GIANT SEEDS OF AN EXTANT AUSTRALASIAN LEGUME LINEAGE DISCOVERED IN EOCENE BORNEO (SOUTH KALIMANTAN, INDONESIA)

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Premise of research. The Neogene collision of the Australian tectonic plate (Sahul) with Southeast Asia (Sunda) restructured the vegetation of both regions. The rarity of plant macrofossils from Sunda has limited the understanding of precollision vegetation and plants that migrated from Sunda to Sahul. Despite the importance of legumes in the living flora, no Malesian reproductive or pre-Neogene fossils of the Fabaceae are known.

Methodology. We collected 47 plant macrofossils from the Tambak Member of the Tanjung Formation (middle-late Eocene) while surveying the Wahana Baratama coal mine near Satui, South Kalimantan, Indonesian Borneo. These fossils represent Southeast Asian forests before the Sahul-Sunda collision. We studied three isolated large (up to 72 mm in length) seeds from the upper Tambak Member, along with 43 fossil leaves and two palynological samples from the lower Tambak Member.

Pivotal results. We describe the extinct legume *Jantungspermum gunnellii* gen. et sp. nov. The *J. gunnellii* seeds are flattened on one side, bilobed, and heart shaped with a long hilum (~60 mm) overlain on the suture, closely resembling *Castanospermum*, the Australian black bean tree. The leaves represent seven morphotypes, which include Fabaceae but are otherwise unidentifiable. One specimen preserves in situ cuticle. The palynoflora includes diverse ferns and palms, Typhaceae, Onagraceae, and forest taxa, including Podocarpaceae, Sapindaceae, and Fabaceae, indicating a largely freshwater coastal swamp environment in the lower Tambak Member.

Conclusions. The *Jantungspermum* seeds are double the length of *Castanospermum* seeds, representing a closely related but extinct papilionoid taxon. The discovery suggests a Sundan precollision history, a much later Sunda-Sahul migration, and an eventual Asian extinction for the *Castanospermum* lineage, which today inhabits coastal rainforests of northern Australasia. The seeds represent the only known fossil relative of *Castanospermum*, the oldest legume fossils from Malesia, and one of the largest fossil angiosperm seeds. The new seeds, leaves, and palynomorphs provide a window into Eocene Malesian vegetation and rare macrofossil evidence of Sundan history for a living Australasian lineage.

Keywords: biogeography, Borneo, *Castanospermum*, Fabaceae, fossil seeds, Sahul-Sunda interchange.

Online enhancements: appendixes.

Introduction

The collision of the Australian tectonic plate (Sahul) into Southeast Asia (Sunda), beginning in the late Oligocene, led to one of the largest biotic exchanges of the Cenozoic (Morley 2000, 2018; Hall 2013, 2017; Kooyman et al. 2019; Joyce

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et al. 2021*a*; Skeels et al. 2023). The floristic interchange fundamentally restructured the tropical Southeast Asian and West Pacific vegetation and is considered a major contributor to the immense diversity seen in the region today (de Bruyn et al. 2014; Kooyman et al. 2019; Joyce et al. 2021*b*). The threatened biodiversity of the Malay Archipelago is comparable to and may exceed that of the Neotropics when standardized for land area, yet it is much less studied (Slik et al. 2015, 2018; Cámara-Leret et al. 2020; Joyce et al. 2020; Raven et al. 2020; Brummitt et al. 2021; Hagen et al. 2021).

Unlike the Neotropical and African rainforests, where a greater proportion of biodiversity is attributed to in situ speciation throughout the Cenozoic, the rainforests of the West Pacific and Southeast Asia attained much of their modern biodiversity through floristic interchanges facilitated by tectonic collisions (Whitmore 1987; Morley 1991, 2000, 2011, 2018; Ashton 2014; Hall 2017). The two most important Cenozoic events were the India-Asia and Sahul-Sunda collisions (Schuster 1972; Morley 2000, 2002, 2003; Klaus et al. 2016; Kooyman et al. 2019; Huang et al. 2021). The Eocene India-Asia collision is thought to have replaced the low-diversity Paleogene floras with many of the characteristic tree lineages of today's Southeast Asian lowland forests (e.g., Dipterocarpaceae and *Alangium*, Cornaceae; Morley 1982, 2000; Bansal et al. 2022). Extant plant lineages in Asia that arrived from the Australian plate, primarily during the Sahul-Sunda collision, are most commonly found in montane forests, and some occur in kerangas (heath) habitats (e.g., *Dacrydium*, Podocarpaceae, and *Gymnostoma*, Casuarinaceae; Robbins 1961; Zamaloa et al. 2006; Wilf 2012; Ashton 2014; Kooyman et al. 2019; Brambach et al. 2020). These Sahul-sourced lineages have been well studied as a result of decades of fossil sampling in Australia and the once-connected Gondwanan continents (e.g., South America, Antarctica, New Zealand; for summaries of Gondwanan-sourced taxa, see Hill 1994; Hill et al. 1999; Kooyman et al. 2014, 2019).

Conversely, there is little direct macrofossil evidence for migrations from Southeast Asia into Australasia that are associated with the Neogene Sahul-Sunda collision. Macrofossils provide critical data for testing biogeographic hypotheses (Crisp et al. 2011; Wilf and Escapa 2015; Carruthers and Scotland 2021), but most Sunda-to-Sahul dispersal hypotheses for individual taxa are inferred from palynological and molecular data (Sniderman and Jordan 2011; Yap et al. 2018, 2020; Brambach et al. 2020; for examples of hypothesized Sunda-to-Sahul taxa, see Morley 2000, 2012, 2018; Li et al. 2009; Su and Saunders 2009; Crisp et al. 2010; Grudinski et al. 2014; Federman et al. 2015; Thomas et al. 2017; Liu et al. 2021; Peng et al. 2021; Holzmeyer et al. 2023). Pollen and spores present the most readily available plant fossil data in Southeast Asia (e.g., Germeraad et al. 1968; Muller 1968; Morley and Flenley 1987; Morley 1998, 2013; Moss and Kershaw 2000; Lelono and Morley 2011; Berry 2022); however, palynomorphs commonly cannot be identified with high taxonomic precision and are prone to taphonomic biases, including long transport distances, low spatial and temporal resolution (Behrensmeyer et al. 2000; Cleal et al. 2021), and preservation biases in certain important groups (e.g., Dipterocarpaceae and many Fabaceae; Bera 1990; Huang 1999; Dixit and Bera 2013; Wilf et al. 2022). Sahul versus Sunda source hypotheses for Asian and Australasian plant lineages have been the subject of many recent biogeographic studies (e.g., Trethowan 2021; Trethowan et al. 2023; and those cited above) as well as a long series of seminal papers (Müller 1842; Wallace 1860, 1869, 1876; Huxley 1868; Stapf 1894; Lydekker 1896; Mayr 1944; Robbins 1961; van Steenis 1964; Hartley 1986; Whitmore 1987; reviewed in Ali and Heaney 2021).

The majority of Cenozoic paleobotanical (macrofossil) collections in the Malay Archipelago were made well over 100 years ago (e.g., Göppert 1854, 1864; Geyler 1877, 1887; von Ettingshausen 1883; Crié 1888; Kräusel 1929*a*). Modern sampling in Southeast Asia has been limited (see reviews in Kräusel 1929*b*; Bande and Prakash 1986; van Konijnenburg-van Cittert et al. 2004; van Gorsel 2014, 2020; Claude 2017; Wilf et al. 2022), especially in Malesia, the region that contains most hyperdiverse ever-wet Asian rainforests (Malesia includes peninsular Malaysia and the Malay Archipelago; Zollinger 1857; van Steenis 1979; Webb et al. 2010; Kooyman et al. 2019). Cenozoic fossil wood has been found in Indonesia and mainland Southeast Asia, and it often can be identified to extant tree families (e.g., Kräusel 1922, 1926; Boureau 1950; Schweitzer 1958; Mandang and Kagemori 2004; Andianto et al. 2021), but temporal and ecological information is limited because fossil wood often undergoes extensive predepositional transport and later reworking (Behrensmeyer et al. 2000). Furthermore, the fossil wood is mostly Neogene (or lacks a reliable age), recording plant lineages present after the onset of the Sunda-Sahul collision. Compression fossils, mostly leaves with rare reproductive structures, often preserve nearly in situ snapshots of plant communities (Burnham 1989, 1990; Wing and DiMichele 1995). Wilf et al. (2022) provided a rare contemporary report of compression floras from the Pliocene of Brunei, but historical collections of Cenozoic Malesian compression fossils are in need of modern taxonomic revision (Göppert 1864; Heer 1874, 1881; Geyler 1877, 1887; Kräusel 1929*b*; Posthumus 1929; Krijnen 1931; Scrivenor 1941).

Legumes (Fabaceae) are critical components of rainforest ecosystems globally; they are nitrogen-fixing plants (trees, shrubs, lianas, and herbs) that thrive in both disturbed and pristine ecosystems, and their pods are a key food source for many animals (Gentry 1993; Crews 1999; Gei et al. 2018; Mathesius 2022). Fabaceae are very diverse but less abundant in Southeast Asian lowland rainforests than in their Neotropical or African counterparts (Gentry 1988; Raes et al. 2013; Menge et al. 2019) because the Asian wet tropics are dominated by trees of Dipterocarpaceae, followed by families such as Euphorbiaceae and Fabaceae (Ho et al. 1987; Newbery et al. 1996; Slik et al. 2003; Ashton et al. 2021). The fossil record of Fabaceae in Malesia is depauperate, and no reliable nonwood macrofossils from this family are known there (see more in "Discussion").

One rainforest legume tree with no fossil record is *Castanospermum* (Papilionoideae). Known as the Australian black bean tree or the Moreton Bay chestnut tree, *Castanospermum* is a coastal taxon found today in northeastern Australasia (New South Wales and Queensland, Australia; New Britain, Papua New Guinea; New Caledonia; and Vanuatu; fig. 1; Lim 2012; Utteridge and Jennings 2022). *Castanospermum australe* A.Cunn. ex Mudie is the only living species in the genus, which grows up to 40 m in height and is dominant in old-growth and disturbed riparian forests (Floyd 1990; Lott 1997; Kitching et al. 2010). *Castanospermum* naturally disperses its seeds through water (via buoyant, salt-tolerant pods that are often consumed by freshwater pleurodire turtles; Smith et al. 1990; Gunn and Dennis 1999; Smith

Fig. 1 Distribution of the extant legume *Castanospermum* (area encircled by dashed lines) and location of the fossil site (star), the Wahana Baratama coal mine near Satui in South Kalimantan, Indonesia.

and Kinnear 1999; Armstrong and Booth 2005); however, Aboriginal groups extended the range of *Castanospermum* inland through deliberate propagation during the Holocene (Rossetto et al. 2017; Roberts et al. 2021).

Here, we report the first fossil seeds and leaves in more than a century from the Cenozoic of what is now Indonesia. The middle-late Eocene fossils and associated pollen samples from South Kalimantan, Indonesian Borneo, represent a time well before the Neogene Sunda-Sahul collision (Lohman et al. 2011; Crayn et al. 2015; Hall 2017). We emphasize the seed fossils, which represent an extinct genus and species closely related to extant *Castanospermum* and comprise the first fossil record for this lineage, the oldest definite legume fossils from Malesia, and the first macrofossil evidence from precollision Sunda of an extant Sahul lineage.

Material and Methods

Study Area and Geologic Setting

The Tanjung Formation is the oldest unit of a sedimentary succession that fills the Barito and Asem Asem Basins of southern Borneo (Kalimantan, Indonesia; figs. 2, 3). The Proto-Barito Basin most likely formed through rifting and subsidence during the early Cenozoic. The basin was later divided by the uplift of the Meratus Mountain complex in the mid-Cenozoic, forming the modern-day Barito and Asem Asem Basins (van de Weerd and Armin 1992; Witts et al. 2012; Faturrakhman et al. 2021). The Tanjung Formation consists of (from oldest to youngest) the Mangkook, Tambak (studied here), and Pagat Members (fig. 3), which have been dated in the Barito Basin to range from the late middle Eocene to the early Oligocene using biostratigraphic data

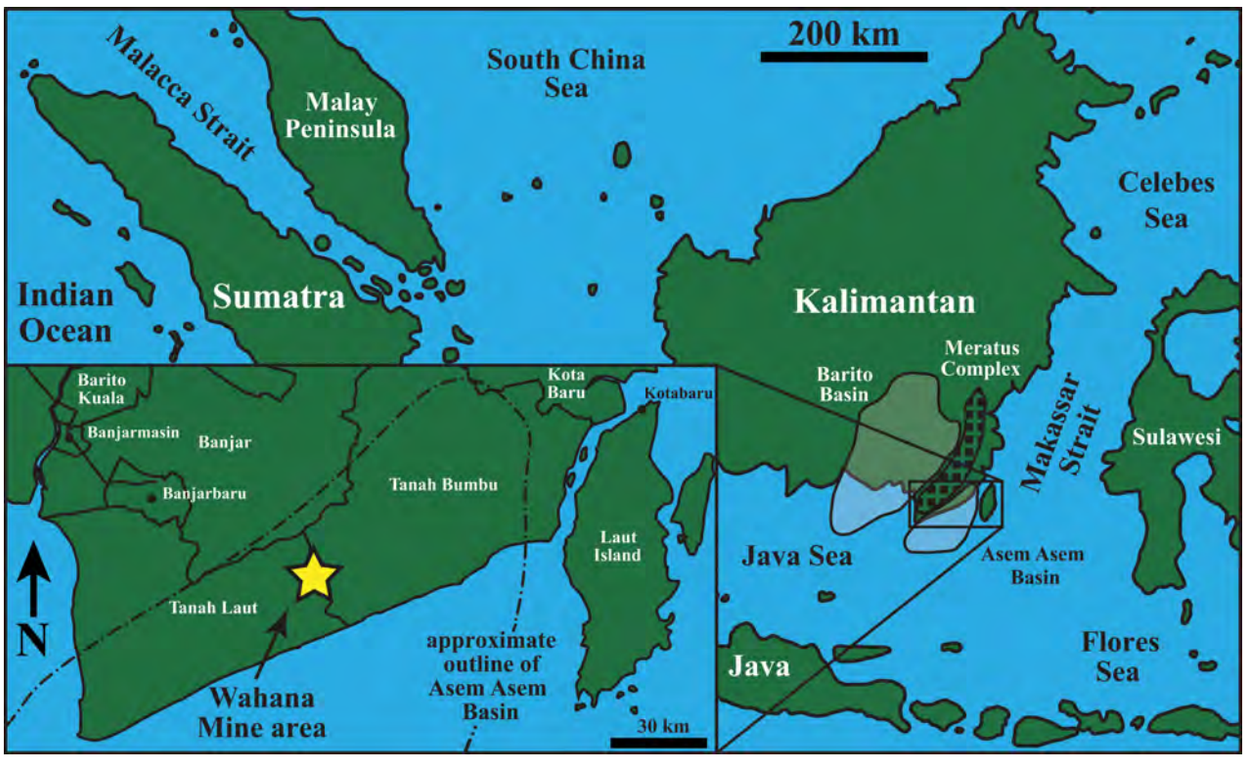


Fig. 2 Map of the Barito and Asem Asem Basins and the Meratus Mountain complex in western Malesia. Inset shows the Wahana Baratama coal mine (star; adapted from Zonneveld et al. 2024*a*, 2024*b*).

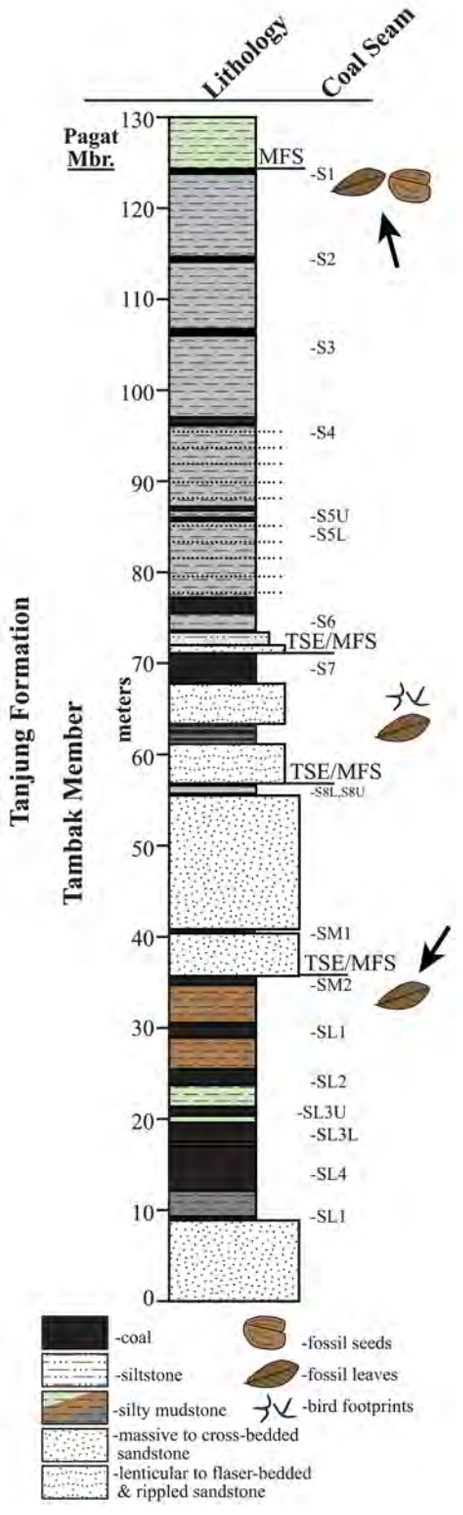


Fig. 3 Stratigraphic section of the Tambak Member of the Tanjung Formation at the Wahana Baratama coal mine. Arrows indicate the stratigraphic positions of plant fossil collection sites PW1404 (leaves and palynology samples, lower arrow) and PW1405 (seeds and leaves, upper arrow). Additional fragmentary fossil leaves were observed near fossilized bird tracks (Zonneveld et al. 2024*b*) between PW1404 and PW1405 but were not collected. Mudstone colors approximately represent those of the outcrop. The S, SL, and SM coal seam labels are the names used for the respective strata targeted by miners (adapted from Zonneveld et al. 2024*a*, 2024*b*). MFS = marine flooding surface; TSE = transgressive surface of erosion.

from foraminifera and palynology (Witts et al. 2012). The Pagat Member in the Asem Asem Basin, overlying the Tambak Member strata containing the fossils reported here in the same coal mine, has most recently been constrained to the late Eocene (Priabonian) using biozonations from large benthic foraminifera (Zonneveld et al. 2024*b*). Thus, all fossils reported here have a minimum age of late Eocene (Priabonian, ca. 33.9–37.7 Ma) and a maximum age of late middle Eocene (Bartonian, ca. 40 Ma; Witts et al. 2012).

Geyler (1877) studied plant compression fossils collected near Pengaron (van Gorsel 2020), probably from the Tanjung Formation in the Barito Basin (fig. 2); all require taxonomic revisions. Coal geologists have since noted the presence of plant macrofossils in the coaly strata of the Tanjung Formation, but they did not collect or study them (Moore and Ferm 1992; Davis et al. 2007; Fikri et al. 2022). Otherwise, since Geyler (1877), no paleobotanists have studied the formation's plant macrofossils until now. Pollen and spore taxa from the Tambak Member, collected in the neighboring Barito Basin, preserved evidence of swampy vegetation dominated by palms (*Nypa* and indeterminate Arecaceae) with additional likely forest taxa, including cycads, various ferns, Podocarpaceae, Sapotaceae, Anacoloseae (Olacaceae), Bombacoideae (Malvaceae), *Polygonum* (Polygonaceae), and *Blumeodendron* (Euphorbiaceae; Witts et al. 2012; Kristyarin et al. 2016; Winantris et al. 2017; Faturrakhman et al. 2021). There are no previous palynological reports from the Tanjung Formation in the Asem Asem Basin.

During a rapid paleontological reconnaissance in August 2014, we collected 47 plant fossils from spoil piles sourced from known stratigraphic levels in temporary mine exposures of the lower and upper Tambak Member in the Wahana Baratama coal mine located in the Satui Regency of South Kalimantan, Indonesia (Asem Asem Basin; figs. 2, 3). The fossil sites were PW1404 (lat. 3.72864°S, long. 115.29898°E) and PW1405 (lat. 3.73037°S, long. 115.29628°E). The Tambak Member is the source of the bituminous coals mined in this region, which represent coastal peat swamps (Moore and Ferm 1988, 1992; Davis et al. 2007; Fikri et al. 2022). The leaf fossils were collected from carbonaceous shale and siltstone interbeds in the coaly lower Tambak Member. Two preliminary palynology samples were later taken and processed from blocks containing leaf fossils from quarry PW1404. The upper Tambak Member, the source of the seed fossils (quarry PW1405), consists primarily of sandy mudstone lacking coal and represents a transition to offshore coastal, brackish environments seen in the overlying Pagat Member (Witts et al. 2012; Zonneveld et al. 2024*a*). Palynological samples were not collected from the seed horizon, because of the oxidized nature of the sediments and the likely low pollen yield. Other fossils previously reported from the Tambak Member of the Wahana Baratama mine include pleurodire turtles, catfish, a crab claw, and trace fossils of crustaceans, bivalves, annelids, and shorebirds (Zonneveld et al. 2024*a*, 2024*b*). The overlying Pagat Member locally contains a small sample of chondrichthyans, diverse large benthic foraminifera, and an abundant invertebrate

fauna of echinoids, corals, crustaceans, bivalves, and gastropods (Zonneveld et al. 2024*a*).

Fossil Specimens, Repositories, Preparation, and Imaging

Fossil specimens and repositories. The three seed fossils collected from the Tanjung Formation were recovered from two blocks at the same stratigraphic level (fig. 3). The blocks contain the large three-dimensionally preserved seed casts (two of them completely free of the matrix) and their associated compressed integuments. The casts are also somewhat compressed, and one of them is embedded in the matrix and could not be safely prepared or extracted. The casts preserve the near three-dimensional shapes of the seeds. The seed coats, which retain most of the informative taxonomic characters as well as the inverse seed shapes, are seen on the matrix as three-dimensional partial compressions for all the seed specimens. No remnants of the fruit body (thought to be a legume, the fruit type of all Fabaceae) were preserved. Because most other fossil Fabaceae seeds are much smaller and found still in their pods, not as isolated fossils (e.g., Herrera et al. 2019; Herendeen et al. 2022), fossil comparisons are difficult. We compared the fossil seeds to known three-dimensionally preserved fossil angiosperm seeds through a literature search and specimens of extant taxa (see "Extant specimens").

The 42 leaf compression fossils (plus one unidentifiable axis fragment) were found in the lower coal-bearing portion of the Tambak Member (fig. 3). The fossil leaves are poorly preserved, with many lacking tertiary or higher-order venation, but we report them here to supplement the palynoflora from the same horizon and to serve as references for future work about this little-known location. Additional fragmentary leaf remains were observed throughout the section but were not collected (fig. 3).

All fossils and associated pollen slides (see "Fossil preparation") are accessioned at the Institut Teknologi Bandung (ITB) in Bandung, Indonesia, following their study on loan to the Pennsylvania State University Paleobotany Laboratory and to Biostratigraphic Associates (for palynology samples). A macrofossil specimen and photographic inventory is provided in a figshare data supplement to this work (see "Data Availability").

Fossil preparation. The fossil seeds are fragile and were not prepared after field collection to avoid damaging them. The fossil leaves were prepared using standard air tools (PaleoTools Micro Jack 2 and PaleoAro; PaleoTools, Brigham City, UT) at the Pennsylvania State University Paleobotany Laboratory to remove excess matrix. In situ cuticle was isolated from one leaf fossil specimen (LabPal.ITB/024-A/DAUN/1408). The cuticle was visibly flaking off the leaf, and ca. 20 pieces (varying in size from ~4 to ~80 mm^2) were removed using forceps. The cuticle was submerged in 30% HCl for 7 d and rinsed with deionized water three times. Next, the coalified plant tissue was removed from the cuticle by soaking in bleach (7.5% NaOCl) for 24 h. The abaxial and adaxial cuticles were dehydrated using a graded ethanol concentration series (50%, 75%, 99%) in a 1.5-mL centrifuge tube. Each cuticle specimen was slide mounted using Cytoseal XYL (Thomas Scientific, Swedesboro, NJ).

The palynology samples were collected from two rock slabs bearing leaf fossils (LabPal.ITB/011/DAUN/1408 and LabPal.ITB/032/DAUN/1408; palynology samples are referred to by slab field numbers PW1404-11 and PW1404-32, respectively) and processed (by J. E. A. Marshall, University of Southampton) using standard methods. Samples were rough crushed to fragments that were a few millimeters in size, and 5 g were placed in a 500-mL plastic bottle. The samples were reacted with HCl (37%) to remove any carbonates. This was followed by decant washing to remove Ca^{2+}, a single treatment in 30 mL of HF (60%) to dissolve silicates, and decant washing to neutralize. This was followed by a brief treatment in hot HCl (37%) to solubilize neoformed fluorides. The samples were then rapidly diluted into approximately 200 mL of water, sieved at 6 μm before being stored in a vial in MilliQ water (Sigma-Aldrich, St. Louis, MO), and later mounted in Elvacite 2044 (Mitsubishi Chemical, Tokyo). The samples were dominated by large fragments of plant debris. In an attempt to concentrate the smaller angiosperm pollen, the residues were further processed by sieving at 50 μm and mounting additional slides of the 6–50-μm size fraction.

Fossil imaging and computed tomography scanning. All macrofossils (and comparative extant material) were imaged using Nikon D90 and D700 DSLR cameras under polarized light (Nikon, Melville, NY). A GE Phoenix v|tome|x L (Universal Systems, Solon, OH) was used for computed tomography (CT) scans (raw scan data are available with open access on figshare [https://10.6084/m9.figshare.23713524]; see "Data Availability") of two of the three seed fossils at the Pennsylvania State University State Center for Quantitative Imaging; one was embedded in the matrix, and one was a free seed cast. The embedded seed was scanned at 260 kV and 550 μA at a resolution of 57.5 μm. The free seed cast was scanned at 240 kV and 200 μA at a resolution of 45 μm. A 0.5-mm tin filter was used on the source for both scans. The scan data were processed using Avizo (Thermo Fisher Scientific, Hillsboro, OR), Dragonfly (Object Research Systems, Montreal), and MeshLab (Cignoni et al. 2008) software.

The cuticles were examined and imaged using both transmitted light and epifluorescence microscopy, Nikon LV100 compound microscope with a DS-Ri1 camera, and Nikon NIS-Elements software (ver. 3) with an X-Cite 120 epifluorescence illumination unit (EXFO Electro-Optical Engineering, Quebec City) and an Endow GFP Longpass Emission green filter (exciter HQ470/40, dichroic Q495LP BS, emitter HQ500LP; set 41018, Chroma Technology, Rockingham, VT). Vertical *z*-stacking of cuticle images was done using Adobe Photoshop CC (continuous release versions, align and blend functions; Adobe, San Jose, CA). The cuticular characters used here follow Dilcher (1974).

The palynology slides were examined and imaged using transmitted light (Olympus CX41 microscope and C-7070 camera; Olympus, Tokyo). CorelDRAW (Corel, Ottawa), Helicon Focus (*z*-stacking functions; Helicon, Kharkiv, Ukraine), and Adobe Photoshop CC were used to compose illustrations showing the light micrographs for selected palynomorphs (all other figures were created using Adobe Photoshop CC and Illustrator CC). Counts of 300 specimens were made for both palynology samples. All plant and nonplant palynomorphs were recorded. Additional coverslips were used to scan for any palynomorphs not recorded in the original counts, and these were recorded as presence/absence.

Extant Specimens and Analysis

Extant specimens. We compared the seed fossils using several databases and regional field guides of extant and fossil seeds to determine family-level affinities (van der Burgh 1978, 1983;

Tiffney 1984; Knobloch and Mai 1986; Eriksson et al. 2000*a*, 2000*b*; Kattge et al. 2011, 2020; Cooper and Cooper 2013; Cervantes et al. 2019; Ganhão and Dias 2019; Pothasin et al. 2022 and references therein). We also used the Kirkbride et al. (2000) legume seed and fruit identification key on the Intkey DELTA software platform and the TRY plant trait database (https://www.try-db.org; Kattge et al. 2011, 2020) to find potential extant relatives with seed morphologies similar to those of the fossils. The Watson and Dallwitz (1991) Intkey DELTA key to angiosperm families did not have sufficient characters to distinguish the seed fossils. Angiosperm seeds with notably different morphological features from the fossils (e.g., seed shape, asymmetry, hilum shape) were systematically removed, leaving only Fabaceae (as described in "Remarks").

Comparisons with extant Fabaceae were done at the United States National Seed Herbarium (BARC) in the Herbarium of the National Arboretum in Washington, DC. Identification characters used for this study (table 1) were modified from Kirkbride et al. (2000, 2003, 2004), Gunn (1984, 1991), Azani et al. (2017), and Koppooscian and Isely (1966). We used Azani et al. (2017) as our taxonomic framework for Fabaceae. Botanical authorities are referenced in the text only if necessary to define new taxa because of the large number of genera discussed, but nomenclatural authorities follow standard botanical databases, such as Tropicos (https://www.tropicos.org), Kew's Plants of the World (https://powo.science.kew.org), and cited paleobotanical works for fossils. A phylogenetic analysis including the isolated fossil seeds was not conducted because no prior matrix with sufficient phylogenetic coverage and seed characters exists, and creating one de novo is outside the scope of the current project. Extant seed specimens were photographed using the same techniques as the fossils (see "Fossil imaging and computed tomography scanning"), and discrete characters of comparable taxa were measured (table 1). Published seed length and width measurements were used for size comparisons and were preferred over seed volume and mass because of the compression of the fossil seeds and the lack of published volume and mass data for many taxa, including *Castanospermum*. Length was measured as the longest major axis of the seed body, and width was then measured as the longest dimension orthogonal to length (as defined by Kirkbride et al. 2000, 2003).

To compare the fossil leaves with those of potential living relatives, we used the Wilf et al. (2021) open-access image dataset of ca. 26,000 cleared and X-rayed leaves. For extant cuticle comparisons, we used the Cuticle Database (http://cuticledb.eesi.psu.edu; Barclay et al. 2007, 2012), Metcalfe and Chalk (1950), and Wilkinson (1979). Additional material, such as herbarium specimens, was not used when studying the leaves, because the poor preservation for plant macrofossils guaranteed that no detailed statements of affinity were possible (see "Data Availability"; app. A; apps. A, B are available online), in turn providing no leads to help identify the in situ cuticle.

Morphotyping of fossil leaves. We used the leaf architecture characters defined in the *Manual of Leaf Architecture* (Ellis et al. 2009), and we tagged images of each fossil with the associated characters using Adobe Bridge (continuous release versions; Adobe) keywords, as described by Rossetto-Harris et al. (2022). Fossils with the same combinations of leaf architectural character states were designated as distinct morphotypes (see app. A; "Data Availability"). Morphotypes allow for the description of likely leaf species without requiring taxonomic identification (Dilcher 1974; Johnson et al. 1989; Ash et al. 1999; Wilf 2008). Leaves that lacked any distinctive preserved characters (ca. 56%) were deemed unidentifiable ("indet."). Each morphotype was given a distinct number preceded by the prefix "TT." No new nomenclature is proposed for the fossil leaves. Insect damage was also surveyed across the leaves (e.g., Labandeira et al. 2007), but only one tentative occurrence of a possible gall was observed. Length and width measurements were recorded for morphotypes with less than 1 cm of lamina length or width estimated as missing. All images are available with open access on figshare (https://10.6084/m9.figshare.23713524; see "Data Availability").

Results

Systematics

Family—Fabaceae Lindl.

Subfamily—Papilionoideae DC.

Genus—Jantungspermum *Spagnuolo et Wilf gen. nov.*

Type species—Jantungspermum gunnellii *Spagnuolo et Wilf sp. nov.*

Generic diagnosis. Seeds bilobed, D shaped, larger than 50 mm in length. Suture linear, wrapping around seed between the lobes. Hilum long, linear, overlain on the suture, terminating on the ventral side of the seed.

Etymology. The generic name refers to the heart-like shape of the seeds and the language of their country of origin, combining *jantung*, meaning heart (Indonesian), and *spermum*, meaning seed.

Jantungspermum gunnellii *Spagnuolo et Wilf sp. nov. (Figs. 4–6)*

Specific diagnosis. Seeds large, bilobed, flattened on the ventral side, and convex on the dorsal side. Seed length is up to >70 mm; seed width is up to >50 mm. Suture longitudinal, linear, wrapping around much of the seed body. Hilum long, linear, overlain on the suture through its length, terminating on the ventral side of the seed. Hilar groove medial, linear. Embryonic axis differentiated from seed, nestled between lobes, straight, parallel to the major axis of the seed.

Holotype. LabPal.ITB/033/BIJI/1408a, LabPal.ITB/033/BIJI/1408b, and LabPal.ITB/033/BIJI/1408c, including a cast and its corresponding and counterpart seed coat compressions in the matrix (figs. 4*A*–4*C*, 4*E*–4*G*, ht, 6*A*–6*D*).

Paratypes. LabPal.ITB/034/BIJI/1408a and LabPal.ITB/034/BIJI/1408b, including a cast still embedded in the matrix and its corresponding seed coat compression on the counterpart block (figs. 4*A*, 4*B*, 4*D*, 4*E*, pt1, 6*E*–6*H*), in the same split slab as the holotype; LabPal.ITB/036/BIJI/1408a and LabPal.ITB/036/BIJI/1408b, including a cast and corresponding seed coat compression in a separate block from the same type locality (fig. 5).

Type locality. Tambak Member, Tanjung Formation, Wahana Baratama mine, Satui Regency, South Kalimantan, Indonesia (quarry PW1405; location: lat. 3.73037°S, long. 115.29628°E; elevation: 13 m asl; figs. 2, 3). The fossils were discovered and collected on August 25, 2014.

Repository. Institut Teknologi Bandung, Bandung, Indonesia.

Table 1

Comparisons of *Jantungspermum gunnellii* to Extant Fabaceae Seeds

Species	Specimen[a]	Length (mm)[b]	Width (mm)[c]	L:W ratio	Hilum length (mm)	Embryonic axis		Outline	Outline in transect[e]	Geographic range of genus[f]
						Shape[d]	Orientation[d]			
Jantungspermum gunnellii	LabPal.ITB/033/BIJI/1408 LabPal.ITB/034/BIJI/1408 LabPal.ITB/036/BIJI/1408	72	58	1.24	105	Straight	Parallel	Bilobed, cicer-like, obovate	Cicer-like	Borneo (Eocene)
Castanospermum australe	BARC000053	37.7	30.4	1.24	24.5	Straight	Parallel	Bilobed	Cicer-like	Australasia
	BARC000054[g]	35.7	32	1.12	...	Straight	Parallel	Circular	Cicer-like	Australasia
Afgekia sericea	BARC000035	16.6	14.3	1.16	22.6	Oblique	Oblique	Circular	Compressed	South China, Myanmar, Thailand
Airyantha schweinfurthii	BARC000036	11.3	8.2	1.38	2	Oblique	Oblique	Elliptic	Compressed	Tropical Africa, Borneo
Alexa sp.	BARC000039	25.9	21.5	1.20	3.8	Straight	Parallel	Elliptic	Flattened	Neotropics
Alexa imperatricis	BARC000038	39.2	38	1.03	8.5	Straight	Parallel	Circular	Cicer-like	Neotropics
Angylocalyx braunii	BARC000041	18.64	9.7	1.92	2.2	Rounded	Oblique or perpendicular	Elliptic	Compressed	Tropical Africa
Angylocalyx oligophyllus	BARC000042	20.16	9.6	2.10	2.1	Rounded	Oblique or perpendicular	Elliptic	Compressed	Tropical Africa
Antheroporum pierrei	BARC000045	16.3	13.2	1.23	3.2	Right-angled	Oblique	Elliptic	Compressed	South China, Myanmar, Thailand
Bowringia callicarpa	BARC000046	12.9	10.6	1.22	3.8	Straight	Parallel	Circular	Compressed	Western Africa, Madagascar, southern China
Callerya cinerea	BARC000044	20.2	13.6	1.49	6.4	Oblique	Oblique	Elliptic	Compressed	Tropical and subtropical Asia, India, Australia
Camoensia brevicalyx	BARC000049	36.4	26.1	1.39	9.1	Straight	Parallel	Obovate, elliptic	Flattened	West Africa
Camoensia scandens	BARC000048	27.5	17.1	1.61	6.4	Straight	Parallel	Oblong	Compressed	West Africa
	BARC000050	30.4	25	1.22	7.4	Straight	Parallel	Ovate	Flattened	West Africa
Canavalia gladiata	BARC000047	29.4	17.7	1.66	22	Oblique	Oblique	Elliptic	Compressed	Pantropical
Candolleodendron brachystachyum	BARC000051	15.6	11.9	1.31	4.3	Deflected	Oblique	Cicer-like	Cicer-like	French Guiana
Clathrotropis brachypetala	BARC000056	62.3	37.8	1.65	3.3	Oblique	Oblique	Elliptic	Compressed	Neotropics
Clathrotropis sp.	BARC000056	50.8	40.9	1.24	5.9	Oblique	Oblique	Cicer-like	Cicer-like	Neotropics

Cordyla africana	BARC000055	30.8	22	1.40	5.8	Straight	Parallel	Elliptic	Compressed	Tropical Africa, Madagascar
Dioclea reflexa	BARC000057	35.2	29.4	1.20	64.8	Usually oblique	Usually oblique	Cicer-like	Compressed	Pantropical
Dipteryx punctata	BARC000058	23.6	14.2	1.66	3.1	Straight	Parallel	Elliptic	Compressed	Neotropics
Dussia martinicensis	BARC000059	25.7	15.2	1.69	4.4	Oblique	Oblique	Elliptic	Compressed	Neotropics
Erythrina acanthocarpa	BARC000060	18.5	18	1.03	3.9	Oblique	Oblique	Cicer-like	Compressed	Pantropical, pansubtropical
Leucomphalos capparideus	BARC000061	18.1	12.22	1.48	4.7	Straight	Parallel	Bilobed	Compressed	West Africa
Mildbraediodendron excelsum	BARC000062[h]	55.9	32.5	1.72	...	Straight	Parallel	Elliptic	Compressed	Tropical Africa
Millettia sp.	BARC000063	27.6	25.1	1.10	13.2	Oblique	Oblique	Cicer-like	Compressed	Tropical Africa, Asia
	BARC000063	20.7	20.3	1.02	5.3	Oblique	Oblique	Cicer-like	Compressed	Tropical Africa, Asia
Mucuna sp.	BARC000064	35.7	34	1.05	83.4	Oblique	Oblique	Circular	Compressed	Pantropical, pansubtropical
Ormosia coutinhoi	BARC000065	32.6	29.6	1.10	36	Straight	Variable	Circular	Compressed	Global tropics (except Africa)
Ormosia jamaicensis	BARC000066	17.6	15.1	1.17	4.8	Straight	Variable	Circular	Compressed	Global tropics (except Africa)
Oxyrhynchus trinervius	BARC000068	18.9	15	1.26	30.5	Oblique	Oblique	Cicer-like	Terete	Central America, New Guinea
Strongylodon sp.	BARC000069	22.2	20.3	1.09	45.8	Oblique	Oblique	Circular, cicer-like	Terete	Madagascar, tropical Asia, India, Sri Lanka, Australasia, Polynesia
Swartzia vaupesiana	BARC000070	31.9	26.7	1.19	63.3	Parallel	Parallel	Circular	Compressed, terete	Neotropics
Uleanthus erythrinoides	BARC000071	17.6	12.5	1.41	1.3	Straight	Parallel	Obovate	Flattened	Neotropics
Xanthocercis madagascariensis	BARC000073	16.8	13.3	1.26	3.4	Straight	Oblique or parallel	Elliptic	Compressed	Southern Africa, Madagascar

[a] Specimens are from the US National Seed Herbarium (BARC) in the Herbarium of the National Arboretum in Washington, DC, or the Institut Teknologi Bandung (ITB) in Bandung, Indonesia.

[b] Defined as the longest axis of the seed (see "Methods"; Kirkbride et al. 2003).

[c] Defined as the longest axis perpendicular to the length of the seed (see "Methods"; Kirkbride et al. 2003).

[d] Defined by Kirkbride et al. (2003). Orientation is measured with respect to the length of the seed.

[e] Cross-sectional shapes defined by Kirkbride et al. (2000).

[f] Defined by Kirkbride et al. (2003).

[g] Specimen is without a seed coat, so hilum cannot be measured.

[h] Hilum was not measured because it was poorly preserved on the peeling seed coat.

Etymology. The specific epithet honors the late Gregg Gunnell, a prominent vertebrate paleontologist (Smith 2017) and valued friend and colleague.

Detailed description. Seeds are large (up to 72 mm × 55 mm), bilobed (cicer-like), and D shaped in cross-section from having a convex dorsal side and a flattened ventral side, with a length-to-width ratio of 1.3 : 1 (figs. 4–6). The seeds are bilaterally symmetrical across the suture line with variable shapes and interpreted as overgrown (seeds grow in the pod to fill available space without predetermined shape; Azani et al. 2017). The suture is longitudinal and linear (up to 105 mm × 3 mm) and wraps around the seed (figs. 4*F*, 4*G*, 5*B*, 5*C*, 6*E*–6*H*). The hilum is elongate and linear (up to 105 mm × 4 mm), preserved in the seed coat compressions, and overlain on the suture (figs. 4*A*, 4*B*, 5*A*). The hilar groove is linear, faintly preserved, and positioned longitudinally and medially in the hilum. The hilum terminates on the flattened ventral side of the seed. Fleshy aril, pleurogram, and pseudopleurogram are not preserved or are absent. Only the paratype specimen LabPal.ITB/036/BIJI/1408b preserves evidence of the embryonic axis that is nestled between lobes, differentiated from the seed, straight, and parallel to the length of the seed (ca. 6 mm wide; fig. 5*F*). The preserved seed density is uniform throughout, with no noticeable internal features and only sand cast material observed, as seen in CT scan data (for raw CT scan data, see "Data Availability"). The embedded paratype seed (LabPal.ITB/034/BIJI/1408a) is more elliptical and less compressed (ca. 45 mm wide, with the apex missing; maximum preserved thickness: ~16 mm; figs. 4*D*, 6) than the holotype specimen (ca. 72 mm × 55 mm; maximum preserved thickness: ~8 mm; figs. 4*C*, 6) or the second paratype specimen (fig. 5).

Remarks. To delineate the family-level identification of *Jantungspermum*, we systematically compared the fossil seeds with comparable extant taxa, including Arecaceae (e.g., *Borassus*), Lauraceae (*Eusideroxylon* and *Persea*), Meliaceae (*Xylocarpus*), Sapindaceae (*Aesculus*), Sapotaceae (*Pouteria*), Anacardiaceae (*Mangifera*), and Malvaceae (*Pachira*), among many others (for a list of sources, see "Material and Methods"). For those with similar sizes or shapes, only Fabaceae species have a long and linear hilum that wraps around the seed body. *Jantungspermum gunnellii* has characters distinct to Fabaceae and Papilionoideae (Kirkbride et al. 2003; Azani et al. 2017), including its overgrown shape, linear hilum, and hilar groove (figs. 4–7). Seed shape variation within legume species and even single pods is quite common (Singh and Pokhriyal 2001; Singh and Sofi 2011); all three specimens have the same hilum features and D-shaped cross section; thus, we designated all as the same taxon despite minor differences in aspect.

Within Fabaceae, only a handful of genera have bilobed (cicer-like) seeds, including *Castanospermum* and *Leucomphalos*, or D-shaped (in cross section) seeds, including *Clathrotropis*, *Erythrina*, *Millettia*, *Alexa*, *Candolleodendron*, and *Castanospermum* (fig. 7*C*–7*H*; table 1; Kirkbride et al. 2003). Only *Castanospermum* seeds are both bilobed and D shaped, matching *J. gunnellii*. Several taxa have a long hilum that almost entirely wraps around the seed, including some (or all) species of *Castanospermum*, *Dioclea*, *Millettia*, *Strongylodon*, *Mucuna*, *Swartzia*, and *Afgekia* (fig. 7*L*–7*S*; Kirkbride et al. 2003); however, among those listed, only *Castanospermum* possesses a hilum aligned on the longitudinal suture in the bilobed seed. Many legume taxa have seed sizes comparable to those of *J. gunnellii*; some genera that reach 25 mm or longer in length include *Mora*, *Mildbraediodendron*, *Mucuna*, *Alexa*, *Angylocalyx*, *Entada*, *Canavalia*, and *Clathrotropis* (see table 1; fig. 7*F*–7*K*; Mathesius 2022). However, only *Castanospermum* seeds (fig. 7*A*–7*E*) share the same combination of characters with *J. gunnellii*, namely a cicer-like, D-shaped, bilobed, presumably overgrown shape; a hilum overlain on the suture that longitudinally wraps around the seed; and a straight embryonic axis parallel to the seed body between the seed lobes.

Although the seeds of *J. gunnellii* share many morphological characters with those of *Castanospermum*, there are some noticeable differences. The hilum terminates on the ventral side of the seeds of *J. gunnellii*, but it most often extends to the dorsal side of the seeds of *Castanospermum*. Additionally, the seeds of *J. gunnellii* are approximately double the average length of the seeds of *Castanospermum* (72 and 33 mm, respectively; table 1; Kirkbride et al. 2000, 2003). *Castanospermum* seeds also exhibit significant variability in their roundness and lobation, but similar variation is seen in *Jantungspermum* seeds (figs. 4–6). Several of these shared seed characters are observed in other legume groups (table 1), most notably extreme seed size (seen in multiple Fabaceae subfamilies). Nonetheless, no other known plant but *Castanospermum*, extant or extinct, shares the same aforementioned combination of seed characters displayed in *Jantungspermum*. The previously mentioned differences justify the need for a new genus and suggest that *J. gunnellii* was a distinct Eocene papilionoid legume closely related to extant *Castanospermum*.

Among fossil Fabaceae, most taxa are represented by leaflets, pods, or wood specimens. Isolated seed fossils are rare for the family, which makes comparisons with *Jantungspermum* difficult. Almost all known legume fossil seeds are preserved as coalified compressions within fossil pods or, less commonly, as compressed casts in the pods (e.g., Herendeen and Dilcher 1992; Magallón-Puebla and Cevallos-Ferriz 1994; Calvillo-Canadell and Cevallos-Ferriz 2005; Wang et al. 2010; Yabe and Nakagawa 2018). Some of the only other known isolated, three-dimensionally preserved fossil legume seeds are specimens of *Entada palaeoscandens* from the Oligocene and Neogene of India and New Zealand (Awasthi and Mehrotra 1995; Agarwal 2003; Conran et al. 2014). *Entada palaeoscandens* seeds are large (43 mm × 43 mm; Conran et al. 2014) and heart shaped but lack the long linear hilum and D-shaped morphology of *Jantungspermum*. Similar to *Castanospermum*, the seeds of *E. palaeoscandens* were probably water dispersed (hydrochorous), but they were more likely adapted to long-distance, fully marine dispersal (sea beans).

Leaf Fossil Morphotypes

The leaf fossil collection from the lower Tambak Member of the Tanjung Formation (fig. 8; app. A) includes 33 slabs with 43 fossil leaves. This small collection includes seven dicot morphotypes, although some of the unidentifiable leaves have features suggesting additional floral diversity. No fern, gymnosperm, or definite monocot leaf fossils are present. Of the categorized leaf fossils, 63% of the specimens are attributed to Fabaceae leaflets (morphotype TT01; fig. 8*A*–8*C*) that do not resemble

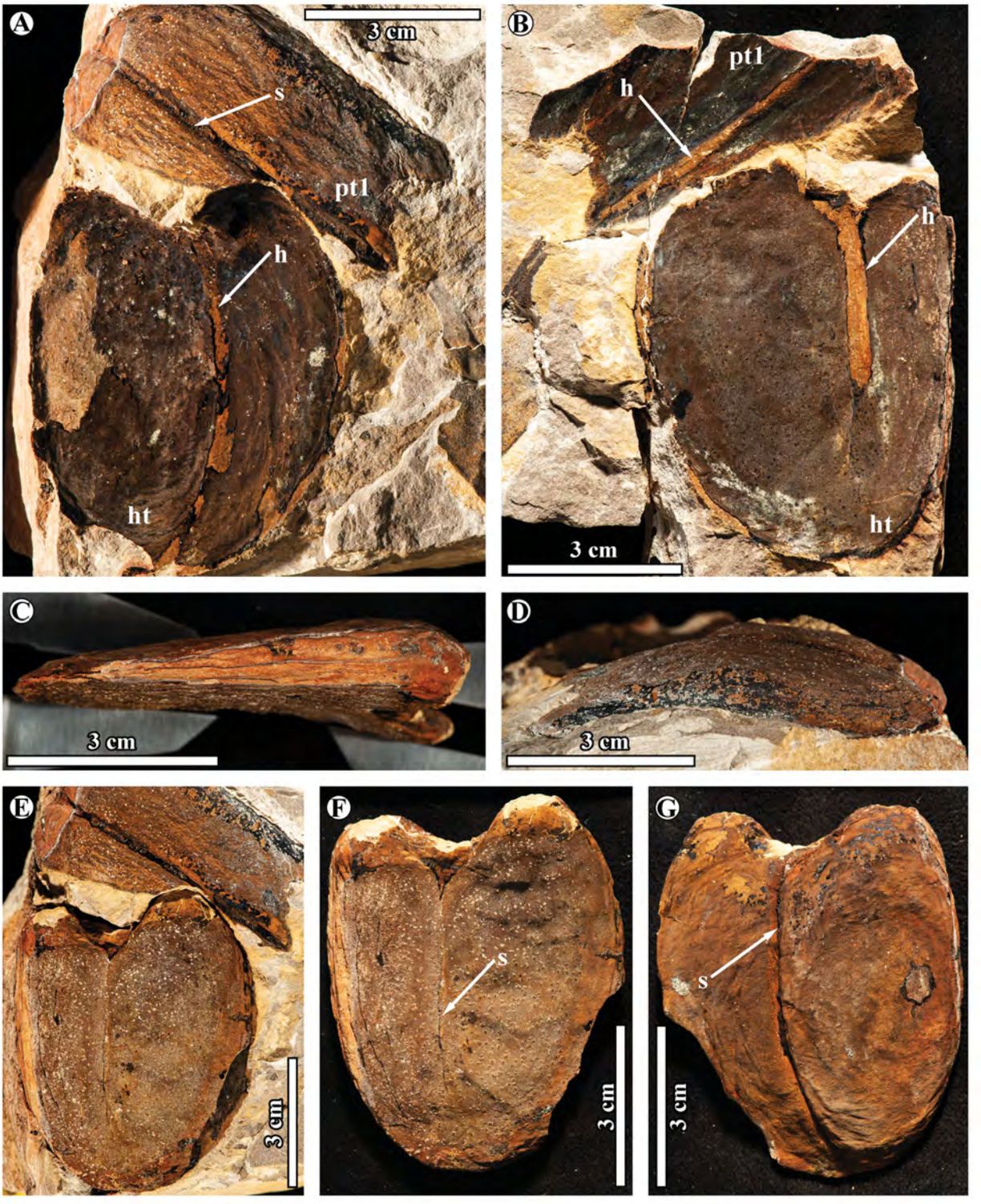


Fig. 4 *Jantungspermum gunnellii* gen. et sp. nov. *A*, Seed coat compression of holotype (ht) specimen (LabPal.ITB/033/BIJI/1408a; inner view of dorsal side) and seed cast of embedded first paratype (pt1) specimen (LabPal.ITB/034/BIJI/1408a) in dorsal view, showing the hilum (h) and the suture (s). *B*, Seed coat compressions of holotype (LabPal.ITB/033/BIJI/1408b; inner view of ventral side) and embedded paratype (LabPal.ITB/034/BIJI/1408b; inner view of dorsal side) specimens on the counterpart block. *C*, Lateral view of the holotype cast specimen (LabPal.ITB/033/BIJI/1408c) to show preserved three-dimensional seed thickness. *D*, Lateral view of embedded paratype cast specimen (LabPal.ITB/034/BIJI/1408a) to show three-dimensional seed thickness. *E*, Natural cast of holotype specimen (LabPal.ITB/033/BIJI/1408c) restored to the position found, fitting its seed coat, in ventral view (compare with *A* and *B*). *F*, *G*, Ventral (*F*) and dorsal (*G*) views of the seed cast shown in *E* (LabPal.ITB/033/BIJI/1408c).

Fig. 5 Second paratype specimen of *Jantungspermum gunnellii* gen. et sp. nov. (LabPal.ITB/036/BIJI/1408a, LabPal.ITB/036/BIJI/1408b). *A*, Seed coat compression of specimen (LabPal.ITB/036/BIJI/1408a; inner view of ventral side), showing the hilum (h). *B*, *C*, Dorsal (*B*) and ventral (*C*) views of the seed cast (LabPal.ITB/036/BIJI/1408b), showing the suture (s). *D*, *E*, Side views of the seed cast. *F*, Apical view of the seed cast, showing the embryonic axis (ea). *G*, Basal view of the seed cast, showing the suture.

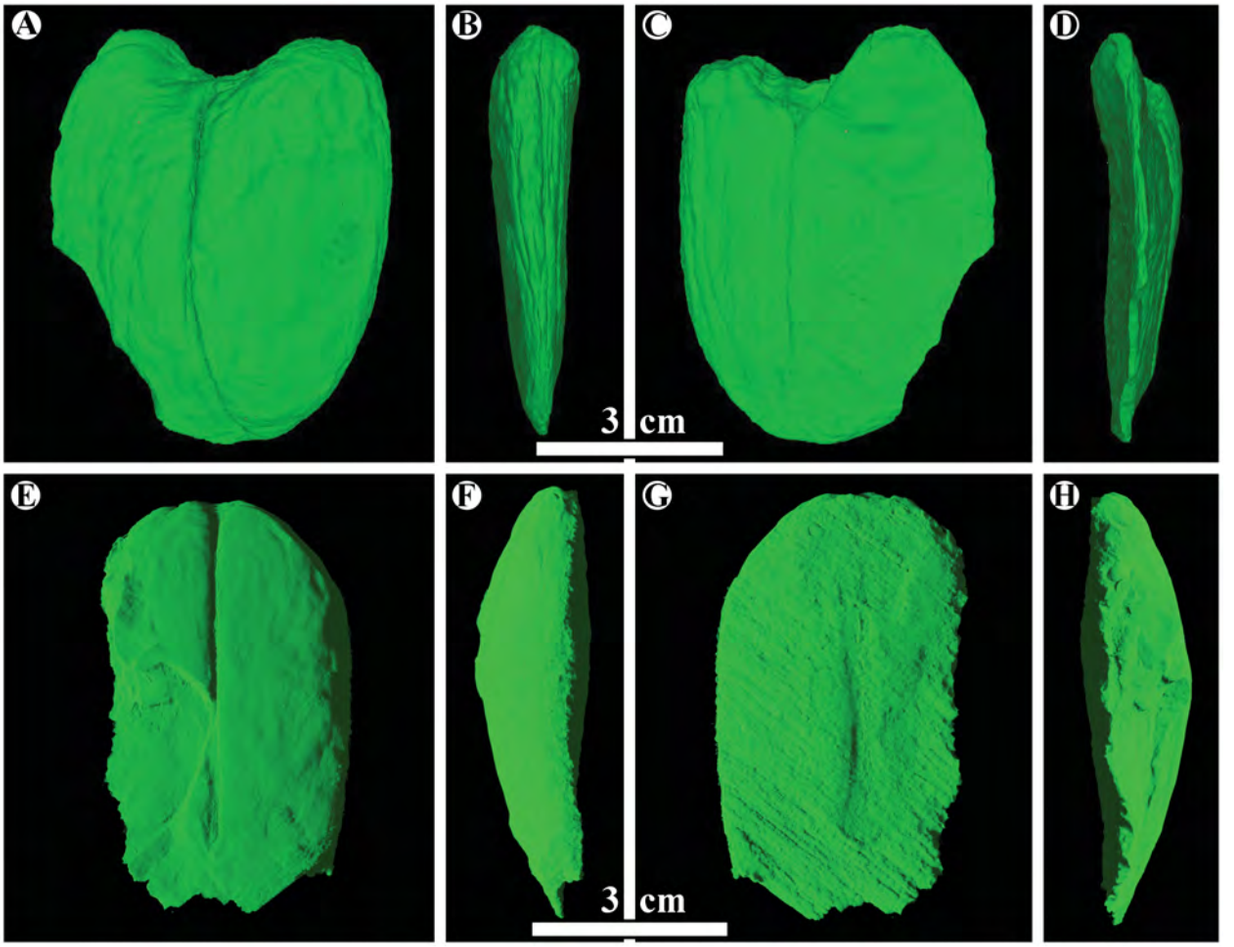


Fig. 6 Rotational views of computed tomography scans of the holotype (LabPal.ITB/033/BIJI/1408c; *A–D*) and paratype (LabPal.ITB/034/BIJI/1408a; *E–H*) seed casts of *Jantungspermum gunnellii* gen. et sp. nov.

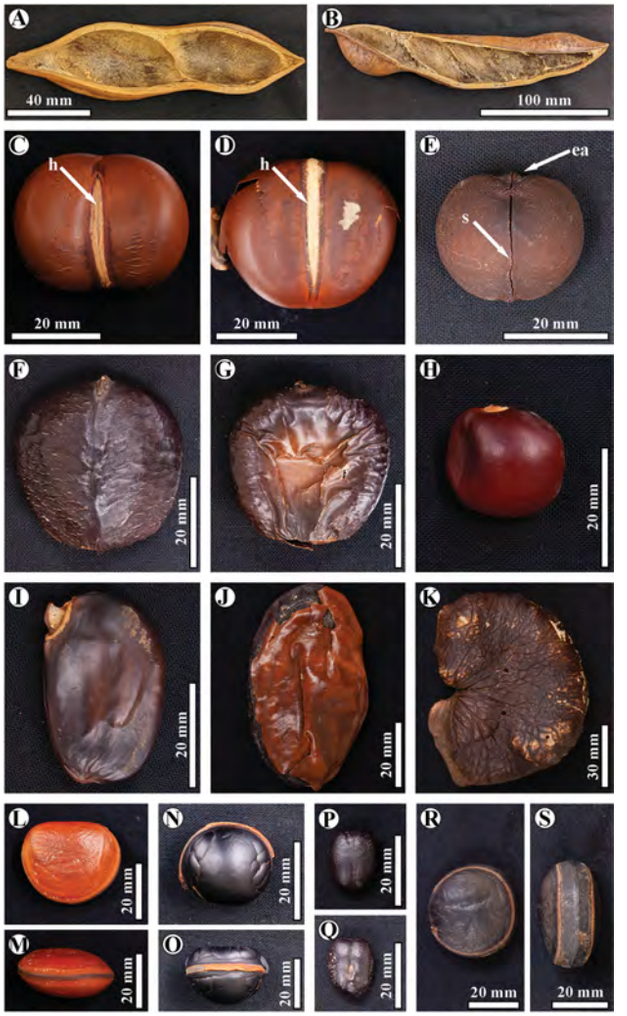


Fig. 7 Seed specimens of extant *Castanospermum* (*A–E*) and the most comparable legume taxa (*F–S*). *A*, Small seed pod of *Castanospermum australe* that held two seeds (BARC000081[A]). *B*, Large seed pod of *C. australe* that held five seeds (BARC000081[B]). *C*, *D*, Seeds of *C. australe* (BARC000053 and BARC000074) showing the hilum (h). *E*, Seed of *C. australe* (BARC000054) with the seed coat removed, showing the suture (s) and the embryonic axis (ea). *F*, *G*, Dorsal and ventral views of *Alexa* sp. seed (BARC000039). *H*, Seed of *Erythrina acanthocarpa* (BARC000060). *I*, Seed of *Camoensia brevicalyx* (BARC000049). *J*, Seed of *Clathrotropis* sp. (BARC000056). *K*, Seed of *Inocarpus* sp. (BARC000082). *L*, *M*, Seed of *Dioclea reflexa* (BARC000057). *N*, *O*, Seed of *Strongylodon* sp. (BARC000069). *P*, *Q*, Seed of *Xanthocercis madagascariensis* (BARC000073). *R*, *S*, Seed of *Mucuna* sp. (BARC000064).

those of extant *Castanospermum*. Detailed descriptions of each leaf morphotype can be found in appendix A.

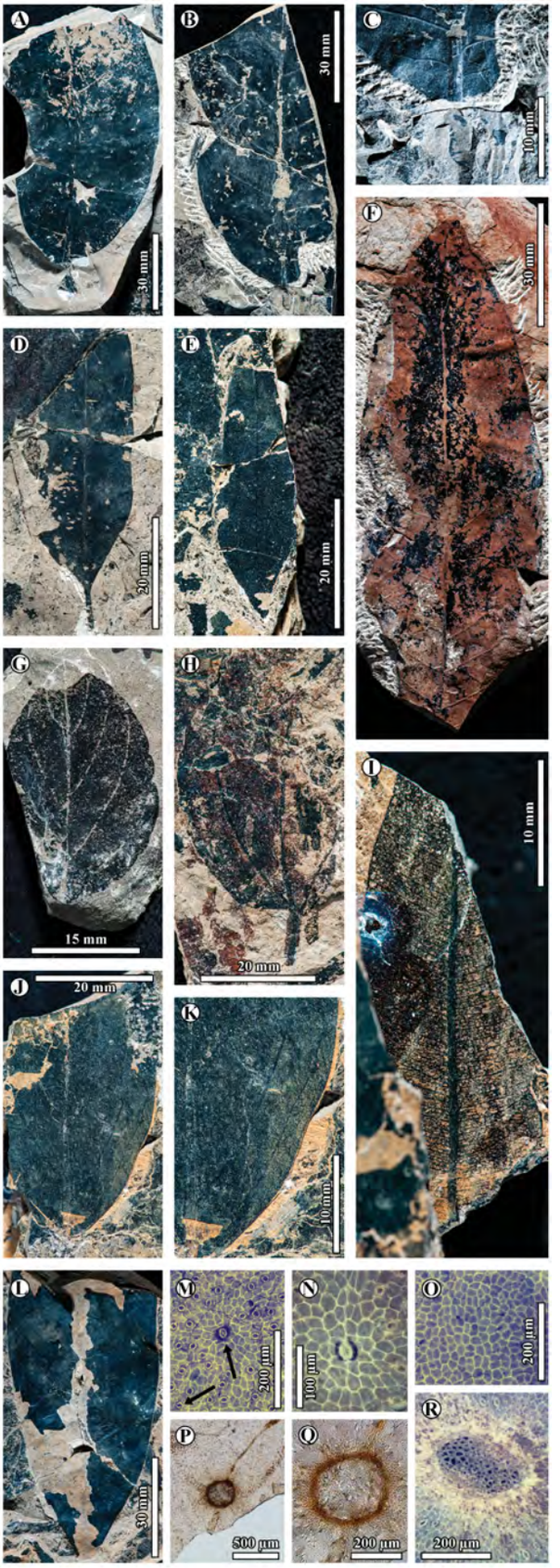
Palynology

The palynology samples from the lower Tambak Member (fig. 9), the source of our leaf fossils (figs. 3, 8), are detailed in appendix B and further discussed below (see "Discussion"). They are dominated by fungal bodies, along with palynomorphs from nine fern families, three monocot families, Podocarpaceae, and ca. nine eudicot families (without representation of papilionoid Fabaceae or the biogeographically significant family Dipterocarpaceae). Together, the palynoflora indicate a low-energy, mostly freshwater swamp paleoenvironment dominated by palms and ferns, consistent with previous reconstructions of the lower Tambak Member from stratigraphy, coal geology, and biomarkers (Guy-Ohlson 1992, 1998; Faturrakhman et al. 2021; Fikri et al. 2022; Zonneveld et al. 2024*a*). The palynomorphs include apparently new occurrences for *Pandaniidites* (possible Pandanaceae; see Stockey et al. 1997; Rozefelds et al. 2022), *Arenga* (*Arengapollenites* sp., Arecaceae), Typhaceae, Onagraceae, Apocynaceae, and Convolvulaceae in the Tanjung Formation.

Discussion

Jantungspermum gunnellii is the oldest reliable legume fossil from Malesia. The oldest definite legume fossils globally are from the earliest Paleocene of the New World, including the United States (Colorado), southern Argentina, and Colombia (Iglesias et al. 2007; Brea et al. 2008; Herrera et al. 2019; Lyson et al. 2019). The earliest fossils of Papilionoideae—the subfamily including *Jantungspermum*, *Castanospermum*, and ca. 70% of all living legume species (Azani et al. 2017)—are from the latest Paleocene of Wyoming (Herendeen et al. 2022). By the Eocene, five of the six extant legume subfamilies had fossil representatives that were discovered in North America, South America, Asia, India, Europe, and Africa (e.g., Bhattacharyya 1985; Senesse and Gruas-Cavagnetto 1990; Herendeen and Crane 1992; Herendeen and Jacobs 2000; Shukla and Mehrotra 2016; Martínez 2018; Herendeen and Herrera 2019; Jia et al. 2021).

The macrofossil record of Southeast Asian legumes, like almost all plant groups in the region, is scant and requires revision. The original paleobotanical survey of the Tanjung Formation by Geyler (1877) reported a Fabaceae leaflet or possible pod fragment (*Leguminosites*), which is fragmentary and poorly preserved and does not resemble TT01. Additional reports of leaf fossils associated with Fabaceae came from Heer (1881) from the Paleogene of West Sumatra (attributed to *Leguminosites*, *Dalbergia*, and *Cassia*) and from Geyler (1887) from the Neogene of Labuan Island in northern Borneo (attributed to *Cassiophyllites*). All these foliage fossils lack features diagnostic of Fabaceae, such as a horizontally striated pulvinus or pulvinulus (e.g., fig. 8*B*, 8*C*; app. A; Pan et al. 2023), and cannot be assigned to Fabaceae with confidence. Neogene (and Tertiary) wood fossils attributed to Fabaceae have been reported from Java, Borneo, and Sumatra (Kramer 1974; Bande and Prakash 1986; Mandang et al. 2021); however, these specimens often have poor age control and postdate the onset of Sunda-Sahul biotic interchange. Regional legume fossils are better known outside of Malesia and generally north of the wet tropics, including northern Vietnam, Thailand, Myanmar, and southern China (e.g., Edwards 1923; Prakash 1973, 1979; Prakash and Bande 1980; Vozenin-Serra 1981; Licht et al. 2014; Wang et al. 2014; Feng et al. 2015; Xu et al. 2015; Nguyen et al. 2022, 2023). Thus, the *Jantungspermum* seeds and Fabaceae leaflets reported here are the only definite Paleogene Fabaceae macrofossils from Malesia.



Despite the large size of the fossils, relatively few Fabaceae genera can reach seed sizes comparable to (or larger than; e.g., some *Entada* spp.) those of *Jantungspermum*, and most legume seeds are 5–15 mm along their longest axis (Gunn 1984, 1991; Kirkbride et al. 2003; Mathesius 2022). Today, large-seeded plants are correlated with water and animal dispersal, tree growth form, and tropical environments (Moles et al. 2005, 2007; Eriksson 2008; Sims 2010; Stevenson et al. 2023). Tropical trees with larger seeds also tend to disperse farther than higher-latitude trees with smaller seeds (Chen et al. 2019; de Jager et al. 2019). Over geologic time, angiosperms have evolved the largest range in seed size compared to those of gymnosperms and extinct seed plants; angiosperm seed size exponentially increased following the Cretaceous-Paleogene mass extinction event and may have peaked in the Eocene (Wing and Boucher 1998; Eriksson et al. 2000*a*; Sims 2012; Benton et al. 2022). To our knowledge, *Jantungspermum* is the largest Fabaceae seed fossil and one of the largest nonpalm (Gómez-Navarro et al. 2009) angiosperm seed fossils ever described.

Jantungspermum may have had similar ecological traits to living *Castanospermum*. Today, *Castanospermum* disperses its seeds using buoyant and salt-tolerant pods that can travel kilometers in rivers and oceans, especially after storm events (Smith et al. 1990; Gunn and Dennis 1999; Smith and Kinnear 1999). Unlike their pods, *Castanospermum* trees are not salt tolerant and are restricted to freshwater riparian habitats, limiting their dispersal compared to that of more salt-tolerant plants, such as the Cocoseae (Arecaceae) or *Barringtonia* (Lecythidaceae; Morley 2000, 2018). The seed fossils of *Jantungspermum* were recovered from the upper Tambak Member in a coastal, probably brackish depositional paleoenvironment (different from the more freshwater environment inferred for the lower Tambak Member; fig. 3; Zonneveld et al. 2024*a*, 2024*b*), which suggests that their pods traveled a significant distance from a riparian parent plant before disintegrating and dropping their seeds. The pods of *Castanospermum* are large (10–40 cm in length; fig. 7*A*, 7*B*) and contain up to five seeds each. Assuming that there was a similar number of seeds

Fig. 8 Leaf fossils (for morphotype descriptions, see app. A; apps. A, B are available online). *A*, *B*, TT01 legume morphotype with striated petiolule (LabPal.ITB/025-A/DAUN/1408, LabPal.ITB/012/DAUN/1408). *C*, Detail of pulvinulus of TT01 with faint horizontal striations (LabPal.ITB/012/DAUN/1408). *D*, *E*, TT02 dicot morphotype (LabPal.ITB/016-C/DAUN/1408, LabPal.ITB/018/DAUN/1408). *F*, TT03 dicot morphotype (LabPal.ITB/030-A/DAUN/1408). *G*, TT04 dicot morphotype with widely spaced, recurved secondary veins (LabPal.ITB/001/DAUN/1408b). *H*, TT05 dicot morphotype with three actinodromous primary veins and a flattened petiole (LabPal.ITB/023/DAUN/1408). *I*, TT06 dicot morphotype with high-angle, thinly gauged, and densely spaced secondary veins terminating in a fimbrial vein, along with random reticulate tertiary venation (LabPal.ITB/021-B/DAUN/1408). *J*, *K*, TT07 dicot morphotype with recurved secondary veins and random reticulate tertiary veins (LabPal.ITB/021-A/DAUN/1408). *L*, Dicot specimen with cuticle preserved (LabPal.ITB/024-A/DAUN/1408). *M*, Abaxial cuticle extracted from LabPal.ITB/024-A/DAUN/1408 under epifluorescence microscopy. Arrows indicate stomata (lower left) and possible hydathode (center). *N*, Detail of a possible hydathode under epifluorescence. *O*, Adaxial cuticle under epifluorescence. *P*–*R*, Gall-like structure on minute veins under transmitted light (*P*, *Q*) and epifluorescence (*R*).

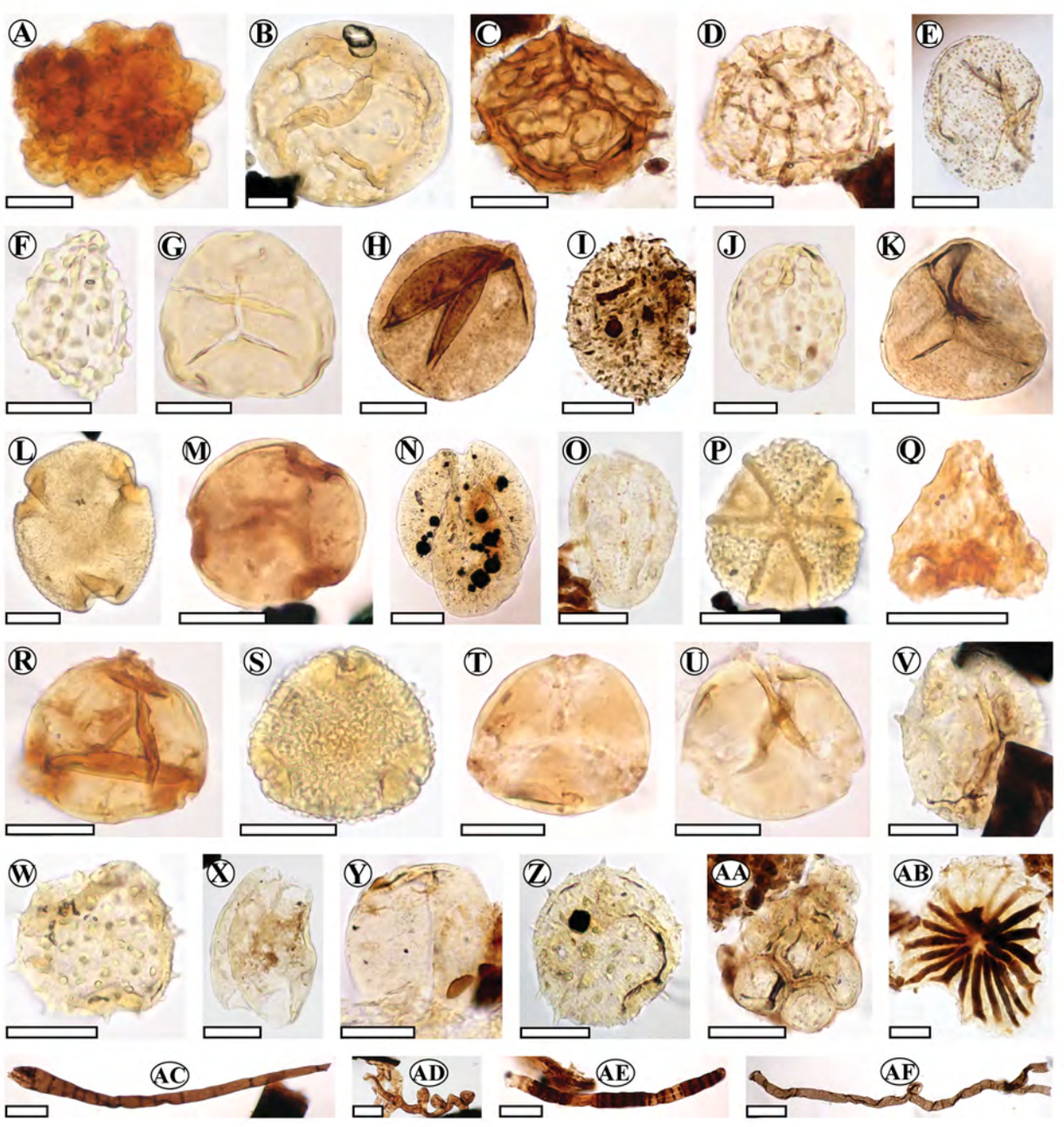


Fig. 9 Selected palynotaxa from the lower Tambak Member of the Tanjung Formation. *A*, *B*, Algae. *A*, *Botryococcus braunii*. *B*, *Zygnema*-type algal body. *C*, *Lycopodiumsporites* sp. *D–K*, Ferns. *D*, *Asplenium* sp. *E*, *Blechnum* sp. *F*, *Verrucatosporites usmensis*. *G*, *Cyathidites* sp. *H*, Osmundaceae. *I*, *Drynaria* sp. *J*, *Verrucatosporites favus*. *K*, *Acrostichum* sp. *L–U*, Eudicots. *L*, *Lanagiopollis microrugulatus*. *M*, *Cricotriporites* sp. *N*, *Perfotricolpites digitatus*. *O*, Possible Fabaceae species. *P*, *Margocolporites vanwijhei*. *Q*, Possible Olacaceae species. *R*, *Corsinipollenites* sp. *S*, *Pometiapollenites* sp. *T*, *Syncolporites* sp. *U*, *Triporopollenites*. *V–AA*, Monocots. *V*, *Arengapollenites* sp. *W*, *Spinizonocolpites echinatus*. *X*, *Longapertites* sp. *Y*, *Palmaepollenites kutchensis*. *Z*, *Pandaniidites* sp. *AA*, *Typha* sp. pollen cluster. *AB*, Peltate trichome. *AC–AF*, Fungi. *AC*, *Quilonia* sp. *AD*, *Meliolinites* sp. *AE*, *Scolecosporites* sp. *AF*, Fungal hypha. For a complete list of the palynomorphs with their affinities, see table B1 (available online). Scale bars = 20 μm.

per pod in *Jantungspermum*, the largest pods could have reached close to a 1 m in length. Taken together, we reconstruct *J. gunnellii* as an extinct riparian legume tree species with water-dispersed propagules.

Jantungspermum gunnellii is the only known fossil relative of *Castanospermum* and presumably its larger tribe Angylocalyceae—one of the earliest-diverging papilionoid clades (Cardoso et al. 2013; Azani et al. 2017). The closest extant relatives

of *Castanospermum*, determined mostly through molecular data (Cardoso et al. 2012, 2013; Azani et al. 2017), are found in Africa (*Angylocalyx*, *Xanthocercis*) and the Neotropics (*Uleanthus*, *Alexa*; Kirkbride et al. 2003). *Jantungspermum* extends the past range of Angylocalyceae into Southeast Asia, where the tribe is notably absent today, but the new fossils are not sufficient to support dispersal scenarios for the entire tribe, and we restrict our biogeographic inferences to the *Jantungspermum-Castanospermum* lineage. Without the new fossils, there would be no reason to suspect that the lineage, with an extant Gondwanan-style distribution (fig. 1), was present in Eocene Sunda or that it had migrated into Australasia through the Sahul-Sunda collision (see the introduction).

During the late Eocene, Borneo was connected to mainland Southeast Asia, and Australia was remote and still adjacent to Antarctica (Hall et al. 2008; Baldwin et al. 2012; Hall 2012, 2013, 2017). Even considering the likely hydrochorous seeds of *Jantungspermum*, arrival in Sunda from Australia by the late Eocene would be nearly impossible considering the latitudinal range involved, and there is no general fossil evidence of a floral (or faunal) Sahul-Sunda interchange until the Miocene (Burnham 1990; Lohman et al. 2011; Macphail and Hill 2018; Morley 2018; Kooyman et al. 2019; Skeels et al. 2023). Additionally, there is no fossil evidence of *Castanospermum* in Australia, which is substantially more paleontologically sampled than Malesia (Hill 1994), before the Sunda-Sahul interchange. The most parsimonious explanation for the presence of *Jantungspermum* in late Eocene Sunda and *Castanospermum* in modern Australasia is a Sundan precollision history for the lineage, a dispersal into Sahul after the late Oligocene onset of the Sunda-Sahul collision, and a later Asian extinction. Thus, *Jantungspermum* and *Castanospermum* provide the first example of a probable Sunda-to-Sahul migration from the paleobotanical record. Many Sunda-to-Sahul taxa (suggested from pollen or molecular data; see the introduction) originated in Afro-Arabia, India, Eurasia, or other regions before migrating from Sunda to Sahul (e.g., *Ctenolophon*, Ctenolophonaceae; Morley 2000, 2018). However, without any other macro- or microfossils related to *Jantungspermum*, we have no basis to extrapolate its earlier history.

The seeds and leaves also provide the first macrofossil floristic data on the terrestrial ecosystems of Eocene Borneo in over 100 years, complementing the coastal and marine vertebrate, invertebrate, microplankton, and trace fossil assemblages from the Tanjung Formation (Zonneveld et al. 2024*a*, 2024*b*; see "Study Area and Geologic Setting"). The leaves, dominated by Fabaceae leaflets, preserve small fragments of a presumably once-diverse flora. Though rare, better-preserved specimens (e.g., TT06; fig. 8*I*) and in situ cuticle preservation (fig. 8*L*–8*R*) show promise for future work. The palynoflora (fig. 9; app. B) records a diverse fern assemblage composed of at least nine families and many life history modes, such as ground cover (*Pteris*, some *Thelypteris*, and some *Blechnum*), possible tree ferns (Osmundaceae and some *Blechnum*), mangrove swamp associates (*Acrostichum* and *Thelypteris*), aquatics (*Ceratopteris*), climbers (*Pyrrosia* and some *Stenochlaena*), and epiphytes (*Asplenium* and *Drynaria*), none of which has yet been recovered in the macroflora. The Tanjung Formation palynoflora also preserves at least seven distinct Arecaceae taxa (app. B), which supports the hypothesis that Eocene Southeast Asia was an ancient hot spot for palm diversity (Huang et al. 2020). *Alangium*, *Caesalpinia*, Olacaceae (specifically *Anacolosa*), and Onagraceae (specifically *Ludwigia*) are hypothesized to have out-of-India and later Sunda-to-Sahul biogeographic histories (Phadtare and Thakur 1990; Morley 2000, 2018; Prasad et al. 2018; Farooqui et al. 2019; Huang et al. 2021). Both ideas are consistent in timing with their presence here in the middle-late Eocene of Borneo. Last, the absence of Dipterocarpaceae—the dominant tree family in modern Malesian lowland forests—in the macro- and microfossil record is an important feature to note because its rise to dominance in Southeast Asian rainforests is still poorly understood (Ashton et al. 2021); however, this absence is not definitive because of the small sample size.

Conclusions

We describe *Jantungspermum gunnellii* Spagnuolo et Wilf gen. et sp. nov., a papilionoid legume closely related to *Castanospermum*, as well as seven leaf morphotypes and a diverse palynoflora from the Tanjung Formation of South Kalimantan, Indonesia. The plant macrofossils are the first (other than wood fossils) reported from the Cenozoic of Indonesia and the Paleogene of all of Malesia in over 100 years. The macrofossils and the palynology highlight the paleobotanical potential of the Tanjung Formation (and Southeast Asia as a whole) and the need for additional paleobotanical research in the biodiverse region. These fossils are fragments from the coastal plant communities represented in the middle-late Eocene Tambak Member of the Tanjung Formation, which adds to recent discoveries of ichnofossils and marine biotas (Zonneveld et al. 2024*a*) from the same location to increase understanding of ecosystems and biodiversity present in Southeast Asia between the India collision and the Sahul collision. *Jantungspermum* seeds, legume leaflets, and Fabaceae palynomorphs together fill in a critical gap in the scant Paleogene legume fossil record of Southeast Asia, compared with the rich records elsewhere. *Jantungspermum gunnellii* is the only known fossil relative of *Castanospermum*, which is only found today in the coastal rainforests of Australia and its neighboring islands (Kitching et al. 2010). The discovery of *Jantungspermum* provides rare macrofossil evidence of the Sunda-to-Sahul plant migration and the role of the *Castanospermum* lineage in the floristic interchange that led to the immense living biodiversity of Southeast Asia and tropical Australasia (Lohman et al. 2011; de Bruyn et al. 2014; Kooyman et al. 2019).

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Data Availability

Additional images of fossil and extant seeds, fossil leaves, CT scan data, and data tables are available open access on figshare (https://10.6084/m9.figshare.23713524).

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