

Fruit morphology, anatomy and relationships of the type species of *Mastixicarpum* and *Eomastixia* (Cornales) from the late Eocene of Hordle, southern England

STEVEN R. MANCHESTER^{1*} and MARGARET E. COLLINSON²

¹Florida Museum of Natural History, Dickinson Hall, P.O. Box 117800, Gainesville, Florida, U.S.A.;
 e-mail: steven@flmnh.ufl.edu

²Department of Earth Sciences, Royal Holloway University of London, Egham, Surrey TW20 0EX,
 United Kingdom

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ABSTRACT. The Mastixiaceae (Cornales) were more widespread and diverse in the Cenozoic than they are today. The fossil record includes fruits of both extant genera, *Mastixia* and *Diplopanax*, as well as several extinct genera. Two of the fossil genera, *Eomastixia* and *Mastixicarpum*, are prominent in the palaeobotanical literature, but concepts of their delimitation have varied with different authors. These genera, both based on species described 93 years ago by Marjorie Chandler from the late Eocene (Priabonian) Totland Bay Member of the Headon Hill Formation at Hordle, England, are nomenclaturally fundamental, because they were the first of a series of fossil mastixioid genera published from the European Cenozoic. In order to better understand the type species of *Eomastixia* and *Mastixicarpum*, we studied type specimens and topotypic material using x-ray tomography and scanning electron microscopy to supplement traditional methods of analysis, to improve our understanding of the morphology and anatomy of these fossils. Following comparisons with other fossil and modern taxa, we retain *Mastixicarpum crassum* Chandler rather than transferring it to the similar extant genus *Diplopanax*, and we retain *Eomastixia bilocularis* Chandler [= *Eomastixia rugosa* (Zenker) Chandler] and corroborate earlier conclusions that this species represents an extinct genus that is more closely related to *Mastixia* than to *Diplopanax*.

KEYWORDS: fruits, *Mastixia*, *Diplopanax*, fossil, Late Eocene, Tertiary

INTRODUCTION

Both extant genera of the cornalean family Mastixiaceae have distinctive endocarps that are readily recognizable in the fossil record. Although geographically limited to Asia (*Diplopanax* and *Mastixia*) and Malesia (*Mastixia*) today, both genera are well documented by fossil fruits in the Cenozoic of Europe (Mai 1970, Martinetto 2011, Hably & Erdei 2013) and North America (Tiffney & Haggard 1996, Stockey et al. 1998). In addition, a complex of extinct mastixioid genera with endocarps similar to those of *Mastixia* and *Diplopanax*

has been recognized (reviewed in Kirchheimer 1957, Mai 1993).

Generic and specific nomenclature for fossil mastixioid fruits is complicated because many of the fossil genera and species were named before the fruit morphology and relationships of the extant representatives were well understood. The living genus *Diplopanax* Hand.-Mazz was named (Handel-Mazzetti 1933) subsequent to the designation of the extinct genera *Mastixicarpum* and *Eomastixia* by Chandler (1926), but initially it was thought to represent Araliaceae, and its affinities to *Mastixia* were only recognized 50 years later (Zeng 1983,

* Corresponding author

Eyde & Xiang 1990). Meanwhile, fossil fruits with similar morphology had been assigned to other genera such as *Tectocarya* Kirchheimer (1936), *Mastixiopsis* Kirchheimer (1936), *Mastixiodiocardium* Scott (Scott 1954, Manchester 1994) and others. The recognition and distinction of various fossil mastixioid genera were informed by degrees of departure from what was then considered to be the only modern genus – *Mastixia*. Names proliferated, with up to 16 genera and 40 species in the literature on European fossil mastixioid fruits. Some were subsequently synonymized, however, and Mai (1993) reduced the number of European fossil mastixioid genera to seven, including five extinct genera plus fossil species of the two extant genera. Difficulties remain, however, because some of the earliest-described taxa – important because of their nomenclatural priority – are less well known anatomically than some of the later-described examples.

Fossil mastixioid genera were first recognized by Chandler (1926) from the late Eocene of Hordle, England. Based upon lignified fruits, she established two new genera that were subsequently found to be widespread in the European Tertiary: *Eomastixia* and *Mastixicarpum*. The circumscription of these genera was subsequently revised as new species from other sites were added (Kirchheimer 1957, Holý 1975, Mai 1993), and by Chandler (1962) when she examined larger collections of topotypic material from Hordle as well as material from other sites. Chandler's work, both in 1926 and 1962, was careful and detailed, but limited by the tools of the time for imaging fine-structure details. Her descriptions were based on optical observations of fruits in surface view and variously fractured to reveal internal anatomy of the fruit and seed features, and informed by careful comparative work on available extant taxa.

For the present article we review the morphology and anatomy of the extant *Mastixia* and *Diplopanax* and provide detailed comparative studies of the morphology and anatomy for the type species of *Eomastixia* and *Mastixicarpum*, based on fruits from the original locality at Hordle, England. New anatomical details revealed by x-ray tomography and scanning electron microscopy improve our understanding of the relationships among these modern and fossil taxa, confirming that *Eomastixia* is close to *Mastixia* and that *Mastixicarpum* is similar to but distinct from *Diplopanax*.

MATERIALS AND METHODS

Specimens. Fruits of extant *Mastixia* and *Diplopanax* were borrowed from herbaria of the US National Museum, Washington, DC (US); Royal Botanic Gardens, Kew, Richmond, Surrey, UK (K); the Komarov Botanical Institute, Saint Petersburg (LE), and the Missouri Botanical Garden, St. Louis (MO). Fossil specimens are housed in the palaeobotany collections, Earth Department, Natural History Museum London (NHMUK; specimen numbers prefixed “V.”). Geological occurrence and locality details may be found in the original published sources (Chandler 1926, 1962, Reid & Chandler 1933), reviewed and updated by Collinson (1996) and Cleal et al. (2001). The Hordle samples (Hordle bed 10) are from the Totland Bay Member of the Headon Hill Formation of late Eocene (Priabonian) age.

Light and scanning electron microscopy. Extant and fossil fruits were studied using natural fracture surfaces and transverse sections cut with a paper-thin diamond blade mounted on a Microslice II annular saw. Naturally fractured surfaces were also studied by scanning electron microscopy (SEM) using a Hitachi S-4000 instrument at the University of Florida.

Micro-computed tomography (micro-CT). For anatomical investigation of extant material, selected fruits were examined by micro-CT at the Imaging and Analysis Centre, NHMUK, using a Nikon Metrology HMX ST 225. These included a fruit from the type material of *Mastixia pentandra* (K704731) and another from type material of *M. euonymoides* (K704785), plus two other fruits of *Mastixia euonymoides* (G. Watt 5899, K). To protect specimens and avoid using adhesive, the fruits were first wrapped in cling film and then inserted carefully into Oasis TM (foam used in flower arranging) for stability during the scan. Scanning was undertaken using a tungsten reflection target at accelerating voltage of 90 kV and current of 290 μ A, with an exposure time of 708 ms (giving a scan time of 38 minutes). No filters were used and 3142 projections were taken over a 360° rotation. Voxel sizes of the resulting datasets were 12 or 13 μ m depending on specimen size. Three-dimensional volumes were reconstructed using CT Pro (Nikon Metrology, Tring, UK) and TIFF stacks were exported using VG Studio Max (Volume Graphics GmbH, Heidelberg, Germany). Datasets were visualized, and images and videos were captured, using Avizo 8.1 (FEI Visualization Science Group, Bordeaux, France). Images were adjusted uniformly overall for contrast and brightness using Adobe Photoshop® CS2 or CS6. Micro-CT scan datasets are archived at NHMUK.

Synchrotron radiation x-ray tomographic microscopy (SRXTM). For improved resolution of anatomical details, SRXTM was applied to selected fossil specimens and fruits of extant *Mastixia* using the TOM-CAT beamline of the Swiss Light Source, Paul Scherrer Institut, Villigen, Switzerland, in March 2015 (fossils) and February 2016 (extant). For extant *Mastixia*, one fruit from type material of each of *M. pentandra* (K704731) and *M. euonymoides* (K704785) was scanned. For fossil *Mastixicarpum crassum* specimens, the holotype V20074a [figured by Chandler 1962: pl. 19, fig. 19] (detached valve in a separate scan from main fruit),

V68593i and V68593ii (two halves of the same specimen, re-registered from V20076 duplicate material) from Hordle were scanned. Both syntypes of *Eomastixia bilocularis* (V20079a, V20079b, labeled *E. rugosa* in the collection) were scanned, as was V40768 from the Bournemouth Freshwater Beds, which was figured by Chandler (1962: pl. 18, fig. 23).

Specimens examined by SRXTM were first wrapped in cling film and polyester batting to act as a stabilizing cocoon, then gently inserted into the bulb of a plastic disposable pipette which had been glued onto a brass pin. Extant *Mastixia* fruits were imaged using a 300 µm thick LuAG Ce scintillator screen (FEE, Idar-Oberstein, Germany) to convert x-rays to visible light. Samples were scanned using a X1.25 microscope objective, digitized by a sCMOS camera (PCO.edge 5.5; PCO GmbH, Kelheim, Germany) at 18 keV and an exposure time per projection of 50 milliseconds. For each scan, 1501 projections (2560 × 2160 pixels) were acquired over 180°. Tomographic data were reconstructed on a Linux PC cluster using a gridding procedure and a highly optimized routine based on the Fourier transform method (Marone et al. 2010, Marone & Stampanoni 2012) using standard absorption contrast. The theoretical pixel size is 5.2 µm. Fossil specimens were investigated in a similar manner, but with some differences as follows. The fossils were imaged using a 100 µm thick LAG Ce scintillator screen and scanned using a X2 microscope objective at 13, 17 or 20.5 keV and an exposure time 40 or 50 milliseconds per projection. In addition to standard absorption contrast reconstructions, tomographic volumes with higher contrast were also computed after phase retrieval of each projection (according to Paganin et al. 2002). The theoretical pixel size is 3.25 µm. Reconstructed images were processed at Royal Holloway University of London using Avizo 8.1 and 9.1 (FEI Visualization Science Group, Burlington, Massachusetts) for Windows 7 and further edited for contrast and brightness using Adobe Photoshop CS 5.1.

EXTANT FRUITS

Mastixia Blume

Mastixia Blume has two subgenera, Subg. *Mastixia* (11 spp.) and Subg. *Manglesia* (2 spp.). Subgenus *Mastixia* has a single whorl of 4–6 stamens and possesses fruits with a narrow dorsal infold, whereas Subgenus *Manglesia* flowers have eight stamens in two whorls, and fruits with a wider dorsal infold (Matthew 1976).

Mastixia fruits (Pl. 1) are unilocular (unlike some of the extinct mastixioid genera which range from 1- to 5-locular) and single-seeded, with a stony endocarp surrounded by a fleshy to leathery layer of mesocarp and a thin epicarp (Kirchheimer 1936, Eyde 1963). In the transition from ovary to fruit, a prominent longitudinal infold develops along the dorsal

side of the endocarp, which becomes the germination valve. This is seen on the surface of the endocarp as a narrow longitudinal slit. This infold intrudes the locule along the plane of bisymmetry, giving a horseshoe shape to the locule as seen in cross section (Pl. 1, figs 2, 4, 9, 10). Surface morphology of the fruit stone, as documented in various extant species by Kirchheimer (1936), ranges from smooth (*M. pentandra* Bl., *M. philippinenensis* Wang) to finely creased (*M. rostrata* Bl.) to knobby (*M. tetrapetala* Merrill; figured as *M. crassifolia* in Kirchheimer 1936). The dorsal infold of the endocarp is tightly closed and lacks intruded mesocarp (unlike *Diplopanax* and some of the fossil genera). In Subg. *Mastixia* the infold is narrow and parallel-sided (e.g. Pl. 1, figs 2–5), whereas in Subg. *Manglesia* the infold is wider and convex-sided (e.g. Pl. 1, figs 8–10).

A pair of unbranched vascular strands in the endocarp, which Eyde (1963) referred to as “ovular traces”, follows the margins of the germination valve and passes through the endocarp from base to the apical placenta. These traces are readily evident in transverse sections of the fruits and are represented in mature fruits by a canal on either side of the trough-shaped locule (Pl. 1, figs 2, 4, 9, 10). Eyde noted that this feature distinguishes *Mastixia* from *Nyssa* and other Cornales. Although he was unable to investigate *Diplopanax* at that time, it is now known that these genera differ in this respect – *Diplopanax* (Pl. 2) lacks the prominent pair of ovular traces. The *Mastixia* species that Kirchheimer (1936) and Eyde (1963) described were all representatives of subg. *Mastixia*, e.g. those shown here in Pl. 1, figs 2–5. We have confirmed that the same feature, paired ovular bundles, occurs in *Mastixia euonymoides* (Pl. 1, figs 9–11) of subg. *Manglesia*, as well as in the various fossil species of *Mastixia* reported by Mai (1970).

X-ray tomographic investigation, as well as standard light microscopy, shows that the germination valve margins of *Mastixia* are cryptic (e.g. Pl. 1, figs 4, 10). A well defined zone of separation tissue like that which delimits the germination valve in *Diplopanax* (e.g. Pl. 2, figs 5, 8) is not seen in *Mastixia*. Nevertheless, the valve opens lengthwise from the apex at maturity (Pl. 1, fig. 7), separating by shearing along or adjacent to those ovular bundles following a zone of very thick-walled longitudinal fibers (Eyde 1963).

Table 1. Extant collections studied

Taxon	Herbarium	Collector information	Location	Notes
<i>DIPLOPANAX</i>				
<i>Diplopanax vietnamensis</i> Averyanov & T.H. Nguyen	LE	V.X. Phuong, L. Averyanov, N.X. Tam, Nguyễn Tien V.	South Vietnam: Bach Ma National Park., Thua Thien Hue Prov., Phu Loc District, Bach Ma Mt., Hai Vong Dai peak. 16°11'46"N, 107°51'45"E at elev. 1300–1350 m	Transverse section
<i>Diplopanax stachyanthus</i> Hand.-Maz.	LE	Nguyễn Tien Ban 121 (May 29, 1977)	Northern Vietnam: Vinh Phu Province (Tam Dao II)	Loan from A. Takhtajan to R. Eyde, transverse sections
<i>D. stachyanthus</i>	US 317051	Jinhua Shi 1 (Oct. 21, 1988)	China: Huaping Nature Reserve, Longsheng Co., Guangxi Prov.	Transverse sections
<i>MASTIXIA</i> SUBG. <i>MASTIXIA</i>				
<i>Mastixia pentandra</i> Blume subsp. <i>scortechinii</i> (King) K.M. Matthew	K 704731	Clematis 919 (July 1886)	Peninsular Malaysia: P. [Brotong] Reserve Perak	Examined by CT & SRXTM
<i>Mastixia pentandra</i>	MO	H.N. Whitford 208 (May 1904)	Philippines: Bataan, Luzon	Cited as <i>M. philippinensis</i> spp. <i>philippinensis</i> by Matthew 1976. Transverse section
<i>Mastixia philippinensis</i> Wangerin ssp. <i>philippinensis</i>	US	W. Stern 2147	Philippines	Microtome transverse section of fruit by R.H. Eyde
<i>MASTIXIA</i> SUBG. <i>MANGLESIA</i>				
<i>Mastixia euonymoides</i> Prain	Kew H645/95	H.G. Watt 5899, (February 7, 1882)	India: Kupra, Manipur	Transverse fracture
<i>Mastixia euonymoides</i>	Kew 704785	M. Shaik, s.n.	Myanmar: Kachin Hills	Examined by CT & SRXTM

The pericarp of *Mastixia* includes three main zones (Pl. 1, figs 2–5, 9–11), as summarized by Eyde (1963):

1) the inner sclerified endocarp,

2) a surrounding intermediate zone with parenchyma and stone cells intermixed, which we term mesocarp (commonly soft and fleshy), and

3) an outer leathery skin, or epicarp.

Secretory cavities and/or canals are common in the mesocarp in both extant subgenera but are rare or absent in the endocarp. Although longitudinal secretory canals are common in the mesocarp of some species (Eyde 1963), Kirchheimer (1936) indicated that they are absent in *M. subcaudata*. We observed numerous narrow elongate secretory canals extending longitudinally from base to apex through the mesocarp of *M. euonymoides* (Pl. 1, fig. 11), but mostly just small rounded or ovoid secretory cavities scattered through the mesocarp of *M. pentandra* (not figured).

Diplopanax Handel-Mazzetti

Diplopanax has two extant species, distributed in southern China and Vietnam (Eyde & Xiang 1990, Averyanov & Nguyễn 2002),

both of which we investigated for fruit morphology (Pl. 2). Fruits of this genus, like those of extant *Mastixia*, are unilocular with an elongate dorsal germination valve that runs the full length of the fruit with a prominent infold that intrudes the locule, resulting in a locule that is C- or U-shaped in cross section (Pl. 2, figs 5–8). Compared to *Mastixia*, however, the fruits are much larger, and have vascular bundles scattered through the stone rather than concentrated in a pair of ovular bundles. The substantial mesocarp (e.g. Pl. 2, fig. 9) adheres firmly to the endocarp and is corky rather than fleshy. The plane of separation tissue (isodiametric sclereids or parenchyma), demarcating the margins of the germination valve, is easily visible and runs directly to the limbs of the locule in *Diplopanax* (e.g. Pl. 2, figs 5, 8, 10, 11), whereas in *Mastixia* a separation tissue is absent or indistinct. In *Mastixia*, the dorsal infold is narrow and formed chiefly by the endocarp wall, without intrusion of the mesocarp, but in *Diplopanax* the infold is wider and consists of both endocarp and mesocarp. Scattered sinuous secretory canals are prominent in the mesocarp, each of them containing a narrow vascular strand with annularly thickened

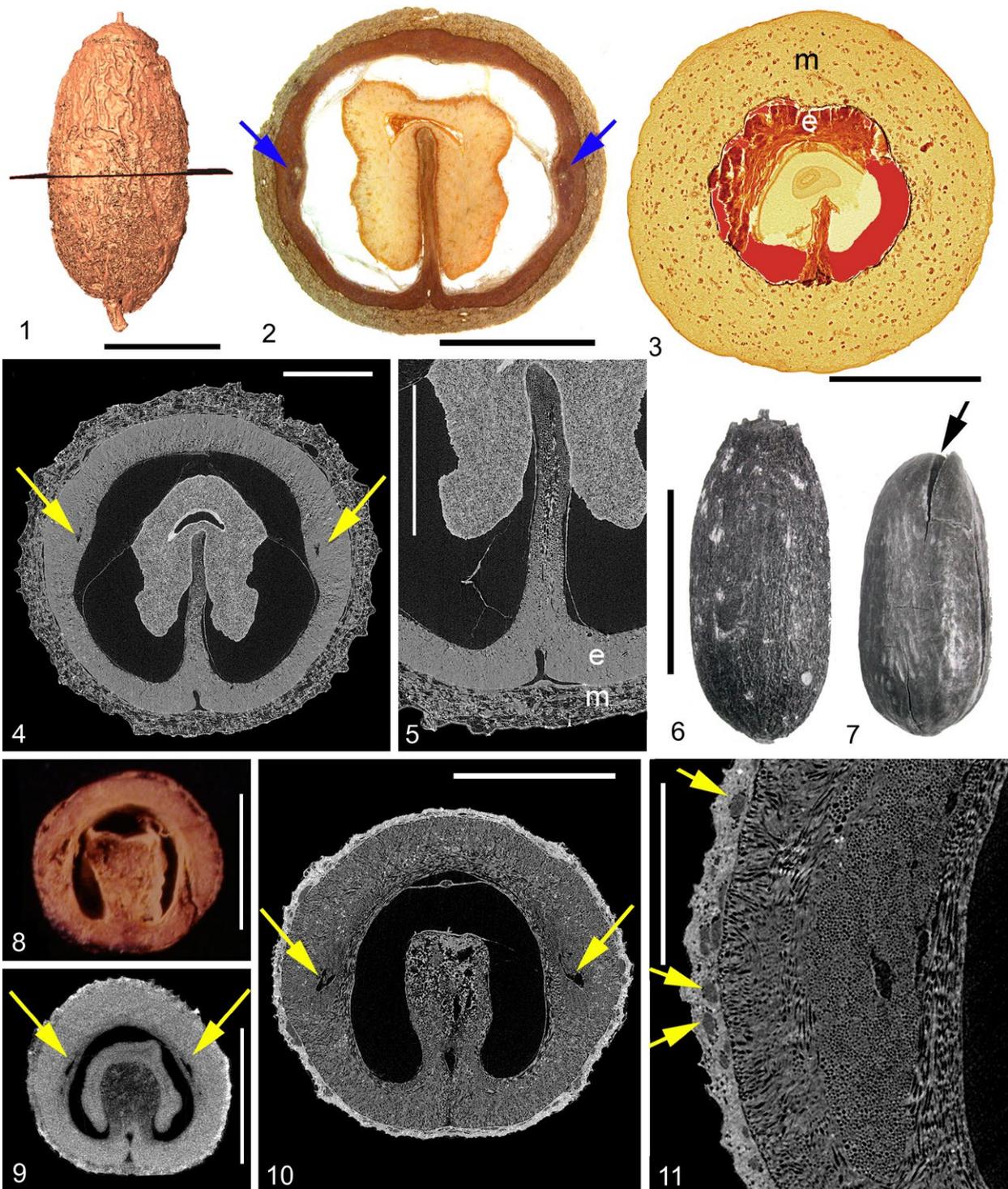


Plate 1. Fruits of extant species of *Mastixia* subgenus *Mastixia* (figs 1–5) and subgenus *Manglesia* (figs 6–11). **1.** *Mastixia pentandra* Bl. Isosurface rendering from SRXTM showing pedicel at base, calyx rim and persistent style at apex, K: 704731; **2.** *M. pentandra*, transverse section, transmitted and reflected light, showing narrow dorsal infold intruding the locule, and two ovular traces (arrows); mesocarp and endocarp nearly equal in thickness, MO: HN Whitford 208, Attaan, Luzon; **3.** *Mastixia philippinensis* Wangerin. Transverse microtome section, transmitted and reflected light of fruit with thick, soft mesocarp (**m**) surrounding the fragmentary darker endocarp tissue (**e**) and central seed intruded by dorsal infold of the endocarp. The portion of the endocarp colored red was torn away by the microtome blade, US: Stern 2147; **4, 5.** *M. pentandra*. SRXTM transverse slice. Arrows indicate ovular traces. Note small slit in narrow, parallel-sided dorsal infold, absence of mesocarp intrusion into infold, small resin bodies in mesocarp, and horseshoe-shaped locule. Endocarp (**e**) and mesocarp (**m**) distinctly separated; epicarp forming a thin wrinkled layer external to mesocarp, K: 704731; **6–8.** *Mastixia euonymoides* Prain, K: H645/95 H.G. Watt 5899, Kupra, Manipur, India; **6.** Complete fruit with apical calyx rim and persistent style; **7.** Endocarp with meso- and epicarp removed. Dorsal furrow on right side; initial split of germination valve is visible near apex (arrow); **8.** Transverse section, showing curved locule and wide dorsal infold, reflected light; **9.** *M. euonymoides*. Micro-CT scan transverse slice. Ovular trace canals indicated by arrows. Note wide dorsal infold in contrast with fig. 5, K: H645/95 HG Watt 5899; **10, 11.** *Mastixia euonymoides* by SRXTM, K: 704785; **10.** Transverse slice. Ovular trace canals indicated by arrows. Note convex-sided, wide dorsal infold; **11.** Same, detail of pericarp anatomy. Arrows indicate resin ducts in mesocarp. Scale bars: 1, 6 (applies also to 7) = 1 cm; 2–5, 8–9 = 5 mm; 10 = 3 mm; 11 = 3 mm

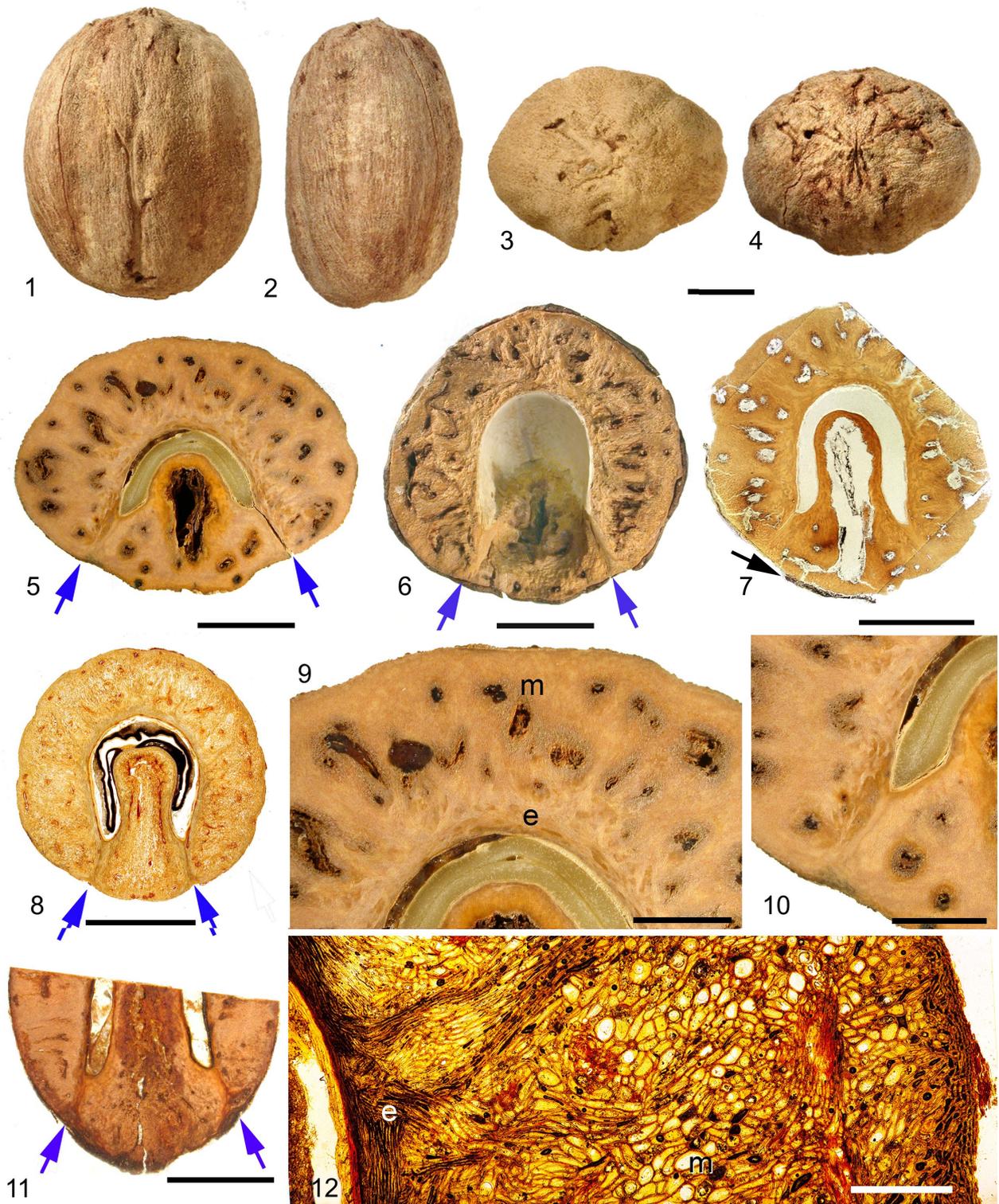


Plate 2. Extant *Diplopanax* fruit stones. 1–4. *Diplopanax vietnamensis* Averyanov & Nguyen. Stone in dorsal, lateral, basal and apical views, reflected light. LE: VX Phuong, HLF 929 [UF1155], Southern Vietnam; 5. Same, equatorial transverse slice showing seed and germination valve. Note scattered vascular bundles/secretory canals in mesocarp, reflected light, showing C-shaped locule and numerous scattered canals. Arrows indicate margins of dorsal germination valve. Note disrupted tissue in dorsal infold; 6. *Diplopanax stachyanthus* Hand.-Maz. Fruit fractured transversely, with seed and germination valve detached. Note scattered canals. Arrows indicate margins of dorsal germination valve, LE: Nguyen Tien Ban 121, Northern Vietnam; 7. Another fruit from same collection as fig. 6 in thin section by transmitted light. Note remains of thin epicarp at arrow; 8. *D. stachyanthus*. Thin section by transmitted light. Arrows indicate margins of dorsal germination valve, US 317051: Jinhua Shi no. 1, Guangxi Prov., China; 9, 10. *D. vietnamensis*, detail of endocarp from section in fig. 5, showing distinction between fibrous endocarp (e) and mesocarp (m) containing scattered canals (fig. 9), and demarcation of germination valve (fig. 10); 11. *D. stachyanthus*, same specimen as fig. 8. Longitudinal coronal section of lower half of fruit. Arrows indicate margins of germination valve; 12. *D. stachyanthus*, increased magnification of transverse section in fig. 8 extending from locule (left side) to remnants of epicarp (right side), with endocarp (e) and mesocarp (m) indicated. Scale bars: 4 (applies also to 1–3), 5–8, 11 = 1 cm; 9, 10 = 5 mm; 12 = 1 mm

elements. The secretory canals follow sinuous tracts in the mesocarp in both species of *Diplopanax* (Pl. 2, figs 5, 6, 9).

The wall of *Diplopanax* fruits consists of three distinct layers. We apply terminology for these layers similar to that which Kirchheimer (1935a) used in describing the pericarp of the related extinct genus *Tectocarya*: an inner fibrous zone comprising the endocarp, a thicker surrounding layer of soft tissue labeled mesocarp, and the outer skin, which he termed exocarp and we refer to as epicarp (Pl. 2, figs 9, 12). In treating various fossil mastixioids, Mai (1993) recognized only endocarp (inner sclerified part of the pericarp) and epicarp, including both the soft tissue and outer skin. Still another alternative is to treat the soft tissue as part of the endocarp and to consider that the mesocarp is confined to a thin fleshy layer (often collapsed in dried fruits) intergrading with the epicarp. Although care must be taken as to homologies in developing a character matrix for all cornalean fruits, here we continue to apply the traditional terms as elaborated below:

1) The endocarp is composed primarily of fibers; those near the locule mostly arranged horizontally and periclinally, but those in the outer part in tracts oriented longitudinally to anticlinally. This tissue includes fibrous lobes or longitudinal ribs extending outward into the mesocarp (Pl. 2, fig. 9).

2) The mesocarp is thicker than the endocarp and composed of small isodiametric cells in the inner part, transitioning to a thick layer of anticlinally oriented rice grain-shaped cells mixed with isodiametric cells, grading peripherally to small rounded isodiametric cells. Numerous scattered vascular bundles and secretory canals with reddish content run obliquely through this layer of mesocarp in various orientations, especially in the outer one-third (Pl. 2, figs 5–9). Isodiametric parenchyma cells surround the sinuous canals (Pl. 2, figs 10, 12).

3) The epicarp is composed of smaller flattened cells (2–5 seriate) comprising a thin dark skin (Pl. 2, figs 6, 7, 12). Whereas in *Mastixia* the ovular bundles are confined to two main strands following the margins of the germination valves, in *Diplopanax* there are typically multiple (15 or more) narrow vascular bundles extending longitudinally through the non-valve portion of the endocarp adjacent to the locule.

FOSSIL MATERIAL

Mastixicarpum Chandler

Mastixicarpum Chandler 1926

Diagnosis. “Fruit ovoid to ellipsoid; endocarp woody, 1-loculed, closely invested by the epicarp; longitudinal infold projecting into the inner cavity, but without corresponding external sulcus; associated, however, with a large, longitudinal germination valve extending along the whole length of the endocarp; locule C- or U-shaped on cross section; radial excrescences of its sclerenchymous tissue irregularly penetrating the softer woody tissue of epicarp, presenting sometimes an implication of an external network-ornamentation.”

This genus was established based on *Mastixicarpum crassum* from the late Eocene of Hordle (Chandler 1926). Subsequently, the generic concept was expanded as additional species were assigned, including *Mastixicarpum limnophilum* (Unger) Kirchheimer (1941), *M. cacaooides* (Zenker) Mai (1993) and *M. Oregonensis* Manchester (Manchester 1994, Tiffany & Haggard 1996). After fruits of modern *Diplopanax* became known, Eyde and Xiang (1990) emphasized the morphological overlap between *Mastixicarpum* and *Diplopanax*. Mai (1993) considered them to be congeneric, although he did not make formal recombinations. His student, Czaja (2003), transferred *Mastixicarpum limnophilum* (Unger) Kirchheimer to *Diplopanax* as *D. limnophilus* (Unger) Czaja (see also Ševčík et al. 2007), but the type species of the genus, *Mastixicarpum crassum*, has not been so transferred. The question remains as to whether the genus *Mastixicarpum* should be completely abandoned, as required if the type species is truly congeneric with *Diplopanax*, or if there are sufficient distinctions to maintain two genera. This depends on a thorough comparison between the type species, *M. crassum* Chandler, and the extant taxa.

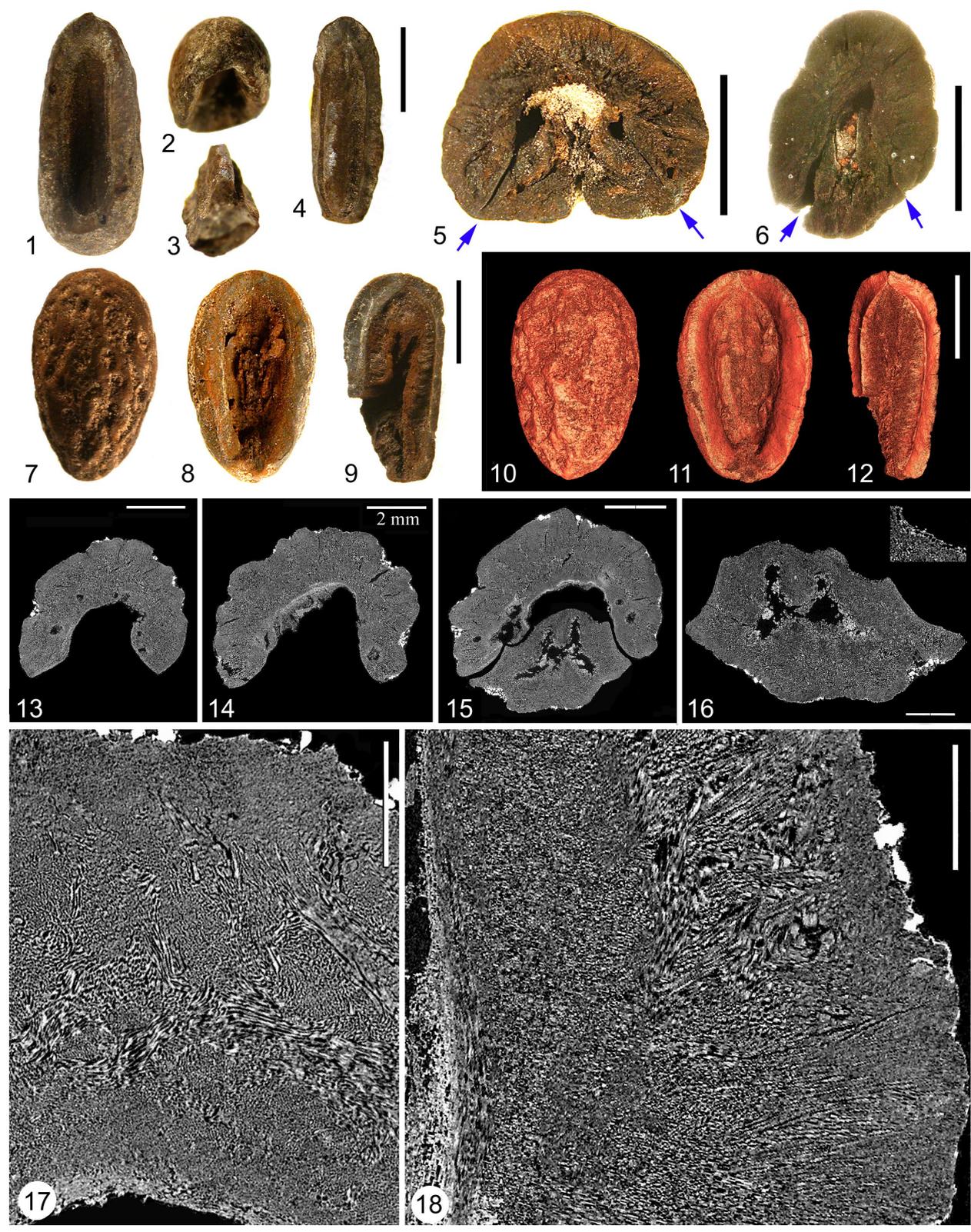
Mastixicarpum crassum Chandler 1926

Plates 3, 4

Basionym. *Mastixicarpum crassum* Chandler 1926, Monogr. Palaeont. Soc. 2. London, p. 36, pl. 6, fig. 5a–d. Chandler 1962, p. 128, pl. 18, figs 1–3, pl. 19, figs 1–3.

We examined numerous specimens of *Mastixicarpum crassum* from Hordle. The fruits are small (1–1.5 cm long) relative to those of extant species of *Diplopanax* (4.5 cm long) and as compared to other European Tertiary species that were subsequently placed in *Mastixicarpum* (1.8–4.5 cm long; Mai 1993). As in

Diplopanax, the stone of *M. crassum* lacks the pair of prominent ovular traces following the outlines of the germination valve that is characteristic of *Mastixia*. In *Mastixicarpum crassum*, distinct planes of separation tissue define the margins of the germination valve (Pl. 3, figs 5, 6, 15; Pl 4, figs 2, 3, 6) – as in *Diplopanax*



(Pl. 2, figs 5, 8, 10). Also in *M. crassum*, the dorsal infold includes intruded mesocarp tissue as well as endocarp (demonstrated by loss of tissue in Pl. 3, figs 15, 16, and by distinctive non-fibrous tissue in the center of the valve infold in Pl. 4, figs 3, 4, 6) – another feature shared with extant *Diplopanax* (Pl. 2, figs 5, 7, 8). However, *Diplopanax* is characterized by numerous secretory canals throughout the mesocarp (Pl. 2, figs 5–10). X-ray tomography has enabled anatomy to be studied throughout the specimens of *M. crassum*, which have been shown to have hardly any canals (Pl. 3, fig. 13; Pl. 4, fig. 3), with some planes of section lacking them entirely (Pl. 4, fig. 4).

The holotype, reillustrated here (Pl. 3, figs 7–18), consists of a stone plus its detached germination valve. The anatomy revealed by virtual transverse sections of the holotype includes a uniseriate inner layer of cuboidal cells lining the locule (Pl. 3, fig. 16 inset), surrounded by a substantial layer of interwoven fibers, mostly longitudinal in orientation, which comprises about 1/5 of the thickness of the stone wall (Pl. 3, figs 17, 18). The rest of the wall appears to be composed of numerous discrete bundles of fibers that are oblique to longitudinal in orientation (Pl. 3, figs 17, 18). The holotype has a rough exterior surface, (Pl. 3, figs 17 top, 18 right) and is interpreted as having lost the outer layers of anticlinally oriented sclereids seen in other, less abraded, specimens. A more complete specimen (V68593; Pl. 4, figs 1–8) shows the same kind of tissue surrounding the locule, composed of interwoven fibers, mostly longitudinal (Pl. 4, figs 5–8). Outside this layer is a narrow zone of numerous bundles of fibers that are oblique to longitudinal in orientation. In addition,

this specimen preserves a thicker outer zone of mostly isodiametric sclereids and/or parenchyma in radial alignment (Pl. 4, figs 5, 8). Tissues filling the dorsal infold consist mostly of shortly elongate sclereids and parenchyma, lacking fibers (Pl. 3, fig. 16, Pl. 4, fig. 6). A lacuna can form in the central part of the infold (Pl. 3, figs 15, 16), as in modern *Diplopanax* (Pl. 2, fig. 5).

The organization of tissues in *Mastixicarpum crassum* stones, from the locule outward, as shown in Pl. 4, figs 5, 8, is as follows:

1. Uniseriate locule lining of cuboidal cells 35–50 µm diameter (arrow in Pl. 4, fig. 6 and inset Pl. 3, fig. 16).

2. A layer about 250 to 500 µm thick composed of mostly longitudinally oriented fibers, grading into numerous bundles of fibers that are oblique to longitudinal.

3. A zone about 300–500 µm thick composed almost exclusively of isodiametric cells (sclereids or parenchyma),

4. A zone of radially oriented elongate parenchyma and/or sclereids.

Discussion. The question remains as to whether the genus *Mastixicarpum* should be subsumed within the extant genus *Diplopanax*. Similarities include the unilocular morphology, well-defined germination valve with distinct separation tissue, and lack of the paired ovular bundles characteristic of *Mastixia*. However, there are differences, too. Fruits of *M. crassum*, the type species, are much smaller than those of the extant species and other European fossil species placed in *Diplopanax*. The scattered canals that are characteristic and numerous in the mesocarp of *Diplopanax* (Pl. 2) are only present in extremely low numbers in *M. crassum*

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Plate 3. *Mastixicarpum crassum* Chandler from the late Eocene of Hordle, England. 1–4. V20074c; 1. Stone in dorsal view with germination valve removed, exposing the locule; 2. Apical view of specimen from fig. 1, showing smooth, rounded ventral surface and locule concavity exposed by detachment of germination valve; 3. Detached germination valve of the same specimen, apical view; 4. Same, germination valve viewed from the inner surface, with broad median ridge representing the dorsal infold; 5. Transversely fractured fruit showing single curved locule and lines of weakness at margins of germination valve (arrows), V20075(a); 6. Transversely fractured fruit, somewhat distorted by lateral compression, V42186(3). Arrows indicate lines of weakness at margins of germination valve; 7–18. V20074a, holotype; 7. Stone viewed from ventral side showing rough eroded surface; 8. Viewed from dorsal side with germination valve removed; 9. Germination valve from the holotype; 10–18. Images from SRXTM; 10–12. Isosurface renderings corresponding to the reflected light images in figs 7–9; 13, 14. Successive digital transverse sections of the endocarp without the dorsal germination valve; 15. Digital transverse section of the endocarp and germination valve, reassembled to show the complete original configuration with C-shaped locule in transverse section; 16. Digital transverse section of the germination valve composed mainly of isodiametric cells, with some tissue loss and with a uniseriate locule lining of cuboidal cells (inset enlargement); 17. Detail of endocarp wall, transverse section, showing transition from vertically oriented fibers adjacent to the locule (lower part of figure) to a thick layer of isodiametric cells traversed by tortuous tracts of fibers and/or ducts. Note incomplete external surface (top of image) due to abrasion of mesocarp; 18. Detail of endocarp wall, sagittal longitudinal section, showing transition from longitudinal fibers adjacent to the locule (left side) to thick layer of isodiametric cells traversed by tortuous tracts of fibers and/or ducts. Scale bars: 4–6, 9, 12 (also applies to 1–3, 7, 8, 10, 11) = 5 mm; 13–15 = 2 mm; 16 = 1 mm; 17, 18 = 0.5 mm

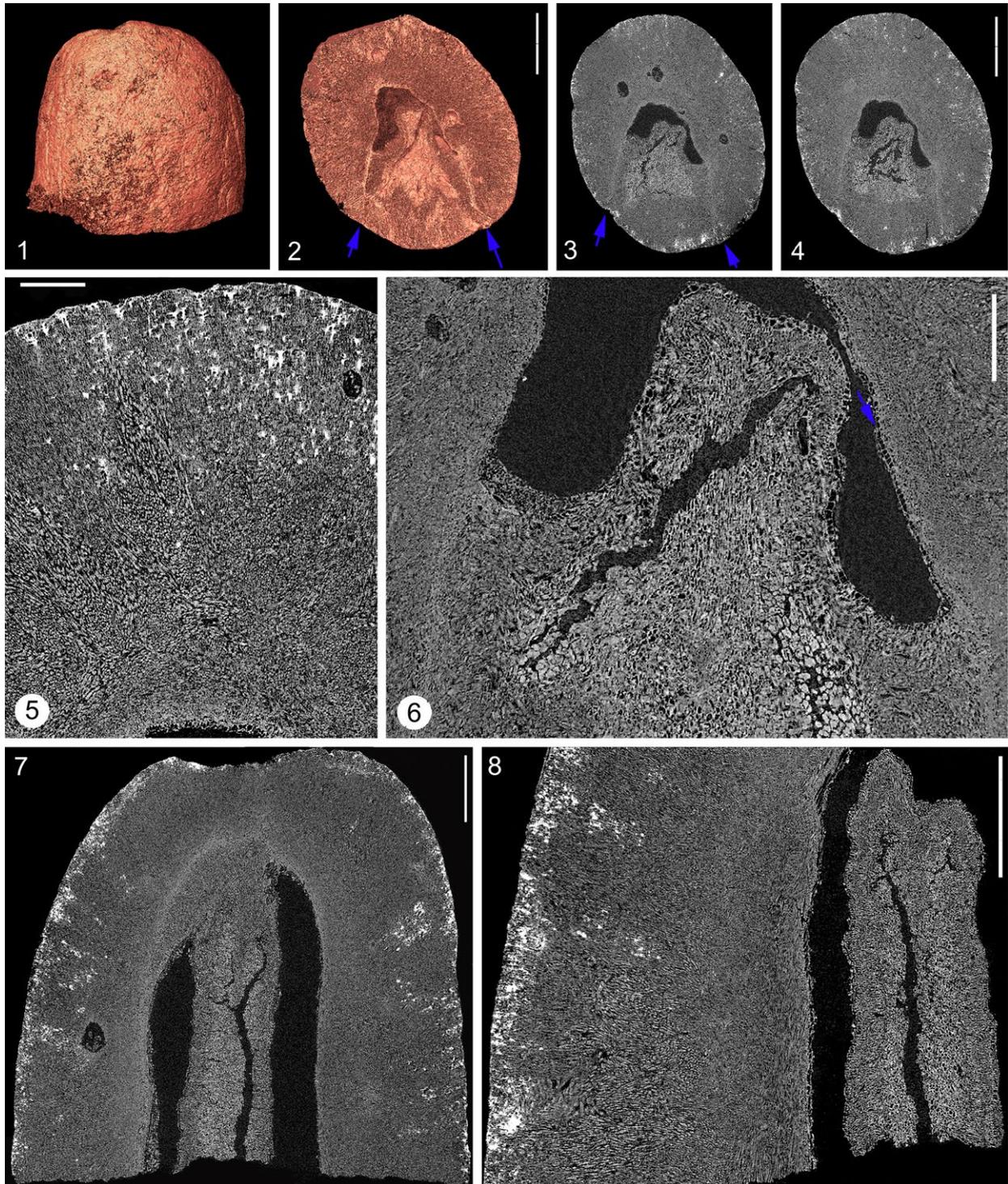


Plate 4. *Mastixicarpum crassum* Chandler from Hordle investigated by SRXTM, V68593. **1.** Isosurface rendering of half of fruit, ventral view; **2.** Isosurface rendering of transversely fractured fruit. Arrows indicate margins of dorsal germination valve; **3, 4.** Successive digital transverse sections showing the C-shaped locule, well-defined germination valve (margins indicated by arrows), and thick fruit wall with scattered cavities attributed to decay; **5.** Enlargement of ventral wall of stone in digital section showing anatomical structure between locule (lower part of figure) and the external surface. Cells are mainly isodiametric near the locule, transitioning to elongate and radially aligned in external portion. Tortuous tracts of cells and/or ducts seen in outer half of wall; **6.** Detail of dorsal infold in germination valve in digital transverse section showing parenchyma cells. Note cuboidal cells lining the locule (arrow); **7.** Digital longitudinal, coronal section through endocarp wall and germination valve; **8.** Detail of section parallel to that of fig. 7. A vertical desiccation crack is visible along the dorsal infold (right side of image). Note parenchymatous cells of the infold and anticlinally aligned cells of the outer wall. Scale bars: 2, 4 (also applies to 1, 3) = 2 mm; 5, 6 = 500 μ m; 7, 8 = 1 mm

(Pl. 3, fig. 13; Pl. 4, fig. 3); indeed, some planes of section in *M. crassum* do not show any canals (Pl. 4, fig. 4).

Hence, our view is that *Mastixicarpum* should be retained as a genus. Although the type species of the genus is distinct from fruits

of extant *Diplopanax*, some of the fossil species previously treated as *Mastixicarpum* clearly represent *Diplopanax*, notably *Diplopanax limnophilus* (Unger) Czaja (2003). Other fossil material of these genera will be discussed in a forthcoming revision of mastixioid fruits from the London Clay flora (Manchester & Collinson, in preparation).

Eomastixia Chandler

Emended diagnosis (Chandler 1962, p. 124). “Fruits belonging to the section Mastixioideae of the family Cornaceae; endocarps two or more loculed, syncarpous, germinating by dorsal valves which extend to the whole length of the locule. Valves bearing on the internal surface a median longitudinal infold which corresponds with a groove on the external surface.”

Diagnosis addendum (Holý 1975, p. 138). “Endocarps 1–4 loculed; more or less conspicuously ribbed, rugose; with resin ducts on the surface; epicarp smooth on the surface, thin or thick, detachable of woody endocarp to a various extent.”

Eomastixia was established based on the species *E. bilocularis* from Hordle by Chandler (1926). Four decades later, Chandler (1962) emended the generic diagnosis to include fruits with two or more locules, and revised the name to *Eomastixia rugosa* (Zenker) Chandler, based on agreement with Kirchner (1957) that an earlier-described species, *Baccites rugosus* Zenker from Altenburg, Thuringia, Germany, was conspecific with the Hordle material. Nevertheless, the type species for *Eomastixia* remains that designated in the original publication, namely *E. bilocularis* from Hordle. Subsequently described genera, including *Diplomastixia* Kirchn., *Ganitrocera* Kirchn. and *Plexiplica* Kirchn., were placed in synonymy with *Eomastixia* by Holý (1975), because of similarities in their original diagnoses but without detailed anatomical justification. Therefore it is important to document more details about the type species.

Eomastixia bilocularis Chandler 1926

Plates 5–7

Basionym. *Eomastixia bilocularis* Chandler 1926, Monogr. Palaeont. Soc., 2. London, p. 37, pl. 6 fig. 6a-3. Subsequently illustrated as *Eomastixia rugosa* (Zenker) (Chandler

1962, p. 126, pl. 18, fig. 9–16, pl. 19, figs 1–3; specimens from Hordle).

Lectotype. Two specimens were illustrated by Chandler (1926) but neither was designated as holotype. We here designate V20079b as the lectotype (Pl. 6, figs 1, 2, 5–12). It originally was figured by Chandler (1926: pl. 6, fig. 6b) and subsequently refigured by her (Chandler 1962: pl. 19, fig. 2). Only the basal half of the originally figured specimen now survives. The remaining syntype of Chandler (1926: pl. 5, fig. 6a), V20079a, is also refigured here for comparison (Pl. 5, figs 3–12).

The type material of *Eomastixia bilocularis* has two locules that are C-shaped in cross section (Pl. 5, figs 9, 10, V20079a; Pl. 6, figs 1, 2, 6–9, V20079b). The Hordle collections also include trilocular specimens (e.g. Pl. 6, fig. 3), and Chandler (1962) illustrated conspecific specimens from the middle Eocene of Bournemouth with up to four locules. The endocarp is gently longitudinally ribbed (Pl. 5, figs 3, 5, Pl. 6, fig. 5). The endocarp wall is thick and woody, composed largely of fibers and elongate sclereids with a few embedded masses of fine parenchyma, and scattered vascular traces. A uniseriate layer of cuboidal cells lines the locule. A narrow longitudinal dorsal slit in the endocarp corresponds to the infold of each locule (Pl. 5, fig. 9; Pl. 6, figs 1, 8). The surrounding mesocarp is composed of isodiametric cells about 25 µm in diameter; it penetrates into the furrows and irregularities of the endocarp and includes globose to longitudinally elongate cavities containing yellow semi-translucent resin. The dorsal infold tissue is composed mostly of fibers and isodiametric sclereids and in the Hordle material generally is “closed”, lacking intrusion of mesocarp tissue. A pair of ovular bundles corresponding to each carpel runs through the endocarp parallel to the margins of the germination valves (Pl. 5, figs 9, 10; Pl. 6, figs 9, 10; Pl. 7, figs 9, 10).

Separation tissue defining the margins of the germination valves extends from the limbs of the locule to the outside of the endocarp, as seen in x-ray tomography (Pl. 6, figs 2, 6–10). Scattered spherical to irregular or slightly axially elongate resin cavities occur in the mesocarp or at the endocarp-mesocarp transition (Pl. 6, figs 9, 10); in many specimens this resin-containing layer is partially or completely missing. Scattered but distinct resin-containing cavities are also seen well in

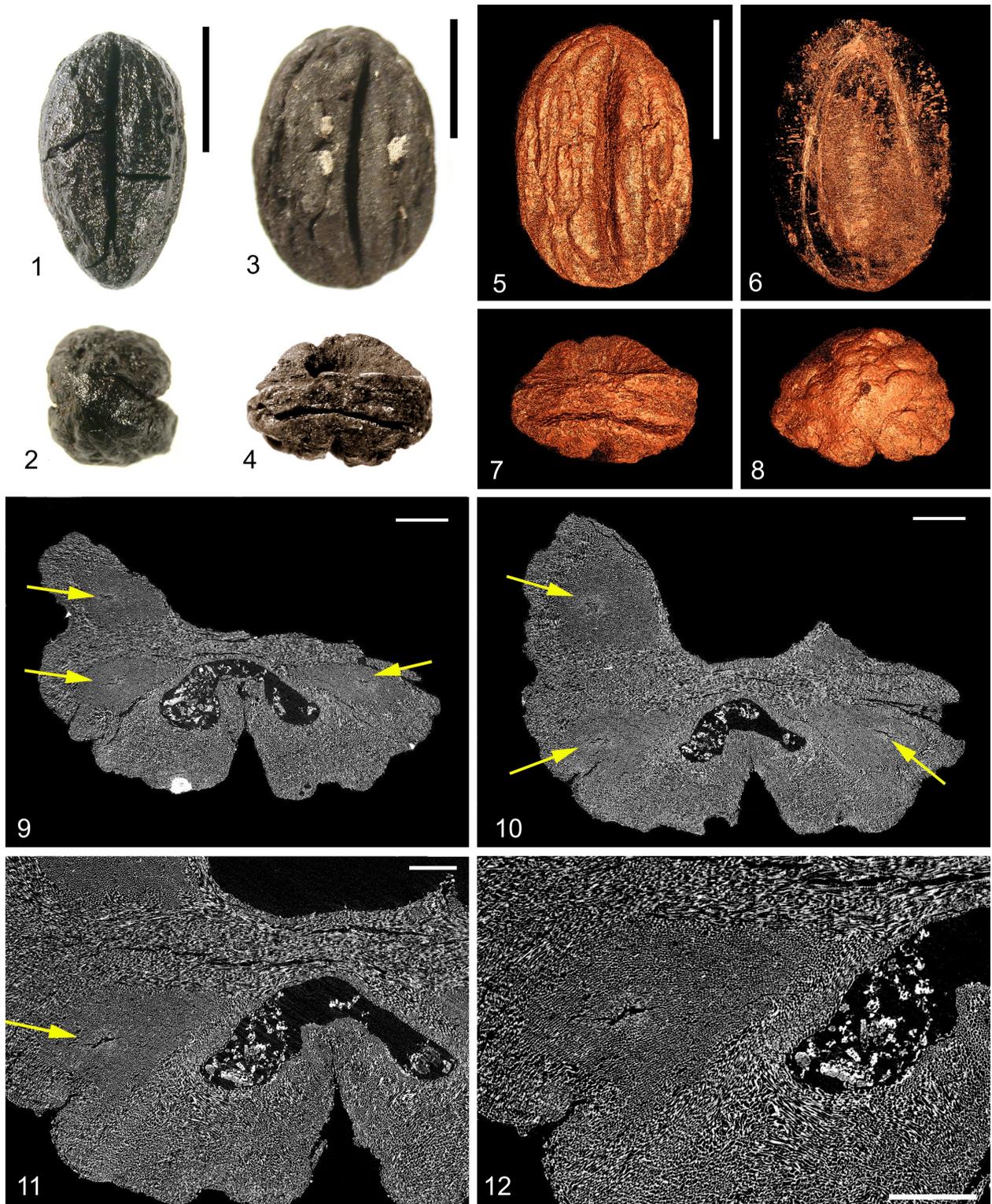


Plate 5. Late Eocene *Eomastixia bilocularis* Chandler from Hordle. **1.** Stone in lateral view showing groove separating two carpels, V20082(4); **2.** Apical view of the stone in 1, showing outline of two carpels; **3.** Stone in lateral view with median groove of germination valve, V20079a, syntype; **4.** Apical view of same. Curved slit demarcates gaping germination valve; **5.** Isosurface rendering of the stone in fig. 3; **6.** Partly translucent rendering of the same specimen, showing course of the ovular bundles following the germination valve; **7.** Apical view of the endocarp in fig. 5; isosurface view in same orientation as fig. 4; **8.** Basal view, isosurface rendering; **9–12.** SRXTM digital transverse sections of the same specimen as in figs 3–8, V20079a; **9.** Transverse section of bilocular specimen with one locule still intact; most of the other half including germination valve missing. Note positions of ovular bundles (arrows); **10.** Another transverse section, nearer to the base of the fruit, showing outlines of both locules, and positions of three of the ovular bundles (arrows); **11, 12.** Detail of transverse sections, showing collapsed canal of the ovular bundle (arrow) and organisation of tissues surrounding the locules. Scale bars: 1, 3, 5 (also applies to 2, 4, 6–8) = 5 mm; 9, 10 = 1 mm; 11, 12 = 0.5 mm

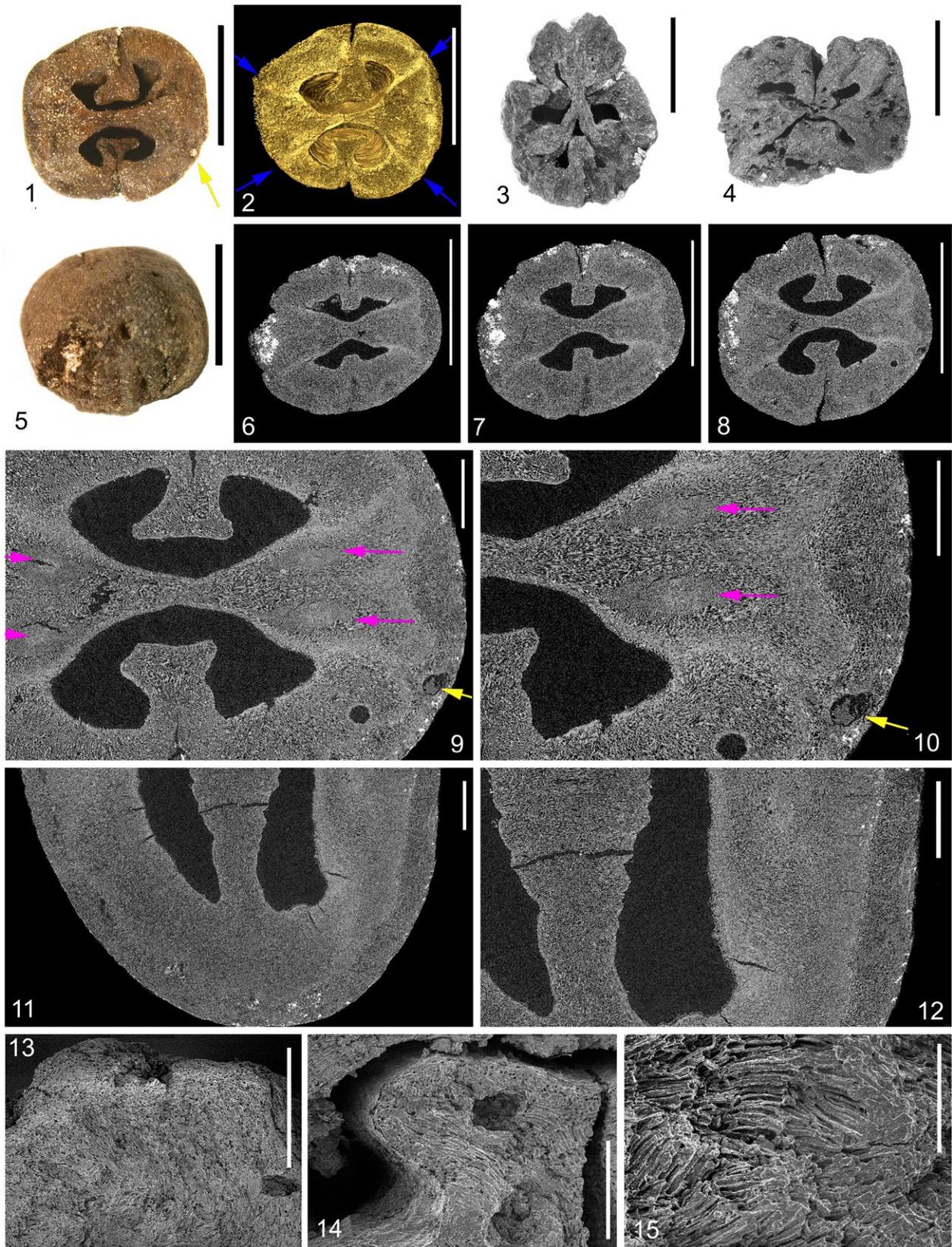


Plate 6. Late Eocene *Eomastixia bilocularis* Chandler from Hordle. **1.** Bilocular fruit in equatorial transverse fracture, view showing two C-shaped locules by reflected light. Arrow indicates a resin cavity within a patch of preserved mesocarp. Lectotype, designated here, V20079b; **2.** Same, isosurface rendering from SRXTM. Note the germination valve margins (arrows); **3.** Trilocular fruit, transversely broken, V40778; **4.** Bilocular fruit, transversely fractured, V20082(2); **5.** Base of specimen in figs 1, 2, reflected light; **6–8.** Successive digital transverse sections of lectotype from near base to near equator, SRXTM. Note almost closed dorsal infolds with median slits, V20079b; **9, 10.** Increased magnification from fig. 8, with pink arrows indicating position of ovular bundles. Germination valve margins adjacent to bundles. Clear distinction between mesocarp and endocarp. A resin cavity within mesocarp indicated by yellow arrow; **11, 12.** Longitudinal coronal sections; **13, 14, 15.** Detail from fig. 4, of infold, SEM, V20082(4). Scale bars: 1–8 = 5 mm; 9–13 = 1 mm; 14 = 400 μ m; 15 = 200 μ m

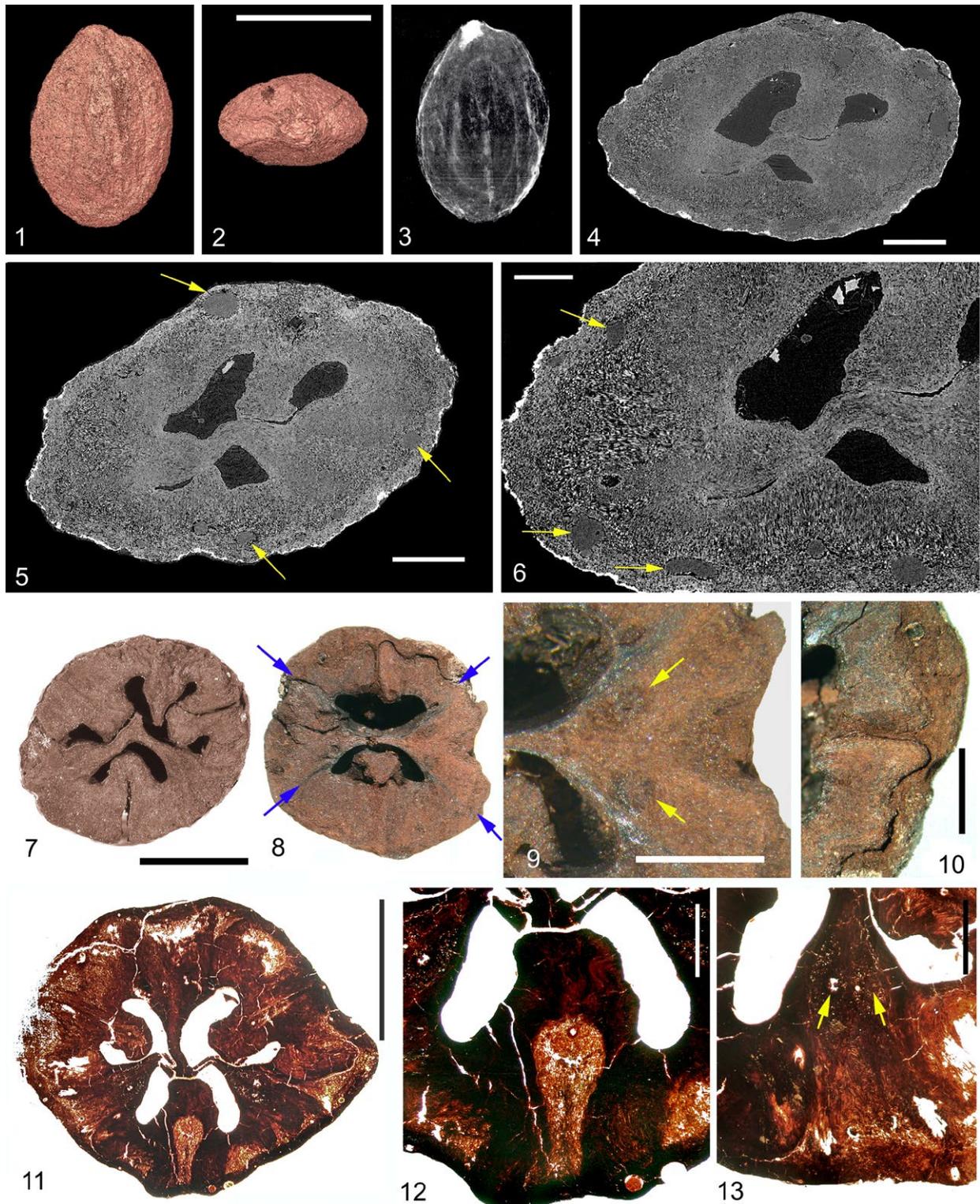


Plate 7. *Eomastixia* from the middle Eocene of Bournemouth, England, and from the Oligocene of Borna, Germany. **1–6.** *Eomastixia bilocularis* Chandler fruit from Bournemouth, V40768, SRXTM. **1, 2.** Isosurface renderings of fruit in ventral and apical views, note apical/perianth disk. **3.** Volume rendering of fruit viewed ventrally with partial translucency showing elliptical outline of locule. **4.** Obliquely transverse digital section near apex showing both locules partly compressed and lower one less well developed. Note resin cavity in dorsal infold of upper locule [slice 1316]. **5.** Obliquely transverse digital section near equator showing both locules [slice 1550]. Arrows indicate resin cavities. Note partially disrupted tissue in dorsal infold of upper locule; **6.** Enlargement from digital section close to position of fig. 5 showing resin cavities, some arrowed; **7–13.** *Eomastixia rugosa* (Zenker) Chandler. Borna, Saxony, Germany [coll. F. Kirchheimer], V26452(1); **7.** Trilocular fruit cut transversely, reflected light; **8.** Bilocular fruit cut transversely, reflected light. Arrows indicate margins of two germination valves; **9.** Detail of endocarp from fig. 8, showing two ovular bundle areas (arrows); **10.** Detail from fig. 8, showing boundary of mesocarp and endocarp; **11.** Thin section from specimen in fig. 7, showing anatomical details; **12.** Detail from fig. 11 of one of the three C-shaped locules and corresponding infold of the germination valve with intruded mesocarp. Note resin cavity (with orange fill) in mesocarp and an adjacent cavity from which resin has been lost (bottom right of image); **13.** Detail from fig. 11 of tissue between adjacent locules. Scale bars: 2, 7, 11 (also applies to 1, 3, 8) = 5 mm; 4, 5, 12, 13 = 1 mm; 6 = 0.5 mm; 9, 10 = 2 mm

a specimen from the middle Eocene Bournemouth Freshwater Beds (V40768) Pl. 7, figs 4–6). *Eomastixia* specimens from the middle Eocene of Messel, Germany, having up to five locules, also have resin-filled cavities in a similar position in the fruit, but they are typically more abundant, larger, in a more continuous layer around the fruit, and also often more elongate than in English material (Collinson et al. 2012: pl. 28, figs c–e, k, pl. 29, figs a, b; van Aarssen et al 1994: figs 2b–e). Although the *Eomastixia* specimens from Hordle are known from endocarps largely denuded of external tissues, Chandler (1962) provided details of the mesocarp and epicarp morphology based on three fruits from the Bournemouth Freshwater beds. In those specimens the epicarp displays a smooth outer surface (e.g. Pl. 7, figs 4–6).

Discussion. The Hordle *Eomastixia* fruits compare well with those from Germany that were formerly described as *Plexiplica* (Kirchheimer 1935b, 1936) and *Ganitrocera* (Kirchheimer 1934, 1936). In all of these, a pair of ovular bundle canals straddles each of the germination valves; this is an additional character supporting the merger of those genera within *Eomastixia* as previously executed by Holý (1975) and Mai (1993). Franz Kirchheimer provided some specimens of *Plexiplica rugosa* (Zenker) Kirchl. from Borna, Germany, to Chandler for comparison with *Eomastixia*. Chandler agreed with him that those specimens, now housed at the Natural History Museum (Pl. 7, figs 7–13), were conspecific, and therefore revised her assignment of the Hordle specimens from *Eomastixia bilocularis* Chandler to *Eomastixia rugosa* (Zenker) Chandler (1962). Transverse sections of Kirchheimer's specimens (Pl. 7, figs 7–13) reveal mostly the same anatomical features observed in the Hordle material, including a well-defined pair of ovular bundles for each of the two or three locules (e.g. Pl. 7, fig. 9). It is possible, however, that Kirchheimer's material represents a different species, because the mesocarp is seen to intrude into the dorsal infolds (Pl. 7, fig. 11, 12), a feature not observed in the Hordle specimens. Hence we treat the Borna Oligocene specimens with the designation *Eomastixia rugosa* (Zenker) Chandler, but retain the original name *Eomastixia bilocularis* Chandler for the Hordle and Bournemouth material.

Compared with the two extant genera of Mastixiaceae, *Eomastixia* falls closer to

Mastixia than to *Diplopanax*, based on the massive endocarp and the presence of two ovular bundles per locule. The mesocarp lacks the prominent scattered canals seen in *Diplopanax*. However, the well-defined separation layer at the margin of each germination valve seen in *Eomastixia* is more similar to the condition in *Diplopanax* than what we observed in extant *Mastixia*. Chandler (1962 p. 125) stated, "These woody endocarps with long dorsal germination valves bearing median longitudinal infolds are clearly related to *Mastixia* but differ from this living genus in having almost invariably more than one locule. In view of the tendency for a larger number of locules to occur in extinct representatives than in living members of a genus, the distinction between *Mastixia* and *Eomastixia* may be an artificial one which will ultimately have to be discarded." In our current understanding, however, *Eomastixia* is well supported as a genus distinct from *Mastixia*, not only by the greater number of locules but by the presence of larger resin cavities in the endocarp and mesocarp, and germination valve margins that do not intersect with the ovular bundles. In *Eomastixia* we have not observed distinct secretory ducts of the kind seen in the extant genera, but instead we see scattered globular resin cavities in the mesocarp or endocarp-mesocarp border. Whether this represents a genuine anatomical distinction or an artifact of preservation is not entirely clear. The contents in the fossils are hardened and yellowish, like amber, whereas the contents of the secretory canals of the extant fruits do not appear to be resinous. The extinct genus *Retinomastixia* Kirchheimer, with unilocular fruits similar to *Mastixia*, bears resin similar in appearance to that of *Eomastixia* but in much greater quantities, in large cavities within the endocarp (Mai 1993).

CONCLUSIONS

Mastixicarpum and *Eomastixia* both deserve continued recognition as genera of Mastixiaceae that are distinct from other fossil genera and from both of the extant genera. Although the type species of *Mastixicarpum* justifies retention of that genus, most other species previously placed in the genus are more appropriately treated as *Diplopanax*. *Eomastixia* was widespread in the European Tertiary, with multiple recognized species (Holý

1975, Mai 1993). The genus persisted into the Neogene and was well represented especially by the species *E. saxonica* (Menzel) Holý as summarized by Holý (1975), Mai (1993) and Ševčík et al. (2007). We hope that the clarification of these genera will help improve our understanding of the broader fossil record of Mastixiaceae, which extends to the late Cretaceous (Knobloch & Mai 1986), with remarkable Cenozoic diversity in both Europe (Mai 1993) and North America (Manchester 1994, Tiffney & Haggard 1996, Stockey et al. 1998). Improved understanding of the rich Cenozoic record, combined with newly documented Cretaceous occurrences, provides excellent opportunities for tracing the diversification and biogeographic history of the Mastixiaceae and other Cornales (Atkinson 2018, Atkinson et al. 2017, 2018).

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