



EARLIEST EVIDENCE OF ANIMAL-DISPERSED NUTS IN THE JUGLANDACEAE: *ZODICARYA* GEN. NOV. FROM THE PALEOCENE OF NORTH AMERICA AND EARLY EOCENE OF ENGLAND

MIN DENG¹, MARGARET E. COLLINSON², WEI-PING ZHANG³, STEVEN R. MANCHESTER^{4,*}

¹ School of Ecology and Environmental Science, State Key Laboratory for Vegetation Structure, Function and Construction (VegLab), Yunnan Key Laboratory of Plant Reproductive Adaptation, Evolutionary Ecology and Institute of Biodiversity, Yunnan University, Kunming 650500, China.

² Department of Earth Sciences, Centre of Climate and Atmosphere, School of Life and Environmental Sciences, Royal Holloway University of London, Egham, Surrey, TW20 0EX, UK; Natural History Museum, Cromwell Road, London SW7 5BD, UK.

³ State Key Laboratory of Plant Diversity and Specialty Crops, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China.

⁴ Florida Museum of Natural History, University of Florida, Dickinson Hall, P.O. Box 117800, Gainesville, Florida, U.S.A.; email: steven@flmnh.ufl.edu.

* corresponding author

Deng, M., Collinson, M. E., Zhang, W.-P., Manchester, S. R. (2026): Earliest evidence of animal-dispersed nuts in the Juglandaceae: *Zodicarya* gen. nov. from the Paleocene of North America and Early Eocene of England – Fossil Imprint, 82(1): 60–74, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (online).

Abstract: Fruit morphology and anatomy are critical for delimitation of tribes and genera within Juglandaceae. In this study, we re-examined the holotypes of *Juglandicarya cantia* E. REID et M. CHANDLER 1933 from the Early Eocene London Clay flora of England and *J. simplicarpa* MANCHESTER 1987 from the Middle Paleocene of the Fort Union Formation of Wyoming, USA using micro-CT scanning to uncover additional morphological and anatomical characters and reassess their affinities relative to extant genera. These fossils are significant as they are among the earliest known large, wingless nuts in the fossil record of Juglandaceae. Although they resemble modern *Juglans* and *Carya* in overall nut morphology, key anatomical differences distinguish them from the extant genera. Micro-CT analysis reveals that the nutshell of *J. cantia* consists of densely packed isodiametric sclereids and lacks lacunae, unlike extant species of *Juglans*. Nuts of both *J. cantia* and *J. simplicarpa* lack internal longitudinal ribs and have only a weakly developed to absent secondary septum differentiating them from extant species of *Carya*. The genus *Juglandicarya*, as traditionally circumscribed, is non-monophyletic, and the morphological traits of *J. cantia* and *J. simplicarpa* differ significantly from those of the lectotype, *J. lubbocki* E. REID et M. CHANDLER. We therefore propose a new genus, *Zodicarya* gen. nov., and establish the new combinations *Zodicarya cantia* (E. REID et M. CHANDLER) M. DENG, M. E. COLLINSON et MANCHESTER comb. nov. and *Z. simplicarpa* (MANCHESTER) M. DENG et MANCHESTER comb. nov. By analogy with extant *Juglans*, *Carya*, and *Alfaroa*, we infer that the large, wingless nuts of *Zodicarya* were adapted for animal-dispersal, indicating that these traits, which are not known in Cretaceous members of the family, evolved in the early Cenozoic. We also summarize the biogeographic history of *Zodicarya* in Europe and North America during the Paleogene.

Keywords: Fruit anatomy, micro-computed tomography (Micro-CT), systematics, Eocene, walnuts

Received: February 6, 2024 | Accepted: September 2, 2024 | Issued: October 7, 2026

Introduction

The family Juglandaceae has a rich and well-documented fossil record that allows us to trace most of the extant genera back to the early Cenozoic. In addition, several fossil genera have been recognized, some of which are clearly extinct, and others that accommodate fossils insufficiently known to determine whether they represent one of the extant genera (Manchester 1987). The extinct genera, e.g., *Polyptera* MANCHESTER et DILCHER (Manchester and Dilcher 1997),

Cruciptera MANCHESTER (Manchester 1991), *Paleooreomunnea* DILCHER, F. W. POTTER et CREPET (Dilcher et al. 1976), *Beardia* L. L. ELLIOTT, MINDELL et STOCKEY (Elliott et al. 2006) and *Alatonucula* HERMSEN et GANDOLFO (Hermesen and Gandolfo 2016), exhibit features diagnostic of the family, but do not belong to any of the eight modern genera. Due to limits of preservation and overlap of morphological characters, some fossils have been more difficult to assess and to determine whether they represent extinct or extant genera. Reid and Chandler (1933) erected the genus *Juglandicarya* E. REID et M. CHANDLER

for fossils of “fruits which, although clearly referable to the Juglandaceae, are of doubtful generic relationship both to living genera and to one another.”

Juglandicarya was conserved against the pre-existing name *Hybothya* ENDL. and its type species was designated as *J. lubbockii* E. REID et M. CHANDLER (Doweld 2013, Herendeen 2015, Wilson 2016). Among the four species that Reid and Chandler (1933) assigned to *Juglandicarya*, two (*J. cantia* and *J. crassa*) have relatively large nuts (12 mm, and 14 mm high, respectively) and thus are similar to extant nuts of *Juglans* and *Carya*. The other two species, *J. lubbockii*, and *J. depressa*, have smaller nuts (8–8.5 mm and 5–6 mm high, respectively) and might represent the eroded remains of winged fruits. In particular, *J. depressa* appears likely to represent nuts of the extant genus *Cyclocarya* ILJINSK. with the disk-like wing mostly eroded away (Manchester 1987). In its traditional sense, *Juglandicarya* is likely non-monophyletic, including species that may fall within different clades of the Juglandaceae.

Most of the extinct and extant genera of the family possess winged fruits adapted for wind dispersal (Stone 1993). Larger wingless juglandaceous nuts first appear as extinct taxa in the mid-Paleocene to Early Eocene. Extant *Juglans* L. and *Carya* NUTT., first appear in the Middle and Late Eocene. (e.g., Tiffney and Manchester 2022, Manchester et al. 2024). The other animal-dispersed member of the family, *Alfaroa* STANDL., has not yet been recognized in the fossil record.

Brown (1962) informally recognized an additional species of *Juglandicarya* based on nutshell molds and casts from the Paleocene of Wyoming, USA. Manchester (1987) named them as *J. simplicarpa*, and stated that the species is “virtually indistinguishable in size and morphology from *J. cantia* of the Early Eocene London Clay of southern England and it is possible that the two were in fact conspecific. However, the North American species is preserved only as siltstone casts and molds and direct anatomical comparison with the pyritized British species is not possible.” (Manchester 1987: 15). Although the Paleocene *J. simplicarpa* is important for marking the earliest known age for such morphology, the lack of anatomical preservation limits the resolution of comparisons with extant and fossil species. Thus, the pyritized Early Eocene London Clay material is fundamental for understanding histological details. Only one specimen (the holotype of *J. cantia*) is currently intact and micro-CT scanning provides an important opportunity to document internal anatomy for the first time.

Our recent work applied micro-CT scanning to document the nut morphology and anatomy of extant *Carya* and *Juglans* species for comparison with fossils (Deng et al. 2024, Manchester et al. 2024). The fossil nuts of *J. cantia* and *J. simplicarpa* are characterized by smooth shells lacking external grooves or ridges, and they also lack prominent internal ribs. Such features are especially similar to those observed in *Carya poilanei* (A. CHEV.) J.-F. LEROY and *Juglans ailantifolia* (MAKINO) REHDER, but no detailed comparative study of the nuts of these species was previously conducted.

Here we augment our understanding of *Juglandicarya cantia* and *J. simplicarpa* by applying high-resolution micro-CT methodology to document their morphology and anatomical features in comparison with extant genera of the

Juglandaceae. Because of differences from the type species of *Juglandicarya*, we establish a new genus – *Zodicarya*, and propose the new combinations *Zodicarya cantia* and *Z. simplicarpa*. We also use micro-CT scanning to investigate nuts of extant Juglandaceae genera for comparison in order to explore the systematic placement of selected fossil taxa and clarify key diagnostic features evaluating related fossil nuts. In addition, we review other fossils that have been assigned to *Juglandicarya*.

Material and methods

Geological setting

We studied the single surviving specimen of *Juglandicarya cantia*, the holotype designated by Reid and Chandler (1933), which was collected by Bowerbank from the London Clay of Sheppey, southern England. The London Clay fossil plants are preserved as pyritized fruits and seeds that are naturally freed from the surrounding clay matrix by wave action owing to the exposures being along the modern-day seacoast. The London Clay Formation on the Isle of Sheppey is estimated to be ca. 53.5 to 51.5 Ma within the Ypresian stage of the Early Eocene (Collinson et al. 2016).

Juglandicarya simplicarpa specimens were collected by cleaving siltstones at Paleocene sites in the Fort Union Formation of Wyoming, USA, including Hells Half Acre (the type locality), and Signor Ridge in the Wind River Basin and Linch in the Powder River Basin (Manchester 1987). Locality numbers cited are from the Florida Museum of Natural History (UF loc.) and United States Geological Survey (USGS loc.) with coordinates in Brown (1962) and Manchester (2014). The precise age in the Paleocene has not been confirmed, but the holotype was collected from the same stratigraphic sequence studied palynologically by Nichols and Ott (1978, 2006) and falls within their zone P4 which has been interpreted as Middle Paleocene (fig. 2 in McKenna and Lillegraven 2005, Nichols 2009). Specimens from the Linch site are in the Lebo Member of the Fort Union Formation – also at the level of zone P4 and hence considered Middle Paleocene (Nichols 1994).

Specimens studied and their preparation

The fossils we investigated are housed in the paleobotanical collections of the Natural History Museum, London (NHMUK), the Florida Museum of Natural History at the University of Florida, Gainesville (UF) and the Smithsonian Natural History Museum, Washington, DC (USNM).

The type specimen of *J. cantia* from the London Clay flora was micro-CT scanned using a Nikon Metrology HMX ST 225 system. Scanning was undertaken using a tungsten reflection target, at an accelerating voltage of 220 kV and current of 200 mA, with an exposure time of 708 ms (giving a scan time of 38 min). A copper filter (2.0 mm thick) was applied to reduce beam hardening. A total of 3,142 projections were taken over a 360° rotation. The voxel size of the resulting

datasets varied from 8 to 15 μm . 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). The fossils of *J. simplicarpa* were micro-CT scanned at the College of Engineering Nanoscale Research Facility, University of Florida, using a GE Phoenix V/tome/xm240 CT scanner with a diamond-tungsten reflection target under a voltage of 120 kV, current of 440 μA , with a voxel size of 56 μm .

For comparative analysis, five extant nuts of *C. poilanei* and two nuts of *J. aillantifolia* var. *cordiformis* were studied by micro-CT scanning using the same equipment at UF with settings of 60 kV, 340 μA , and 0.200 s exposure time, 2,200 images, at a resolution of 42 μm (*J. poilanei*) and 60 kV, 480 μA , and 0.131 s exposure time, 2,200 images, at a resolution of 32 μm (*J. aillantifolia*). The specimens of extant species used for CT-scan are deposited in the paleobotany modern fruit/seed reference collection (UF) and herbarium (FLAS) of the Florida Museum of Natural History, Gainesville, Florida.

Micro-CT datasets were analyzed using VG Studio Max 3.1 (Volume Graphics GmbH, Heidelberg, Germany) to produce volume renderings, isosurface renderings, virtual sections, and three-dimensional image reconstructions. The original micro-CT scan datasets of *J. simplicarpa* and the extant nuts are archived at FLMNH and exemplary datasets were uploaded to MorphoSource (<https://www.morphosource.org/>). Micro-CT scan datasets of *J. cantia* are archived at the Natural History Museum, London (NHMUK) Imaging and Analysis Center. Terminology for fruit anatomy of Juglandaceae follows that of Manning (1940, 1978) and Manchester (1987).

The new names of species are registered with a unique PFN number in the Plant Fossil Names Registry, hosted and operated by the National Museum, Prague.

Systematic palaeontology

Order Fagales

Family Juglandaceae

Genus *Zodicarya* M.DENG, M.E.COLLINSON et MANCHESTER gen. nov.

Pls 1, 2

Type Species. *Zodicarya cantia* (E.REID et M.CHANDLER) M.DENG, M.E.COLLINSON et MANCHESTER, comb. nov.

Plant Fossil Names Registry Number: PFN003663.

Generic Diagnosis. Nut globose to ellipsoidal, unilocular, single-seeded, rounded basally and apically, smooth without external ribs or grooves, bisected longitudinally by a median plane of germinal separation. Nut moderate in size (≥ 1 cm diameter). Primary septum prominent, extending upwards from the base, at right angles to the plane of nutshell separation. Secondary septum absent or poorly developed. Locule with smooth contours, apically pointed, pyriform in lateral view, deeply bilobed from the base (by the primary septum) or slightly 4-lobed when a secondary septum is

present, with straight or slightly convex apical shoulder region. Nutshell and septa lacking lacunae.

Etymology. Abbreviation of *Zodiakos* (Gr referring to animals) + *Carya*, (Gr referring to walnut trees) (Brown 1956). This name alludes to our concept that this nut was adapted for animal dispersal.

Zodicarya cantia (E.REID et M.CHANDLER)

MANCHESTER, M.DENG et M.E.COLLINSON comb. nov.

Pl. 1

Basionym. *Juglandicarya cantia*, E.Reid et M.Chandler (1933): 142–143, pl. 3, figs 5, 6.

Holotype. NHMUK v. 22121 (Pl. 1, Figs 1–17; Reid and Chandler 1933: pl. 3, figs 5, 6)

Paratype. NHMUK v. 22122 [missing; Reid and Chandler 1933: pl. 3, fig. 7]

Plant Fossil Names Registry Number: PFN003662.

Emended specific diagnosis. Fruit a unilocular, single-seeded nut. Nut globose, 12 mm high $\times$ 12 mm wide, rounded basally and apically, smooth without external ribs or grooves. Nutshell thickest in the apical region, thickness gradually decreasing toward the base, without lacunae, composed of isodiametric sclereids. Primary septum prominent (ca 0.17–0.33 mm in thickness), at right angles to the plane of separation of the two halves of the nut. Secondary septum absent (holotype) or weakly developed (paratype). Locule with smooth contours, deeply bilobed from the base due to the primary septum, and with straight or slightly convex apical shoulder region.

Locality. Isle of Sheppey, northern coast of Kent, England, U.K.

Stratigraphic horizon and age. London Clay Formation, Ypresian, Early Eocene.

Zodicarya simplicarpa (MANCHESTER)

M.DENG et MANCHESTER, comb. nov.

Pl. 2

Basionym. *Juglandicarya simplicarpa*, Manchester (1987): 14, fig. 4A–D.

Holotype. UF 15740e-4860a (Pl. 2, Figs 1–6), designated by Manchester (1987).

Paratypes. USNM 313747, 312920 (Pl. 2, Fig. 12), 312944 (Pl. 2, Fig. 13) and 387384, designated by Manchester (1987).

Plant Fossil Names Registry Number: PFN003680.

Emended diagnosis. Fruit a unilocular, single-seeded nut. Nut globose-ellipsoidal, 12–22 mm high, 11–14 mm wide; exterior of nutshell smooth; primary septum prominent

1.1–1.7 mm thick, at right angles to the plane of separation of the two halves of the nut. Secondary septum absent to weakly developed. Locule bilobed at lower 2/3, entire or slightly emarginate at the base, sometimes giving 4 lobes at the extreme base; apical shoulder region straight or slightly convex; contours of locule smooth without grooves. Anatomy not preserved. Nutshell apparently without lacunae.

Additional informative specimens. UF18257-21877 (Pl. 2, Figs 7–9), UF15740e-23166, (Pl. 2, Fig. 11) 23169 (Pl. 2, Fig. 10), 23176 (Pl. 2, Figs 14, 15), UF15757a-69855 (Pl. 2, Figs 16–19).

Type Locality. Hells Half Acre (UF loc. 15740e), Natrona County, Wyoming, USA.

Additional localities. Ethete (USGS loc. 5917), and Signor Ridge (UF loc. 15757a), Fremont County, Wyoming and Linch (UF loc. 18257), Johnson County, Wyoming.

Stratigraphic horizon and age. Fort Union Formation, Tiffanian, Middle Paleocene.

Descriptions and comparisons

Nut morphology of *Zodicarya*

(Pls. 1, 2)

Zodicarya cantia from the London Clay flora is characterized by a globular nut 12 mm in diameter. The holotype was naturally fractured along the plane of germinal separation, exposing the locule cast (Pl. 1, Figs 1–8). The nutshell is smooth without nodulations or grooves (Pl. 1, Figs 2–8). The thickness of the nutshell ranges from 2.5–2.7 mm in the upper portion and becomes gradually thinner towards the base of the nut (ca. 0.7 mm) (Pl. 1, Figs 1, 3). Despite good cellular preservation, no cavities or lacunae were detected in the nutshell (Pl. 1, Figs 6, 9–17). The locule shows a smooth contour with no longitudinal grooves, cavities or ridges; the locule cast has a straight to convex-rounded apical shoulder region, and is two-lobed at base (Pl. 1, Figs 1, 4, 7). The primary septum is thick, but internally degraded in the placental area (owing to either decomposition prior to pyritization or subsequent pyrite decay) (Pl. 1, Figs 11, 13, 14), hindering analysis of the placental bundles. The secondary septum is absent in the holotype. However, the paratype specimen (now missing), was figured and described by Reid and Chandler (1933, in Pl. 3, Fig. 7) who noted that the base of the locule cast exposed in face view showed a slight emargination of the cotyledon lobe indicating a weak secondary septum intrusion. This indicates some variation from no secondary septum to a weakly expressed secondary septum in the species. The nutshell is composed of large isodiametric sclerenchyma cells that are best preserved in the outer nutshell (Pl. 1, Figs 16–17).

Another species with large nuts, *Juglandicarya crassa* (BOWERB.) E. REID et M. CHANDLER, was recognized by Reid and Chandler (1933) based on specimens first described by Bowerbank (1840) as *Cupressinites crassus*. The nut was

estimated at 14 mm long and 19 mm broad. Although this species appears to align with our concept of *Zodicarya*, we have refrained from proposing a new combination because the original specimen is no longer available, and no additional specimens have been recovered. It could, in fact, be conspecific with *J. cantia*, given that their sizes both fall within the size range observed among the more plentiful specimens assigned to *Z. simplicarpa* (see below).

Fossils of *Zodicarya simplicarpa* of the Paleocene Fort Union Formation in Wyoming, USA, are preserved as sedimentary casts and molds, lacking histological detail. The nuts vary from globose to ovoid-ellipsoid, and range in size from 11–14 mm in width and 12–22 mm in length. The exterior of the nutshell mold is rounded and smooth without prominent ribs and grooves (Pl. 2, Figs 8, 10, 17, 18). Two primary seed lobes are well developed in the locule cast; the lobes can be entire or slightly emarginate at the base, indicating lack or only or weak development of a secondary septum (Pl. 2, Figs 2, 3, 6, 12). The apical shoulder region is straight or slightly convex; contours of the locule casts are smooth indicating that endocarp lacked inner ribs (Pl. 2, Figs 2–7, 11–13). If lacunae had been present in the nutshell, we would expect that they would be preserved as sedimentary infillings in some of the specimens; however, no lacunae casts have been found, in either physically broken or CT-scanned material, suggesting that the nut wall, which is represented only by the empty space between the locule cast and the external mold of the nutshell, was originally composed of solid tissue that lacked lacunae, as is observed directly in the better-preserved nut of *Z. cantia*.

Nut morphology of extant *Carya* and *Juglans*

We base our comparison with extant species of *Juglans* and *Carya* in part upon our previously presented micro-CT scan analyses (Deng et al. 2024, Manchester et al. 2024). Additionally, we provide here new observations of extant *Carya poilanei* (Pl. 3, Figs 1–11) and *Juglans ailantifolia* (Pl. 3, Figs 12–19).

Carya poilanei, native to Vietnam and southern China (Zhang et al. 2022), has subglobose nuts 23–27 mm high and 23–24 mm wide with a smooth nutshell surface (Pl. 3, Fig. 1). The nutshell is about 3.0–3.5 mm thick, and includes prominent parenchymatous lacunae (Pl. 3, Figs 2–7). The edge of the suture zone is not thickened. The vasculature trace in the primary septum of the nut is uniform, with two main vascular bundles (funicular strands) entering from the basal pedicel attachment area. These bundles soon diverge from each other, arch peripherally toward the apex, and then bifurcate so that one branch reaches the upper cavity (Pl. 3, Fig. 2) and another branch extends along the apical margin of the primary septum just below the cotyledon to join with the placenta (Pl. 3, Figs 2, 3). These features have also been observed previously in most species of *Carya* except for *C. sinensis* (Leroy 1955, Deng et al. 2024). The interior of the nutshell is smooth without longitudinal ribs as indicated by the surface rendering (Pl. 3, Figs 8, 9, 11). The primary vascular bundle extends into the secondary septum at the placenta, and then stretches down to the basal region (Pl. 3, Fig. 3). The secondary septum is well developed at the base (Pl. 3, Figs 3,

6–7); hence the basal portion of the locule is divided into four lobes (Pl. 3, Fig. 7, 9, 10). This species has attracted interest previously because of similarities to the extinct European species, *C. ventricosa* (Mai 1981, Deng et al. 2024).

Juglans ailantifolia var *cordiformis*, native to Japan, is known as the heartnut because of its heart-shaped nuts (Pl. 3, Figs 15, 19). The nuts we studied measured 27–31 mm high and 22–25 mm wide. The nutshell lacks the four longitudinal corners or edges commonly observed in *Carya* and the external nutshell surface is smooth (Pl. 3, Fig 12) in contrast to most other extant *Juglans* species. As is characteristic for *Juglans*, the paired placental bundles in the primary septum follow an axial course to the placenta (Pl. 3, Fig. 13). The interior of the nutshell is smooth without longitudinal ribs (Pl. 3, Figs 14–19). As in other species of *Juglans*, the lacunae in the nutshell and septum are interconnected apically and lobed with well-defined edges (Pl. 3, Figs 16, 19).

Discussion

Systematic position of *Zodicarya* and comparisons with other taxa

The nut morphology of *Zodicarya* is consistent with the general characteristics of Juglandaceae, being unilocular with a partial primary septum bearing a perforation near the apex accommodating the placental area, and a plane of weakness along which the nutshell separates at germination that is perpendicular to the primary septum (Manning 1978). Additionally, micro-CT scans reveal that the nutshell of *Zodicarya cantia* is composed of isodiametric sclereids, an anatomical synapomorphy diagnostic of subfamily Juglandoideae (Manos and Stone 2001), supporting its placement within this clade. Members of Engelhardioideae (*Alfaroa*, *Engelhardia*, *Oreomunnea*, and *Beardia*), by contrast, have nutshells composed of fibers (Manos and Stone 2001, Elliott et al. 2006).

Comparisons with other species of *Juglandicarya*

Manchester (1987) reevaluated systematic relationships among the four species previously assigned to *Juglandicarya*, and considered the genus with that composition to be polyphyletic, with varied affinity to other genera. For example, *Juglandicarya lubbocki* from England exhibits a four-lobed locule base and introrse dorsal vascular bundles, resembling the extinct winged fruit genus *Cruciptera* (Manchester 1991). However, the type specimen is missing, and crucial anatomical details, such as nutshell structure and presence of lacunae, remain unknown. *Juglandicarya depressa* consists of small, abraded, pyritized nutlets. No wings were preserved, but its quadrangular shape and presence of longitudinally oriented fibers on the surface of the nutlets that converge upon the equator from the base and apex indicate a possibility of a surrounding circular wing, possibly related to *Cyclocarya* (Manchester 1987). Nevertheless, due to limited preservation, it remains classified within the fossil genus *Juglandicarya* (Manchester 1987, Pigg et al. 2023).

Juglandicarya gruetii was originally described by Vaudois-Miéja (1978) based on molds and casts from the Eocene Anjou flora at Saint-Saturnin-sur-Loire, France. However, recent micro-CT analyses have demonstrated that the type specimen represents a pentacarpellate capsule, structurally unrelated to Juglandaceae. Consequently, it was reassigned to a distinct genus, *Vaudoisia* (Strullu-Derrien et al. 2022). Thomasson (1987) assigned a fossil nut from the Late Miocene of northeastern Nebraska to *Juglandicarya* sp. The specimen is relatively large (1.9 cm high, 1.9 cm wide), with a smooth rounded shoulder of the locule and undeveloped secondary septum. While its overall shape is superficially similar to that of *Z. cantia*, the presence of prominent lacunae in the basal part of the nutshell (see fig. 6-6 in Thomasson 1987) clearly indicates affinity with *Juglans*. The nutlets recently reported as *Juglandicarya* sp. from the latest Paleocene of the north-central Paris Basin (Smith et al. 2014) are small (5.5 mm high, 4.0 mm wide) and likely derived from a winged fruit. Micro-CT images from their figures (see fig. 4J in Smith et al. 2014) reveal that the locule cast is divided into 2–3 lobes or has several grooves in the lower $\frac{1}{3}$ on both sides of the primary septum, suggesting the presence of interior ribs on the nutshell or potentially a prominent secondary septum, traits more consistent with extant *Pterocarya*.

In summary, the fossil genus *Juglandicarya* encompasses morphologically heterogeneous fossils with divergent affinities across Juglandaceae (Reid and Chandler 1933, Manchester 1987). In light of these findings and newly obtained anatomical evidence, we propose recognizing *Zodicarya* as a distinct genus to accommodate *J. cantia* and *J. simplicarpa*, which form a coherent and morphologically diagnosable group.

Comparisons with extant Juglandoideae

As mentioned above, *Zodicarya cantia* is anatomically aligned with the subfamily Juglandoideae, based on its nutshell structure composed of isodiametric sclereids rather than fibers, a synapomorphy of the subfamily (Manos and Stone 2001, Manos et al. 2007). Manchester (1987, 1989) hypothesized that *Zodicarya simplicarpa* and *Z. cantia* (then treated as *Juglandicarya*) were probably aligned with Hicorieae because the nuts cooccur with *Carya*-like pollen (*Caryapollenites*, e.g., Nichols and Ott 1978) but predate the occurrence of *Juglans* pollen.

A key diagnostic feature of Juglandaceae nuts is septum configuration (Manning 1940, 1978). In *Zodicarya*, the secondary septum is either absent or only weakly developed, resulting in a bilobed seed chamber at the nut base, occasionally with slight emargination of the two main lobes. This condition is shared with genera such as *Casholdia* (Crane and Manchester 1982), *Platycarya*, *Cyclocarya* and some species of *Juglans* and *Carya* (our observation of micro-CT scan datasets submitted to morphosource.org); however, the nutlets of the former three genera are substantially winged. The non-winged nuts and relatively large fruit size of *Zodicarya* are features shared with *Juglans* and *Carya*.

The interior of the *Zodicarya* nutshell is smooth, without ribs, a trait shared with *Juglans* (Pl. 3, Figs 14–19). This

differs from most *Carya* species, where longitudinal interior ribs are well-developed in the nutshell (Leroy 1955, Deng et al. 2024). An exception is East Asian *Carya poilanei*, which lacks interior ribs but has a prominent secondary septum in the lower ¼ of the nut (Pl. 3, Figs 3, 6, 7) dividing the seed chamber into four lobes at the base (Pl. 3, Fig. 10), unlike the simpler, usually bilobed structure seen in *Zodicarya* (Pl. 3, Figs 3, 6, 7, 10).

Nuts of *Zodicarya* are smoothly rounded, with no indication of the four longitudinal corners that coincide with the margins of the deciduous husk valves of *Carya*. *Juglans* nuts have persistent, nondeciduous husks and their nutshells lack the four corners typically seen in *Carya*. Husks in both of these genera are derived from the bract and bracteoles of the flower (Manning 1940). Although husks are not preserved in *Zodicarya* we infer from the smoothness of the nut surface that the husk was indehiscent.

The presence or absence of lacunae is another important diagnostic characteristic of subfamily Juglandoideae. Except for *Platycarya*, lacunae can occur in all other extant genera of the subfamily, including *Pterocarya* and *Cyclocarya* (observations from our micro-CT scan data available at morphosource.org). The configuration differs, however; the lacunae occur only in the upper portion of the nutshell (above the placenta) in *Cyclocarya*, or inside the primary septum in *Pterocarya*. In contrast, the nutshell of *Zodicarya* completely lacks lacunae (Pl. 1, Figs 9–13), clearly distinguishing it from extant species of *Juglans* and *Carya*.

Vascular bundle arrangement within the primary septum is another diagnostic character for distinguishing *Carya* and *Juglans*. In *Juglans* the paired funicular strands follow an axial course mostly parallel to each other within the primary septum and merge at the placental area, while in *Carya* the strands diverge from one another within the primary septum and display a peripheral course before arching back to the placental area (Leroy 1955, Deng et al. 2024). Unfortunately, cellular preservation is poor in the critical area of the septum in the holotype of *Z. cantia* obscuring the vascular bundle course (Pl. 1, Figs 11, 13, 14). Also it is unclear whether the species originally possessed septal lacunae as seen in the primary septum of *Juglans*. Despite this limitation, a pair of small notches observed at the placentation level of the primary septum in *Z. cantia* (Pl. 1, Fig. 11) likely represents remnants of placental vascular bundles. These are reminiscent of the well-defined vascular bundles at the seed-placenta junction of the primary septum of extant *Juglans* species (Deng et al. 2024). *Carya*, in contrast, has diffuse, tuft-like placental vasculature. The primary septum of *Juglans* sect. *Cardiocaryon* and sect. *Trachycaryon* is typically thick and woody and the secondary septum is not developed (Manchester 1997), another similarity with *Zodicarya*.

Zodicarya appears to show greater overall similarity to *Juglans* (especially sect. *Cardiocaryon*) than to *Carya*, particularly in septum structure, surface morphology, and absence of interior ribs. However, the lack of lacunae, an otherwise defining feature of *Juglans*, represents a clear distinction. The combination of features supports the interpretation of *Zodicarya* as a separate and extinct evolutionary lineage within the Juglandoideae.

Comparison with other fossil genera of Juglandoideae

We also evaluated the possibility that *Z. cantia* and *Z. simplicarpa* belong to the fossil genus *Globocarya* DOWELD, a genus characterized by spheroidal, smooth-surface nuts of moderate size (4.5–10.9 mm in length) and a thick woody shell without lacunae (Doweld 2016). *Globocarya* was established as a replacement for *Sphaerocarya* P.I.DOROF. (Dorofeev 1970) (a junior homonym; Doweld 2016). *Globocarya nikitinii* (P.I.DOROF.) DOWELD, the type species, is from the Miocene of western Siberia (Doweld 2016). Nutshell anatomy of the type species, *Globocarya nikitinii* reveals an outer layer of isodiametric sclereids and an inner layer of thin-walled cells, confirming its affinity with Juglandoideae (Dorofeev in Budantsev 1994). However, its secondary septum extends to 1/4–1/3 of the locule height and divides the seed chamber into four prominent lobes, which is unlike the bilobed locule of *Zodicarya*. Considering the differences in size and locule configuration, we conclude that *Globocarya* and *Zodicarya* are distinct genera.

Two other species formerly assigned to *Sphaerocarya* by Dorofeev (1970) and reviewed with additional imagery in Budantsev (1994) also differ from *Zodicarya*. *Sphaerocarya uralensis* P.I.DOROF., with small nuts (4.5–7.7 mm), a secondary septum in the lower ¼ of the locule and inferred remnants of wings, was later reassigned to a separate genus, *Boreocarya* by Doweld (2016). *B. nucifera* (LUDWIG) DOWELD has small nuts (ca. 5–8 mm) with distinct thin equatorial ridges and persistent “exocarp” remains, suggesting winged morphology and potential affinity with *Cyclocarya* (Martinetto 1998). Fossil nuts of *Carya buranica* ILJINSK. et AKHMET. from the Eocene-Oligocene transition of Kazakhstan (Averyanova et al. 2022, Pl. 1, Figs 9, 10, 13–17) show a smooth, unribbed locule closely resembling that of *Zodicarya*. However, the lack of internal information regarding vascular traces in the primary septum and the presence or absence of lacunae in the nutshell precludes a more precise comparison or systematic placement.

Zhang et al. (2022) performed a total-evidence analysis combining molecular and morphological data on the extant and fossil species of Juglandaceae, yielding a phylogenetic tree topology similar to that of Manos et al. (2007), in which *Juglandicarya simplicarpa* (now *Z. simplicarpa*) and *J. lubbocki* formed a clade sister to (*Beardia vancoverensis* + *Carya*). Of the 73 morphological traits used for total evidence analysis, only 17 were scored for *Zodicarya*, with six unambiguous fruit traits. However, four wing-related traits were over-weighted by being scored independently four times, and the remaining seven traits (e.g., style, bracts and staminate flowers) are unknown for *Zodicarya*, limiting the robustness of its placement. Moreover, the fibrous nutshell of *Beardia*, in contrast to the isodiametric sclereids, suggests an affinity with Engelhardioideae rather than Juglandoideae.

Despite extensive fossil evidence, the systematic affinities of many juglandaceous fossil taxa remain unresolved due to a lack of fine anatomical data. Our comparative analysis of both extant and fossil Juglandoideae indicates that *Zodicarya* is probably closest to *Juglans* sect. *Cardiocaryon*, but it also exhibits morphological distinctions from both *Juglans* and *Carya*. These features support the recognition of *Zodicarya* as a separate, now-extinct lineage within Juglandoideae.

Ecological significance

The large, wingless nuts of *Zodicarya* strongly suggest adaptation to animal dispersal – a trait that reflects broader evolutionary trends within Fagales from abiotic to biotic dispersal strategies. Stone (1973) identified two major reproductive syndromes within the order: (1) wind-dispersed, lightweight, winged nutlets with minimal protection, adapted to open environments (e.g., *Betula*, *Platycarya*), and (2) large, heavy, indehiscent nuts with thick, protective shells and substantial food reserves, adapted for animal dispersal and successful seedling establishment in shaded habitats (e.g., *Juglans*, *Quercus*).

Within Juglandaceae, the transition from winged, wind-dispersed fruits to large, animal-dispersed nuts occurred independently in the subfamilies Engelhardioideae and Juglandoideae. Stone (1973) further proposed two major evolutionary pathways: one from *Engelhardia* and *Oreomunnea* (winged) to *Alfaroa* (large, unwinged); and another from the biwinged *Pterocarya* and circular-winged *Cyclocarya* (Iljinskaya 1953), ultimately to the typical walnut (*Juglans*) and hickory nut (*Carya*), which are large fruits protected by a lignified shell and a thick husk (Stone 1973: 379). These hypotheses have been supported by molecular phylogenetic investigations (Zhang et al. 2022, 2013). Recent anatomical and paleobotanical research has revealed additional independent transitions toward biotic dispersal syndromes in *Beardia* (Engelhardioideae), *Globocarya*, *Sphaerocarya* and *Zodicarya* (Juglandoideae), highlighting the repeated, convergent evolution of animal-mediated dispersal in response to similar ecological pressures.

Micro-CT analysis of *Zodicarya* reveals that the thick, hard nutshell was composed of densely packed isodiametric sclereids, indicating that mechanical defenses against frugivory had already evolved by the Paleocene. Although pyritization obscures fine details of the inner shell anatomy, the preserved nutshell structure suggests a clear functional adaptation for seed protection. In comparison, modern *Juglans* and *Carya* exhibit more specialized nutshell anatomies characterized by interlocking polylobate sclereids and inner weakly lobed sclereids (Antreich et al. 2019, 2022, Huss et al. 2020, Xiao et al. 2021). These features, together with internal lacunae, enhance defense against predation (Patil et al. 2022). Variations in nutshell density allow differential water absorption, generating internal tension that facilitates controlled cracking at specific sites during germination (Huss and Gierlinger 2021). The development of polylobate sclereids in modern *Juglans* and *Carya* and lacunae in the nutshell of these genera represent key innovations and a derived condition that optimizes both the physical defenses of the nut and the efficiency of germination.

Although *Zodicarya* lacks both lacunae and the complex sclereid organization found in modern *Juglans* and *Carya*, its robust, homogeneous nutshell likely provided effective protection against frugivores of the time. It thus represents an early and distinct example of convergent evolution toward animal-dispersed fruit morphology within Juglandaceae. This example highlights both evolutionary innovation within Juglandoideae and the parallel ecological responses observed across both subfamilies of Juglandaceae in adapting to similar biotic dispersal trends during the early Cenozoic.

The ecological context of this transition is closely tied to the diversification of effective animal dispersers. The Early Eocene to Oligocene was a critical period for the radiation and ecological expansion of rodent groups (e.g., cricetids, dipodids, and ctenodactylids), which likely played a key role in the dispersal of large-fruited plants (Wood 1959, Fabre et al. 2012, Wu et al. 2012, O’Leary et al. 2013). Although rodents originated in the Early Paleocene (Meredith et al. 2011), their major diversification occurred during the Eocene, with a second wave during the Eocene–Oligocene transition likely driven by global climate change (Li et al. 2022). This period also saw increased land connectivity across Eurasia, which facilitated faunal and floral exchanges (Ni et al. 2020). In parallel, the diversification of corvid birds during the mid-Cenozoic likely further enhanced long-distance dispersal capacity for large-seeded taxa (Aggerbeck et al. 2014, Garcia-Porta et al. 2022). These overlapping radiations of animal dispersers likely exerted strong selective pressure on fruit traits in lineages such as *Zodicarya*.

Biogeography

Recent phylogenetic and biogeographic analyses suggest that the Juglandaceae originated in the Northern Hemisphere with contrasting evolutionary trajectories between the temperate subfamily Juglandoideae and the tropical subfamily Engelhardioideae (Zhang et al. 2022). Fossil evidence indicates that during the Paleocene and Eocene, North America harboured the highest diversity of juglandaceous genera, followed by successive expansion into Europe and eventually Asia (Manchester 1987). This supports the hypothesis that temperate Juglandoideae lineages dispersed early between North America and Europe via the North Atlantic Land Bridge (NALB) during the Late Paleocene to Early Eocene. These lineages subsequently diversified at higher latitudes, especially during the Miocene, coinciding with the evolution of frost tolerance in several major clades (Zhang et al. 2022). This scenario is further supported by fossil evidence from high latitude floras, including *Juglans* in the Eocene of Axel Heiburg Island and Greenland (Manchester et al. 2024). Genera such as *Carya* and *Juglans* likely migrated between North America and Europe via the NALB, which served as a key corridor for floristic exchange between these continents during the early Cenozoic (Tiffney 1985, Zhang et al. 2013, 2022) and even into the Neogene (Denk et al. 2010, 2023). The occurrence of *Zodicarya* fossils in both the Middle Paleocene of Wyoming and the Early Eocene London Clay flora of southern England suggests that this extinct genus traversed the NALB during the same time interval.

Farther east, *Carya buranica*, which as we noted above, very closely resembles and might belong to *Zodicarya*, was recently recorded from a paleoflora in Kazakhstan dating to the Eocene–Oligocene transition. This central Asian flora represents the earliest known Turgai-type assemblage – characterized by forest elements comparable to those of the London Clay flora but indicative of a cooler climate (Averyanova et al. 2022). This suggests that *Zodicarya* or close relatives may have extended their ranges into Asia by the Oligocene, following dispersal routes similar to those of *Carya*, *Juglans*,

Pterocarya and other temperate Juglandoideae (Manchester 1987, Reid and Chandler 1933).

The paleogeographic history of *Zodicarya* reflects its early role in the expansion of Juglandoideae across the Northern Hemisphere and its subsequent restriction or extinction. Its fossil occurrences complement broader patterns of transcontinental plant migration, climate-driven dispersal filtering, and convergent adaptation to animal-mediated seed dispersal during the early Cenozoic.

Acknowledgements

We thank the staff of the Natural History Museum, London for access to the London Clay fossil plant collections and for undertaking the CT scan on the London Clay specimen, Terry Lott for help with manuscript formatting, Bruce Tiffney and Edoardo Martinetto for helpful review comments and Zuzana Heřmanová for editing expertise.

References

- Aggerbeck, M., Fjeldsa, J., Christidis, L., Fabre, P. H., Jonsson, K. A. (2014): Resolving deep lineage divergences in core corvid passerine birds supports a proto-Papuan island origin. – *Molecular Phylogenetics and Evolution*, 70: 272–285. <https://doi.org/10.1016/j.ympev.2013.09.027>
- Antreich, S. J., Huss, J. C., Xiao, N., Singh, A., Gierlinger, N. (2022): The walnut shell network: 3D visualisation of symplastic and apoplastic transport routes in sclerenchyma tissue. – *Planta*, 256(3): 49. <https://doi.org/10.1007/s00425-022-03960-w>
- Antreich, S. J., Xiao, N., Huss, J. C., Horbelt, N., Eder, M., Weinkamer, R., Gierlinger, N. (2019): The puzzle of the walnut shell: A novel cell type with interlocked packing. – *Advanced Science*, 6(16): 1900644 (6 pp.). <https://doi.org/10.1002/advs.201900644>
- Averyanova, A., Tarasevich, V. F., Popova, S., Utescher, T., Su, T., Mosbrugger, V. (2022): Late Rupelian flora of the Zaissan Depression (Eastern Kazakhstan). – *Review of Palaeobotany and Palynology*, 304(2022): 104721 (13 pp.). <https://doi.org/10.1016/j.revpalbo.2022.104721>
- Bowerbank, J. (1840): A history of the fossil fruits and seeds of the London Clay. – John Van Voorst, London, pp. 410–412.
- Brown, R. W. (1956): *Composition of Scientific Words*. – Smithsonian Institution Press, Washington, D.C., 882 pp.
- Brown, R. W. (1962): Paleocene flora of the Rocky Mountains and Great Plains. – Professional Paper, United States Geological Survey, 375: 1–119, 169 pls. <https://doi.org/10.3133/pp375>
- Budantsev, L. J. (1994): Magnoliophyta fossilia Rossiae et civitatum finitimarum. 3. Leitneriaceae – Juglandaceae. – Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg, 118 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-permineralized fruits and seeds from the London Clay Formation (Ypresian) conserved in silicone oil: A critical evaluation. – *Botany*, 94(9): 697–711. <https://doi.org/10.1139/cjb-2016-0078>
- Crane, P. R., Manchester, S. R. (1982): An extinct juglandaceous fruit from the Upper Palaeocene of southern England. – *Botanical Journal of the Linnean Society*, 85(2): 89–101. <https://doi.org/10.1111/j.1095-8339.1982.tb00587.x>
- Deng, M., Kvaček, J., Heřmanová, Z., Manchester, S. R. (2024): Comparative nut morphology and biogeographic implications of *Carya ventricosa* from the Miocene of Europe. – *International Journal of Plant Sciences*, 185(2): 109–128. <https://doi.org/10.1086/728185>
- Denk, T., Bouchal, J. M., Guner, H. T., Coiro, M., Butzmann, R., Pigg, K. B., Tiffney, B. H. (2023): Cenozoic migration of a desert plant lineage across the North Atlantic. – *New Phytologist*, 238(6): 2668–2684. <https://doi.org/10.1111/nph.18743>
- Denk, T., Grímsson, F., Zetter, R. (2010): Episodic migration of oaks to Iceland: Evidence for a North Atlantic “land bridge” in the latest Miocene. – *American Journal of Botany*, 97(2): 276–287. <https://doi.org/10.3732/ajb.0900195>
- Dilcher, D. L., Potter, F. W., Crepet, W. L. (1976): Investigations of angiosperms from the Eocene of North America: Juglandaceous winged fruits. – *American Journal of Botany*, 63(5): 532–544. <https://doi.org/10.2307/2441817>
- Dorofeev, P. I. (1970): Vklad v taksonomiyu nekotorykh iskopayemykh Juglandaceae [A contribution to the taxonomy of certain fossil Juglandaceae]. – *Botanicheskii Zhurnal* (St Petersburg), 55: 1596–1604. (in Russian)
- Doweld, A. B. (2013): Proposal to conserve the name *Juglandicarya* against *Hybothya* with a conserved type (fossil Juglandaceae). – *Taxon*, 62(4): 843–843. <https://doi.org/10.12705/624.24>
- Doweld, A. B. (2016): *Boreocarya* and *Globocarya*, new names in the extinct Juglandaceae of Northern Eurasia. – *Acta Palaeobotanica*, 56(2): 519–521. <https://doi.org/10.1515/acpa-2016-0010>
- Elliott, L. L., Mindell, R. A., Stockey, R. A. (2006): *Beardia van-couverensis* gen. et sp. nov. (Juglandaceae): Permineralized fruits from the Eocene of British Columbia. – *American Journal of Botany*, 93(4): 557–565. <https://doi.org/10.3732/ajb.93.4.557>
- Fabre, P.-H., Hautier, L., Dimitrov, D., Douzery, E. J. P. (2012): A glimpse on the pattern of rodent diversification: A phylogenetic approach. – *BMC Evolutionary Biology*, 12(1): 88. <https://doi.org/10.1186/1471-2148-12-88>
- García-Porta, J., Sol, D., Pennell, M., Sayol, F., Kaliontzopoulou, A., Botero, C. A. (2022): Niche expansion and adaptive divergence in the global radiation of crows and ravens. – *Nature Communications*, 13(1): 2086. <https://doi.org/10.1038/s41467-022-29707-5>
- Herendeen, P. S. (2015): Report of the Nomenclature Committee on Fossils: 9. – *Taxon*, 64(6): 1306–1312. <https://doi.org/https://doi.org/10.12705/646.14>
- Hermesen, E. J., Gandolfo, M. A. (2016): Fruits of Juglandaceae

- from the Eocene of South America. – *Systematic Botany*, 41(2): 316–328.
<https://doi.org/10.1600/036364416x691830>
- Huss, J. C., Gierlinger, N. (2021): Functional packaging of seeds. – *New Phytologist*, 230(6): 2154–2163.
<https://doi.org/10.1111/nph.17299>
- Huss, J. C., Antreich, S. J., Bachmayr, J., Xiao, N., Eder, M., Konnerth, J., Gierlinger, N. (2020): Topological interlocking and geometric stiffening as complementary strategies for strong plant shells. – *Advanced Materials*, 32(48): 2004519 (7 pp.).
<https://doi.org/10.1002/adma.202004519>
- Ilijinskaya, I. A. (1953): Monograph of the genus *Pterocarya* Kunth. – Trudy Botanicheskogo Instituta im Komarova Akademii Nauk SSSR, series 1, Flora i Sistematika Vysshikh Rastenii, 10: 7–123.
- Leroy, J.-F. (1955): Study of the Juglandaceae. Attempt to find a concept of the morphology of the female flower and the fruit. – *Memoire du Museum National d'Histoire Naturelle*, Paris, 6B: 246–246.
- Li, Q., Li, Q., Xu, R.-C., Wang, Y.-Q. (2022): Rodent faunas, their paleogeographic pattern, and responses to climate changes from the early Eocene to the early Oligocene in Asia. – *Frontiers in Ecology and Evolution*, 10: 955779 (17 pp).
<https://doi.org/10.3389/fevo.2022.955779>
- Mai, D. H. (1981): Der Formenkreis der Vietnam-nuss (*Carya poilanei* (Chev.) Leroy) in Europa. – *Feddes Repertorium*, 92:339–385.
<https://doi.org/10.1002/fedr.19810920502>
- Manchester, S. R. (1987): The fossil history of the Juglandaceae. – *Monographs in Systematic Botany from the Missouri Botanical Garden*, St Louis, 21: 1–137.
<https://doi.org/10.5962/bhl.title.154222>
- Manchester, S. R. (1989): Early history of the Juglandaceae. – *Plant Systematics and Evolution* 162 (1-4): 231–250.
<https://doi.org/10.1007/bf00936919>
- Manchester, S. R. (1991): *Cruciptera*, a new Juglandaceous winged fruit from the Eocene and Oligocene of western North America. – *Systematic Botany*, 16(4): 715–725.
<https://doi.org/10.2307/2418873>
- Manchester, S. R., Dilcher, D. L. (1997): Reproductive and vegetative morphology of *Polyptera* (Juglandaceae) from the Paleocene of Wyoming and Montana. – *American Journal of Botany*, 84(5): 649–663.
<https://doi.org/10.2307/2445902>
- 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., Dilcher, D. L. (1997): Reproductive and vegetative morphology of *Polyptera* (Juglandaceae) from the Paleocene of Wyoming and Montana. – *American Journal of Botany*, 84(5): 649–663.
<https://doi.org/10.2307/2445902>
- Manchester, S. R., Wilson, R., Liu, Y.-S., Basinger, J. F. (2024): Arctic walnuts! Nuts of *Juglans* (Juglandaceae) from the Middle Eocene of Axel Heiberg Island, Northern Canada. – *International Journal of Plant Sciences*, 185(5): 453–473.
<https://doi.org/10.1086/730541>
- Manning, W. E. (1940): The morphology of the flowers of the Juglandaceae. II. The pistillate flowers and fruit. – *American Journal of Botany*, 27(10): 839–852.
<https://doi.org/10.2307/2438058>
- Manning, W. E. (1978): The classification within the Juglandaceae. – *Annals of the Missouri Botanical Garden*, 65(4): 1058–1087.
<https://doi.org/10.2307/2398782>
- Manos, P. S., Soltis, P. S., Soltis, D. E., Manchester, S. R., Oh, S.-H., Bell, C. D., Dilcher, D. L., Stone, D. E. (2007): Phylogeny of extant and fossil Juglandaceae inferred from the integration of molecular and morphological data sets. – *Systematic Biology*, 56(3): 412–430.
<https://doi.org/10.1080/10635150701408523>
- Manos, P. S., Stone, D. E. (2001): Evolution, phylogeny, and systematics of the Juglandaceae. – *Annals of the Missouri Botanical Garden*, 88(2): 231–269.
<https://doi.org/10.2307/2666226>
- Martinetto, E. (1998): East Asian elements in the Pliocene-Pleistocene floras of Italy. – In: Zhang, A. L., Wu, S. G., Raven, P. H., Iwatsuki, K., Kubitzki, K. (eds), *Proceedings of the First International Symposium of Floristic Characters and Diversity of East Asian Plants*, July 25th – 27th 1996, Kunming, Yunnan, China, pp. 71–87.
- McKenna, M.C., Lillegraven, J. A. (2005): Problems with Paleocene Palynozones in the Rockies: Hell's Half Acre Revisited. – *Journal of Mammalian Evolution*, 12(1): 23–51.
<https://doi.org/10.1007/s10914-005-4864-x>
- Meredith, R. W., Janecka, J. E., Gatesy, J., Ryder, O. A., Fisher, C. A., Teeling, E. C., Goodbla, A., Eizirik, E., Simao, T. L. L., Stadler, T., Rabosky, D. L., Honeycutt, R. L., Flynn, J. J., Ingram, C. M., Steiner, C., Williams, T. L., Robinson, T. J., Burk-Herrick, A., Westerman, M., Ayoub, N. A., Springer, M. S., Murphy, W. J. (2011): Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. – *Science*, 334(6055): 521–524.
<https://doi.org/10.1126/science.1211028>
- Ni, X., Li, Q., Zhang, C., Samiullah, K., Zhang, L., Yang, Y., Cao, W. (2020): Paleogene mammalian fauna exchanges and the paleogeographic pattern in Asia. – *Science China Earth Sciences*, 63(2): 202–211.
<https://doi.org/10.1007/s11430-019-9479-1>
- Nichols, D. J. (1994): Palynostratigraphic correlation of Paleocene rocks in the Wind River, Bighorn, and Powder River Basins, Wyoming. – *Wyoming State Geological Survey Public Information Circular*, 33: 17–29.
- Nichols, D. J. (2009): On the palynomorph-based biozones in Paleogene strata of Rocky Mountain basins. – *The Mountain Geologist*, 46(3): 105–124.
- Nichols, D. J., Ott, H. L. (1978): Biostratigraphy and evolution of the *Momipites-Caryapollenites* lineage in the early Tertiary in the Wind River Basin, Wyoming. – *Palynology*, 2: 93–112.
<https://doi.org/10.1080/01916122.1978.9989167>
- Nichols, D. J., Ott, H. L. (2006): Neotypes for Paleocene species in the *Momipites-Caryapollenites* pollen lineage. – *Palynology*, 30(1): 33–41.
<https://doi.org/10.2113/gspalynol.30.1.33>
- O'Leary, M. A., Bloch, J. I., Flynn, J. J., Gaudin, T. J., Giallombardo, A., Giannini, N. P., Goldberg, S. L., Kraatz, B. P., Luo, Z.-X., Meng, J., Ni, X., Novacek, M. J., Perini,

- F. A., Randall, Z. S., Rougier, G. W., Sargis, E. J., Silcox, M. T., Simmons, N. B., Spaulding, M., Velazco, P. M., Weksler, M., Wible, J. R., Cirranello, A. L. (2013): The placental mammal ancestor and the post-K-Pg radiation of Placentals. – *Science*, 339(6120): 662–667.
<https://doi.org/10.1126/science.1229237>
- Patil, A. Y., Hegde, C., Savanur, G., Kanakmood, S. M., Contractor, A. M., Shirashyad, V. B., Chivate, R. M., Kotturshettar, B. B., Mathad, S. N., Patil, M. B., Soudagar, M. E. M., Fattah, I. M. R. (2022): Biomimicking nature-Inspired design structures – An experimental and simulation approach using additive manufacturing. – *Biomimetics* (Basel), 7(4): 186.
<https://doi.org/10.3390/biomimetics7040186>
- Pigg, K. B., DeVore, M. L., Taylor, W. (2023): New features of *Cyclocarya brownii* Manchester & Dilcher from the Late Paleocene of North Dakota, USA. – *International Journal of Plant Sciences*, 184(4): 282–303.
<https://doi.org/10.1086/724496>
- Reid, E. M., Chandler, M. E. J. (1933): The London Clay Flora. British Museum (Natural History), London.
<https://doi.org/10.5962/bhl.title.110147>
- Smith, C. C., Reichman, O. J. (1984): The evolution of food caching by birds and mammals. – *Annual Review of Ecology, Evolution, and Systematics*, 15: 329–351.
<https://doi.org/10.1146/annurev.es.15.110184.001553>
- Smith, T., Quesnel, F., De Plöeg, G., De Franceschi, D., Métais, G., De Bast, E., Solé, F., Folie, A., Boura, A., Claude, J., Dupuis, C., Gagnaison, C., Iakovleva, A., Martin, J., Maubert, F., Prieur, J., Roche, E., Storme, J.-Y., Thomas, R., Tong, H., Yans, J., Buffetaut, E. (2014): First clarkforkian equivalent land mammal age in the latest Paleocene basal Sparnacian facies of Europe: Fauna, flora, paleoenvironment and (bio)stratigraphy. – *PLoS ONE*, 9(1): e86229.
<https://doi.org/10.1371/journal.pone.0086229>
- Stone, D. E. (1973): Patterns in the evolution of amentiferous fruits. – *Brittonia*, 25(4): 371–384.
<https://doi.org/10.2307/2805641>
- Stone, D. E. (1993): Juglandaceae. – In: Kubitzki K., Rohwer J. G., Bittrich V. (eds), *Flowering Plants, Dicotyledons: Magnoliid, Hamamelid and Caryophyllid Families*. Springer, Berlin, Heidelberg, pp. 348–359.
https://doi.org/10.1007/978-3-662-02899-5_43
- Strullu-Derrien, C., Spencer, A. R. T., Kenrick, P., Judd, W. S., De Franceschi, D., Manchester, S. R. (2022): Revisions to the Eocene carpoflora of Anjou, western France, with new data from X-ray tomography. – *Botany Letters*, 169(4): 454–465.
<https://doi.org/10.1080/23818107.2022.2101518>
- Thomasson, J. R. (1987): Late Miocene plants from northeastern Nebraska. – *Journal of Paleontology*, 61(5): 1065–1079.
<https://www.jstor.org/stable/1305347>
- Tiffney, B. H. (1985): The Eocene North Atlantic land bridge: Its importance in Tertiary and modern phytogeography of the Northern Hemisphere. – *Journal of the Arnold Arboretum* 66: 243–273.
<https://doi.org/10.5962/bhl.part.13183>
- Tiffney, B. H., Manchester, S. R. (2022): The early middle Eocene Wagon Bed carpoflora of central Wyoming, U.S.A. – *Fossil Imprint*, 78: 51–79.
<https://doi.org/10.37520/fi.2022.004>
- Vaudois-Miéja, N. (1978): Nouvelle étude paléocarpologique de l'anjou. Révision bibliographique des Juglandaceae fossiles. – *Review of Palaeobotany and Palynology*, 25(3): 269–294.
[https://doi.org/10.1016/0034-6667\(78\)90031-3](https://doi.org/10.1016/0034-6667(78)90031-3)
- Wilson, K. L. (2016): Report of the General Committee: 15. – *Taxon*, 65(5): 1150–1151.
<https://doi.org/10.12705/655.14>
- Wood, A. E. (1959): Eocene radiation and phylogeny of the rodents. – *Evolution*, 13(3): 354–361.
<https://doi.org/10.2307/2406112>
- Wu, S., Wu W., Zhang, F., Ye, J., Ni, X., Sun, J., Edwards, S. V., Meng, J., Organ, C. L. (2012): Molecular and paleontological evidence for a post-Cretaceous origin of rodents. – *PLoS One* 7(10): e46445 (11 pp.).
<https://doi.org/10.1371/journal.pone.0046445>
- Xiao, N., Felhofer, M., Antreich, S. J., Huss, J. C., Mayer, K., Singh, A., Bock, P., Gierlinger, N. (2021): Twist and lock: Nutshell structures for high strength and energy absorption. – *Royal Society Open Science*, 8(8): 210399 (12 pp.).
<https://doi.org/10.1098/rsos.210399>
- Zhang, J.-B., Li, R.-Q., Xiang, X.-G., Manchester, S. R., Lin, L., Wang, W., Wen, J., Chen, Z.-D. (2013): Integrated fossil and molecular data reveal the biogeographic diversification of the Eastern Asian-Eastern North American disjunct hickory genus (*Carya* Nutt.). – *PLoS ONE*, 8(7): e70449 (13 pp.).
<https://doi.org/10.1371/journal.pone.0070449>
- Zhang, Q.-Y., Ree, R. H., Salamin, N., Xing, Y.-W., Silvestro D. (2022): Fossil-informed models reveal a Boreotropical origin and divergent evolutionary trajectories in the walnut family (Juglandaceae). – *Systematic Biology*, 71(1): 242–258.
<https://doi.org/10.1093/sysbio/syab030>
- Zhang, W.-P., Bai, W.-N., Zhang, D.-Y. (2022): The rediscovery of *Carya poilanei* (Juglandaceae) after 63 years reveals a new record from China. – *PhytoKeys*, 188: 73–82.
<https://doi.org/10.3897/phytokeys.188.77242.suppl1>

Explanation of the plates

PLATE 1

Zodicarya cantia (E.Reid et M.Chandler) M.Deng, M.E.Collinson et Manchester comb. nov. from the early Eocene London Clay Formation, England, holotype, NHMUK V 21121.

- 1, 2. Front and lateral view, reflected light.
- 3–17. Images from micro-CT scanning.
- 3–8. Isosurface rendering of nut showing the smooth, thick nutshell, medial primary septum (black arrows), and smooth form of the locule.
3. Front view of nut opened along the natural separation plane, showing the protruding smooth locule cast.
4. Apical view of nut.
5. Basal view.

6. Basal view with translucency showing locule configuration and thick nutshell.
- 7, 8. Lateral views showing the hemispherical, smooth nut shell on one half and protruding smooth lobes of the locule cast on the other side where the nutshell has been lost.
- 9–17. Virtual sections.
- 9–11. Transverse sections at the basal 1/3 of the placenta (Fig. 9), at the middle of the placenta (Fig. 10), and at the top of the placenta (Fig. 11). The section planes are indicated in Fig. 14 by the yellow, orange and blue lines, respectively; white arrows indicate cavities in the primary septum resulting from decay.
- 12–14. Virtual longitudinal sections of nut parallel to the primary septum; section planes indicated by the red lines from left to right in Fig. 11; white arrows indicate decayed area; red arrows indicate areas that are possibly the remains of placental bundles.
15. Longitudinal section parallel to separation plane (perpendicular to the primary septum; in the plane indicated by the long green line in Figs 11, 14), showing smooth shoulder, thick primary septum and cavity resulting from decay (white arrows).
16. Enlargement of nutshell, transverse section at the level indicated by blue line in Fig. 14; yellow arrows indicating the continuous span of isodiametric sclereids
17. Enlargement of nutshell in longitudinal section in plane indicated by the short green line in Fig. 14. The observation of cells with exclusively circular outlines in this plane, at right angles to that of Fig. 16, indicates these cells are isodiametric and hence cannot be interpreted as fibers. L = locule; Se = primary septum. Scale bars = 5.0 mm in 1.–15.; 2 mm in Figs 16., 17.

PLATE 2

Zodicarya simplicarpa (MANCHESTER) M.DENG et MANCHESTER comb. nov. from the Paleocene Fort Union Formation of Wyoming. Position of the primary septum indicated by black arrows and the weakly developed secondary septum by white arrows. L = locule lobes.

- 1–6. Holotype, Hells Half Acre, Wyoming, UF15740e-4860a.
1. Locule cast with prominent median cleavage representing the primary septum, reflected light.
2. Surface rendering in same orientation as Fig. 1.
3. Basal view of surface rendering, showing horizontal basal cleavage indicating weakly developed secondary septum (white arrows) in addition to the prominent primary septum (upper black arrow).
4. Virtual transverse section, showing the weakly developed secondary septum (white arrows).
5. Surface rendering, depth map image of the nutshell ventral surface as viewed through the matrix, opposite to the view in Fig. 1 and Fig. 2, two chambers of the locule separated by primary septum.
6. Lateral view of the locule cast, surface rendering, depth map image.
- 7–9. Specimen from Linch, Wyoming, UF18257-21877.

7. Sedimentary cast showing two lobes of the locule separated by primary septum, reflected light.
8. Corresponding nut mold (counterpart to that in Fig. 7), showing the smooth ellipsoidal shape, surface rendering from micro-CT scan.
9. Micro-CT virtual transverse section of the same specimen as Fig. 7 and Fig. 8 with both parts reassembled, showing that only one half of the nut was deposited. The arched black line and median vertical line is the void remaining from decay of the nutshell and septum.
10. Nut mold with smooth contours from Hells Half Acre, reflected light, UF15750E-23169.
11. Apical view of locule cast from transversely compressed nut, reflected light, UF15740E-23166.
12. Locule cast preserved at right angles to the plane of separation, USNM312920, USGS locality 9112.
13. Locule cast showing median groove representing the primary septum, USNM312944, USGS locality 5917.
- 14–15. Specimen from Hells Half Acre, Wyoming, showing two nuts with locule casts in different orientations, apical and lateral by reflected light (14), and surface rendering from micro-CT scanning (15), UF15740e-23176.
- 16–19. Nut from Signor Ridge, Wyoming, UF15757a-69855.
16. Equatorial transverse virtual section two halves of the nut, separated along the plane of germinal splitting, with primary septum indicated by arrows.
17. Surface rendering in lateral view, showing slightly ridged surface texture.
18. Same in basal view.
19. Surface rendering, ventral view of one half of the nutshell with primary septum indicated (SE). Scale bars = 5.0 mm.

PLATE 3

Nuts of extant *Carya poilanei* (A.CHEV.) J.-F.LEROY and *Juglans ailantifolia* var. *cordiformis* (MAKINO) REHDER by micro-CT.

- 1.–11. *Carya poilanei*. BNU20211005, Coll. W.-P. Zhang and D.-Y. Zhang 5 Oct. 2021, Jianshui county, China [23°23'40.42"N; 102°51'34.42"E].
1. Surface rendering of nut in lateral, apical and basal view.
2. Median longitudinal section of nut parallel to primary septum; red arrows indicate the traces of the vascular bundle in the primary septum.
3. Median longitudinal section of nut parallel to separation plane, with plane of section indicated by red line in Fig. 2. Blue arrows indicate the vascular bundle diffusing from the placenta and stretching into the secondary septum.
- 4–7. Transverse sections from the nut top to the bottom, section planes indicated by horizontal lines in 2.
8. Virtual cast of locule, lateral view, with separation plane facing the viewer.
9. Apical view of virtual locule cast.
10. Basal view of virtual locule cast.
11. Lateral view of virtual locule cast, rotated 90 degrees from Fig. 8, with primary septum facing the viewer.

- 12–19. *Juglans ailantifolia* var. *cordiformis*. Cultivated, Russell, Iowa, USA (UF mod. ref. coll. UF2881).
12. Surface rendering, lateral view, showing smooth nutshell surface.
 13. Median longitudinal section parallel to primary septum with lacunae indicated by asterisks; red arrows indicate the traces of the vascular bundle in the primary septum.
 14. Transverse section at the placenta with lacunae of the nutshell and septum indicated by asterisks; section plane indicated by green line in Fig. 13.
 15. Median longitudinal section parallel to separation plane, with section plane indicated by red line in 13.
 16. Lateral view of virtual locule cast, with separation plane line facing the viewer.
 17. Apical view of virtual locule cast.
 18. Basal view of virtual locule cast.
 19. Lateral view of virtual locule cast, with primary septum facing the viewer.
- In Figs 10, 11, 16, and 19 the locule (yellow) is overlain by a virtual image of the nutshell at 95 % transparency, showing the low density tissue (fuzzy white) in Figs 10–11 and the well-defined lacunae in the nutshell and primary septum (light blue). Scale bars = 5 mm.





