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REVISION OF SAHNIOCARPON HARRISII CHITALEY & PATIL BASED ON NEW SPECIMENS FROM THE DECCAN INTERTRAPPEAN BEDS OF INDIA

E. M. V. Nambudiri¹, William D. Tidwell², and Shya Chitaley³

Abstract—New specimens of Sahniocarpon harrisii Chitaley & Patil were collected from the Deccan Intertrappean beds at Mohgaon Kalan in central India. These specimens form the basis for this reinvestigation of the species and an emended diagnosis. A tuberculated seed coat, a chalazal haustorium, and the bitegmic nature of the testa can be observed in the new specimens. These features were not included in the original description. Although the extant genera of Clusiaceae and Sahniocarpus are not similar in all aspects, they are close enough to tentatively assign Sahniocarpus to this tropical family.

Well-preserved plant fossils, a majority of them angiospermic, have been noted from the Deccan Intertrappean beds exposed at Mohgaon Kalan in central India. The fossil plants from this locality include woods, roots, leaf impressions, flowers, and fruits. Petrified wood is the predominant fossil material from these beds, whereas fruiting structures are rare.

The first fruiting structure documented from the Mohgaon Kalan locality was Enigmocarpus parviflorus, a multilocular, many-seeded loculicidal capsule described by Sahni (1943). Since this publication, only a few additional dicot fruits have been reported from this locality by later workers. Jain (1964) and Nambudiri (1969) described fossil species of Indocarpus that were related to modern genera of Guttiferae, and two new genera of fossil fruits with malvaceous affinities were detailed by Chitaley and Nambudiri (1973) and Chitaley and Sheikh (1971).

The only other dicot fruit known from the Deccan Intertrappean series at this locality is Sahniocarpus harrisii Chitaley & Patil (1971). Additional specimens of this species collected by EMVN from the same Intertrappean beds exposed at Mohgaon Kalan, Chhindwara district, Madhya Pradesh, India (Fig. 1), are described here. The reinvestigation and subsequent emended diagnosis of Sahniocarpus are based on these new specimens.

The age of the Deccan Traps has long been a subject of much debate. Geologists, such as Krishnan (1969) and Wadia (1966), generally regard the Deccan volcanism as an Upper Cretaceous activity. This view was held by many researchers until Crooksank (1937) and Sahni (1937) reviewed the paleontological and geochemical data and, based upon their findings, suggested an Early Tertiary age for these beds. Plant fossils such as Nipadites (Nypa) (Rode 1933), the freshwater alga, Chara (Malcolmson 1837, Rao and Rao 1935), and palms are indicative of an Early Tertiary age (Sahni 1937). Because of mass extinctions associated with the iridium anomaly, the Cretaceous-Tertiary boundary has recently received much attention. Through this research much radiometric data have been generated concerning the Deccan Traps. The Potassium-Argon dates from these rocks suggest that the volcanic activity spanned a considerably longer time period than originally thought. Alexander (1981) reviewed the K-Ar dates for the Deccan Traps in the Chhindwara area, the collecting locality for the Sahniocarpus fruits, and suggested an age of 47 Ma for the volcanic Trap strata. This is in agreement with Sahni's original interpretation that the Intertrappean beds at Mohgaon Kalan, Chhindwara district, is of Early Tertiary age. Paleomagnetic studies of the Deccan Traps note a reversely magnetized lower and a normally magnetized upper traps (Athevale et al. 1963, Clegg et al. 1956, Verma and Pulliah 1967). Geomagnetic field reversal, an Upper Cretaceous phenomenon, is recognized in both continental and oceanic sequences and is easily discerned in the North Indian Ocean.

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sequence (Scalter and Fischer 1974). However, data accumulated from plant fossils suggest that the Intertrappean beds in the Chhindwara area are Paleocene to Early Eocene in age.

**Systematic Paleobotany**

*Sahniocarpus harrisii* Chitaley & Patil (1971)

**Specific diagnosis** (emended).—Fruit round to oval (6.5 x 7.5 mm), pentalocular, septicidal capsule; pericarp (0.85–1.6 mm thick) divided into outer zone (0.35–0.7 mm) of fleshy or hard tissues (each cell 27–36 μm in size) and an inner zone of fleshy or aerenchymatous cells; dehiscence along the septae, septae five, meeting at the center of the fruit; placentation axile; each locule single-seeded; seeds obovate, anatropous, with 3 attenuated, chalazal outgrowths; seeds endospermic, bitegmic, testa (115 μm wide), tuberculated; embryo axis (3071 x 629 μm) with a radicle towards the micropylar end, embryonic leaves, plumule and a chalazal haustorium at the chalazal end; seeds attached to the base of the axile placental by a short funicle (592 μm long).

**Description**

This permineralized fruit (7 x 7.2 mm) is a round to oval, pentalocular, septicidal capsule (Figs. 2, 3). The dry pericarp (1.5 mm thick) is differentiated into an outer zone of comparatively hard tissues and an inner fleshy zone (Fig. 18). The locules are separated by five septae (Figs. 5, 6). At the distal end of the fruit, the locules split along septal margins (septicidal dehiscence; Fig. 4). A single, anatropous seed, completely infilling the locule (Fig. 9), is added to the base of the axile placental by a short (592 μm long) funicle (Fig. 14). Each seed is obovate with a narrow micropylar end and a broad chalaza (Fig. 5). At the chalazal end, these seeds have three triangular, attenuated, stony outgrowths (Figs. 4,
The testa is hard and bitegmic, derived from outer and inner integuments (Figs. 7, 10, 12, 15). The outer integument is tuberculated by fleshy outgrowths arising from the testa (Fig. 12). The cotyledonary cells are poorly preserved. The embryo axis (3071 µm long and 629 µm wide) is comparatively large and is differentiated into a radicle, located at the micropylar end, and a plumule at the chalazal end (Fig. 9). Embryonic leaves, arising from the plumule and formed by the differentiation of the shoot apex, are clearly visible. An elongated haustorium is attached to the embryo at the chalazal end (Fig. 9).

PERICARP.—The pericarp is differentiated into outer and inner layers (Fig. 18). The outer pericarp is formed of polygonal, thick-walled, compactly arranged cells (mean diameter of 35.5 µm). This tissue is covered by a single-layered epidermis, composed of rectangular cells (12 µm). This epidermis is occasionally covered by cuticle. Conversely, cells of the inner pericarp (24.2 µm) are formed exclusively of thin-walled, round to oval, or polygonal cells. Vascular bundles traverse the inner pericarp.

VASCULATURE OF THE FRUIT.—The main lateral vascular bundle can be traced throughout the inner pericarp (Fig. 13). This vascular bundle in transverse section (126 µm × 97 µm) shows two main metaxylem vessel elements (20 µm) and four to five protoxylem vessel elements (14 µm). A layer of sclerotic tissues surrounds each bundle (Fig. 13). This main vasculature of the fruit supplies branches into the septae, which are composed of parenchymatous cells. Longitudinally oriented vessel elements of the septum have spiral wall thickenings (Fig. 11). Although cells of the phloem tissue are not easily discernible, it is assumed that the thin-walled cells in the vascular bundles are functional phloem cells.

SEEDS.—The testa (115 µm wide) is formed from the outer and inner integuments of the bitegmic ovules (Figs. 7, 10, 12, 15). Two to five layers of highly thick-walled cells form the outer testa. Apparently due to attenuated appendages, the testa attains a maximum thickness at the chalazal end. Cells of these appendages are exclusively thick walled. The inner testa is comparatively less sclerotic. Eight to ten layers of round to polygonal cells form the inner testa. A distinct layer of barrel-shaped cells (31 µm × 16.5 µm), separating the outer from the inner testa (Figs. 7, 10, 12, 15), is developed from the innermost layer of the outer integument. Outer walls of these cells are thin walled, whereas the inner and tangential walls are thickened (Fig. 15). Cells of the testa in surface view are elongated with sinuous cell walls (Fig. 8).

Round to oval, fleshy outgrowths (Fig. 12), similar to elaiosomes (Esau 1979), give the seeds a tuberculated appearance. These tubercles are formed of thin-walled, polygonal cells. Like septal cells, cells of the elaiosomes have undergone considerable degradation due to the attack of fungi. In fact, fungal mycelia and spores are clearly visible inside the fruit and seeds. The anatropous nature of the seeds is ascertained by the presence of a micropyle (14 µm wide) located near the funicle (Figs. 10, 14). Both outer and inner integuments take part in the formation of the micropylar duct. Vascular bundles are clearly visible at the chalaza.

EMBRYO.—The embryo (3071 µm × 629 µm) completely fills the seed cavity. Cells of this embryo are polygonal (wherever preserved), thin walled, and parenchymatous.
Figs. 3–8. Sahniocarpus harrisii Chitaley & Patil: 3. Fruit in l.s. showing septicidal dehiscence, nature of pericarp, seed coat, and embryo axis (4.5X); 4. Fruit in l.s. showing dehiscence at the distal end (26X); 5. Fruit in l.s. showing three seeds; the central seed is attached to the base of the axile placenta by a short funicle (15X); 6. Fruit in t.s. shows each locule containing a single seed (7X); 7. Testa in oblique section showing the outer and inner integuments (140X); 8. Cells of testa in surface view (300X).
Figs. 9–13. *Sahniocarpon harrisii* Chitaley & Patil: 9, Seed in l.s. showing embryo axis; cells of the radicle (r), plumule (p) with embryonic leaves (e), and a haustorium (h) attached to the chalazal region (30X); 10, Seed in l.s. to show the micropyle (m) formed of outer and inner integuments (130X); 11, Vascular bundle in the pericarp showing vessel elements with helical thickenings (20X); 12, Testa in l.s. showing elaiosomes (es) (250X); 13, Pericarp in l.s. showing vascular bundles (120X).
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Comparisons and Affinities

On comparison with the several dicotyledonous fruits from the Deccan Intertrappean series, it is clear that these permineralized fruit specimens are, in fact, *Sahniocarpon harrisii*. Sahni (1943) described a loculicidal capsule, *Enignocarpon parijai*, having lythraceous and sonneratiaaceous affinities. *Sahniocarpon harrisii* differs from *Enignocarpon parijai* in having single-seeded locules and also in being a septicidal rather than a loculicidal capsule. *Enignocarpon* has several seeds per locule. In addition, the hypostase tissue in *Enignocarpon* is absent in *Sahniocarpon harrisii*. The other dicotyledonous fruits known from these Intertrappean beds are *Indocarpa intertrappea* Jain (1964), *I. mahabalei* Nambudiri (1969), *Harrisocarpon sahni* Chitaley & Nambudiri (1973), and *Daberocarpon gerhardii* Chitaley & Sheikh (1971). *Daberocarpon gerhardii* is a multilocular fruit with a single seed in each locule. Chitaley and Sheikh (1971) suggested affinities for this genus of fruit with such malvaceous genera as *Abutilon indicum*, *Malva parisiiflora*, *Malva sylvestris*, *Malvastrum* sp., *Sida cordifolia*, and *Sida rhombifolia*.

*Harrisocarpon sahni* is also a septicidal capsule but contains two seeds per locule. *Sahniocarpon harrisii* is different from both species of *Indocarpa* in having a stony seed coat as compared to the sarcotesta in *Indocarpa*. Moreover, *Indocarpa* is a multi-seeded, septifragal capsule.

Chitaley and Patil (1971) stated that the *Sahniocarpon* pericarp is fleshy with aerenchymatous cells in the inner layers of the pericarp. The specimens described here, however, indicate that the pericarp is divisible into an outer zone of hard tissues and an inner zone of fleshy tissues. The pericarp in these new specimens lacks air chambers. Such differences are, perhaps, induced by ecological conditions and should not be used for discriminating at specific levels. The abundance of aerenchymatous tissue in the specimens described by them suggests that the parent plants were perhaps growing around several small lakes that formed an integral part of the Deccan landscape during the Intertrappean time. Another feature of interest is the nature of the testa. Chitaley and Patil (1971) mentioned that the testa is composed of three zones, the outer and inner zones of thin-walled parenchymatous cells and a central zone of elliptical cells with radial wall thickenings. Except for the sclerotic outer and inner testa, the structure of the seed coat as described by Chitaley and Patil (1971) is somewhat similar to the new specimens. A layer of barrel-shaped cells, separating the outer and inner testa, is the innermost layer of the outer integument. Ontogenetically, bitegmic seeds of Cruciferae develop a similar structure in their testa (Vaughn and Whitehouse 1971). Esau (1979) suggested that if subepidermal parenchyma is present in the outer integument, they are either crushed or become thick walled. Such thick-walled cells may have formed during the development of the seed coat in these new specimens of *Sahniocarpon*. The seeds are anatropous in both *Sahniocarpon* and our new specimens, but in the latter the seeds are attached to the base of the axile placenta by a funicle. For purpose of clarity, we have used the term funicle rather than raphe (Chitaley and Patil 1971). The raphe is a ridge formed by adnation of the funiculus with the ovule (Esau 1979). While such minor differences exist between the type specimens of *Sahniocarpon harrisii*, it is evident that the specimens described here belong to the genus *Sahniocarpon*. There are features in the new specimens that were not originally described by Chitaley and Patil (1971) for *Sahniocarpon harrisii*, such as, the tuberculated seed coat, the chalazal haustorium, and the bitegmic nature of the testa. The specific diagnosis of the *Sahniocarpon harrisii* has been, therefore, emended to include these additional characteristics.

Several features present in the *Sahniocarpon* fruit may be primitive. The majority of angiosperms (84.6% of dicotyledons; Davis 1966) have anatropous ovules. Although Sporne (1974) suggested that orthotropous ovules should be regarded primitive, Eames (1961) and Takhtajan (1969) noted that orthotropous ovules were derived from the anatropous condition and should be considered advanced. There is a general agreement, however, that bitegmic ovules are primitive in comparison with the unitegmic ovules (Joshi 1939, Maheswari 1950). Many angiosperous...
Figs. 14–18. Sahniocarpon harrisii Chitaley & Patil. 14. Seeds in l.s. showing attachment to the axile placentation (42X); 15. Testa in l.s. showing outer (oi) and inner (ii) integuments (320X); 16. Seed in l.s. showing cellular nature of the embryo axis (100X); 17. Seeds in t.s.; the seed at the top of the picture is in surface view (26X); 18. Fruit in l.s. showing pericarpic tissues (35X).
families represented in the Cretaceous floras, as well as 62% of extant dicotyledons, have two distinct integuments producing the seed coat (Sporne 1974). A sarcostesta (Corner 1953) is considered more primitive (van der Pijl 1955) than a sclerostesta as in Sahniocarpon. Sporne (1974) noted that the septa in axile placentation is a single unit formed by fusion of individual, involute carpels.

Members of both Guttiferae and Lecythidaceae are present in the fossil floras of India. Jain (1964) and Nambudiri (1969) described species of dicotyledonous fruit resembling Guttiferae. Indocarpa and the Sahniocarpon specimens were collected from the same Transrappean locality at Mahgaon Kalan. Lakhanpal and Bose (1951) described leaves of Garcenia and Calophyllum (Guttiferae) from the Tertiary beds in Rajasthan. Wood genera such as Kayeoxylon assamicum (Chowdhury and Tandon 1949) and Guttiferoxylon indicum (Ramanujam 1960) also occur in the Tertiary beds of India. Shallom (1960) reported Barringtonoxylon deccanense, a fossil wood assignable to Lecythidaceae, from the Deccan Transrappean beds of India.

On comparison with extant genera, the Sahniocarpon fruit is found to resemble fruits of members of the families Clusiaceae (Guttiferae sensu stricto; Cronquist 1968, 1981) system in which subfamilies Clusioideae and Hypericoideae have been included under the family Clusiaceae. The subfamily Clusioideae has capsular fruits, as in Sahniocarpon, with 3–5 carpels forming the fruit. These subfamilies have 1–numerous seeds attached to the base of the axile placenta. Moreover, the seeds are bitegmic. The difference between Sahniocarpon and the several genera of Clusioideae is that micropyles in seeds of the modern genera of this subfamily are formed entirely of their outer integuments (Table 1, Davis 1966). Sahniocarpon differs from Hypericoideae as well, the major difference between them being the number of seeds in each locale of the fruit. In Lecythidaceae, the ovules are anatropous. They are bitegmic but the micropyle is formed only of the inner integument (Venkateswarulu 1952). Although the genera of Clusiaceae are not similar to Sahniocarpon in all aspects, the resemblances between the extant genera of this family and Sahniocarpon are close enough to tentatively assign this genus to the Clusioideae of the tropical family Clusiaceae.

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<th>CHARACTER</th>
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<th>HYPERICOIDEAE</th>
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<tr>
<td>Fruit</td>
<td>Capsule, berry, or drupe</td>
<td>Capsule or berry</td>
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<tr>
<td>Number of locules</td>
<td>1–many</td>
<td>3–5</td>
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<tr>
<td>Number of ovules</td>
<td>1–many</td>
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<td>Orientation of ovules</td>
<td>Usually straight</td>
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<td>Nature of ovules</td>
<td>Anatropous, hemianatropous</td>
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<tr>
<td>Placentation</td>
<td>Axile, basal, or infrequently parietal</td>
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<td>Seeds</td>
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<td>Formed of both integuments</td>
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<tr>
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LITERATURE CITED


