



MASTIXIOID FRUITS (CORNALES) FROM THE EARLY EOCENE LONDON CLAY FLORA: MORPHOLOGY, ANATOMY AND NOMENCLATURE REVISION

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Abstract: Following on the seminal works of Reid and Chandler in 1933 and Chandler in 1961, morphology and anatomy of fossil mastixioid fruits from the early Eocene London Clay of southern England were reanalyzed with the benefit of new methods in comparison with extant genera of Mastixiaceae and with other fossil representatives from Europe and North America. The species named *Mastixia cantiensis* E.REID et M.CHANDLER was based on a heterogeneous assemblage of specimens, all representing Mastixiaceae, some of which truly represent *Mastixia* whilst others correspond to *Diplopanax* and *Mastixiopsis*. The holotype of *M. cantiensis* E.REID et M.CHANDLER corresponds to extant *Diplopanax* rather than *Mastixia*. Therefore, this species is moved out of *Mastixia* and is treated as *Diplopanax cacaooides* (ZENKER) comb. nov. Nine species of mastixioid fruits are currently recognized in the London Clay flora: *Mastixia parva* E.REID et M.CHANDLER, *M. cf. oregonensis* (R.A.SCOTT) TIFFNEY et HAGGARD, *Diplopanax cacaooides*, *Tectocarya grandis* (E.REID et M.CHANDLER) comb. nov., *Mastixiopsis nyssoides* KIRCHH., *Exbeckettia mastixioides* (E.REID et M.CHANDLER) gen. et comb. nov., *Lanfrancia subglobosa* E.REID et M.CHANDLER, *Portnallia bognorensis* M.CHANDLER, and *Langtonia bisulcata* E.REID et M.CHANDLER. These include the oldest known representatives of the genera *Diplopanax*, *Tectocarya* and *Mastixiopsis* and contribute to our understanding of the former morphological diversity and palaeobiogeography of the Mastixiaceae.

Key words: *Beckettia*, biogeography, *Diplopanax*, *Exbeckettia*, *Lanfrancia*, *Langtonia*, *Mastixia cantiensis*, Mastixiaceae, *Mastixiopsis*, *Portnallia*, taxonomy, *Tectocarya grandis*

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Introduction

The early Eocene London Clay flora of southern England is well known for its diverse flora of pyritized fruits and seeds (Bowerbank 1840, Reid and Chandler 1933, Chandler 1961, 1964, 1978, Collinson 1983) that has been important in establishing early fossil records of many modern families and genera and providing important insights to early Eocene paratropical conditions and biogeographic patterns (Collinson and Cleal 2001). Angiosperm families well represented in the London Clay flora include Arecaceae, Annonaceae, Lauraceae, Magnoliaceae, Juglandaceae, Sabiaceae, Menispermaceae, and Icacinaceae. The flora was also rich in representatives of the order Cornales, including *Alangium* LAM., *Cornus*, *Curtisia*, *Nyssa* and several species of Mastixiaceae (Reid and Chandler 1933, Chandler 1961, 1964, Eyde 1997, Manchester et al. 2007, 2010). Here, we focus on the London Clay species of Mastixiaceae. This family includes two extant genera, *Mastixia* BLUME and

Diplopanax HAND.-MAZZ, and is sister to Davidiaceae and Nyssaceae within the Cornales as supported by molecular sequence data (Xiang et al. 2011, Fu et al. 2019, Thomas et al. 2021). The fossil record of mastixioid fruits can be traced to the Late Cretaceous (Knobloch and Mai 1986, Atkinson et al. 2017, 2019) and its diversification appears to have peaked in the Eocene (Manchester et al. 2015). In agreement with Xiang et al. (2011), Atkinson (2018), Fu et al. (2019), Thomas et al. (2021), we prefer recognition of Mastixiaceae at the family rank, contrary to recent APG classification subsuming it within a broad concept of Cornaceae (APG IV 2016).

The striking abundance and diversity of mastixioid fruits in the early Eocene London Clay flora was first recognized by Reid and Chandler (1933). Their observation was biogeographically informative because the clade is now restricted to Asia and Malesia. Multiple genera were recognized by Reid and Chandler, in contrast with the single modern genus, *Mastixia*, known at the time. The mastixioid

affinity of extant *Diplopanax*, which was initially considered to belong to Araliaceae (Handel-Mazzetti 1933), was not recognized until much later (Zeng 1983, Eyde and Xiang 1990, Averyanov and Nguyen 2002).

Subsequent to Reid and Chandler's work, mastixioid fruits were also recognized to be abundant and diverse in the Tertiary deposits of mainland Europe (Kirchheimer 1934, 1935, 1936, 1938a, b, 1941, 1957, Mai 1970, 1987, 1993, Holý 1975, Martinetto 2011, Hably and Erdei 2013). Such fruits were also identified from the Paleocene and Eocene of North America (Scott 1954, Manchester 1994, Tiffney and Haggard 1996, Stockey et al. 1998, Huegele and Manchester 2019, 2020). By the 1950s, up to 16 genera and 40 species of fossil mastixioid fruits had been recognized (Kirchheimer 1957). However, some were subsequently synonymized; e.g., Holý (1975) and Mai (1993) reduced the number of European fossil mastixioid genera to seven, including the representatives of the two extant genera plus five extinct genera (reviewed by Martinetto 2011). Difficulties remained, though, because some of the earliest described taxa, important because of their nomenclatural priority, were less well known, anatomically, than some of the later described taxa. Recently, we provided revised circumscriptions of the earliest described fossil mastixioid genera, *Mastixicarpum* and *Eomastixia* M.CHANDLER (Chandler 1926, 1962) based on type material from the late Eocene of Hordle, England (Manchester and Collinson 2019).

Fossil fruits of the Mastixiaceae have already proven to be critical in investigations of the phylogeny and evolution of the Cornales (Atkinson 2018, Atkinson et al. 2019). For nomenclatural clarity, it is important to revisit the London Clay taxa, which include some of the earliest named extinct genera and species of this family. In the present article, we revisit the mastixioids from early Eocene London Clay, with particular attention to internal morphological and anatomical features revealed by physical fractures and sectioning augmented by micro-CT scanning. Reid and Chandler (1933) recognized four genera and six species of mastixioid fruits, including the modern genus *Mastixia* and three extinct genera. Chandler (1961) added another genus, *Portnallia*. A review of these taxa is presented below.

Materials and methods

Specimens were examined from the London Clay flora, housed in the palaeobotany collections, Earth Sciences Department, Natural History Museum London (NHMUK; specimen numbers prefixed "V."). Comparisons with fossils from other sites included those in collections of the Museum für Naturkunde, Berlin, (specimens cited with the prefix, MNB), Florida Museum of Natural History, University of Florida (UF), and the Smithsonian Natural History Museum (USNM). Modern specimens of *Mastixia* and *Diplopanax* were borrowed from herbaria of the US National Museum, Washington, DC, the Komarov Botanical Institute, Saint Petersburg and the Royal Botanic Gardens, Kew Richmond, Surrey, UK (K). Transverse sections near the equator of the fruits are particularly useful for distinguishing mastixioid taxa and have been provided whenever possible for the comparative figures in this article.

In a recent article (Manchester and Collinson 2019), we illustrated examples and summarized observations of fruit morphology and anatomy for both extant subgenera of *Mastixia* and both modern species of *Diplopanax* as a comparative basis for interpreting fossil remains. Here we apply the same terminology.

The London Clay fruits and seeds are preserved as pyrite permineralizations. They are stored in silicon oil to retard oxidation and pyrite decay. For optimal reflected light images, specimens were immersed in xylene during photography, with oblique lighting provided by a pair of small desk lamps. Internal morphology and anatomy of extant and fossil fruits were studied both from natural fracture surfaces and with transverse sections cut with a paper-thin annular diamond blade mounted on a Microslice II saw. Images were taken with a Nikon Coolpix 950 digital camera. Selected pyritized specimens (excluding type and figured specimens) were physically sawn with a thin-bladed annular diamond saw and etched on one face with nitric acid following the procedure that Kenrick (1999) summarized based on earlier literature including Collinson and Ribbins (1977), to reveal anatomical structure by reflected light microscopy. Although highly informative in the detail provided, Ribbins and Collinson (1978) cautioned against this approach which can accelerate the process of pyrite breakdown.

We re-examined type specimens using micro-computed tomography (micro-CT). For anatomical investigation, selected fruits were examined by micro-CT at the Imaging and Analysis Centre, NHMUK in 2015, using a Nikon Metrology HMX ST 225. 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®. Micro-CT scan datasets are archived at NHMUK Imaging and Analysis Center.

Geological occurrence, dating and locality data may be found in the original published sources (Reid and Chandler 1933, Chandler 1961, 1962), reviewed and updated by Collinson and Cleal (2001) and Collinson et al. (2016).

Taxonomic survey

We present the taxa in order of relationship to the two extant genera, treating the fossil species, *Diplopanax cacoides* first, followed by a species of the related extinct genus, *Tectocarya*. Then *Mastixia* is presented, followed by members of other extinct genera in the following sequence: *Exbeckettia* gen. nov., *Lanfrancia* E.REID et M.CHANDLER, *Mastixiopsis* KIRCHH., *Portnallia* M.CHANDLER, and *Langtonia* E.REID et M.CHANDLER.

Current status of *Mastixia cantiensis* E.REID et M.CHANDLER

The London Clay species named *Mastixia cantiensis* by Reid and Chandler (1933) was based on a heterogeneous assemblage of specimens, all representing Mastixiaceae,

Table 1. Nomenclatural fate of re-investigated specimens of *Mastixia cantiensis* E.REID et M.CHANDLER.

Catalogue number Natural History Museum, London	Illustrations in Reid and Chandler 1933	Current assignment; figures herein
V. 22953 Holotype	pl. 25, figs 1, 2	<i>Diplopanax cacaooides</i> (ZENKER) comb. nov.; Text-fig. 1a–d, h–j
V. 22954	pl. 25, fig. 3	<i>Diplopanax cacaooides</i> (ZENKER) comb. nov.; Text-fig. 1e, f
V. 22955	pl. 25, fig. 4	<i>Mastixia</i> cf. <i>oregonensis</i> (R.A.SCOTT) TIFFNEY et HAGGARD; Text-fig. 4d, g
V. 22956	pl. 25, fig. 5	Indet. locule cast
V. 22957	pl. 25, fig. 6	Indet. locule cast
V. 22960(1)	cited p. 450	<i>M. cf. oregonensis</i> (R.A.SCOTT) TIFFNEY et HAGGARD; Text-fig. 4a–c
V. 22963(1)	cited p. 450 but not figured	<i>Mastixiopsis nyssoides</i> KIRCHH.; Text-fig. 5c, e, g

but some of which truly represent *Mastixia* whilst others correspond to *Diplopanax* and *Mastixiopsis* (Tab. 1). Unfortunately for nomenclatural stability, the holotype of *M. cantiensis* corresponds to extant *Diplopanax* rather than to *Mastixia*. Therefore, this species must be moved out of *Mastixia*, and transferred to *Diplopanax cacaooides* (ZENKER) comb. nov. The epithet *cacaooides* of Zenker (1832) has priority over *cantiensis* of Reid and Chandler (1933).

Systematic palaeobotany

Genus *Diplopanax* HAND.-MAZZ., 1933

Diplopanax cacaooides (ZENKER) MANCHESTER et M.E.COLLINSON comb. nov.

Text-fig. 1a–f, h–j

- 1832 *Baccites cacaooides* ZENKER, p. 10, pl. 1, figs (E) and 4–8, 11–16.
 1933 *Mastixia cantiensis* E.REID et M.CHANDLER, p. 448, pl. 25, figs 1–3 only.
 1978 *Mastixicarpum cacaooides* (ZENKER) MAI in Mai and Walther, p. 120, pl. 44, figs 13–22.
 1993 *Mastixicarpum cacaooides* (ZENKER) MAI; Mai, p. 59.

B a s i o n y m . *Baccites cacaooides* ZENKER (Zenker 1832: Beiträge zur Naturgeschichte der Urwelt, p. 10, pl. 1, figs (E) and 4–8, 11–16; Altenburg, Weisselster Basin, Germany).

Plant Fossil Registry Number. PFN002904 (for new combination).

Nomenclature. Rather than making a new combination which would preserve the epithet *cantiensis*, we are required to use an epithet that was established earlier by Zenker (1832) because the specimens from Weisselster Basin, Germany (Mai and Walther 1978) and the London Clay are conspecific.

Description and remarks. The holotype of *Mastixia cantiensis* (Text-fig. 1a–d, h–j) conforms to the extant genus *Diplopanax* in having clearly defined planes of weakness demarcating the germination valve (Text-fig. 1h, i), and by the dispersed rather than paired ovular bundles as illustrated and described earlier for the extant species (pp. 54–57 and pl. 2 in Manchester and Collinson 2019). The fruits of this fossil species are unilocular, ovoid to cylindrical, rounded basally and rounded or truncate apically, 17 to 32 mm long and

12 to 22 mm wide. The locule is horseshoe-shaped in cross section. The germination valve is elongate. The endocarp wall is up to 9 mm thick, composed of radial fibres, with scattered vascular bundles and secretory canals (Text-fig. 1h–j), but usually without larger cavities.

Synonyms of *Diplopanax cacaooides* cited by Mai 1993 include *Platymastixia cacaooides* (ZENKER) KIRCHH. (Kirchheimer 1934: 790, fig. 21) and *Mastixicarpum compactum* KIRCHH. (Kirchheimer 1935) from the Weisselster Basin, Germany (Mai and Walther 1978). For comparison with the London Clay specimens (Text-fig. 1a–f, h–j), we illustrate a specimen from the Miocene of Wiesa, Germany (Text-fig. 1g). With the exception of the type material of *Mastixicarpum* M.CHANDLER from Hordle, most other species formerly attributed to that genus are now considered to represent *Diplopanax* (Eyde and Xiang 1990, Czaja 2003, Manchester and Collinson 2019). Czaja (2003) recognized a common Miocene species, *D. limnophilus* (UNGER) CZAJA (see also Ševčík et al. 2007). Similar *Diplopanax* fruits were also present in the Eocene of western North America (e.g., late Eocene *Diplopanax* sp. from late Eocene Quimper Sandstone, Oak Bay, Jefferson Co., Washington; fig. 33 in Manchester et al. 2009). *Diplopanax eydei* STOCKEY, LePAGE et PIGG described from the middle Eocene of Princeton, British Columbia, Canada (Stockey et al. 1998), conforms in general morphology, but has smaller fruits and preserves a thick epicarp of isodiametric cells not observed in other modern and fossil species of the genus. In our current understanding, the London Clay occurrence is significant as the oldest representative of the genus *Diplopanax*.

Genus *Tectocarya* KIRCHH., 1935

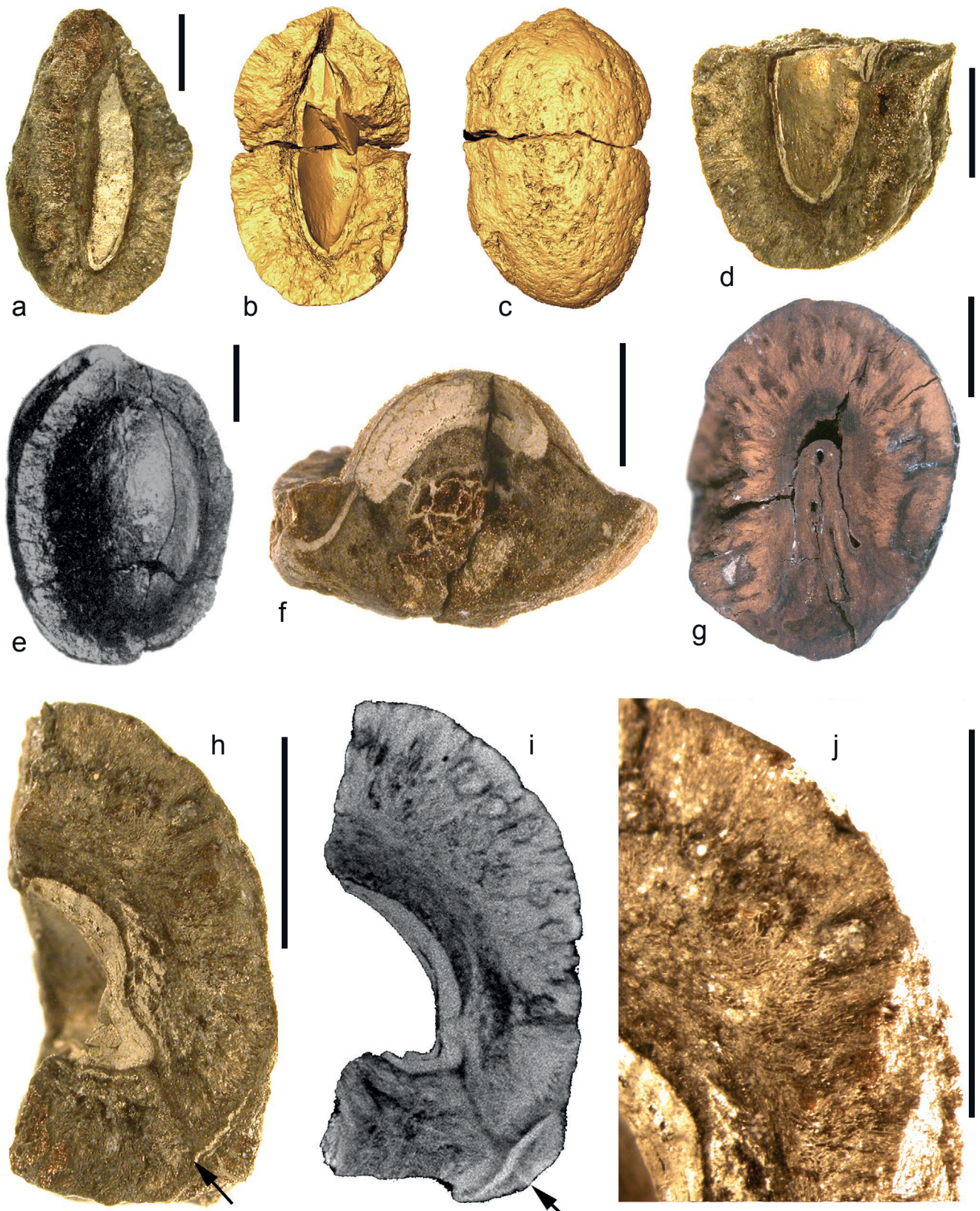
Tectocarya grandis (E.REID et M.CHANDLER) MANCHESTER et M.E.COLLINSON comb. nov.

Text-fig. 2a–n

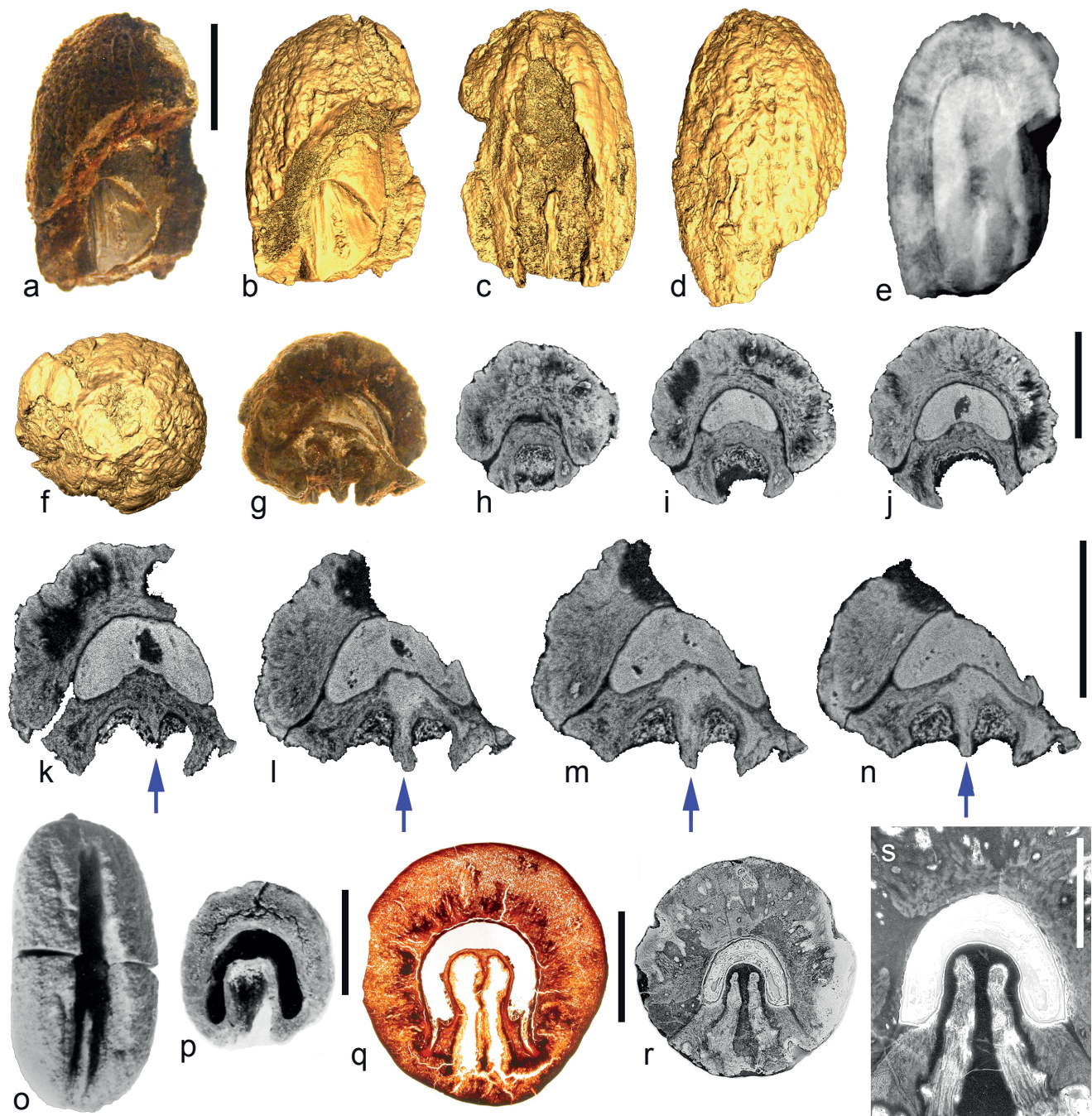
B a s i o n y m . *Mastixia grandis* E.REID et M.CHANDLER (Reid and Chandler 1933: The London Clay flora, p. 450, pl. 25, figs 7–9).

Holotype. V.22968 (Natural History Museum, London).

Plant Fossil Registry Number. PFN002905 (for new combination).



Text-fig. 1. *Diplopanax cacaooides* (ZENKER) comb. nov. a–d: [Holotype of *Mastixia cantia* E.REID et M.CHANDLER, V.22953]. a: Lateral view of longitudinally broken specimen, reflected light. b–d: Surface renderings from micro-CT data. b: Lateral view of longitudinal fracture surface. c: Same specimen rotated to show external surface. d: Enlargement of lower half from (a, b), reflected light. e, f: Specimen figured originally as a paratype of *M. cantia*, V.22954 (Reid and Chandler 1933: pl. 25, fig. 3), reflected light. e: Ventral view with much of the endocarp wall fallen away exposing smooth convex ventral surface of locule cast. f: Transversely fractured surface, showing thick wall of the endocarp, and dehiscence plane leading to the left limb of the locule. g: Transversely sectioned, laterally compressed specimen from Miocene of Wiesa, Germany for comparison, Senckenberg Museum, SM.B. 21034/I. h–j: Digital transverse sections from micro-CT data of the Holotype V.22953. h: Transverse fracture surface from (b), showing curved locule and zone of weakness defining the germination valve (arrow), reflected light. i: Same orientation with clear demarcation of the separation plane of the germination valve (arrow), digital section from micro-CT scan. j: Enlargement from (h). Scale bars 5 mm.

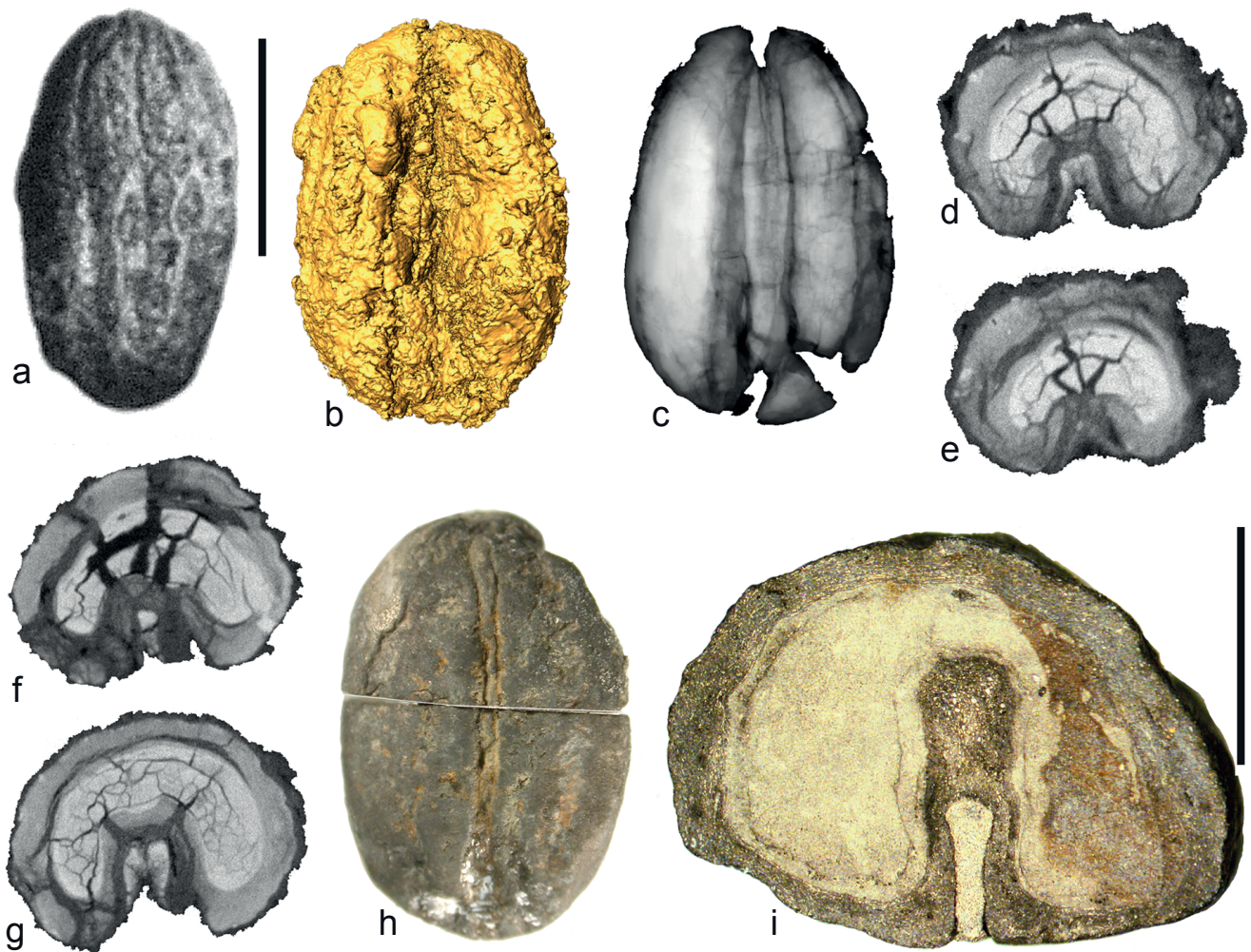


Text-fig. 2. *Tectocarya* spp. a–n: *Tectocarya grandis* (E.Reid et M.Chandler) comb. n. Holotype V.22968. a: Lateral view of broken endocarp, reflected light. b–d: Longitudinal views, surface renderings from micro-CT data. e: Translucent volume renderings. f: Apical view, surface rendering. g: View of transversely broken surface showing curved locule, reflected light. h–n: Successive digital transverse sections. Note septum in the dorsal infold (arrows). o, p: *Tectocarya rhenana* KIRCHH., Miocene of Germany, dorsal view and transverse section [Holotype of *Mastixoidea tectocaryoides* KIRCHH., Alfred Mine near Konzendorf, photo by Dieter Mai] (Synonym of *T. rhenana* MAL, 1993). q: *T. rhenana* transverse section. from Mine Alfred, Düren, Germany, coll. Claire A. Brown 1952, USNM 355632. r, s: *Tectocarya* sp. from late Eocene of Post, Oregon, USA, physical transverse section, reflected light. UF279-50014. [Surface views of same specimen shown in Manchester and McIntosh 2007: figs 62, 63]. Scale bars 1 cm in (a–r), 0.5 cm in (s).

Remarks. We studied the holotype of this species, V. 22968, by light microscopy of the exposed surfaces and by micro-CT scanning. It lacks the pair of prominent ovular bundles diagnostic of *Mastixia* and its close relatives *Eomastixia* and *Retinomastixia* KIRCHH. The separation planes of the germination valve margins directly intercept the locule limbs, indicating similarity to *Diplopanax* and to the fossil-genus, *Tectocarya*. The preserved part of the

pericarp is resolved into two main layers, a dense layer of mostly periclinally oriented fibres lining the locule, about 1/5 of the wall thickness, and a thick outer layer with fibres and sclereids predominantly anticlinally in orientation with scattered, variously oriented vascular strands and canals.

Digital transverse sections of the *T. grandis* holotype (Text-fig. 2h–n) show that the dorsal infold has a median septum of fibres dividing the surrounding parenchymatous



Text-fig. 3. *Mastixia parva* E.REID et M.CHANDLER. a–g: Holotype, V. 22972. a: Ventral view (original illustration from pl. 25, fig. 13 of Reid and Chandler 1933), reflected light. b–g: from micro-CT data. b: Dorsal view of specimen in (a) now suffering from encrustation due to pyrite decay; isosurface rendering. c: Translucent volume rendering, dorsal view showing two limbs of the locule and longitudinal groove. d–g: Digital transverse sections at various positions showing c-shaped locule, longitudinal dorsal infold, endocarp wall, and degradational cracks. h, i: V. 22983(1). h: Dorsal view showing longitudinal infold. i: Physical transverse section showing c-shaped locule and longitudinal dorsal infold. Scale bars 5 mm in (a–h), applies also to (b–g), 2 mm in (i).

tissue into two longitudinal pockets (Text-fig. 2k–n) – a feature diagnostic of *Tectocarya* KIRCHH. (Kirchheimer 1935, 1936, 1957; herein Text-fig. 2o–s). Although the holotype of London Clay species is hereby reassigned to *Tectocarya*, the second specimen listed and figured under the name *Mastixia grandis* by Reid and Chandler (1933: 451, pl. 25, fig. 9; V. 22969; herein Text-fig. 5d, f, h) appears to represent a distinct taxon, possibly *Mastixiopsis*.

Tectocarya was previously reported only from the Miocene, with three species distinguished by features of fruit shape, size, sculpture and relative thickness of endo- and mesocarp (Kirchheimer 1935, 1936, 1957, Mai 1993). This genus is morphologically and anatomically similar to *Diplopanax*, but the distinct median septum of the dorsal infold characteristic of *Tectocarya* (Text-fig. 2o, q, r) has not been observed in the extant species of *Diplopanax* (cf. pl. 2, figs 1–12 of Manchester and Collinson 2019).

Tectocarya grandis represents the first recognition of an early Eocene species of *Tectocarya*. The specimen is from the Isle of Sheppey, UK where the age range of the London Clay is between 53.5 and 51.5 Ma (Collinson et al. 2016). Another Eocene example, from the late Eocene of Post, Oregon,

USA, formerly misassigned to *Mastixicarpum occidentale* MANCHESTER (Tiffney and Haggard 1996, Manchester and McIntosh 2007), is also clearly recognizable as *Tectocarya* based on the septum in the dorsal infold (Text-fig. 2r, s). The holotype of *M. occidentale* from the Clarno Nut Beds (Manchester 1994) is retained in *Mastixicarpum*, however, and does not represent *Tectocarya*.

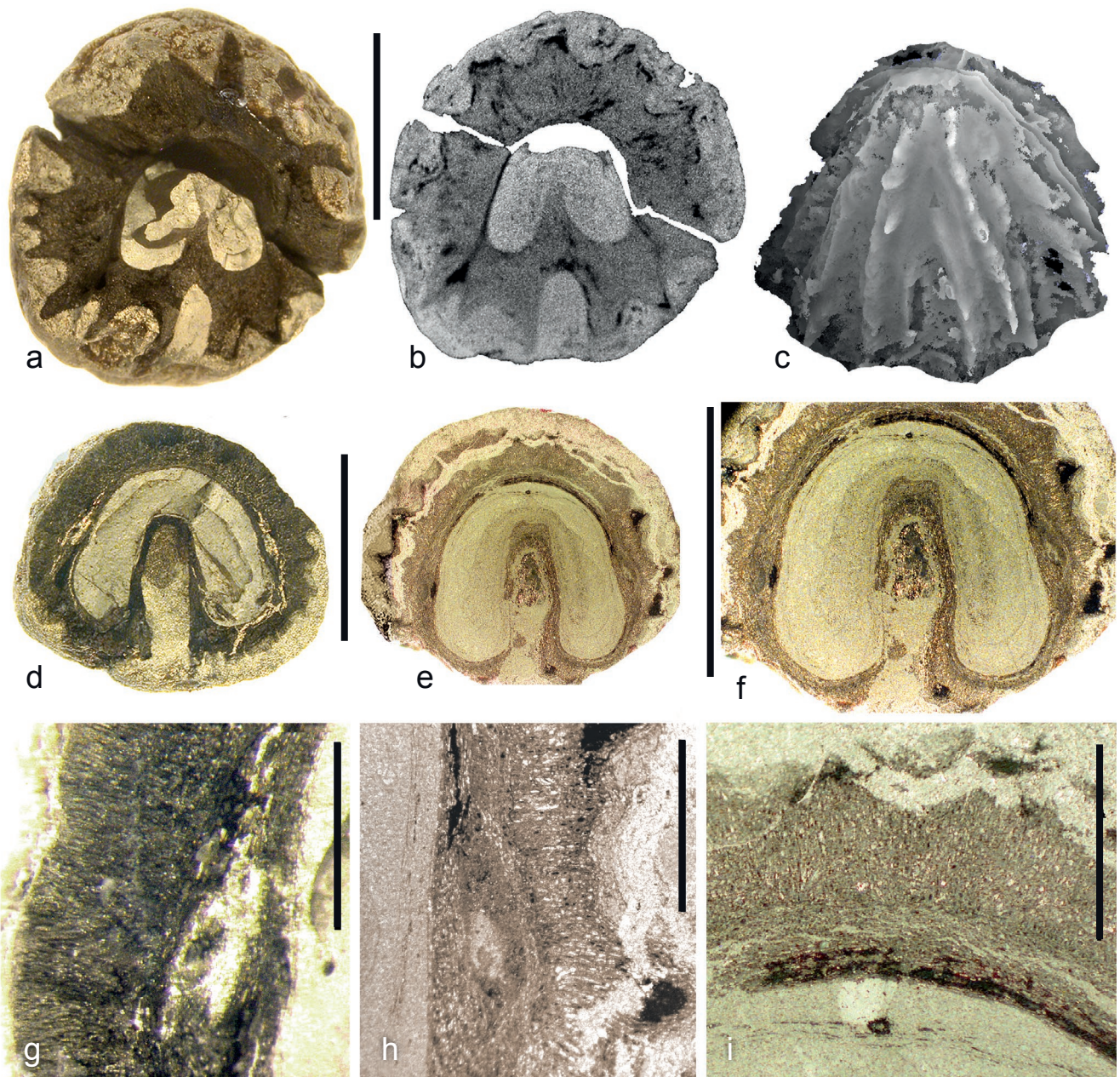
Genus *Mastixia* BLUME, 1826

Mastixia parva E.REID et M.CHANDLER, 1933

Text-fig. 3a–i

Holotype. V.22972 (Natural History Museum, London).

Remarks. This is one of the oldest occurrences of the extant genus, *Mastixia*. The holotype has degraded from pyrite decay since it was initially imaged by Reid and Chandler (cf. Text-fig. 3a, b), but micro-CT scanning still reveals the internal structure (Text-fig. 3c–g). The unilocular, single-seeded fruits have endocarps 7–10 mm long, with a relatively smooth surface, and a few shallow

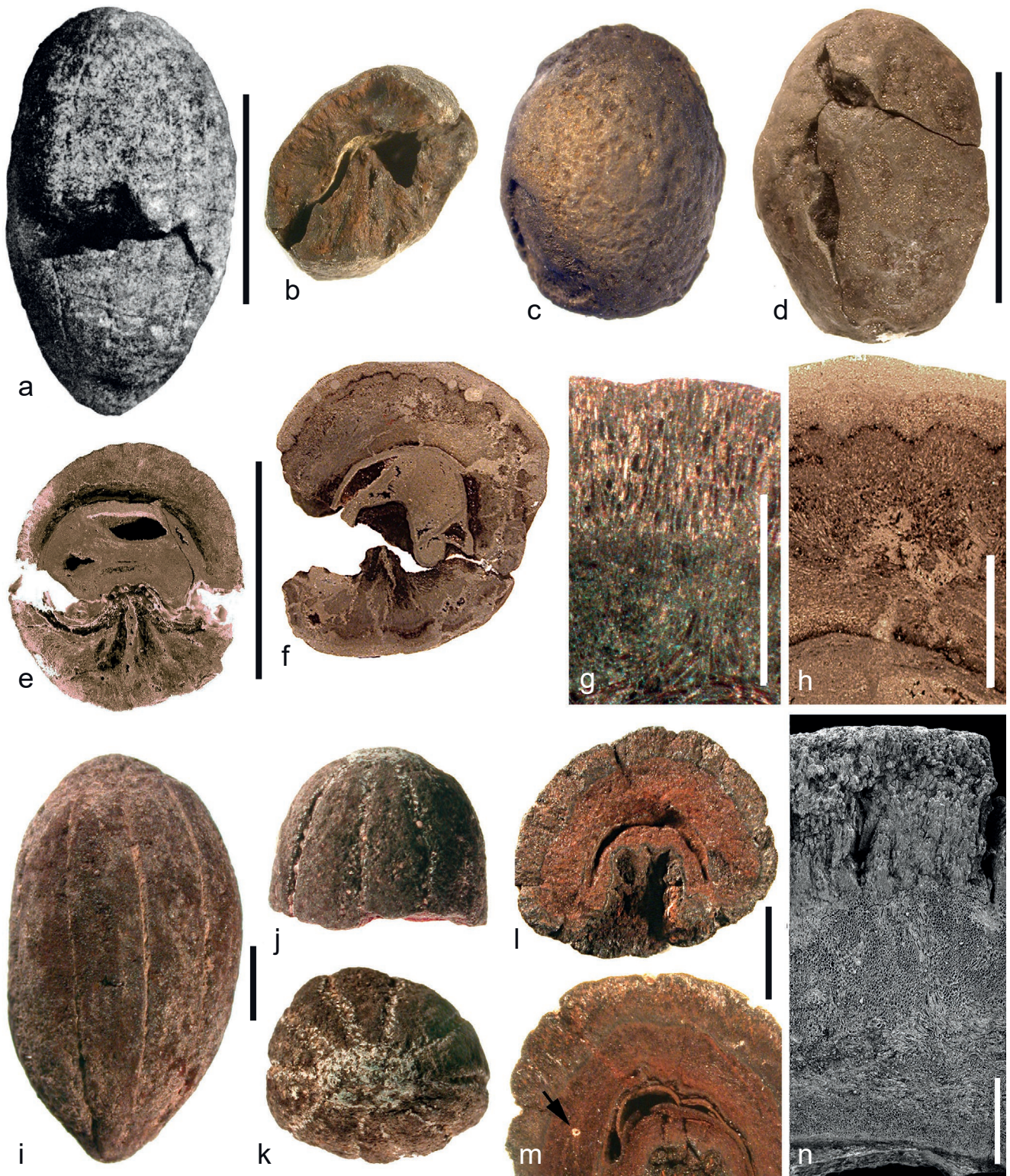


Text-fig. 4. *Mastixia* cf. *oregonensis* (R.A. SCOTT) TIFFNEY et HAGGARD from the London Clay, originally included within the concept of *M. cantiensis*. a–c: V. 22960(1). a: Transverse fracture, showing c-shaped locule, dorsal infold, and sculptured endocarp, reflected light. b: Transverse digital section from micro-CT scan data. c: Surface view of ribbed endocarp extracted from micro-CT data. d: Transverse fracture, reflected light, V. 22955 (originally illustrated in pl. 25, fig. 4 of Reid and Chandler 1933). e, f: Transverse physical section, V. 22963(2) showing U-shaped locule and longitudinal dorsal infold. g–i: reflected light. g: Detail from left of (d). h, i: Detail from right of (f). Scale bars 5 mm in (a–f), 1 mm in (g–i).

longitudinal furrows. Reid and Chandler (1933) observed a circular scar at the apex marking the limit of an accrescent calyx. They described the mesocarp as 0.6 to 0.98 mm thick, formed of polygonal or rounded cells, typically ca 30 μm in diameter. The endocarp opens at germination by a large longitudinal dorsal valve with a median longitudinal groove on its external surface (Text-fig. 3h) corresponding with a deep longitudinal dorsal infold projecting into the locule as a rounded ridge, forming a c-shaped locule as viewed in transverse section (Text-fig. 3d–g, i). The wall is about 0.8 mm thick, formed of a layer of transversely aligned elongate cells and parenchyma. The locule lining is composed of transversely aligned fibres. As in extant

Mastixia, the separation zones of the germination valve run tangential to the limbs of the locule.

Additional examples that appear likely to represent the same or a very similar species were called simply “*Mastixia* sp.” by Manchester (1994) from the middle Eocene Clarno Nut Beds locality of Oregon. Those specimens clearly show the pair of ovular bundle canals running parallel to the germination valve margins (Manchester 1994: pl. 10, fig. 2) – a characteristic feature of this extant genus. Other species of *Mastixia* came to prominence later in the European Tertiary, including *Mastixia rattazzii* MARTINETTO in the Oligocene and *M. amygdaliformis* (SCHLOTH.) KIRCHH. (Hably and Erdei 2013), *M. lusatica* MAI, and *M. thomsonii* MAI (Mai 1970) in the Miocene.



Text-fig. 5. *Mastixiopsis nyssoides* KIRCHH. a, b, g–n: Organic preservation. a, b: Lignitic, unpermineralized, early Eocene Dorset Pipe clays at Arne, V. 40762. a: Ventral view (original illustration from pl. 18, fig. 1 of Chandler 1962). b: Transverse fracture, somewhat distorted by compression. c–f: Pyrite permineralization. c: Ventral view, V. 22963(1) from Sheppey, originally listed as *Mastixia cantiensis*. d: Lateral view, V. 22969 from Sheppey (identified as *Mastixia grandis* by Reid and Chandler 1933: pl. 25, fig. 8). e: Equatorial transverse physical section from (c). f: Equatorial transverse physical section from (d). g: Detail of pericarp from (e), showing endocarp formed of dense fibrous tissue, surrounded by mesocarp of anticlinally oriented larger cells. h: Detail of pericarp from (f). i–n: Type material from Eocene of Riestadt, Germany, MNB. i: Ventral view. j, k: Ventral and apical views of holotype. l: View of the transversely fractured surface from (j) showing horseshoe shaped locule. m: Equatorial transverse physical cut of the specimen in (i); note yellow resin cavity (arrow). n: Scanning electron microscopy of pericarp from (l) with locule lining at lower edge of image. Note dense endocarp tissue composed of small cells (fibres and sclereids), extending about 3/5 of distance to periphery, surrounded by mesocarp of larger, anticlinally oriented cells. Scale bars 1 cm in (a–f), (i–k), 1 mm in (g), 2 mm in (h), 3 mm in (l), m, 250 μ m in (n). Bar in (d) applies also to (c). Bar in (l) also applies to (m). Bar in (i) also applies to (j) and (k).

***Mastixia cf. oregonensis* (R.A. SCOTT) TIFFNEY et
HAGGARD, 1996**
Text-fig. 4a–i

- 1954 *Mastixioidiocarpum oregonense* R.A. SCOTT, p. 84, pl. 16, figs 16–18.
1994 *Mastixioidiocarpum oregonense* R.A. SCOTT; Manchester, p. 43, text-fig. 10B, pl. 10, figs 4–11.
1996 *Mastixia oregonensis* (R.A. SCOTT) TIFFNEY et HAGGARD, p. 42, pl. 2, figs 1–3.

Remarks. Although the holotype that Reid and Chandler (1933) designated for *Mastixia cantiensis* belongs instead to *Diplopanax* (see above), some of the paratypes they identified to *Mastixia cantiensis* are readily distinguished from *Diplopanax* in having prominent endocarp sculpture and a pair of prominent ovular bundle canals in the endocarp adjacent to the germination valve margins. In particular, the specimens V. 22955 (Reid and Chandler 1933: pl. 25, fig. 4), V. 22960(1) (Text-fig. 4a–c), and V. 22963(2) (Text-fig. 4e–f) resemble the fossil genus *Mastixioidiocarpum* R.A. SCOTT, previously described from the Eocene Clarno Formation of Oregon, USA (Scott 1954, Manchester 1994). That fossil genus was subsumed into *Mastixia* by Tiffney and Haggard (1996), who noted that the only difference from modern species of the genus is the more prominently sculptured endocarp. Tiffney and Haggard (1996) also attributed similar fruits from the late Eocene LaPorte flora of California to the extant genus.

A clear distinction between the Oregon species and the London Clay specimens has not been seen, but the London Clay specimens typically show less prominent sculpture due to abrasion. We treat specimens of this kind as *Mastixia cf. oregonensis*. In Europe, such prominently sculptured fossil endocarps are present in some species of *Eomastixia* but are rare in *Mastixia*. Most similar are *Mastixia thomsonii* MAI from the Miocene of Konzendorf and Düren, Germany (Mai 1970) and *M. rattazzii* MARTINETTO (Martinetto 2011) from the Oligocene of Germany and Italy, respectively.

Genus *Mastixiopsis* KIRCHH., 1936

***Mastixiopsis nyssoides* KIRCHH., 1936**
Text-fig. 5a–g

Remarks. *Mastixiopsis* is an extinct genus which was first recognized from the Eocene of Riestedt, Germany (Kirchheimer 1936). The fruits are unilocular with a locule that is curved in cross section (Text-fig. 5l, m). The germination valve extends over the entire length of the endocarp (Kirchheimer 1936). We reexamined the type material and used Scanning electron microscopy to document the pericarp anatomy (Text-fig. 5n). The endocarp is a dense tissue composed of fibers and sclereids and is surrounded by a thick mesocarp of larger anticlinally oriented cells (Text-fig. 5l–n).

In his concept of *Mastixiopsis nyssoides* KIRCHH., Mai (1993) included a specimen called “*?Mastixia cantiensis* M. CHANDLER, 1962 (non Reid and Chandler 1933)” by Chandler (1962: 122–123, pl. 18, figs 1–3) from the early Eocene Dorset Pipe clays at Arne, UK. That specimen is refigured here (Text-fig. 5a, b). However, Mai was unable to study the original material and stated “without the knowledge

of the originals, it is not possible to decide whether this determination is also correct for the typical *Mastixia cantiensis* E. REID et M. CHANDLER (1933) from the London Clay.” (Mai 1993: 59). We encountered two additional specimens of the same kind from the London Clay of Sheppey. One of them (Text-fig. 5c, e, g) was listed as a specimen of *M. cantiensis* by Reid and Chandler (1933), and the other (Text-fig. 5d, f, h) was cited by the same authors as the paratype of *Mastixia grandis* REID et CHANDLER (the holotype of which we now treat as *Tectocarya grandis*). We re-examined the type material of *Mastixiopsis* from Riestedt for comparison (Text-fig. 5i–n).

The type material of *Mastixiopsis nyssoides* from the Eocene of Riestedt shows prominent external longitudinal grooves (Text-fig. 5i–k). These grooves are also seen in the Arne specimen (Text-fig. 5a using pl. 18, fig. 1 in Chandler 1962), but they are not obvious on the outside of the pyritized Sheppey specimens (Text-fig. 5c, d). The undulatory contact between the epicarp and mesocarp as seen in transverse sections (Text-fig. 5f, h) may be an indication of those grooves but the spacing lacks the uniformity of the grooves in Text-fig. 5a and Text-fig. 5i–k. The anatomical composition of the London Clay specimens conforms well with those from Riestedt, including the mesocarp of anticlinally oriented elongate cells and the more dense inner sclerenchymatous layers forming the endocarp. Future CT study of the Riestedt and Arne specimens and the London Clay specimen in Text-fig. 5e, f, h will be helpful to confirm if all of these belong to the same taxon.

Genus *Exbeckettia* MANCHESTER et M.E. COLLINSON
gen. nov.

Type. *Exbeckettia mastixioides* (E. REID et M. CHANDLER) MANCHESTER et M.E. COLLINSON comb. nov.

Plant Fossil Names Registry Number.
PFN002684 (for new genus).

***Exbeckettia mastixioides* (E. REID et M. CHANDLER)**
MANCHESTER et M.E. COLLINSON comb. nov.
Text-fig. 6a–l, 7a–g

Basionym. *Beckettia mastixioides* E. REID et M. CHANDLER (Reid and Chandler 1933: The London Clay flora, p. 456, pl. 25, figs 28–36).

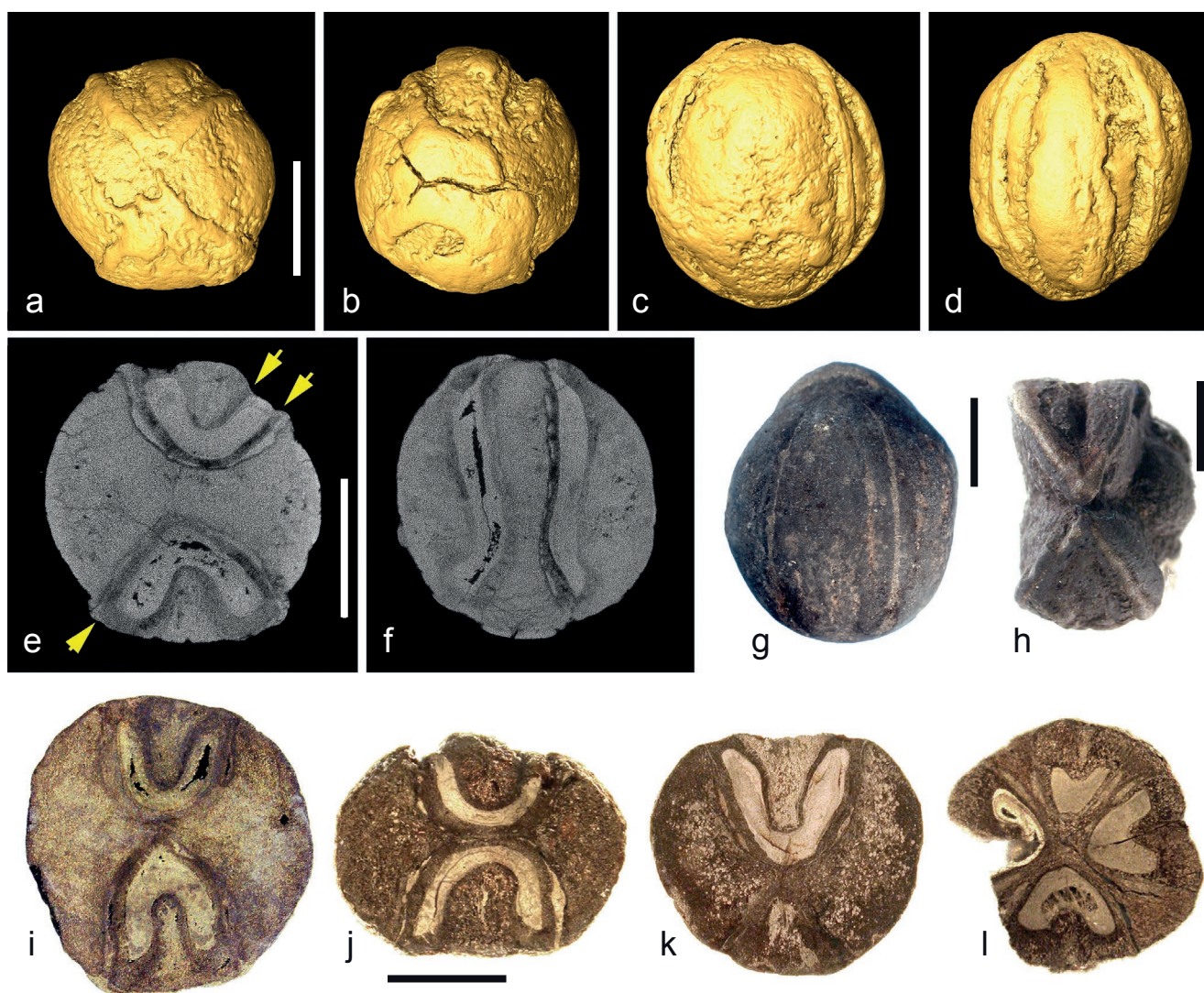
Holotype. V.23002 (Natural History Museum, London).

Plant Fossil Names Registry Number.
PFN002909 (for new combination).

Nomenclature. A new generic name: *Exbeckettia* MANCHESTER et M.E. COLLINSON is proposed because the name *Beckettia* E. REID et M. CHANDLER (Reid and Chandler 1933) is a junior homonym of the moss genus *Beckettia* MÜLLER (Müller 1898).

Emended diagnosis. Diagnosis as presented by Reid and Chandler 1933 is hereby emended slightly to include two to four locules (compared to bilocular to rarely trilocular fruits in the original diagnosis).

Remarks. Reid and Chandler (1933) established this genus and species for subglobular or broadly ovoid fruits



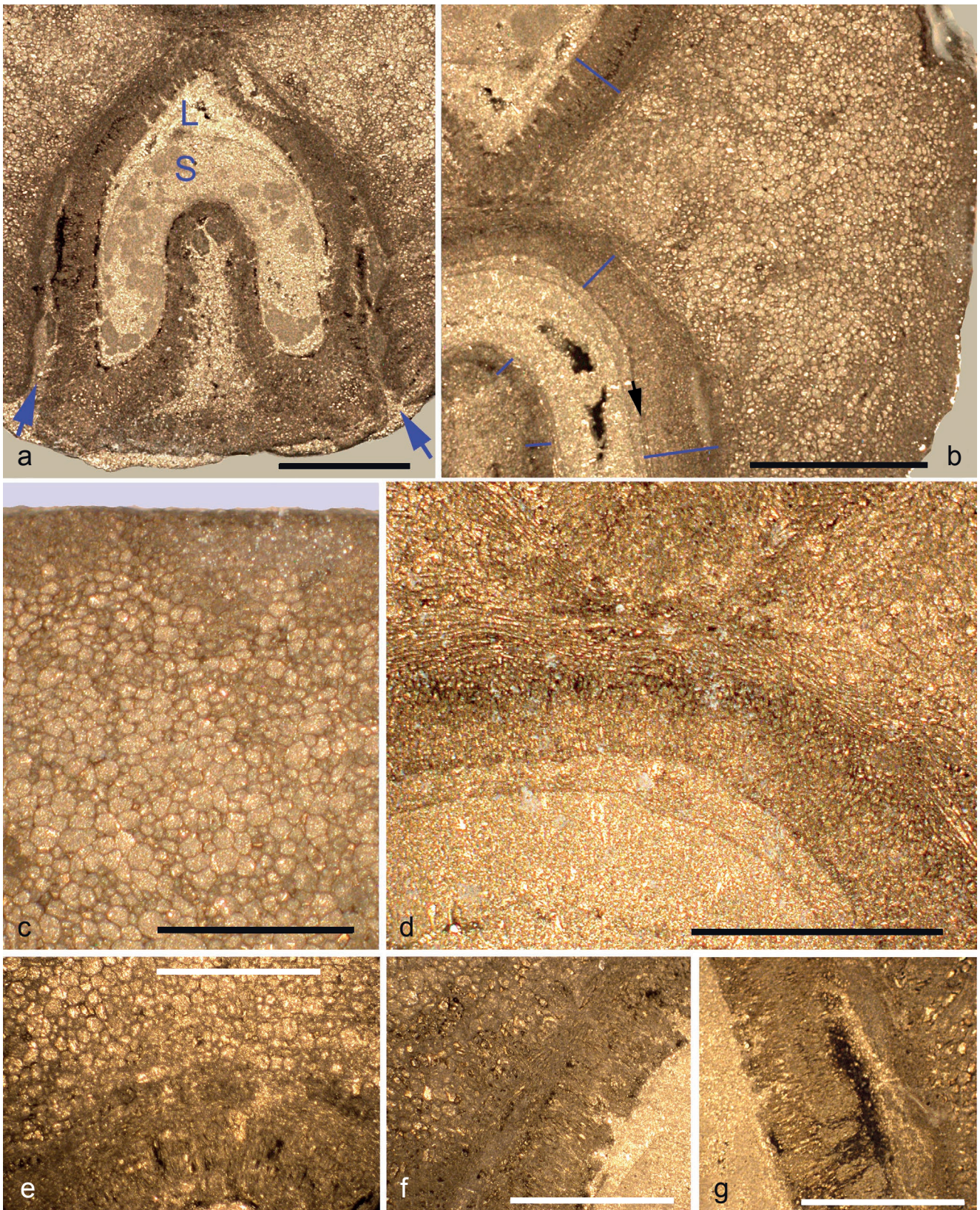
Text-fig. 6. *Exbeckettia mastixioides* (E.REID et M.CHANDLER) comb. nov. from the London Clay. a–f: Holotype, V. 23002, bilocular fruit. a–d: Surface renderings from micro-CT data. a: Apical view. b: Basal view. c: Lateral view with dorsal surface of locule facing forward. d: lateral view with interlocular septum facing forward. e, f: Digital sections from micro-CT data. e: transverse equatorial showing U-shaped locules and distinct dark endocarp (arrows). f: Median longitudinal intercepting both locules. g: lateral view of bilocular fruit with interlocular septum facing forward. V. 23013(3). h: Apical view of bilocular fruit with two exposed locule casts, V. 23013(1). i–l: Fruits in physical transverse section showing U-shaped locules and distinct locule lining. i: Bilocular fruit shown in (g). j: Bilocular fruit, V. 23007. k: Fruit with one locule larger than the other, V. 23006. l: Tetralocular fruit, V. 22993. Scale bar 5 mm in (a–l), bar in (a) applies also to (b–d), bar in (e) applies also to (f), bar in (j) applies to (i–l).

with two to three locules, the locules U-shaped in cross section, each with an elongate dorsal germination valve (e.g., Text-figs 6e, h, i–k, 7a). In addition, we noticed one tetralocular specimen that had previously been classified as *Lanfrancia*, which conforms to *Exbeckettia* in its anatomical composition (Text-fig. 6l). The fruits are 13–15 mm long and 11.5–13 mm wide. The single seed within each locule bears a ventral raphe as expected in Mastixiaceae. The endocarp surrounding each locule is smooth-surfaced with a relatively thin wall (0.8 to 1 mm thick on the ventral and lateral surfaces and 0.4 mm thick within the dorsal infolds). The bulk of the fruit stone appears to be mesocarp composed of parenchyma cells rather than fibres (Text-fig. 7b, c). A layer of horizontally oriented periclinal fibres (up to 4 cells thick) lines the locule except in the dorsal infold area (Text-fig. 7b). Similar fibres, also oriented horizontally, but in layers up to 10 cells thick, form the outer part of the endocarp wall (Text-

fig. 7d–g). Most of the endocarp is formed of longitudinally elongate, rice grain-shaped sclereids about 3–4 times longer than wide, which appear approximately circular in cross section, arranged in radial files, along which degradational splitting may occur (Text-fig. 7a, f, g).

A pair of canals, apparently marking the pathway of ovular bundles, runs longitudinally through the endocarp. The margins of the germination valve run tangential or parallel to the arms of the locule (Text-figs 6e, i–l, 7a), rather than intersecting directly with the locule, suggesting that they may have detached as pyrenes, rather than functioning in germination splitting, but as Reid and Chandler (1933) already discussed, it is possible that this is an artefact of preservation.

Reid and Chandler (1933) observed that the seed coat has two layers: an outer coat formed of many layers of polygonal cells 50 µm in diameter, as seen in impressions on



Text-fig. 7. *Exbeckettia mastixioides* (E.Reid et M.Chandler) comb. nov. Details of anatomy in transverse section on cut surfaces from bilocular fruit shown in Text-fig. 6i, V. 23013(3). a: Details of seed (S), locule (L), distinct endocarp planes of separation (arrows). b: Detail of endocarp adjacent to the locule, and surrounding mesocarp. Blue lines indicate thickness of sclerenchyma lining the locule. Note layer of horizontally oriented periclinal fibres a few cells thick, lining the locule (arrow). c: Enlargement showing parenchyma cells of the mesocarp decreasing in diameter toward the periphery. d: Enlargement showing fibres and sclereids of the endocarp. e: Sharp contact between endocarp and mesocarp. f, g: Detailed anatomy of endocarp including locule lining, and contact with mesocarp. Scale bars 2 mm in (a), (b), 1 mm in (c–g).

the locule cast, and with a columnar arrangement, as seen in radial sections of the seed, and an inner coat two cells thick of small obliquely aligned cells that produce a finely striate surface.

The dorsal infolds of *Exbeckettia* are broad and the central area of each infold is occupied by mostly large isodiametric parenchyma cells or sclereids with smaller cells distributed peripherally (e.g., Text-fig. 7b, c). Surrounding and infilling between the sclerenchymatous endocarps is a large area of parenchymatous tissue, composed of rounded isodiametric cells that include large cells interspersed among smaller cells (Text-fig. 7c, e). Reid and Chandler (1933) considered this tissue to be a part of the endocarp, however we treat this tissue as “mesocarp” because of its parenchymatous composition and striking similarity to the tissue surrounding the endocarp of the unilocular fossil, *Diplopanax eydei* STOCKEY, PIGG et LEPAGE (Stockey et al. 1998). The parenchymatous tissue is not traversed by vascular bundles nor secretory canals. Despite excellent preservation, no resin cavities or canals are seen in *Exbeckettia*.

Reid and Chandler (1933) considered the relationship of this genus to *Mastixia* to be clear but emphasized that the fossil is distinguished by having more than one locule and by the mass of coarse parenchyma which mainly fills the angular spaces between the locules. The presence of an ovular bundle on either side of each locule, and of planes of separation running tangential to the lateral endocarp wall are additional similarities with *Mastixia*.

Mai (1993) adopted a broad concept of *Beckettia*, into which he sunk the London Clay genera *Portnallia* and *Lanfrancia* and added some Cretaceous species (Knobloch and Mai 1986, Mai 1993). If his interpretation is followed then these would all belong now under the name *Lanfrancia*, due to the fact that *Beckettia* was a junior homonym. However, we do not agree with Mai’s (1993) interpretation that these species were congeneric. *Lanfrancia* is distinguished by more fibrous endocarps and apparently lacks the pair of ovular bundle channels expected to straddle each locule. Also, the tissue that forms between adjacent locules of *Lanfrancia* is not the same kind of parenchyma. In our current treatment we have also retained *Portnallia* as a distinct genus with justification provided below.

Genus *Lanfrancia* E.REID et M.CHANDLER, 1933

***Lanfrancia subglobosa* E.REID et M.CHANDLER, 1933**

Text-fig. 8a–o

Remarks. *Lanfrancia* was distinguished by Reid and Chandler (1933) from *Exbeckettia* (then *Beckettia*) in lacking the large wedges of parenchymatous tissue between locules. In addition, the fruits of *Lanfrancia* do not show the obvious pair of ovular traces adjacent to each locule – a difference from extant and fossil *Mastixia*, as well as from *Exbeckettia* and *Eomastixia*. Three to five layers of horizontal fibres line the U- to V- or C-shaped locules of *Lanfrancia* (e.g., Text-fig. 8k, m), but the remainder of the endocarp is formed by rounded sclereids as seen in transverse section (Text-fig. 8j–m) and longitudinal section (Text-fig. 8n, o).

Reid and Chandler (1933) noted the similarity of *Lanfrancia* to *Eomastixia*, but considered that it differed by having more locules. Later this difference was negated

as Chandler (1962) showed that 3- and more-loculed fruits of *Eomastixia* occur at the type locality (Manchester and Collinson 2019). Reid and Chandler also noted a possible difference in mode of germination. The *Lanfrancia* specimens were observed to fall apart into pyrenes, rather than staying together and germinating by valves – a feature they acknowledged could be due to their pyritic preservation, differing from the carbonaceous preservation of the type material of *Eomastixia*. *Lanfrancia* corresponds to *Eomastixia* in the fibrous composition of the septa and dorsal infold regions, the closed dorsal infolds (with little or no intrusion of mesocarp). Whereas *Eomastixia* includes resin cavities (Collinson et al. 2012, Manchester and Collinson 2019), we have not observed these in *Lanfrancia*.

Genus *Portnallia* M.CHANDLER, 1961

***Portnallia bognoensis* M.CHANDLER, 1961**

Text-fig. 9a–o

- 1961 *Portnallia bognoensis* M.CHANDLER, p. 285, pl. 28, figs 39–44 (V. 30422 b).
1961 *Portnallia sheppeyensis* M.CHANDLER, p. 286, pl. 28, figs 45, 46, pl. 29, figs 1–3.
1986 *Beckettia bognoensis* (M.CHANDLER) ERW.KNOBLOCH et MAI, p. 107.
1986 *Beckettia sheppeyensis* (M.CHANDLER) ERW.KNOBLOCH et MAI, p. 107.

Holotype. V.30421 (Natural History Museum, London).

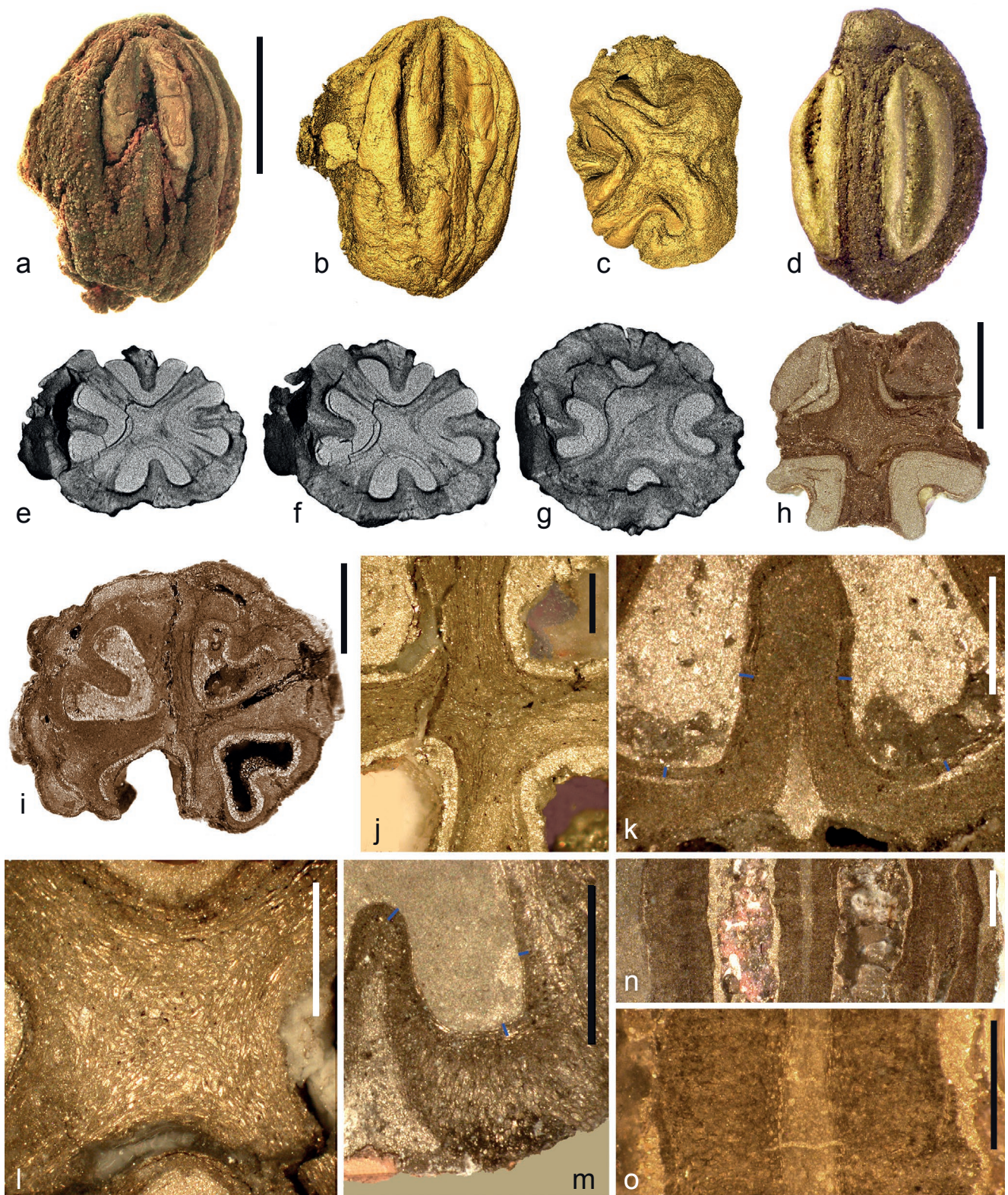
Remarks. The genus *Portnallia* was established by Chandler (1961) for subglobular to ovoid 2- to 3- to 4-locular endocarps distinguished by their smaller size (4–6 mm long) relative to *Exbeckettia* (13–15 mm long) and *Lanfrancia* (12 mm long). Chandler recognized two species, differing from each other in size (3.5–6 mm long in *P. bognoensis*, vs. 6–7.5 mm in *P. sheppeyensis*), but she added “Should more abundant material become available in the future, the validity of *Portnallia sheppeyensis* as a species should be reviewed...” (Chandler 1961: 287). Transverse sections of the two species show striking similarities in form of the locule and the narrow fibrous intervening septae (Text-fig. 9b, e, g, i, m–o). Knobloch and Mai (1986) treated both species of this genus as conspecific and transferred them to *Beckettia*. However, as mentioned above, the name *Beckettia* was earlier established for a genus of moss, so the name with priority in the case of a merger of these genera would be *Portnallia*. However, we do not support the merger of these genera, because the fruit stones of *Exbeckettia* are characterized by large areas of isodiametric cells between adjacent locules, whereas those of *Portnallia* are composed mainly of fibres. We retain *Portnallia* as a distinct entity from *Lanfrancia* because of its much smaller size (about half the length).

Genus *Langtonia* E.REID et M.CHANDLER, 1933

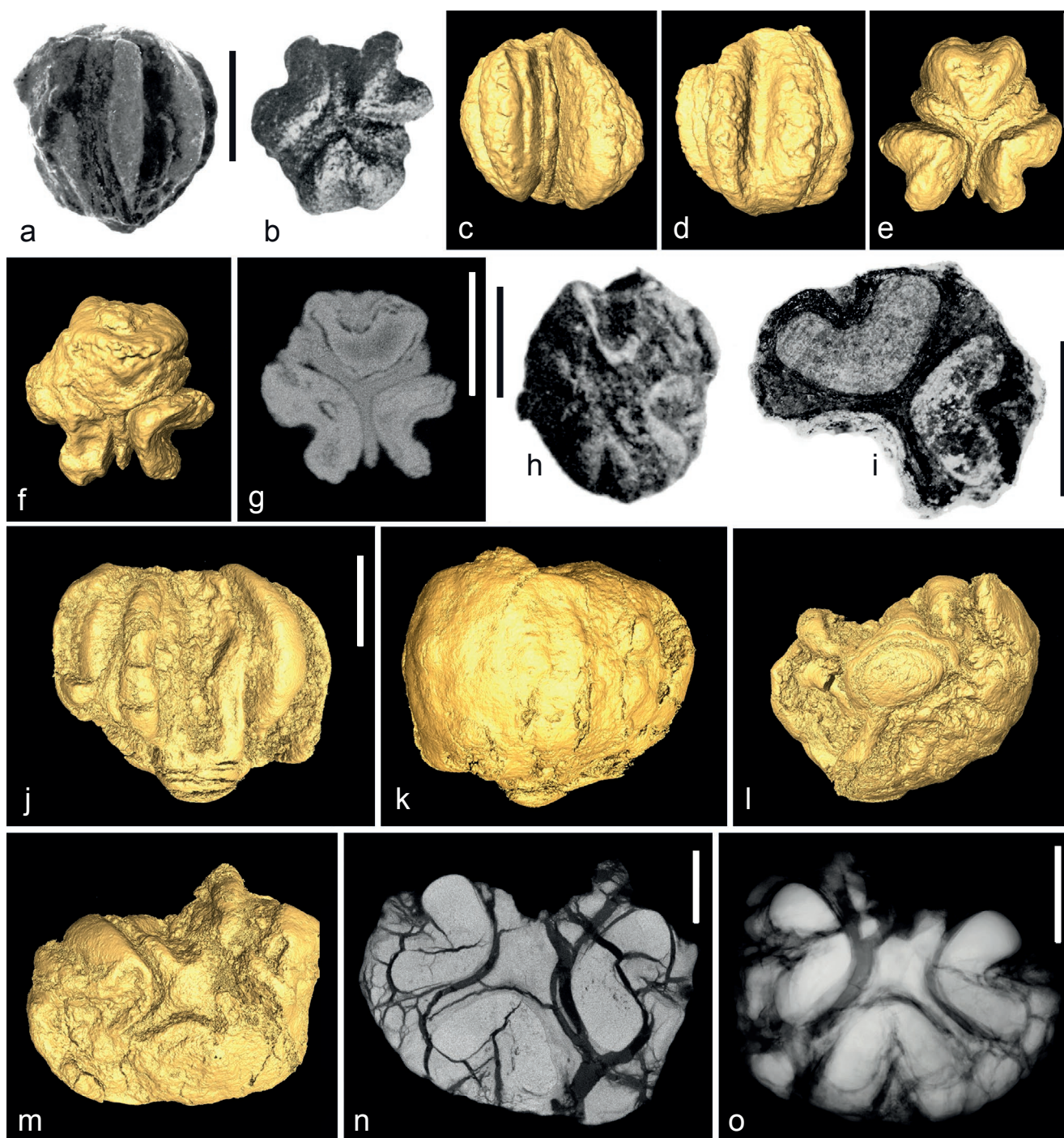
***Langtonia bisulcata* E.REID et M.CHANDLER, 1933**

Text-fig. 10a–j

Holotype. V.22984 (Natural History Museum, London).



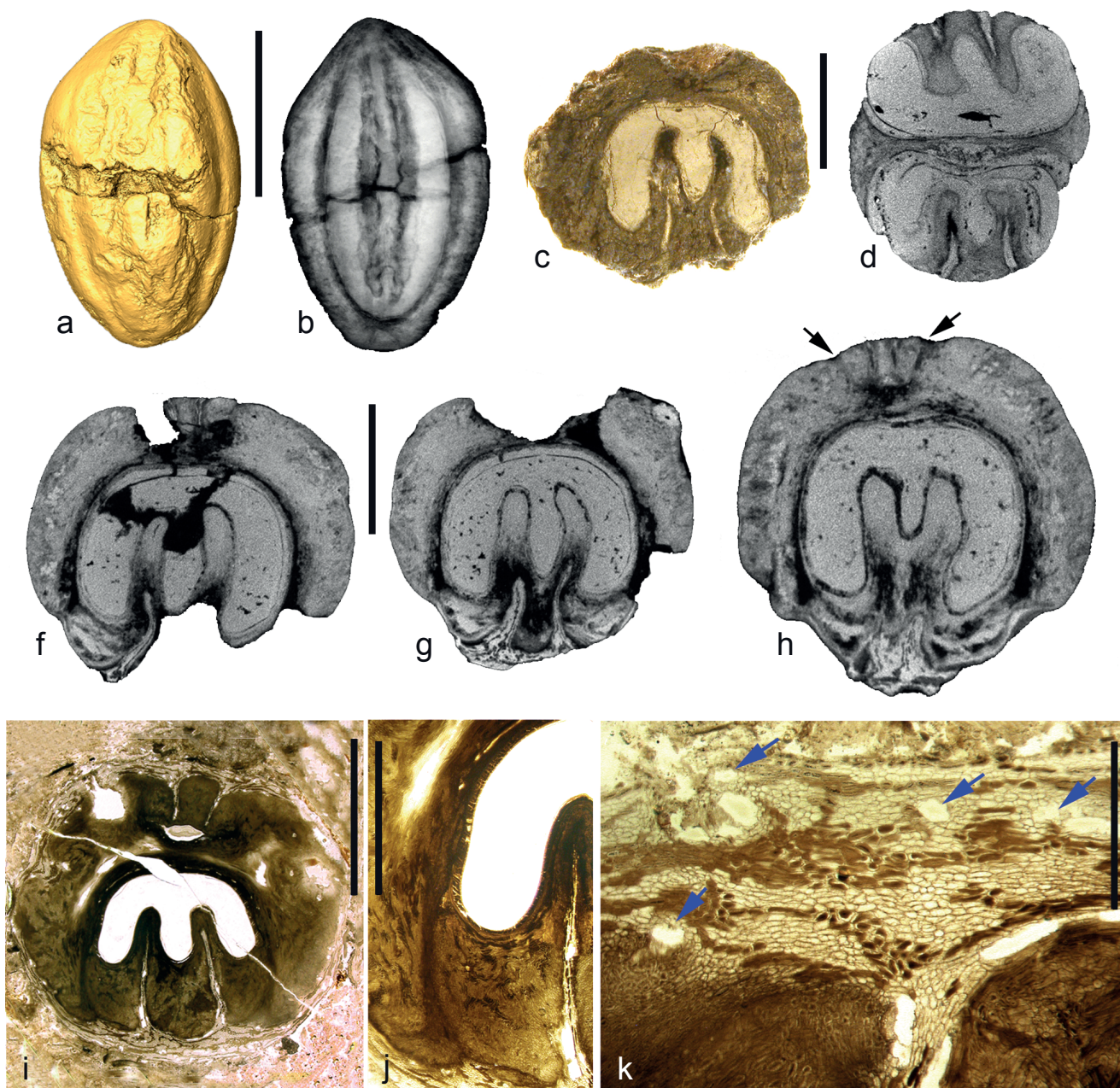
Text-fig. 8. *Lanfrancia subglobosa* E.REID et M.CHANDLER. a–c, e–g: Holotype V. 23014. a: reflected light. b, c: Surface renderings from micro-CT data. a, b: Lateral views with dorsal surface of locule facing forward and locule casts protruding in upper part. c: Apical view. d: Fruit showing two locule casts the dorsal surfaces of which face to the left and the right, V. 30417(1). e–g: Successive digital transverse sections showing four u to v to c-shaped locules from micro-CT data. h: Physical transverse section of specimen in (d). i–k: Physical transverse section, V. 30419 from Herne Bay, blue lines in K indicating limits of fibre layer lining the locule. l: Detail from (h), showing sclerenchyma composing the septa and central axis. m: Transverse section, enlargement from (i), showing anatomy of tissues adjacent to the dorsal infold. Blue lines indicate limits of the fibre layer lining the locule. n: Part of (m) recut, tangential section transecting the dorsal infold (central), both limbs of the locule cast, and peripheral parts of the pericarp on either side. o: Detail from (n), showing anatomy of the infold. Scale bars 5 mm in (a–h) (a–g share the same bar), 3 mm in (i), 1 mm in (j–m), 0.5 mm in (n), 0.2 mm in (o).



Text-fig. 9. *Portnallia*. a–j: *P. bognorensis* M.CHANDLER. a–g: Holotype, V. 30421. a: Oblique lateral view with dorsal surface of locule cast facing towards right side. b: Basal view (original illustration from pl. 28, fig. 40 of Chandler 1961). c–g: Micro CT data. c–f: Surface renderings. c: Lateral view with interlocular septum facing forward. d: lateral view with dorsal surface of locule facing forward. e: Basal view. f: Apical view. g: Digital transverse section near equatorial position showing (c) to u-shaped locules. h: Apical view of tetralocular fruit, V. 30423 (original illustration from pl. 28, fig. 42 of Chandler 1961). i: Transverse section of specimen in (h), reflected light. j–o: *P. sheppeyensis* M.CHANDLER, Holotype V. 30428, here synonymized with *P. bognorensis*, from micro-CT data. j–m: Surface renderings. j: Lateral view with interlocular septum facing forward. k: Lateral view with dorsal surface of locule facing forward. l: Basal view. m: Apical view. n: Digital equatorial transverse section showing the three preserved locules and extensive cracking due to pyrite decomposition. o: Translucent volume rendering, apical view showing (c) to u-shaped locules. Scale bars 2 mm, bar in (a) applies also to (b), bar in (e) applies to also to (c, d), bar in (g) applies also to (f), bar in (j) applies to applies also to (k–m).

Remarks. *Langtonia* was established and identified as an extinct mastixoid genus by Reid and Chandler (1933). *Langtonia bisulcata* fruits are elongate-ellipsoidal with smooth to shallowly ridged surface. The fruits have endocarps composed of tortuous fibres (Text-fig. 10g–j)

surrounded by a thin mesocarp and epicarp covering (Text-fig. 10j). Endocarps vary greatly in size from 9 to 20 mm long in the London Clay (Reid and Chandler 1933) and from 16 to 35 mm long in the Clarno Nut Beds (Manchester 1994). The fruits are bilocular, sometimes with both locules well



Text-fig. 10. *Langtonia bisulcata* REID et CHANDLER. a, b, e–g: Holotype, V. 22984, from micro-CT data. a: Dorsiventral view surface rendering. b: Dorsiventral view translucent volume rendering showing outline of locule cast. c: Equatorial transverse fracture showing paired dorsal infolds and locules with shape of a ϵ in cross section, reflected light, V. 22993. d: Digital transverse section from micro-CT data, of fruit with two well developed ϵ -shaped locules, V. 22985. e–g: Successive digital transverse sections with one well developed ϵ -shaped locule and infolds of the abortive locule visible in (g) (arrows). h–j: Physical transverse thin sections of specimen from middle Eocene Clarno Formation, Oregon, USA with well-preserved mesocarp including longitudinal canals in (j) (arrows), USNM 424875; Scale bars 0.5 cm in (a, b), 2.5 mm in (c–g), 5 mm in (h), 2 mm in (i), 1 mm in (j); (a, b) share same scale bar; (c, d) share same scale bar; (e, f, g) share same scale bar.

developed (Text-fig. 10d), but commonly with one of the locules abortive (Text-fig. 10c, g, h). Unlike the other extant and fossil genera of Mastixiaceae, each germination valve of *Langtonia* has two dorsal infolds resulting in a locule that has the shape of a ϵ in cross section (Text-fig. 10c–h). Contrary to the situation in *Mastixia* and *Eomastixia*, where ovular bundles follow the germination valve boundaries, the vascular bundles of *Langtonia* are scattered, situated mainly in the septal area in the endocarp on the ventral side of each locule. The germination valves lack prominent vascular bundles. The locule is lined by a uniseriate layer of relatively large rectangular cells (Text-fig. 10i).

Kirchheimer (1957) questioned the affinity of *Langtonia* to Mastixiaceae because of the double infolds which are not seen in any other mastixioids. However, the woody endocarps with elongate germination valves, and pendulous anatropous seeds with ventral raphe (Reid and Chandler 1933: pl. 25, fig. 21, Manchester 1994: pl. 11, fig. 5) support Reid and Chandler's assignment. The endocarps have elongate germination valves that extend the full length of the locule as in extant Mastixiaceae, contrasting with the apically confined valves of Nyssaceae (*Amersinia* MANCHESTER, P.R.CRANE et GOLOVN., *Camptotheca* DECNE., and *Nyssa* L.; fig. 12 in Manchester and Hickey 2007).

In western North America the same genus and species is known from permineralized fruits in the Eocene Clarno Formation (Manchester 1994) and by the distinctive endocarp molds and locule casts from Paleocene Fort Union Formation (Tiffney and Haggard 1996). Although well represented in the London Clay, *Langtonia* has not been observed in the carpofloras of continental Europe. Most specimens are preserved with only the endocarp remaining, but one of the Clarno specimens with intact soft tissue (Text-fig. 10h–j) shows the presence of longitudinal canals (Text-fig. 10j) similar to those seen in extant *Mastixia* (Manchester and Collinson 2019: pl. 1, fig. 11).

Conclusions

The diversity of Mastixiaceae in the London Clay flora was even greater than previously recognized. Both extant genera, *Mastixia* (2 spp.) and *Diplopanax*, are now recognized, plus six extinct genera: *Exbeckettia*, *Lanfrancia*, *Langtonia*, *Mastixiopsis*, *Portnallia*, and *Tectocarya* for a total of eight genera and nine species. This diversity, together with that of Alangiaceae (Reid and Chandler 1933, Feng et al. 2009), Cornaceae (Reid and Chandler 1933, Manchester et al. 2010), Nyssaceae (Reid and Chandler 1933, Zhou et al. 2020), and Curtisiaceae (Manchester et al. 2007), indicates that the Cornales were prominent in the early Eocene London Clay flora. Judging from the growth habits of modern relatives, these plants were probably trees, and coexisted in the London Clay community along with other arborescent taxa including Juglandaceae, Lauraceae and Magnoliaceae. The other most diverse families in the London Clay carpoflora, including Menispermaceae (16 genera, 18 species; Collinson and Cleal 2001), Icacinaceae (7 genera, 21 species; Stull et al. 2016), and Vitaceae (5 genera, 25 spp.; Collinson and Cleal 2001) probably were mostly lianas.

A few million years prior to deposition of the London Clay flora, the Paleocene floras of western North America were home to a diversity of cornalean taxa, including *Cornus*, *Davidia* BAILL., *Amersinia*, *Browniea* MANCHESTER et L.J.HICKEY, *Langtonia* and *Mastixia* as known from the Paleocene Fort Union Formation (Tiffney and Haggard 1996, Manchester et al. 1999, Manchester 2002, Manchester and Hickey 2007, Manchester 2014) and Denver Formation (Huegele and Manchester 2020). By middle Eocene time, the Clarno flora in western North America included *Alangium*, *Cornus*, *Nyssa*, *Mastixia*, *Langtonia* and *Mastixicarpum* (Manchester 1994), while in Europe, the Messel flora of Germany included *Alangium*, *Nyssa*, and at least four mastixioids (Collinson et al. 2012). The recognition of “Asian” genera in the late Cretaceous and Paleogene of Europe and North America underscores the necessity to include fossil data in evaluating the biogeographic history of the cornalean clade (Atkinson 2018, Atkinson et al. 2017, 2019, Fu et al. 2019).

The Mastixiaceae were especially diverse and abundant in Paleogene of Europe and North America, although they today are restricted to the Indomalayan region (sensu Takhtajan 1969). Despite their richness in the Paleogene of North America, there are no known post-Eocene

occurrences of mastixioids in North America. By contrast, in Europe, the abundance and diversity of mastixioids was maintained or even increased into the Neogene. Although we are not aware of post-Eocene records of *Langtonia*, another extinct genus, *Retinomastixia*, was well represented in later European floras along with *Mastixia*, *Eomastixia*, and *Diplopanax* (Kirchheimer 1938b, Gregor 1978, Mai 1993). As yet, mastixioid fruits have not been recovered from Asian Tertiary floras. The question remains, when did *Diplopanax* and *Mastixia* arrive to the regions where they occur today?

Acknowledgements

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References

- APG IV. (2016): An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. – *Botanical Journal of the Linnean Society*, 181: 1–20.
<https://doi.org/10.1111/boj.12385>
- Atkinson, B. A. (2018): The critical role of fossils in inferring deep-node phylogenetic relationships and macro-evolutionary patterns in Cornales. – *American Journal of Botany*, 105(8): 1401–1411.
<https://doi.org/10.1002/ajb2.1084>
- Atkinson, A., Stockey, R. A., Rothwell, G. W. (2017): The early phylogenetic diversification of Cornales: Permineralized cornalean fruits from the Campanian (Upper Cretaceous) of western North America. – *International Journal of Plant Sciences*, 178(7): 556–566.
<https://doi.org/10.1086/692766>

- Atkinson, B. A., Martínez, C., Crepet, W. L. (2019): Cretaceous asterid evolution: fruits of *Eydeia jerseyensis* sp. nov. (Cornales) from the upper Turonian of eastern North America. – *Annals of Botany*, 123(3): 451–460. <https://doi.org/10.1093/aob/mcy170>
- Averyanov, L. V., Nguyen, T. H. (2002): *Diplopanax vietnamensis*, a new species of Nyssaceae from Vietnam—one more living representative of the Tertiary flora of Eurasia. – *Novon*, 12: 433–436. <https://doi.org/10.2307/3393114>
- Bowerbank, J. S. (1840): A history of the fossil fruits and seeds of the London Clay. – John Van Voorst, London, 144 pp.
- Chandler, M. E. J. (1926): The Upper Eocene flora of Hordle, Hants Part II. – *Monographs of the Palaeontographical Society*, London, 78(363): i–vii, 33–52, pls V–VIII. <https://doi.org/10.1080/02693445.1926.12035598>
- Chandler, M. E. J. (1961): The Lower Tertiary floras of southern England. I. Palaeocene Floras. London Clay Flora (Supplement). Text and Atlas. – British Museum (Natural History), London, 354 pp., 34 pls. <https://doi.org/10.5962/bhl.title.110079>
- Chandler, M. E. J. (1962): The lower Tertiary floras of southern England. II. Flora of the Pipe-clay series of Dorset (Lower Bagshot). – British Museum (Natural History), London, 176 pp., 29 pls. <https://doi.org/10.5962/bhl.title.110079>
- Chandler, M. E. J. (1964): The lower Tertiary floras of southern England. IV. A summary and survey of findings in the light of recent botanical observations. – British Museum (Natural History), London, 151 pp., 4 pls.
- Chandler, M. E. J. (1978): Supplement to the Lower Tertiary floras of southern England, Part 5. – *Tertiary Research Special Paper*, 4: 1–47.
- Collinson, M. E. (1983): Fossil plants of the London Clay (The Palaeontological Association Field Guides to Fossils No. 1). – The Palaeontological Association, London, 121 pp.
- Collinson, M. E., Adams, N. F., Manchester, S. R., Stull, G. W., Herrera, F., Smith, S. Y., Andrew, M. J., Kenrick, P., Sykes, D. (2016): X-ray micro-computed tomography (micro-CT) of pyrite-permineralised fruits and seeds from the London Clay Formation (Ypresian) conserved in silicone oil: a critical evaluation. – *Botany*, 94: 697–711. <https://doi.org/10.1139/cjb-2016-0078>
- Collinson, M. E., Cleal, C. J. (2001): Early and early middle Eocene (Ypresian–Lutetian) palaeobotany of Great Britain. – In: Cleal, C. J., Thomas, B. A., Batten, D. J., Collinson, M. E. (eds), *Mesozoic and Tertiary palaeobotany of Great Britain* (Geological Conservation Review Series No. 22). Joint Nature Conservation Committee, Peterborough, pp. 187–226.
- Collinson, M. E., Manchester, S. R., Wilde, V. (2012): Fossil fruits and seeds of the Middle Eocene Messel biota, Germany. – *Abhandlungen der Senckenberg Gesellschaft für Naturforschung*, 570: 1–250.
- Collinson, M. E., Ribbins, M. M. (1977): Pyritised fern rachides in the London Clay. – *Tertiary Research*, 1(4): 109–113.
- Czaja, A. (2003): Paläokarpologische Untersuchungen von Taphozönosen des Unter- und Mittelmiozäns aus dem Braunkohlentagebau Berzdorf/Oberlausitz (Sachsen). – *Palaeontographica*, Abt. B, 256: 1–148.
- Eyde, R. H. (1997): Fossil record and ecology of *Nyssa* (Cornaceae). – *Botanical Review*, 63: 97–123. <https://doi.org/10.1007/BF02935928>
- Eyde, R. H., Xiang, Q.-Y. (J.). (1990): Fossil mastixioid (Cornaceae) alive in eastern Asia. – *American Journal of Botany*, 77: 689–692. <https://doi.org/10.1002/j.1537-2197.1990.tb14455.x>
- Feng, C.-M., Manchester, S. R., Xiang, Q.-Y. (J.). (2009): Phylogeny and biogeography of Alangiaceae (Cornales) inferred from DNA sequences, morphology, and fossils. – *Molecular Phylogenetics and Evolution*, 51(2): 201–214. <https://doi.org/10.1016/j.ympev.2009.01.017>
- Fu, C. N., Mo, Z. Q., Yang, J. B., Ge, X. J., Li, D. Z., Xiang, Q.-Y. (J.), Gao, L. M. (2019): Plastid phylogenomics and biogeographic analysis support a trans-Tethyan origin and rapid early radiation of Cornales in the Mid-Cretaceous. – *Molecular Phylogenetics and Evolution*, 140: 106601 (16 pp.). <https://doi.org/10.1016/j.ympev.2019.106601>
- Gregor, H. J. (1978): Revision der Arten von *Retinomastixia* Kirchheimer aus dem europäischen Tertiär. – *Mitteilungen der Bayerische Staatssammlung für Paläontologie und Historische Geologie München*, 18: 143–152.
- Hably, L., Erdei, B. (2013): A refugium of *Mastixia* in the late Miocene of eastern Central Europe. – *Review of Palaeobotany and Palynology*, 197: 218–225. <https://doi.org/10.1016/j.revpalbo.2013.06.003>
- Handel-Mazzetti, H. F. (1933): *Plantae novae Chingianae*, III. – *Sinensia*, 3: 185–198.
- Holý, F. (1975): Representatives of the family Mastixiaceae Calestani 1905 in the Bohemian Tertiary. – *Acta Musei Nationalis Pragae, Series B – Historia Naturalis*, 31(3-5): 123–147.
- Huegele, I. B., Manchester, S. R., (2019): Newly recognized diversity of fruits and seeds from the Late Paleogene flora of Trinity County, East Texas, USA. – *International Journal of Plant Sciences*, 180(7): 681–708. <https://doi.org/10.1086/704358>
- Huegele, I. B., Manchester, S. R. (2020): An early Palaeocene carpo-flora from the Denver Basin of Colorado, USA, and its implications for plant-animal interactions and fruit size evolution. – *International Journal of Plant Sciences*, 181(6): 646–665. <https://doi.org/10.1086/707727>
- Kenrick, P. (1999): Opaque petrification techniques. – In: Jones, T. P., Rowe, N. P. (eds), *Fossil plants and spores: modern techniques*. Geological Society, London, pp. 87–91.
- Kirchheimer, F. (1934): Neue Ergebnisse und Probleme paläobotanischer Brunkohlensforschung. – *Braunkohle*, 33: 769–774, 788–793.
- Kirchheimer, F. (1935): Weitere Mitteilungen über Früchte und Samen aus deutschen Braunkohlen II. – *Braunkohle*, 34: 289–294.

- Kirchheimer, F. (1936): Zur Kenntnis der Früchte rezenter und fossiler Mastixioideen. – Beihefte zum Botanischen Centralblatt, Abt. B, 55: 275–300.
- Kirchheimer, F. (1938a): Umbelliflorae: Cornaceae (Fossilium Catalogus, II: Plantae. Pars 23). – Dr. W. Junk Verlag für Naturwissenschaften, Gravenhage, 188 pp.
- Kirchheimer, F. (1938b): Beiträge zur näheren Kenntnis der Mastixioideen-Flora des deutschen Mittel- bis Oberoligozäns. – Beihefte zum Botanischen Centralblatt, Abt. B, 58: 303–375.
- Kirchheimer, F. (1941): Bemerkenswerte Funde der Mastixioideen-Flora. – Braunkohle, 40: 610–617.
- Kirchheimer, F. (1957): Die Laubgewächse der Braunkohlenzeit. – W. Knapp, Halle (Saale), 783 pp.
- Knobloch, E., Mai, D. H. (1986): Monographie der Früchte und Samen in der Kreide von Mitteleuropa. – Rozprawy Ústředního ústavu geologického, 47: 5–219.
- Mai, D. H. (1970): Subtropische Elemente im europäischen Tertiär I. – Paläontologische Abhandlungen Abt. B, 3(3-4): 441–503.
- Mai, D. H. (1987): Neue Arten nach Früchten und Samen aus dem Tertiär von Nordwestsachsen und der Lausitz. – Feddes Repertorium, 98: 105–126.
<https://doi.org/10.1002/fedr.4910980106>
- Mai, D. H. (1993): On the extinct Mastixiaceae (Cornales) in Europe. – Geophytology, 23: 53–63.
- Mai, D. H., Walther, H. (1978): Die Floren der Haselbacher Serie im Weissester-Becken (Bezirk Leipzig, DDR). – Abhandlungen der Staatliches Museums für Mineralogie und Geologie, 28: 1–200.
- Manchester, S. R. (1994): Fruits and seeds of the Middle Eocene Nut Beds flora, Clarno Formation, Oregon. – Palaeontographica Americana, 58: 1–205.
- Manchester, S. R., (2002): Leaves and fruits of *Davidia* (Cornales) from the Paleocene of North America. – Systematic Botany, 27(2): 368–382.
- Manchester, S. R. (2014): Revisions to Roland Brown's North American Paleocene flora. – Acta Musei Nationalis Pragae, Series B – Historia Naturalis, 70(3-4): 153–210.
<https://doi.org/10.14446/AMNP.2014.153>
- Manchester, S. R., Chen, Z.-D., Lu, A.-M., Uemura, K. (2009): Eastern Asian endemic seed plant genera and their paleogeographic history throughout the Northern Hemisphere. – Journal of Systematic Evolution, 47(1): 1–42.
<https://doi.org/10.1111/j.1759-6831.2009.00001.x>
- Manchester, S. R., Collinson, M. E. (2019): Fruit morphology, anatomy and relationships of the type species of *Mastixicarpum* and *Eomastixia* (Cornales) from the late Eocene of Hordle, southern England. – Acta Palaeobotanica, 59: 51–67.
<https://doi.org/10.2478/acpa-2019-0006>
- Manchester, S. R., Crane, P. R., Golovneva, L. B. (1999): An extinct genus with affinities to extant *Davidia* and *Camptotheca* (Cornales) from the Paleocene of North America and eastern Asia. – International Journal of Plant Sciences, 160(1): 188–207.
<https://doi.org/10.1086/314114>
- Manchester, S. R., Grimsson, F., Zetter, R. (2015): Assessing the fossil record of Asterids in the context of our current phylogenetic framework. – Annals of the Missouri Botanical Garden, 100: 329–363.
<https://doi.org/10.3417/2014033>
- Manchester, S. R., Hickey, L. J. (2007). Reproductive and vegetative organs of *Browniea* gen. n. (Nyssaceae) from the Paleocene of North America. – International Journal of Plant Sciences, 168(2): 229–249.
<https://doi.org/10.1086/509661>
- Manchester, S. R., McIntosh, W. C. (2007): Late Eocene silicified fruits and seeds from the John Day Formation near Post, Oregon. – Paleobios, 27(1): 7–17.
- Manchester, S. R., Xiang, Q.-Y. (J.), Xiang, Q.-P. (2007): *Curtisia* (Cornales) from the Eocene of Europe and its phytogeographical significance. – Botanical Journal of the Linnean Society, 155: 127–134.
<https://doi.org/10.1111/j.1095-8339.2007.00680.x>
- Manchester, S. R., Xiang, X.-P., Xiang, Q.-Y. (J.). (2010): Fruits of Cornelian Cherries (Cornaceae: *Cornus* subg. *Cornus*) in the Paleocene and Eocene of the Northern Hemisphere. – International Journal of Plant Sciences, 171(8): 882–891.
<https://doi.org/10.1086/655771>
- Martinetto, E. (2011): The first mastixioid fossil from Italy and its palaeobiogeographic implications. – Review of Palaeobotany and Palynology, 167: 222–229.
<https://doi.org/10.1016/j.revpalbo.2011.08.004>
- Müller, C. (1898): Symbolae ad Bryologiam Australiae II. – Hedwigia, 37: 77–112.
- Reid, E. M., Chandler, M. E. J. (1933): The London Clay flora. – the British Museum (Natural History), London, 561 pp., pls I–XXXIII.
<https://doi.org/10.5962/bhl.title.110147>
- Ribbins, M. M., Collinson, M. E. (1978): Further notes on pyritised fern rachides from the London Clay. – Tertiary Research, 2(1): 47–50.
- Scott, R. A. (1954): Fossil fruits and seeds from the Eocene Clarno Formation of Oregon. – Palaeontographica, Abt. B, 96: 66–97.
- Ševčík, J., Kvaček, Z., Mai, D. H. (2007): A new mastixioid florula from tektite-bearing deposits in South Bohemia, Czech Republic (middle Miocene, Vrábče Member). – Bulletin of Geosciences, 82(4): 429–436.
<https://doi.org/10.3140/bull.geosci.2007.04.429>
- Stockey, R. A., LePage, B. A., Pigg, K. B. (1998): Permineralized fruits of *Diplopanax* (Cornaceae, Mastixioideae) from the middle Eocene Princeton chert of British Columbia. – Review of Palaeobotany and Palynology, 103: 223–234.
[https://doi.org/10.1016/S0034-6667\(98\)00038-4](https://doi.org/10.1016/S0034-6667(98)00038-4)
- Stull, G. W., Adams, N. F., Manchester, S. R., Sykes, D., Collinson, M. E. (2016): Revision of Icacinaceae from the Early Eocene London Clay flora based on X-ray micro-CT. – Botany, 94(9): 713–745.
<https://doi.org/10.1139/cjb-2016-0063>
- Takhtajan, A. (1969): Flowering plants origin and dispersal. – Smithsonian Institution Press, Washington, 310 pp.
- Tiffney, B. H., Haggard, K. K. (1996): Fruits of Mastixioideae (Cornaceae) from the Paleogene of western North America. – Review of Palaeobotany and Palynology, 92: 29–54.
[https://doi.org/10.1016/0034-6667\(96\)00104-2](https://doi.org/10.1016/0034-6667(96)00104-2)

- Thomas, S. K., Liu, X., Du, X.-L., Dong, Y., Cummings, A., Pokorny, L., Xiang, Q.-Y. (J.), Leebens-Mack, J. H. (2021): Comprehending Cornales: phylogenetic reconstruction of the order using the Angiosperms353 probe set. – *American Journal of Botany* 108(7): 1112–1121. <https://doi.org/10.1002/ajb2.1696>
- Xiang, Q.-Y. (J.), Thomas, D. T., Xiang, Q. P. (2011): Resolving and dating the phylogeny of Cornales—effects of taxon sampling, data partitions, and fossil calibrations. – *Molecular Phylogenetics and Evolution*, 59(1): 123–138. <https://doi.org/10.1016/j.ympev.2011.01.016>
- Zeng [Tseng], C.-J. (1983): The systematic position of *Diplopanax* Hand.-Mazz. – *Acta Phytotaxonomica Sinica*, 21: 151–152.
- Zenker, J. C. (1832): Beiträge zur Naturgeschichte der Urwelt: Organische Reste (Petrefacten) aus der Altenburger Braunkohlen-Formation, dem Blankenburger Quadersandstein, jenaischen bunten Sandstein und böhmischen Übergangsgebirge. – Friedrich Mauke, Jena, 67 pp.
- Zhou, W., Xiang, Q.-Y. (J.), Wen, J. (2020): Phylogenomics, biogeography, and evolution of morphology and ecological niche of the eastern Asian-eastern North American *Nyssa* (Nyssaceae). – *Journal of Systematic Evolution*, 58: 571–603. <https://doi.org/10.1111/jse.12599>