Botanical Journal of the Linnean Society, 2019, **190**, 260–280. With 6 figures.

Fossil palm fruits from India indicate a Cretaceous origin of Arecaceae tribe Borasseae

KELLY K. S. MATSUNAGA[1], STEVEN R. MANCHESTER[2], RASHMI SRIVASTAVA[3], DASHRATH K. KAPGATE[4] and SELENA Y. SMITH[1*]

[1]*Earth and Environmental Sciences, University of Michigan, Ann Arbor, MI, USA*
[2]*Florida Museum of Natural History, Gainesville, FL, USA*
[3]*Birbal Sahni Institute of Palaeosciences, Lucknow, India*
[4]*Department of Botany, J.M Patel College, Bhandara, Maharashtra, India*

Received 26 November 2018; revised 3 March 2019; accepted for publication 20 April 2019

The fossil record of palms (Arecaceae) is essential for understanding the deep evolutionary and geographical history of the family. We studied palm fruit fossils from the *c.* 67–64-Myr-old Deccan Intertrappean Beds of India to infer the systematic relationships of the fossils and their relevance to palm evolution. Using X-ray micro-computed tomography, physical sectioning techniques and a total-evidence phylogenetic analysis, we show that these fossils represent a crown group member of subtribe Hyphaeninae (tribe Borasseae, subfamily Coryphoideae) allied with the extant genera *Satranala* and *Bismarckia*, now endemic to Madagascar. These fossils, synonymized here as *Hyphaeneocarpon indicum*, provide evidence for the existence of crown group Hyphaeninae during the late Maastrichtian–early Danian. This pre-dates prior age estimates for the Hyphaeninae crown node by nearly 40 Myr and implies an earlier divergence of Borasseae. The presence of *Hyphaeneocarpon* in India shows that Borasseae have persisted in the Indian Ocean region for > 64 Myr. This study illustrates the utility of palm fruit characters for placing fossils in a phylogenetic context and has important implications for understanding the evolution and diversification of Borasseae and the palaeobiogeography of palms.

ADDITIONAL KEYWORDS: biogeography – Deccan – Maastrichtian – MrBayes – palaeobotany – Palaeocene – palm phylogeny – X-ray micro-computed tomography (μCT).

INTRODUCTION

Palms (Arecaceae) are found today throughout tropical regions worldwide occupying a variety of environments ranging from arid deserts to tropical rainforests (Dransfield *et al.*, 2008). Currently, Arecaceae comprise *c.* 2600 species classified into five subfamilies and 181 genera (Baker & Dransfield, 2016). Additionally, they have a rich fossil record extending back to the Late Cretaceous; unequivocal palm fossils first appear during the Turonian (*c.* 94–90 Ma) and are geographically widespread by the Maastrichtian (*c.* 72–66 Ma; Gee, 2001; Harley, 2006; Dransfield *et al.*, 2008). Subsequently, they achieved a global distribution, extending into high-latitude regions such as Alaska and Antarctica during the warm and equable climatic conditions of the Eocene (Sluijs *et al.*, 2009; Pross *et al.*, 2012; Suan *et al.*, 2017). The fossil record of palms thus represents an important source of data for understanding the deep evolutionary history of the family and terrestrial environments of the geological past.

The Maastrichtian–Danian (*c.* 67–64 Ma) Deccan Intertrappean Beds of India host plant fossil assemblages with numerous palm macrofossils (Bonde, 2008; Kapgate, 2009; Srivastava, 2011). Located primarily in central India, these localities preserve the remains of palm stems, leaves, roots, pollen, inflorescences and fruits, indicating that palms were an important component of the vegetation of central India during the Late Cretaceous and Palaeocene, during which time India was geographically isolated from other major landmasses (Ali & Aitchison, 2008; Chatterjee, Goswami & Scotese, 2013). Today palms do not comprise a significant component of the vegetation of central India. Although the flora of India includes

---

*Corresponding author. E-mail: sysmith@umich.edu *c.* 96 species in 20 genera (Kulkarni & Mulani, 2004), Modern palms in India are thought to have descended from relatively recent colonizations rather than an ancient flora (Baker & Couvreur, 2013). However, little is known about the taxonomic composition of historical palm assemblages and the role of India in the evolutionary and biogeographical history of Arecaceae.

Over the course of nearly a century of study on the Deccan flora, *c.* 168 fossil species have been assigned to Arecaceae, including 85 species based on stem specimens, 37 on fruits, 28 on leaves, roots and inflorescence axes, and 18 on palynomorphs (Bonde, 2008; Kapgate, 2009). These diverse assemblages could be essential for understanding the evolutionary tempo in palm diversification, historical biogeography of palm lineages and transitions in the terrestrial vegetation of India through time. For example, recent re-examination of *Palmocarpon drypeteoides* (Mehrotra, Prakash & Bande) Manchester, Bonde, Nipunage, Srivastava, Mehrotra & Smith revealed morphological characters diagnostic of subtribe Attaleinae, which is currently most diverse in South America and with no representatives in India or elsewhere in Asia (Manchester *et al.*, 2016). However, the systematic affinities of most of the palm fossils in the Deccan Intertrappean beds are poorly understood, as is the extent to which the number of described palms accurately represents the true species richness in these fossil assemblages. Morphological studies and taxonomic revisions are therefore essential for understanding the Deccan floras and applying them to broader questions of palm evolution.

In this study we re-examined five previously described fossil palm species, in light of new specimens recovered from the Deccan Intertrappean Beds at Dhangaon, Keria and Mohgaonkalan: *Hyphaeneocarpon indicum* Bande, Prakash & Ambwani; *Palmocarpon arecoides* Mehrotra; *Arecoidocarpon kulkarnii* Bonde; *A. palasundarensis* Bonde; and *Pandanusocarpon umariense* Bonde (Bande, Prakash & Ambwani, 1982; Mehrotra, 1987; Bonde, 1990a, b, 1995). We used comparative anatomy to investigate the taxonomic affinities of the new fruit specimens and to evaluate conspecificity of the previously described fossils, which exhibit some shared features. To understand their systematic relationships and significance in an evolutionary and biogeographical context, we included the fossils in a total-evidence phylogenetic analysis of extant palms. Palms exhibit significant diversity and convergence in fruit structure and other features. It can therefore be difficult or unwieldy to evaluate objectively whether some combinations of characters are unique to clades, have evolved multiple times or are possibly plesiomorphic. Phylogenetic analyses can also help to frame more precise systematic hypotheses, such as placement of fossils in the stem or crown of a group and alliances with particular extant taxa. This information can facilitate inferences of historical biogeography and character evolution and inform node calibrations in future dating analyses, providing valuable information on the diversification of palms in deep time.

MATERIAL AND METHODS

Locality and age

The Deccan Volcanic Province (DVP) comprises a sequence of continental flood basalts (traps) formed during the late Maastrichtian to early Danian (*c.* 67–64 Ma, chrons 30N–29N; Hooper, Widdowson & Kelley, 2010; Renne *et al.*, 2015; Schoene *et al.*, 2015), exposed across central and western peninsular India. Intertrappean sedimentary layers, which occur between some basalt flows and represent quiescent intervals between volcanic episodes, frequently contain permineralized plants preserved three-dimensionally in chert deposits. More than 50 plant fossil-bearing localities have been discovered during the last century, most of which are concentrated in central India in the states of Maharashtra and Madhya Pradesh and occur primarily in the north-eastern portion of the Deccan Main Plateau or in the Mandla subprovince (Fig. 1; Kapgate, 2009; Smith *et al.*, 2015). Where magnetostratigraphic data are available, many of these localities fall within Chron 29R, which straddles the Cretaceous–Palaeogene (K-Pg) boundary (M. Widdowson, pers. comm., 2018). Although more precise ages of most macrofossil localities are poorly constrained, many are considered either late Maastrichtian or early Danian depending on their location in the DVP, stratigraphic continuity with dated outcrops and palynomorph content (Samant & Mohabey, 2009). Specifically, the localities exposed in the north-eastern Deccan Main Plateau and south-western part of the Mandla subprovince are currently considered late Maastrichtian, whereas those in the eastern region of the Mandla subprovince are probably all early Danian (Shrivastava, Duncan & Kashyap, 2015; Smith *et al.*, 2015).

Specimens studied

Specimens were examined from existing and new collections. Fossils come from six localities in the DVP: Mohgaonkalan, Keria, Dhangaon, Palasundar, Umaria and Shahpura. The new macrofossil specimens (UF19415-69208, UF19415-62614, UF19438-68879, UF19329-62153) originate from the Keria, Mohgaonkalan and Dhangaon localities of the Deccan

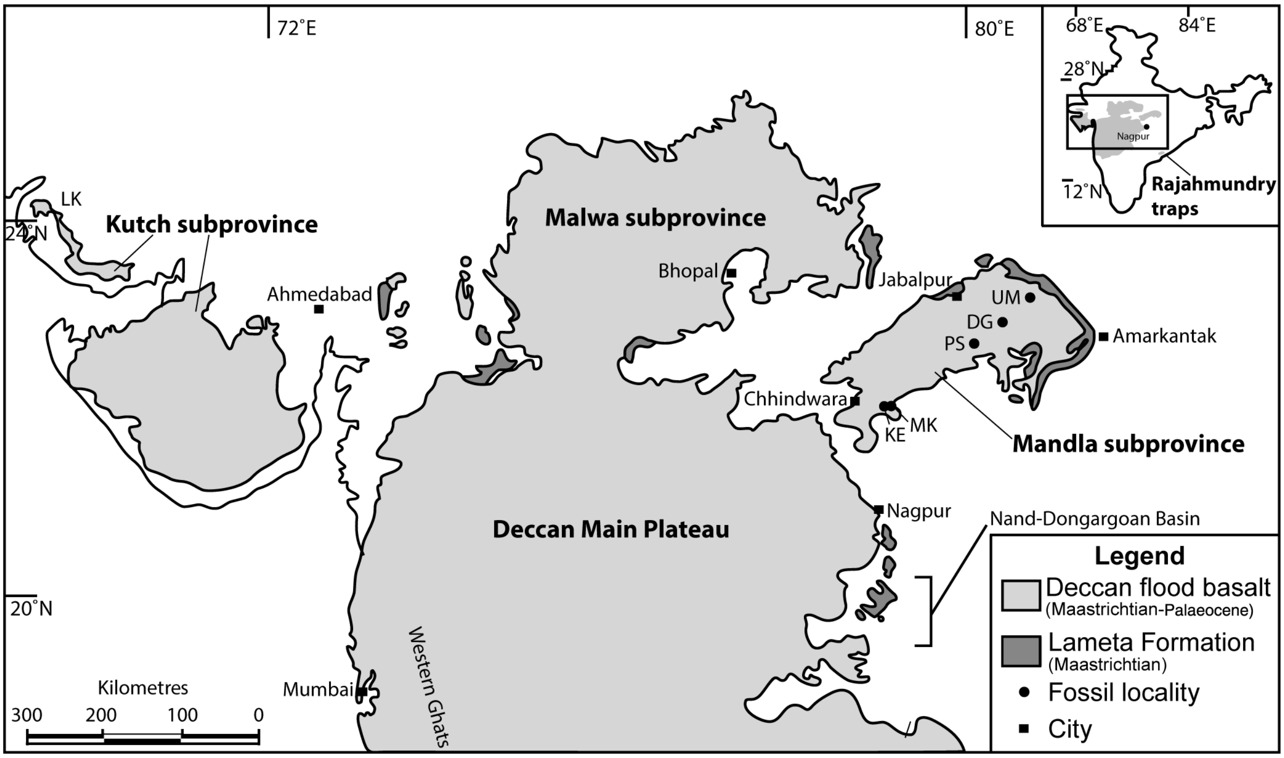


Figure 1. Deccan Intertrappean Bed localities in which *Hyphaeneocarpon indicum* fossils occur. Note that all the localities are in the Mandla subprovince of the Deccan Volcanic Province. The Shahpura locality was not included in the map, as its precise location is not certain, but at the map scale shown it would probably overlap the dot for the Umaria locality. Abbreviations: KE, Keria; MK, Mohgaonkalan; PS, Palasundar; DG, Dhangaon; UM, Umaria (modified from Smith et al. 2015).

Intertrappean Beds of India. Keria (coordinates: 21.9984°N, 79.173633°E) and Mohgaonkalan (coordinates: 22.023583°N, 79.186733°E) are located in the south-western edge of the Mandla subprovince of the DVP, in the state of Maharashtra, whereas Dhangaon (coordinates: 22.84083333°N, 80.44333333°E) is further east in the Mandla subprovince in the state of Madhya Pradesh. The specimens are curated in the palaeobotanical collections of the Florida Museum of Natural History in Gainesville, Florida, USA (UF). Other specimens examined by us and revised here represent previously described species from several other localities. These include specimens curated at the Agarkhar Research Institute (ARI) in Pune, India, of *Arecoidocarpon kulkarnii* (Bonde, 1990a; Mohgaonkalan locality, ARI5285), *A. palasundarensis* (Bonde, 1995; Palasundar, ARI5288) and *Pandanusocarpon umariense* (Bonde, 1990b; Umaria, ARI5284), and *Hyphaeneocarpon indicum* (Bande *et al.*, 1982; Shahpura) from the Birbal Sahni Institute of Palaeosciences (BSIP) in Lucknow, India (BSIP 35408, slide 6182). The distribution of these localities in Mandla subprovince indicates varying ages: Keria and Mohgaonkalan, which are considered part of the same intertrappean bed, are probably Maastrichtian, whereas the other localities located further east in Mandla subprovince are all probably early Danian. The precise location in Mandla district (Madhya Pradesh) of the Shahpura locality from which the *H. indicum* holotype was described was not specified (Bande *et al.*, 1982), but it is probably in the vicinity of the Umaria locality, near the town of Shahpura, and is thus probably also Danian.

Extant comparative material included fruit specimens of *c.* 80 species representing most genera sampled in the phylogenetic analysis, including all genera of Borasseae. Specimens were obtained either on loan or examined in the herbarium collections at the Royal Botanic Gardens, Kew (K), L.H. Bailey Hortorium Herbarium (BH) and Fairchild Tropical Botanic Garden (FTG), or collected in the filed at Fairchild Tropical Botanic Garden. Specimens of *Bismarckia nobilis* Hildebr. & H.Wendl., *Satranala decussilvae* Beentje & J.Dransf., *Medemia argun* (Mart.) Württemb. ex H.Wendl., *Borassus flabellifer* L., *Borassodendron machadonis* (Ridl.) Becc. and

Hyphaene thebaica (L.) Mart. were further studied using X-ray micro-computed tomography (μCT; see below) to better understand their anatomical similarities with *Hyphaeneocarpon* Bande, Prakash & Ambwani and to identify potential synapomorphies.

Fossil fruits from Keria, Mohgaonkalan and Dhangaon were studied using a combination of serial peels (cellulose acetate or butyl acetate) mounted on microscope slides for documenting anatomy and μCT to observe three-dimensional structure. The μCT scans were performed at the University of Michigan CTEES facility using a Nikon XT H 225ST industrial μCT system with a Perkin Elmer 1620 X-ray detector panel and a tungsten reflection target. Depending on the specimen, scans were set at 68–130 kV, 130–175 μA, and used 0–0.5 mm of copper filter, which reduces strong artefacts in reconstructed images by suppressing lower energy X-rays. Pixel size varied from *c*. 12.0 to 16.5 μm. The μCT scans of figured extant species, *Bismarckia nobilis* and *Satranala decussilvae* (K000300252; Figs 4C, 6D–E), were scanned on the same system using 58–60 kV and 155–175 μA, with 27–31 μm pixel size resolution. Scans were acquired using Inspect-X and reconstructed using CT Pro 3D (Nikon Metrology), which uses an FDK (Feldkamp-Davis-Kress) type algorithm. The reconstruction software takes the 2D projection images acquired by the X-ray detector and generates a 3D image represented by grey values distributed in a volumetric space. Reconstructed datasets were analysed with Avizo 9 Lite 3D software (FEI). We refer to sections obtained from the reconstructed μCT data as digital sections. Videos based on μCT scans, raw scan data (image stacks) and associated metadata are archived and freely accessible at MorphoSource (www.morphosource.org) under project number 634.

PHYLOGENETIC ANALYSIS

A genus-level morphological and molecular dataset focused on Coryphoideae was assembled to test the systematic relationships of the fossil in the subfamily, while considering possible affinities with other groups. Taxon sampling was based on the dataset of Baker *et al.* (2009) and included exemplar species of each genus in subfamilies Coryphoideae, Nypoideae and Calamoideae and one species representing each tribe of subfamilies Ceroxyloideae and Arecoideae. *Dasypogon bromeliifolius* R.Br. and *Kingia australis* R.Br. (Dasypogonaceae) were also included as outgroups in the molecular partitions, for a total of 85 sampled taxa. The molecular dataset included four plastid (*matK*, *rbcL*, *rps16*, *trnL-trnF*) and two nuclear (*PRK*, *RPB2*) markers, all obtained from GenBank (Supplementary materials). Coding sequences (*rbcL*, *matK*, *ndhF*) were aligned using MUSCLE (v.3.8) and adjusted minimally by hand in AliView (v.1.25). Non-coding sequences (*rps16*, *trnL-trnF*, *PRK*, *RPB2*) were aligned initially using MAFFT and refined with PRANK, if necessary; for these sequences, this procedure produced better alignments than manually adjusting MUSCLE results.

The morphological matrix used to incorporate the fossil into the phylogenetic analysis contained 110 characters scored for 83 taxa (*Dasypogon bromeliifolius* and *Kingia australis* were not included as there are insufficient published fruit data, and we could not obtain specimens; Supporting Information File S2). This matrix was modified from that of Baker *et al.* (2009) to reflect the taxon sampling of this study and updated generic concepts in Arecaceae. The original dataset of Baker *et al.* (2009) contained 105 vegetative and reproductive characters, to which we added five additional fruit characters; the original character coding and scoring were left unmodified. The new characters were added primarily to elucidate placement of the fossils in Borasseae. Preliminary analyses using the unmodified matrix of Baker *et al.* (2009) showed strong support for placement of the fossil with subtribe Hyphaeninae, but with relationships otherwise unresolved. The new characters include: seed number per fruit (one, up to three or more than three), endocarp origin within the pericarp (from the inner zone, i.e. locular epidermis, or middle zone of pericarp), germination structure shape (circular or slit/elongate), germination structure type [pore, valve (e.g. *Satranala*) or operculum] and basal intrusion of endocarp into the seed (absent or present). Scoring of the five added characters was based on descriptions in the literature and observations of herbarium material. The fossil species was scored for 20 characters. Although the fossil could not be scored for some morphological characters, all the morphological characters were retained in the analysis to aid in placing extant genera for which DNA sequence data are sparse. In most cases, morphological characters and all DNA sequences were sampled from the same species. However, some sequences were not available for all focal species and were instead taken from closely related, congeneric taxa (Supporting Information). The morphological matrix and aligned DNA sequences were concatenated using SequenceMatrix (v.1.8), with all external gaps coded as question marks.

Phylogenetic analysis of the combined dataset was performed using Markov chain Monte Carlo (MCMC) methods in MrBayes (v.3.2.6) on the CIPRES Science Gateway (Miller, Pfeiffer & Schwartz, 2010). We used PartitionFinder2 with AICc model selection (Akaike information criterion, correcting for sample size) and the ‘greedy’ search function to estimate the optimal partitioning scheme for the DNA sequence data limited to the models available in MrBayes (Supporting

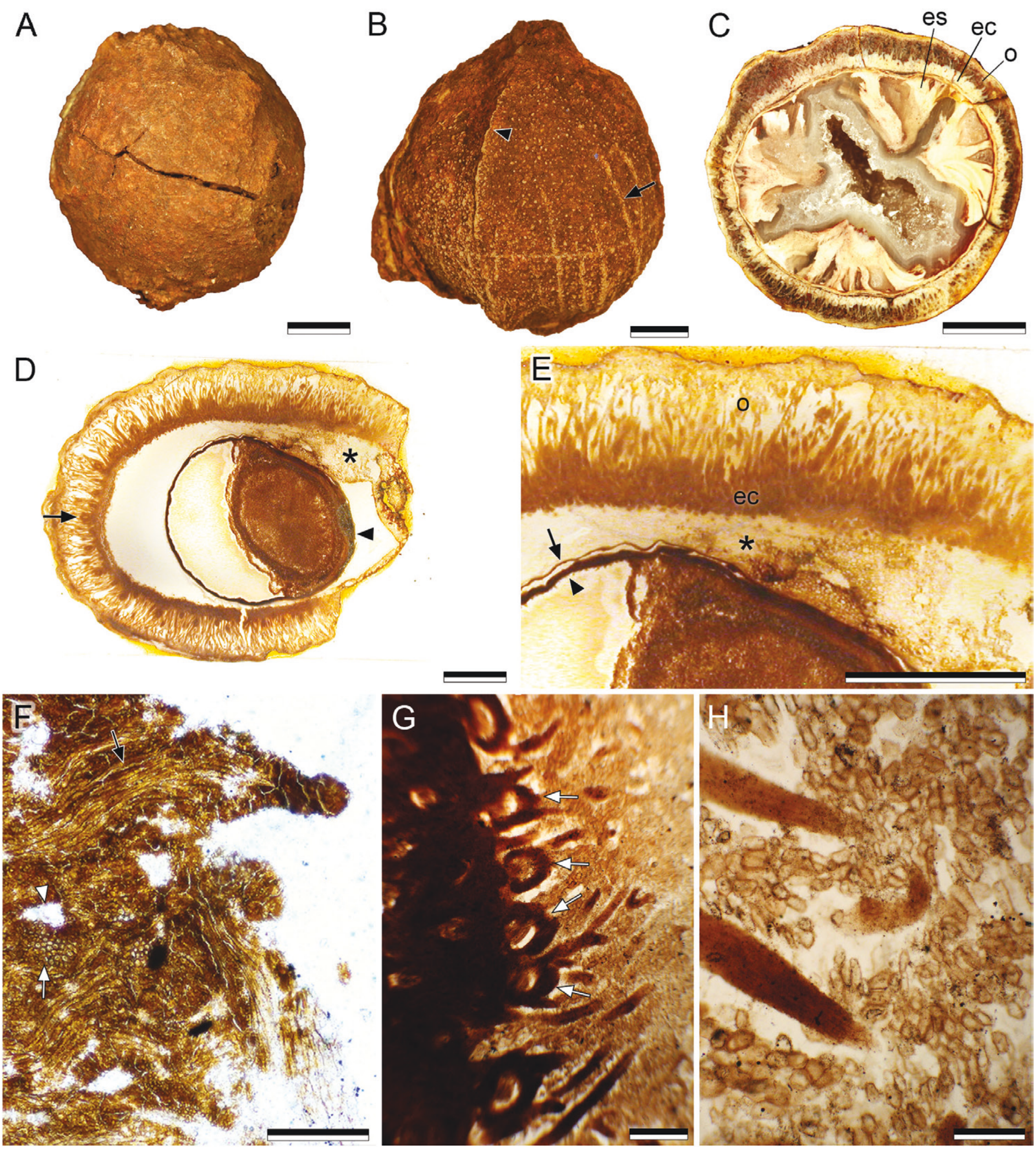


Figure 2. Fruit and pericarp structure of *Hyphaeneocarpon indicum*. A, B, external view of fruits isolated from matrix. The specimen shown in B is missing the outermost pericarp, exposing large longitudinal fibrovascular bundles on endocarp surface (arrow). Note ridge formed by germination pore on upper half of fruit (arrowhead). Specimens UF19415-62614 (A) and UF 19415–69208 (B). Scale bar = 5 mm. C, polished transverse surface section of specimen shown in A. Note endosperm of seed is partially preserved. Specimen UF19415-62614. Scale bar = 5 mm. D, transverse section through holotype of *H. indicum*. Note parenchymatous inner zone of pericarp (asterisk) preserved between the seed (arrowhead) and endocarp, large longitudinal fibrovascular bundles to outside of endocarp (arrow), and relatively large size of specimen. Specimen BSIP 35408 (peel). Scale bar = 5 mm. E, detail of three pericarp layers shown in D. Note that layer interpreted

Information; Guindon *et al.*, 2010; Lanfear *et al.*, 2012, 2017). For comparison, we also ran PartitionFinder2 including all substitution models and found that for some partitions, substitution models not available in MrBayes yielded the highest AICc scores. In most cases these models had comparable AICc scores (ΔAIC < 2), but for two partitions (*matK* positions 1 and 2) the ΔAIC between the best fit and available models was as high as 5. Because the objective of the analysis was to place the fossil in a phylogenetic context, we accepted these higher ΔAIC scores because the difference in substitution models was probably inconsequential relative to our goals. The morphological data were analysed with the MKv model. Across all partitions, the rate prior was set to 'variable' to allow for different relative transition rates (ratepr = variable) and the following model parameters were unlinked: transition/transversion ratio (tratio), substitution rates of the GTR model (revmat), character state frequencies (statefreq), gamma shape parameter (shape) and proportion of invariable sites (pinvar). We used the default settings in MrBayes for all other parameters. Tree searches comprised two independent MCMC runs with four chains each (three hot, one cold), running for 20 million generations and sampling every 100 generations, with burnin left at the default 25%. The standard deviation of split frequencies was < 0.02 when runs terminated, and convergence of MCMC runs was confirmed using Tracer (v.1.6).

RESULTS

SYSTEMATIC PALAEOBOTANY

Arecaceae, subfamily Coryphoideae, tribe Borasseae, subtribe Hyphaeninae

Hyphaeneocarpon Bande, Prakash & Ambwani, emend. Matsunaga, S.Y.Sm., Manch., Srivastava & Kapgate.

Emended generic diagnosis

Fruits globose to slightly oblong, single-seeded, with two abortive carpels basally. Abortive ovules/seeds basally attached in locules. Pericarp with three zones: inner zone parenchymatous, absent at maturity; middle zone of interwoven fibre bundles forming endocarp; outer zone parenchymatous with radially oriented fibre bundles from endocarp. Epicarp thin, smooth. Endocarp enclosing fertile and locules of abortive carpels separately, forming pyrenes; elongate apical germination pore above fertile locule. Seeds with intact seed coat surrounded by the locular epidermis, with prominent basal groove from intrusion of the endocarp. Endosperm homogeneous. Embryo apical. Stigmatic remains basal, near locules of abortive carpels.

Type: Hyphaeneocarpon indicum Bande, Prakash & Ambwani emend. Matsunaga, S.Y.Sm., Manch., Srivastava & Kapgate.

Basionym: Hyphaeneocarpon indicum Bande, Prakash & Ambwani, The Palaeobotanist 30: 307. 1982.

Synonymy: Arecoidocarpon kulkarnii Bonde, Palaeobotanist 38: 213, 1990, *Arecoidocarpon palasundarensis* Bonde, Birbal Sahni Centenary Vol.: 67, 1995, *Pandanusocarpon umariense* Bonde, Proceedings 3IOP Conference, Melbourne 1988: 60, 1990, *Palmocarpon arecoides* Mehrotra, Geophytology 17: 205. 1987.

Holotype: BSIP 35408 (Fig. 2D, E), Bande *et al.*, 1982: figs 1–7.

Other specimens studied: UF19415-69208 (Figs 2B, 5G–I), UF19415-62614 (Figs 2A, C, 3D, E, 5C, D), UF19438-68879 (Figs 3B, 4A, B, F, 5A, B, E, F), UF19329-62153 (Fig. 2F).

Type locality, stratigraphy and age: Shahpura, Mandla District, Madhya Pradesh; Deccan Intertrappean Beds, India, late Maastrichtian–early Danian.

Other occurrences: Dhangaon, Keria, Mohgaonkalan, Palasundar, Umaria; Deccan Intertrappean Beds, India, late Maastrichtian–early Danian.

Emended specific diagnosis: As for genus. Fruits 1.5–4.0 cm long, 1.5–3.0 cm wide. Pericarp up to 9.0 mm

---

as the locular epidermis (arrow) is positioned between inner pericarp and seed coat (arrowhead). Scale bar = 5 mm. F, light micrograph showing endocarp anatomy consisting of interwoven bundles of fibre, visible in longitudinal (black arrow) and transverse sections (white arrow). Note lacunae dispersed throughout this tissue (arrowhead), which may have been filled with parenchyma. Specimen UF19329-62153 (peel). Scale bar = 100 μm. G, light micrograph focused on large longitudinal fibrovascular bundles to outside of endocarp (arrows). Note large size of these bundles relative to endocarp fibre bundles. Specimen ARI 5288 (thin section; *Arecoidocarpon palasundarensis*). Scale bar = 200 μm. H, light micrograph from thin section. Detail of outer pericarp zone showing parenchyma cells and fibre bundles. Specimen ARI 5288 (thin section; *A. palasundarensis*). Scale bar = 200 μm. Abbreviations: es, endosperm; ec, endocarp; o, outer pericarp zone.

thick, thinner at maturity. Inner pericarp zone up to 4.0 mm thick or absent at maturity. Endocarp 0.5–1.5 mm thick, composed of fibre bundles 75–200 µm in diameter; fibre bundles extending into outer pericarp of similar diameter. Individual fibres *c.* 8–12 µm in diameter. Parenchyma cells of outer pericarp zone isodiametric to elongate, up to 50 µm wide and 100 µm long. Seeds *c.* 9–11 mm in diameter.

Description

The fruits are globose to subglobose and range from *c.* 1.5 to 2.5 cm in diameter (Fig. 2A–D). Fruits collected from the Mohgaonkalan and Keria localities tend to be smaller, *c.* 1.5 cm wide, whereas those from other localities tend to be larger. Fruit sizes for new material and published specimens are summarized in Table 1.

The pericarp ranges in thickness from *c.* 2.0 to 9.0 mm. The large variation results from a combination of the size of the fruits, developmental stage and taphonomic factors such as dehydration or compression. The pericarp can be divided into three zones that probably correspond to the mesocarp, although developmental stages needed for determining exact homology are not preserved. We recognize an ephemeral inner parenchymatous zone, a sclerenchymatous middle zone, and an outer zone of radial fibre bundles and parenchyma (Fig. 2E–H). Additionally, to the inside of the pericarp there is a thin layer associated with the seed coat that is probably the locular epidermis. To the outside a thin epicarp is sometimes preserved.

The inner zone is variable in thickness (up to 4.0 mm) and consists of thin-walled parenchyma cells (Fig. 2E). This tissue is only clearly visible in one specimen, but remnants of it are present in most other well-preserved specimens between the middle pericarp layer and the locular epidermis. It probably represents a tissue present only in immature fruits, a feature common in some groups of palms (see discussion section 'Taxonomic affinities inferred from fruit morphology'; Romanov *et al.*, 2011). Note that the fruit with the thickest documented pericarp (9.0 mm at the widest point) is preserved at a developmental stage in which this inner layer is still prominent; this fruit is also probably somewhat compressed and possibly somewhat obliquely sectioned, probably exaggerating thickness on some axes.

The middle zone is composed of densely interwoven bundles of fibres that form a thick, sclerenchymatous layer (Figs 2C–F, 3D, G). Conventionally, most of the literature on palms refers to any hard inner layer of the fruit as an endocarp. We follow this convention here, noting that the developmental origin of the endocarp is variable in the family and can be derived from the locular epidermis, various regions of the mesocarp or both (Murray, 1973; Bobrov *et al.*, 2012b). In these fossils the functional 'endocarp' originates from the mesocarp; evidence for this is based on a thick zone of parenchyma to the inside of the sclerenchymatous 'endocarp' in some stages of development (the 'inner zone' described above). Individual fibres of the endocarp are *c.* 8.0–12.0 µm in diameter, with narrow lumina, and form thick bundles *c.* 50–100 µm wide (Fig. 2F). Small lacunae are sometimes present in between some of the fibre bundles of the endocarp, which may have been occupied by parenchyma cells as documented by Bonde (1995). To the outside of the endocarp is a single ring of large fibrovascular bundles, which run longitudinally from the base of the fruit to the apex (Fig. 2D, G). These fibrovascular bundles directly abut the endocarp and sometimes appear partially embedded in it. In specimens for which the outer layer of the pericarp is not preserved, these bundles can be clearly seen on the surface of the endocarp (Fig. 2B).

Some fibre bundles of the endocarp extend radially into the outer zone of the pericarp, oriented perpendicular to the outer surface of the fruit (Figs 2C, D, 3D). This outer zone is otherwise parenchymatous, consisting of thin-walled cells that are elongate to nearly isodiametric, up to 50 µm wide and 100 µm long (Fig. 2H). The epicarp is thin, membranous and typically poorly preserved.

Seeds are globose, 9.0–11.0 mm in diameter, with a basal indentation corresponding to an inward protrusion of the endocarp (Fig. 3A–C). Several large fibro-vascular bundles run vertically through this protrusion to vascularize the seed, indicating that seeds are basally attached within fruits (Fig. 3B, C). In many palms, ovule placentation in the ovary may differ from the seed attachment observed in mature fruits and thus seed attachment should not be used to infer ovule placentation (Dransfield *et al.*, 2008). The densely interwoven fibres of the endocarp form part of this protrusion. At the periphery of each seed two membranous layers are seen: the inner one constituting the seed coat itself and the outer one representing the locular epidermis of the fruit (Fig. 3D, E). The seed coat and locular epidermis are both thin and too poorly preserved to resolve anatomical details. The endosperm is homogeneous (non-ruminate); i.e. it lacks deep invaginations of the seed coat seen in some palms (Fig. 3F). Embryos, when preserved, are positioned apically within the seed (Fig. 3G). Anatomical preservation of embryos is insufficient to resolve additional details.

The µCT scanning revealed that each fruit has two abortive carpels represented by small locules at the extreme base, just above the remnants of the perianth (Fig. 4). In one specimen the locules contain

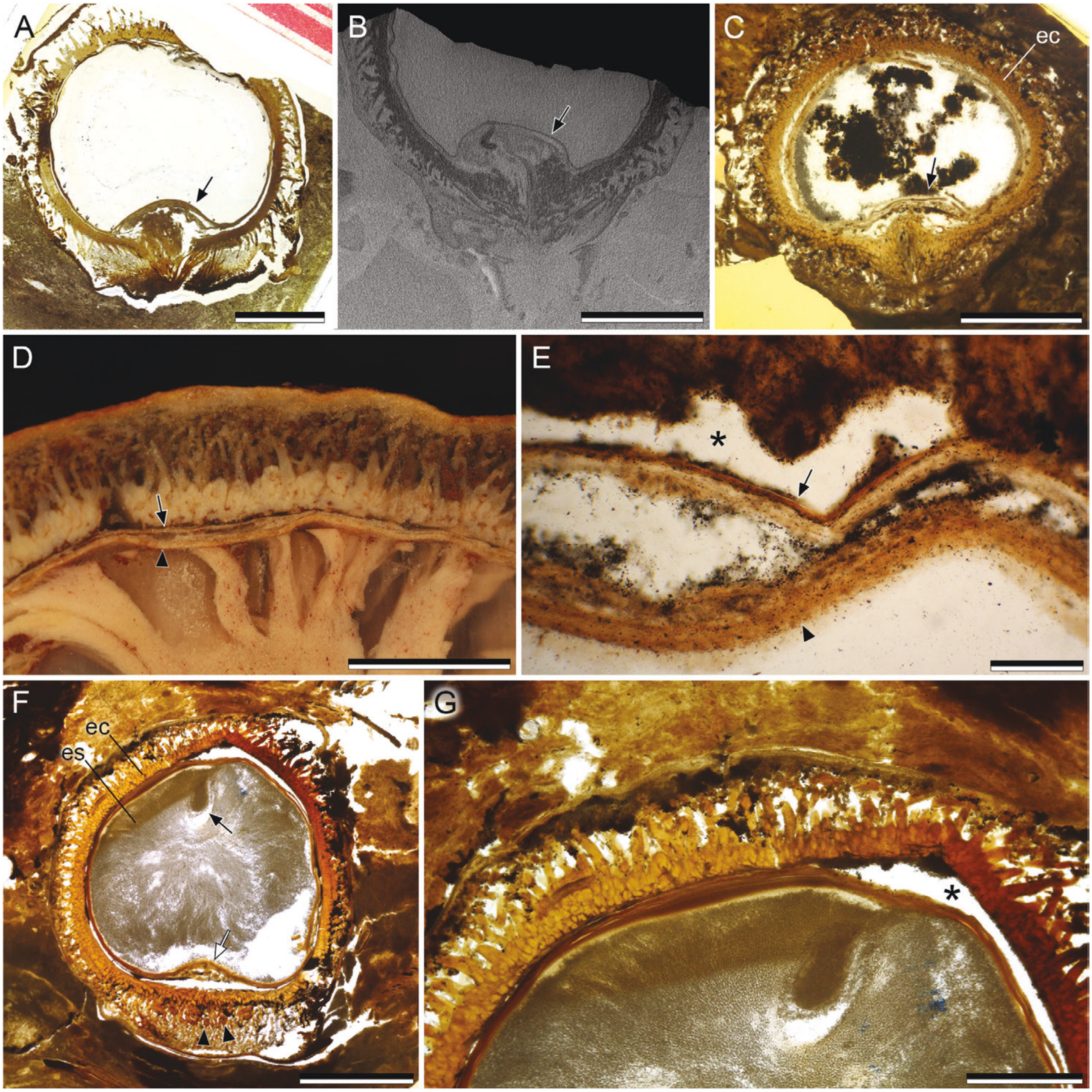


Figure 3. Seed structure of *Hyphaeneocarpon indicum*. A–C, longitudinal sections showing basal intrusion of pericarp into seed (arrows). Specimen in B is a digital longitudinal section from a µCT scan, while A and C are light micrographs of thin sections. Specimens ARI 5288 (thin section; *Arecoidocarpon palasundarensis*) (A), UF19438-68879 (B), ARI 5285 (thin section; *Arecoidocarpon kulkarnii*) (C). Scale bars = 5 mm. D, detail of fruit in Figure 2C in which pericarp and part of seed are preserved. Note two layers surrounding endosperm: outer, locular epidermis (arrow), inner, seed coat (arrowhead). Specimen UF19415-62614. Scale bar = 2 mm. E, detail of locular epidermis (arrow) and seed coat (arrowhead). Preservation of this specimen is not sufficient to determine anatomical composition of these tissues. Note that the locular epidermis and seed coat are pulled away from the endocarp in E and G, leaving a gap (asterisk). ARI 5288 (thin section; *A. palasundarensis*). Scale bar = 250 µm. F, G, fruit with entire seed preserved, including endosperm and embryo (black arrow). Edge of basal protrusion is captured in plane of section (white arrow) and several longitudinal vascular bundles are seen in transverse section (arrowheads). Specimen ARI 5285 (thin section; *A. kulkarnii*). Scale bar = 5 mm. Abbreviations: es, endosperm; ec, endocarp.

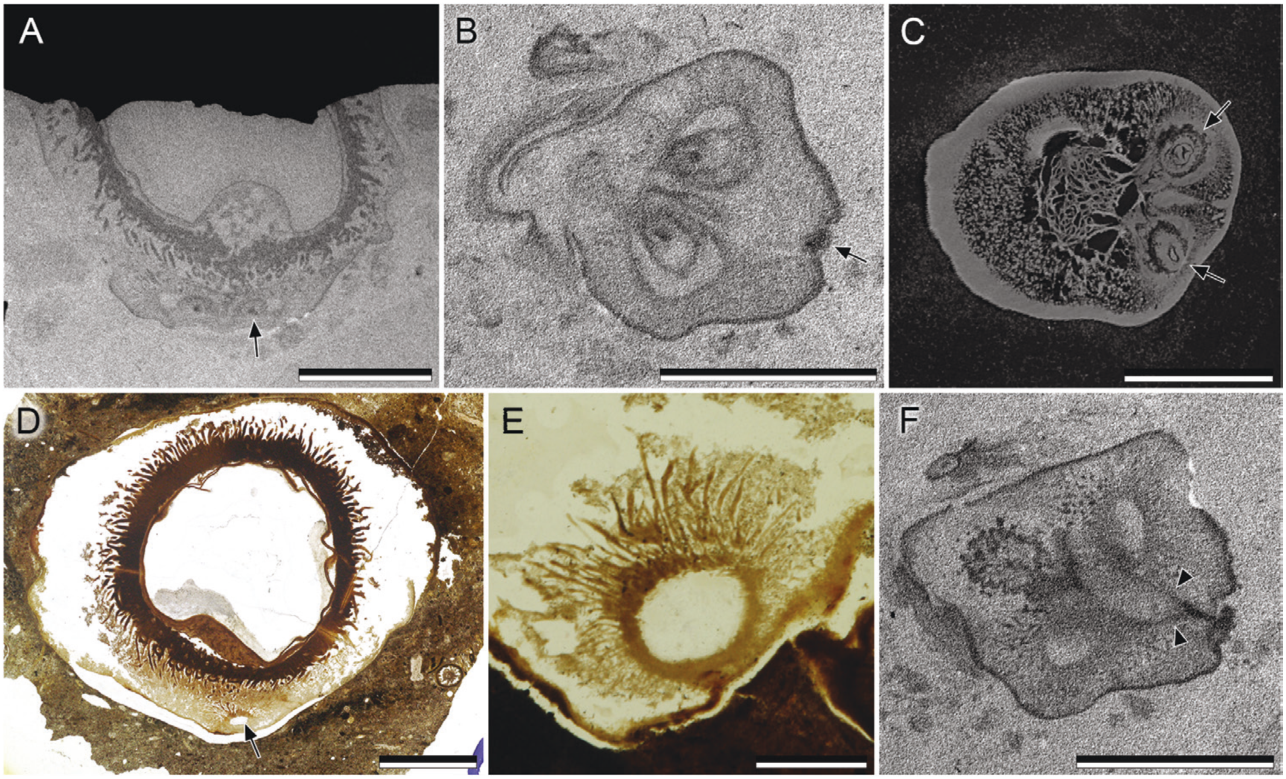


Figure 4. Abortive carpels of *Hyphaeneocarpon indicum*. A, digital longitudinal section of fruit showing two locules of aborted carpels below fertile locule (arrow). Each locule contains an ovule or abortive seed. Specimen UF 68879. Scale bar = 5 mm. B, digital transverse section through locules of abortive carpels in fruit shown in A. Note indentation on edge of fruit (arrow) corresponding to stigmatic remains seen more clearly in F. Specimen UF 68879. Scale bar = 5 mm. C, digital transverse section through the base of an extant *Bismarckia nobilis* fruit with two abortive carpels (arrows), for comparison with *Hyphaeneocarpon*. Note presence of thin endocarp around each locule. Scale bar = 5 mm. D, light micrograph of thin section in which the locule of an abortive carpel is visible at the base of the fruit, below the fertile locule (arrow). Specimen ARI 5288 (thin section; *Arecoidocarpon palasundarensis*). Scale bar = 5 mm. E, detail of abortive locule seen in D from another section in same series. Note endocarp structure, from which thin fibre bundles radiate, which is identical to that of fertile locules. Specimen ARI 5288 (thin section; *A. palasundarensis*). Scale bar = 5 mm. F, digital longitudinal section through base of fruit shown in A and B. Plane of section passes through two locular canals extending to surface of fruit (arrowheads), indicating position of stigmatic remains. Specimen UF 68879. Scale bar = 5 mm.

ovules or abortive seeds, which appear to be attached basally (Fig. 4A, B). Each locule is surrounded by a layer of small, interwoven fibre bundles, with some fibre bundles radiating outwards in a pattern identical to the fertile locule (Fig. 4C, D). This feature indicates that the endocarp encloses each seed separately (forming multiple pyrenes), rather than forming a continuous tissue around all locules. Although each locule has a separate endocarp, the outer parenchymatous zone is continuous between the fertile and abortive locules. Together these features indicate that the fruits developed from flowers with three fused carpels at maturity and were not apocarpous or pseudomonomerous like some modern palms.

Although surficial remnants of the stigma are not clearly visible on the external surface of fruits, serial digital sections were used to detect remnants of locular canals and infer the position of stigmatic remains. In digital transverse sections of the specimen with well-preserved abortive carpels, we observed thin channels connecting the locules of the aborted carpels to the external surface of the fruit; these channels converge just below the epidermis (Fig. 4E). Similar channels can be seen in fruits of many extant species connecting the locules to the stigmatic remains (K. K. S. Matsunaga, pers. obs.). The position of these channels indicates that the fruits have basal stigmatic remains.

At the apical end of each fruit the endocarp forms a long ridge with a narrow gap at the apex that spans approximately one-third of the circumference of the fruit (Fig. 5A–F). This structure is consistently observed in the fruits and its position relative to the embryo suggests it is an apical germination pore.

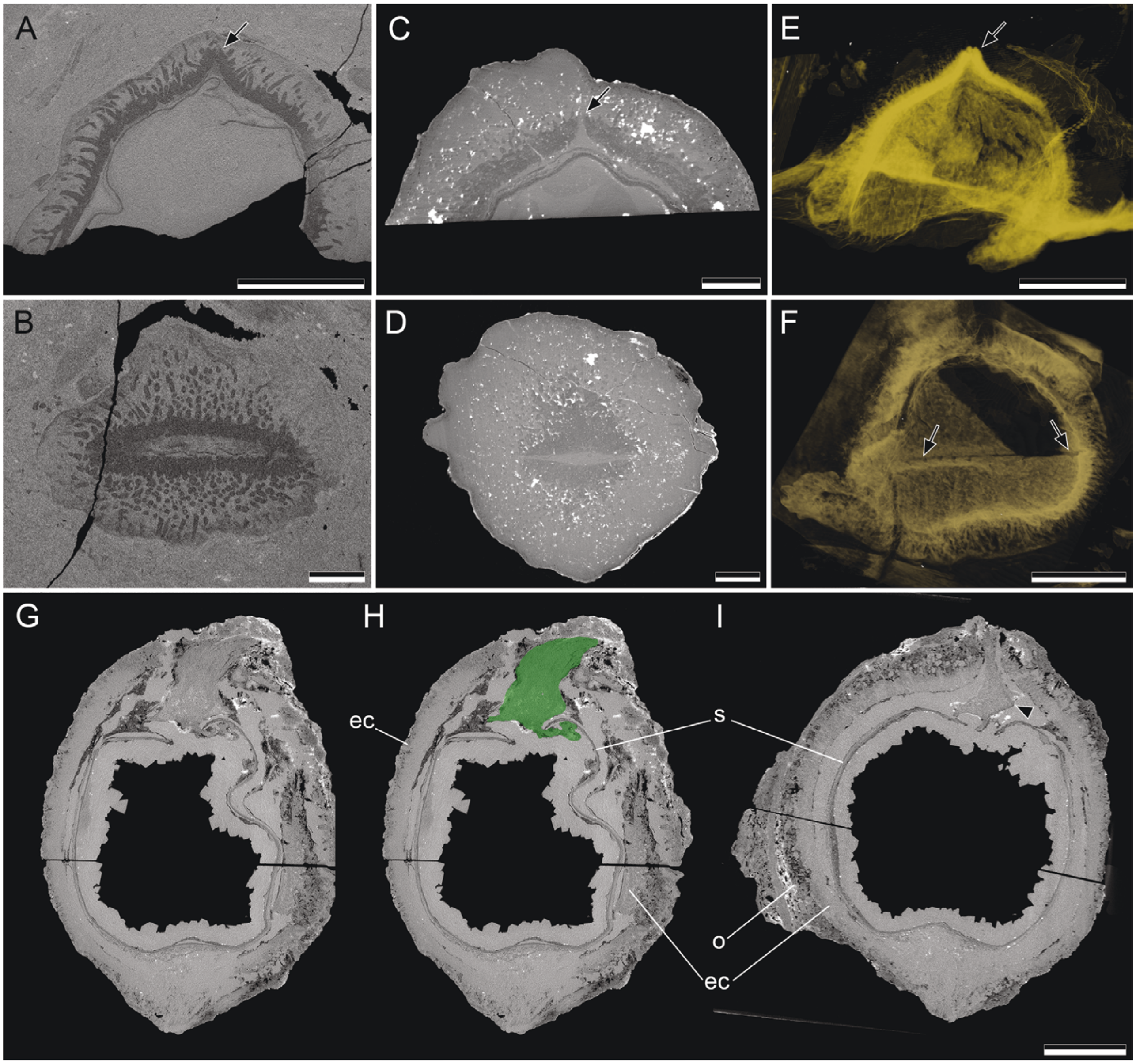


Figure 5. Germination pores of *Hyphaeneocarpon indicum*. A–F, endocarp germination pores (arrows) seen in digital longitudinal (A, C) and corresponding transverse sections (B, D) and from lateral and apical perspectives of volume-rendered specimen (E, F). Note narrow, elongate shape of pore seen in transverse section (B, D), prominent ridge it forms (E), and length of pore revealed by volume rendering, showing pore extending nearly half of fruit circumference (F). G, H, digital longitudinal section through fruit shown in Figure 2A, revealing preserved seedling highlighted in green in H. Tissues of seedling can be traced to inside seed coat (arrow). Note that much of outer pericarp is not preserved and that part of endocarp is broken on the right-hand side of the section. Specimen UF 19415–69208. I, longitudinal section of specimen shown in G and H, rotated 90° to show germination pore through which seedling (arrowhead) protrudes. Scale bar = 5 mm. Abbreviations: ec, endocarp; s, seed coat; o, outer pericarp zone.

One specimen with an attached seedling preserved confirms this (Fig. 5G–I). The specimen consists of an isolated fruit with part of the pericarp missing on one side, exposing the endocarp. The centre of the seed is hollow and only the seed coat is preserved. Digital longitudinal sections reveal a structure protruding from the top of the fruit, through the aperture in the endocarp. The structure is laterally flattened (Fig. 5I), conforming to the elongate shape of the germination pore, and contains longitudinal strands probably representing vascular tissues or fibres. Although the seed is poorly preserved, tissues of the seedling can be traced to the inside of the seed coat. Mode of germination, whether remote tubular, remote ligular or adjacent ligular, could not be determined.

PHYLOGENETIC ANALYSIS

The 50% majority rule consensus tree summarizing the posterior distribution of our analysis is well resolved and generally conforms to previously published trees, with some differences (see Discussion). Borasseae are resolved as monophyletic (posterior probability = 1), with *Hyphaeneocarpon* nested in subtribe Hyphaeninae with strong support (posterior probability = 0.99). In Hyphaeninae, *Hyphaeneocarpon* forms a clade with the extant genera *Bismarckia* Hildebr. & H.Wendl. and *Satranala* J.Dransf. & Beentje (posterior probability = 0.93) that is sister to *Hyphaene* Gaertn. and *Medemia* Württemb. ex H.Wendl. In this tree, *Hyphaeneocarpon* is most closely related to *Satranala*, support for which is low compared to other nodes, but moderate for a relationship based solely on morphological characters (posterior probability = 0.53).

DISCUSSION

JUSTIFICATION FOR SYNONYMY OF SPECIES

Several characters shared by the new specimens and the five previously described fossil species indicate they most probably represent occurrences of a single species (Table 1). These characters include: (1) endocarp consisting of interwoven fibre bundles; (2) a single layer of large longitudinal fibro-vascular bundles to the outside of the endocarp; (3) fibre bundles that radiate from the endocarp into the outer, parenchymatous zone of the mesocarp; (4) a prominent basal protrusion of the pericarp into the seed; and (5) a thin seed coat attached or appressed to locular epidermis (sometimes described as a two-layered seed coat). Other characters that are important but not documented in all specimens include the apical embryo, apical germination pores, seedlings, abortive carpels and the inner zone of parenchyma in the pericarp. The variability in observation of these features is due to differences in development, preservation quality or the methods used to study specimens. With respect to study methods, some characters may be present in the previously described species, particularly the abortive carpels, germination pore and large longitudinal bundles, but are not documented because visualizing them requires specific planes of section that are easy to acquire with μCT data but are generally not feasible using physical sectioning techniques.

The five diagnostic characters listed above are all present in the recently collected Keria and Dhangaon specimens and in the previously published specimens attributed to *Arecoidocarpon kulkarnii* (Bonde, 1990a; Fig. 3C, F, G), *A. palasundarensis* (Bonde, 1995; Figs 2G, H, 3A, E, 4D, E) and *Pandanusocarpon umariense* (Bonde, 1990b). In addition, we observed abortive carpels and germination pores in specimens of *A. palasundarensis* not shown in the original published images. *Hyphaeneocarpon indicum* was described from a single specimen, from which one transverse section was taken (Bande *et al.*, 1982; Fig. 2D, E). All of the key characters were documented, except the basal protrusion of the pericarp (the physical section did not pass through the base of the fruit). *Palmocarpon arecoides* (Mehrotra, 1987) is also described from a single specimen and is the least thoroughly described example. The features that indicate *P. arecoides* is probably conspecific with the aforementioned taxa are similarities in the size of the fruits, the presence of a basal protrusion of the pericarp into the seed, and the overall structure of the pericarp consisting of an inner sclerified layer and an outer parenchymatous layer containing fibre and fibrovascular bundles. The orientation of the fibre bundles in the outer layer is not clear from the published descriptions and images, overall preservation of the fruits is poor, and we were unable to examine or obtain new images of the original specimens. Despite this, we include *P. arecoides* in synonymy with the other species owing to the presence of the basal protrusion and the general structure of the pericarp.

Based on these morpho-anatomical similarities and considerations described above, we treat *Arecoidocarpon kulkarnii*, *A. palasundarensis*, *Hyphaeneocarpon indicum*, *Palmocarpon arecoides*, *Pandanusocarpon umariense* and the new specimens from Dhangaon and Keria as conspecific. We have included them here in the synonymy presented for *Hyphaeneocarpon indicum* Bande, Prakash & Ambwani emend. Matsunaga, S.Y.Sm., Manch., Srivastava & Kapgate, based on the first name to be validly published. Another species, *Palmocarpon insigne* Mahabale from Mohgaonkalan (Mahabale, 1950), appears similar to *Hyphaeneocarpon indicum* and is also probably conspecific. However, it lacks nomenclatural priority, because it was never validly published, and we do not include it in synonymy with the other species because the illustration and description lack sufficient detail to identify it unequivocally as *Hyphaeneocarpon*, and we were unable to locate the original specimen.

Table 1. Comparison of described species and new specimens included in synonymy as *Hyphaenocarpon indicum*

Species	Locality	Size (cm; length × width)	Endocarp: interwoven fibre bundles	Pericarp: longitudinal vascular bundles	Pericarp: radial fibre bundles	Embryo or seedling	Abortive locules	Basal intrusion of endocarp	Evidence of germination pore
Arecoidocarpon kulkarnii Bonde, 1990a	Mohgaonkalan	1.6 × 1.4	+	+	+	+	–	+	+
Arecoidocarpon palasundarensis Bonde, 1995	Palasundar	2.0 × 2.2	+	+	+	–	+	+	+
Hyphaeneocarpon indicum Bande *et al.*, 1982	Shahpura	4.0 × 2.3–3.2	+	+	+	–	–	–	–
Palmocarpon arecoides Mehrotra, 1987	Samnapur	≥2.0 × 2.2–2.3	?	?	?	–	–	+	–
Pandanusocarpon umariense Bonde, 1990b	Umaria	2.1–2.5 × 1.8–2.0	+	+	+	–	–	+	+
New specimen	Keria	≥1.0 × ≥1.3	+	+	+	–	–	+	+
New specimens	Dhangaon	1.7–2.3 × 1.5–≥2.0	+	+	+	+	?	+	+
New specimen	Mohgaonkalan	*c.* 2.0 × 1.4	+	+	+	–	+	+	+

Important features for recognizing synonymy and for systematic placement are listed, including pericarp structure, embryo position and germination pores. Fruit size is also included to show the range of fruit sizes observed in the different specimens. For some specimens, exact height and width were difficult to determine, as the outer pericarp is frequently missing or partially preserved (indicated by ≥). The symbol '+' denotes a feature that was observed in published descriptions, figures or in the actual specimen. '–' indicates a character either not preserved or not observed in the available preparations of the specimen (e.g. only one or a few sections made). '?' was used in situations where a feature could not be observed due to insufficient detail in published descriptions and/or relevant material not being available for study.

VARIATION IN FRUIT SIZE

Fruits exhibit considerable variation in size between the different localities (Table 1). The smallest specimens are from the Keria and Mohgaonkalan localities (*c*. 1.5 cm), whereas the largest is the type specimen of *Hyphaeneocarpon indicum* from Shahpura. The latter was described as *c*. 4.0 cm long and 3.2 cm in diameter at the widest point, but the fruits are somewhat compressed, which may exaggerate the size measurements. Most fruits are *c*. 2.0–2.5 cm in diameter. We do not consider the size variation to be grounds for recognizing two different species, because there is no strong bimodal pattern in fruit size, and we have not found any characters that distinguish the smaller specimens from Keria and Mohgaonkalan from the others. In modern palms fruit size does sometimes vary between species, but it can also vary within and between individuals. Moreover, disparity in fruit size of the fossils may reflect developmental, preservational or local environmental differences. Among palms, fruit size tends to increase as the seed matures and the endosperm transitions from a free-nuclear to a cellular phase (DeMason, Sekhar & Harris, 1989), and therefore some of the size variation could reflect fruit maturity. However, this does not fully explain the range in observed fruit size because some of the smaller specimens appear to have mature seeds (Fig. 3F), whereas the largest specimen is probably slightly immature (Fig. 2D; see below). Temporal differences could also account for this variation, as the Mohgaonkalan and Keria localities are part of the Deccan Main Plateau and currently are considered late Maastrichtian, whereas the other localities are all in the eastern Mandla subprovince and are probably early Danian; so far, *Hyphaeneocarpon indicum* is the only plant species known to occur at localities in both regions. It is therefore possible that the smaller size of some fruits is related to environmental or other biotic changes that occurred over the K-Pg boundary in India, but this would need to be tested further.

TAXONOMIC AFFINITIES INFERRED FROM FRUIT MORPHOLOGY

Owing to significant morphological diversity among palm fruits, there are few clear characters with which palm fruits can be universally recognized. However, the following characters of the fossils strongly indicate relationships with Arecaceae: fruits indehiscent, single-seeded, derived from three fused uni-ovulate carpels (one of which forms the mature fruit), presence of albuminous seeds with small conical embryos, and a pericarp with a sclerenchymatous endocarp and longitudinal fibrovascular bundles (Dransfield *et al.*, 2008; K. K. S. Matsunaga pers. obs.). Several additional key characters are present that constrain the probable affinities of the fossil taxon to subfamily Coryphoideae, tribe Borasseae, subtribe Hyphaeninae: (1) syncarpous gynoecium with three carpels; (2) fruit single-seeded, derived from one of the carpels; (3) pericarp with a thick zone of parenchyma to the inside of the endocarp in some developmental stages; (4) endocarp composed of interwoven fibre bundles that radiate into outer parenchymatous zone of pericarp; (5) embryo apical; (6) apical germination pore in endocarp; and (7) basal stigmatic remains (Dransfield *et al.*, 2008; Romanov *et al.*, 2011).

Gynoecium structure and development are variable among modern palms, but the most prevalent and likely ancestral condition is for the gynoecium to be syncarpous and trimerous at anthesis (Moore & Uhl, 1982; Dransfield *et al.*, 2008). However, some palms consistently produce more than three carpels (e.g. Phytelepheae), several genera of coryphoid palms have only a single carpel (most Cryosophileae) and many members of Arecoideae are pseudomonomerous, with two of the carpels aborting usually early in floral development (e.g. tribes Areceae and Euterpeae). In most genera that have three carpels at anthesis only one of the seeds matures; in some of these taxa the abortive carpels are obvious in mature fruits, forming basal bulges or protuberances (e.g. *Hyphaene*, *Bismarckia*). Therefore, despite the basic condition being trimery of the gynoecium, palm fruits are most commonly single-seeded (Moore & Uhl, 1982; Dransfield *et al.*, 2008).

The fossils of *Hyphaeneocarpon* have a gynoecium of three carpels, two of which are abortive but easily seen at the base of mature fruits. This indicates that *Hyphaeneocarpon* is unlikely to belong to a group of palms that are either pseudomonomerous or unicarpellate. The inner layer of parenchyma between the endocarp and seed (Fig. 2D, E) helps to further refine potential affinities. This tissue is found in fruits of many modern members of Coryphoideae and in *Nypa* Steck (Nypoideae) and *Eugeissona* Griff. (Calamoideae; Romanov *et al.*, 2011; Bobrov *et al.*, 2012a, b). In such fruits, this inner layer is initially thick but compresses as the seed matures during the final phases of fruit development; on reaching maturity the seed completely displaces the parenchyma and fills the entire space within the endocarp. Furthermore, this inner parenchyma is not present in other taxa with thick endocarps such as Cocoseae, in which the endocarp develops from the innermost layers of the pericarp (Dransfield *et al.*, 2008; Bobrov *et al.*, 2012b). The ephemeral nature of this tissue helps to explain why we did not observe it in most specimens (e.g. Figs 2C, 3F) and why the locular epidermis is often pulled away from the endocarp in mature fruits

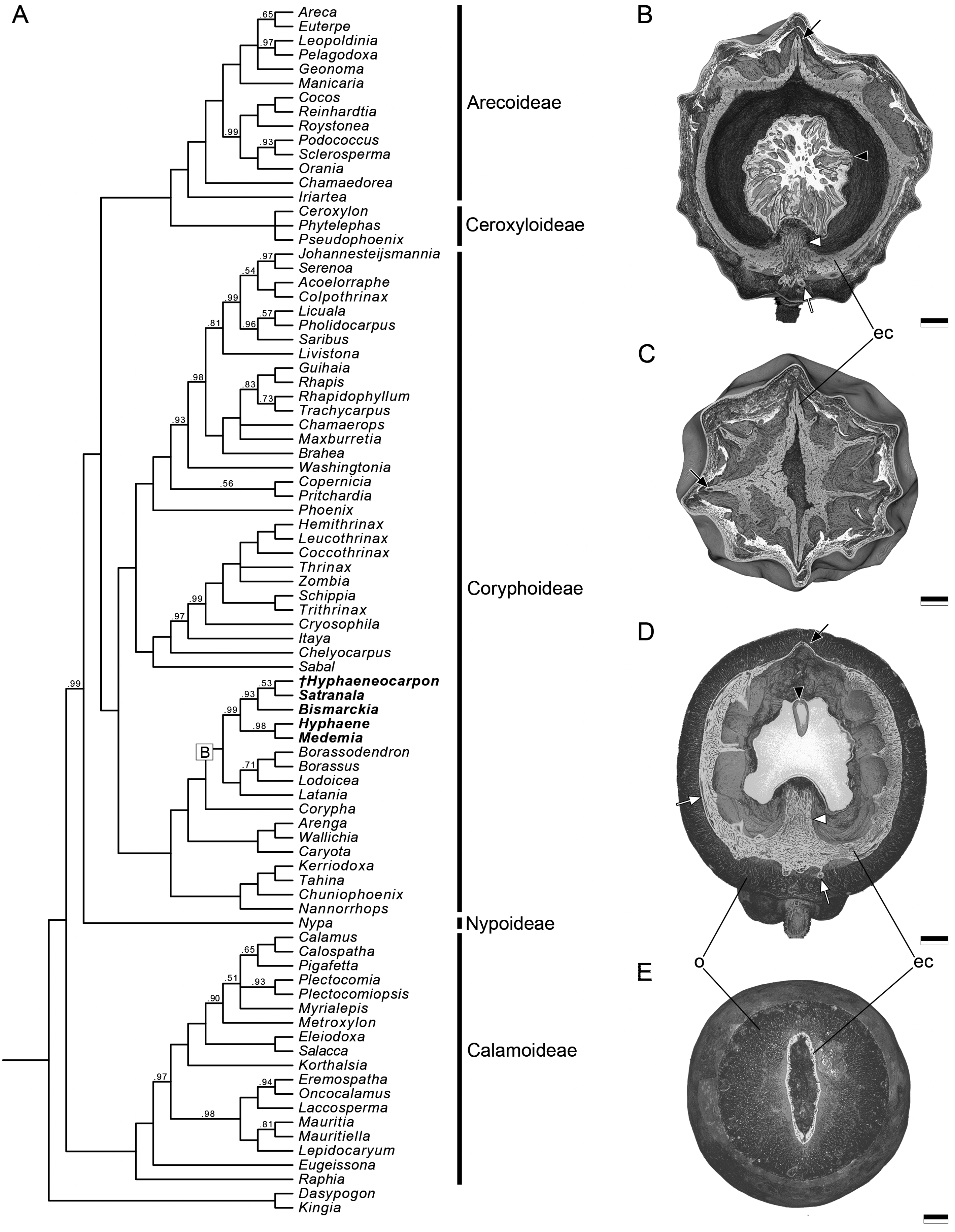
(Fig. 3E, G). Among palms that exhibit this inner parenchyma, affinities with Coryphoideae are most likely. Fruits of *Nypa* and *Eugeissona* are highly distinctive and inconsistent with the morphology of the *Hyphaeneocarpon* fossils. *Nypa* fruits are derived from an apocarpous gynoecium and have an obovate, angular shape related to their dense aggregation in globose heads (Bobrov *et al.*, 2012b). *Eugeissona* and all modern Calamoideae have an epicarp composed of helically arranged imbricate scales, a character not present in these fossils (Dransfield *et al.*, 2008; Bobrov *et al.*, 2012a). Other features including gynoecium morphology and the positions of stigmatic remains, embryo and germination pore make affinities with *Eugeissona* or *Nypa* highly unlikely.

Subfamily Coryphoideae comprise two clades: the ‘syncarpous clade’ and a second group containing *Sabal* Adans., *Phoenix* L., and tribes Cryosophileae and Trachycarpeae, all of which are apocarpous except for *Sabal* (Fig. 6A; Dransfield *et al.*, 2008; Baker *et al.*, 2009; Faurby *et al.*, 2016). The syncarpous condition of *Hyphaeneocarpon* is consistent with the syncarpous clade, which includes 16 genera in four tribes: Caryoteae, Chuniophoeniceae, Corypheae and Borasseae. Among these tribes, only Borasseae have thick endocarps composed of interwoven fibre bundles, apical embryos and apical germination pores consisting of thin zones of the endocarp (Dransfield *et al.*, 2008; Romanov *et al.*, 2011). Borasseae include eight genera in two subtribes: Hyphaeninae (*Hyphaene*, *Bismarckia*, *Medemia* and *Satranala*) and Lataninae (*Latania* Comm. ex Juss., *Lodoicea* Comm. ex DC., *Borassus* L. and *Borassodendron* Becc.). Members of Lataninae produce three-seeded fruits, although seed number in *Lodoicea* is variable, with each seed surrounded by a separate endocarp, forming pyrenes. Stigmatic remains are consistently apical. In contrast, fruits of Hyphaeninae are typically single-seeded, with the abortive carpels forming bulges at the base of the fruit (Fig. 6D); sometimes, more than one seed develops, producing a deeply lobed fruit resembling two smaller ones conjoined at the base. Stigmatic remains are basal in Hyphaeninae. Fossils of *Hyphaeneocarpon*, which are single-seeded with basal stigmatic remains, are therefore much more similar to Hyphaeninae than to Lataninae.

Several other characters of *Hyphaeneocarpon* are also seen in Hyphaeninae. (1) the pericarp of both *Bismarckia* and *Hyphaene* has fibre bundles that extend radially from the endocarp into a predominantly parenchymatous zone of the pericarp (Fig. 6D). (2) In *Bismarckia* and *Satranala* fruits, the endocarp protrudes into the base of the seed (Fig. 6B–E). (3) The germination pores of *Bismarckia* and *Satranala* are elongate and form a ridge, rather than being circular as in other members of Borasseae (note: germination pores in *Medemia* also appear to be slightly elongate, but do not form a ridge; Fig. 6B–E). This ridge is much shallower and broader in *Bismarckia* than in *Satranala* or *Hyphaeneocarpon*. In *Satranala* the ridge runs around much of the circumference of the fruit, and instead of germinating through the pore, the endocarp splits to release the entire seed; among palms this germination mode is unique to *Satranala* (Dransfield *et al.*, 2008). (4) In *Bismarckia* and *Satranala* there is a single layer of large longitudinal fibrovascular bundles in the outermost zone of the endocarp. In *Bismarckia* these bundles are visible in longitudinal and transverse sections through the endocarp (Fig. 6D), whereas in *Satranala* the bundles form the crests of the longitudinal ridges of the endocarp, as seen in transverse section (Fig. 6C). Based on these features, *Hyphaeneocarpon* is much more similar to *Satranala* and *Bismarckia* than it is to *Hyphaene* and *Medemia*. However, one notable difference is the absence of sculpturing in *Hyphaeneocarpon* endocarps; the endocarp is smooth, lacking the deep ridges formed externally in *Satranala*, or protruding internally into the seed as in *Bismarckia* (Fig. 6B, D). Overall, all the characters described above indicate strongly that the *Hyphaeneocarpon* fossils have close affinities with Hyphaeninae. This is congruent with the conclusions of Bande *et al.* (1982), who, in their original description of *H. indicum*, placed it in Hyphaeninae based on similarities in pericarp anatomy, notably the presence of parenchyma to the inside of the endocarp. Although Bande *et al.* (1982) thought it more closely resembled *Hyphaene*, our comparisons based on additional specimens and several new characters suggest greater similarity with *Bismarckia* and *Satranala*, the latter of which was not discovered until 1995 (Dransfield & Beentje, 1995).

PHYLOGENETIC ANALYSIS

We conducted a phylogenetic analysis to test the systematic relationships of *Hyphaeneocarpon* among palms and to obtain complementary information about its phylogenetic position. In our analysis *Hyphaeneocarpon* is positioned in Hyphaeninae, forming a well-supported clade with the extant genera *Satranala* and *Bismarckia*. This clade is united by the following morphological synapomorphies, the first two of which were scored in the morphological matrix: (1) presence of an elongate germination pore or valve that usually forms a ridge; (2) endocarp that protrudes into the seed basally, forming a distinctive groove; and (3) a single layer of large longitudinal fibrovascular bundles embedded in the endocarp. Furthermore, *Hyphaeneocarpon* resolves as sister to *Satranala* with moderate support given the limited morphological characters scored (posterior probability = 0.53).


A
.65
Areca
Euterpe
.97
Leopoldinia
Pelagodoxa
Geonoma
Manicaria
Cocos
Reinhardtia
.99
Roystonea
.93
Podococcus
Sclerosperma
Orania
Chamaedorea
Iriartea
Arecoideae
Ceroxylon
Phytelephas
Pseudophoenix
Ceroxyloideae
.97
Johannesteijsmannia
.54
Serenoa
Acoelorraphe
.99
Colpothrinax
.57
Licuala
.81
.96
Pholidocarpus
Saribus
Livistona
Guihaia
.98
.83
Rhapis
.73
Rhapidophyllum
Trachycarpus
.93
Chamaerops
Maxburretia
Brahea
Washingtonia
.56
Copernicia
Pritchardia
Phoenix
Hemithrinax
Leucothrinax
Coccothrinax
Thrinax
Zombia
.99
Schippia
Trithrinax
.97
Cryosophila
Itaya
Chelyocarpus
Sabal
Coryphoideae
.99
.53
†Hyphaeneocarpon
.93
Satranala
.99
Bismarckia
.98
Hyphaene
Medemia
B
Borassodendron
.71
Borassus
Lodoicea
Latania
Corypha
Arenga
Wallichia
Caryota
Kerriodoxa
Tahina
Chuniophoenix
Nannorrhops
Nypa
Nypoideae
Calamus
.65
Calospatha
Pigafetta
.51
.93
Plectocomia
Plectocomiopsis
.90
Myrialepis
Metroxylon
Eleiodoxa
Salacca
Korthalsia
Calamoideae
.97
.94
Eremospatha
Oncocalamus
.98
Laccosperma
.81
Mauritia
Mauritiella
Lepidocaryum
Eugeissona
Raphia
Dasypogon
Kingia
B
ec
C
D
o
ec
E

However, we consider this relationship highly uncertain, as the *Hyphaeneocarpon–Satranala–Bismarckia* group collapsed into a polytomy in some iterations of our analysis. Moreover, the vegetative morphology of *Hyphaeocarpon* is currently unknown and therefore it is possible its phylogenetic position could change with the addition of more characters such as those of the stems and leaves. Nevertheless, we consider *Hyphaeneocarpon* to be a reliable fossil for calibrating the crown group of Hyphaeninae in future dating analyses. Although *Hyphaeneocarpon* might be used to calibrate divergence of *Satranala* and *Bismarckia*, we feel there is too much uncertainty in the relationships between the three genera to justify using *Hyphaeneocarpon* as a calibration for that node. In contrast, there is little uncertainty in the position of *Hyphaeneocarpon* in the crown group of Hyphaeninae and we feel it would be appropriate as a crown node calibration for the subtribe, with an age of 67–64 Ma.

The overall topology recovered in our analysis is consistent with those of previously published phylogenetic trees with respect to subfamily- and tribe-level relationships among palms and conforms to current genus-level classifications in those larger clades. Moreover, our analysis corroborates some relationships for which conflicting results have been obtained in other studies and recovers similar areas of uncertainty. For instance, the relationships between genera of Hyphaeninae agree with those of some previous analyses, wherein *Bismarckia* and *Satranala* form a clade sister to one comprising *Hyphaene* and *Medemia* (Asmussen *et al.*, 2006; Baker *et al.*, 2009; Faurby *et al.*, 2016). Our analysis shows strong support for these relationships, with *Hyphaeneocarpon* part of the *Bismarckia–Satranala* group. In contrast, relationships in Trachycarpeae and Calamoideae are poorly supported, consistent with uncertainties observed in previous studies (e.g. Asmussen *et al.*, 2006; Baker *et al.*, 2009; Bacon, Baker & Simmons, 2012; Barrett *et al.*, 2016; Faurby *et al.*, 2016). The lack of resolution in these groups may be related to the paucity of DNA sequence data available to us on GenBank for some genera in Calamoideae and Trachycarpeae and may generally reflect the need for more data in resolving intergeneric relationships of palms (Faurby *et al.*, 2016). Therefore, despite fairly high support in our analysis for some nodes in these groups, we treat our results for Calamoideae and Trachycarpeae cautiously. However, these uncertainties do not change our confidence in the affinities of *Hyphaeneocarpon* with Hyphaeninae.

Other occurrences of Borasseae in the Deccan Intertrappean Beds

Several other fossils from the Deccan Intertrappean Beds have been assigned to or compared with Borasseae, some of which originate from the same localities in which *Hyphaeneocarpon* occur. They include leaves of *Sabalites dindoriensis* R.Srivastava, G.Srivastava, & D.L.Dilcher and *Amensoneuron borassoides* Bonde, petioles of *Palmocaulon hyphaeneoides* Shete & Kulkarni and stems of *Palmoxylon hyphaeneoides* Rao & Shete (Shete & Kulkarni, 1980; Bonde, 1986; Rao & Shete, 1989; Srivastava, Srivastava & Dilcher, 2014). Vegetative structures alone, particularly leaves, are generally insufficient for confident systematic placement among palms (Read & Hickey, 1972), but some of these fossils potentially represent Borasseae.

Fossils of *Sabalites dindoriensis* consist of impressions of costapalmate leaves with unarmed petioles and an associated inflorescence (Srivastava *et al.*, 2014). Strongly costapalmate leaves lacking spines are found in several coryphoid genera (Dransfield *et al.*, 2008), and although the robust unbranched inflorescence associated with *S. dindoriensis* resembles those of Borasseae, possible affinities with other groups cannot be ruled out entirely. These fossils originate from the Ghughua

Figure 6. Phylogenetic relationships of *Hyphaeneocarpon indicum*. A, majority rule consensus tree drawn as a cladogram. Node labels are posterior probabilities, and all unlabelled nodes have a posterior probability of 1. Borasseae stem labelled 'B', genera of subtribe Hyphaeninae indicated with bold text. B–E, volume rendering of μCT scans of extant species *Satranala decussilvae* (B, C) and *Bismarckia nobilis* (D, E), digitally sliced to show internal structure. B, lateral view of *S. decussilvae* fruit cut in longitudinal section showing the apical germination pore (black arrow), basal intrusion of endocarp into seed (white arrowhead) and large longitudinal vascular bundles cut in transverse section (white arrow). Note that seed (black arrowhead) is dry and shrivelled up inside the endocarp. C, apical view of *S. decussilvae* fruit cut in transverse section along ridge formed by germination pore, showing its elongate shape. Note large longitudinal vascular bundles that run along apex of each endocarp ridge (arrow). Specimen K000300252. D, lateral view of *B. nobilis* fruit cut in longitudinal section showing apical germination pore (black arrow), basal intrusion of endocarp into seed (white arrowhead), and large longitudinal vascular bundles intercepted in transverse and oblique longitudinal section (white arrows). The seed is dry and shrivelled up inside endocarp, but embryo is still visible (black arrowhead). Note structure of outer pericarp zone, with numerous fine radial fibre bundles, and two basal bulges corresponding to abortive carpels. E, apical view of *B. nobilis* fruit cut in transverse section along ridge formed by germination pore, showing its elongate shape. Note similarities with comparable sections from *Hyphaeneocarpon indicum* in Figure 5. All scale bars = 5 mm. Abbreviations: ec, endocarp; o, outer pericarp zone.

locality, which is near the Umaria locality in which *Hyphaeneocarpon* occurs. *Amensoneuron borassoides* is a palmate or costapalmate leaf impression with some vein structure preserved, originating from the Mohgaonkalan locality where some fruits of *Hyphaeneocarpon* occur (Bonde, 1986). However, the specimen consists of a single lamina fragment and lacks additional features helpful for identification. *Palmocaulon hyphaeneoides* is a permineralized palm petiole exhibiting anatomical similarities to Borasseae (Shete & Kulkarni, 1980). Taxonomic affinities with other groups of palms are possible, but the anatomical similarities documented by the original authors do indicate potential relationships with Borasseae.

Palmoxylon hyphaeneoides was described from a basal stem segment bearing numerous roots, and based on comparisons with modern palms it was considered by Rao & Shete (1989) to resemble *Hyphaene*. We applied the original description of *P. hyphaeneoides* to the dataset of anatomical descriptors of palm stem anatomy compiled by Thomas & De Franceschi (2013). Using the relevant anatomical characters documented by Rao & Shete (1989), *Palmoxylon hyphaeneoides* exhibits stem anatomy consistent with several groups of coryphoid palms including Borasseae, *Sabal*, Trachycarpeae and Chuniophoeniceae, as well as *Nypa*, and thus its placement in Borasseae is equivocal.

IMPLICATIONS FOR DIVERGENCE TIME ESTIMATES – LATE CRETACEOUS DIVERSIFICATION OF CROWN CORYPHOIDEAE?

Placement of *Hyphaeneocarpon* in Hyphaeninae (Borasseae) has implications for elucidating the evolutionary tempo and historical biogeography of Coryphoideae and of palms more generally. Currently the oldest macrofossil assigned to Borasseae, *Hyphaene kappelmanni* A.D.Pan, B.F.Jacobs, J.Dransf. & W.J.Baker (Pan *et al.*, 2006), is late Oligocene (28–27 Ma), significantly younger than *Hyphaeneocarpon*, which is late Maastrichtian–early Danian (67–64 Ma). With *H. kappelmannii* employed as a calibration for stem Hyphaeninae, molecular dating analyses have estimated the age of the Borasseae stem node to between 49 and 29 Ma and the Hyphaeninae crown node to between 26 and 13 Ma (Baker & Couvreur, 2013). The position of *Hyphaeneocarpon* in crown Hyphaeninae indicates a much earlier origin of Borasseae and Hyphaeninae than analyses using the *H. kappelmanii* calibration have so far predicted, indicating an origin of the Hyphaeninae crown group by 67–64 Ma, *c.* 40 million years earlier than current estimates. This implies an even earlier origin of Borasseae, probably in the Late Cretaceous.

The age of *Hyphaeneocarpon* is interesting in the context of the fossil record of palms. The earliest palm macrofossils and much of the Late Cretaceous fossil record consist of costapalmate leaf fossils assigned to the form genus *Sabalites* G.Saporta (Berry, 1914; Harley, 2006). Although these provide compelling evidence for Coryphoideae in the Cretaceous (costapalmate leaves are today restricted to Coryphoideae), leaf and stem fossils generally cannot be assigned below the subfamily level and are often placed in form genera (Read & Hickey, 1972). Reproductive structures, which potentially can provide strong evidence for divergence of crown lineages, are not seen in abundance until around the Eocene (Harley, 2006; Dransfield *et al.*, 2008, and references therein) and many earlier occurrences of palm fruits are, in our opinion, unreliable records for major groups of Arecaceae owing to the absence of clear diagnostic characters in the fossils. Moreover, most molecular dating studies, for which relatively few reliable fossil calibrations are available, place much of the diversification of Coryphoideae in the Cenozoic (Couvreur, Forest & Baker, 2011; Bacon *et al.*, 2012; Baker & Couvreur, 2013). An exception to this paucity of reproductive organs in the early fossil record are seeds of *Sabal bigbendense* Manchester, Wheeler, & Lehman and *Sabal bracknellense* (Chandler) Mai from the Campanian of Texas (Manchester, Lehman, & Wheeler, 2010). These are indistinguishable from modern *Sabal* seeds and were found in association with costapalmate leaf compressions. The *Sabal* fossils, along with the *Hyphaeneocarpon* fossils from India, together suggest that there was a much more extensive Late Cretaceous diversification of crown Coryphoideae than indicated by both molecular dating analyses and the fossil record of vegetative organs. This could extend to other subfamilies as more of the Deccan palms are described and revised; a recent study of fossils now assigned to *Palmocarpon drypeteoides* indicates Attaleinae (Cocoseae, Arecoideae) had diverged by the Maastrichtian–Danian (Manchester *et al.*, 2016). Further analyses are needed to determine the precise influence of these fossils on divergence time estimates, but *Hyphaeneocarpon* will serve as a reliable and probably highly informative calibration.

BIOGEOGRAPHICAL IMPLICATIONS

Today members of Borasseae are found throughout the Indian Ocean region, from Africa into Southeast Asia (Dransfield *et al.*, 2008). Most genera are geographically restricted. *Bismarckia* and *Satranala* are endemic to Madagascar, *Medemia* is found only in the deserts of southern Egypt and northern Sudan, *Lodoicea* is endemic to the Seychelles, *Latania* is endemic to the Mascarene Islands, and

Borassodendron is distributed in parts of Southeast Asia. The exceptions are *Borassus*, which is one of the most widespread palm genera, stretching from Africa to Southeast Asia, and *Hyphaene*, found throughout Africa, Madagascar, the Middle East and India (Bayton, Obunyali & Ranaivojaona, 2003; Dransfield *et al.*, 2008). The fossil record of Borasseae contains only a few occurrences, all from within its modern distribution. In addition to *Hyphaene kappelmannii* from Ethiopia, there is *Borassus*-type pollen from Kenya (late Oligocene to early Miocene; Vincens, Tiercelin & Buchet, 2006) and two fruit fossils assigned to the group: *Hyphaene coriacea* Gaertn. from Uganda (late Miocene; Dechamps, Senut & Pickford, 1992) and *Hyphaeneocarpon aegypticum* Vaudois-Miéja & Lejal-Nicol from Egypt (Aptian; Vaudois-Miéja & Lejal-Nicol, 1987). However, the specimens of *H. aegypticum* are of uncertain affinity (Pan *et al.*, 2006) and are questionably palms, and until they can be re-examined do not represent a reliable record for the group. The fossils of *Hyphaeneocarpon indicum* from the Maastrichtian–Danian of India are thus the oldest reliable record of Borasseae.

The close affinities of *Hyphaeneocarpon* with two genera endemic to Madagascar are curious from a biogeographical perspective, because India and Madagascar were joined as a single continent throughout the Early Cretaceous after the breakup of Gondwana (Ali & Aitchison, 2008; Chatterjeee *et al.*, 2013). The syncarpous clade of Coryphoideae, to which Borasseae belongs, is hypothesized as having a Laurasian origin, with subsequent spread of Borasseae stem lineages into the Indian Ocean where the diversification of the tribe subsequently occurred (Dransfield *et al.*, 2008; Baker & Couvreur, 2013). If this hypothesis is correct, the ancestor of *Hyphaeneocarpon* could have entered India either via dispersal from Madagascar, or during the separation of Madagascar and India around the Turonian (*c.* 90 Ma). Alternatively, the *Hyphaeneocarpon–Bismarckia–Satranala* clade or its ancestors may have been more widespread in the past, persisting to modern times only in Madagascar. Regarding dispersal vectors, modern representatives of Borasseae have large, typically animal-dispersed fruits (mammals, large birds; Zona & Henderson, 1989) and are considered poor dispersers (Baker & Couvreur, 2013). The Indian fossils, although smaller than fruits of most modern Borasseae, are structurally similar to those of extant members and lack features suggesting different dispersal adaptations. These considerations raise intriguing and unanswered questions about the role of dispersal versus vicariance in the biogeographical history of Borasseae and the identity of fruit dispersers, because these events pre-date the evolution of modern mammalian and avian vectors.

CONCLUSIONS

We document the morphology and anatomy of several new palm fruit specimens from the Deccan Intertrappean Beds of India and revise the taxonomy of five previously described species, placed here in synonymy as *Hyphaeneocarpon indicum*. X-ray µCT scans revealed several key characters essential for systematic placement of the fossils in subtribe Hyphaeninae of tribe Borasseae, including the presence of abortive carpels and germination pores with seedlings. Phylogenetic analysis further indicated affinities with the extant genera *Bismarckia* and *Satranala* in Hyphaeninae, which are today endemic to Madagascar. This is the oldest reliable occurrence of Borasseae in the fossil record. Our results indicate that divergence of Hyphaeninae occurred by the late Maastrichtian–early Danian, and Borasseae have persisted in the Indian Ocean region since the end of the Cretaceous. Inclusion of this fossil in dating analyses will be necessary to determine the influence of these fossils on the predicted ages of other phylogenetic nodes, but they nevertheless suggest a more extensive Late Cretaceous diversification of palms than was previously known. This highlights the importance of the Deccan palms, and fruit fossils more generally, in elucidating the deep evolutionary history of Arecaceae.

ACKNOWLEDGEMENTS

We are grateful to Dr S. D. Bonde and Dr P. G. Gamre for providing access to type specimens and thin sections at the Agharkar Research Institute, Pune, Dr R. C. Mehrotra for access to the type material housed at the Birbal Sahni Institute, Lucknow, and Dr Bandana Samant for donation of specimens. We thank Dr Brett Jestrow (Fairchild Tropical Botanic Garden Herbarium), Dr Anna Stalter (L.H. Bailey Hortorium Herbarium), Dr Kevin Nixon (L.H. Bailey Hortorium Herbarium), Mr Harry Smith (Royal Botanic Gardens, Kew) and Dr William Baker (Royal Botanic Gardens, Kew) for access to modern comparative material. This study includes data produced in the CTEES facility at University of Michigan, supported by the Department of Earth & Environmental Sciences and College of Literature, Science, and the Arts. Funding for this research was provided by USA National Science Foundation grants DEB 1701645 to K.K.S.M. and S.Y.S., EAR 1338295 to S.Y.S. and EAR 1338285 to S.R.M.

REFERENCES

Ali JR, Aitchison JC. 2008. Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166–35 Ma). *Earth-Science Reviews* **88:** 145–166.

Asmussen CB, **Dransfield J**, **Deickmann V**, **Barfod AS**, **Pintaud J-C**, **Baker WJ. 2006.** A new subfamily classification of the palm family (Arecaceae): evidence from plastid DNA phylogeny. *Botanical Journal of the Linnean Society* **151:** 15–38.

Bacon CD, **Baker WJ**, **Simmons MP. 2012.** Miocene dispersal drives island radiations in the palm tribe Trachycarpeae (Arecaceae). *Systematic Biology* **61:** 426–442.

Baker WJ, **Couvreur TLP. 2013.** Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. *Journal of Biogeography* **40:** 274–285.

Baker WJ, **Dransfield J. 2016.** Beyond *Genera Palmarum*: progress and prospects in palm systematics. *Botanical Journal of the Linnean Society* **182:** 207–233.

Baker WJ, **Savolainen V**, **Asmussen-Lange CB**, **Chase MW**, **Dransfield J**, **Forest F**, **Harley MM**, **Uhl NW**, **Wilkinson M. 2009.** Complete generic-level phylogenetic analyses of palms (Arecaceae) with comparisons of supertree and supermatrix approaches. *Systematic Biology* **58:** 240–256.

Bande MB, **Prakash U**, **Ambwani K. 1982.** A fossil palm fruit *Hyphaeneocarpon indicum* gen. et sp. nov. from the Deccan Intertrappean Beds, India. *The Palaeobotanist* **30:** 303–309.

Barrett CF, **Baker WJ**, **Comer JR**, **Conran JG**, **Lahmeyer SC**, **Leebens-Mack JH**, **Li J**, **Lim GS**, **Mayfield-Jones DR**, **Perez L**, **Medina J**, **Pires JC**, **Santos C**, **Stevenson DW**, **Zomlefer WB**, **Davis JI. 2016.** Plastid genomes reveal support for deep phylogenetic relationships and extensive rate variation among palms and other commelinid monocots. *New Phytologist* **209:** 855–870.

Bayton RP, **Obunyali C**, **Ranaivojaona R. 2003.** A re-examination of *Borassus* in Madagascar. *Palms* **47:** 206–219.

Berry EW. 1914. The Upper Cretaceous and Eocene floras of South Carolina and Georgia. *US Geological Survey, Professional Paper* **84:** 1–200.

Bobrov AVFC, **Dransfield J**, **Romanov MS**, **Romanova ES. 2012a.** Gynoecium and fruit histology and development in *Eugeissona* (Calamoideae: Arecaceae). *Botanical Journal of the Linnean Society* **168:** 377–394.

Bobrov AVFC, **Lorence DH**, **Romanov MS**, **Romanova ES. 2012b.** Fruit development and pericarp structure in *Nypa fruticans* Wurmb (Arecaceae): a comparison with other palms. *International Journal of Plant Sciences* **173:** 751–766.

Bonde SD. 1986. *Amesoneuron borassoides* sp. nov. A borassoid palm leaf from the Deccan Intertrappean bed at Mohgaonkalan, India. *Biovigyanam* **12:** 89–91.

Bonde SD. 1990a. *Arecoidocarpon kulkarnii* gen. et sp. nov., an arecoid palm fruit from Mohgaon Kalan, Madhya Pradesh. *The Palaeobotanist* **38:** 212–216.

Bonde SD. 1990b. A new palm peduncle *Palmostroboxylon umariense* (Arecaceae) and a fruit *Pandanusocarpon umariense* (Pandanaceae) from the Deccan Intertrappean Beds of India. In: Douglas JG, Christophel DC, eds. *Proceedings of the 3rd International Organization of Palaeobotany Conference, Melbourne 1988*. *Melbourne:* A-Z Printers, 59–65.

Bonde SD. 1995. A palm peduncle and fruit from the Deccan Intertrappean Beds of India. In: Pant D, ed. *Proceedings of the Birbal Sahni Birth Centenary International Conference: Symposium on Global Environment and Diversification of Plants through Geological Time: Birbal Sahni Centenary Volume*. Allahabad, India: Society of Plant Taxonomists, 63–69.

Bonde SD. 2008. Indian fossil monocotyledons: current status, recent developments and future directions. *The Palaeobotanist* **57:** 141–164.

Chatterjee S, **Goswami A**, **Scotese CR. 2013.** The longest voyage : tectonic, magmatic, and paleoclimatic evolution of the Indian plate during its northward flight from Gondwana to Asia. *Gondwana Research* **23:** 238–267.

Couvreur TL, **Forest F**, **Baker WJ. 2011.** Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC Biology* **9:** 44.

Dechamps R, **Senut B**, **Pickford M. 1992.** Fruits fossiles pliocènes et pléistocènes du Rift Occidental ougandais. Signification palèoenvironnementale. *Comptes Rendus de l'Académie des Sciences Paris, Série II* **314:** 325–331.

DeMason DA, **Sekhar KC**, **Harris M. 1989.** Endosperm development in the date palm (*Phoenix dactylifera*) (Arecaceae). *American Journal of Botany* **76:** 1255–1265.

Dransfield J, **Beentje HJ. 1995.** *Satranala* (Coryphoideae : Borasseae : Hyphaeninae), a new palm genus from Madagascar. *Kew Bulletin* **50:** 85–92.

Dransfield J, **Uhl NW**, **Asmussen CB**, **Baker WJ**, **Harley MM**, **Lewis CE. 2008.** *Genera palmarum: the evolution and classification of palms*. Richmond: Kew Publishing.

Faurby S, **Eiserhardt WL**, **Baker WJ**, **Svenning JC. 2016.** An all-evidence species-level supertree for the palms (Arecaceae). *Molecular Phylogenetics and Evolution* **100:** 57–69.

Gee CT. 2001. The mangrove palm *Nypa* in the geologic past of the New World. *Wetlands Ecology and Management* **9:** 181–194.

Guindon S, **Dufayard JF**, **Lefort V**, **Anisimova M**, **Hordijk W**, **Gascuel O. 2010.** New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* **59:** 307–321.

Harley MM. 2006. A summary of fossil records for Arecaceae. *Botanical Journal of the Linnean Society* **151:** 39–67.

Hooper P, **Widdowson M**, **Kelley S. 2010.** Tectonic setting and timing of the final Deccan flood basalt eruptions. *Geology* **38:** 839–842.

Kapgate DK. 2009. *Palaeovegetation, palaeophytogeography and palaeoenvironmental study of Central India*. Bhandara: J.M. Patel College of Arts, Commerce & Science.

Kulkarni AR, **Mulani RM. 2004.** Indigenous palms of India. *Current Science* **86:** 1598–1603.

Lanfear R, **Calcott B**, **Ho SY**, **Guindon S. 2012.** Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29:** 1695–1701.

Lanfear R, **Frandsen PB**, **Wright AM**, **Senfeld T**, **Calcott B. 2017.** PartitionFinder 2 : new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* **34:** 772–773.

Mahabale TS. 1950. Palaeobotany in India VII. Some new fossil plants from the Deccan Intertrappeans. *Journal of the Indian Botanical Society* **29:** 31–33.

Manchester SR, **Bonde SD**, **Nipunage DS**, **Srivatava R**, **Mehrotra RC**, **Smith SY. 2016.** Trilocular palm fruits from the Deccan Intertrappean Beds of India. *International Journal of Plant Sciences* **177:** 633–641.

Manchester SR, **Lehman TM**, **Wheeler EA. 2010.** Fossil palms (Arecaceae, Coryphoideae) associated with juvenile herbivorous dinosaurs in the Upper Cretaceous Aguja Formation, Big Bend National Park, Texas. *International Journal of Plant Sciences* **171:** 679–689.

Mehrotra RC. 1987. Some new palm fruits from the Deccan Intertrappean Beds of Mandla District, Madhya Pradesh. *Geophytology* **17:** 204–208.

Miller MA, **Pfeiffer W**, **Schwartz T. 2010.** *Creating the CIPRES Science Gateway for inference of large phylogenetic trees. 2010 Gateway Computing Environments Workshop,* (GCE), 14 Nov. 2010, New Orleans, LA pp 1 - 8.

Moore HE, **Uhl NW. 1982.** Major trends of evolution in palms. *The Botanical Review* **48:** 1–69.

Murray SG. 1973. The formation of endocarp in palm fruits. *Principes* **17:** 91–102.

Pan AD, **Jacobs BF**, **Dransfield J**, **Baker WJ. 2006.** The fossil history of palms (Arecaceae) in Africa and new records from the Late Oligocene (28–27 Mya) of north-western Ethiopia. *Botanical Journal of the Linnean Society* **151:** 69–81.

Pross J, **Contreras L**, **Bijl PK**, **Greenwood DR**, **Bohaty SM**, **Schouten S**, **Bendle JA**, **Röhl U**, **Tauxe L**, **Raine JI**, **Huck CE**, **van de Flierdt T**, **Jamieson SS**, **Stickley CE**, **van de Schootbrugge B**, **Escutia C**, **Brinkhuis H**; **Integrated Ocean Drilling Program Expedition 318 Scientists**. **2012.** Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch. *Nature* **488:** 73–77.

Rao GV, **Shete RH. 1989.** *Palmoxylon hyphaeneoides* sp. nov. from the Deccan Intertrappean beds of Wardha District Maharashtra, India. *Proceedings of the Special Indian Geophytological Conference, Pune, 1986* **1:** 123–128.

Read RW, **Hickey LJ. 1972.** A revised classification of fossil palm and palm-like leaves. *International Association for Plant Taxonomy* **21:** 129–137.

Renne PR, **Sprain CJ**, **Richards MA**, **Self S**, **Vanderkluysen L**, **Pande K. 2015.** State shift in Deccan volcanism at the Cretaceous–Paleogene boundary, possibly induced by impact. *Science* **350:** 76–78.

Romanov MS, **Bobrov AV**, **Wijesundara DS**, **Romanova ES. 2011.** Pericarp development and fruit structure in borassoid palms (Arecaceae-Coryphoideae-Borasseae). *Annals of Botany* **108:** 1489–1502.

Samant B, **Mohabey DM. 2009.** Palynoflora from Deccan volcano-sedimentary sequence (Cretaceous–Palaeogene transition) of central India: implications for spatio-temporal correlation. *Journal of Biosciences* **34:** 811–823.

Schoene B, **Samperton KM**, **Eddy MP**, **Keller G**, **Adatte T**, **Bowring SA**, **Khadri SF**, **Gertsch B. 2015.** Earth history. U–Pb geochronology of the Deccan Traps and relation to the end-Cretaceous mass extinction. *Science* **347:** 182–184.

Shete RH, **Kulkarni AR. 1980.** *Palmocaulon hyphaeneoides* sp. nov. from the Deccan Intertrappean beds of Wardha District, Maharashtra, India. *Palaeontographica Abteilung B* **172:** 117–124.

Shrivastava JP, **Duncan RA**, **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* **224–225:** 214–224.

Sluijs A, **Schouten S**, **Donders TH**, **Schoon PL**, **Röhl U**, **Reichart G-J**, **Sangiorgi F**, **Kim J-H**, **Sinninghe Damsté JS**, **Brinkhuis H. 2009.** Warm and wet conditions in the Arctic region during Eocene thermal maximum 2. *Nature Geoscience* **2:** 777–780.

Smith S, **Manchester SR**, **Samant B**, **Mohabey DM**, **Wheeler E**, **Baas P**, **Kapgate D**, **Srivastava R**, **Sheldon ND. 2015.** Integrating paleobotanical, paleosol, and stratigraphic data to study critical transitions: a case study from the Late Cretaceous–Paleocene of India. *Earth-Life Transitions: Paleobiology in the Context of Earth System Evolution* **21:** 137–166.

Srivastava R. 2011. Indian upper Cretaceous-Tertiary flora before collision of Indian Plate : a reappraisal of central and western Indian Flora. *Memoir of the Geological Society of India* **77:** 281–292.

Srivastava R, **Srivastava G**, **Dilcher DL. 2014.** Coryphoid palm leaf fossils from the Maastrichtian–Danian of Central India with remarks on phytogeography of the Coryphoideae (Arecaceae). *PLoS One* **9:** e111738.

Suan G, **Popescu SM**, **Suc JP**, **Schnyder J**, **Fauquette S**, **Baudin F**, **Yoon D**, **Piepjohn K**, **Sobolev NN**, **Labrousse L. 2017.** Subtropical climate conditions and mangrove growth in Arctic Siberia during the early Eocene. *Geology* **45:** 539–542.

Thomas R, **De Franceschi D. 2013.** Palm stem anatomy and computer-aided identification: the Coryphoideae (Arecaceae). *American Journal of Botany* **100:** 289–313.

Vaudois-Miéja N, **Lejal-Nicol A. 1987.** Paléocarpologie africaine: apparition dés l'Aptien en Égypte d'un palmier (*Hyphaeneocarpon aegyptiacum* n. sp.). *Comptes Rendus de l'Académie des Sciences Paris Série II* **304:** 233–238.

Vincens A, **Tiercelin J-J**, **Buchet G. 2006.** New Oligocene–early Miocene microflora from the southwestern Turkana Basin. Palaeoenvironmental implications in the northern Kenya Rift. *Palaeogeography, Palaeoclimatology, Palaeoecology* **239:** 470–486.

Zona S, **Henderson A. 1989.** A review of animal-mediated seed dispersal of palms. *Selbyana* **11:** 6–21.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

File S1. Excel spreadsheet containing GenBank accession numbers for all sampled species, with each tab separating the sampling for each gene. The last tab lists the species sampled in the morphological matrix.
File S2. Morphological matrix used in the analysis, formatted for Mesquite (https://www.mesquiteproject.org/).
File S3. PartitionFinder2 output for the best-fit partitioning scheme of the molecular sequence data used in our phylogenetic analysis.
File S4. MrBayes input file used in the final analysis.
File S5. Tree file for the 50% majority rule consensus tree output by MrBayes.