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Morphology and anatomy of the angiosperm fruit *Baccatocarpon*, incertae sedis, from the Maastrichtian Deccan Intertrappean Beds of India

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ABSTRACT. Distinctive permineralized fruits of *Baccatocarpon mohgaoense* (Paradkar & Dixit) comb. nov. have been collected from several sites in the late Maastrichtian of the Deccan Intertrappean beds of Central India. We describe the peculiar fruits in detail, based on combined investigations by reflected light and X-ray CT scanning. Three-dimensional renderings and virtual slices confirm that the fruits have two lateral single-seeded locules and a central sterile chamber filled with parenchyma. The endocarp is thin-walled and opens apically longitudinal valves. Here we validate the generic name *Baccatocarpon* Bhowal & Sheikh ex Manchester, Ramteke, Kapgate & S.Y. Smith and recognize a single species, for which the name *Baccatocarpon mohgaoense* (Paradkar & Dixit) comb. nov. has priority. We document the occurrence of this species in cherts from the paleobotanical sites known as Bhutera, Keria, Mahurzari, Mohgoankalan, Paladaun, Marai Patan and Shibla. The systematic affinity of these fruits remains mysterious.

KEYWORDS: Deccan chert, Maastrichtian, Mohgaonkalan, X-ray micro-computed tomography

INTRODUCTION

The Deccan Intertrappean Beds of India preserve a rich fossil record of plants which spans the Cretaceous/Paleogene boundary (Kapgate 2005, Srivastava 2012, Smith et al. 2015). Determining the species composition of the floras in pre- and post-boundary localities will help us to assess plant response to local and global environmental perturbations. India was an isolated island continent at the time of deposition, so these fossil floras also contribute to testing hypotheses regarding the biogeographic affinities of this extinct Indian flora and in determining whether they were endemic plants or rather were allied to those of Africa, Asia or Gondwana.

In the continuing investigation of multiple localities of the Deccan Intertrappean beds of central India (Kapgate 2005, Smith et al. 2015), several plant taxa have been found to be shared among localities considered to represent the late Maastrichtian flora. These include the angiosperms *Enigmocarpon* (Sahni 1943),

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Table 1. Prior names proposed for *Baccatocarpon mohgaoense*

Binomial	Authors	Holotype	Comment	Original specimens
"Sparganium"	Mahabalé 1953	Not applicable	See text	collection of S.D. Bonde, Pune
Grewia mohgaoensis	Paradkar & Dixit 1984	"GRE/DIX 1, 2"	Binomial valid, generic assignment incorrect	lost
Baccatocarpon sharmae	Bhowal & Sheikh 2004	Not designated	Invalid name	lost
Euphorbioceocarpon singhpurii	Bhowal & Sheikh 2006	Not designated	Invalid name	lost

"*Musa*" *cardiospermum* (Jain 1963), *Graminocarpon* (Chitaley & Sheikh 1971), *Indovitis* (Manchester et al. 2013), *Pantocarpon* (Kapgate et al. 2007, Manchester et al. in press), *Sahnipushpam* (revised, Kapgate et al. 2011) and *Viracarpon* (revised, Matsunaga et al. 2018). Here we review another example that is highly distinctive and found in multiple localities, yet obscure in affinities.

The name *Baccatocarpon* was proposed by Bhowal & Sheikh (2004) for a distinctive fruit from the Singpur locality of Madhya Pradesh (MP), India. No holotype was designated and the originally illustrated specimen has been lost; however, the images and description were sufficient to recognize other specimens of the same species, several of which were assigned different names (see Tab. 1). Here we validate this generic name and recognize a single species, for which the name *Baccatocarpon mohgaoense* (Paradkar & Dixit) comb. nov. has priority.

Baccatocarpon mohgaoense was a typical element of the Deccan Intertrappean flora, judging from the observation that it occurs commonly at several localities scattered over a large area of central India, spanning more than 300 km north to south (Fig. 1). We used serial peels and micro-CT scan information to reveal the morphology and anatomy of these fruits in more detail. The purpose of this article is to stabilize the nomenclature of this

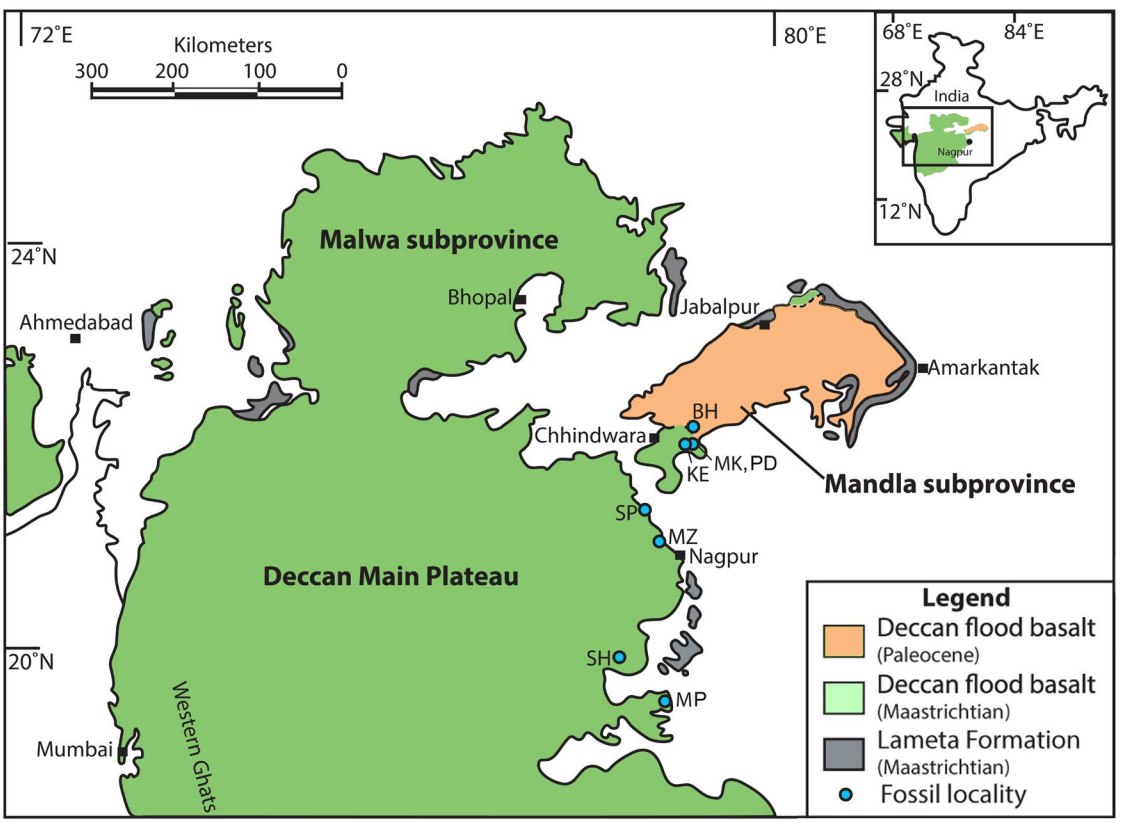

Fig. 1. Map showing the distribution of sites from which *Baccatocarpon mohgaoense* (Paradkar & Dixit) Manchester, Ramteke, Kapgate & S.Y. Smith comb. nov. was collected: Bhutera (BH), Keria (KE), Mohgaonkalan (MK), Paladaun (PD), Marai Patan (MP), Mahurzari (MZ), Shibla (SH), Singpur (SP). Coordinates of localities presented in Table 2. Dark gray and green areas inferred as Maastrichtian; orange inferred as Paleocene. Base map from Samant and Mohabey (2009). Paleocene distribution generalized, inferred from radiometric dates (Shrivastava et. al. 2015) and palynological inferences (Samant et al. 2019)

species by validating the name, to document more clearly the morphology and anatomy of this strange fruit, and to map its geographic distribution among multiple localities of the Deccan Intertrappean chert.

MATERIAL AND METHODS

New specimens were collected from sites of Deccan Intertrappean cherts scattered across central India (Fig. 1), including Bhutera, Keria, Mahurzari, Mohgoankalan, Paladaun, Marai Patan (also called Patan in the literature), Shibla (also called Sibla and Shimbala) and Singpur (Smith et al. 2015). Because of their floristic similarity, most of these sites are likely to be approximately contemporaneous, and are inferred to be late Maastrichtian (e.g. Samant & Mohabey 2009). The Deccan Traps span from the Maastrichtian to the Paleocene, with radiometric ages ranging from ~66.4–65.5 Ma (Sprain et al. 2019) to 64.2 Ma or younger (Shrivastava et al. 2015). The age of individual paleobotanical sites – whether Maastrichtian or Paleocene – has been controversial, as whole-rock basalt dates are not precise enough to secure their position with respect to the Cretaceous/Paleogene boundary. More precise radiometric dates are available from analyses of zircon and plagioclase separates (e.g. Schoene et al. 2019, Sprain et al. 2019), but so far the sites sampled for these dates have not been adjacent to any of the paleobotanical localities from which *Baccatocarpon* has been recovered, and we have inferred late Maastrichtian age based on stratigraphic position and palynological correlations (Samant et al. 2019).

Fruits were found by breaking the chert in the field and/or laboratory with a hammer and etching the fragments with hydrofluoric acid. When a fruit of *Baccatocarpon* was found in a freshly fractured surface, the adjoining pieces were etched and successively peeled to prepare slides for transmitted light microscopy. Peels were made by the paint-on method using butyl acetate solution, following the procedure described in Kapgate et al. (2011) to reveal anatomical details. Some of the same specimens were investigated by X-ray micro-computed tomography (micro-CT). Additional specimens were found fully intact within pieces of chert, revealed by micro-CT scans.

Specimens were photographed by reflected light with a Canon Rebel XSi camera and a DFS 60 mm macro lens. Peel slides were photographed with a combination of transmitted and reflected light using the same camera mounted on a Nikon Labophot microscope. Micro-CT scanning was carried out on selected extant fruits with a GE Phoenix V|tome|xm240 instrument at the University of Florida, and virtual sections were processed with Avizo 9.0 Lite.

SYSTEMATICS

Genus: ***Baccatocarpon*** Bhowal & Sheikh ex Manchester, Ramteke, Kapgate & S.Y. Smith

Generic diagnosis. As for species, presented below.

Type species: ***Baccatocarpon mohgaoense*** (Paradkar & Dixit) Manchester, Ramteke, Kapgate & S.Y. Smith comb. nov.

Species: ***Baccatocarpon mohgaoense*** (Paradkar & Dixit) Manchester, Ramteke, Kapgate & S.Y. Smith comb. nov.

Figs 2–5

Basionym. *Grewia mohgaoensis* Paradkar & Dixit 1984.

Synonymy. All other names that have been applied to this taxon (Tab. 1) were nomina nuda, so they are not included in a formal synonymy. One specimen was misidentified to the extant genus *Sparganium* (Mahabalé

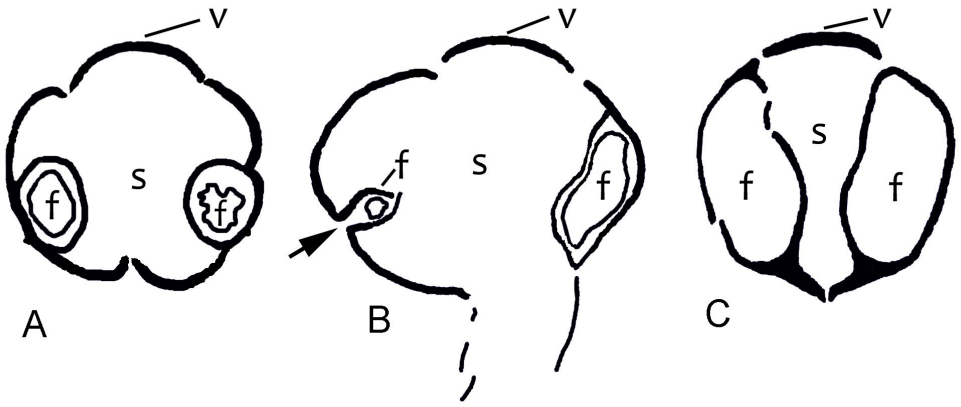

Fig. 2. Diagrammatic representation of previously published specimens of *Baccatocarpon* in different planes of section. **A**. *Grewia mohgaonse* Paradkar & Dixit (1984). Compare with Figs 3A, 4C. **B**. "*Baccatocarpon sharmae*" Bhowal & Sheikh (2004). Compare with Figs 3B, 4D, 5D. **C**. "*Euphorbioceocarpon singhpurii*". Compare with Figs 3F, 4R, S. Labels: f = fertile locule, s = sterile chamber, v = dorsal valve; arrow indicates external opening of a fertile locule

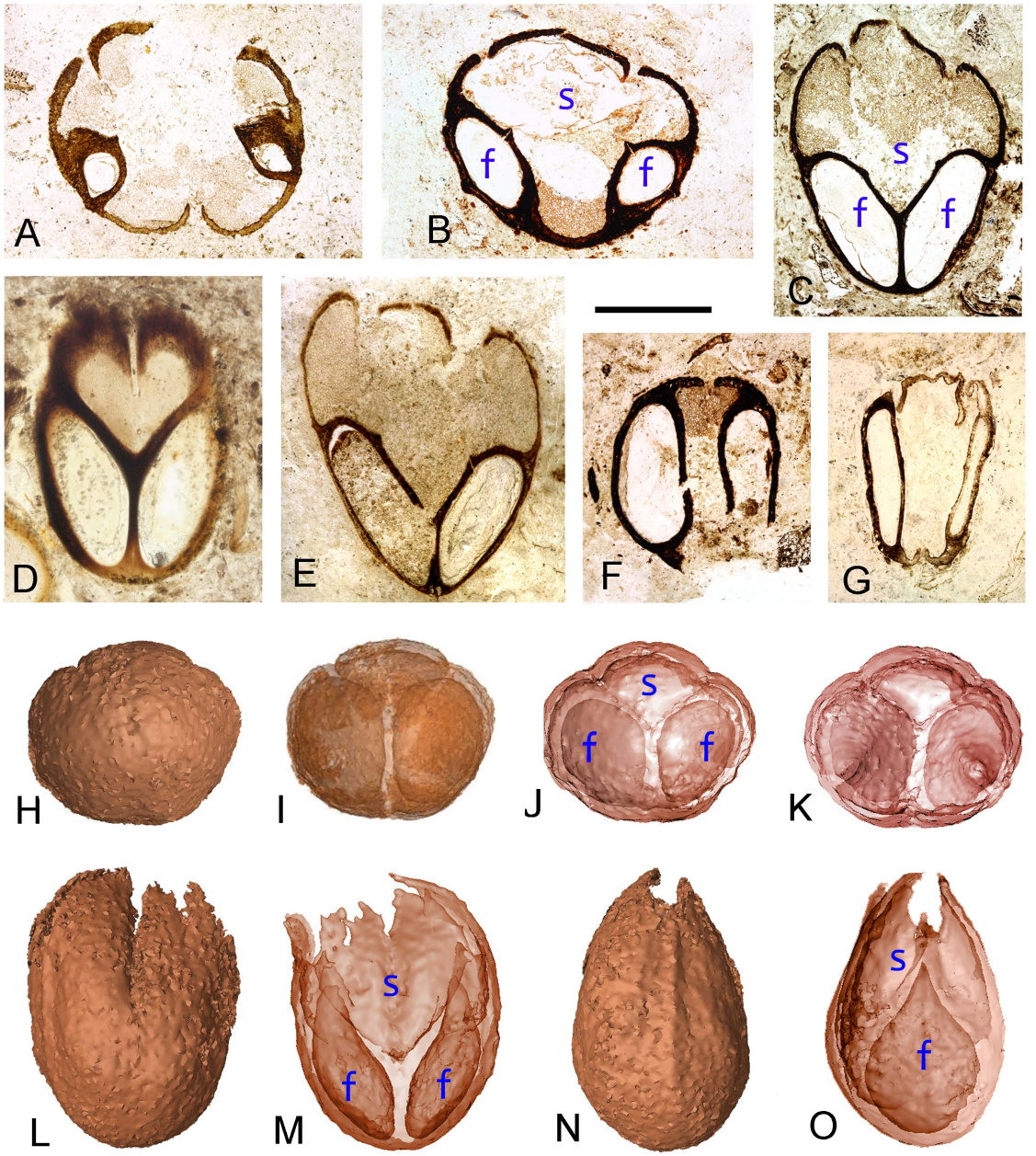

Fig. 3. **A–G**. Morphology of *Baccatocarpon mohgaoense* (Paradkar & Dixit) Manchester, Ramteke, Kapgate & S.Y. Smith comb. nov. **A**, **B**. Specimens from Marai Patan in transverse section. UF19442-62686, UF19442-62687. **C**. Coronal section, Marai Patan. **D**. Specimen from Mohgaonkalan illustrated previously by Mahabalé 1953 fig. 23 as *Sparganium*. **E**. Specimen from Singpur, UF19278-70320. **F**. Oblique longitudinal view, specimen from Marai Patan, UF19442-62688. **G**. Specimen from Bhutera, UF19348-62142. **H–O**. Surface rendering of Marai Patan specimen rotated to different views, UF19442-69830. **H**. Basal view showing smooth rounded surface by reflected illumination. **I**. Same view with translucency to show bases of the two large fertile locules separated by median septum. **J**. Basal view with translucency with portion of the wall removed, showing rounded bases of the two fertile locules, and the intervening sterile locule. **K**. Apical view with portion of the wall removed, revealing the pointed apices of both fertile locules. **L**. Front view, with reflected illumination, showing rounded base and apical separation along longitudinal slits. **M**. Same view, with translucency, revealing both fertile locules. **N**. Lateral view by reflected illumination, showing rounded base and longitudinal ridge. **O**. Same view, rendered translucent, showing pyriform outline of fertile locule. Scale bar = 2 mm. Labels: f = fertile locule, s = sterile locule

1953: Pl. 29, fig. 23) but without a species designation, so this has no relevance for formal synonymy.

Neotype: designated here. UF18311-70434 (Fig. 5A) from Mohgaonkalan, Chhindwara, Madhya Pradesh, India, housed at Florida Museum of Natural History, University of Florida. We selected this specimen because it is from the same locality as the holotype of Paradkar & Dixit (1984), which is now missing.

Additional specimens examined. UF19278-69720, 70320, 70321; UF19279-56229; UF19348-62142; UF19351-70423, 70567; 19438-68872; UF19442-69830, 68935;

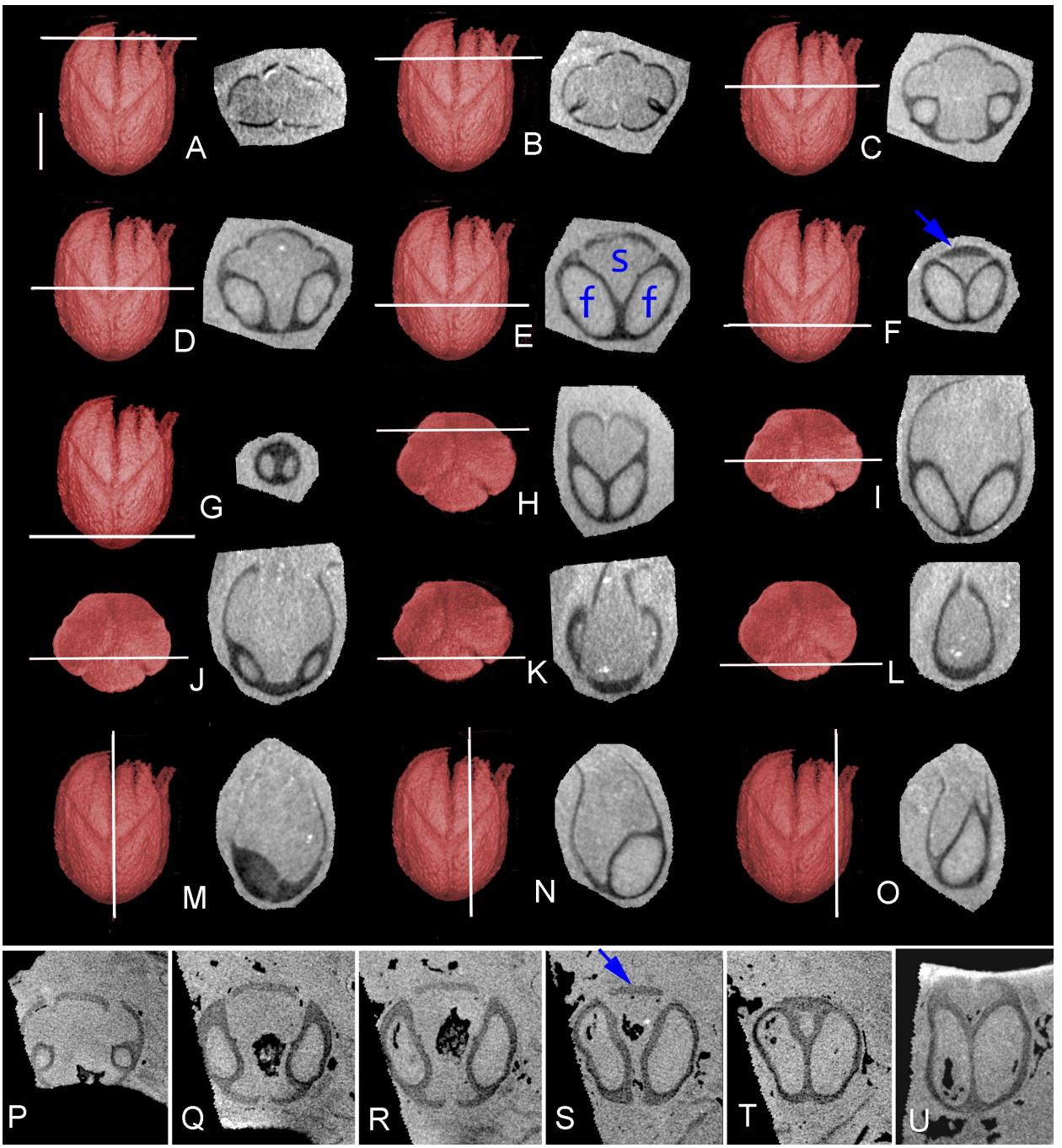

Fig. 4. Morphology of *Baccatocarpon mohgaoense* (Paradkar & Dixit) Manchester, Ramteke, Kapgate & S.Y. Smith comb. nov., **A–L**. A single specimen shown in successive section views, from Marai Patan, UF19442-69830. **A–G**. Serial transverse sections from apex toward base, with levels of sections indicated by the white line on longitudinally oriented volume rendering to the left of each section image; labels in E indicating the sterile (s) and fertile (f) locules, arrow in F denoting the dorsal valve. **H–L**. Serial coronal sections, with levels of sections indicated by white lines on the basal-view volume renderings to the left of each section image. **M–0**. Serial sagittal sections with section level indicated by white lines on the volume renderings to the left. **P–T**. Serial transverse sections from near apex to near base of fruit in chert from Mohgaonkalan, arrow indicating dorsal valve, UF 19438-68872. **U**. Same specimen in coronal section. Scale bar in A = 2 mm (applies to all)

UF19506-69603 at Florida Museum of Natural History.

Type locality, stratigraphy and age. Mohgaonkalan–Deccan Intertrappean Beds, India, late Maastrichtian.

Other occurrences. Keria, Mahurzari, Paladaun, Marai Patan, Shibla, Singpur–Deccan Intertrappean Beds, India, late Maastrichtian (Fig. 1, Tab. 2).

Emended diagnosis. Fruits ellipsoidal, 4.0–5.7 mm long, 4.3–5.4 mm wide, 3.3–3.6 mm deep. Endocarps smooth, lacking vascular strands or ribs, bilaterally symmetrical, with a pair of faint lateral longitudinal keels

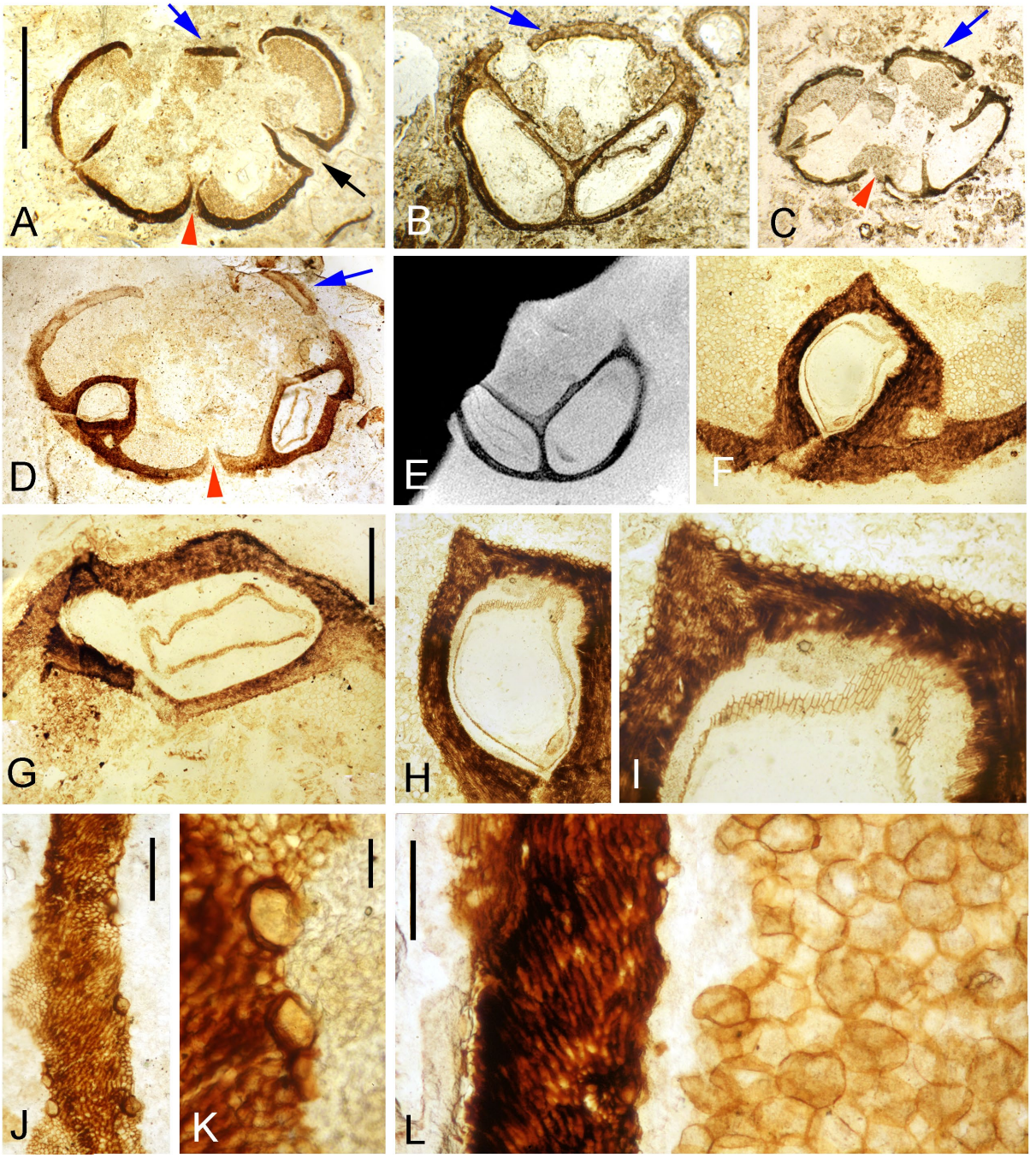

Fig. 5. *Baccatocarpon mohgaoense* (Paradkar & Dixit) Manchester, Ramteke, Kapgate & S.Y. Smith comb. nov. from different sites. Blue arrows indicating dorsal valve, red arrows indicating ventral slit. **A**. Transverse section peel in apical 1/3, Mohgaonkalan, black arrow indicating opened fertile locule. Neotype, UF18311-70434. **B**. Transverse section in basal 1/3, Paladaun UF19506-69603. **C**. Mahurzari, oblique section, UF19279-56229. **D–I**. Specimen from Marai Patan, UF19442-68935. **D**. Oblique-transverse section showing the two fertile locules and sterile central chamber. **E**. Digital longitudinal coronal section from micro-CT data of the same specimen, the upper fracture surface representing the plane at which the sections of D, F–L were peeled. **F–H**. Each of the fertile locules enlarged, showing fibrous septa and single seed inside. **I**. Enlargement showing elongate cells of the seed coat, and fibrous carpel wall. **J**. Enlargement of fibrous endocarp wall. **K**. Transition zone from septum to inner chamber, with idioblasts. **L**. Section through fibrous wall and parenchymatous central chamber. Scale bar = 2 mm in A (applies also to B–E), 500 µm in G (applies also to H, I), 100 µm in J, 20 µm in K, L

and a median groove. Base rounded, apical end tapered and usually splitting open along 4 or 5 longitudinal slits. Fruit with three chambers: a large sterile central chamber filled with parenchyma and a symmetrical pair of lateral, single-seeded locules on either side of the plane of bisymmetry. Fertile locules pyriform, extending about halfway from the rounded base of the fruit toward the apex, sharing a common septum basally but divergent from each other apically, separated by parenchyma tissue of the central chamber. Lateral locules with a slit-like

opening on the distal side (coinciding with lateral longitudinal keel of the fruit) and a keel in the same plane on its proximal side. Pedicel and style not observed, but a circular scar at base, possibly representing the detachment scar.

Endocarp wall 140–240 µm thick, made up of narrow fibers 6–8 µm thick. Septum 120–150 µm thick, also composed of narrow fibers 6–8 µm thick. Idioblasts containing rhomboidal crystals occur at the periphery of the endocarp and lining the sterile locule. Vascular bundles absent or rare in the endocarp wall and septa. Endocarp opening apically by three main longitudinal slits: one on the ventral side separating the two fertile locules, and two on the opposite side defining a dorsal valve.

Comments. These peculiar disseminules present different appearances depending on the orientation and level of the plane of fracture or section (Figs 2, 4). Consequently, their morphology has been interpreted in different ways, leading to multiple taxonomic designations. The publication history of this taxon is summarized in Table 1 and discussed below.

DISCUSSION

Baccatocarpon mohgaoense fruits occur at several localities of the Deccan Intertrappean Beds (Fig. 1). These fruits, embedded in the chert, exhibit very different appearances depending upon the orientation and level in which they are fractured or cut, but successive virtual slices through complete specimens analyzed by micro-CT scanning revealed their internal and external structure (Figs 2, 3). The distinctive features of this fruit are bilateral symmetry, the sterile, parenchyma-filled central chamber (e.g. Fig. 3B, C, 5D, L), the pair of lateral, pyriform, single-seeded locules, and the valve-like opening of the fruit. Nearly all specimens were ruptured open apically by splitting along longitudinal zones of weakness. The endocarps have three main longitudinal zones of apical separation, one of them in the plane of bisymmetry separating the two fertile locules, the other two on the opposite side, defining a prominent dorsal valve that opens apically (Figs 3A, 4C, D). This valve is commonly somewhat opened in mature specimens (Figs 3A, B, 4P–S, 5A–D) but was fixed basally; we did not find them completely detached.

The apical opening of the fruit directly exposed only the parenchyma of the central chamber, with the fertile locules still encapsulated by their sclerenchymatous walls, so that the seeds remained intact within the pair of lateral locules even after the fruit opened apically (Figs 3A–D, 4, 5D). It seems likely that the seeds did not regularly dehisce but instead germinated via distal slits of the carpels aligned with the lateral longitudinal edges of the endocarp (Figs 2B, 5A). Perhaps desiccation of the central chamber created physical tensions that effected the opening of the pericarp associated with germination of the seeds.

PREVIOUS INVESTIGATIONS

This fruit type was first illustrated by Mahabalé (1953), who interpreted it as an example of extant *Sparganium* (his Fig. 12 and Pl. 29, fig. 23; reillustrated here as Fig. 3D). Mahabalé did not provide a species name and he illustrated this specimen together with another kind of fruit (his Pl. 29, fig. 22) that is now treated as *Pantocarpon* (Kapgate et al. 2007). The similarity to *Sparganium* was only superficial; *Sparganium* fruits are indehiscent and obconical with a prominent stylar protrusion not seen in these fossils (Zubkova & Shabes 1985).

Paradkar and Dixit (1984), based on two specimens from Mohgaonkalan, illustrated and described this fruit type and placed it in the modern tilioid genus *Grewia*. Both original specimens of *Grewia mohgaoensis*, including the holotype, are now lost, but the published description and images (e.g. Fig. 2A) are sufficient to match it with subsequently discovered specimens. Paradkar and Dixit (1984) described the fruit as "small, round, two pyrened, two seeded, drupaceous and indehiscent" and 4.4 by 4.0 mm in diameter. The attribution to *Grewia* rested partly on the description of slime cells in the fossil specimens; however, these are not clearly documented in the images provided and could not be verified in the specimens we have studied. Possibly the authors were referring to the layer of idioblasts that we observed to contain rhomboidal crystals lining the sterile locule (Fig. 5K). Paradkar & Dixit's description of the fossil as two-pyrened seems to have been influenced by a comparison with extant *Grewia* fruits. Our sections show that all three carpels are fused, sharing a single endocarp (Fig. 4).

Based on a specimen from Singpur, Bhowal & Sheikh (2004) attempted to establish a new genus and species, "*Baccatocarpon sharmae*", but no holotype nor repository was designated, so the name has remained a nomen nudum according to the International Code of Nomenclature for Algae, Fungi, and Plants (ICN; Turland et al. 2018). The description was based on a specimen exposed in an oblique-transverse fracture near the base of a fruit, showing one of the fertile locules appearing smaller than the other because of the oblique section (Fig. 2B). Apparently the reported dimensions were miscalculated, because the fruit was indicated as less than one millimeter ("792 µm"), but estimates based on other specimens from the same locality as well as other sites indicate that the correct diameter is in the range of 3–5 mm (Tab. 2). Part of the pericarp in Bhowal & Sheikh's specimen is fractured and splayed open, and its outline (Fig. 1B) was interpreted to include the stalk of the fruit. We do not agree with this interpretation and have not seen any specimens with an intact pedicel, even with the aid of current micro-CT scan technology that allows us to examine complete fruits while still fully encased within the chert. We hereby validate the generic name *Baccatocarpon* with the designation of a type specimen from Mohgaonkalan and provision of an emended diagnosis, adopting the original epithet of Paradkar & Dixit (1984): *Baccatocarpon mohgaoense* (Paradkar & Dixit) comb. nov

Two years later, the same authors proposed an additional binomial for this fruit type, "*Euphorbioceocarpon singhpurii*", for another specimen from Singpur (Bhowal & Sheikh 2006). However, it too was invalidly published, lacking designation of a holotype and repository. This specimen, which we consider to represent *Baccatocarpon mohgaoense*, had been fractured and peeled in a nearly transverse plane and was interpreted to show three locules (Fig. 2C). The magnifications and measurements were apparently miscalculated (the fruit was described as only ~1 mm in diameter, and magnifications of the figures were exaggerated times ten). Bhowal & Sheikh (2006) published photos of the specimen showing mesocarp and exocarp that are missing from most other specimens. They also observed: "glandular hairs, both at the apical and distal part of the fruit. On the distal side, only remnants of the hair can be seen whereas at the apical side they are very distinct. They appear entire as well as bifurcated. The tips of the hairs are rounded and made up of thin walled, elongated cell in longitudinal section" (Bhowal & Sheikh 2006: 47). We have not encountered such hairs on any of the material we examined. Paradkar & Dixit's (1984) specimen also showed meso- and exocarp but without such hairs. Perhaps these hairs were usually lost by degradation prior to fossilization in the specimens we studied. It is a pity that Bhowal and Sheikh's specimen and slides are missing, but it is clear that their specimen belonged to the species here referred to as *Baccatocarpon mohgaoense*.

Bhowal & Sheikh (2004) considered but dismissed the possibility that the fruit was bilocular and also discarded the possibility that the fruit might be unilocular with the seed attached to the fruit wall in parietal placentation. Ultimately, they concluded "it is amply clear that the studied fossil is a trilocular fruit with parietal placentation." Our investigation of additional specimens, with the benefit of X-ray micro-CT analyses, confirms that

Table 2. Localities where *Baccatocarpon* was recovered

Locality	Latitude	Longitude	Exemplary specimens
Mohgaonkalan	22°1.415′N	79°1.204′E	UF18311-70434 Neotype
Mohgaonkalan II	22°01.12800′N	79°10.91500′E	UF19438-68872
Paladaun	22°01.28502′N	79°10.42332′E	UF19506-69603
Marai Patan	19°32.18598′N	78°07.53600′E	UF19442-69830 UF19442-68935
Mahurzari	21°13.280′N	79°00.843′E	UF19279-56229
Singpur	21°37.00250′N	78°44.07017′E	UF19278-69720 UF19278-70320 UF19278-70321
Shibla	19°58.141′N	78°40.838′E	UF19351-70423 UF19351-70567
Bhutera	22°06.582′N	79°08.402′E	UF19348-62142

the fruits are three-chambered, with a sterile central chamber and two fertile lateral locules (Figs 2, 3). However, the placentation, whether parietal as interpreted by Bhowal & Sheikh (2004) or axile as interpreted by Paradkar & Dixit (1984), is not certain. Whether the fruit was derived from a bicarpellate or a tricarpellate ovary is uncertain, as we have not seen specimens with intact style and stigma. Because we did not encounter vasculature in the endocarp wall or septum, we infer that the main vasculature passed through external tissues of the mesocarp and/or exocarp that were not preserved in our material.

The suggestion of euphorbiaceous affinity (Bhowal & Sheikh 2004) was based on incompletely known morphology and anatomy. Fruits of Euphorbiaceae are typically trilocular with equal development of the locules, in contrast to the bilateral symmetry of *Baccatocarpon*. Even when one of the carpels of a euphorbiaceous fruit aborts, important morphological differences remain, including the distinct subapical axile placentation and the lack of a dorsal valve. The morphology and anatomy of *Baccatocarpon* are unlike that of schizocarpic capsules typical of Euphorbiaceae and also unlike that of genera with samaras and those with indehiscent drupe-like fruits (e.g. Webster 2014).

AFFINITIES OF *BACCATOCARPON MOHGAOENSE*

Despite the distinctive morphology of these fruits, we have not encountered morphologically matching fruits among extant angiosperms. In our broader comparisons we noted similarities with the apialean family Torricelliaceae. The three extant genera of Torricelliaceae all possess three carpels with a combination of two sterile locules and one central fertile locule, and the fruits open apically by valves (Manchester et al. 2017). The extinct genus *Pantocarpon*, which co-occurs at several localities with *Baccatocarpon*, likely represents Torricelliaceae (Manchester et al. in press). *Pantocarpon* resembles *Baccatocarpon* in having two fertile locules and one sterile locule (rather than one fertile and two sterile as in extant Torricelliaceae; Manchester et al. 2017). However, *Baccatocarpon* lacks the pair of subapical apertures seen in Torricelliaceae. The sterile locule of *Pantocarpon* and the extant genera is empty of tissue at maturity, whereas that of *Baccatocarpon* is filled with parenchyma (Fig. 3A–F). Also, the endocarp in *Baccatocarpon* is composed mostly of fibers, whereas the modern genera of Torricelliaceae have endocarps composed mostly of isodiametric (in *Aralidium*) to somewhat elongate sclereids (Manchester et al. 2017). Because it lacks the synapomorphy of paired endocarp apical apertures, has its sterile locule filled with parenchyma rather than empty, and its endocarp is composed of fibers, it seems that *Baccatocarpon* represents an extinct, unrelated clade, and that the similarities between this fossil and Torricelliaceae are simply due to convergence.

Although *Baccatocarpon mohgaoense* was widespread and relatively common in the late Maastrichtian of central India, we are not aware of any subsequent fossil occurrences, and nothing precisely similar is known in the present-day flora. It therefore seems to have been an endemic Late Cretaceous Indian taxon that succumbed to environmental changes at or near the Cretaceous/Paleogene boundary.

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REFERENCES

BHOWAL M. & SHEIKH M.T. 2004. *Baccatocarpon sharmae* gen. et. sp. nov. A petrified dicot baccate fruit from the Deccan Intertrappean Beds of Singhpur, Madhya Pradesh, India. Trends in Life Sciences (India), 19(1): 25–32.

BHOWAL M. & SHEIKH M.T. 2006. A petrified dicot fruit, *Euphorbioceocarpon singhpurii*, from the Intertrappean Bed of Singhpur, Madhya Pradesh. Gond. Geol. Magz., 21: 47–49.

CHITALEY C.D. & SHEIKH M.T. 1971. An infected grain from the Deccan intertrappean cherts of Mohgaonkalan. J. Indian Bot. Soc., 50: 137–142.

JAIN R.K. 1963. Studies in Musaceae-I. *Musa cardiosperma* sp. nov., a fossil banana fruit from the Deccan Intertrappean Series India. The Palaeobotanist, 12: 45–54.

KAPGATE D.K. 2005 Megafloral analysis of intertrappean sediments with focus on diversity and abundance of flora of Mohgaonkalan, Mandla and adjoining areas of Madhya Pradesh. Gond. Geol. Magz., 20: 31–46.

KAPGATE D.K., PATIL S.P., ILAMKAR N.P. & RAMTEKE D.D. 2007. Investigation of a new petrified trilocular fruit from the Deccan Intertrappean Series of Mohgaonkalan, M.P.: 43–48. In: Trivedi P.C. (ed.), Palaeobotany to Modern Botany. Pointer Publications, Jaipur.

KAPGATE D.K., AWASTHI N., MANCHESTER S. & CHITALEY S. 2011. Inflorescence and flowers of *Sahnipushpum* Shukla from the Deccan Intertrappean beds of India. Acta Palaeobot., 51(2): 207–227.

MAHABALÉ T.S. 1953. Occurrence of *Sparganium* in the Deccan Intertrappeans of Madhya Pradesh, India. Proc. Natn. Inst. Sci. India, 19: 623–629.

MANCHESTER S.R., KAPGATE D.K. & WEN J. 2013. Oldest fruits of the grape family (Vitaceae) from the Late Cretaceous Deccan Cherts of India. Amer. J. Bot., 100: 1849–1859.

MANCHESTER S.R., COLLINSON M.E., SORIANO C. & SYKES D. 2017. Homologous fruit characters in geographically separated genera of extant and fossil Torricelliaceae (Apiales). Int. J. Pl. Sci., 178(7): 567–579.

MANCHESTER S.R., KAPGATE D.K., PATIL S.P., RAMTEKE D., MATSUNAGA K.S. & SMITH S.Y. In press. Morphology and affinities of *Pantocarpon* fruits (Torricelliaceae) from the Maastrichtian Deccan Intertrappean Beds of Central India. Int. J. Pl. Sci.

MATSUNAGA K.S., SMITH S.Y., MANCHESTER S.R., KAPGATE D., RAMTEKE D., GARBOUT A. & VILLARRAGA-GÓMEZ H. 2018. Reinvestigating an enigmatic Late Cretaceous monocot: morphology, taxonomy, and biogeography of *Viracarpon*. Peer J. "6:e4580; DOI 10.7717/peerj.4580" 32 pp.

PARADKAR S.A. & DIXIT V.P. 1984. *Grewia mohgaonse*–a new petrified dicotyledonous fruit from the Deccan Intertrappean beds of Mohgaonkalan, Madhya Pradesh–India. Proc. Ind. Geophytology Conf., Lucknow (1983) Special Publication, 156–162.

SAHNI V.B. 1943. Indian silicified plants 2. *Enigmocarpon parijai* a silicified fruit from the Deccan with a review of fossil history of the Lythraceae. Proc. Ind. Acad. Sci., 17B(3): 59–96.

SAMANT B. & MOHABEY D.M. 2009. Palynoflora from Deccan volcano-sedimentary sequence (Cretaceous-Paleogene transition) of central India: Implications for spatio-temporal correlation. J. Biosci., 34: 811–823.

SAMANT B., KUMAR D., MOHABEY D.M., KAPGATE D.K., MANCHESTER S.R., PATIL S.K. 2019. Palynoflora from intertrappean localities in southeastern part of Deccan volcanic province: taxonomic composition, age and paleogeographic implications. Palaeoworld. [in press/available online]

SCHOENE B., EDDY M.P., SAMPERTON K.M., KELLER C.B., KELLER G., ADATTE T. & KHADRI S.F. 2019. U-Pb constraints on pulsed eruption of the Deccan Traps across the end-Cretaceous mass extinction. Science, 363: 862–866.

SHRIVASTAVA J.P., DUNCAN R.A., KASHYAP M. 2015 Post-K/PB younger ^{40}Ar–^{39}Ar ages of the Mandla lavas: Implications for the duration of the Deccan volcanism. Lithos, 224: 214–224.

SMITH S.Y., MANCHESTER S.R., SAMANT B., MOHABEY D.M., WHEELER E., BAAS P., KAPGATE D., SRIVASTAVA R. & SHELDON N.D. 2015. Integrating paleobotanical, paleosol, and stratigraphic data to study critical transitions: a case study from the Late Cretaceous-Paleocene of India: 137–166. In: Polly P.D., Head J.J. & Fox D.L. (eds), Earth-Life Transitions: Paleobiology in the Context of Earth System Evolution. The Paleontological Society Papers, 21. Yale Press, New Haven, CT.

SPRAIN C.J., RENNE P.R., VANDERKLUYSEN L., PANDE K., SELF S., MITTAL T. 2019. The eruptive tempo of Deccan volcanism in relation to the Cretaceous-Paleogene boundary. Science, 363: 866–870.

SRIVASTAVA R. 2012. Indian upper Cretaceous-Tertiary flora before collision of Indian Plate: A reappraisal of central and western Indian flora. Mem. Geol. Soc. India, 77: 281–292.

TURLAND N.J., WIERSEMA J.H., BARRIE F.R., GREUTER W., HAWKSWORTH D.L., HERENDEEN P.S., KNAPP S., KUSBER W.-H., LI D.-Z., MARHOLD K., MAY T.W., MCNEILL J., MONRO A.M., PRADO J., PRICE M.J. , SMITH G.F. (eds.) 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. DOI https://doi.org/10.12705/Code.2018

WEBSTER G.L. 2014. Euphorbiaceae: 51–216. In: Kubitzki K. (ed.), The families and genera of vascular plants. XI Flowering plants – Eudicots Malpighiales. Springer, New York 331 pp.

ZUBKOVA I.G. & SHABES L.K. 1985. Typhales: 262–264. In: Takhtajan A. (ed.), Anatomia Seminum Comparativa, Vol 1.