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Inflorescences and flowers of *Sahnipushpam* Shukla from the Deccan Intertrappean beds of India

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ABSTRACT. Spicate inflorescences with attached flowers from the Deccan Intertrappean beds at Mahurzari, Nagpur District, Maharastra, India augment our understanding of the late Cretaceous (Maastrichtian) extinct angiosperm genus, *Sahnipushpam*, which was previously documented only from detached flowers and fruits. We studied new specimens as well as earlier published material to advance understanding of the morphology and possible systematic affinities of *Sahnipushpam.* The inflorescence is at least 4.8 cm in length and 6.0–6.5 mm in breadth. The inflorescence axis is 1.2–1.5 mm in diameter, with scattered, vascular bundles. Numerous sessile flowers are closely arranged on the axis. They are small, actinomorphic, and mostly pistillate, sometimes hermaphrodite. A single fused tubular whorl, interpreted as perianth, surrounds the ovary and is quadrangular to subcircular in cross section with lysigenous spaces inside. The androecium includes four stamens with small anthers, positioned in the angles of the perianth. In situ pollen grains, studied by both light and scanning electron microscopy, are 25–30 μm in maximum dimension, oblong to somewhat boat-shaped, extended monosulcate, with a finely reticulate exine. The gynoecium is superior and free from the perianth, tetra- to pentacarpellate with a single locule that is partitioned into 4 or 5 major subunits and further into 8–11 minor subunits, by incomplete, radially oriented septa. The single seed or ovule is multilobed or ruminate due to penetration of major and minor incomplete septa from the ovary. The style is stout with a prominent central canal divided by thin horizontal septa. The stigma is peltate and more or less umbrella-like. The new inflorescence specimens resolve the previous controversy over which side of these unusually shaped flowers and fruits was apical, and confirm that the original interpretation was correct. Despite excellent preservation and many distinctive characters now known for this genus, the systematic affinities relative to living angiosperm families remain elusive. The combination of scattered vascular bundles and monosulcate pollen suggests affinities with the Piperales or with the monocots. Members of extant Piperales are similar in the possession of oil cells and have some members with only one whorl of perianth, but other features of *Sahnipushpam* seem remote from Piperales, and closer to the monocotyledonous family, Araceae, which share tendencies for expanded stigma, small number of stamens, sometimes 4- and 5-carpellate fruits. The similarities with Araceae are scattered among unrelated genera, and may be in part attributable to convergent evolution. The possibility remains that this flower belongs to an extinct family with few if any extant relatives.

KEYWORDS: Angiosperms, spicate inflorescence, flowers, monosulcate pollen, Deccan, India

INTRODUCTION

In 1948, Shukla reported a petrified angiospermous flower from the Deccan Intertrappean beds at Mohgaonkalan in Chhindwara District, Madhya Pradesh. Two years later he gave it the new generic name *Sahnipushpam* (Shukla 1950). He did not, however, provide a specific name, nor a diagnosis or detailed description. Later, many workers studying the Deccan Intertrappean flora from the same area, recovered a large number of additional *Sahnipushpam* flowers preserved in the chert. Detailed, well illustrated accounts were published almost simultaneously in different journals by Verma (1956) and Prakash (1956). Verma (1956) named it *Sahnipushpam shuklai* and indicated nearest affinities with Sonneratiaceae while Prakash (1956) described similar specimens as *S. glandulosum* and compared them with Myrtaceae. Subsequent studies, however, led to the suggestion of affinities with the monocot family Araceae (Prakash & Jain 1964), but some aspects of the flower are not accommodated in any of the modern families that have been suggested so far, and the phylogenetic position of the genus has remained uncertain. Since the specific names *Sahnipushpam shuklai* Verma and *S. glandulosum* Prakash were given for the same kind of flower, Prakash and Jain (1964) pointed out that *S. shuklai* Verma, published a few months earlier in the same year, has nomenclatural priority.

The Deccan Intertrappean beds in which *Sahnipushpam* occurs are sedimentary strata of lacustrine and fluviatile deposition, interbedded between successive basalt flows. The basalts were formed during the latest Cretaceous and Palaeocene as a result of volcanic eruptions and outpouring and subsequent cooling of lava which spread over a greater part of central, south-east and south-west of the peninsular India covering an area of about 525,000 sq. km (Fig. 1). These eruptions occurred over an interval of about 3 million years (ca 67–64 Ma; Hooper et al. 2010). Biogeographic affinities of the Deccan flora are of interest because the Indian subcontinent had not yet affixed to Asia, and is expected to contain elements of Gondwanan affinity, possibly reflecting former connection with Madagascar, and/or unique taxa that differentiated while the subcontinent was isolated from other land masses (e.g. Bajpai 2010).

Flowers of *Sahnipushpam* from Mohgaonkalan were described in increasing detail based on anatomically preserved specimens by Verma (1956), Prakash (1956), Prakash and Jain (1964). These accounts agreed in many features, such as flowers sessile, bisexual, gynoecium syncarpous, superior, pentalocular (although now regarded as unilocular with deeply intruded septa), with a thick style having a prominent stylar canal and an enlarged umbrella-like stigma. However, these publications presented different interpretations of some key characters (Tab. 1). In particular, the tubular structure surrounding the ovary was interpreted as a hypanthium (Verma 1956), or as a calyx tube (Prakash 1956, Prakash & Jain, 1964). Authors also differed in their estimates of the number of stamens and in their interpretation of the pollen morphology. Soon after the above publications appeared, Chitaley (1964) also studied *Sahnipushpam*, and reported a tetracarpellate gynoecium.

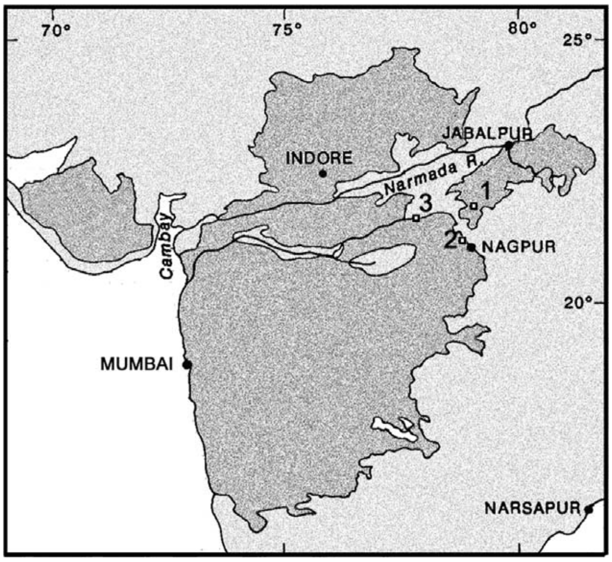

Fig. 1. Western and central India showing extent of Deccan basalts (dark gray), indicating the three localities from which *Sahnipushpam* is known. **1**. Mohgaonkalan, Chhindwara District, Madhya Pradesh, **2**. Mahurzari, Maharashtra Pradesh, **3**. Jaulkheda, Baitul District, Madhya Pradesh. Base map modified from Jaeger et al. (1989)

The genus again came to light after a lapse of about four decades when Ambwani et al. (2001) reinterpreted the structure and orientation of floral parts, disputing the observations of previous authors (Shukla 1948, 1950, Verma 1956, Prakash 1956, Prakash & Jain 1964). Ambwani et al. (2001) postulated that the flower had been described upside down by earlier workers, and that the stamens and pollen were instead lacerated parts of a hypanthium, and fungal spores. This controversial reinterpretation has not been formally challenged until now, and the taxonomic affinities have remained uncertain.

In this article we reconsider the morphology and possible affinities of *Sahnipushpam*

Table 1. Varying interpretation of *Sahnipushpam* characters

	Verma 1956	Prakash 1956	Prakash & Jain 1964	Ambwani et al. 2001	Present authors
Inflorescence type	?	?	?	?	spike
Flower type	hermaphroditic	hermaphroditic	hermaphroditic	? unisexual, female	pistillate & hermaphroditic
Ovary position	superior	superior	superior	superior	superior
Hypanthium	yes	–	–	yes	no
Perianth	no	one whorl	one whorl	none	one whorl
Stamen number	probably many	uncertain	at least 2, probably 4	n.a.	4 (to 5?)
Stamen morphology	basifixed	dorsifixed	position unclear, but dehiscence longitudinal	n.a.	position unclear, but dehiscence longitudinal
Stamen position	perigynous	probably on calyx tube	hypogynous	n.a.	hypogynous
Pollen	elliptical	oblong to +/–boat-shaped, smooth, dicolpate and syncolpate	anisopolar boat-shaped, some grains colpate, or with smaller aperture at both equatorial ends	none	extended monosulcate, microreticulate, tectate-columellate
Carpel number	5	5	4–6	5–6	4–6
Locules	5	5	9–12 apically and basally but joining into 1 in middle	5	1; incompletely partitioned by septa into 8–12 locelli
Ovules	5 (11: 2 per loc. of 4, 3 per fifth loc.)	10–11 (2 per loc. of 4, 3 per fifth loc.)	?	10 (2 per loc.)	1
Style	thick	thick	thick	thick	thick
Stylar canal	yes, septate	yes, septate	yes, septate	not mentioned	yes, septate
Stigma	umbrella-like	disk-like	umbrella-like	umbrella-like	massive umbrella-like, lobed but number of lobes not known
Fruit dehiscence	septifragal	septicidal	?	?	indehiscent
Secretory cavities	in hypanthium	in calyx	in calyx	?	in calyx
Ovary epidermis	studded with numerous round glands	spherical sacs of oil tannin or resin	studded with minute spherical glands	studded with glands	numerous idioblasts (oil cells)

based on the discovery of flowers still intact within inflorescences from the Mahurzari site near Nagpur, supplemented by examination of anatomically well preserved specimens from the type locality of Mohgaonkalan using SEM as well as light microscopy. We provide additional evidence narrowing the likely affinities to the family Araceae.

MATERIAL AND METHODS

This study is based on specimens from two locations, Mohgaonkalan, in Madhya Pradesh, and Mahurzari near Nagpur, Maharashtra Pradesh (Fig. 1). While this article was in review, many *Sahnipushpam* specimens were discovered at a third locality, Jaulkheda, near Amla railroad station in Baitul District, Madhya Pradesh (D.K. Kapgate fieldwork 2011), indicating that the plant was distributed across a region that included these three places which form a nearly equilateral triangle with each site about 160 km from the others (Fig. 1). Precision radiometric dating has not been possible due to a lack of suitable crystals in the enveloping basalts. Nevertheless, the classic Mohgaonkalan chert is most likely Late Maastrichtian based on continuity of outcrops of the main Deccan basalt flows to those of the Jhilmili section 25 km to the northwest, where the chronology has been constrained by overlying Danian Zone PIa planktic foraminifera (Keller et al. 2009, Keller pers. comm. 2011). Based on paleofloristic similarities, the other localities are considered likely to be Maastrichtian as well (Kapgate 2005), although a Paleocene position has not been firmly ruled out. List of fossil plants identified so far from Mahurzari and Mohgaonkalan are given by Bande et al. (1988), Bande & Chandra (1990), and Kapgate (2005).

Mohgaonkalan is the type locality for the genus. We reexamined specimens from the original published material at the Birbal Sahni Institute of Paleobotany, Lucknow (BSIP), and borrowed and sectioned a specimen from the Kansas Natural History Museum. We also collected and sectioned new specimens from the exposure at N22°1.415′, E79°11.204′. These have been deposited at the Cleveland Museum of Natural History (CMNH) and Florida Museum of Natural History (UF). *Sahnipushpam* is among several isolated flower types that have been recognized from the Mohgaonkalan beds including *Sahnianthus* (Shukla 1944a, 1958, Chitaley 1955, Dwivedi & Shukla 1958, Dayal 1967), *Chitaleypushpam* (Paradkar 1971), *Deccananthus* (Chitaley & Kate 1972), *Raoanthus* (Chitaley & Patel 1973), *Chenopodianthus* (Kapgate et al. 2006), and *Tetraplasandranthus* (Kapgate et al. 2009).

It was a matter of great luck that one of us (D.K. Kapgate) found several specimens of inflorescences with intact *Sahnipushpam* flowers in the cherts exposed in a basalt quarry at N21°13.280', E79 0.84'near the village of Mahurzari. This location, previously recorded as Bharatwara by Shukla (1944b) and Prakash (1956), is about 14 km from Nagpur, on Nagpur – Katol road. Mahurzari was previously indicated as a source of *Sahnipushpam* by Prakash and Jain (1964), but the specimens were not illustrated.

The fossils were recovered by physically breaking pieces of chert with hammers, thereby exposing inflorescences, or isolated flowers and fruits in oblique transverse and longitudinal fractures. Serial sections from each broken surface were prepared by the butyl acetate peel technique. The exposed surface of the specimen was first smoothed by rubbing on a glass plate using a slurry of fine grade carborundum powder. It was then etched with a few drops of 40% hydrofluoric acid and then washed gently in running water to remove all traces of acid. After drying a few drops of butyl acetate were placed on the etched surface with care to prevent entrapping small air bubbles in the peel solution. The specimen was held horizontally allowing the peel solution to spread evenly, and then air-dried for 4–6 hours in a dust free environment. The peel was removed by starting an edge with a scalpel or razor blade and then carefully pulling it off by hand. Resulting peels were immediately placed under pressure in a clamp to flatten. By repeating the same technique a succession of peels were produced. In other instances, peels were prepared from sliced surfaces of the chert by the standard cellulose acetate method (Galtier & Phillips 1999). The peels were mounted on microscope slides under cover slips in the usual manner using Canada balsam or D.P.X. synthetic resin.

Cited specimens are stored at the Cleveland Museum of Natural History (CMNH), the Florida Museum of Natural History (UF), the Kansas Natural History Museum, Lawrence, and the Birbal Sahni Institute of Palaeobotany, Lucknow.

SYSTEMATIC POSITION

Division: Angiospermae

Order and family: not resolved

Genus: *Sahnipushpam* Shukla 1950

Type species: *Sahnipushpam shuklai* Verma 1956, emend. (Figs 1 A–I and 2)

Synonym: *Sahnipushpam glandulosum* Prakash 1956, emend. (Pl. 1, figs 2, 4)

EMENDED DIAGNOSIS

Inflorescence spicate, 21 to at least 48 mm long and 6.0–6.5 mm broad bearing sessile flowers. Inflorescence axis 1.2–1.5 mm in diameter, made up of parenchymatous ground tissue and scattered vascular bundles with spiral and reticulate thickening on xylem elements. Flowers actinomorphic, commonly pistillate, sometimes hermaphrodite, 2.5–5.1 mm in length and 1.3–3.2 mm in breadth. Perianth tubular, quadrangular to subcircular in cross section, slightly thick at the base, thin in the middle and thick and fleshy at the apex, composed of isodiametric cells 25–50 µm and occasional globose lysigenous cavities, 90–120 µm. Stamens at least four, positioned near the angles of the perianth; anthers small, dithecate, four-lobed, dehiscing by longitudinal slits. Pollen grains oblong, boat-shaped, 25–30 µm long, 15–20 µm, wide, with a large sulcus extending fully to the poles and slightly beyond. Exine finely reticulate with lumina 2–3 µm in diameter. Gynoecium syncarpous commonly pentacarpellate but ranging from tetra- to hexacarpellate, single seeded. Ovary superior, 1.9–3.5 mm long and 1.5–2.3 mm in diameter, 8–12 chambered at the extreme base and apex, but unilocular in the equatorial region with partial septa extending inward from the periphery. Ovule/seed lobed (ruminate) due to the intrusion of ovary septa; placentation probably basal. Numerous spherical glands [oil cells], 40–55 µm in diameter, interspersed among epidermal cells of the outer ovary wall. Style one, stout and thick (0.9–1.0 mm diam.), sometimes enlarged and bulbous in the region between the ovary and stigma. Stylar canal prominent, 100–200 µm wide often with horizontal or oblique septa. Top of style expanded into an umbrella-like peltate stigma 2.5–3 mm wide with unknown number of lobes. Mature fruit indehiscent, consisting of a single, 5–10 lobed seed.

Specimens and slides studied. BSIP 5505 at the Birbal Sahni Institute, Lucknow, P-21388A, 21388B, 21387, and slides Pm 1290–1315, 1346–1349, 1383, 2824–2828, 4037–4073, 4113–4118, 4242–4255, 4414–4418, 4448–4857, and 5825–5828 at the Cleveland Museum (CMNH), UF 52556, 53767–53769 at the Florida Museum of Natural History (UF), and KUPB E308, at the Kansas Museum of Natural History.

GENERAL DESCRIPTION

The following description is based on the study of successive sections of inflorescences; as well as a number of detached flowers and fruits. The observations of previous authors (Verma 1956, Prakash 1956, Prakash & Jain 1964, Chitaley 1964, Ambawani et. al. 2001) have also been considered and incorporated here when verified through their photographs and/or our observations. Different interpretations of the morphology by these different authors are presented in Table 1 in comparison with our own current interpretation.

Inflorescence. Eight spicate inflorescence specimens have been recovered. The average spike width is 6.0–6.5 mm and the preserved length ranges up to 48 mm, but these are incomplete with portions of the basal and apical parts missing. At least 20 to 32 sessile flowers are borne on the axis. The inflorescences have been fractured and sliced in different planes resulting in transverse, longitudinal, and oblique cross and oblique sections of the flowers (Pl. 1, figs 1–6). We consider these to represent inflorescences, rather than infructescences, because the gynoecia are relatively small, about 2/3 the size of those found isolated and dispersed (7.5–9.0 mm vs 10.0–12.5 mm diameter). Perianth and stigma are faintly preserved surrounding the gynoecia in these inflorescences, but not as well preserved as in the isolated flowers from Mohgaonkalan.

Axis. The inflorescence axis is 1.2–1.5 mm wide. One of the specimens originally sectioned longitudinally showing the attachment of numerous sessile flowers (Pl. 1, figs 1, 2) was subsequently sectioned transversely through the axis (Pl. 1, fig. 6), providing clear documentation of the scattered fibrovascular bundles (Pl. 1, figs 7, 8). These bundles can also be seen in oblique sections of the axis (e.g. Pl. 1, fig. 3). Although the vascular bundles and associated fibres are relatively well preserved due to their lignified tissue, the surrounding parenchymatous tissue is relatively poorly preserved, and in some places the axis is badly crushed, suggestive of herbaceous condition. Each vascular bundle consists of 2–3 protoxylem and 5–6 metaxylem elements. Spiral thickening is seen in protoxylem whereas both spiral and reticulate thickening is present on metaxylem elements (Pl. 1, fig. 9). A single-layered epidermis is preserved in places, and no secondary xylem is developed.

Flowers. The flowers are sessile (Pl. 1, figs 1, 2; Pl. 2, fig. 7), actinomorphic and monochlamydeous and readily recognized by their distinctive radially septate ovary (Pl. 3, figs 2–6, 9–17) and peltate stigma (Pl. 2, figs 1, 2, 6). The flowers attached to the inflorescences are considerably smaller than those found isolated in the chert, suggesting differences in maturity. Perianth is weakly preserved in the inflorescence specimens contrasting with the well lignified fruit tissue, and stamens were not observed in any of the inflorescence specimens.

Bract. Although a possible bract was reported in association with the flower by Prakash (1956), this interpretation was later questioned by Prakash and Jain (1964) who emended the diagnosis to read “flowers ebracteate,” noting that although a large number of straw-like things are found in association with these flowers, none of them has been found in organic connection. Despite the availability now of complete inflorescences, we have not observed obvious bracts. If present, the bracts may have been deciduous prior to fruiting stage.

Receptacle. The basal part of the flower according to Verma (1956), Prakash (1956), Prakash and Jain (1964) is the receptacle, whereas Ambwani et al. (2001) interpreted the upper part of the style and stigma to represent the receptacle. The receptacle is clearly seen in sections of the flowers that are attached on the inflorescence (Pl. 2, figs 3, 5, 6). Longitudinally sectioned flowers show the basal attachment of perianth (Pl. 2, figs 1, 2, 8, 9; Pl. 4, figs 1–4) and sometimes stamen filaments can be seen arising between the base of the ovary and the perianth (Pl. 2, fig. 1, Pl. 4, figs 2–4).

Perianth. Prakash (1956) described the tubular structure surrounding the ovary as calyx while Verma (1956) considered it to be hypanthial, formed by a peripheral extrusion of the receptacular tissue around the ovary. Only a single undivided gamophyllous whorl is observed, forming a tube (Pl. 4, figs 5–9) that is almost straight-sided, up to 4.5 mm long, quite closely adjacent to the ovary but free along its whole length (Pl. 2, figs 1, 2, 4, 9; Pl. 4, figs 1–2). The narrow space between this tube and the ovary accommodates stamens in some specimens (Pl. 4, figs 4–10). Since the anthers are positioned below the apical rim of this tube, the hypanthial interpretation of Verma (1956) seems less plausible than the perianth interpretation. Despite its unusual morphology, we interpret it to represent a modified calyx based on its position, and apparent protective function. It is somewhat thick at the base, thin in the middle and swollen and fleshy at the apex forming a rim-like structure surrounding the base of the style (Pl. 2, figs 2, 6, 8, 9). Because of the unlobed apical edge, it is difficult to ascertain the number of elements which may have given rise to this tubular structure. In most of the transverse sections of the flowers, the tube is quadrangular in outline indicating the number of tepals might have been four, but the vasculature, mentioned below suggests that the number could range to from four to 6. The corners are thicker, slightly projected outward possibly representing the central part of the sepal (Pl. 3, figs 13, 14, 16; Pl. 4, figs 5–10).

Anatomically, the perianth mostly consists of thin-walled parenchymatous tissue, with numerous polygonal, more-or-less isodiametric cells 20–50 μm in diameter (Pl. 3, fig. 19). Epidermal cells are very small and without any trichomes as mentioned by Prakash (1956). No oil cells of the kind seen in the gynoecium were observed in the perianth, but large globose cavities or spaces, 90–120 μm in diameter, apparently of lysigenous nature are frequent within the mesophyll (Pl. 3, fig. 19). There appear to be four to six main vascular traces at the base of the tube (Pl. 3, fig. 17), which divide to become 12 to 15 at the top, as documented by Prakash (1956).

Androecium. Verma (1956) inferred that the flowers of *Sahnipushpam* bore numerous stamens, but did not document this with particular specimens or photographs. Prakash and Jain (1956) reported the presence of stamens in at least twenty specimens that they studied, but all of the specimens were cut or fractured obliquely so that the exact number of stamens could not be counted in any one specimen. However, they noted that individual stamens (only one or two observed per specimen) were positioned in the angles of the usually quadrangular perianth, leading them to conclude that there were probably four stamens per flower. We have observed three specimens with stamens, all from Mogoankalan, like the stamen-bearing specimens previously described and illustrated by other authors. An obliquely sectioned specimens studied through a series of successive peels, demonstrates the presence of four anthers (Pl. 4, figs 5–10). In oblique longitudinal sections at one side of the flower, three of the anthers are seen (Pl. 4, figs 5, 6); as successive serial sections were prepared toward the other side of the flower, a fourth anther appeared (Pl. 4, figs 8, 9), supporting the prediction made by Prakash and Jain (1956).

Anthers are dithecate, four-lobed and four-loculed structures with a small connective (Pl. 4, figs 11, 12). Those we observed are fully mature and dehisced, although a few grains remain in the locules. The anther wall consists of two layers of cells. As seen in a longitudinal section, the outermost layer of the epidermis consists of small somewhat thick-walled more or less isodiametric cells. The inner layers consist of anticlinally elongate cells with radial fibrillar thickenings (Pl. 5, figs 1, 2). No tapetum or intermediary layers are visible. The absence of tapetal cells appears to be due to their disintegration at maturity rather than due to non-preservation. Although all of the anthers appear to be dehisced, groups of pollen grains remain scattered in the anther locules (Pl. 5, fig. 1, 2). Filaments are seen arising from the receptacle in a few longitudinally sectioned specimens (Pl. 4, figs 2–4), as described previously by Prakash and Jain (1964). The stamens have long filaments that arise from the base of the flower, as already indicated by Prakash and Jain (1964), correcting Verma's (1956) inference that the stamens were perigynous.

It is noteworthy than none of the eight inflorescences studied from Mahurzari possess stamens, even though the perianth tube is sometimes preserved (e.g. Pl. 2, figs 6, 8, 9). Also, numerous specimens from Mohgaonkalan lack stamens, despite having well preserved perianth and gynoecium. We now interpret that *Sahnipushpam* was variable in sexuality, including both pistillate flowers and occasional hermaphroditic flowers. We did not recover any exclusively staminate flowers.

Pollen. The pollen grains are oblong to somewhat boat-shaped, 15–20 μm × 25–30 μm (Pl. 5, figs 1–8). Each grain has a large sulcus extending fully to the poles and slightly beyond, with an annular thickening at each end. The colpi are wide and long, extending fully to the poles and, in fact, curving slightly over the poles (Pl. 5, figs 1, 3–7). The surface is finely reticulate with lumina 2–3μm in diameter, and muri 2 μm thick (Pl. 5, figs 7–10. Fractured grains examined by SEM reveal that the wall is about 0.5 μm thick with structure consisting of a perforated tectum, a columnar layer, and a footlayer, each about 0.15 μm thick (Pl. 5, figs 8–10). No triaperturate grains were found.

Earlier investigations of these pollen grains were limited by the resolution of available microscopes. The combination of higher resolution light and scanning electron microscopy has allowed us to dismiss earlier interpretations that the pollen was was dicolpate and syncolpate (Prakash 1956) or may have had a pair of apertures at either equatorial end (Prakash & Jain 1964). Prakash and Jain (1964) observed that a distinct sulcus is seen in some grains but not others, yet in “the majority of pollen grains, however, there is a distinct areolate, possibly aperturate, area with thin, more or less circular zones at either equatorial end.” These bulges, and slits with the appearance of pore-like apertures are seen in light microscopy of the grains we studied (Pl. 5, figs 3, 5, 6) as well as in the illustrations of Prakash and Jain (1964, Pl. 2, figs 8–12). It now appears, however, that the bulge and slits are formed by extremities of the long sulcus, which passes slightly beyond the poles of the grain, a condition referred to as extended monoculcate (Harley & Baker 2001).

Gynoecium. Judging from the number of radial septa penetrating the ovary at the equator (Pl. 3, figs 4, 11, 15) *Sahnipushpam* is usually tetracarpellate or pentacarpellate, and sometimes hexacarpellate (Prakash & Jain 1964). The shape of the ovary in cross section is usually square or diamond-shaped with 4 rounded corners, even when the configuration of septa indicates 5 carpels-probably a feature enfluenced by the close packing of flowers within the spike (Pl. 1, figs 4, 5). The gynoecium measured in dispersed flowers is 4.6–5.0 mm long from base of the ovary to top of the stigma and 2.0 to 2.3 mm in diameter, but those in the inflorescences are only 1.4–2.2 mm long and 1.2–1.9 mm wide.

The cross-sectional configuration varies depending on the level at which the ovary is examined, as shown by the serially sectioned specimen in Pl. 3, figs 1–7. A transverse section near the base of the ovary reveals 9 to 11 nearly equal rounded-triangular locelli arranged in a circle around a central circular cavity (Pl. 3, figs 2, 9, 13, 16, 17). Sectioning the same ovary higher, near the equator (Pl. 3 figs 2, 12, 14), shows that the circle of locelli are interconnected with one another and with the central cavity, and only partially subdivided by radial longitudinal septa extending inward from the periphery. The septa are in two orders: a set of 4–5 primary septa, which extend from the periphery nearly all the way to the center of the ovary, defining 4–5 primary loceli, and a set of secondary septa, that subdivide the primary compartments, extending from the periphery only about halfway toward the center (Pl. 3, figs 4, 5, 11, 15). Usually there is just one secondary septum dividing each primary compartment but in some cases there care two or three secondary septa in a single primary compartment. Sectioning the same ovary close to the apex reveals that the four (or five) major septa interconnect in the center, while the minor septa still extend only ⅓ to ½ of the distance toward the center. At this level, the central cavity area has disappeared (Pl. 3, fig. 4). Thus, what was formerly interpreted to be a multilocular ovary is in reality unilocular with incomplete radial partitions, and the sections interpreted to show an ovule or seed in each of the locelli (Shukla 1950) were actually representing multiple lobes of a single ruminate seed divided by radial intrusions of the ovary wall (Pl. 3, figs 5–12). Prakash and Jain (1964) already observed that the gynoecia are unilocular in the central portion even though they observed the basal and apical parts may be divided into 9-, 10, 11- or even 12 “locules.” Since these compartments all join at the center, the fruits are technically unilocular, but the number of carpels is probably reflected by the number of locelli.

A thin layer that might represent seed coat conforms to, but is free from the locule in some specimens, (e.g. Pl. 3, figs 10, 11, 13). In two specimens, we observed that the cylindrical central chamber is filled with silica which is white in color, whereas the surrounding lobes are translucent, suggesting that a different substance occupied the central chamber (Pl. 3, figs 7, 14). Possibly this was the embryo, while the surrounding lobes were endosperm. The “embryo cavity” is separated from the surrounding locelli by a wall of schlerenchyma at the base of the ovary, but is directly connected to the locelli at midlevels. Earlier authors were concerned about the lack of central vascular bundles to connect with the surrounding "locules", and interpreted that all specimens were poorly preserved in the central zone. The placentation appears instead to have been near the base of the fruit, consisting of a circle of vascular strands at the base of each primary septum (Pl. 3, figs 1, 9.).

The ovary wall is 290–320 µm thick and highly lignified. The wall between the central cavity and the locelli, and that of the septa between locelli are composed of sclerenchyma—mostly longitudinally oriented fibres (Pl. 3, fig. 18, Pl. 4, fig. 13). A characteristic feature is the presence of spherical idioblasts resembling oil cells scattered among the epidermal cells of the wall, protruding like glands at the surface (Pl. 3, fig. 20, Pl. 4, figs 3, 12, 13). These are about 40–55 µm in diameter, more or less equal in size, and often very close to each other (Pl. 2, fig. 10). Otherwise, the epidermis of the ovary consists of small thin-walled isodiametric cells (Pl. 4, fig 13). Below the epidermis there are few layers of thick-walled sclerenchymatous cells, while the inner region consists of many layers of thin-walled parenchymatous cells of varying size, some large and some small (Pl. 3, fig. 19).

A single style arises from the ovary. It is stout, and circular in cross section, 0.8–1.0 mm in diameter (Pl. 3, figs 7, 8). Length including the stigma varies from 0.5 mm to 2.3 mm depending on maturation and the relative length varies from less than 1/3 of the ovary length in immature flowers (Pl. 2, figs 6, 8, 9), to markedly elongate-equal to, or greater than the length of the ovary in mature flowers or fruits (Pl. 2, figs 1, 2, Pl. 4, fig. 1). In most specimens the outline is more or less cylindrical, but some specimens are enlarged and bulbous in the lower ⅔ or more of the length (Pl. 4, figs 1,2). All specimens show a central stylar canal that is prominently septate (Pl. 4, figs 1, 2, 6). The stylar canal is about 200–225 µm in diameter and runs through the middle of the style all along its length. The same kind of septate central canal is also observed in both cylindrical and bulbous styles. When cut obliquely, the canal may appear discontinuous (Pl. 4, figs 2, 6, 7), but successive sections demonstrate that the canal runs from the top of the ovary to the base of the stigma. The septa or partitions are composed of only a few layers elongated thick-walled cells. The style is formed of a non-lignified tissue of small isodiametric cells, similar to that of the perianth, and is readily distinguished from the well lignified tissue of the ovary. A distinct zone of separation indicates that the style and stigma were deciduous or degraded prior to the rest of the fruit (Pl. 2, figs 6, 8, 9).

The style is terminated by a transversely expanded stigma that is usually well thickened (Pl. 2, figs 1, 2), but sometimes thin (Pl. 4, figs 1, 2). In longitudinal section it forms a T shape at its junction with the style, extending out and nearly touching perianth rim (Pl. 2 figs 2, 8, 9), hence covering and protecting the rest of the flower below. It is thick in the centre and thins toward the margin (Pl. 2, figs 1, 2). Viewed transversely the stigma is seen to form a rounded to subangular disk over the top of the flower. The tissue of the stigma consists of loose, thin-walled parenchymatous cells. No papillae or outgrowths were observed on the surface.

Fruit. The fruit is a single-seeded rounded-cuboidal nut, sometimes surrounded by the persistent perianth tube (Pl. 3, figs 14, 15). The distinctive septation of the ovary as described above is maintained in fruit as well. The seed is radially lobed conforming to the partial septa that intrude inward from the pericarp (Pl. 3, fig. 11). Although some of the fruit specimens appear to be fragmentary, most are complete, although the style appears to have regularly detached (Pl. 2, figs 8, 9). We interpret the fruits to be indehiscent as we have not seen any regular pattern of splitting, nor any anatomical lines of weakness that could be interpreted as dehiscence planes. The hollow area at the receptacular end occasionally contains tissues that may represent a developing embryo (Pl. 2, figs 3, 7, Pl. 3, figs 13, 16) and may have served as the opening for germination.

COMPARISON AND DISCUSSION

Regarding the affinities of *Sahnipushpam* with extant taxa, previous workers tried to trace its nearest living counterpart among monocots and dicots, but none could arrive to a definite conclusion. Verma (1956) noticed that most of the characters of the flower are distributed mainly over the different families included in the Myrtiflorae with comparatively closer resemblance to Sonneratiaceae. Prakash (1956) considered it closer to Myrtaceae in many characters, especially in having spherical oil sacs or glands on the ovary wall and what were then interpreted as bicolporate pollen grains. Ambwani et al. (2001), placed the flower under the familial designation Lythraceae, also in the Myrtales but without explanation. However, these and other families of Myrtales have numerous stamens and multiseeded fruits contrasting with *Sahnipushpam*, which, based on our observations, has only four stamens and just one seed.

Sahnipushpam has several features that should help with determination of its systematic placement: flowers in spikes, axis of spike with scattered vascular bundles, perianth in a single fused whorl, stamens few (four, possibly up to five), anthers dehiscing via longitudinal slits, gynoecium superior, ovary unilocular with incomplete radial divisions, style thick, deciduous, traversed by a wide, septate central canal, and a massive stigma. The extended monosculcate pollen morphology of *Sahnipushpam*, should also provide insight to the systematic affinities. Distinctive anatomical features, namely the numerous idioblasts, which we interprets as oil cells, in the epidermis of the ovary and fruit, and the presence of lysigenous cavities in the perianth, should also help in determining the relationships among extant angiosperms. Despite all these features, we have not succeeded to find an obvious match for *Sahnipushpam* among extant angiosperm families.

The distinctive feature of false partitions intruding the locule radially from the periphery converges with a pattern seen in some the Santalales where similar radiating incomplete septa occur in some Loranthaceae (Dixit 1958), and Santalaceae (e.g. *Dendrotrophe varians*, figured on p. 474 of Cooper & Cooper 2004). However, *Sahnipushpam* differs greatly from these families in perianth configuration, pollen ornamentation and aperture configuration; and the peculiar anatomical features of perianth and pericarp. Indeed, affinities with Eudicots in general may be ruled out on the basis monosulcate pollen and scattered vascular bundles.

Two groups of extant angiosperms can possess both monosulcate pollen and scattered vascular bundles: Piperales and Monocots. The order Piperales, having scattered vascular bundles, oil cells common in the ovary wall, and sometimes monosulcate pollen, seem to be a reasonable group to consider for the possible affinities of *Sahnipushpam*. The abundance of oil cells at and adjacent to the epidermis of the ovary and fruit (Pl. 2, fig. 10, Pl. 4, figs 3, 13) closely matches the condition seen illustrated in extant Piperaceae and Saururaceae (figs 83, 84, 118, 127 in Igersheim &Endress 1998). Among the living families of this order Piperaceae and Saururaceae can have spicate inflorescences and a relatively small number of stamens like *Sahnipushpam* but their flowers are perianthless, whereas Aristolochiaceae can have one or two perianth whorls but very different flower morphology. Although pollen of most Piperales is readily distinguished from that of *Sahnipushpam*, that of Saururaceae is somewhat similar in being monosulcate and in the case of *Gymnotheca* has microreticulate ornamentation. However pollen grains in this family are small, 8–14 µm in polar length (Smith & Stockey 2007), about half the size of those in *Sahnipushpam*. Details of gynoecium morphology, including lack of peltate stigma and of false septa also distinguish modern Piperales from *Sanipushpam* (Igersheim & Endress 1998).

Prakash and Jain (1964) previously referred *Sahnipushpam* to the monocot family Araceae, influenced especially by the pollen grains – although with some hesitance because the inflorescence structure had not been confirmed. The presence of spicate inflorescences lacking floral bracts, and higher resolution microscopy of the pollen, confirming the monosulcate configuration and microreticulate ornamentation, further support attribution to Araceae. Pollen of this family is morphologically diverse (Wang & Zhou 2002), including many taxa with inaperturate and smooth to echinate grains, but some in the Gymnostachydoideae, e.g. *Lysichiton*, *Pothos*, and *Symplocarpos*, have monosulcate grains of similar size and microreticulate sculpture to *Sahnipushpam*.

However, aroids do not shed their flowers and fruits to be found in isolated condition as often is the case in *Sahnipushpam*. In addition, the presence of abundant oil cells in the ovary and fruit of *Sahnipushpam* distinguishes the fossil from Araceae and other monocots, with the exception of *Acorus*. The latter genus comprises the only member of Acoraceae, which are now considered sister to all other monocots, has monosulcate pollen somewhat similar to that of *Sahnipushpam*, but it has 2 whorls of perianth, 3 carpels and bears multiple ovules per locule (Buzgo & Endress 2000).

The gynoecia of Araceae are typically 1–3-carpellate, but range to up to 8 locular in Spathicarpeae, and to many locules in *Philodendron* (Mayo et al. 1997). Some genera have a thick stylar region between ovary and stigma (e.g. *Philodendron*), and the stigma can be massive and subcapitate, or broad and disk-like (e.g. *Xanthosoma*), cohering to similar structures of adjoining flowers (Eyde et al. 1967). Perianth can be absent, or consisting of one or two whorls; in some cases tepals are fused into a single cuplike whorl, as in *Anadendrum*, *Holochlamys*, *Pedicellarum*, *Stylochaeton*, some *Pothos*, and some *Spathiphyllum.* Both bisexual and unisexual flowers occur in the family; stamens commonly number 3–5. In *Lysochiton*, the stylar region and tepal apices protect the young fruit, eventually breaking off to reveal ripe seeds (Hultén & St. John 1931). However, the complicated pattern of locule septation combined with a single seed, distinguishes *Sahnipushpam* from extant genera of *Araceae*. We concur with Prakash and Jain (1964), that *Sahnipushpam* is likely most closely similar to the Araceae, although it does not fit neatly within a particular group of the family. The similarities with Araceae are scattered among unrelated genera, and may be in part attributable to convergent evolution. India was a biogeographically isolated island in the late Cretaceous (e.g. Briggs 2003) and its biota may have included unique taxa with only distant relationships to extant families. The possibility remains that *Sahnipushpam* belongs to an extinct family with few if any extant relatives.

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PLATES

Plate 1

Inflorescences of *Sahnipuspam* from Mahurzari locality

1. Longitudinal section of an inflorescence with central axis surrounded by attached flowers in longitudinal and oblique orientations, by reflected light. CMNH-P21388A. Scale bar – 5 mm
2. Same specimen, peel by transmitted light. Arrow indicates level where the specimen was subsequently cut transversely to reveal the features seen in figs 6–7
3. Inflorescence with a portion of thick axis with scattered vascular bundles and numerous flowers in oblique, transverse and longitudinal section, by reflected light. CMNH- P21388B
4. Adjacent plane of section to that in fig. 3, showing closely spaced flowers that are mostly diamond-shaped in cross section, reflected light
5. Peel from the specimen in fig. 3, transmitted light [CMNH peel # PM5826]
6. Corner block cut from the specimen in fig. 2, showing the central axis in both longitudinal (below red line) and transverse view (above red line). Semicircular outline of the inflorescence axis indicated by arrow. CMNH-P21388A

7, 8. Details of inflorescence axis from fig. 6. Transverse view showing scattered fibrovascular bundles, reflected light

9. Tracheary elements with annular thickenings. Longitudinal peel of specimen in fig. 1 [CMNH peel # PM 5841]

Scale bars – 5 mm in 1–6; 0.5 mm in 7, 8; 100 μm in 9

Plate 1

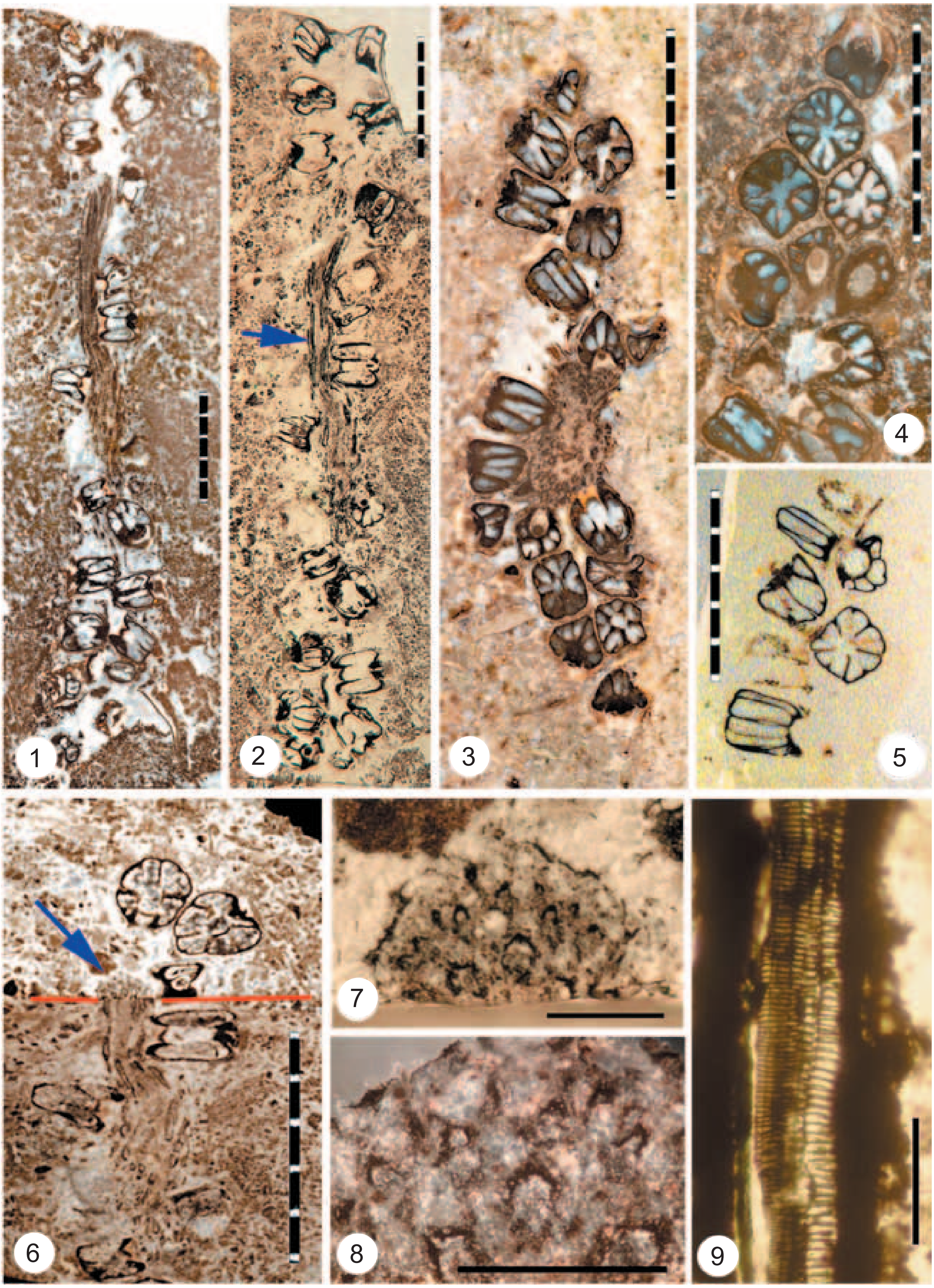

Plate 2

Flowers of *Sahnipushpam* in longitudinal section. 1, 2, 4 from Mohgaonkalan, 3, 6–9 from Mahurzari

1. Two flowers or fruits showing very stout style and enlarged stigma. Degraded hypogynous perianth tube extends about half the length of the gynoecium. UF18311-53767. Scale bar – 3 mm
2. Flower in median longitudinal section showing longitudinal septa of the ovary, wide style with a transversely septate central canal, and prominent peltate stigma. Apical rim of the perianth tube is thickened and contiguous with the adjacent style and stigma. BSIP 5505. Scale bar – 3 mm
3. Detail of gynoecia in oblique, near-basal section from Pl. 1, fig 4. Scale bar – 2 mm
4. Flower showing tubular perianth surrounding the septate ovary. [CMNH slide PM4040]. Scale bar – 3 mm
5. Flower in oblique longitudinal section, intercepting receptacle (R), longitudinal septa within the ovary (o), and thickened part of perianth rim (p) composed of isodiametric cells extending beyond top of the ovary. [CMNH slide PM4037 (FL10/1]. Scale bar – 2 mm
6. Flower in longitudinal section showing pronounced demarcation between dark tissue of the ovary and light-colored thick style and stigma. CMNH P-21388D. Scale bar – 2 mm
7. Flower in oblique section showing basal attachment with vascular bundles of the inflorescence axis, peripheral chambers, and tissue within the central chamber. CMNH- P21388D. Scale bar – 2 mm
8. Flower in longitudinal section showing enlarged apical rim of the perianth, and pronounced truncation of sclerified tissue at apex of ovary. Scale bar – 2 mm
9. Same flower as fig. 8, sectioned along the central axis, intercepting septate stylar canal. Scale bar – 2 mm
10. Gynoecia exposed in surface view by fracture of the infructescence in Pl. 1, fig. 3, oriented with base protruding obliquely (left) and in lateral view (right). Note regularly spaced punctae due to oil cells of the epidermis, and cleavage formed by the partial septa. CMNH- P21388B. Scale bar – 2 mm


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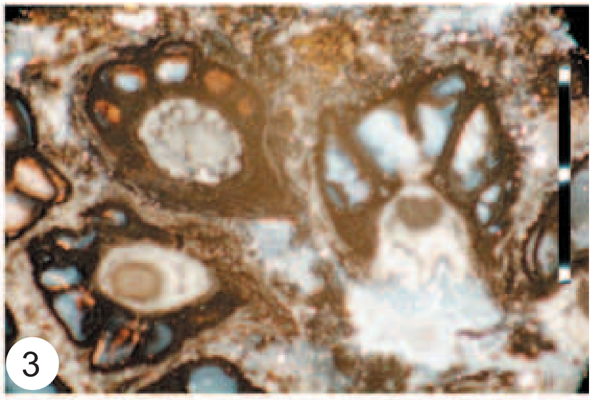
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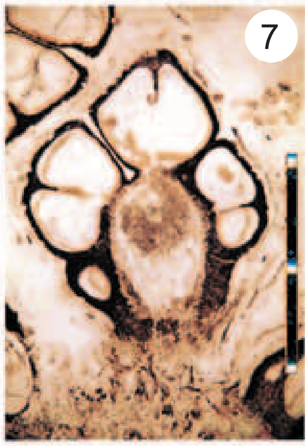
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Plate 3

Sahnipushpam flowers at various levels in transverse section. 1–8, 10, 11, 14, 15, 19, 20 from Mohgaonkalan, 9, 12, 13, 16–18 from Mahurzari

1–7. Successive sections of a single flower arranged from base to apex at same magnification. UF18311-53768. Scale bar in 4 – 1 mm (applies also to 1–7)

1. Basal section through receptacle, with placental vasculature around the central opening. Surrounding perianth is also visible
2. Slightly above the level of section in fig. 2, showing nine septa that divide the seed into 9 basal lobes (in other specimens there tend to be 10 lobes at this level). At this level the septa join into a sclerenchymatous sleeve surrounding the central chamber
3. Here the septa are seen to be incomplete, no longer joining into a central sleeve, and falling into two orders – primary and secondary septa
4. Approximately equatorial section of the ovary, showing 4 primary septa, with interspersed shorter secondary septa
5. Approaching the top of the ovary the primary septa meet in the center, while the secondary septa intrude only part way to the center
6. Top of the ovary with four primary septa and a central channel that links with the stylar channel
7. Transverse section above the ovary, through the style; rim of perianth is also visible
8. Enlargement of style cross section from fig. 7, showing central canal and 5 vascular bundles. Scale bar – 0.5 mm
9. An ovary sectioned transversely near the base showing 5 locelli. CMNH P-21388A. Scale bar – 1.0 mm
10. Obliquely sectioned ovary viewed at the transition between basal compartments and open locule. Seed coat constrained by the septal configuration. CMNH P-21387
11. Same specimen sectioned near the equator, showing partial septa and ruminate seed coat. Basal part of an ovary showing 5-locelli. Secondary septa arise from the middle part of each of the locelli. Scale bar – 1 mm (applies also to 10)
12. Ovary at level of 5 locelli and central chamber. CMNH P-21388B. Scale bar – 1 mm
13. Similar specimen at lower plane of section level of 10 locelli. Note possible embryo tissue in central chamber and membrane (outlining the endosperm?) within the locelli. CMNH- P21388B. Scale bar – 1 mm
14. Flower sectioned at lower level obliquely transverse, through an 11-locellate ovary (higher level of section at left with distinct secondary septa, lower level at right with both primary and secondary septa joining in ring forming a central chamber). Note 4 angles of surrounding perianth. BSIP 5505b. Scale bar – 1 mm
15. Flower in equatorial transverse section showing quadrangular perianth tube and rounded radially septate ovary. CMNH P-26887J Scale bar – 1 mm
16. Flower sectioned near receptacle with seed tissue developed in the center. Scale bar – 1 mm
17. Flower sectioned near base, surrounded by perianth with 5 readily visible vascular bundles. CMNH-P21388B. Scale bar – 1 mm (applies also to 16)
18. Detail from 17 showing fibrous construction of the ovary wall, and parenchymatous inner layer. Scale bar – 250 μm
19. Perianth cross section consisting of parenchymatous tissue with scattered lysigenous cavities. Same specimen as Pl. 4, fig. 15. [CMNH Slide PM5878 (Fl3/15)]. Scale bar – 300 μm
20. Detail of ovary wall with sclerenchymatous tissue. Note oil cells scattered among the epidermal cells forming slight papillae at the surface. Scale bar – 250 μm

Plate 3

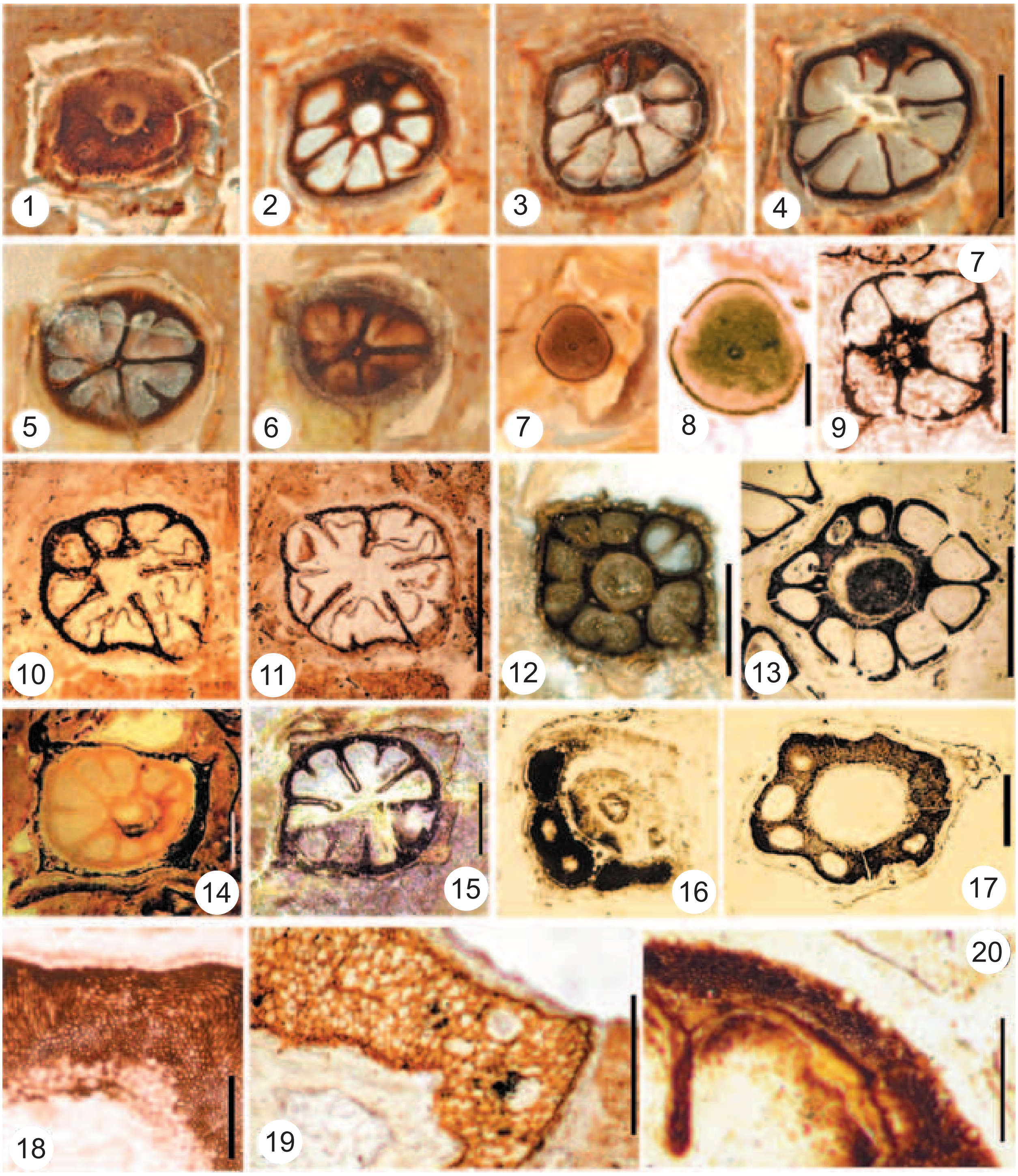

Plate 4

Sahnipushpam flowers with swollen style and septate stylar canal
from Mohgaonkalan illustrated by peels at multiple levels

1. Pistillate flower showing outline of single perianth whorl, septate ovary, basally swollen style and capitate stigma. [CMNH slide # PM4043]. Scale bar – 2 mm
2. Same flower as in fig. 1, peeled closer to the median axis. Note incomplete septa arising from base of locelli, prominent septation of the stylar canal, and thin stamen filament arising from base between gynoecium and perianth on right side. [CMNH slide # PM4040]. Scale bar – 2 mm
3. Detail from fig. 1, showing outline of seed within locule lobe, and well lignified ovary wall with numerous white circular idioblasts. Scale bar – 1 mm
4. Same flower as Pl. 2, fig. 1. showing perianth in profile view with curled tip and stamen filament (arrow). UF18311-53767. Scale bar – 1 mm

5–14. Series of obliquely longitudinal sections through a bisexual flower showing gynoecium, four anthers (arrows), and tubular perianth. CMNH P-21387D. Scale bar in 5 – 2 mm (applies also to 6–10)

5. Outermost section of the series, cutting through a portion of the swollen style corresponding to the upper part of the gynoecium seen in fig. 1. Two anthers are visible inside the front corners of the perianth tube
6. Same flower peeled closer to the floral axis, showing septate ovary seated below the bulbous style. The septate stylar canal appears nearly circular rather than elongate as an artifact of the oblique angle of section. Three opened anthers visible with perianth at top and right side of gynoecium
7. Successive section closer to center portion of gynoecium, showing here the connection between the ovary and swollen part of the style
8. Subsequent section, showing lower part of stylar canal
9. Subsequent section clearly showing an additional anther to left of ovary.
10. Opposite end of the series from fig. 5, well below the anthers, oblique through the basal portion showing uniformly thin perianth tube, basal locelli of the ovary, and central receptacle area

11, 12. Enlargments of dehisced anthers from the flower in figs 5–10. Scale bar = 0.3 mm.

13. Paradermal section of the ovary wall from the flower in figs 5–10, showing abundant enlarged globose oil cells scattered among the epidermal cells. Also showing fibres of the ovary wall underlying the epidermis. Scale bar – 200 μm


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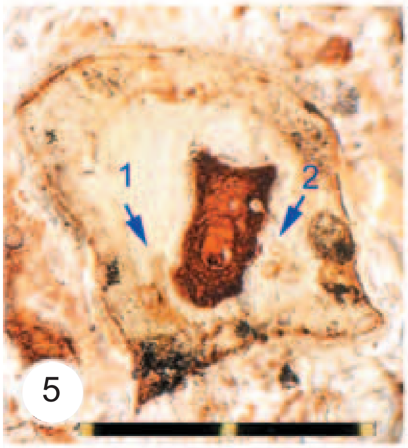
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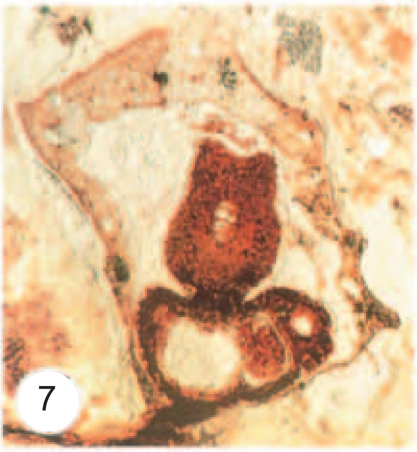
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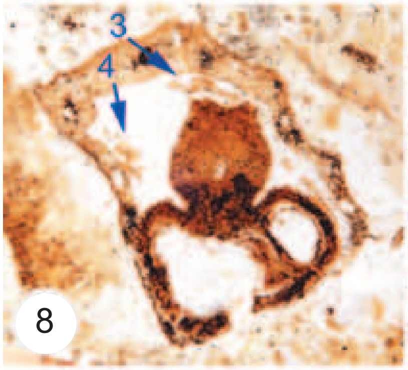
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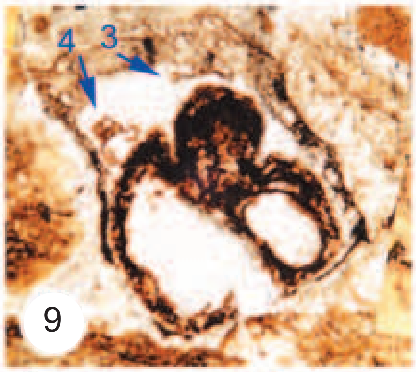
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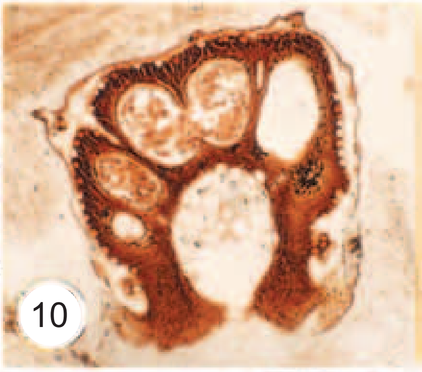
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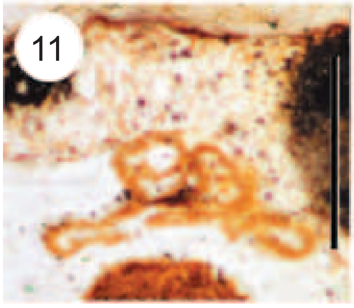
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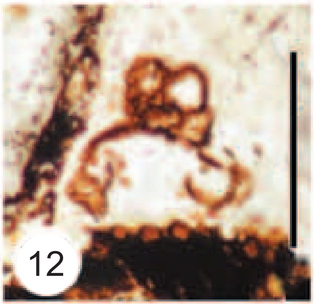
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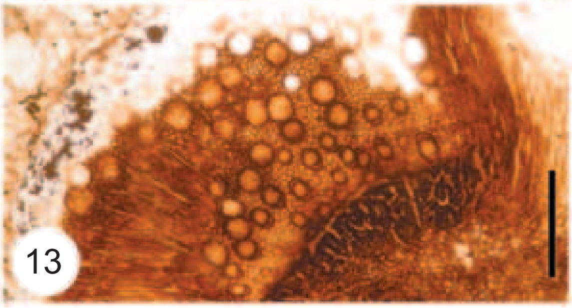
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Plate 5

Pollen from stamens of the bisexual flower in Pl. 4, figs 5–13

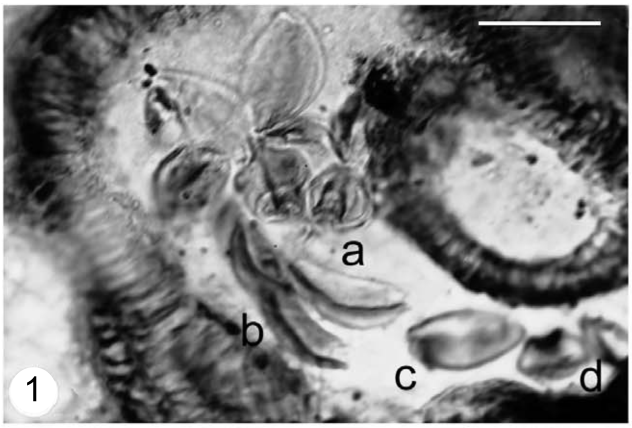
1. Cross section of an anther showing anther wall and elliptical pollen grains, transmitted light microscopy of peel section. Alphabetically labeled grains correspond to the same ones in fig. 2 [CMHH slide PM5866]. Scale bar – 20 µm
2. The same peel as fig. 1, viewed by SEM. Grains a, b, c, d, correspond to those labeled in fig. 1. Scale bar – 20 µm

3–6. Isolated pollen grains found within the anthers.

3, 4. Pollen grain of "c" of figs 1 and 2, in two planes of focus, showing annular thickening at each end, elongate colpus, and finely reticulate surface

5, 6. Two additional pollen grains by light microscopy. Scale bar in fig. 6 – 10 µm, applies also to figs 3–5

7. Same grain as in figs, 1c, 2c, 3 and 4, by SEM, showing microreticulate surface and elongate sulcus. Scale bar – 10 µm
8. Pollen grains in various orientations within anther, some broken showing wall structure. Scale bar – 30 µm
9. Partially collapsed pollen grains broken showing relative thickness of pollen wall. Scale bar – 5 µm
10. Broken pollen grain showing tectate columellate construction of the wall. Scale bar – 1 µm


a
b
c
d
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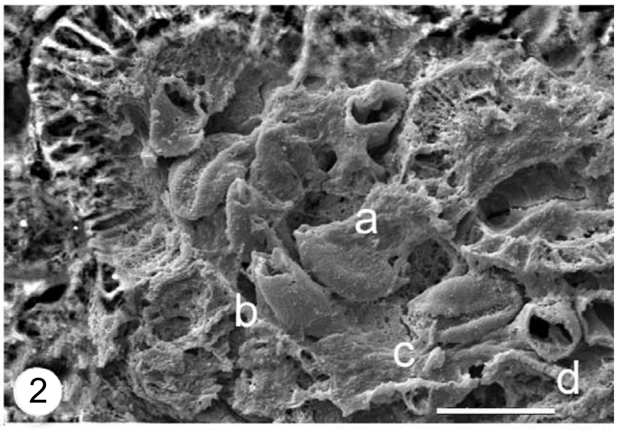
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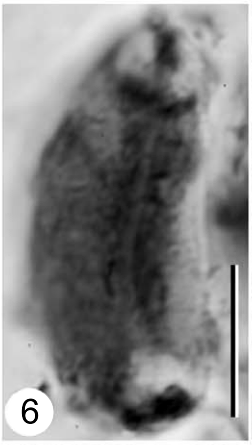
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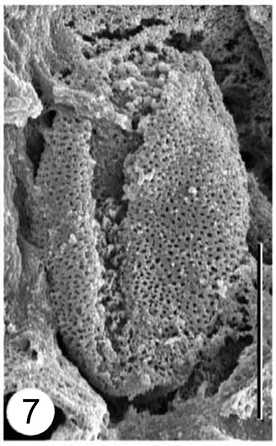
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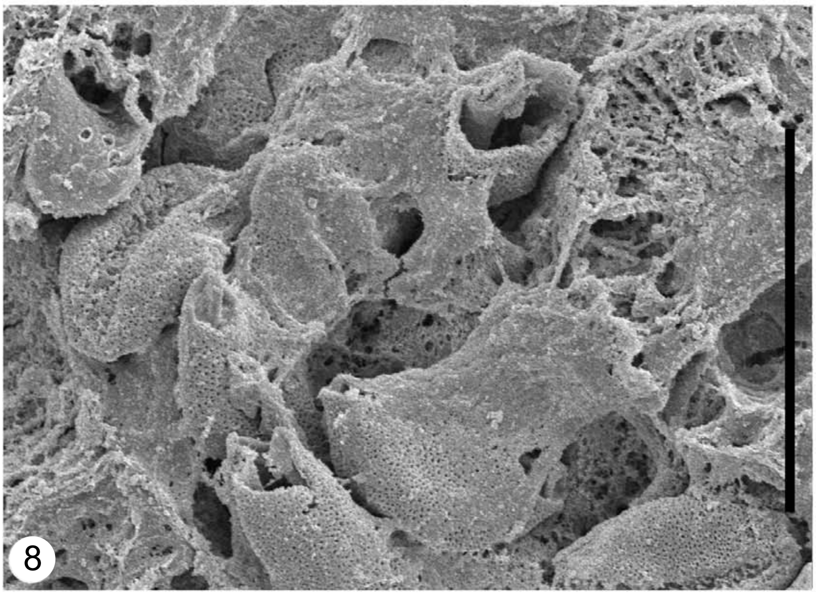
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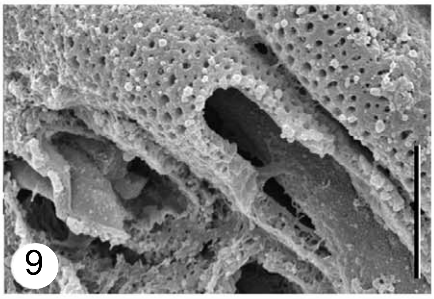
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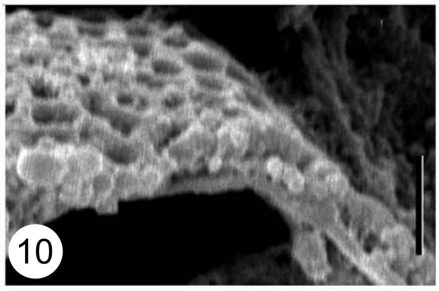
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