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Revisiting *Graminocarpon*, a distinctive monocot seed from the latest Cretaceous Deccan Intertrappean beds of India

STEVEN R. MANCHESTER[1*], DASHRATH KAPGATE[2], KELLY MATSUNAGA[3],
VAISHALI D. NAGRALE[4], DEEPAK RAMTEKE[5], DMITRY SOKOLOFF[6]
and SELENA Y. SMITH[7]

[1] Florida Museum of Natural History, Dickinson Hall, Gainesville, Florida 32611-7800, USA;
e-mail: steven@ufl.edu, ORCID: 0000-0003-0238-7977

[2] Department of Botany, Jashbhai Muljibhai Patel College, Bhandara, 441904-M.S, India;
e-mail: dkapgate@gmail.com, ORCID: 0000-0002-0116-1629

[3] Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045, USA;
and Biodiversity Institute, University of Kansas, Lawrence, Kansas 66045, USA; e-mail: matsunaga@ku.edu,
ORCID: 0000-0002-9533-2934

[4] Post Graduate Department of Botany, Rashtrasant Tukadoji Maharaj Nagpur University, Nagpur, India;
e-mail: vaishalidnagrale@gmail.com

[5] Gondia Education Society High School and Junior College, Mohadi. Dist., Gondia, 4416014-M.S., India;
e-mail: deeplifesc@gmail.com

[6] School of Plant Sciences and Food Security, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 6997801,
Israel; e-mail: dsokoloff@tauex.tau.ac.il, ORCID: 0000-0001-6314-9767

[7] Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, Michigan 48109,
USA; e-mail: sysmith@umich.edu

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ABSTRACT. Disseminules of *Graminocarpon* Chitaley et Sheikh, found at several sites of the Deccan intertrappean cherts in central India, have been reinvestigated based on physical thin sectioning and peeling and by X-ray micro-CT scanning. The globose seeds, measuring 2 to 2.5 mm in diameter, with a prominent furrow on one side and the apparent circular hilum in the center of the furrow, have a thin seed coat composed of two cell layers. The straight cylindrical embryo with no evidence of plumule differentiation is obliquely positioned in the plane of symmetry on the side opposite the furrow and is capped by a circular operculum. The combined morphological features support its recognition as a monocot, but exclude it from the Gramineae/Poaceae. Secure systematic placement is difficult, however, as we failed to find a direct match among extant taxa. The general geometry of the seeds, and position of the embryo and embryo cap presents similarities with the Arecaceae. However, the fossil appears to be unique among monocots, not readily attributed to a modern clade.

KEYWORDS: fossil, monocot, operculate seed, embryo, Late Maastrichtian, palms, grasses

INTRODUCTION

The flora of the Deccan Intertrappean beds of central India documents vegetation that occupied the region when the Indian subcontinent was still mostly isolated from other land masses and positioned equatorially, about 65–67 million years ago during a time of extensive volcanism. Cherts containing well preserved fossil plants have been recovered from about ten main sites of probable late Maastrichtian age across central India (e.g. Smith et al., 2015).

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[*] Corresponding author

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The Deccan flora includes a variety of angiosperm taxa represented by fruits, seeds, and occasional flowers. Monocots were an important part of this diversity and included early grasses (according to investigations of leaf fragments; Prasad et al., 2011), as well as at least two genera of Zingiberaceae (Smith et al., 2021) and several palms (summarized, Manchester et al., 2016, 2022; Matsunaga et al., 2019). Despite excellent morphological and histological preservation, some of the monocots represent extinct clades that have been difficult to place with respect to extant families, such as *Viracarpon* Sahni (Matsunaga et al., 2018) and *Sahnipushpam* Shukla ex Verma (Kapgate et al., 2011). Here we deal with one of the most prevalent seed types of the Deccan Intertrappean paleobotanical sites, *Graminocarpon* Chitaley et Sheikh. Micro-CT scan surface reconstructions and virtual sections demonstrate aspects of the morphology that were not clear from previous studies of physically broken and peeled specimens. The new data indicate it does not belong to the Gramineae/Poaceae and necessitate reconsideration of its affinities.

The genus *Graminocarpon* was established by Chitaley and Sheikh (1971) for small globose disseminules with a prominent longitudinal groove resembling that of a wheat caryopsis. The type species, *Graminocarpon mohgaoense* Chitaley et Sheikh, was described from the classic Mohgaonkalan locality in an article focused mainly on the fungi encountered in sections of the endosperm. The inference that these disseminules represent fruits of a grass has been accepted in subsequent treatments (e.g. Agarwal, 2008; Kapgate, 2012). Another generic name was applied to these structures by Dighe and Kokate (2016), who called them *Coffeocarpon deccanii*.

Graminocarpon mohgaoense is one of the most ubiquitous seeds of the Deccan Intertrappean beds, found at nearly every chert site where any plants are preserved, except for those of somewhat younger age in the Ghughua area per Shrivastava et al. (2015) and Pathak et al. (2017). Recent micro-CT scanning investigations of the Deccan cherts have provided new morphological and anatomical information on *Graminocarpon*, leading us to exclude it from the Gramineae/Poaceae. Here we provide a more detailed treatment of *G. mohgaoense*, based on both optical and X-ray imaging, and summarize the evidence for its systematic placement, perhaps in the Arecaceae.

MATERIAL AND METHODS

Specimens of *Graminocarpon* were studied in cherts from various localities of the Deccan Intertrappean beds, including sites near the village of Mohgaonkalan, in Chhindwara MP [Mohgaonkalan, Paladaun, Keria, and Palatwara, as well as Singpur, Marai Patan, Pudiyal Mohada, Shibla and Amabogoli (Table 1).

Ground thin sections the fossils from Mohgaonkalan, prepared by S.D. Bonde, were studied at the Agharkar Research Institute, Pune (ARI). We prepared additional ground sections and peels from the other sites. A slice of chert from Palatwara in the collection at University of Kansas (KUPB), donated to by D.V. Shukla in 1971 was particularly informative by reflected light and X-ray micro-CT scanning. Newly collected material is archived in the Florida Museum of Natural History at University of Florida, Gainesville (UF).

Micro-CT scan investigations were carried out at the College of Engineering Nanoscale Research Facility of the University of Florida. Initial observations were done at resolutions of 12.24 micrometers on a GE Phoenix V/tome/xm240 CT scanner located at the University of Florida College of Engineering Nanoscale Research Facility, with voltage of 100 kV, current of 100 µA, and exposure times of 500 ms. Higher resolution scans were done at the same facility, using a Zeiss Versa 620 XRM with a resolution of 1.36 µm. Reconstructed Tiff stacks were processed with VG Studio Max to obtain 3D renderings and virtual sections. Micro-CT scan data sets of extant palm fruits and seeds were accessed and analyzed from those archived at morphosource.org (project P776) from the study of Matsunaga and Smith (2021).

Table 1. Localities with *Graminocarpon mohgaoense* and example specimens

	Locality number	Coordinates	Example specimen numbers
Amabagholi	UF19352	21.8788333°N, 78.1948889°E	UF70404
Keria	UF19329	21.9984000°N, 79.1736330°E	UF76090
Mohgaonkalan	UF19438	22.0235833°N, 79.1867333°E	UF68874
Marai Patan	UF19442	19.53643333°N, 78.125600°E	UF70562, 71113, 71117
Paladaun	UF19506	22.0214166°N, 79.1737222°E	UF69603, 69605a, 70744
Palatwara	KUPB sn	20.0288889°N, 79.1986111°E	KUPB E299
Pudiyal Mohada	UF19443	19.57071667°N, 79.032250°E	UF71263a
Shibla	UF19444	19.9690167°N, 78.6806333°E	UF86896, 86900, 86913
Singpur	UF19278	21.6167083°N, 78.7345028°E	UF70319, 70684

We also studied the report of another species, *Graminocarpon stellatus* Dutta et Ambwani (2005). The published illustrations of that species show that it does not conform to the genus *Graminocarpon* but instead appears to be an isolated seed of the myrtalean genus *Enigmocarpon*, which, along with its flower, *Sahnianthus*, is common at the same site of Mohgaonkalan (Hamersma et al., 2025).

RESULTS

SYSTEMATICS

cf. ARECACEAE Bercht. et J. Presl

Graminocarpon Chitaley et Sheikh
emend. Manchester, Kapgate et Nagrale

Figs 1–4

Monocotyledonae

Family cf. ARECACEAE

Graminocarpon
Chitaley et Sheikh emend.

Emended diagnosis. Seed nearly globose with a prominent longitudinal furrow (infold of the seed coat). Circular thickening central to the infold. Embryo short (less than 1/3 of seed diameter), oriented at 30–50 degrees to the furrow on the opposite side of the seed from it, closer to the rounded end of the seed than to the equator. Seed coat thin, non-ruminate (except for the single longitudinal furrow), composed of two uniseriate layers of isodiametric cells, the outer layer with thick-walled cells. External surface or seed ornamented with a hexagonal mesh pattern by the protrusion of individual cells. Circular operculum formed by both layers of the seed coat, positioned directly above the embryo. Endosperm copious, uniform, cellular, composed of isodiametric cells.

Type species. *Graminocarpon mohgaoense* Chitaley et Sheikh.

Graminocarpon mohgaoense
Chitaley et Sheikh

Figs 1–4

Emended diagnosis. As for genus.

Synonymy.

2012 *Graminocarpon intertrappea* DK Kapgate; The Botanique, v. 16: p. 20, holotype number indicated, but its figure not specified.

2016 *Coffeocarpon deccanii* Dighe and Kokate; International Journal of Scientific Research, v. 5: p. 276, pl. 2, figs 1–8.

Holotype, as designated by Chitaley and Sheikh: “2 Dn/Sh.” Department of Botany, Institute of Science, Nagpur, Locality Mohgaonkalan [specimen lost].

Neotype, designated here: UF19438-68874 (Fig. 1H–L).

Additional informative specimens. KUPB E299 (Palatwara, near Mohgaonkalan, containing at least four seeds of *Graminocarpon*, along with other well-preserved angiosperm seeds (studied by reflected light and micro-CT scanning), UF19278-70319 (Singpur, surface exposed, ground sections and peels), UF19329-76090 (Keria, surface exposed seeds), UF19444-86900, 86911, 86912, 86913, 86896 (Shibla surface exposed), UF19442-71113 (Marai Patan, surface exposed).

Description. The seeds are nearly globose, but with a prominent longitudinal infold on one side (e.g. Figs 1L, 2A, B, H, J, 3 N, O) and a circular germination cap near the base on the other side (Figs 1F, 2E–G, 3M). The seeds measure 2.1–2.5 mm in height, 1.9–2.3 mm in width across the infold, and 1.2–2.1 mm in depth. We describe the longitudinal furrow, lying in the plane of bisymmetry, as ventral following the conventions used in *Phoenix* spp. (Biradar and Mahabale, 1969; Iossi et al., 2006). If this orientation is correct, the embryo can be said to lie on the dorsal side of the seed (Figs 2B, D–F, N, 3E, G). The seed has a subtle mucro at one end of the longitudinal axis (Fig. 2H, J, K), while the opposite end (closer to the embryo) is rounded. The embryo and overlying operculum are situated closer to the rounded end of the seed.

The sections do not show any vascular bundles or an obvious raphe, although it might be expected to run lengthwise along half the length of the infold. Another possible interpretation is that the ovule was almost orthotropous without a raphe. A circular pad of tissue, 0.64 mm diameter and 0.14 mm thick in the middle of the infold is interpreted as the hilum (Figs 1D, I, 2C, D, 3F, H–J, 4B). The cells composing this tissue are uniformly small, ~10 µm, and isodiametric.

Endosperm tissue is copious, uniform, cellular, composed of isodiametric cells (Figs 2A–F, 3B–J). There is no evidence of an aleurone layer at the surface of the endosperm or a central cavity in the endosperm. The embryo is

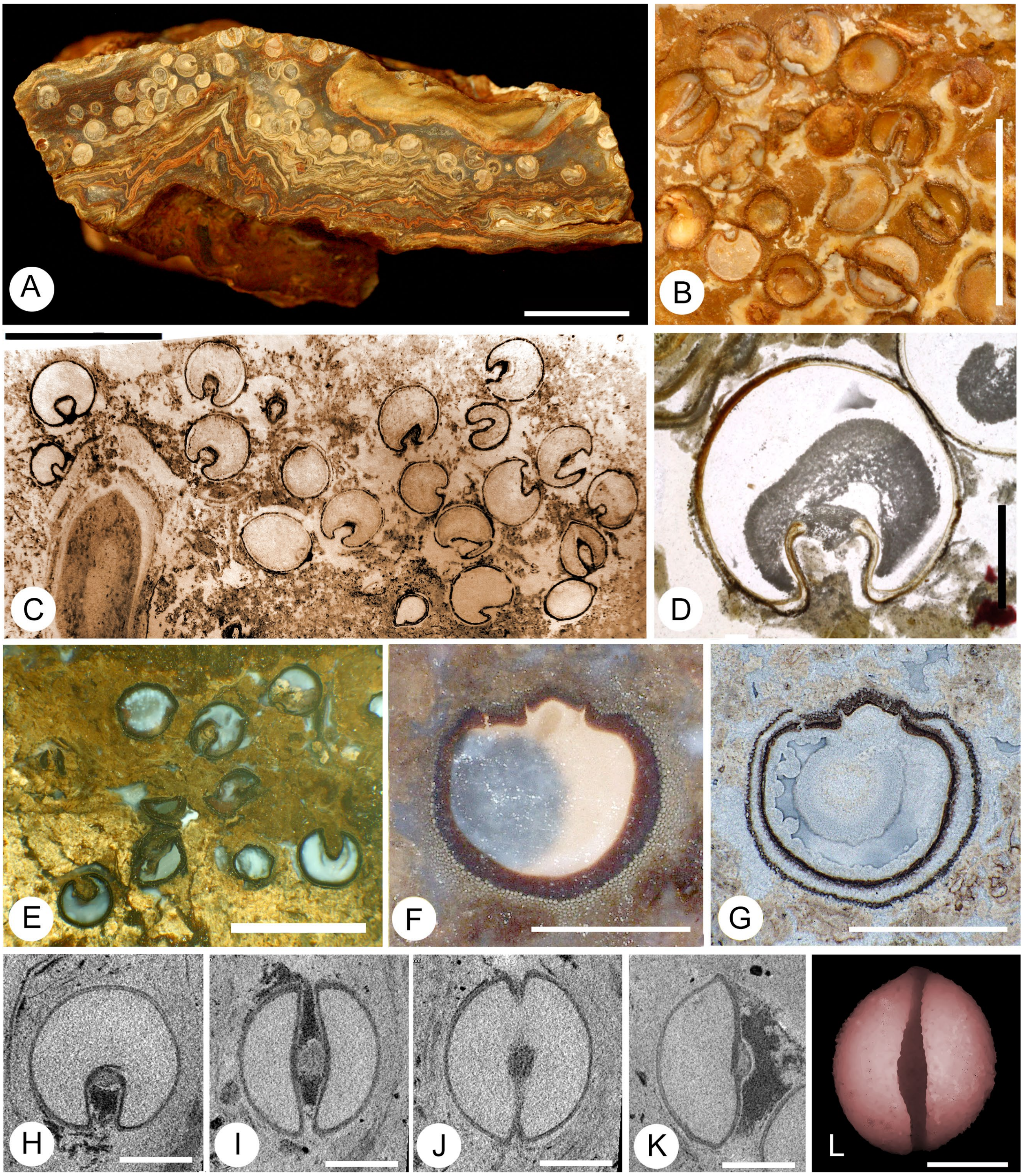

Figure 1. *Graminocarpon mohgaoense* Chitaley et Sheikh seeds from Mohgaonkalan (A–D, H–L) and Singpur (E–G); **A**, **B**. S.D. Bonde Collection, ARI 5307; **A**. Numerous seeds accumulated together, polished surface of chert; **B**. Naturally fractured surface of same piece chert with surface-exposed seeds, showing the infold in various orientations, reflected light; **C**. Another accumulation in chert, peel section, CMNH PM 1508; **D**. Seed in transverse section, ground thin section by reflected light from same specimen as A, B, ARI 5307; **E**. Accumulation of about ten seeds, UF19278-70319; **F**. Tangential section of seed from same specimen as E, intercepting operculum (arrow), with translucency showing the uniseriate external layer of isodiametric cells, and silhouette of the embryo below the operculum, reflected light, immersed in xylene; **G**. The same surface as F, with greater contrast after etching with hydrofluoric acid, rendering it opaque, showing separation of the two main seed layers, and revealing that the operculum is formed by both layers of the seed coat, reflected light; **H–L**. One seed within chert imaged by micro-CT scan, neotype, UF19438-68874; **H**. Virtual transverse section showing furrow of the seed coat; **I**. Virtual coronal section intercepting the longitudinal groove with central placement of the hilum; **J**. Median coronal section parallel to I, skimming the edge of the infold (vertical) and hilum (central); **K**. Sagittal section, showing protrusion of hilum and pointed apex; **L**. Surface rendering, ventral view showing longitudinal furrow. Scale bars = 10 mm in A; 5 mm in B, C, E; 1 mm in D, F–L

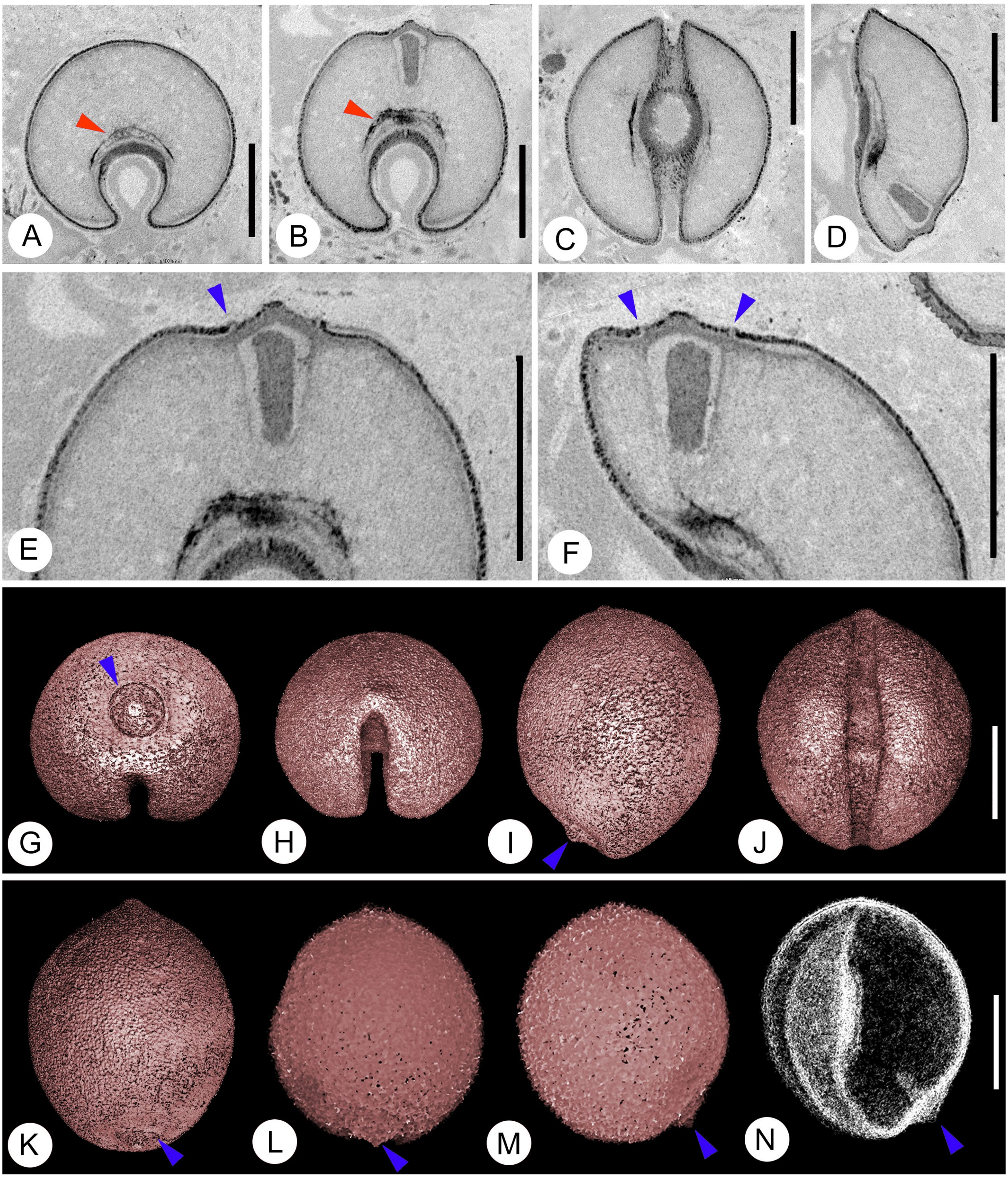

Figure 2. *Graminocarpon mohgaoense* Chitaley et Sheikh seed from Palatwara, KUPB E299-2. **A–F**. Virtual sections; **A**. Equatorial transverse section showing circular outline and ventral furrow; arrow indicates possible hypostase tissue; **B**. Oblique section parallel to embryo, showing prominent ventral furrow below, and bulge of the operculum over the embryo; arrow indicating possible hypostase tissue; **C**. Coronal section traversing the length of the ventral furrow and central circular hilum; **D**. Sagittal section in the plane of bisymmetry, 90° to B and C, intercepting the embryo near base of the seed; **E**, **F**. Enlargements from C, D, showing uniseriate seed coat and isodiametric cells of endosperm Arrows indicate edges of the operculum; **G–K**. Reflective surface rendering of the same specimen from A–F, in varied orientations; **G**. Basal view to the circular embryo cap/operculum (arrow); **H**. Apical view; **I**. Lateral view with operculum to lower left (arrow); **J**. Ventral view with prominent longitudinal groove and apical mucro; **K**. Dorsal view with embryo cap below (arrow); **L**, **M**. Depth map images; **L**. Dorsal view; **M**. Lateral view; **N**. Same view as M, with translucency showing the embryo (arrow). Scale bars = 1 mm

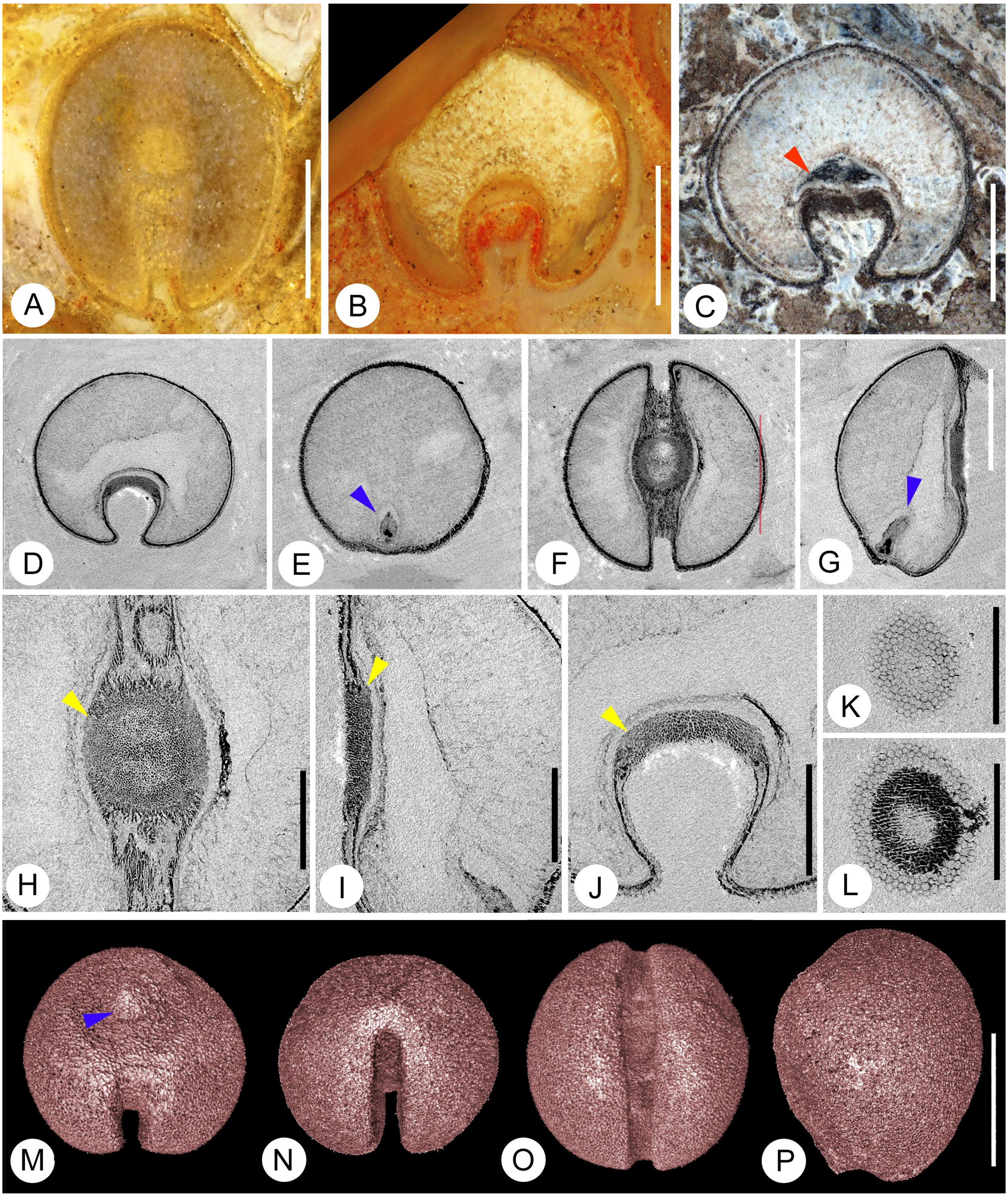

Figure 3. *Graminocarpon mohgaoense* Chitaley et Sheikh seeds from Palatwara (A, B, D–P, KUPB E299), and Keria (C); **A**, **B**. Reflected light, polished surface; **A**. Longitudinal section with vertically oriented ventral furrow visible through translucent silica, KUPB E299-3; **B**. Transverse section showing cellular endosperm and thin seed coat with ventral furrow at bottom of image, KUPB E299-4; **C**. Surface exposed seed in transverse section; arrow indicating possible hypostase, UF19329-76090; **D–L**. Virtual sections from micro-CT scanning, KUPB E299-1; **D**. Equatorial transverse section; **E**. Coronal longitudinal section intercepting the subbasal embryo (arrow); **F**. Coronal section, intercepting both sides of seed separated by the infold, thickened circular hilum in center; **G**. Sagittal section with subbasal embryo (arrow); **H**.Coronal section intercepting the "hilar pad" of isodiametric cells (arrow), and longitudinally elongate cells following the infold; **I**. Sagittal section (right angle to H), showing hilar pad to left, faintly preserved surrounding endosperm; **J**. Transverse section intercepting the hilar pad of isodiametric cells (arrow); **K**, **L**. Successive longitudinal peridermal sections from surface indicate by red line in F; **K**. Outer layer of seed coat with cells in honeycomb arrangement; **L**. Tangential section immediately below the level of K, intercepting three layers: outermost layer of honeycomb cells, inner seed coat layer of horizontally elongate cells, and central circular outline of the edge of the endosperm; **M–P**. Reflective surface rendering images; **M**. Basal view with protruding embryo cap; **N**. Apical view with protuberance adjacent to infold; **O**. Ventral view with median furrow; **P**. Lateral view. Scale bars = 1 mm in A–G (bar in G applies to D–F); M–P (bar in P applies to M–O); 0.5 mm in H–J; 0.05 mm in K, L

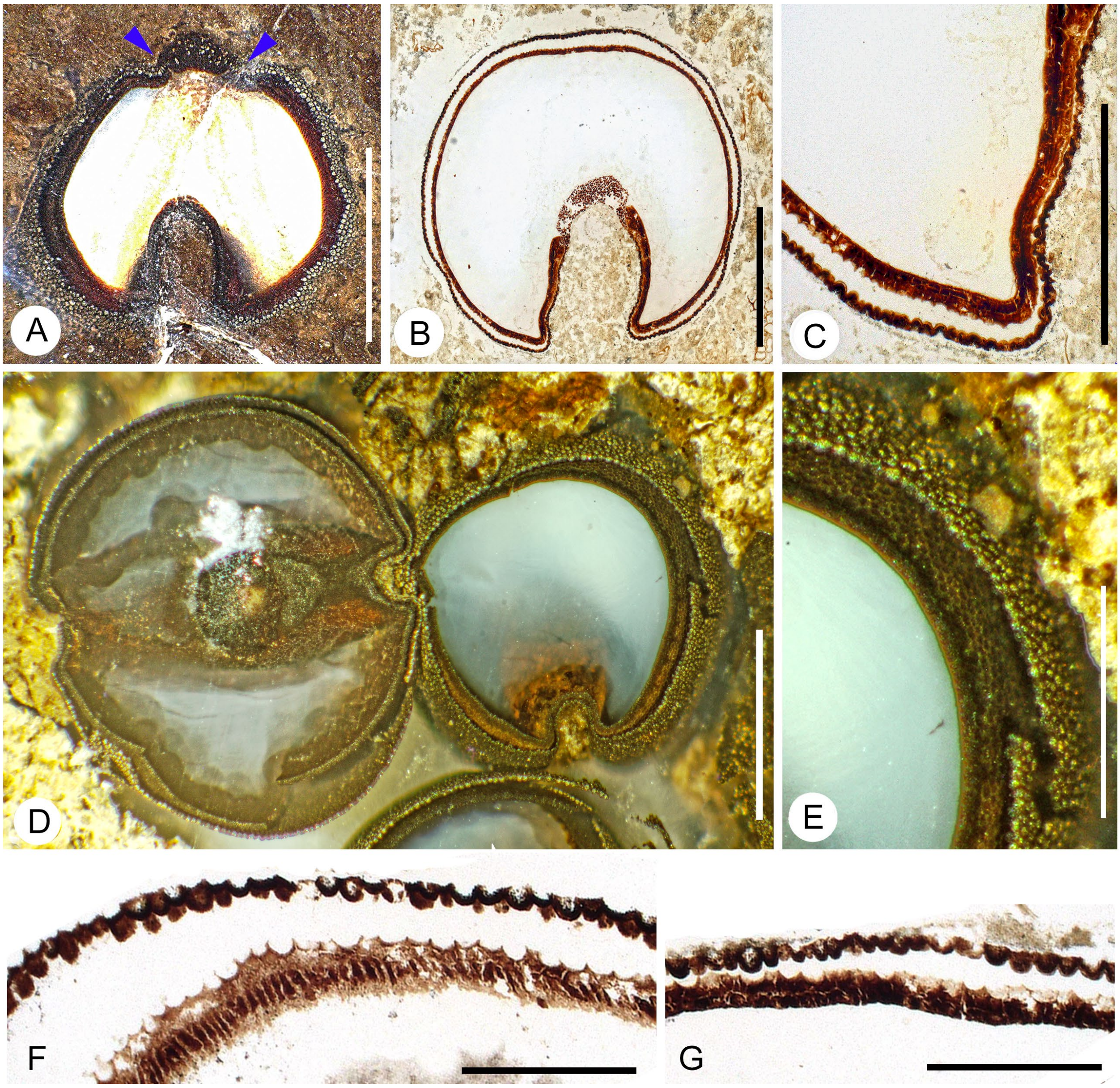

Figure 4. *Graminocarpon mohgaoense* Chitaley et Sheikh seeds from Singpur, UF19278-70319. **A**. Oblique physical section traversing the operculum and infold, immersed in xylene, reflected light; **B**. Transverse peel section showing circular outline, separated seed coat layers, and infold, transmitted light; **C**. Detail of seed coat from B, with two main layers separating; **D**. Portions of three seeds in a polished slab by reflected light. Seed on left shows circular outline of hilum at center of horizontally oriented infold. Seed on right shows the outer uniseriate layer of isodiametric cells in the plane of section and in the surrounding surface visible through translucent silica; **E**. Detail from D showing separating outer layer; **F**, **G**. Peel sections by transmitted light, showing inner and outer layers separated from one another. Scale bars = 1 mm in A–D; 0.5 mm in E; 250 µm in F, G

relatively small, and cylindrical, 0.48 mm long and 0.15 mm wide, positioned on the dorsal surface near the base (Figs 2B, D, N, 3E, J). No obvious differentiated plumule can be seen.

The seed coat is composed of two main layers, an inner layer, presumably representing the tegmen, and an outer layer, interpreted as the testa (Figs 1D, 2E, F, 3C, K, L, 4B–G). Successive paradermal sections show the outer layer of polygonal cells (Fig. 3K, L), and an inner layer of elongate cells (inner portion of Fig. 3L). These layers commonly separate from each other as shown in Fig. 4B–G. Although the two layers can appear to be contiguous when the sectioned surface is viewed with translucency and depth (Fig. 1F), the same surface, upon etching to render it opaque, shows a significant separation between the layers (Fig. 1G; see also Fig. 4D–G). A germinal operculum forms a distinct circular mound 0.5 mm in diameter, to which the embryo is adjoined, on the dorsal side of the seed in the plane of symmetry, opposite from the longitudinal furrow (Figs 1F, G, 2G, I, K–N, 3M).

In the circular area of the putative hilum, several layers of cells can be seen, of which the outer and the inner layer seem to be continuous with the two cell layers of the seed coat (Fig. 3I, J, yellow arrows). Another tissue is visible at a short distance inside the seed, U-shaped in sections perpendicular to the furrow (red arrow in Figs 2A, B, 3C). One possible interpretation is that this tissue was located at the boundary between the chalaza and nucellus and fits the term hypostase in the sense accepted by Shamrov (1998, 2008), but not Tilton (1980) and Rudall (1997).

We have not found *Graminocarpon* seeds with intact surrounding fruit tissue. This statement is based on accepting both of the cellular outer layers as seedcoat. We rejected the hypothesis that the outer layer represents endocarp because both layers contribute to formation of the embryo cap/ operculum (Figs 1G, 4A) and both are aligned with the putative hilar region (Fig. 3I). From this we infer the seeds were borne in fleshy fruits, with easily degraded pericarp, likely attractive for animal dispersal. Accordingly, some of the pericarp characters that would be helpful for placing it systematically are missing.

SYSTEMATIC POSITION

The initial assignment to the grasses (Chitaley and Sheikh, 1971) may have been influenced by the longitudinal furrow, comparable to the groove which often occurs on the ventral side of caryopsis fruits. However caryopses and their enclosed seeds are typically narrow and elongate rather than globose, and the embryos are commonly, although not always, aligned with the long axis. Germination opercula are not documented for extant grasses (Petrova et al., 1985). Some other members of the Poales do possess opercula, including Xyridaceae and Eriocaulaceae (Rudall and Sajo, 1999; Coan, 2006; Nardi et al., 2015; Nardi, 2018).

As reviewed by Grootjen and Bouman (1981b: 265), in plants with operculate seeds “germination is accomplished by the shedding of a lid-like part of the seed coat, after which the radicle protrudes through the opening.” This lid, usually formed by a differentiation of the integuments adjacent to the micropyle, is commonly referred to as an operculum (in German: Samendeckel; Portugese: opérculo). Among angiosperms, operculate seeds occur in some magnoliids including the Nymphaeales (e.g. Collinson, 1980; Sokoloff et al., 2013) and various clades of monocots. Netolitzky (1926) reported them in the families Typhaceae, Pandanaceae, Sparganiaceae, Palmae, Araceae, Lemnaceae, Commelinaceae, Phylidraceae, Liliaceae, Dioscoreaceae, and Zingiberales. Additional examples were cited by Tschirch (1891) in Potamogetonaceae and Restionaceae. Other potential positions within the monocots were considered in this study with reference to the review of extant monocot seeds edited by Takhtajan (1985), but most families could be readily eliminated.

An operculum is well documented in seeds of Zingiberales, typically terminal on the long axis of the seed, and the embryo is elongate (4–5 times longer than wide and extending more than 2/3 the length of the seed) except in Musaceae which have short embryos but pronounced micropylar collars and chalazal chambers (Grootjen and Bouman, 1981a; Benedict et al., 2016). Commelinaceae also have operculate seeds (Grootjen and Bouman, 1981a). However, the rim-like micropylar collar around the operculum distinguishes extant Zingiberales and Commelinaceae from *Graminocarpon*.

The geometry of *Graminocarpon* seeds suggests that comparison with the seeds of palms is appropriate. A morphological survey of palm fruits and seeds representing most extant genera of the Arecaceae using micro-CT imaging was carried out by Matsunaga and Smith (2021). From this work, it can be seen that globose seeds superficially resembling *Graminocarpon* occur in several clades of the family. A ventral intrusion of seed coat, sometimes referred to as a postament, occurs in Calamoideae and Coryphoideae and is particularly common in the latter (Matsunaga and Smith, 2021). Typically in palms the postament is formed of solid tissue, but it can be hollow in *Phoenix*. The longitudinally elongate intrusion seen in *Graminocarpon* superficially resembles that of *Phoenix*. However, the homology of seed tissues distinguishes *Phoenix*, as well as many other palms, from *Graminocarpon*. According to Danilova and Savchenko (1985), most palms have a vascularized outer integument with more than one bundle, and this is visible in the seeds. Also, the seed coat of palms tends to have more than two cell layers. These features differ from what we observe in *Graminocarpon*.

In Genera Palmarum (Dransfield et al., 2008), the term operculum is used exclusively

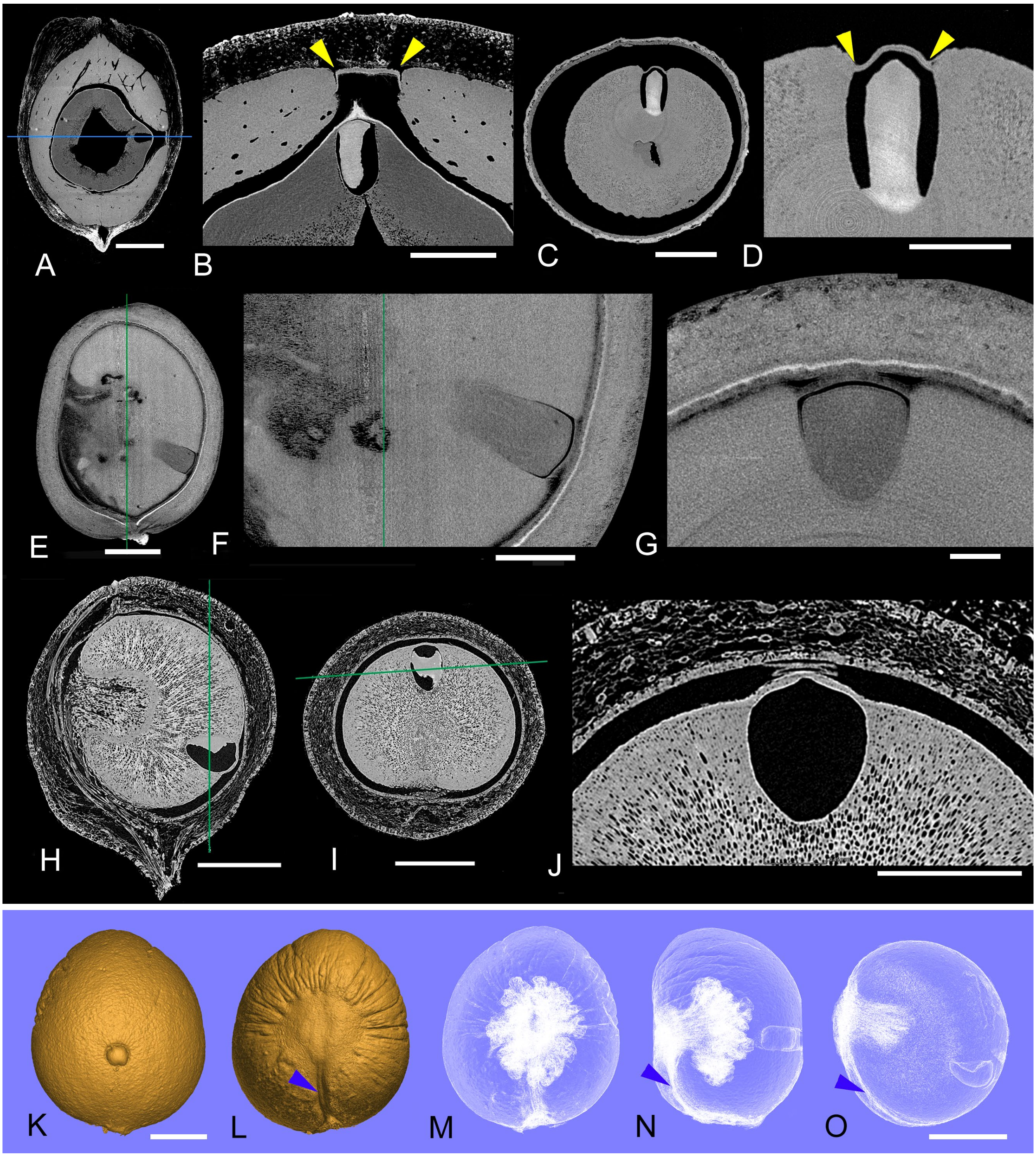

Figure 5. Extant palm fruits for comparison, micro-CT scan imagery. Specimen sources indicated in Appendix supplement 1 of Matsunaga and Smith (2021). **A**, **B**. *Jubaeopsis caffra* Becc. Note that the operculum (arrows) is formed by the endocarp layer of pericarp; **C**, **D**. *Livistona benthamii* F.M.Bailey; **E–G**. *Livistona chinensis* (Jacq.) R.Br. ex Mart. Note that the operculum (arrows) is formed by the seed coat; **H–J**. *Rhapis excelsa* (Thunb.) A.Henry; **K–N**. Digitally extracted seed of *Livistona chinensis* from the fruit shown in E; **K**. Dorsal view with circular embryo cap/operculum; **L**.Ventral view with raphe indicated (arrow); **M**. Same view with translucency showing prominent postament; **N**. Lateral view showing subequatorial embryo (right side), raphe (arrow), and ventrally intruded postament (left side); **O**. Translucent sagittal view of *Rhapis excelsa* seed from the fruit shown in H, showing ventral postament, raphe (arrow), and subbasal embryo (lower right). Scale bars = 10 mm in A; 5 mm in B, E; 2 mm in C, F, H, I, O; 1 mm in D, G, J

in application to what is interpreted as endocarp of the fruit, and not mentioned in relation to the seed. In a CT scan survey including most genera of the palms, Matsunaga and Smith (2021) observed that “endocarp opercula are common throughout Arecoideae and were not found in any other subfamilies.” However, the term operculum has also been applied to structures with similar shape and function formed by the seedcoat in palms. Seedcoat opercula have been reported, for example, in *Phoenix* (Biradar and Mahabale, 1969; Iossi et al., 2006), *Pritchardia* (Pérez, 2009) and *Jubaeopsis* (Robertson, 1977).

In some cases, the attribution of operculum to the seed coat in palms was erroneous. In his investigation of *Jubaeopsis caffra*, Robertson (1977) stated "At the micropyle the inner integument forms an operculum." However, micro-CT scanning of the same species shows that the operculum is formed by the endocarp (Fig. 4A, B). Further investigation of palms with attention to placement and character of seed coat opercula would be desirable. In our comparative work, referring to the micro-CT scan digital slice movies and datasets archived by Matsunaga and Smith (2021) at Morphosource.org, we found some similar, although not identical morphology and anatomy of seeds in *Livistona benthamii* (Fig. 4C–G) and *Rhapis excelsa* (Fig. 4H–J).

DISCUSSION

The dismissal of *Graminocarpon* from Poaceae adds to our understanding of the complex affinities of monocots that were endemic to India about 66 million years ago. Although palms were abundant and are the most diverse plant family encountered among the Deccan plants, they were accompanied by other monocots of less certain affinity including *Sahnipushpam* (Kapgate et al., 2011) and *Viracarpon* (Matsunaga et al., 2018). The affinities of *Graminocarpon*, despite excellent histological preservation, also remain uncertain at this time. As far as currently known, *Graminocarpon* suffered extinction prior to the early Paleogene tectonic collision of the Indian subcontinent with Eurasia.

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ADDITIONAL INFORMATION

CONFLICT OF INTEREST. The authors have declared that no competing interests exist.

ETHICAL STATEMENT. No ethical statement was reported.

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