MORPHOLOGY AND AFFINITIES OF PANTOCARPON FRUITS (CF. APIALES: TORRICCELLIACEAE) FROM THE MAASTRICHTIAN DECCAN INTERTRAPPEAN BEDS OF CENTRAL INDIA

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Premise of research. Permineralized fruits of Pantocarpon Kapgate, Patil, llamkar & Ramteke have been reinvestigated to better understand this abundant component of the Deccan Maastrichtian–Paleocene flora of central India.

Methodology. Peels and X-ray microcomputed tomography (μ-CT) were used to compare the morphology and anatomy of the silicified fruits with that of possible extant relatives.

Pivotal results. We show, for the first time, the surface morphology of these fruits, which are encased within opaque chert, and clarify additional characters of morphology and anatomy. By varying the orientation of digital sectioning planes through the fruit using μ-CT data, we show that five different generic names (Pantocarpus and the junior synonyms Bicarpelarocarpus, Electriocarpus, Loganiocarpus, and Verbenaceocarpus) were previously applied to the same entity, each based on holotypes studied in different physical planes of section. Several distinctive characters, including tricarpellate syncarpous fruits, paired apical apertures, empty sterile locules, single-seeded fertile locules, and longitudinal germination valves, are shared with the extant eudicot family, Torricelliaceae (Apiales). The pair of endocarp apertures resembles that in Aralidium and Torricellia. There are some obvious differences, however, from fruits of the three living genera. In Torricellia, Melanophylla, and Aralidium, there are two sterile locules (lateral) and a single fertile one (median), whereas in Pantocarpus, there are two fertile locules (lateral) and a single sterile one (median).

Conclusions. Recognition of Pantocarpus as a potential member of Torricelliaceae is interesting because it would be the most ancient record known for the family (next youngest being middle Eocene, ca. 47 Ma) and provides additional biogeographic information. The occurrence of this taxon in India at about 66 Ma, when the subcontinent was still isolated from other major landmasses, indicates that this region may have played a role in early evolution of the family, which is now disjunct between Madagascar, China, and Malesia.

Keywords: Deccan chert, Maastrichtian, Mohgaonkalan, X-ray microcomputed tomography.

Introduction

The family Torricelliaceae H.H. Hu, of the order Apiales, has an interesting modern distribution, disjunct between Madagascar, East Asia, and Malesia with one genus in each region: Melanophylla Baker, Torricellia DC (conserved name; alternate prior spelling was Torricelia), and Aralidium Miq., respectively. The monophyly of these genera within Torricelliaceae has been confirmed by molecular data (e.g., Plunkett 2003; Kårehed 2003; Soltis et al. 2018) and supported by various morphological synapomorphies, particularly in fruit morphology (Manchester et al. 2017). The fruits vary in shape and size but all are trilocular, with one fertile locule and two sterile locules (Manchester et al. 2017). Torricellia fossils have been recognized based on well-preserved fruits from the Eocene of western North America (Manchester 1999; Manchester et al. 2017) and Eocene to Miocene of Europe (Meller 2006; Collinson et al. 2012). The recognition of early torricelliaceous fossils has broader implications for understanding the evolutionary history of Asterids because the Apiaceae have a relatively sparse fossil record (Manchester et al. 2015).

We have been investigating anatomically preserved silicified plants from the Deccan Intertrappean beds of central India to obtain information on the ecosystem composition in India across
the Cretaceous-Paleogene boundary, a time when India was geographically isolated as an island, and to assess the response of the biota to the global changes occurring at this time (Smith et al. 2015; Samant et al. 2020). Among the more common and characteristic elements of the Deccan fruit and seed flora is a distinctive small trilocular fruit that we now infer to represent Torricelliaceae.

The fossils were originally attributed to the extant genus *Sparganium* L. (Typhaceae), without a specific assignment, by Mahabalé (1953, pl. 29, fig. 22), but the actual botanical affinities have remained elusive. The fruits differ from those of *Sparganium* in the position and number of locules and in various other morphological features introduced in the present study. The binomial with nomenclatural priority for these fossils is *Pantocarpon deccanense* Kapgate, Patil, Ilamkar & Ramteke (2007), based on specimens from the classic Mohgaonkalan lagerstätte in Chhindwara, Madhya Pradesh, India. In this article, we provide the first three-dimensional renderings of these fossils along with digital slices in transverse and longitudinal orientations from X-ray microcomputed tomography (μ-CT) scanning. The improved understanding of the fruit morphology revealed the need for a synonymic revision, which is presented here. This reduces the diversity of taxa recorded from the Deccan fruit and seed flora but enriches our understanding of the geographic distribution of *Pantocarpon* among multiple localities of the Deccan chert, indicating that the genus was widespread in the late Maastrichtian of India. We also offer a new interpretation of its taxonomic affinity relative to extant eudicots and assign the genus to Torricelliaceae based on new characters revealed by μ-CT scanning.

### Material and Methods

We found the fossils at several localities of the Deccan intertrappean beds, including Bhutera, Keria, Mohgaonkalan, Paldau, Marai Patan, Shibla, and Singpur (fig. 1; table 1). Fruits were found in the field and laboratory by cracking the fossiliferous chert with hammers and inspecting fresh fracture surfaces for intercepted botanical remains. Discovered specimens were etched with hydrofluoric acid for better contrast in photography, and successive serial peels were prepared by the paint-on acetate peel method summarized by Kapgate et al. (2011). Specimens and prepared peel slides are cataloged in the Paleobotanical Collection of the Florida Museum of Natural History at the University of Florida (UF), Gainesville, Florida.

The extensive series of basalt flows known as the Deccan traps spans from Maastrichtian to Paleocene with radiometric ages ranging from about 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 outcropping in interbeds between basalt flows—whether Cretaceous or Cenozoic—has been debated because whole-rock basin dates are insufficiently precise to secure their position with respect to the Cretaceous-Paleogene boundary. The more precise radiometric dates obtained from detrital zircons (e.g., Schoene et al. 2019) and plagioclase separates (e.g., Sprain et al. 2019) are from sites in the Western Ghats, far to the west of the paleobotanical sites; those ages cannot be correlated directly to the paleobotanical sites that outcrop along the eastern margin of the Deccan main plateau and into the Mandla lobe (fig. 1). We infer that paleobotanical sites such as Ghuhgua, Shahpura, and Parapani (Kapgate 2005), in the eastern part of the Mandla lobe, are Paleocene based on 40Ar/39Ar dating of plagioclase (Shrivastava et al. 2015). Those sites are, so far, lacking any occurrences of *Pantocarpon* fruits. The *Pantocarpon*-bearing sites are situated on the eastern margin of the Deccan main plateau and in the western part of the Mandla lobe (fig. 1). These are consistent in floras composition, including such taxa as *Baccatocarpon*, *Enigmocarpon*, *Graminocarpon*, *Indovitis*, and *Sahnipushpan*, and have been considered likely to be late Maastrichtian in age based on stratigraphic position and palynological inferences (Samant et al. 2020).

Specimens were μ-CT scanned to discover *Pantocarpon* fruits embedded within the chert. We used a GE Phoenix V/tome/xm240 CT scanner, with a tungsten reflection target and 0.5-mm copper filter, located at the University of Florida College of Engineering Nanoscale Research Facility. Voltage and current were adjusted to specimen size, with voltage ranging from 100 to 180 kV and current ranging from 50 to 90 μA, with up to 1700 images of a single specimen and resolution ranging from 14 to 60 μm. Resulting image stacks were processed with Avizo Lite version 9.1 to produce volume renderings, surface renderings, and digital sections. The best example data sets are accessible as TIFF stacks and 3-D surface renderings at https://morphosource.org under the project “Deccan Plant Reproductive Structures,” for example, https://www.morphosource.org/Detail/SpecimenDetail/show/specimen_id/21963.

### Results

#### Systematics

**Family—Torricelliaceae**

**Genus—Pantocarpon** Kapgate, Patil, Ilamkar & Ramteke *emend.* Manchester, Kapgate, Patil, Ramteke & S.Y. Smith

**Type Species—** *Pantocarpon deccanense* Kapgate, Patil, Ilamkar & Ramteke, *emend.* Manchester, Kapgate, Patil, Ramteke & S.Y. Smith (Figs. 2–4, 5D)

*Emended generic diagnosis.* Fruit ovoid, trilocular with two pyriform fertile locules arising from the base, each containing one seed; central locule larger than the others, sterile, empty, longitudinally bilobed, occupying the apical half of the fruit. Base of fruit rounded with an abrupt hypanthial rim about one-fifth up from base to apex. Fruits with two longitudinal planes of bisymmetry: a major plane bisecting both fertile locules and a minor plane aligned with the septum that divides the two fertile locules. A prominent keel is developed along the major plane of symmetry. A pair of less prominent but well-defined keels runs from base to apex on both sides of the minor plane of symmetry. Planes of weakness extending longitudinally along each of the keels delimit four lateral valves—one pair for each fertile locule. Pericarp 150–160 μm thick, with a mesocarp composed of isodiametric parenchyma and endocarp composed of sclereids. Apex of endocarp with two prominent circular apertures, one on either side of the keel. Prominent vascular bundles absent in septum and wall of endocarp. Seeds conforming to the shape of the locule, pendulous, bitemgic.
Type Species—Pantocarpon deccanense Kapgate, Patil, Ilamkar & Ramteke emend. Manchester, Kapgate, Patil, Ramteke & S.Y. Smith (Figs. 2–4, 5D)

Basionym. Pantocarpon deccanii Kapgate, Patil, Ilamkar & Ramteke, pp. 43–48 in Palaeobotany to Modern Botany, PC Trivedi, ed. 2007.

Synonyms. Bicarpelarocarpon singhpuri Bhowal & Sheikh. The Palaeobotanist vol. 57, p. 438, pl. 1, figs. 1–8, 2008. Plectroniocarpon intertrappeanse Kokate, Upadhye, & G.V. Patil. The Botanique vol. 14(1), p. 41, pl. 1, figs. 1–10, 2010. Loganio- carpon deccanense Kokate, Upadhye & Bhadange. Geophytology vol. 43, pp. 105–108, pl. 1, figs. 1–8, 2013. Verbenaceocarpon mahabalei Dhabarde, Sheikh, & Kolhe. J. Bio. Innov. vol. 1(1), pp. 3, 4, pl. 1, figs. 1–9, 2012. Trilocu- locarpon bhuteriense Ramteke & Gedam. Int. J. Res. Biosci. Agri. Techn. vol. 5(2), pp. 639, 640, pls. 1, 2, 2017.

Holotype. SKPP/Trf2/ Deposited at Department of Botany, J. M. Patel College, Bhandara (as designated by Kapgate et al. 2007). Duplicate peels and prepared slides of the holotype are housed at Florida Museum of Natural History under the catalog number UF18311-70522.

Other material studied. Florida Museum of Natural History UF18311-62133, 70371, 70431, 70432, 70436, 70484, 70522, 70523, 71293, UF19438-68875, 69404.

Table 1

| Locality      | Coordinates (lat., long.) | Reference(s) | Specimen(s)                  |
|---------------|---------------------------|--------------|------------------------------|
| Bhutera       | 22°06.582N, 79°08.402E    | Ramteke and Gedam 2017 | ...                          |
| Keria         | 21°59.79333N, 79°10.29167E| ...           | UF19329-70433, 70459, 70460, 70695 |
| Mohgaonkalan  | 22°1.415N, 79°1.204E      | Kapgate et al. 2007; | UF18311-62133, 70371, 70431, 70432, |
|               |                           | Kokate et al. 2010   | 70436, 70484, 70522, 70523, 71293, |
|               |                           |                 | UF19438-68875, 69404          |
| Marai Patan   | 19°32.18598N, 78°07.53600E| ...           | UF19442-69829, 70482, 70483   |
| Paladaun      | 22°01.28502N, 79°10.42332E| ...           | UF19506-70453                |
| Shibla        | 19°58.141N, 78°40.838E   | ...           | UF19331-62137, 70733          |
| Singpur       | 21°37.00250N, 78°44.07017E| Bhowal and Sheikh 2008; | UF19279-70318, 70433         |

Fig. 1 Map showing the distribution of sites from which Pantocarpon has been collected: Bhutera (BH), Keria (KE), Mohgaonkalan and Paladaun (MK), Marai Patan (PA), Shibla (SH), and Singpur (SP). Coordinates of localities are presented in table 1. Dark gray and green areas inferred as Maastrichtian; orange area inferred as Paleocene. Base map from Samant and Mohabey (2009). Paleocene distribution generalized, inferred from Shrivastava et al. (2015), and palynological inferences from Samant et al. (2020).
Fig. 2  *Pantocarpon deccanense* fossil fruits. **A–F**, Surface renderings of a fruit embedded in chert from the Mohgaonkalan locality, based on microcomputed tomography data, UF19438-68873. **A, B**, Specimen in longitudinal view with major plane of symmetry parallel to the page, with 100% opacity in **A** to show surface morphology but increased translucency in **B** to show outlines of the three locules. Arrows in **A** indicate inferred hypanthium margin. **C, D**, Specimen rotated 90°, now with minor plane of bisymmetry parallel to the page, with opacity 100% in **C** and showing the prominent keel; opacity reduced in **D** to show pyriform outline of fertile locule. Arrows in **C** indicate inferred hypanthium margin. **E**, Nearly same view as **C**, with apical end rotated forward to reveal the two apical apertures. **F**, Apical view showing keel in major plane of bisymmetry and two apical apertures. **G–P**, Successive transverse sections from near base to near apex. **G–K**, Transecting both fertile locules. **L–P**, Transecting apical part of fertile locules plus the central sterile locule. **Q–U**, Successive longitudinal sections parallel to the major plane of bisymmetry. Arrows in **Q** mark rim of the hypanthium; arrow in **U** denotes apical endocarp aperture. **V–Z′**, Successive longitudinal sections at right angles to **Q–U**, parallel to the minor plane of bisymmetry. Arrows in **Y** indicate apical apertures. Section in **V** is median, transecting the septum in basal half. Scale bars = 1 mm. Scale bar in **A** also applies to **B–F**, scale bar in **G** also applies to **H–U**, and scale bar in **V** also applies to **W–Z′**.
The fruits are ovoid, oval in longitudinal view, and elliptical-hexagonal in transverse view, 1.0–1.6 mm wide, 2.0–2.7 (3.0) mm high (fig. 2). They are trilocular with two pyriform lateral locules arising from the base (figs. 2L–2U, 3B, 3H–3K) that are fertile, each containing one seed (figs. 2B, 2Q–2U, 3B, 3H–3K). The central locule is empty, larger than the others, and bilobed (fig. 3D), sometimes with a thin median septum preserved (fig. 3G) occupying the apical half of the fruit. The base of the fruit is rounded with an abrupt hypovalent rim about one-fifth of the way from base to apex, where the fruit wall surface begins gradual tapering toward the apex (figs. 2A–2C, 2Q, 3A–3D).

There are two longitudinal planes of bisymmetry: a major plane bisecting both fertile locules (figs. 2A, 2B, 3A, 3B) and a minor plane aligned with the septum that divides the two fertile locules (figs. 2C, 2D, 3C, 3D). A prominent keel (forming an angle of 95°–100° as viewed in transverse section) is developed in the major plane of symmetry and runs from base to apex on both sides (figs. 2C–2F, 3C, 3D). A pair of less prominent keels (forming angles of 120°–130° as viewed in transverse section) runs from base to apex on both sides of the minor plane of symmetry (fig. 3A). The keel edges, collectively, give a compressed hexagonal appearance to the cross-sectional view (figs. 2G–2L, 3L, 3M). Planes of weakness extending longitudinally along each of the keels delimit four valves—one pair for each fertile locule (fig. 3N). No obvious basal scar or pedicel was observed, but some specimens show an intact apical protrusion likely representing the styles (fig. 3A–3D).

The apex of the endocarp is marked by two prominent circular apertures, one on either side of the keel (fig. 2E, 2F, 2U, 2Y). The pericarp is 150–160 μm thick, divided into an endocarp wall (50–70 μm thick) and septa composed mainly of small isodiametric sclereids (2.5–3.8 μm in diameter) and occasional peripheral idioblasts bearing rhomboidal crystals and a surrounding mesocarp (30 μm thick) composed of isodiametric parenchyma cells (100–125 μm in diameter; fig. 3O, 3P). Septa and the endocarp wall are lacking obvious vasculature. Vertical tubes occur within the mesocarp, running parallel to the longitudinal ridges of the endocarp (fig. 3O, 3P). These may be the positions of former vascular strands, not preserved, or alternatively might represent secretory canals. There is one seed in each of the two lateral locules that conforms to the shape of the locule (fig. 3H–3O). Seeds are pendulous (fig. 3I), bitegmic (fig. 3J, 3M, 3O, 3Q, 4A, 4B), 380–540 μm wide, and 608–800 μm long (fig. 3H, 3I). The seed coat is composed of a smooth inner membrane and a uniseriate outer layer of tracheoid fibers (terminology from Schmid 1986) that are about 2.2 μm thick with prominent annular thickenings (fig. 4B).

**Discussion**

Three-dimensional renderings of the fruits from X-ray μ-CT scan data (figs. 2A–2F, 3A–3F) show an interesting morphology with a pair of pyriform single-seeded fertile locules arising from the base and straddling a sterile median, apically positioned locule, with a keel in the major plane of symmetry and a pair of large circular apertures at the apex on either side of the keel. Prior interpretations of the fruit morphology have varied according to the orientation and level of physical fractures, sections, and peels through which the fruits were observed. However, with these three-dimensional data, we can see exactly how Pantocarpon fruits take on different appearances depending on the orientation of the plane of section and proximity of slices to the fruit margin so that the same specimen may appear two, three, or four loculed (fig. 2). The complex fruit structure has led to other names being applied subsequently to Pantocarpon, which we synonymize above. These include Verbenaceocarpon mahabalei Dhabare, Sheikh & Kolhe (2012) and Bicarpelarocarpon singhpuri Bhowal & Sheikh (2008) based on specimens from Singpur, Loganiocarpon decanense Kokate, Upadhya & Bhandare (2013) and Electranoocarpon intertrappeanse Kokate, Upadhya, & G.V. Patil (2010) from Mohgaonkalan; and Triloculocarpon bhuteriens Ramteke & Gedam (2017) from Bhutera.

Specimens sectioned longitudinally, parallel with the major plane of bisymmetry, show three locules, as in the virtual sections in figure 2Q–2U. This trilocular configuration is seen in sections of the holotype of Pantocarpon decanense, as figured by Kapgate et al. (2007) and here (fig. 3H). An apparent bicorial configuration is seen when the specimens are sectioned more or less transversely in the basal half of the fruit (fig. 2L–2K). This is the view that led to the interpretation of these fossils as the monocot Sparganiurn (Mahabalé 1953, pl. 29, fig. 22; refigured here in fig. 3L) and as Verbenaceae (Dhabare et al. 2012). Bicarpelarocarpon of Bhowal and Sheikh (2008) was described based on a specimen serially peeled obliquely through the equatorial region, intercepting at first two of the locules (a lateral and the central one) and then part of the third locule.

Still another genus was proposed based on a holotype that was studied in longitudinal sections oriented parallel to the minor plane of bisymmetry: Plectroniocarpon intertrappeanse (Kokate et al. 2010). With the aid of μ-CT scan visualization, we show that the same specimen that gives the familiar views of Pantocarpon when sectioned parallel to the major plane of bisymmetry (fig. 2Q–2U) will show instead the configuration described as Plectroniocarpon when the plane of section is reoriented by 90° to be parallel to the minor plane of bisymmetry (fig. 2V–2Z).

Anatomy of the pericarp is well preserved in the specimen figured from Bhutera (Ramteke and Gedam 2017, pl. 1, fig. 2). These authors also show a section intercepting placentation of...
Fig. 3  *Pantocarpon deccanense* fossil fruits. A–G, Fruit from Marai Patan, UF19442-69829, 3-D renderings and virtual slice images of a single specimen from microcomputed tomography scan. A, B, Lateral view with major plane of bisymmetry parallel to the page, rendered opaque (A) and translucent (B), showing paired fertile locules arising from the base and larger sterile locule toward the apex. Note prominent stylar projection at apex. C, D, Lateral view with minor plane of bisymmetry parallel to the page, rendered opaque (C) and translucent (D), showing bilobed sterile locule in upper part. Note prominent stylar projection at apex. E, F, Apical view with prominent apertures, rendered opaque (E) and translucent (F). G, Digital section of the same fruit in nearly transverse section. H–K, Physical longitudinal sections, peels by reflected light. H, Holotype of *P. deccanense* in orientation similar to that in figure 2S, Mohgaonkalan, UF18311-70522. I, Longitudinal section (LS), UF19442-70638a1, from Keria. J, Oblique LS of specimen from Marai Patan, UF19442-70566. K, Oblique LS of specimen from Mohgaonkalan, UF18311-70436. L–P, Physical transverse sections (TS). L, Specimen originally figured as *Sparganium* by Mahabalé (1953), sectioned transversely in basal one-third intercepting the two fertile locules, each with a
the seeds (pl. 1, fig. 1C). They, like Kapgate et al. (2007), interpret the placentation to be axile, but it could alternatively be parietal (Dhabarde et al. 2012). The seeds are pendulous from the apex of each fertile locule (fig. 3).

Kapgate et al. (2007) described the fruit as being derived from a superior ovary but without explanation of the evidence. The abrupt horizontal rim about one-fifth of the way from the base of the fruit, where the wall surface begins its gradual taper toward the apex, appears likely to be the edge of a hypanthium (fig. 2A, 2C, 2Q), suggesting a partly inferior ovary. If the currently proposed affinity to Torricelliaceae is correct, then we would expect these fruits to have developed from an inferior ovary (Yembatureva and Konstantinova 2013).

Dehiscence was described as loculicidal (Kapgate et al. 2007). This is supported by specimens showing separation along the longitudinal edges of the fertile locules (fig. 2X). However, despite examining numerous specimens, we have not encountered any fruits with the seeds dehisced. It is more likely that germination, rather than dispersal, occurred via the separation of these valves. The sterile locule is consistently empty, without any preserved parenchyma tissue (fig. 3H–3K, 3N). Kapgate et al. (2007) noted that the large middle locule, without any seed formation, may have provided buoyancy for water dispersal.

The pair of prominent apical holes in the endocarp (figs. 2E, 2F, 3E, 3F) was not mentioned in previous accounts because these apertures were difficult to observe in the obliquely fractured and peeled specimens, but they are clearly seen in specimens viewed by X-ray μ-CT of the chert. Both of these holes enter to the empty sterile central chamber. The function of these holes is not obvious. Presumably, these apertures would have been covered by epicarp of the fruit, as in extant fruits of Torricelliaceae (Manchester et al. 2017), rather than being open to the environment.

**Systematic Affinities**

The original suggestion that these fruits represent extant *Sparganium* (Mahabalé 1953) can be discarded now that the complex morphology is more completely understood. *Sparganium* fruits have only one or two locules, have monocotyledonous embryos, and lack sterile locules, germination valves, and endocarp apertures. Several characters of *Pantocarpon* match those of fruits in the extant apialean family, Torricelliaceae. These include tricarpellate syncarpous fruits, a pair of apical apertures, empty sterile locules, single-seeded fertile locules, septae that lack obvious vascular strands, and longitudinal germination valves (Manchester et al. 2017).

The pair of well-formed terminal apertures is particularly similar to that in *Aralidium* and *Torriceilla*; more elongate paired apertures occur in *Melanophylla*. There are some obvious differences, however, from the three living genera of Torricelliaceae (fig. 5). In *Torriceilla*, *Melanophylla*, and *Aralidium*, there are

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Fig. 4  Anatomical detail. A, Endocarp wall (left) and seed coat (right). Note peripheral idioblasts in the endocarp. UF19442-70638a3. B, Paradermal section through testa composed of tracheid fibers with annular thickening. UF18311-70436. Scale bars = 100 μm (A), 50 μm (B).
two sterile locules (lateral) and a single fertile one (median), whereas in *Pantocarpon*, there are two fertile locules (lateral) and a single sterile locule (median; fig. 5A–5C vs. fig. 5D). There is also a discrepancy in size. With a maximum length of 3 mm, these fruits are much smaller than those of the extant genera, the smallest of which is *Torricellia* (5 mm long). However, similar size differences occur among the extant genera, with *Melanophyllum* (12–13.5 mm) more than twice as long as *Torricellia*, and *Aralidium* (26–28 mm long) about twice as long as *Melanophyllum*. Clearly, fruit size is flexible within this family, although relatively consistent within genera.

In modern genera of Torricelliaceae, the apertures are equally distributed, with one for each of the two sterile locules. In *Pantocarpon*, the two apertures both connect to a single sterile locule and are positioned on either side of the major plane of bisymmetry (fig. 5D). In some cases, however, we observed what appears to be a thin septum bisecting the sterile locule (fig. 3D, 3G). An additional difference is the presence of two germination valves (three longitudinal planes of splitting from apex) per fertile locule in the fossil (fig. 5D) versus one germination valve (two longitudinal planes of splitting from apex) per fertile locule in the extant Torricelliaceae (fig. 5A–5C). Last, the uniseriate layer of tracheid fibers in the seed coat distinguishes this fossil from the extant representatives of Torricelliaceae. Tracheid fibers occur as a characteristic feature of seed coat inner or outer layers in various angiosperm families (e.g., Calycanthaceae, Lauraceae, Myristicaceae, Papaveraceae, Dilleniaceae, Burseraceae, Rutaceae, Onagraceae, Lythraceae and Vitaceae; Corner 1976) but do not occur in extant Torricelliaceae and, to our knowledge, have not been documented in families of the Apiales (Corner 1976).

**Distribution**

*Pantocarpon deccanense* fruits are known from Mohgaon-kalan (Kapgate et al. 2007), Singpur (alternative spelling, Singhpur; e.g., *V. mahabalei* of Dhabarde et al. 2012), and Bhutera (e.g., *T. bhuteriense* of Ramteke and Gedam 2017). In addition, we have collected new specimens of *Pantocarpon* from Keria, Marai Patan, Paladaun, Singpur, and Shibla (table 1), showing this was a relatively widespread plant within the Deccan ecosystem (fig. 1). These sites are floristically similar and are thought to have been deposited in the late Maastrichtian, in contrast with paleobotanical sites farther to the east in the Mandla subprovince that have not yielded *Pantocarpon* fruits such as Ghughua, Umaria, Palasunder, and Parapani, which are among basalt flows dated as Paleocene (Shrivastava et al. 2015). As yet, we have not observed such fruits in fossil deposits outside of India.

Other fossil Torricelliaceae are found in North America and Europe, but they are much younger than *Pantocarpon*; the oldest are from middle Eocene sites (ca. 47 Ma) in Europe (Messel, Germany [Collinson et al. 2012]) and western North America (Clarno Formation, OR [Manchester 1999; Manchester et al. 2017]; Roslyn Formation, WA [Manchester 1999]). The inferred presence of Torricelliaceae in India at about 66 Ma, when the subcontinent was still isolated from other major landmasses, indicates that India may have played a role in the early evolution of this family, which is now disjunct between Madagascar, China, and Malesia.

**Conclusion**

X-ray μ-CT data helped reconcile the affinities of *Pantocarpon*, as well as identify junior synonyms that were erected because of the complex morphology that can be misleading depending on the plane of section. This contributes to our overall understanding of plant diversity in the Deccan Intertrappean beds of India. Recognition of *Pantocarpon* as a potential member of Torricelliaceae is interesting because it constitutes the most ancient record known for the family, with the next youngest being middle Eocene, and provides additional biogeographic information. The fruits of *Pantocarpon* from the latest Cretaceous Deccan Intertrappean beds suggest that India may have played an important role in the early evolution of Torricelliaceae, which is now disjunct between Madagascar and Asia.

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