

Endocarps of *Parinari* (Chrysobalanaceae) from the Neogene of Northeastern Thailand

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ABSTRACT. Five fossil endocarps were collected from late Miocene fluvial deposits in a commercial sandpit in Northeastern Thailand. The endocarps were studied with light microscopy and scanning electron microscopy (SEM) and compared with recent and fossil endocarps. We conclude that the endocarps are *Parinari* (Chrysobalanaceae) and propose two new species, *P. hilliana* and *P. khoratensis*. These provide the first record of *Parinari* fruits from Asia and the Pacific region and indicate that the genus was already pantropical by the Miocene with previous reports of Miocene *Parinari* endocarps from Africa (Ethiopia) and the Neotropics (Panama).

KEYWORDS: *Parinari*, Chrysobalanaceae, Chaloe Phra Kiat, sandpits, Nakhon Ratchasima, Thailand

INTRODUCTION

Chrysobalanaceae R.Br. currently consists of 27 genera and 531 species of trees and shrubs. The family is mainly tropical with the majority of species, 422, in the Neotropics, 66 species in tropical Africa, and 43 species in tropical Asia and Oceania (Bardon et al., 2016). Four species within the family extend north or south of the tropics in the southeastern United States, southern Brazil, and southern Africa (Prance and White, 1988; Prance and Sothers, 2003). Thirty-nine species of *Parinari* Aubl. are currently accepted: 18 species in tropical America, six in tropical Africa, 15 in tropical Asia, the Pacific region, and northern Queensland, Australia, and one disjunct species in South America and Africa. These occupy tropical forests, ranging from deciduous dipterocarp forests, to lowland rainforests, and to swamp forests (Prance and Sothers, 2003).

Based on plastid genome data calibrated with fossils of Chrysobalanaceae, Bardon et al. (2016) concluded an African or Southeast Asian origin of Chrysobalanaceae, inferring an Eocene stem age of 49.2 mya, with the first arrival of the family in the Neotropics during the Oligocene. They further inferred an early Oligocene stem age of their Clade A, comprising *Neocarya* (DC.) Prance ex F. White, *Parinari*, and possibly *Bafodeya*, and the stem age of *Parinari*, splitting from *Neocarya*, at 25.6 Ma in the late Oligocene. Bardon et al. (2016) suggested that *Parinari* originated in Africa because of the African distribution of the sister genus *Neocarya*, with subsequent dispersal to Southeast Asia, and later dispersal from Southeast Asia to the Neotropics. In a more extensive plastid genomic study, including 11 of 39 species of *Parinari* (Chave et al., 2020), *Parinari* was monophyletic and formed a clade with *Neocarya*, with *Bafodeya* Prance ex F. White forming a basal clade

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with *Kostermanthus* Prance. The stem age of *Parinari* with separation from *Neocarya* was estimated to be 28 Ma, with diversification at 7.6 Ma. The place of origin of the genus *Parinari* was less clear-cut. The two earliest subclades of the 11 species were Neotropical, with the subclade of the 6 remaining species distributed in Africa, Southeast Asia, and Oceania, implying a possible Neotropical origin. The pantropical distribution of the genus may have arisen from trans-oceanic dispersal (Chave et al., 2020).

Plant macrofossils, including wood, fruits, seeds, and bamboo were discovered in a commercial sandpit in Chaloe Phra Kiat District, Nakhon Ratchasima Province, Northeastern

Thailand, in layers thought to be late Miocene in age. Among these specimens were five endocarps of *Parinari* (Chrysobalanaceae). We describe two new species based on these fossil endocarps, the first records of fruits of this genus reported from Asia or the Pacific region, and discuss the biogeographic inferences that can be made.

MATERIALS AND METHODS

LOCALITY AND AGE

The fossil fruits were collected with other fruits, seeds, bamboo, and wood in deposits from a commercial sandpit in Phra Phut Subdistrict, Chaloe Phra



Figure 1. A. Map of Southeast Asia, showing fossil locality, Phra Phut sandpit, in Northeastern Thailand, and distributions of extant species of *Parinari* in mainland Southeast Asia; B. Details of fossil locality along the Mun River (star indicates Phra Phut sandpit); C. Phra Phut sandpit, Phra Phut Subdistrict, Chaloe Phra Kiat District, Nakhon Ratchasima Province, Thailand (dashed line indicates the lower levels where the fruits were collected)

Kiat District, Nakhon Ratchasima Province, in North-eastern Thailand (14°59'54"N latitude, 102°14'43"E longitude) (Fig. 1A–C), approximately 16 km east of Nakhon Ratchasima city and 230 km northeast of Bangkok. The sandpit, referred to as Phra Phut sandpit (or sandpit No. 11) (Fig. 1C), is one of more than ten sandpits near the Mun River, a tributary of the Mekong River (Nishioka and Vidthayanon, 2018). The fossils recovered from these sandpits in the Chaloe Phra Kiat, Non Sung, Chakkarat, and Phimai districts, Nakhon Ratchasima, range in age from middle Miocene to late Pleistocene (Yang and Grote, 2018; Handa et al., 2020). The endocarps in this study were collected from the lower grey silty and sandy fluvial deposits of the Phra Phut sandpit (Fig. 1C). The nearby Somsak sandpit (sandpit No. 8) is one of the most important sandpits in Chaloe Phra Kiat District, and has yielded numerous mammalian fossils (Chaimanee et al., 2006). The fossiliferous Tha Chang beds in this sandpit were separated into a lower stratigraphic unit of sand and organic-rich clay (reduced zone) and an upper stratigraphic unit of yellowish sand and gravel (oxidized zone). The mammalian fossils from the lower unit were considered to be late Miocene in age (6–9 Ma) and often contained sulphide minerals, such as FeS₂ (pyrite) (Nishioka et al., 2020). Nishioka et al. (2020) also considered the lower layers in Takut Khon sandpit (sandpit No. 10), adjacent to Phra Phut sandpit, to be of similar age to Somsak sandpit. They reported the bovids *Solenoportax falconeri* and *Pachyportax giganteus* from Takut Khon sandpit. In addition, Duangkrayom et al. (2017) reported the first record of the late Miocene zygodont proboscidean, *Zygodon* sp., also from Takut Khon sandpit. More recently, during 2017–2019, numerous additional species of mammalian fossils were recovered from the lower unit of Phra Phut sandpit and considered to be late Miocene (Duangkrayom, unpublished data). The fossil fruits from the lower unit of Phra Phut sandpit, including those described here, are partly coalified and also coated with and infilled with pyrite, similar to the fossils in the lower, late Miocene unit of Somsak sandpit. We therefore conclude an age of late Miocene for the endocarps.

METHODS

Selected fossil endocarps were treated with 48% HF to remove the siliceous matrix. All the fruits were stored in a solution of 50% ethanol : 30% glycerol : 20% water. Some specimens were washed with water and air dried.

Two of the fossil fruits and recent fruits of *Parinari anamensis* Hance were observed with scanning electron microscopy (SEM). Pieces of endocarp were attached to SEM stubs and coated with gold for 4 minutes. They were then observed and photographed with a Zeiss Auriga field emission scanning electron microscope at 5 kV at Suranaree University of Technology, Nakhon Ratchasima, or at 10 kV at the Synchrotron Light Research Institute (Public Organization), Nakhon Ratchasima. Measurements of cells were made using SEM photographs with IrfanView (Version 4.58 32 bit, 2021) software.

SYSTEMATICS

ANGIOSPERMAE

EUDICOTS

Order Malpighiales

Juss. ex Bercht. and J. Presl, 1820

Family Chrysobalanaceae R. Br., 1818
in J.H. Tuckey, Narr. Exped. Zaire 433
(Brown, 1818)

Genus *Parinari* Aublet, 1775

Parinari Aubl., Hist. Pl. Guiane Fr. 1: 514, t. 204–206 (1775)

Type species. *Parinari campestris* Aubl. (1775)

Parinari hilliana Grote sp. nov.

Holotype. NRRU-F01010019 (Pl. 1, figs 1,4; Pl. 2, figs 1, 4, 7, 10).

Paratype. NRRU-F01010020 (Pl. 1, fig. 7).

Repository. Northeastern Research Institute of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, Nakhon Ratchasima, Thailand.

Type locality. Phra Phut sandpit (sandpit No. 11), Phra Phut Subdistrict, Chaloe Phra Kiat District, Nakhon Ratchasima, Thailand (14°59'54"N latitude, 102°14'43"E longitude).

Stratigraphic horizon. Greyish sandy deposits of the lower reduced unit, Tha Chang beds. Late Miocene in age.

Etymology. The epithet honours Arthur Hill, whose studies of the mechanisms of seed germination from stony fruits, including those of *Parinari* (Hill, 1933, 1937), was an inspiration to the first author.

Diagnosis. Endocarps, transversely broadly oblong in side view, nearly transversely elliptic in cross section, but slightly concave on one side. Surface smooth or slightly pitted, without furrows or ridges, or with a few furrows on one side. Two basal elliptic germination plugs, each covering a seminal cavity, not beaked between the plugs. Two seminal cavities separated by a septum and lined with hairs. Two small openings between the two plugs. Endocarp wall thick, consisting of swirling bundles



Plate 1. Fossil and recent endocarps of *Parinari*. **1.** *Parinari hilliana* (NRRU-F01010019, holotype), basal view showing one germination valve, one germination valve removed showing seminal cavity, arrows indicating small openings, presumably for vascular bundles; **2.** *Parinari khoratensis* (NRRU-F01010021, holotype), basal view showing two germination valves; **3.** *P. khoratensis* (NRRU-F01010023), basal view showing two germination valves; **4.** *P. hilliana* (NRRU-F01010019), side view; **5.** *P. khoratensis* (NRRU-F01010021), side view; **6.** Recent *P. anamensis*, basal view showing two germination valves (arrows); **7.** *P. hilliana* (NRRU-F01010020), side view; **8.** *P. khoratensis* (NRRU-F01010023), side view; **9.** Recent *P. anamensis*, side view; **10.** *P. hilliana* (NRRU-F01010019), cross section, showing two seminal cavities; **11.** *P. khoratensis* (NRRU-F01010022), cross section, showing two seminal cavities; **12.** Recent *P. anamensis*, cross section, showing two seminal cavities. Scale bar = 10 mm (1–12)

of fibers and ellipsoidal sclereids, giving a marbled, or marbled, appearance.

Description. Endocarp, transversely broadly oblong in side view, nearly transversely elliptic in cross section, but slightly concave on one side, 19.6–20.8 mm high, 22.5–23.4 mm wide, height/width (H/W) ratio 0.84–0.92, 13.5–15.6 mm thick, width/thickness (W/T) ratio 1.31–1.73. Surface smooth or slightly pitted, without deep furrows or ridges, or a few furrows on one side

(NRRU-F01010020). Two basal elliptic germination plugs, 11.0–12.0 mm long by 5.2–7.7 mm wide, each covering a seminal cavity, separated by 4.4–4.9 mm and lacking a beak between the plugs. Two small openings between the 2 plugs, presumably for vascular bundles, suggesting that the plugs are basal. Endocarp wall thick, 2.0–4.4 mm, and the 2 seminal cavities separated by a septum 0.8–0.9 mm thick. Seminal cavities 7.8–8.0 mm wide by 4.8–9.2 mm thick (N = 2). The endocarp wall consisting of swirling

Table 1. Characteristics of extant and fossil endocarps of Chrysobalanaceae similar to those of *P. hilliana* and *P. khoratensis*

Species	Seminal cavities	Endocarp interior	Release of embryo	Endocarp	Endocarp surface	Locality	Age	Reference
<i>Parinari hilliana</i> Grote	2 ^a	Hairs, long, slender, twisted	2 basal germination plugs	Transversely broadly oblong, 2.0–2.1 cm high	Smooth or slightly pitted, furrows absent or only on one side	Northeastern Thailand	Late Miocene	This study
<i>Parinari khoratensis</i> Grote	2	Hairy	2 basal germination plugs	Broadly oblong or broadly elliptic; beak between plugs, 2.2–3.0 cm high	Deep longitudinal elongate furrows, some extending the length of the endocarp and some shorter and discontinuous	Northeastern Thailand	Late Miocene	This study
<i>Neocarya macrophylla</i> (Sabine) Prance	2	Fine, soft wool	2 small basal germination plugs	Transversely broadly oblong, beak between plugs; cavities within endocarp	Rough, fibrous, with ridges	Western and North-eastern Africa	Extant	Hill, 1937; Prance and White, 1988
<i>Parinari anamensis</i> Hance	2	Hairy	2 basal germination plugs	Broadly ellipsoid or broadly oblong, 2.0–4.0 cm high	Longitudinal ridges and deep grooves	Thailand, Cambodia, Laos, Vietnam	Extant	Kostermans, 1965; Prance and White, 1988; this study
<i>Parinari costata</i> (Korth.) Blume subsp. <i>rubiginosa</i> Ridley) Prance	2	Hairy	2 basal germination plugs	Drupe ellipsoid, 4.2 cm high, 3.3 cm high	–	Southern Thailand, Myanmar, Malaysia, Philippines	Extant	Prance and Sothers, 2003; this study
<i>Parinari rigida</i> Kosterm.	2	Lanate	2 basal germination plugs	Drupe irregularly ellipsoid, 5 cm high, 4 cm wide, base tapered almost into a stipe	–	Southern Thailand, Peninsular Malaysia, Borneo, Sumatra	Extant	Prance, 1989
<i>Parinari antiquum</i> Tiffney	2	Short round-tipped papillae	2 plugs	Elongate-ovoid; 2.2–3.2 cm high, isodiametric and elongate cavities in outer part of endocarp	Smooth to slightly fibrous and rough	Fejej, Ethiopia	Early-middle Miocene	Tiffney et al., 1994
<i>Parinari</i>	2	–	2 basal stoppers	Elliptic or obovate, sometimes narrowly elliptic or ovate, 1.9–3.0 cm high	Anastomosing longitudinal grooves and ridges	Colombia	Middle Miocene	Wijninga, 1996
<i>Colombicarpon biloculare</i>	2	Interdigitating cells	2 plugs	–	–	Colombia	Tertiary	Wijninga, 1996; Jud et al., 2016
<i>Parinari</i> sp. 2	2	Woolly trichomes	2 basal germination plugs	Elliptic drupe, 3.7–5.3 cm high, 1.3–2.0 cm wide	–	Costa Rica	Pleistocene	Lott et al., 2011; Jud et al., 2016
<i>Parinari panamensis</i> Jud, Nelson, and Herrera	2	Hairs	2 basal germination plugs	Ellipsoidal to oblong, 21–40 mm high	Smooth to shallowly pitted, with shallow irregular, longitudinal grooves	Panama	Early Miocene	Jud et al., 2016

^a Two seminal cavities in the fruit arising from a false dissepiment (secondary septum) dividing a locule

bundles of fibers and ellipsoidal sclereids, giving a marmorate appearance.

The layer of the endocarp facing the seminal cavity consisting of parallel rows of fibers several cells thick, with a dense layer of hairs in the seminal cavity; the outer boundary with a zone of spherical or slightly ellipsoidal idioblasts (up

to 33 µm long). The remaining outer layer of the endocarp consisting of thick swirling bundles of fibers and clusters of elliptic sclereids (up to ca 47 µm long). These two layers appear to correspond to the second layer (L2) and outermost layer (L3), respectively, of endocarps of *Parinari* spp. described by Jud et al. (2016).

Affinities. Genera with biloculate endocarps and germination plugs include *Operculicarya* H. Perrier, *Pourpartia* Comm. ex Juss., and *Sclerocarya* Hochst. (Anacardiaceae R.Br.) and *Parinari* and *Neocarya* (Chrysobalanaceae) (Prance and White, 1988; Herrera et al., 2018). However, the endocarps of the anacardiaceous genera have apical germination plugs and lack hairs in the locules. Fruits of Chrysobalanaceae are drupes with a single locule or 2 seminal cavities derived from a false dissepiment (secondary septum). Some genera show special mechanisms of release of the embryo, whereas other genera do not. The inner layer of the endocarp facing the seminal cavities is often hairy (Table 1; Supplementary File¹). Only 2 genera in the family have basal obdurators or germination plugs, *Parinari* and *Neocarya* (Prance and White, 1988). These two genera also have hairy linings of the seminal cavities (Hill, 1937; Prance and Sothers, 2003), both features of which are found in the fossil endocarps. The endocarp wall of *Neocarya*, however, contains many cavities (Prance and White, 1988), a characteristic not found in the fossils. The endocarps are also marmorate in *Maranthes* Blume (Kostermans, 1965), but the endocarps of that genus have lateral plates rather than basal plugs (Prance and White, 1988). Therefore, the fossil endocarps can be placed in the genus *Parinari* of Chrysobalanaceae. *Parinari hilliana* differs from *Parinari anamensis*, the only extant species occurring in Northeastern Thailand, which possesses longitudinal ridges and deep grooves on the outer surface of the endocarp and is convex on both sides. *Parinari costata* (Korth.) Blume subsp. *rubiginosa* (Ridley) Prance, with a dried fruit 4.2 cm long and 3.3 cm wide, including a thin mesocarp, and *P. rigida* Kosterm., with fruits 5 cm long and 4 cm wide, including a thin mesocarp, both occur in southern Thailand, but have larger endocarps than the fossil endocarps (Prance, 1989; this study).

Fossil endocarps of *Parinari* are known from the Miocene of Ethiopia and the early Miocene to Pleistocene of Central and South America (Table 1). *Parinari antiquum* Tiffney (Tiffney et al., 1994) was described from the early-middle Miocene of Fejej, Ethiopia, based on fossil drupes and locule casts. These

differ from our fossils in having isodiametric and elongate cavities in the outer part of the endocarp. In addition, the locule linings have short, round-tipped papillae rather than hairs. *Colombicarpon biloculare* Reid from the Tertiary of Colombia is considered tentatively to be *Parinari*, but differs in having locules lined with digitating cells (Wijninga, 1996; Jud et al., 2016). Lott et al. (2011) described 2 fossil drupes from a Pleistocene deposit along the banks of the Rio Puerto Viejo, Heredia Province, Costa Rica, which they referred to as *Parinari* sp. 2. However, the dimensions do not appear to match our fossils. These drupes are elliptic, 3.7–5.3 cm long, and 1.3–2 cm wide, with exocarp and mesocarp each 1 mm thick, so the endocarps presumably would be more elongate than ours. A section of one drupe shows an endocarp that is circular in cross section. *Parinari panamensis* Jud, Nelson, and Herrera (Jud et al., 2016), from early Miocene sites in Panama, is based on a large collection of fossil endocarps. The endocarps are ellipsoidal to oblong, 21–40 mm long and 15–27 mm wide, nearly circular in cross section, and possess longitudinal grooves on the outside of the endocarp, unlike those of *P. hilliana*.

Parinari khoratensis

Grote sp. nov.

Holotype. NRRU-F01010021 (Pl. 1, figs 2, 5).

Paratypes. NRRU-F01010022 (Pl. 1, fig 11; Pl. 2, figs 2, 5, 8, 11), NRRU-F01010023 (Pl. 1, figs 3, 8).

Repository. Northeastern Research Institute of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, Nakhon Ratchasima, Thailand.

Type locality. Phra Phut sandpit (sandpit No. 11), Phra Phut Subdistrict, Chaloem Phra Kiat District, Nakhon Ratchasima, Thailand (14°59'54"N latitude, 102°14'43"E longitude).

Stratigraphic horizon. Greyish sandy deposits of the lower reduced unit, Tha Chang beds. Late Miocene in age.

Etymology. Khorat is the common name of the province of Nakhon Ratchasima, where the specimens were collected.

Diagnosis. Endocarp, broadly oblong or broadly elliptic in side view, transversely

¹ Supplementary File 1: Genera of Chrysobalanaceae and characteristics of the endocarps

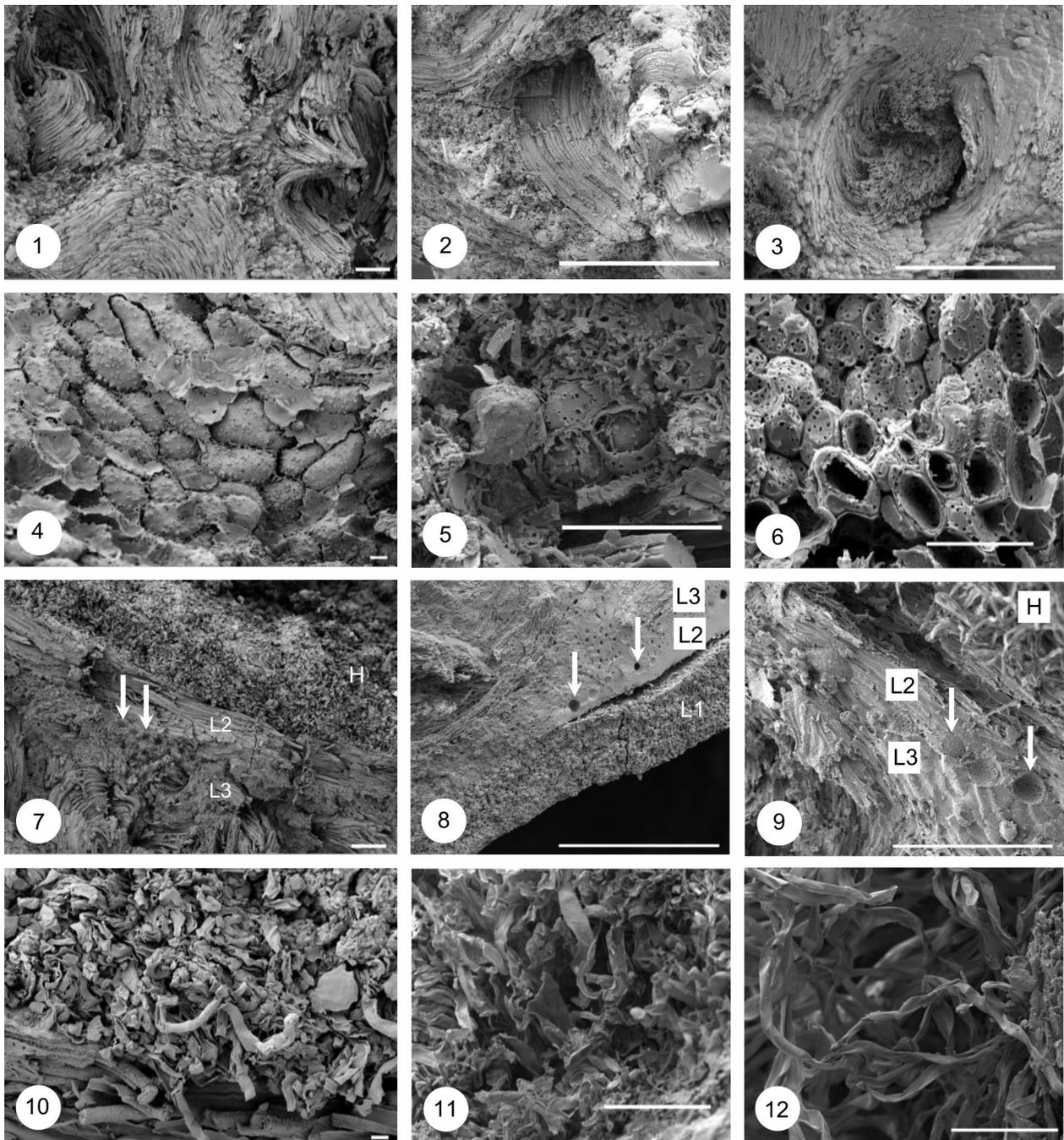


Plate 2. Scanning electron micrographs of fossil and recent *Parinari* spp. **1.** *P. hilliana* (NRRU-F01010019), outer layer of endocarp, showing swirls of fibers and sclereids; **2.** *P. khoratensis* (NRRU-F01010022), outer layer of endocarp, showing swirls of fibers and sclereids; **3.** Recent *P. anamensis*, outer layer of endocarp, showing swirls of fibers and sclereids; **4.** *P. hilliana* (NRRU-F01010019), outer layer of endocarp, showing clusters of sclereids; **5.** *P. khoratensis* (NRRU-F01010022), outer layer of endocarp, showing clusters of sclereids; **6.** Recent *P. anamensis*, outer layer of endocarp, showing clusters of sclereids; **7.** *P. hilliana* (NRRU-F01010019), showing second endocarp layer (L2), with hairs (H) in the seminal cavity and idioblasts (arrows), and outer endocarp layer (L3); **8.** *P. khoratensis* (NRRU-F01010022), showing inner endocarp layer (L1), second endocarp layer (L2) with idioblasts (arrows), and outer endocarp layer (L3); **9.** Recent *P. anamensis*, showing second endocarp layer (L2), with hairs (H) in the seminal cavity and idioblasts (arrows), and outer endocarp layer (L3); **10.** *P. hilliana* (NRRU-F01010019), showing hairs in seminal cavity; **11.** *P. khoratensis* (NRRU-F01010022), showing hairs in seminal cavity; **12.** Recent *P. anamensis*, showing hairs in seminal cavity. Scale bar = 10 μm (4, 10); 50 μm (5, 6); 100 μm (1, 7, 11, 12); 300 μm (2, 9); 500 μm (3, 8)

elliptic to subcircular in cross section. Surface with elongated furrows. Two elliptic germination plugs, each covering a seminal cavity, with a beak between the two plugs. Two seminal cavities separated by a septum and lined with hairs. Endocarp wall thick, consisting of

swirling bundles of fibers and ellipsoidal sclereids, giving a marmorate appearance.

Description. Endocarps, broadly oblong or broadly elliptic in side view, transversely elliptic to subcircular in cross section, 21.5–29.7 mm

high, 20.7–24.8 mm wide, H/W ratio 1.04–1.20, 14.5–21.3 mm thick, W/T ratio 1.16–1.43. Surface with deep longitudinal elongate furrows, some extending the length of the endocarp and some shorter and discontinuous. Two elliptic germination plugs, 9.8–15.8 mm long by 4.8–10.6 mm wide, 3.0–3.5 mm thick, separated by 3.9–5.0 mm, each covering a seminal cavity, with a beak-like structure between the two plugs. Endocarp wall thick, up to 4.1 mm, with two seminal cavities separated by a septum 1.0 mm thick. Seminal cavities 8.2–8.7 mm wide by 3.8–8.0 mm thick (N = 2). Endocarp wall consisting of swirling bundles of fibers and ellipsoidal sclereids, giving a marmorate appearance.

The layer of the endocarp facing the seminal cavity with indeterminate cell types, with a dense layer of hairs in the seminal cavity; the outer boundary of this layer with a zone of spherical idioblasts. The remaining outer endocarp layer external to this layer consisting of thick swirling bundles of fibers and clusters of ellipsoidal sclereids. These two layers appearing to correspond to the second layer (L2) and outermost layer (L3), respectively, of endocarps of *Parinari* spp. described by Jud et al. (2016). A layer of small cells forming the inner layer of the germination plugs appearing to correspond to the innermost endocarp layer (L1) of Jud et al. (2016).

Affinities. As in *Parinari hilliana*, these fruits have diagnostic characters of *Parinari* and *Neocarya*, namely endocarps with two germination plugs, two seminal cavities, and hairs inside the seminal cavities (Table 1). The layer of cells corresponding to the L1 layer of *Parinari* endocarps, which forms the inner layer of the basal germination plugs (Jud et al., 2016), indicates that the plugs are basal. The beak-like structure at the base of the endocarp between the basal plugs is similar to that in *Neocarya macrophylla* (Sabine) Prance ex F. White. However, the endocarp wall of the fossils does not have cavities as found in *N. macrophylla*, so the fossils are concluded to be *Parinari*. These endocarps differ from *P. halliana* in the following characters: the height greater than the width (H/W ratio greater than 1), both sides convex, without a concavity on one side, a beak-like structure between the germination plugs, and deep longitudinal furrows externally on both sides. They are similar to

endocarps of *P. anamensis*, but have a distinct beak between the germination plugs. *Parinari costata* subsp. *rubiginosa* and *P. rigida*, both of which occur in southern Thailand, have larger endocarps than the fossil endocarps (Prance, 1979; this study).

Parinari antiquum (Tiffney et al., 1994), from the early-middle Miocene of Fejej, Ethiopia, differs from our fossils in having isodiametric and elongate cavities in the outer part of the endocarp, a feature not present in our fossils. In addition, the locule linings have short, round-tipped papillae rather than hairs (Table 1). *Colombicarpon biloculare* from the Tertiary of Colombia and considered tentatively to be *Parinari* (Wijninga, 1996; Jud et al., 2016) differs in having locules lined with digitating cells. Fossil drupes of *Parinari* sp. 2 of Lott et al. (2011) from a Pleistocene deposit in Costa Rica appear to differ in shape from our fossils, being more elongate (see above). Endocarps of *Parinari panamensis* (Jud et al., 2016) from the Miocene of Panama are ellipsoidal to oblong, 21–40 mm long and 15–27 mm wide, more elongate than our fossils.

DISCUSSION

SYSTEMATICS OF CHRYSOBALANACEAE AND *PARINARI*

Parinari Aubl., 1775 (Aublet, 1775) was first described based on two species, *P. campestris* Aubl. and *P. montana* Aubl. (Prance and White, 1988). Aublet mentioned a bilocular ovary but did not seem to place much importance on it. Hooker and Bentham (1849) considered “the spurious dissepiment which separates the ovules” as “the essential character of *Paranarium* [= *Parinari*]”. Various authors before and after this included many bilocular species in *Parinari*, even when they differed in many other characters. Some species with unilocular ovaries were also included in *Parinari*. This expanded concept of *Parinari* subsequently has been divided into 7 genera by resurrecting old genera or proposing new genera: *Parinari* sensu stricto, *Bafodeya*, *Atuna* Rafinesque, *Exellodendron* Prance, *Maranthes* Blume, *Neocarya* and *Kostermanthus* (Prance, 1972, 1979; White, 1976; Prance and White, 1988). Some species of *Parinari* have also been transferred to other genera, including *Hunga* Pancher ex Prance and *Magnistipula* Engl.

(White, 1976; Prance, 1979). The fruits in all of these genera lack basal germination plugs, except for *Neocarya*, and those of *Kostermantus* have a single seminal cavity (Prance, 1979; Prance and White, 1988). The reduced *Parinari* is currently comprised of 39 species (Prance and Sothers, 2003). The endocarps of both *Parinari hilliana* and *P. khoratensis* are in agreement with those of this reduced circumscription of the genus. These revisions and realignments of genera should be kept in mind when evaluating the older records of fossils attributed to Chrysobalanaceae. Likewise, *Licania* Aubl. was found to be polyphyletic and was divided into nine presumed monophyletic genera, by the reintroduction of old generic names or proposal of new genera (Prance and Sothers, 2003; Sothers and Prance, 2014; Sothers et al., 2016) (Supplementary File 1).

FOSSIL RECORD OF *PARINARI* AND *PARINARIOXYLON*

Jud et al. (2016) presented a table on the fossil record of Chrysobalanaceae and their evaluation of the familial status of these fossils. Here we restrict our description to those fossils purported to be *Parinari* or related (as *Parinariosyylon*). Fossil wood of *Parinariosyylon itersonii* Pfeiffer and Van Heurn was reported from the Pliocene of west Java in 1928, and later from the Miocene of the Omo Basin, Ethiopia by Lemoigne in 1978 (Jud et al., 2016). *Parinariosyylon cuddalorese* Awasthi was reported from late Miocene Cuddalore Sandstones near Pondicherry, India, and from the middle Miocene Warkalli beds, Kerala, India (Awasthi, 1969; Srivastava and Aswasthi, 1996; Jud et al., 2016). *Parinariosyylon neyveliense* Awasthi and Agarwal was reported from the Neyveli lignite in Tamil Nadu, India, variously considered to be Miocene (Singh et al., 1992) or Paleocene–Eocene (Elayaraja and Kumarasamy, 2019). *Parinariosyylon splendidum* Trivedi and Ahuja was reported from Miocene–Pliocene deposits from the Siwaliks near Kalagarh, Uttarakhand State, India (Trivedi and Ahuja, 1979). Wood of *Parinariosyylon panamensis* Jud, Nelson and Herrera is from the early Miocene of Panama (Jud et al., 2016). Jud et al. (2016) confirmed that all of the above-mentioned records of fossil wood, except for *P. itersonii* from Ethiopia, could be reliably placed in Chrysobalanaceae. However,

they cautioned assigning wood to specific extant genera in the family in the absence of clear diagnostic characters. Srivastava and Awasthi (1996) likewise questioned the inclusion of *P. itersonii* from Ethiopia within the Chrysobalanaceae because of the presence of vasicentric aliform parenchyma, which is absent from this family. Awasthi and Agarwal (1986) wrote that the affinity of *P. splendidum* was doubtful based on anatomical characters. As to the affinity of *P. neyveliense*, Awasthi and Agarwal (1986) mentioned that the fossil wood anatomically matches wood of several genera of Chrysobalanaceae. However, since the only extant genus of this family on the Indian mainland was *Parinari*, they assumed that the fossil wood was *Parinari*. The recent Indian species referred to were *Parinari indicum* (Bedd.) Bedd. and *P. travancorica* Bedd. However, these species have been transferred to *Atuna* as *Atuna indica* (Bedd.) Kosterm. and *A. travancorica* (Bedd.) Kosterm., respectively (Kostermans, 1969), therefore the fossil may not be most closely related to *Parinari*. Srivastava and Awasthi (1996) mentioned that *Parinariosyylon cuddalorese* shares a gross anatomical similarity with several genera but is closer to wood of *Parinari*, particularly *Parinari corymbosa* (Blume) Miq. (= *Maranthes corymbosa* Blume) and *Parinari salomonensis* C.T. White (= *Parinari papuana* C.T. White subsp. *salomonensis* (C.T. White) Prance).

Fossil leaves assigned to *Parinari* include *Parinari* sp. 1 from the Pleistocene of Costa Rica (Horn et al., 2003; Lott et al., 2011) and *Parinari kathgodamensis* Prasad from the middle Miocene Siwalik deposits, of Kathgodam, Uttarakhand, India (Srivastava et al., 2015). Chaney (1933) provisionally identified leaves as *Parinarium* (= *Parinari*) sp. from the middle Tertiary of Uganda. Jud et al. (2016) mentioned the difficulty of assigning fossil leaves to specific genera of Chrysobalanaceae or even to the family.

Only a few fossil fruits have been attributed to *Parinari*. *Parinari antiquum* (Tiffney et al., 1994) was described from the early-middle Miocene of Fejej, Ethiopia, based on fossil drupes and locule casts. The locule linings have short, round-tipped papillae rather than hairs. Wijninga and Kuhry (1990) referred to endocarps from the Pliocene of Colombia as cf. *Parinari*-type. The endocarps have two valves running from the top to the base, which appear to differ

from extant *Parinari* endocarps with basal valves or plugs. We consider the association to *Parinari* doubtful as did Jud et al. (2016). Wijninga (1996) described endocarps identified as *Parinari* from deposits in Colombia considered to be middle Miocene in age. The endocarps had two basal stoppers and a surface with anastomosing longitudinal grooves and ridges; the characteristics of the locules were not mentioned. Wijninga (1996) also wrote that endocarps of *Colombicarpon biloculare* from the Tertiary of Colombia, attributed to Anacardiaceae by Andrews (1970), were probably *Parinari*. However, the locules were reported to be lined with digitate cells and not hairs (Jud et al., 2016). Lott et al. (2011) described 2 fossil drupes from a Pleistocene deposit along the banks of the Rio Puerto Viejo, Heredia Province, Costa Rica that they referred to as *Parinari* sp. 2. *Parinari panamensis* (Jud et al., 2016) from three early Miocene sites in Panama is based on a large collection of fossil endocarps. Fruits of *Parinari curatellifolia* Planch. ex Benth. were collected from a Holocene archaeological site in Zambia (Phillipson, 1976). Although leaves of *Parinari* and wood of *Parinarioxylon* have been reported from the Miocene of India, and *Parinarioxylon* from the Pliocene of Java, Indonesia, fossil endocarps have not been reported from Asia or the Pacific region prior to the present study.

BIOGEOGRAPHIC INFERENCES

As mentioned above, Bardon et al. (2016) suggested that *Parinari* originated in Africa, and that from there it dispersed to Southeast Asia, and later from Southeast Asia to the Neotropics. Chave et al. (2020) stated that the site of origin of the genus was less certain, perhaps in the Neotropics. The previous fossil record based on endocarps, which can be more reliably identified to genus than leaves or wood, showed the presence of *Parinari* in the Neotropics by the early Miocene and in Africa (Ethiopia) by the early or middle Miocene. The present study indicates that the genus was also present in continental Southeast Asia by the late Miocene, showing that the genus was pantropical by that time. These results are concordant with trans-oceanic dispersal across the Pacific and/or Atlantic Ocean by the Miocene, but do not indicate the directions or timing of dispersal.

At present, three species of *Parinari* occur in Thailand. *Parinari anamensis* occurs in central, northern, and northeastern Thailand, as well as in Cambodia, southern and central Laos, and southern Vietnam. *Parinari costata* subsp. *rubiginosa* occurs in southern and southeastern Myanmar, Peninsular Malaysia, Borneo and with one record in southern Thailand (Gardner et al., 2015). *Parinari rigida* Kosterm. is found in far southern Thailand, with one record, and in Peninsular Malaysia, Sumatra and Borneo. An additional 3 species have ranges that include Peninsular Malaysia: *Parinari elmeri* Merr., *Parinari oblongifolia* and *Parinari parva* Kosterm (Prance, 1989).

Parinari anamensis today occurs in deciduous dipterocarp, mixed deciduous and dry evergreen forests (Forest Biodiversity Division, s.d.). However, other species of *Parinari* in southern Thailand and Peninsular Malaysia are found in communities including lowland rainforest, hill forest, and heath and swamp forests (Prance and White, 1988; Prance and Sothers, 2003). Because of the variety of environments in which *Parinari* can thrive, the environment encountered by *P. hilliana* and *P. khoratensis* is uncertain.

CONCLUSIONS

Although endocarps of *Parinari* are distinctive, there have been very few reports of fossil endocarps of this genus. This study provides an additional record of *Parinari* endocarps, the first in Asia and the Pacific region. This demonstrates the presence of this genus in Asia during the late Miocene. Although the place of origin and subsequent dispersal of the genus is uncertain, these fossils indicate that by the Miocene, *Parinari* was pantropical, occurring in the Neotropics, Africa, and Southeast Asia, likely the result of trans-oceanic dispersal. Fossil leaves and wood from Asia have been reported, but while these can confirm the presence of the family Chrysobalanaceae, the identity at the generic level is less certain. Although these two newly proposed species occur in the current range of the genus, they show a greater diversity of the genus in the more northern part of the range in Asia, where currently only *Parinari anamensis* is found in northern Thailand and Indochina and *P. costata* in Myanmar.

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