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Oldest fruit of Phyllanthaceae from the Deccan Intertrappean Beds of Singpur, Madhya Pradesh, India

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ABSTRACT. A permineralized fruit from the latest Cretaceous of central India is recognized as a member of the malpighialean family Phyllanthaceae. The fruit is a tricarpellate, septicidal capsule 2.8 mm in diameter possessing two ellipsoidal seeds per locule. The pericarp includes two main layers, each uniseriate and composed mainly of columnar cells. This fruit, named *Phyllanthocarpon singpurensis* gen. et sp. nov., confirms the presence of Phyllanthaceae in India ca 66 million years ago, well prior to its tectonic fusion with Eurasia, and is an early record for the euphorbioid clade in Malpighiales.

KEYWORDS: Phyllanthaceae, Euphorbiaceae, Malpighiales, fossil fruit, Deccan Intertrappean beds, Maastrichtian, Late Cretaceous

INTRODUCTION

The Euphorbiaceae s.s., Putranjivaceae, and Phyllanthaceae are closely related families that were formerly treated as Euphorbiaceae s.l. (Wurdack et al. 2004, Hoffmann et al. 2006). Together with Pandaceae and Picrodendraceae, these families form a prominent clade within the order Malpighiales. The fossil record of this group is relatively meager, although fossil fruits of Euphorbiaceae s.s. have been traced back to the Eocene in England (Reid & Chandler 1933, Collinson & Cleal 2001), Germany (Collinson et al. 2012), and North America (Dilcher & Manchester 1988, Manchester & McIntosh 2007). The oldest known fruit of Phyllanthaceae, from the late Cretaceous of central India, was the subject of a conference abstract (Mistri et al. 1992); however, the genus and species name introduced in that abstract remained a nomen nudum because the binomial was never validly published. We validate the name *Phyllathocarpon* here, and provide new photographic and descriptive documentation.

The specimen was recovered from chert at the locality of Singpur, ca 60 km northwest of Nagpur, central India. Singpur is among numerous paleobotanical localities exposed in the Deccan Intertrappean beds of central India representing flora that existed immediately prior to and following the Cretaceous-Tertiary boundary (Prakash 1960, Smith et al. 2015). The Singpur locality is likely of late Maastrichtian age based on the palynological correlation (Samant et al. 2008).

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MATERIAL AND METHODS

The chert containing the silicified fruit was collected among loose pieces exposed at the edge of a farming field near Singpur (alternate spelling Singhpur), at 21°36.958′N, 78°43.827′E. The site is probably close to the chert locality known as Sauser in the older literature (e.g., Prakash 1960). Upon breaking the chert with a hammer in the field, the fruit was clearly seen in its nicely preserved state. Both counterparts of the specimen were successively etched with hydrofluoric acid, painted with a collodion solution, and peeled to prepare slides for transmitted light microscopy, following the procedure described in Kapgate et al. (2011). The original specimen and most of the original peels have been lost, but three of those peels were recovered and donated to the Paleobotanical Collection of the Florida Museum of Natural History, University of Florida (UF) in Gainesville, Florida. These peels provided the images shown in this article, supplementary to the line diagram published with the original abstract (Mistri et al. 1992). Photomicrographs were prepared with a Canon Rebel 450 digital camera mounted on a Nikon labophot microscope. Fruits of extant genera of Phyllanthaceae were examined at the herbarium of Missouri Botanical Garden. Micro-CT scanning was carried out on selected extant fruits with a GE Phoenix V|tome|xm240 instrument at the University of Florida, and virtual sections were processed with Avizo 9.0 Lite.

The palynoflora of the Singpur locality was investigated by Samant et al (2008). Another angiosperm fruit was described from the same locality and called *Euphorbioceocarpon* (*nomen nudum*; Bhowal & Sheikh 2006), but the affinities of that fruit to Euphorbiaceae and Phyllanthaceae are, in our opinion, remote. Other megafossils from the same locality were called *Verbenaceocarpon* (Dhabarde et al. 2012) and *Baccatocarpon* (*nomen nudum*; Bhowal & Sheikh 2004).

SYSTEMATICS

Malpighiales

Phyllanthaceae

Phyllanthocarpon Mistri, Kapgate & Sheikh ex Kapgate & Manchester **gen. nov.**

Diagnosis. Fruit a trilobed, trilocular, septicidal capsule with two seeds per locule. Placentation axile. Pericarp composed of two prominent uniseriate columnar layers. Seeds ellipsoidal to somewhat trigonal with a prominent layer of columnar cells forming the seed coat.

Type species. *Phyllanthocarpon singpurensis* Kapgate & Manchester sp. nov.

Phyllanthocarpon singpurensis sp. nov.

Pl. 1, figs 1–7

Diagnosis. Fruit a trilobed, tricarpellate capsule, 2.8 mm in equatorial diameter, with rounded locules and a longitudinal groove aligned with each of the three septae. Fruit wall 70 to 90 μm thick, composed of two main lignified layers, both uniseriate and approximately equal in thickness, composed primarily of anticlinal columnar cells. These layers invaginate between adjacent locules to form the septae, and form a slight ridge at the midline of each carpel. Seeds six, two per locule, ellipsoidal to trigonal, 450–675 μm wide, 925–1000 μm in dorsiventral dimension, height uncertain. Seed coat 18–25 μm thick, composed of a prominent layer of mostly anticlinal columnar cells 14–24 μm high. The configuration of these cells varies from more or less isodiametric over the circular chalaza to radially and periclinally elongate. A thin inner layer, apparently cutinized, has separated from the prominent mechanical layer and borders the endosperm.

Holotype. PBM/Ang/4 originally deposited at Botany Department, Institute of Science, Nagpur, India, was unfortunately discarded. Surviving duplicate peel slides from the holotype are stored at the Florida Museum of Natural History under catalog number UF19278-53557 (type status designated here).

Horizon. Dhuma Formation, Deccan Trap Group, Late Maastrichtian.

Locality. Singpur, Madhya Pradesh, India.

DESCRIPTION

The specimen is a well-preserved trilocular fruit exposed in a transverse fracture. The fruit is 2.8 mm in diameter and contains six seeds, arranged two per carpel (Pl. 1, figs 1–2). The pericarp consists of two layers of approximately equal thickness, each composed of columnar cells. The columnar cells in these layers are ca 35–45 μm high and 10–20 μm in diameter. Each of the three septae is ca 90–100 μm thick and is bipartite, formed by the invagination of the columnar endocarp layers of adjacent locules (Pl. 1, figs 3, 5). A well-defined narrow median gap within each septum represents the plane of dehiscence (Pl. 1, figs 1–3). The septae

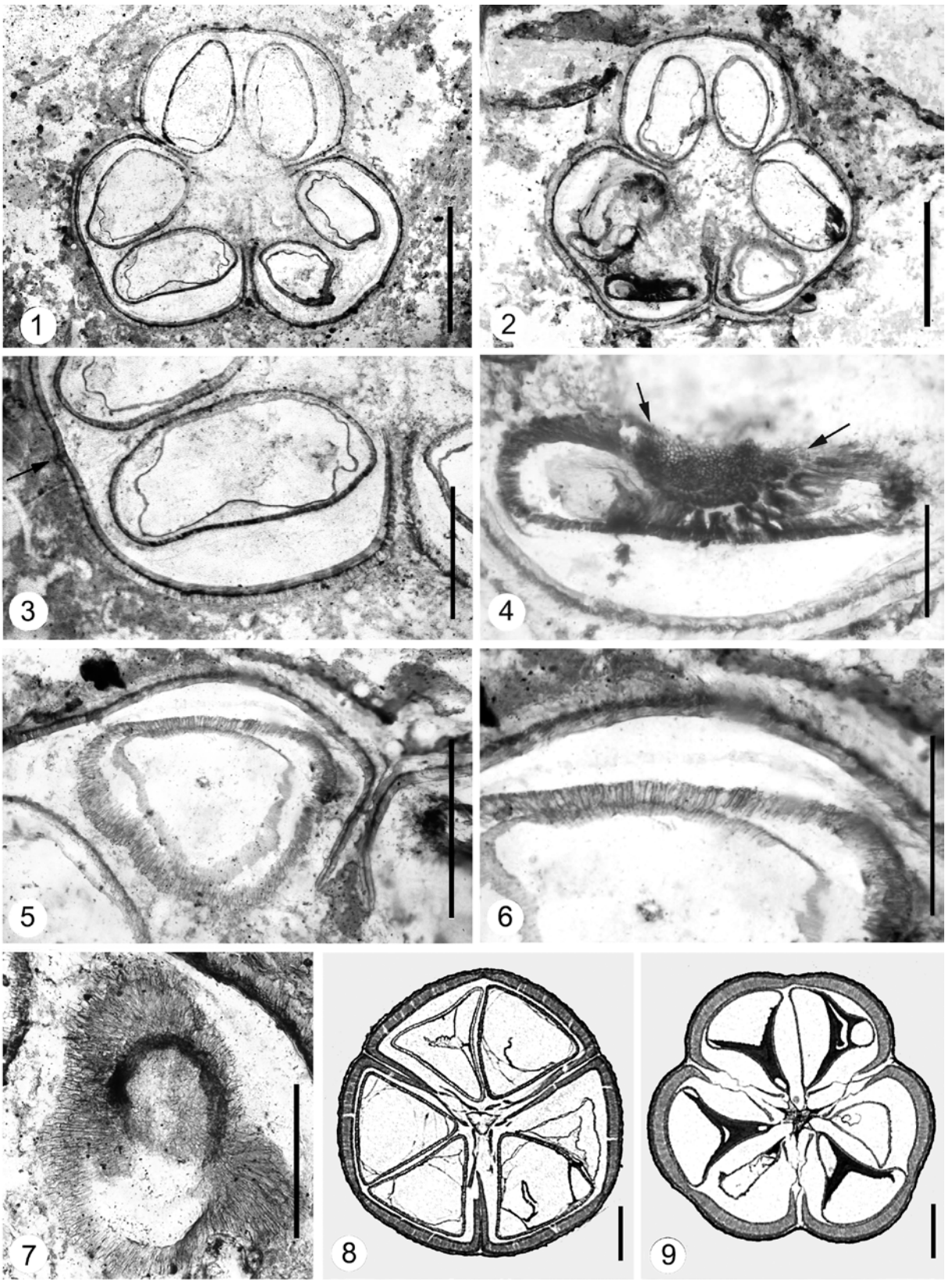

Plate 1. **1–7**. Fruit of *Phyllanthocarpon singpurensis* sp. nov. Holotype, UF19278-53557. **1**. Transverse section near equator, showing thin, two-layered pericarp and three locules with two seeds in each, scale bar = 1 mm; **2**. Transverse section closer to apex, with most seeds in sectional view, one at lower left sectioned peridermally near base, scale bar = 1 mm; **3**. Detail from fig. 1, showing biseriate pericarp, intruding septum, and intact seeds. Arrow indicates ridge of carpel suture, scale bar = 500 µm; **4**. Detail of seed from fig. 2, with arrows delimiting chalazal rim, scale bar = 250 µm; **5**, **6**. Successive enlargements of seed from fig. 2, showing columnar layers of seed coat and pericarp, scale bars = 500 µm, 250 µm; **7**. Seed showing circular chalaza, scale bar = 250 µm; **8–9**. Transverse sectional views of extant Phyllanthaceae fruits for comparison; **8**. Fruit of extant *Leptopus chinensis* in virtual transverse slice from CT scan data, MO 4482861, scale bar = 500 µm; **9**. Fruit of extant *Phyllanthus cochichinensis* in virtual transverse section from CT scan data. MO 4112051, scale bar = 500 µm

do not join at the center of the fruit in the nearly equatorial transverse sections available. This is taken as an indication of septicidal dehiscence whereby the septae had begun to separate at the center of the fruit to facilitate seed dispersal. A slight median ridge on each carpel is aligned with the center of each locule, representing the line of carpel suture (Pl. 1, fig. 3).

Available sections do not show the placentation, but the arrangement of seeds is consistent with the axile placentation seen in extant Phyllanthaceae (cf. Gagliardi et al. 2014, fig. 2b). The seeds in section appear oval to rounded-trigonal in outline and measure ca 675 to 1000 μm in diameter (Pl. 1, figs 1–5), and have a well-delimited circular scar at one end (Pl. 1, fig. 4, 7).

IDENTIFICATION

The fossil represents a fruit that formed from a tricarpellate, syncarpous ovary with two ovules per carpel. Trilocular, capsular fruits with septicidal, loculicidal and septifragal dehiscence and prominent columnar layers in the pericarp are a typical condition in Euphorbiaceae s.s., Phyllanthaceae, and some Picrodendraceae, although berries also occur in some genera of these families. Fruits of Euphorbiaceae have a single ovule per carpel, whereas the other two families are characterized by two ovules per carpel (e.g., Gagliardi et al. 2014, Hoffmann et al. 2006, Wurdack et al. 2004). According to these criteria, the fossil, clearly showing two seeds per carpel, conforms to Phyllanthaceae and/or Picrodendraceae. Hoffmann et al. (2006) and Reveal et al. (2007) considered that the latter two families are sister taxa and could be merged into one family but hesitated to do so because the older name Picrodendraceae would take priority for the combined family name, contrary to the preferred name of Phyllanthaceae.

Tricarpellate, explosively dehiscent capsular fruits with two seeds per chamber are characteristic of members of the family Phyllanthaceae (Hoffmann et al. 2006), but the family also includes berry-like fruits and in many genera only one of the two ovules per locule develops into a seed, thus producing fruits that resemble those of Euphorbiaceae s.s. Stuppy (1995) provided a table comparing selected characters of fruits and seeds among extant genera of Phyllanthaceae. Genera typified by tricarpellate, capsular fruits and typically two seeds per locule include *Actephila* Blume, *Andrachne* L., *Dicoelia* Benth., *Dissiliaria* F. Muell. ex Baill., *Kairothamnus* Airy Shaw, *Leptopus* Decne (Pl. 1, fig. 8), *Phyllanthus* L. (Pl. 1, fig. 9), *Poranthera* Rudge, *Reverchonia* A. Gray, *Sauropus* Blume, *Savia* Willd., *Whyanbeelia* Airy Shaw & B. Hyland, *Zimmermannia* Pax, and *Zimmermanniopsis* Radcl.-Sm.. The genus *Phyllanthus* L. resembles the described fossil fruit in most of its characters, and the species *Phyllanthus simplex* Retz, *P. niruri* L. and *P. debilis* Willd. are particularly similar in size and morphology. We have not made exhaustive comparisons with all extant genera, however. Direct comparison with herbarium material is partly impeded by the fragmentary nature of dried explosively dehiscent capsules, whereas the fossil was preserved in a state prior to complete dehiscence. Documentation of additional fresh or pickled fruits would be desirable for direct comparison with the well-preserved fossil.

The prominent mechanical layer of seed coat in this fossil is the exotegmen, which forms the main mechanical layer in the seed coat of most extant phyllanthaceous seeds (Tokuoka & Tobe 2001). Stuppy (1995) and Tokuoka & Tobe (2001) surveyed seed coat anatomy among extant members of Phyllanthaceae, leading to the recognition of six categories based on the configuration of cells composing the exotegmic layer (Tokuoka & Tobe 2001). The exotegmen can be composed of a palisade of cells that are transversely elongate (Type 1, e.g., *Reverchonia arenaria* A. Gray, *Spondianthus preussii* Engl.), or cuboidal cells (Type 2, e.g., *Drypetes* Vahl, and *Sibangea* Oliv.). The exotegmic cells can be stellate to undulate in transverse outline (Type 3, e.g., *Savia* Willd., *Actephila excelsa* (Dalzell) Mull. Arg). The layer can be multicellular with tangentially oblong cells (Type 4, e.g., *Sauropus androgynus* Merr.), or composed of linear tracheoidal cells (Type 5, e.g., *Keayodendron bridelioides* (Mildbr. Ex Hutch. & Dalziel) Leandri), or of ribbon-like cells (Type 6, e.g., *Pseudolachnostylis maprouneifolia* var. *dekindtii* (Pax) Radcl.-Sm., *Lingelsheimia frutescens* Pax, *Maesobotrya floribunda* Benth.). These categories are readily recognized, and are often consistent within a genus. The seeds of

this fossil show the Type 1 configuration of columnar cells (Pl. 1, fig. 6), which occurs in *Amanoa* Aubl., *Andrachne* L., *Glochidion* J.R. Forst. & G. Forst., *Spondianthus* Engl., and some *Phyllanthus* L. (Tokuoka & Tobe 2001).

Glochidion is among some traditional genera subsumed within a broader concept of *Phyllanthus* based on phylogenetic analyses using ITS and MatK data (Kathriarachchi et al. 2006). Considering the above discussion and comparison it can be said that the present fossil fruit corresponds to the Phyllanthaceae and is particularly similar to some species of modern *Phyllanthus*, but it is not possible to assign the fossil fruit with confidence to an extant genus; hence the assignment to the new fossil genus *Phyllanthocarpon* is preferred.

Other fossil fruits with confirmed euphorbiaceous affinity have been recognized from the early Eocene of the London Clay in southern England (Reid & Chandler 1933), the middle Eocene of Messel near Darmstadt, Germany (Collinson et al. 2012), the middle Eocene of Tennessee, USA (Dilcher & Manchester 1988), and the late Eocene John Day Formation of Oregon, USA (Manchester & McIntosh 2007). However, this occurrence from India is the oldest example of the Euphorbiaceae alliance to be confirmed from the fossil record to date.

Woods with affinities to Euphorbiaceae and Phyllanthaceae have been reported previously from other outcrops of the Deccan Intertrappean beds. *Bischofinium deccanii* Bande (1974), from the probable early Paleocene site of Parapani, Dindori District, Madhya Pradesh, displays a suite of anatomical features consistent with the extant phyllanthaceous genus *Bridelia* (Wheeler et al., in press). Contrasting with the capsular fruit of *Phyllanthocarpon*, *Bridelia* has berry-like fruits rather than capsules. The wood thus provides corroborative evidence that the family was present on the Indian subcontinent by the late Cretaceous.

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