Fossil fruits and seeds from the early Eocene lower Lillebælt Clay Formation, Hinge clay pit, Denmark

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Newly discovered fossil fruits and seeds from the lower part of Member L2 of the Lillebælt Clay Formation at Hinge clay pit, Denmark, provide the first diverse plant macrofossil assemblage from this unit. The material includes 39 specimens retrieved by sieving of approx. 5000 kg of a thin sapropel layer and adjacent clay occurring within the lower part of the *Azolla*-bearing interval and is dated to the latest Ypresian, Chron C22n, approximately 49 Ma. The assemblage includes named or tentatively named taxa assigned to five species in two (possibly three) genera of Vitaceae; *Eurya* sp. and *Cleyera* sp. (Pentaphylaceae); *Rhamnospermum bilobatum* (incertae sedis); Mastixiaceae; Magnoliaceae; Icacinaceae and 20 additional taxa of seeds, fruits or endocarps for which the modern relatives are unclear. The assemblage is notable for its occurrence in an offshore, bathyal depositional environment, implying long-distance transport from surrounding land areas into the eastern North Sea Basin. Comparison with Eocene floras from the United Kingdom and Germany (Messel) shows both similarities and striking differences. Several families common in coeval floras, including Menispermaceae and others, are not recorded in the Hinge assemblage. These absences are probably due mainly to taphonomic modification of the assemblage during the transport and early diagenesis, but rarity of taxa and preparation technique may also play a role. Other explanations for differences may be differing ages and/or ecologic distributions of the compared floras. The assemblage provides a rare window into late early Eocene vegetation around the North Sea Basin while also emphasizing the strong taphonomic filtering that shaped the fossil record at Hinge.

Keywords: Fruits, Seeds, Eocene, Lillebælt Clay Formation, Denmark, North Sea Basin

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The present paper describes newly discovered very well preserved 49 million years old (latest Ypresian, Early Eocene) fossil fruits and seeds from Denmark. The fossils have been collected from the clay pit at Hinge (Fig. 1A). They derive from a thin sapropel layer and the immediately under- and overlying sapropelic clay (Fig. 1B, C), occurring in the lower part of Member L2 of the Lillebælt Clay Formation (Fig. 1D). The fruits and seeds have been transported from surrounding land areas and deposited in deep, probably bathyal, water ~ 200 km or farther from nearest coast. No plant macrofossils, fruits and seeds have previously been recorded in the Lillebælt Clay Formation, apart from sporadic, pyritized driftwood occurring mainly in sapropelic intervals of Member L2 (CH-C pers. obs.), and a single pyritized fruit (endocarp) of *Iodes multireticulata* (Icacinaceae) found loose at Trelde Næs (Fig. 1A). The aim of this paper is therefore to document the presence, diversity and preservation of these newly discovered plant remains and to raise

awareness of them as a basis for future more detailed taxonomic, comparative and imaging studies.

In contrast, a diverse macrofauna has been described from the Lillebælt Clay Formation, in particular during the last c.50 years. The fauna includes crustaceans (Collins & Jakobsen 2003; Jakobsen & Andersen 2025), molluscs (Schnetler & Heilmann-Clausen 2011), echinoderms (Rasmussen 1972), bony fishes (Schwarzhans 2007; Carnevale *et al*. 2022; Schwarzhans & Nielsen 2023 (otoliths)), cartilaginous fishes (Ward 1994; Carlsen & Cuny 2014; Pollerspöck *et al*. 2023), and rare brachiopods, annelids, corals, birds and turtles (Hoch 1975). Various parts of the fauna were documented by Bonde (1995) and Bonde & Jakobsen (2004), while general overviews are given in Bonde (1968), Bonde *et al.* (2008), and Heilmann-Clausen (2017). A diverse ichnofauna of coprolites was documented by Hunt *et al.* (2026).

As concerns micro- and nannofossils, organic-walled dinoflagellate cysts are well preserved throughout the Lillebælt Clay Formation and form the main tool for biozonation and age interpretation in the lower, non-calcareous members L1–L4 (Heilmann-Clausen 1978, 1988, Heilmann-Clausen & Costa 1989, Heilmann-Clausen & van Simaeys 2005). Pollen and spores are well preserved, but have never been described, except for megaspores and massulae of the aquatic fern *Azolla jutlandica*, which occur in Member L2 and are crucial for dating of the present material (see below and Heilmann-Clausen 1978; Collinson *et al*. 2010; Heilmann-Clausen *et al*. 2010). Foraminifers and calcareous nannofossils are present in the upper calcareous members L5 and L6 (Perch-Nielsen 1971; Dinesen 1972; Dinesen *et al*. 1977; Thiede *et al*. 1980; Thomsen *et al*. 2012).

Geological setting and age

The Danish land area is situated in the eastern part of the Cenozoic North Sea Basin (e.g., Nielsen *et al*. 1986; Ziegler 1990). During the Eocene, the basin was bordered to the northeast and east by the Fennoscandian, Baltic and Polish platforms, to the south by the Mittelgebirge Highs in Germany, and in the west the Shetland and Anglo-Welsh highs in the British Isles (Knox *et al*. 2010). The precise position of the northern and eastern coastlines is highly uncertain as any nearshore and terrestrial deposits have been removed by Neogene – Quaternary erosion due to Neogene uplift and Quaternary glaciations. The tentative position of the coastline is shown in Fig. 1A.

Relatively deep marine waters (generally bathyal) covered the present Danish land area during the Eocene (e.g., Ward 1994; Schnetler & Heilmann-Clausen 2011; King 2016; Heilmann-Clausen 2017; Pollerspöck *et al.* 2023). This may be due to a long-term thermal subsidence of the British Isles and part of the North Sea Basin caused by the onset of seafloor spreading between Greenland and the British Isles (Knox 1996).

A variable number of marine connections existed between the basin and the North Atlantic in the southwest, the evolving Norwegian-Greenland Sea in the north, and the Peri-Tethys in the southeast (e.g., Dercourt *et al*. 2000; Knox *et al*. 2010; King *et al.* 2013). A strong and extended warming period, the Early Eocene Climatic Optimum (EECO) occurred during the late early – late Ypresian. In this period the waterways became particularly well established and allowed an influx of warm oceanic waters to the North Sea and a ventilation of the latter (King *et al.* 2013). The improved oceanic connections are probably a result of the very high eustatic sea-level especially in mid Ypresian time (Miller *et al.* 2005), combined with thermal subsidence in the western parts of the area, cf. above. The environment in the offshore part of the North Sea became fully marine to nearly oceanic in character. The present Danish land area was situated in the offshore part (Fig. 1A), and thin, hemipelagic and condensed clay units were deposited here during most of the Ypresian. The Ypresian units include the Røsnæs Clay Formation and lower members L1 and L2 of the Lillebælt Clay Formation (Fig. 1D; King 2016; Heilmann-Clausen 2017). The members L1–L6 of the Lillebælt Clay Formation were originally defined as informal beds (Heilmann-Clausen *et al*. 1985) but were subsequently formalized as members by King (2016).

The presence of a diverse benthic fauna (see above) and bioturbation indicate that the sea-floor was moderately to well ventilated. Variation between reddish and greenish sediment colours, parallelled with variation in the content of Fe and Mn, point to shifting oxygen content of the bottom waters; the reddish Fe and Mn-richer intervals being best ventilated (Heilmann-Clausen *et al.* 1985). In the lower part of Member L2 organic-rich clay and a couple of thin sapropels are known from all localities and indicate that anoxic conditions periodically developed at this time. The thickest of the sapropels (2–5 cm) overlies two closely spaced volcanic ash layers and forms a regional marker bed (Heilmann-Clausen *et al.* 1985). The fossil fruits and seeds described here are excavated from this sapropel and a few centimeters of the adjacent sapropelic clay (Fig. 1D and Fig. 2).

The age of the fruits and seeds is well established on basis of the presence of the aquatic fern *Azolla*, dinoflagellate cyst zonation and magnetostratigraphy, as outlined below. A unique offshore marine influx of *Azolla* spores is recorded in numerous research and industrial boreholes in the Norwegian-Greenland Sea and central and northern North Sea (e.g., Bujak & Mudge 1994; Eldrett *et al.* 2004). The *Azolla* event is

likewise recorded in Denmark where it is represented by *A. jutlandica* Collinson *et al.* (2010). It occurs in the lower part of Member L2 (Fig. 2), and the lower part of its range includes the sapropel with the fruits

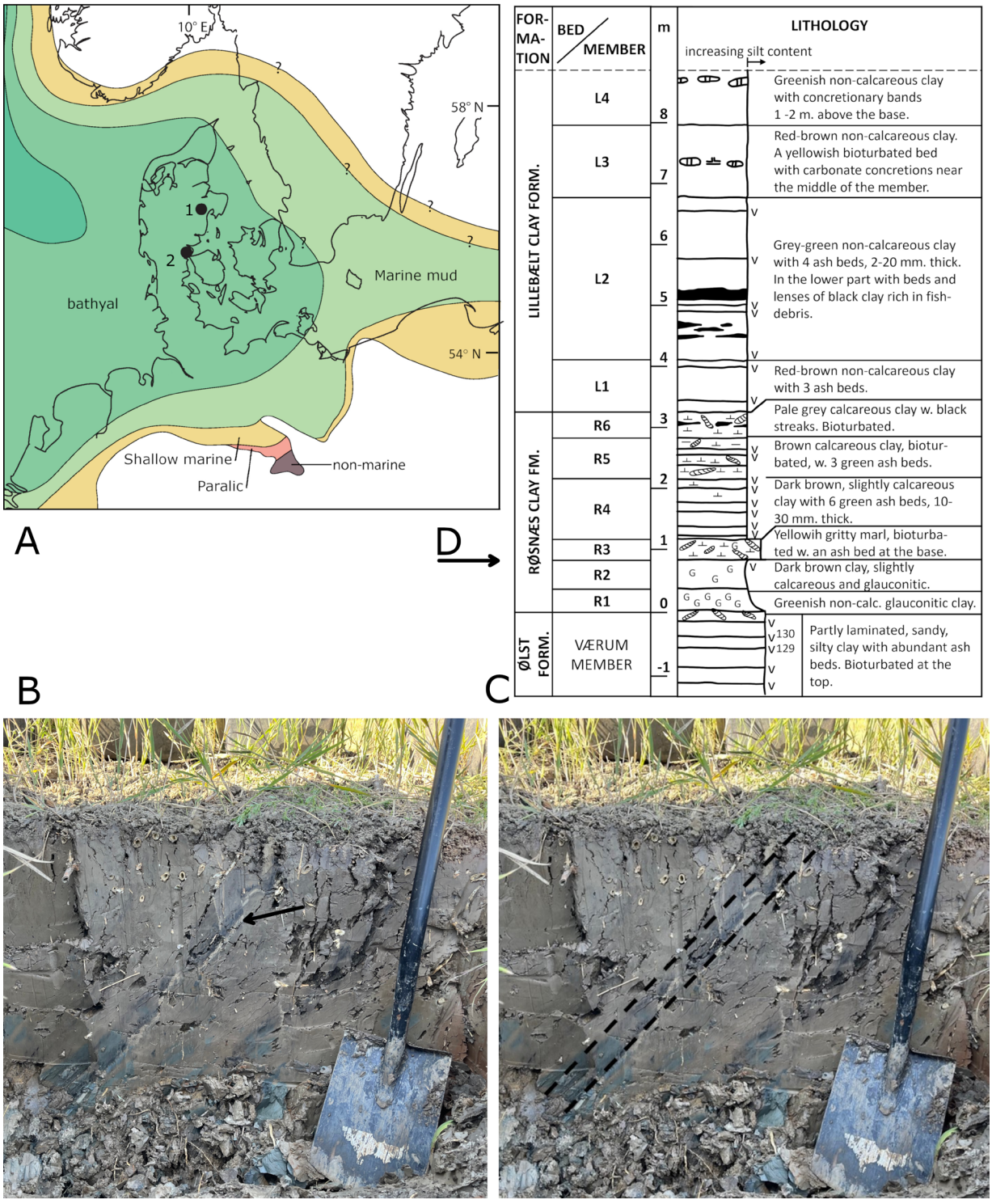


Fig. 1. A. Map of Denmark and surrounding countries with a paleogeographic reconstruction of the late Ypresian eastern North Sea. 1, Hinge clay pit; 2, Trelde Næs peninsula. Modified from Heilmann-Clausen (2020). B and C, sampling site at Hinge showing the sapropel between the two dashed lines (which yielded the fruits and seeds) overlying a thin argillized ash layer (at arrow in B). D, section of the topmost Ølst, Røsnæs Clay, and lower Lillebælt Clay formations at Hinge. The sampled sapropel is at ~ 5 m. Modified from Heilmann-Clausen *et al.* (1985). Beds R1 to R6 and L1 to L6 were formalized as members in King (2016).

and seeds studied herein (Heilmann-Clausen 1978; Collinson *et al.* 2010).

Magnetostratigraphy in the Hinge section shows that the boundary between Chron C22n and Chron C21r is within the *Azolla*-bearing interval (Heilmann-Clausen *et al*. 2010; Fig. 2). This is precisely the same situation as in the Norwegian-Greenland Sea where the Chron C22n-C21r boundary is likewise indicated within the *Azolla*-interval (Brinkhuis *et al*. 2006). Dinoflagellate cyst zonations in Denmark (Fig. 2; Heilmann-Clausen 1988) and the Norwegian-Greenland Sea (Eldrett *et al.* 2004) are also similar and, in terms of the recent dinoflagellate cyst zonation of King (2016 fig. 17 and p. 594, not fig. 12), place the lower part of the *Azolla* event in Zone DE9b and the top of the *Azolla* event in the overlying Zone DE10.

In summary, the fruit and seed-bearing sapropel belongs to lowermost part of the *Azolla* interval, dinoflagellate cyst Zone DE9b and upper part of magnetochronozone C22n (Fig. 2). The age of the chron-C21r/C22n boundary is 49.037 MA (Speijer *et al*. 2020). The age of the fruits and seeds can therefore be firmly established as latest Ypresian, with a numerical age of ~49 Ma (Fig. 2).

The entire Member L2 may be correlated with the upper part of the inner neritic to marginal marine Wittering Formation in southern England (Schnetler & Heilmann-Clausen 2011; King 2016) and lower part of the likewise inner neritic Aalter Sand Formation in Belgium (Steurbaut *et al.* unpublished).

Material and methods

Sample collection, processing and study

The figured specimens are housed in the Natural History Museum of Denmark in Copenhagen (NHMD 2115491 to NHMD 2115522). Over a four-year period from 2021–2024, approximately 5000 kg of sedimentary material from the Lillebælt Clay Formation, Member L2 containing a sapropel clay layer, was systematically collected from the Hinge clay pit. The sapropel clay layer varied in thickness from a few centimeters up to six centimeters. The amount of the sapropel clay layer collected is estimated to be approximately 1000 kg, with the remaining 4,000 kg consisting of adjacent clay material evenly distributed on either side of the sapropel layer. The material was collected following written permission and formal approval from the owner of the clay pit, Leca Danmark A/S. The bulk material (without prior drying) was manually broken into fragments not larger than 10 cm and submerged in large plastic containers (dimensions: 30 × 45 × 70 cm) filled with tap water. Mechanical agitation with a three-prong cultivator was applied every second or third day to facilitate

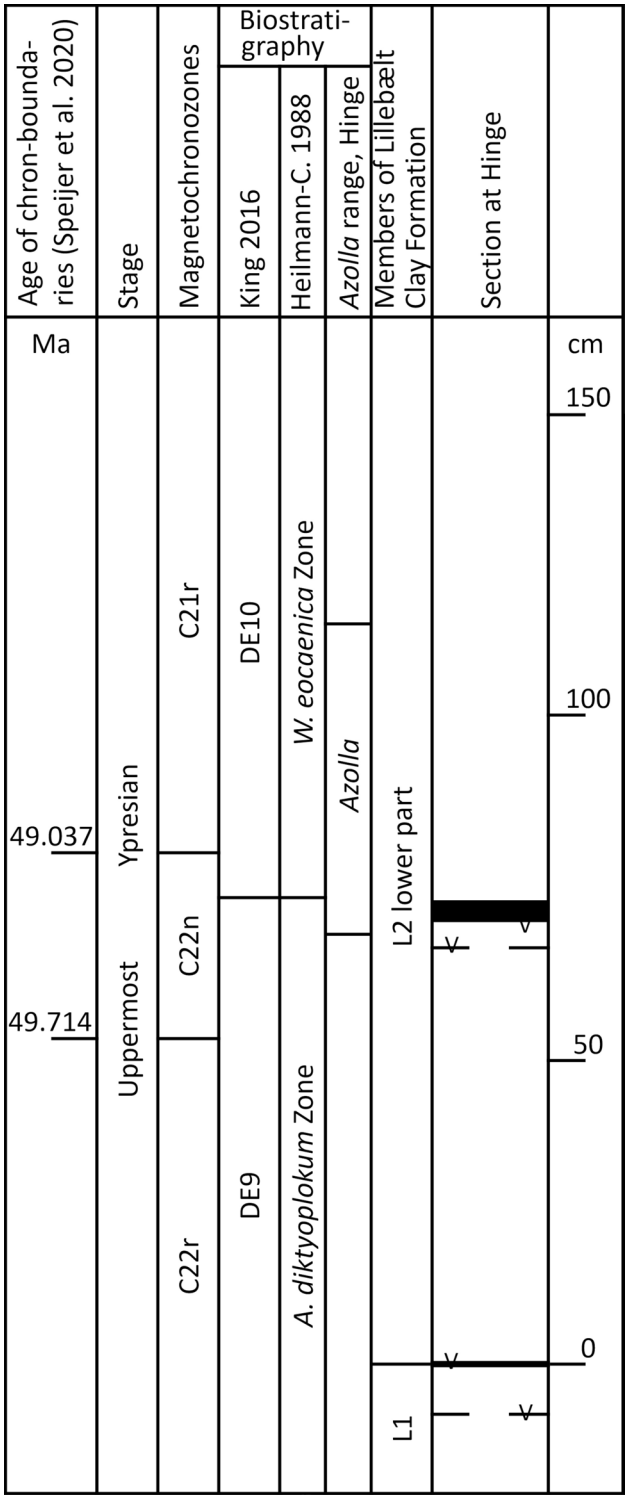


Fig. 2. Lower part of Member L2 at Hinge, with sampled sapropel (black) at ~70 cm. V=argillized volcanic ash layers. Bio-, magneto- and chronostratigraphy are also shown. Magnetostratigraphy and *Azolla* occurrence are from Heilmann-Clausen *et al.* (2010). Member L2 correlates with upper part of the Wittering Formation in southern England (see text).

dissolution of the clay matrix.

After 4–6 weeks, the partially disaggregated sediment was processed using custom-built sieves (dimensions: 30 × 50 cm). The upper sieve had a 10 × 10 mm mesh, while the lower sieve had a finer 3 × 3 mm mesh. Material placed on the upper sieve was thoroughly rinsed with cold tap water. All the water and dissolved material were collected and filtered through double-layered nylon stockings (Denim 20) to retain fossils and fine undissolved particles. A few larger fossils were hand collected on the finer sieve. The nylon stockings had mesh openings of 0.3 × 0.3 mm. Any larger sediment pieces remaining on the sieves after rinsing with water were re-submerged and subjected to further mechanical agitation with the three-prong cultivator for additional weeks, followed by the same filtration procedure.

Subsequent processing

The retained material in the nylon stockings was sequentially rinsed to remove as much sediment as possible. Initially, cold running water was passed through the stockings while gently massaging the stockings by hand for approximately 15 minutes, until the effluent ran clear. This was followed by a brief rinse with lukewarm water (2 minutes). A small quantity of liquid dish detergent (~5 ml) was then added, and the material was gently agitated for 2 minutes. After a 5-minute soak, cold running water was used to remove any remaining detergent.

The material was then transferred to a plastic container (dimensions: 7 × 20 × 30 cm) filled with water. The material was stirred to dislodge adhering particles such as fossils and sand. Floating organic matter was carefully decanted, and this step was repeated until most organic material was removed. The remaining clear water was carefully decanted, and the separated material was oven-dried at 90°C for approximately 45 minutes or until fully dry. Final sorting was performed under a binocular microscope (Efix) with 7-10 times magnification.

Imaging

High-resolution imaging was conducted using an automated focus stacking setup. A full-frame Canon EOS RP camera was mounted vertically on a WeMacro 100 mm focus stacking rail. The optical system included a Raynox DCR 150 tube lens in combination with one of the following objectives: Mitutoyo QV (2.5X / 0.14 NA) or a Mitutoyo M Plan Apo (10X / 0.28 NA). For larger specimens alternative systems used were a LAOWA 25mm F2.8 Ultra Macro (5X), or a Canon RF 100 mm F2.8 L MACRO IS USM. The choice of objectives depended on the size of the seed. Illumination was provided by a custom LED array (4 units, each with 81 LEDs). Image acquisition and rail control were managed via Helicon Remote software, and final image rendering was performed using Helicon Focus 7 (Method C: Pyramid, Smoothing Level 2).

Results

The fossil material retrieved from the sieving of 5000 kg of sediment includes 39 specimens of well-preserved fruits and seeds. This material is illustrated in Figs 3–6. The small number of fruits and seeds retrieved from such a large sediment sample indicates that they are very rare in this offshore sedimentary environment. Due to the small number of specimens retrieved, mostly including only one or a few specimens of each form, the systematic identification is tentative. Most specimens remain unidentified at genus or species level, and many are identified only as distinct morphotypes of unknown affinity.

Key characteristics and suggested systematic affinities of the fruit and seed flora

Family VITACEAE

Genera of Vitaceae have seeds with a very distinctive morphology (Chen & Manchester 2011). The overall profile of many of the seeds is round or oval to pyriform with an oval to rounded chalazal scar on the dorsal surface and a pair of infolds on the ventral surface. Some genera have seeds with an elongate oval chalaza whilst in others the chalaza is almost round. Some seeds have an ornamented surface whilst others can be almost smooth (Chen and Manchester 2011). Seeds of some species of *Ampelocissus* are indistinguishable from those of *Vitis* (Chen and Manchester 2011).

Five Vitaceae seed morphologies can be distinguished in the Hinge material. All the morphologies can be accommodated within the genus *Vitis*. Vitaceae morphology 1 might alternatively be a species of the genus *Ampelopsis* seeds of some species of which are indistinguishable from seeds of *Vitis* (Chen and Manchester 2011). Variations in the seed morphology described below suggest that these seeds might represent five different species.

Vitaceae morphology 1
One specimen, Fig. 3A (NHMD 2115491)

Seed with rugose ornament of pronounced radiating ridges, some discontinuous, on both surfaces. Broken and missing apex and base but

original profile probably almost round. Short ventral infolds. Oval chalaza nearer apex.

Vitaceae morphology 2
One specimen, Fig. 3B (NHMD 2115492)

Seed smooth, elongate oval with very long narrow, slightly curved ventral infolds. Very slight apical notch. No basal groove. Chalaza almost central on dorsal surface. Narrow beak at the base.

Vitaceae morphology 3
Three specimens, Fig. 3C (NHMD 2115493)

Seed with smooth ventral surface and faint radiating rugae on the dorsal surface. Very short, broad ventral infolds; apical notch with apical groove; basal groove. Chalaza nearer apex on dorsal surface. Distinct beak at the base.

Vitaceae morphology 4
One specimen, Fig. 3D (NHMD 2115494)

Seed smooth, almost round with short broad ventral infolds. No apical or basal groove. Chalaza central on dorsal surface. Distinct beak at the base.

Vitaceae morphology 5
One specimen, Fig. 3E (NHMD 2115495)

Seed smooth, small and almost round with very short, narrow, ventral infolds. No apical or basal groove. Chalaza almost central on dorsal surface. Distinct beak at the base

Family Pentaphylaceae

***Eurya* sp.** (genus formerly included in Theaceae)
Two specimens, Fig. 4B (NHMD 2115496) and Fig. 4D (NHMD 2115497)

Seeds campylotropous, laterally flattened, probably originally but also enhanced by compaction. Seeds rounded to oval in outline; surfaces with an obvious reticulum of rectangular to square cells in rows which curve and parallel the seed profile. Seeds narrowing slightly or strongly at the origins of those cell rows. One specimen is almost equiaxial in profile, the other is more elongate in one dimension.

***Cleyera* sp.** (genus formerly included in Theaceae)
One specimen, Fig. 4A (NHMD 2115498)

Seed campylotropous, laterally flattened, probably originally but also enhanced by compaction. Seed almost oval in outline but with one edge more or less straight with a pronounced central indentation probably marking the position of the micropyle and hilum. Seed surfaces with an obvious reticulum of rectangular to square upraised cells in rows which curve and parallel the seed profile.

Incertae sedis

***Rhamnospermum bilobatum* Chandler**
One specimen, Fig. 4C (NHMD 2115499)

This enigmatic taxon of unknown systematic affinity is characterised by the bilobed organisation which is clearly evident in the Hinge specimen. Small rect-

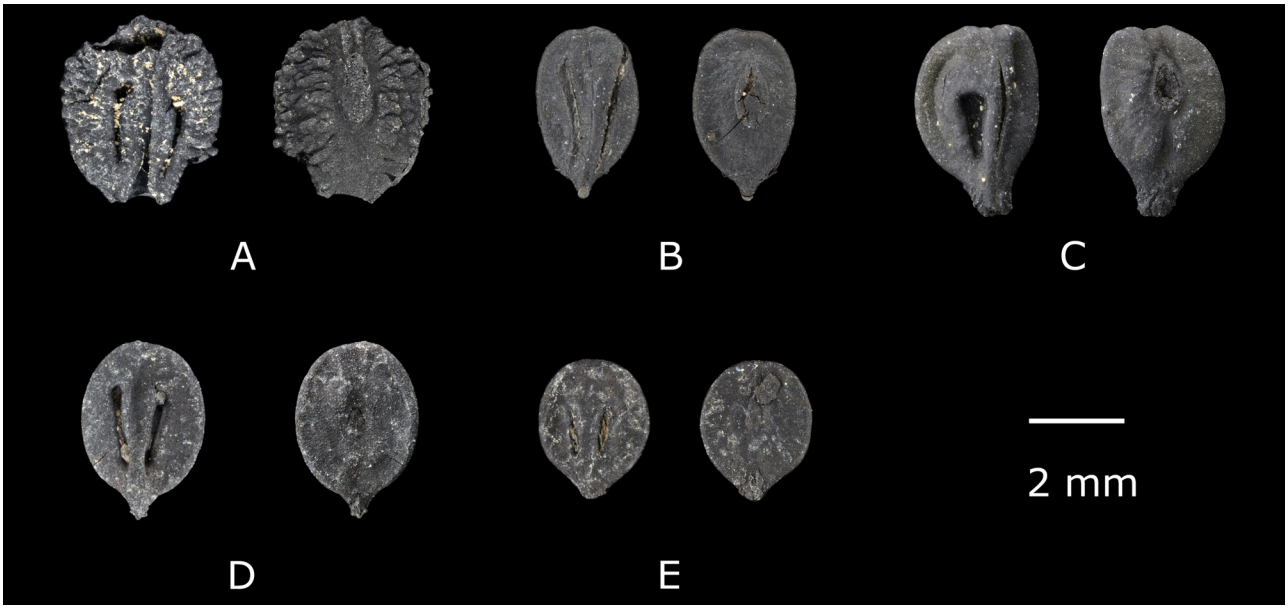


Fig. 3. Vitaceae seeds from the Hinge assemblage, showing five distinct morphologies. For each ventral surfaces are shown on the left and dorsal surfaces on the right. For further details see text.

angular cells are seen lower right of the right hand figure, also typical of this taxon. The taxon occurs throughout the Paleogene in the UK. For further details of this taxon see Collinson (1983a appendix p. 213).

Family MASTIXIACEAE

Mastixiaceae endocarp
One specimen, Fig. 4E (NHMD 2115500)

This specimen is smaller than typical Mastixiaceae endocarps but the longitudinal ridges (one central straight and two lateral curved) on the left figure suggest the presence of an elongate germination valve on an endocarp. The specimen is thick-walled. There is no evidence of resin either in canals or scattered.

Family MAGNOLIACEAE

***Magnolia* sp. seed**
One specimen, Fig. 4F (NHMD 2115501)

Seed flattened, obovate with a slightly pointed base (micropylar area) and a slightly flattened apex. The apex bears a small circular chalazal scar.

Family ICACINACEAE

Icacinaceae endocarp
One specimen, Fig. 4G (NHMD 2115502)

Endocarp ovoid, flattened, with a central linear feature extending from base to half the length of the endocarp. Surface reticulate with an irregular network of raised areas. Area at upper right is not interpreted as an original feature but is considered to be damage,



Fig. 4. Selected fossil seeds and endocarps from the Hinge assemblage, including Pentaphylaceae (A,B,D), *Rhamnospermum bilobatum* (C), Mastixiaceae (E), Magnoliaceae (F) and Icacinaceae (G). Opposite surfaces are shown for A-E and only one surface for F and G. The 1 mm scale refers to A–D and 10 mm scale to E–G. For further details see text.

possibly a bite mark.

Unidentified morphotypes

Morphotypes of uncertain or unknown systematic affinity are listed and key features noted below. The number of specimens of each morphotype is also stated.

Fig. 5A (NHMD 2115503). Unidentified morphotype 1. Small fruit interpreted as a capsule, apical and basal view illustrated. Rounded overall profile and five locules. Surface slightly corroded – one specimen.

Fig. 5B (NHMD 2115504). Unidentified morphotype 2. Half specimen of a probable thick-walled seed with external longitudinal ridges of varying thickness. Very thick wall; cavity lined with a cuticle-like layer with small rectangular cell walls. Indentation at one end interpreted as former position of attachment (hilum) and narrow canal at opposite end interpreted as position of micropyle – one specimen.

Fig. 5C (NHMD 2115505). Unidentified morphotype 3. Thick-walled seed or endocarp, if the terminal feature is an original scar then this may be a seed of

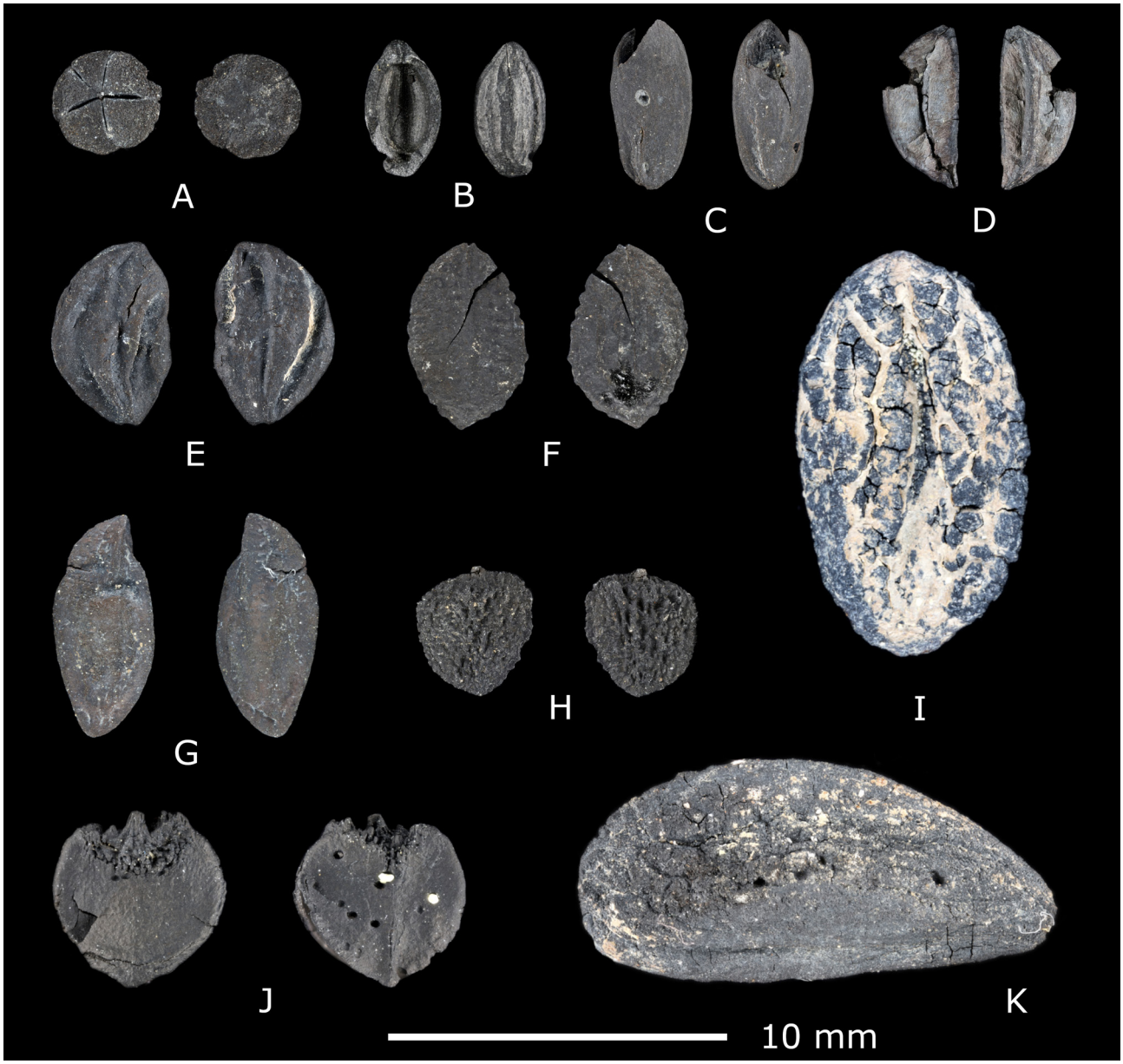


Fig. 5. Selected specimens from the Hinge assemblage. These include a capsule (A, apex and base), a probable Hamamelidaceae seed (C); other thick-walled specimens (B, D-J) and a probable single-seeded Vitaceae fruit (K). Opposite surfaces are shown on the left and right for C-H and J with only one surface shown for I and K and both sides of one broken half for B. For further details see text.

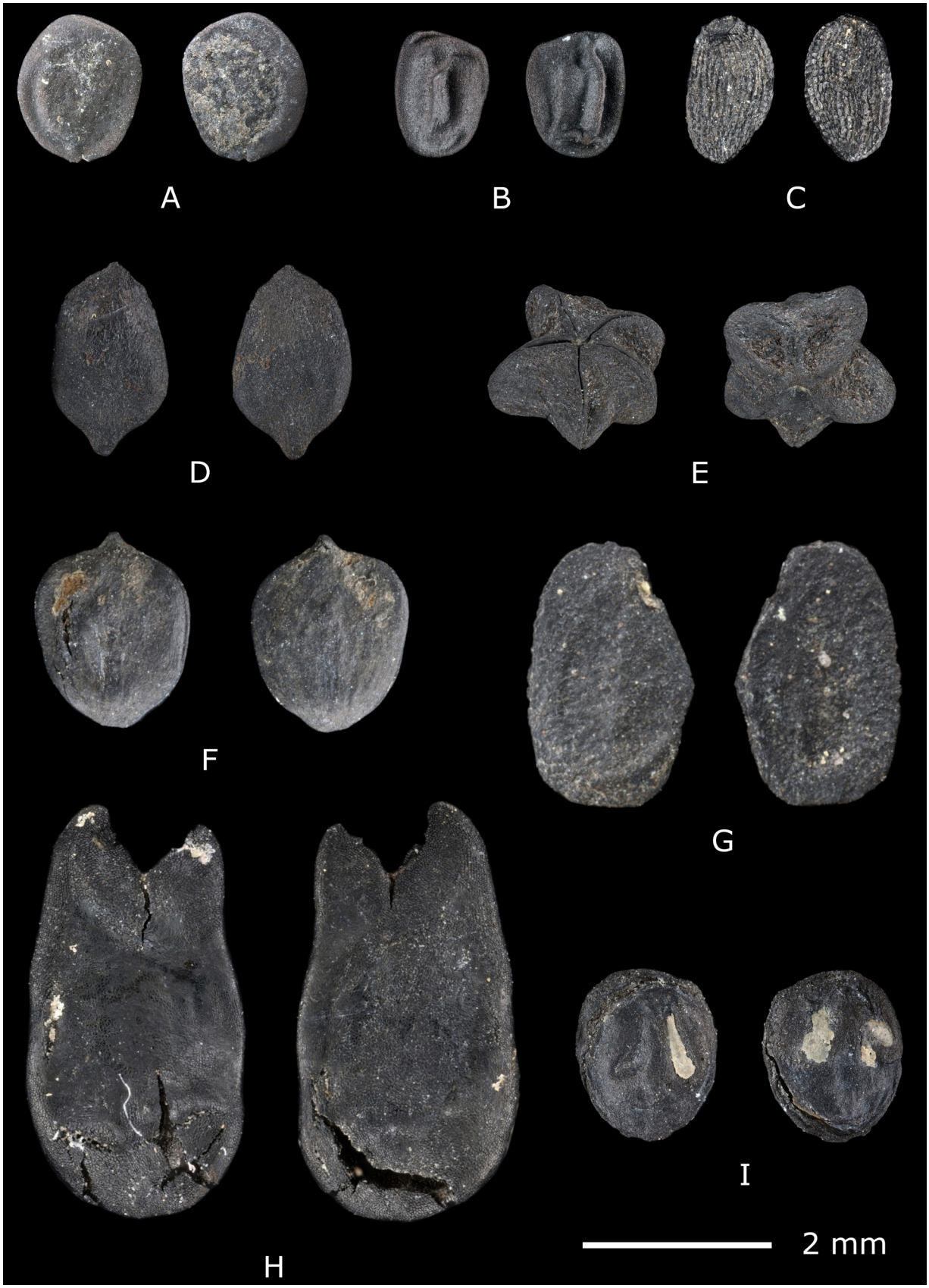


Fig. 6. Various specimens from the Hinge assemblage including a five-loculed capsule (E) and *Carpolithus* species 31 of Collinson *et al.* 2012a (H). Others are unidentified. Opposite surfaces are shown on the left and right. For further details see text.

the Hamamelidaceae (see e.g. *Corylopsis* in Collinson *et al*. 2012a). However, the terminal feature on the specimen illustrated may be breakage – one specimen.

Fig. 5D (NHMD 2115506). Unidentified morphotype 4. Endocarp or seed, semicircular in profile with one straight and one curved margin. Surface pattern of very fine parallel ridges aligned obliquely across all of one side (left figure) and the left half of the other side (right figure) – one specimen.

Fig. 5E (NHMD 2115507). Unidentified morphotype 5. Endocarp or seed, infolds may be original or a consequence of compaction – one specimen. No obvious surface pattern.

Fig. 5F (NHMD 2115508). Unidentified morphotype 6. Inferred seed with horizontally wrinkled rugose surface, possible terminal features at pointed ends which might represent hilum and micropyle – one specimen.

Fig. 5G (NHMD 2115509). Unidentified morphotype 7. Endocarp or seed, narrowing at both ends and with a longitudinal ridge on each surface possibly indicating originally part of a group (e.g. within a fruit) – one specimen.

Fig. 5H (NHMD 2115510). Unidentified morphotype 8. Endocarp or seed with irregularly deeply pitted external surface – one specimen.

Fig. 5I (NHMD 2115511). Unidentified morphotype 9. Large, thick walled, probable endocarp. Many cracks with sediment infill giving an appearance of a reticulum which may not be an original feature – one specimen.

Fig. 5J (NHMD 2115512). Unidentified morphotype 10. Inferred half of woody fruit. Outer surface (left image) with faint depressions possibly indicating original surface pattern. Inner surface (right image) with irregularly spaced holes possibly indicative of insect boring – one specimen.

Fig. 5K (NHMD 2115513). Possibly a single-seeded fruit of Vitaceae – the specimen is very similar to *Crassivitisemen* Collinson *et al*. 2012a. A CT scan to determine internal structure would be needed to confirm this identification. Elongate indentation oriented from left to right in lower part of image is interpreted as a vascular strand as in *Crassivitisemen* – one specimen.

Fig. 6A (NHMD 2115514). Unidentified morphotype 11. Very small seed, round in profile, almost flat, surface superficially appears smooth but at higher magnification shows a very fine reticulate pattern composed of very small cells only obvious where their outer periclinal walls are missing. Possible former attachment represented by the slight slit at the base – one specimen.

Fig. 6B (NHMD 2115515). Unidentified morphotype 12. Very small elongate oval seeds with obvious surface reticulum composed of quite large cells with upstanding anticlinal walls. Cells elongated parallel with the seed longest axis and arranged in longitudinal rows. Terminal scar in left image apex interpreted as possible attachment (hilum) – five specimens.

Fig. 6C (NHMD 2115516). Unidentified morphotype 13. Seeds very similar to 6A but surface more wrinkled suggesting a more 3D original morphology – two specimens.

Fig. 6D (NHMD 2115517). Unidentified morphotype 14. Very small, elongate oval, seeds or endocarps, narrowing to a point at either end. No obvious surface pattern or surface scars – two specimens.

Fig. 6E (NHMD 2115518). Unidentified morphotype 15. Very small five-loculed capsule with each locule deeply indented. Separation slits seen in apex of left image (inferred apical view) indicate incipient septicidal dehiscence. Numbers of seeds per locule not known. External similarity with *Epacridicarpum* Chandler (Epacridaceae) but seed number per locule is not known for the Hinge material so it is not appropriate to apply that generic name – one specimen.

Fig. 6F (NHMD 2115519). Unidentified morphotype 16. Very small probable seed or endocarp. Inferred apex slightly pointed – one specimen.

Fig. 6G (NHMD 2115520). Unidentified morphotype 17. Very small probable seed with rugose surface and angled probable hilar surface in upper part – one specimen.

Fig. 6H (NHMD 2115521). *Carpolithus* species 31 Collinson *et al*. 2012a. The overall external morphology of this species is fully described in Collinson *et al.* 2012a based on material from the late early or early middle Eocene of Messel, Germany. Detail of the internal anatomy obtained using SRXTM was described in Collinson *et al.* (2012b) and illustrated in their figures 4 e-k. The specimen illustrated here shows only a slight indication of the characteristic longitudinal ridge (right image) which should be present on one surface but does show very clearly the terminal cleft (inferred apex) and the characteristic oblique ridge near the inferred apex (right image) – one specimen.

Fig. 6I (NHMD 2115522). Unidentified morphotype 18. Very small probable seed, compressed, rounded in profile. The indentations on the left image are probably not original features. No visible surface cellular pattern – one specimen.

Discussion

Unexpected absences and possible explanations

Comparison may be made with Eocene floras, (e.g. summarised in Chandler 1964, Collinson 1983a,b, Collinson pers. obs.) which include many from marine depositional settings in the south eastern United

Kingdom, an area which was geographically close to Denmark in the Eocene as now. A number of flowering plant families and genera which occur in the UK Eocene are absent from this new Danish flora. These include the following abundant and/or frequently recorded flowering plant families in the UK Eocene: Anacardiaceae, Annonaceae, Apocynaceae, Arecaceae (including *Nypa*), Burseraceae, Cornaceae, Cyclanthaceae, Cyperaceae, Euphorbiaceae, Juglandaceae, Lauraceae, Lythraceae, Mastixiaceae, Menispermaceae, Rutaceae, Tapisciaceae, Toricelliaceae and genera of uncertain systematic affinity namely *Hightea*, *Lagenella*, *Lagenoidea* and *Wetherellia*.

Some of these absences may be due to growth habit, rarity in the original vegetation, or occurrence in a habitat probably more than 200 km away from the depositional catchment area (Fig. 1A) such that their potential fossils did not reach this Danish depositional setting or did not occur within the sampled sediment volumes. One or more of these factors may explain the absence of Menispermaceae endocarps most of which have very characteristic morphologies and would have been easily recognised if they were present in this Danish flora. Furthermore, their sizes fall well within the range of specimens studied here. They typically occur in fairly small numbers in fossil assemblages in the UK (Collinson pers. obs. including NHMUK collections). At Messel some genera of Menispermaceae are represented only by single specimens and the largest number for a species at Messel is 12 specimens (for *Palaeosinomenium ornamentum* Collinson *et al.* 2012a).

Some absences may be a consequence of a large (e.g. greater than 20 mm) or very small (less than 2 mm) disseminule size. One example is the large fruits of the mangrove palm *Nypa*. In the deposits in the foreshore at Bracklesham Bay, West Sussex, UK, with the right tidal and beach sand conditions, it has been possible in the past to see many *Nypa* fruits of various sizes exposed *in situ* (Collinson 1993). However, a typical visit to this locality, or a bulk sediment sample comparable to those studied here, would be extremely unlikely to record *Nypa*. Another example is the very small elongate (approx. 2 mm x 1mm) and lightweight dominantly cuticular fossil fruits of *Cyclanthus* (Smith *et al.* 2008) which may be missing owing to the washing and sieving process used here.

Other absences might be explained for preservational reasons. For example, the Annonaceae specimens from the London Clay Formation of the UK (e.g. Collinson 1983b) are frequently preserved as internal casts in iron pyrites of the endosperm (storage tissue), which has very characteristic, easily recognisable, complex surface patterns. By contrast, the testa surface of modern seeds is smooth and simple and fossils with that outer testa preserved might not be recognized as Annonaceae. However, there are no specimens in the Hinge flora of appropriate size or 3D shape to belong to the Annonaceae. Notably, Annonaceae are also missing from the late early or early middle Eocene Messel flora of Germany (Collinson *et al.* 2012a and Collinson personal observations of new material in the Senckenberg Museum collections, Frankfurt, 2025).

Conclusions

The Hinge clay pit assemblage is the first diverse record of fossil fruits and seeds from the Lillebælt Clay Formation. It derives from a sapropel in the lower part of Member L2, within the lower *Azolla*-bearing interval, and is dated to the latest Ypresian, Chron C22n, approximately 49 Ma. With only 39 specimens retrieved in 5000 kg of sediment, fossil fruits and seeds are rare. The assemblage includes named or tentatively named taxa assigned to five species and two or three genera of Vitaceae (including *Vitis,* possibly *Ampelopsis* and *Crassivitisemen*); Pentaphylaceae (*Eurya* sp. and *Cleyera* sp.); *Rhamnospermum bilobatum (incertae sedis)*, Mastixiaceae, Magnoliaceae, Icacinaceae and 18 distinctive unnamed morphotypes of seeds, fruits or endocarps. Its occurrence in bathyal marine sediment at Hinge shows that the terrestrial plant remains were transported at least 200 km from the nearest land-mass into the offshore eastern North Sea Basin and preserved under locally anoxic conditions. As would be expected the material has been modified by taphonomic processes during the long-distance transport and, possibly, also by the preparation method. Absence of some expected taxa for floras of this age may be due to rarity in the original vegetation or growth distant from the depositional site. The flora shares elements with Eocene floras from the United Kingdom and Messel, Germany, but also lacks several families common in those assemblages. The Hinge flora substantially expands the Danish Eocene palaeobotanical record and demonstrates the value of large-volume sampling and sieving of sapropelic intervals. Further collecting and also SEM and CT investigation may refine systematic identification and improve comparison with other north-west European Eocene floras.

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