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Angiosperm affinities of *Surangea* from the late Cretaceous Deccan Intertrappean Beds of central India

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ABSTRACT. The genus *Surangea* Chitaley et Sheikh, based on permineralized specimens from the Deccan Intertrappean Beds of central India, was originally considered to represent a fern megasporangium. Reexamination of original material and new specimens has revealed that the structures are capsular fruits with well-defined seeds, rather than megasporangia. We describe *Surangea* fruits in detail, based on peels and micro-CT scanning, and document its distribution among multiple localities of the Deccan Intertrappean Beds. The fruits are pentacarpellate septicidal capsules with ~8–12 seeds per locule. The seeds are prominently ornamented with parallel ridges and have a curved embryo/endosperm cavity and a prominent aril. This set of features indicates eudicotyledonous affinities for *Surangea.* In particular, the combination of septicidal capsules, axile placentation and arillate campylotropus seeds suggests affinity with the order Myrtales, but it does not fit cleanly within an extant family. *Surangea* fruits add to the diversity of angiosperms known from this late Maastrichtian flora. It joins several other fruit types known from the Deccan flora that do not fall neatly into extant families, possibly representing parts of an endemic community that succumbed to environmental stress associated K-Pg boundary events and/or subsequent northward rafting of the Indian subcontinent.

KEYWORDS: arillate seeds, Maastrichtian, Mohgaonkalan, Pentapetalae, pentalocular septicidal capsule

INTRODUCTION

Interbeds within the Deccan basalt series in central India are well known for cherts containing abundant silicified plant remains, including algae, pteridophytes, angiosperms and occasional gymnosperms (reviewed, Kapgate, 2005; Smith et al., 2015). These cherts are important for providing a window into the local paleoecosystems of the latest Cretaceous and earliest Paleogene when the Indian subcontinent was isolated as it moved northwards (Hu et al., 2016; Morley, 2018). Not only is this a time of global environmental transition, but the Deccan flora has potential to offer insights into the history of the Indian vegetation and to what extent this vegetation shows biogeographic affinities with Africa or Asia, or is endemic.

Among these exceptionally well-preserved plant fossils is a distinctive reproductive structure described as *Surangea mohgaoensis* by Chitaley and Sheikh (1971) from the classic

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Mohgaonkalan site. Originally, this species was interpreted to represent a fern megasporangium. New specimens and renewed investigation of the type material has revealed that *Surangea* is an angiosperm fruit rather than a fern megasporangium. This adds to the diversity of angiosperms known from this equatorial flora that was deposited in the latest part of the Cretaceous (late Maastrichtian). Here we describe the morphology of *Surangea* fruits and seeds in more detail based on serial peels and micro-CT scanning, summarize the localities from which this plant is now known and consider the systematic affinities of this extinct genus.

MATERIALS AND METHODS

We studied slides of the holotype and new specimens from Mohgaonkalan (22°01.415′N, 79°11.204′E) of Chhindwara District, M.P., India. In addition, fruits were discovered from the nearby Keria (21°59.904′N, 79°10.418′E) and Paladaun (22°01.285′N, 79°10.423′E) sites. Isolated seeds were studied from Ambabagholi (21°52.730′N, 78°11.693′E) in Chandrapur District, Maharashtra. All of these sites are considered most likely to be latest Cretaceous, late Maastrichtian (Smith et al., 2015).

Fruits and occasional isolated seeds were discovered by breaking the black chert and etching it with hydrofluoric acid. The etching process altered the surface color from black to brown, allowing fruits to be recognized by examination in reflected light with a hand lens. After exposure by initial fracture of the chert both counterpart pieces were serially peeled by etching with hydrofluoric acid and applying acetate sheets to the etched surface wetted with acetone. When dried, the acetate peels were manually pulled away (peeled) from the chert surface, trimmed with scissors, and mounted on a glass slide with a glass coverslip using Canada Balsam as mounting medium. Resulting slides were studied and photographed with transmitted and reflected light microscopy on Nikon Labophot and Wild M4000 photomacroscope with a Canon Rebel 450 digital camera.

Micro-CT scanning was carried out with a Zeiss Versa 620 XRM scanner at the College of Engineering Nanoscale Research Facility of the University of Florida. Best results were achieved with a voxel size of 2.0327 µm, using 80 kv with and 125 µA with a 4X objective, a LE5 filter with 3200 images at exposure times of 10 seconds. Virtual sections and segmentation of the fruits and seeds were prepared with Volume Graphics Studio Max version 3.1 (Heidelberg, Germany). Resulting surface files were exported in ply format and visualized with depth mapping and X-ray rendering in Meshlab (http://www.meshlab.net/). Relevant TIFF stacks, movies and .ply files have been archived at Morphosource.org (search term *Surangea*; project Deccan Plant Reproductive Structures).

SYSTEMATICS

Clade PENTAPETALAE D.E. Soltis P.S., Soltis et W.S. Judd

Order MYRTALES?

Family. Incertae Sedis

Genus. ***Surangea*** Chitaley et Sheikh emend. D. Ramteke, S.Y. Smith, Kapgate & Manchester

Figs 1–3

Emended diagnosis. Fruit a pedicellate, globose capsule, 4.7–5.0 mm diameter, pentalocular, containing numerous seeds. Fruit wall thin (92–105 µm), composed of isodiametric cells ~20 µm in diameter. Central vascular axis ~300 µm diameter from which radiate five thin septa. Locules each containing ~8–12 seeds with axile placentation. Seeds reniform, broadly rounded distally, narrowed proximally, 1.1–1.3 mm long, 0.8 mm wide, 1.0 mm deep, laterally compressed, with a single plane of symmetry (sagittal). Transverse, subparallel blade-like ridges, ~60–90 µm high, ornament the lateral and apical portions of the seed. Embryo/endosperm cavity strongly curved, nearly U-shaped in the sagittal plane but with unequal limbs. A distinctive, smooth, inflated, band of arillate tissue containing enlarged cells is adpressed to the seed coat at the proximal and lateral surfaces of the seed. Seed coat composed of a prominent uniseriate inner layer of columnar or cuboidal thin-walled cells 15–20 µm high, 10–18 µm wide, that conforms to the contour of the main seed cavity, and an outer layer 8–25 µm thick, depending on whether measured to valleys or crests of the ornamentation, composed of denser, darker cells.

Species. ***Surangea mohgaoensis*** Chitaley et Sheikh emend. D. Ramteke, S.Y. Smith, Kapgate & Manchester

Type species. *Surangea mohgaoensis* Chitaley et Sheikh emend.

Basionym. *Surangea mohgaoensis* Chitaley et Sheikh 1972. Geophytol., 1: 123, 124, 125, text-figs 1–4, pl. 1, figs 1–8.

Synonymy. *Spinocarpon mohgaoense* Kapgate 2013. Geophytol., 43: 52, 56, pl. 1, figs 1–7; pl. 2, figs 1–7.

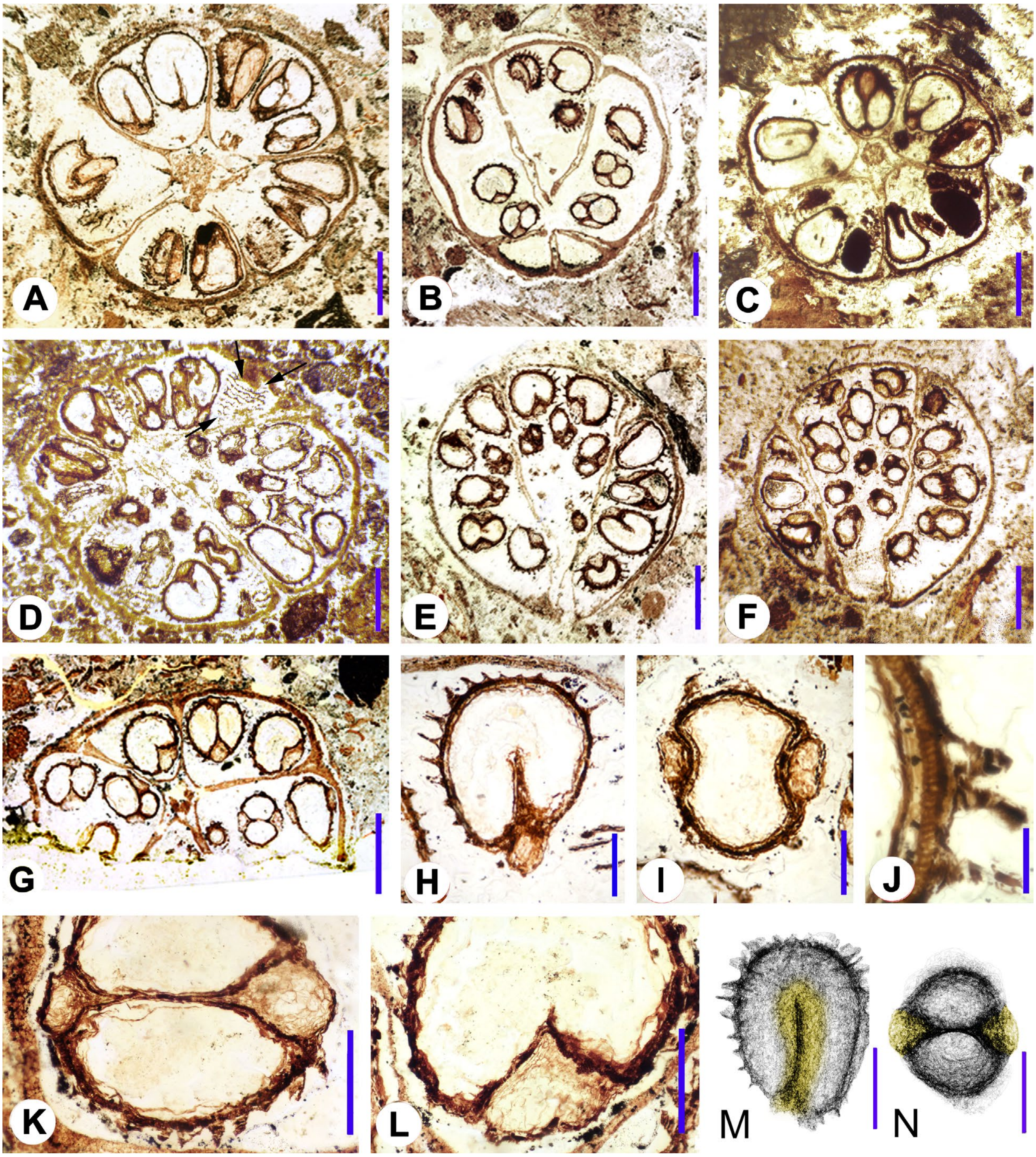

Figure 1. *Surangea mohgaonensis* fruits and seeds. **A–L**. Acetate peel sections by combined reflected and transmitted light microscopy; **A–C**. Specimens from Mohgaonkalan; **A**. Transversely sectioned fruit showing thick pentagonal central axis and thin radial septa delimiting five locules, containing seeds with their narrow hilar ends facing inward, indicating axile placentation, UF 18311-62124; **B**. Holotype, peel cutting obliquely through five locules, delimited by narrow septa, CMNH PM-1388; **C**. Transverse section showing central vasculature and five locules, UF 18311-62124; **D**. Specimen from Paladaun, peel intercepting seeds at various levels. Note tangential section of seed coat periphery with ridged ornamentation appearing as parallel lines (upper right). UF 19506-70519; **E**. Specimen from Mohgaonkalan, UF 18311-70429; **F**. Obliquely sectioned fruit from Keria, UF 19329-62155; **G**. Section at level showing more clearly the five locules from Mohgaonkalan, UF 18311-62123; **H–L**. Details of individual seeds from Keria, UF 19329-62155; **H**. Single seed in lateral section showing curved cavity and basal aril; **I**. Seed in transverse section showing central cavity and peripheral aril; **J**. Detail of seed coat; **K**, **L**. Detail of seeds showing large cells composing the aril; **M**, **N**. Seed reconstructed in 3D, digitally extracted from micro-CT data from the specimen in F; surface rendering in lateral and apical views with translucency; aril shaded yellow. Scale bars = 1 mm in A–G; 250 µm in H, I, K–L; 100 µm in J, 500 µm in M, N

N o m e n c l a t u r e. The type species was initially presented with the spelling mohgaoense; however, according to the feminine gender of the generic name, the epithet should be corrected to mohgaonensis. Orthographic errors such as this are to be corrected according to the botanical code of nomenclature (Turland et al., 2018).

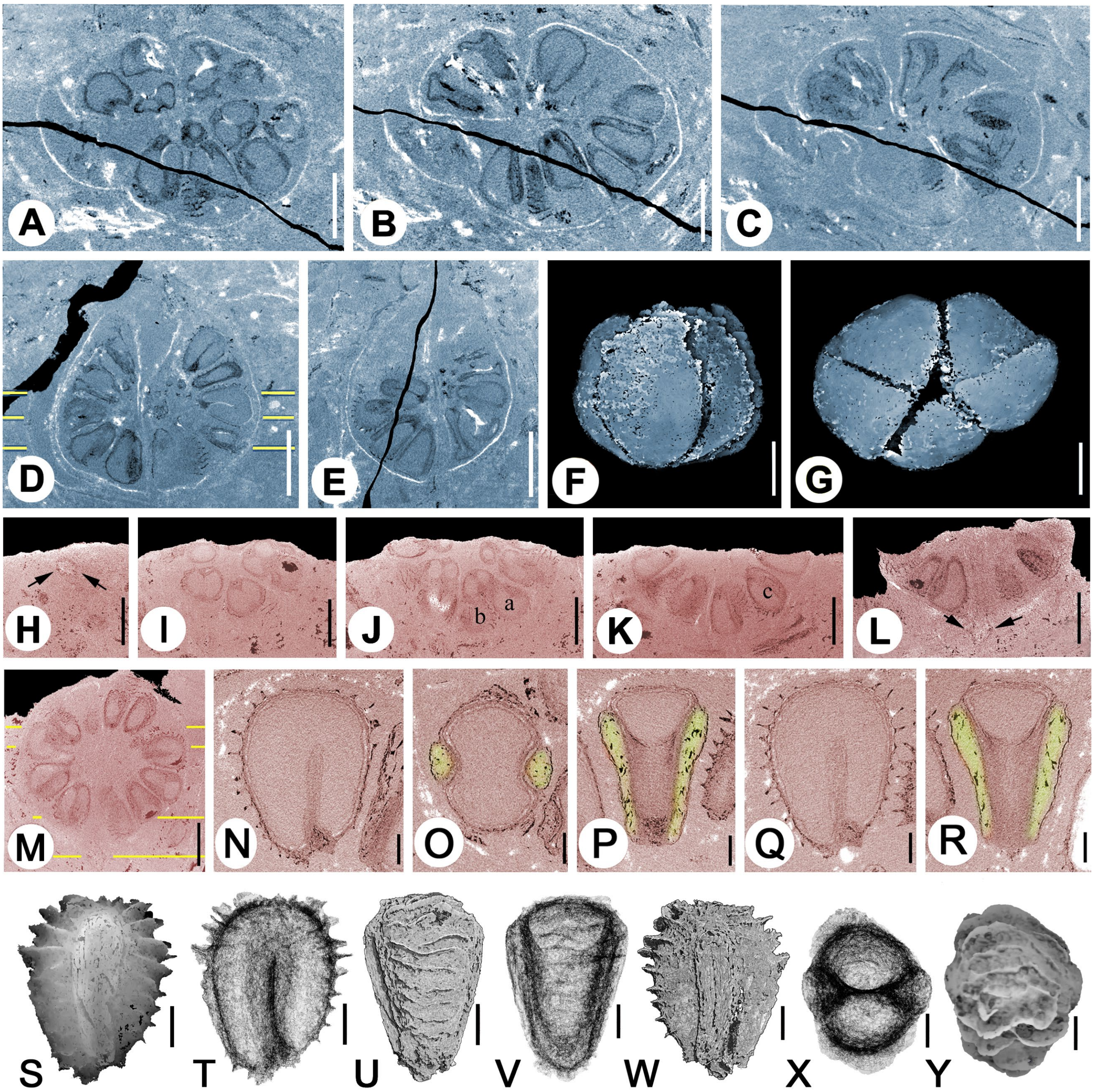

Figure 2. *Surangea mohgaonensis* fruit and seeds. Virtual serial sections and extracted seed from micro-CT scan data. **A–G**. Fruit from Mohgaonkalan, UF18311-19116; **A–C**. Successive transverse sections moving apically according to registration lines in D, showing thin fruit wall, and seeds in apparent axile placentation; **D**, **E**. Longitudinal sections at right angles to one another; **F**, **G**. Lateral and basal views of the pentacarpellate septicidal capsule, digitally extracted from the chert, depth map rendering; **H–Y**. Specimen from Keria; same as that shown by light microscopy (Fig. 1F, H–L), UF 19329-62155; **H–K**. Successive transverse sections arranged from pedicel (H, arrows), near base (I), slightly above equator (J) to apical one third (K) at levels indicated in M showing the organization of seeds within each of the locules; seeds labeled "a–c," are enlarged in N–Y; **L**. Median longitudinal section in plane of the pedicel (arrows) and central axis; **M**. Median longitudinal section at right angles to the plane of L, with registration lines indicating the planes of H–K; **N–P**. Seed "a" in sagittal, transverse and coronal section, aril indicated in yellow; Q, R. Seed "b" in sagittal and coronal section, aril indicated in yellow; **S–Y**. Seed "c," digitally extracted showing surface sculpture by depth map rendering (S, Y), opaque surface rendering (U, W) and translucent surface rendering (T, V, X), rotated through sagittal (S, T, W), coronal (U, V) and apical (X, Y) orientations. Scale bars = 1 mm in A–M, 0.2 mm in N–Y

Emended diagnosis. As above for the genus.

Holotype. "3Dn/Sh, Department of Botany, Institute of Science, Nagpur." (Chitaley and Sheikh, 1972). The specimen is missing but duplicate peel slides of the holotype were studied: CMNH PM-1388, CMNH PM-1566 and UF18311-62123.

Additional specimens studied. UF 18311-62124, 69116, 70429 from Mohgaonkalan; UF 19329-62155 from Keria; UF 19506-70519 from Paladaun; UF19352-62148 from Ambabagholi (Coordinates in Material and Methods).

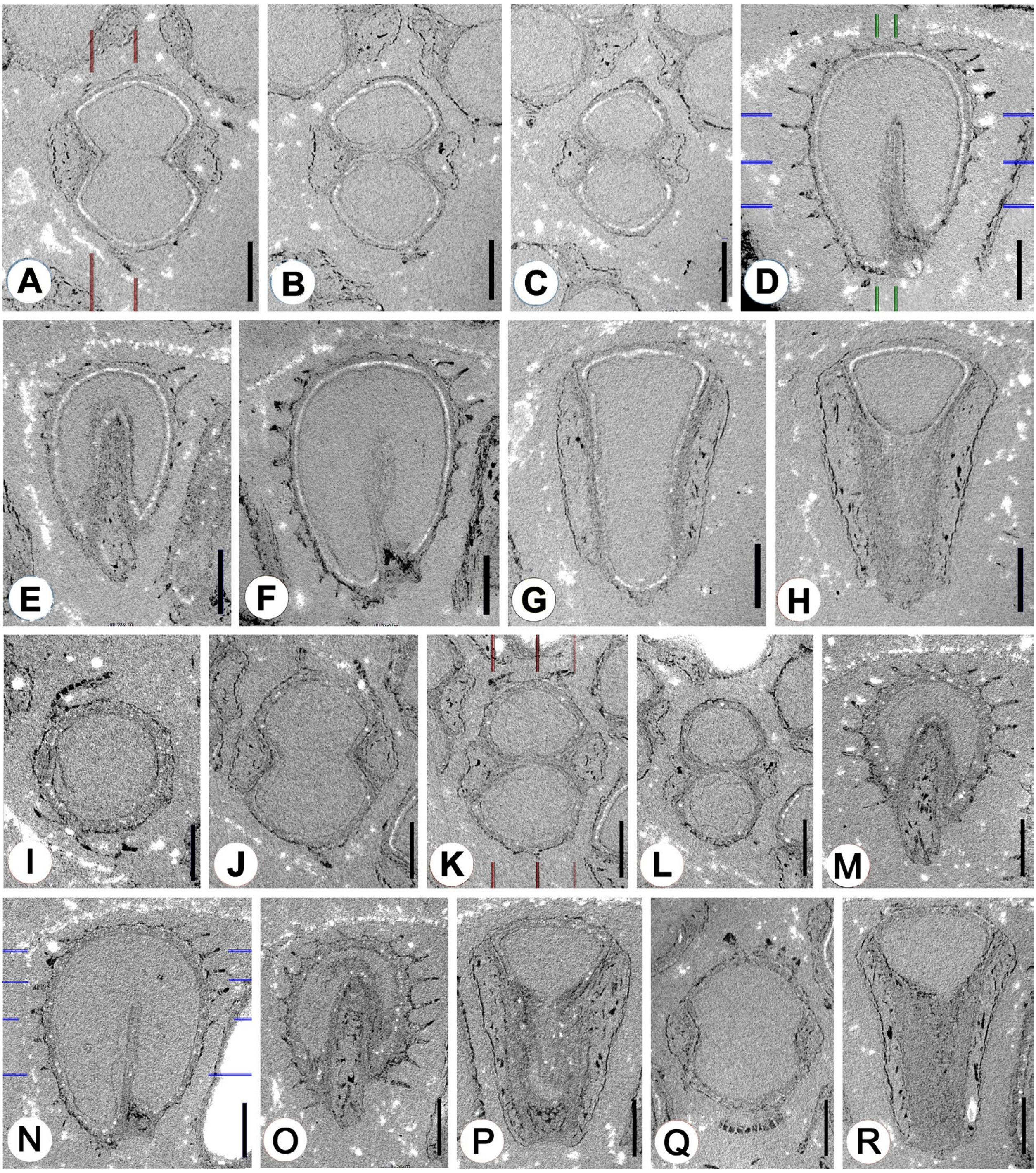

Figure 3. *Surangea mohgaonensis* seeds in digital section from micro-CT scan of a fruit from Keria, UF 19329-62155 (same specimen as Fig. 2H–Y). **A–H**. Seed "d" in transverse (A–C), sagittal (D–F) and coronal (G, H) sections. Registration lines in A and D show the planes of section represented in E, F and A–C, G, H, respectively; **I–P**. Seed "e" in transverse (I–L), sagittal (M–O) and median coronal (P) section. Registration lines in K and N show the planes of section represented in figures M–O and I–L, respectively; **Q**, **R**. Seed "f" in transverse section at apical one-third showing ornamentation of seed coat (Q), in median coronal section (R), intercepting the aril on both lateral margins. Scale bars = 0.25 mm

DISCUSSION

The holotype was originally interpreted as a pteridophytic synangium with five chambers and eight to nine spiny tetrads of spores per chamber. Since the initial description in 1971, more specimens of *Surangea* have been recovered from the type locality of Mohgaonkalan, and from other sites in the local area (Keria, Paladaun) and more distant (Ambabagholi). The specimens represent mature capsular fruits rather than sporocarps and the contents can now be recognized as seeds rather than megaspores because they have a strongly curved internal cavity and an aril-like structure not known for spores. Although the seeds were previously reported to be spiny (Kapgate, 2013), and they appear so when viewed in broken pieces and peel sections (e.g. Fig. 1H), the study of successive peels and of micro-CT scanning results (Fig. 2) reveals that the seeds are ornamented with parallel sharp ridges rather than spines (Figs 1M, 2S, W). Tangential sections of the seed coat periphery show the parallel ridges (Fig. 1D). The ridges are 60 to 90 µm high and about 90–100 µm apart with rounded troughs between them (Figs 2S–U, W, 3D, F, M–O).

One of the fruits we studied by micro-CT scan had opened apically and appears to have lost seeds from the apical portions of the locules (Fig. 2C–E). In addition to fruits with intact seeds, the dispersed seeds of *Surangea* are occasionally recovered from the chert. These were interpreted as spiny fruits and named *Spinocarpon mohgaoense* by Kapgate (2013), but they match in size and morphology to the ridged seeds seen in situ within fruits of *Surangea*. Distinctive features of these capsular fruits include the relatively thin pericarp and septa (Fig. 1A–G), the globose to oblate form (Fig. 2F, G, J, M) and the central column with several vascular bundles (Fig. 1C, G), bearing seeds that are arranged in what appears to be axile placentation (Figs 1A, G, 2B, D). Dehiscence was not loculicidal, as there is no separation plane in the pericarp at the middle of each locule; instead the capsules show initial splitting along the septa (Figs 1A–G, 2A–D), indicating septicidal dehiscence. Style and perianth are not persistent on any of our specimens but a terete protrusion observed by micro-CT scan, continuous with the central axis, is interpreted as the pedicel (Fig. 2H, L, M), and is widened beneath the fruit, suggesting that the perianth was hypogynous. The lack of prominent vasculature on the fruit wall (a feature commonly associated with epigyny) also suggests that the perianth was hypogynous and the ovary thus superior.

The seeds are distinctive in their shape and ornamentation (Fig. 2S–Y). The embryo/endosperm cavity may appear C- or J-shaped when sectioned obliquely (Fig. 1A–E, H), but CT-scan imagery confirms that they are nearly U-shaped in sagittal section, but with one arm slightly longer than the other (Figs 1M, 2N, Q, T, W, 3D, N), curved around a partition formed by invagination of the seed coat from the proximal end. The seed coat includes a prominent uniseriate layer of columnar or cuboidal thin-walled cells (Fig. 1J, white layer in Fig. 3A–H) and an outer layer of indistinctly preserved cells forming the external ornamentation of sharp parallel ridges (Fig. 1J). A smooth, elongate outgrowth is adpressed to the seed coat on both lateral margins extending from the proximal end toward the distal margin of the seed following the coronal plane (Fig. 1M, N). It is composed of large thin-walled cells (Fig. 1K, L) that are well seen when the seeds are sectioned in transverse (e.g. Figs 1I, K, 2O, 3A–C, J–L, Q) and in coronal (e.g. Figs 2P, R, 3G, H, P, R) planes. These outgrowths are not seen in median sagittal sections, but are intercepted in sagittal planes that are tangential to the periphery (Fig. 3E, M, O). We interpret them to be an aril. The surface of the aril is smooth, whereas the main portion of the seed is sharply ridged. The embryo and endosperm tissues are not preserved, but a thin undulatory cuticle lines the embryo cavity (Fig. 1H–L).

SYSTEMATIC PLACEMENT

Several features of the fruit and seed morphology provide clues to the systematic position of *Surangea*. The consistently 5-locular syncarpous fruits indicate development from pentacarpellate ovaries, from which we may infer placement within the Pentapetalae of the Eudicots. Septicidal capsules with axile placentation also support this placement. Additional clues to the systematic position of *Surangea* include the strongly curved embryo/endosperm cavities indicating campylotropous seeds and the aril-like structure on the seeds. In the search for related extant taxa, we sought those with pentacarpellate capsular fruits with hypogynous perianth, axile placentation and curved arillate seeds. In the superasterids these features can be found in Aizoaceae (Caryophyllales) and Ericales, while in the rosids they occur in the Myrtales.

The Aizoaceae range in carpel number from one to 20 (commonly 2–5), and are superior to inferior, with multiple seeds per locule. The seeds range from anatropous to campylotropus (Hartmann, 1993). The seed surface varies from smooth to ridged (Kanwal et al., 2009) and the fruits can be berries or capsules.

The capsular fruits are rarely septicidal, more commonly circumsissle or loculicidal in dehiscence. Although arillate seeds are observed in subfamily Sesuvioideae, the aril covers almost the entire seed (Hartmann, 1993). Ericalean fruits can be pentacarpellate and sometimes have septicically dehiscent capsules, but we did not observe seeds morphologically similar to those of *Surangea* in this order.

In the rosids, arillate seeds with curved embryo cavities occur in the Myrtales such as Myrtaceae and Melastomataceae. Although Corner (1976) described the seeds of Melastomataceae as exarillate, he also stated there are "a few genera with thickened raphe (? vestigial aril)" (p. 192). According to Vyshenskaya (1996), the raphe tissue is succulent, or spongy, sometimes arilloid [see the longitudinal diagrams of seeds in figs 45 to 53 in Vyshenskaya (1996), which show the larger cells surrounding the raphe interpreted as arilloid], e.g. in the subfamily Melastomatoideae, such as in *Astronia, Blakea*, and in some genera of Sonerilieae, e.g. *Amphiblemma, Calvoa, Gravesia, Oxyspora, Bertolonia, Salpinga, Medinilla, Miconia, Dissotis, Monochaetum*. Seeds of Melastomataceae are diverse in their ornamentation (Ocampo and Almeda, 2013; Ocampo et al., 2022), including sometimes ridged like *Surangea* (e.g. *Arthrostema*; fig. 15 in Whiffin and Tomb, 1972). Fruits of Melastomataceae, when capsular rather than baccate, are loculicidally rather than septicidally dehiscent, indicating that *Surangea* does not belong to this family. Septicidal capsules occur in a few genera of the myrtalean family, Lythraceae, but the seeds are not campylotropous and are not arillate (Graham, 2007; Graham and Graham, 2014).

The embryo-endosperm cavity in the extant taxa of Melastomataceae and Lythraceae are usually just straight or J-shaped, contrary to the U-shaped cavity with nearly equal limbs observed in *Surangea* (Ocampo et al., 2022). Seeds of Myrtaceae can be anatropous, hemitropous or campylotropous (Wilson, 2011). The embryos of Myrtaceae vary from straight to J- to C- or U-shaped (Landrum and Sharp, 1989), but the strongly curved ones generally occur in baccate, rather than capsular fruits. The capsular fruits of Myrtaceae are loculicidally dehiscent (Wilson, 2011), thus differing from the septicidal capsules of *Surangea*. Hence, the fossil fruit might fit within the Myrtales, but it does not fit cleanly within an extant family.

CONCLUSION

Recognition of *Surangea* as a new kind of fruit increases the diversity of angiosperms known from the Deccan Intertrappean cherts. Although it is clearly assignable to the Pentapetalae clade, its more precise affinities, potentially as a myrtalean rosid, remain uncertain. *Surangea* joins several other angiosperm fruits of the Deccan Cherts whose precise extant affinities remain obscure, including *Baccatocarpon* Bhowal et Sheikh (Manchester et al., 2019), *Indocarpa* Jain (Jain, 1964), *Sahniocarpon* Chitaley et Patil (Chitaley and Patil, 1973), *Sahnipushpam* Shukla (Kapgate et al., 2011) and *Scaevolacarpon* Kokate, Upadhye, et Patil (Kokate et al., 2010). These co-occurred with other genera that are indeed assignable to modern families such as *Indovitis* Manchester, Kapgate et Wen (Vitaceae; Manchester et al., 2013), *Momordiocarpon* Deshmukh et Kokate (Zingiberaceae; Smith et al., 2021), *Hyphaeneocarpon* Bande, Prakash et Ambwani, *Tricoccites* Rode (Arecaceae; Matsunaga et al., 2019; Manchester et al., 2022).

If *Surangea* represents a clade that was isolated on the Indian subcontinent, it could have become extinct in response to the Deccan volcanism and environmental changes at the K-Pg boundary (e.g. Sprain et al., 2019), or later as the land mass moved northward through different climate zones and collided with Eurasia (e.g. Ding et al., 2017; Klaus et al., 2016), facilitating new competition from the introduction of Laurasian taxa.

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