Nut of *Juglans bergomensis* (Balsamo Crivelli) Massalongo in the Miocene of North America

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ABSTRACT. A new occurrence of fossil butternut is recognized based on a permineralized highly scabrate walnut from the middle Miocene of western Washington, USA. The specimen fits the circumscription of *Juglans bergomensis* (Balsalmo Crivelli) Massalongo, a species that was widespread in Europe and Asia during the Neogene. The occurrence near Brady, Washington, supplements the previously recognized occurrence from Banks Island, Canada, indicating a distribution in mid-latitude western North America as well as Europe and Asia during the Miocene.

KEYWORDS: *Juglans bergomensis*, butternut, Juglandaceae, Miocene, Washington

INTRODUCTION

The Juglandaceae DC. ex Perleb, or walnut family, is a diverse family with ten extant genera spread out predominately in the Northern Hemisphere but also extending southwards into parts of South America and New Guinea (Manning 1978, Manchester 1987). Fossil fruits of both extant and extinct genera are present by the Paleocene (Iljinskaya 1953, Manchester 1981, Crane & Manchester 1982, Manchester & Dilcher 1982), and extinct relatives have been recognized back to the Cenomanian (Friis et al. 2011). The namesake genus, *Juglans* L., belongs to the subfamily Juglandoideae Eaton, tribe Juglandeae Rchb. and subtribe Juglandinae D.E. Stone and P.S. Manos. *Juglans* is divided into three sections: sect. *Juglans* Dode (Persian or English walnuts), sect. *Rhysocaryon* Dode (black walnuts) and sect. *Cardiocaryon* Dode (butternuts). Phylogenetic work by Stone et al. (2009) indicates that sections *Cardiocaryon* and *Juglans* form a clade that is sister to sect. *Rhysocaryon*. Occasionally, the North American butternut, *J. cinerea* L., is treated as its own section, sect. *Trachycaryon* Dode ex Mann. It has also been hypothesized

to be nested among black walnuts based on chloroplastic DNA (Aradhya et al. 2007, Dong et al. 2017) and sister to *Cardiocaryon* based on chromosomal ITS (Dong et al. 2017), however, these results may differ from the nuclear topologies in part due to problems associated with inheritance strictly from the maternal lineage via hybridization (Greiner et al. 2015). For our purposes we adopt the phylogeny of Stone et al. (2009), supported by morphology as well as nuclear DNA (ETS, ITS and the second intron of the LEAFY gene).

The oldest previously described fossil nut of *Juglans* is *J. clarnensis* Scott (sect. *Rhysocaryon*), based on numerous specimens from the middle Eocene of Oregon (Scott 1954, Manchester 1994). Ongoing work on specimens from the middle Eocene of Axel Heiberg Island, Canada, indicate another occurrence of the genus, which appears likely to represent sect. *Cardiocaryon* (Wilson et al. 2006, J.F. Basinger pers. comm. 2017). The paleobotanical record of nuts indicates that the genus had spread to Europe and Asia by the Miocene (Miki 1953, Nirei 1975, Mai 1995, Kunzmann

& Mai 2005, Standke 2008) and was established in South America by the late Miocene or early Pliocene (Brown 1946).

The modern natural distribution of sect. *Cardiocaryon* is disjunct between eastern North America (with a single species, *J. cinerea*) and eastern Asia (e.g., *J. ailantifolia* Carr., *J. mandshurica* Maxim.). This disjunction is clearly due to extinction across parts of large areas from its former distribution range, because the fossil record indicates a broader range of the section during the Paleogene and Neogene (Miki 1953, Kirchheimer 1957, Manchester 1981, 1987, van der Ham 2015). Some authors treated the European and Asian fossils as members of the extant North American species *J. cinerea* (e.g. Unger 1950, Kryshtofovich 1915, Szafer 1954). Traditionally, however, many of the occurrences were treated as distinct species, so that those in Japan, Siberia, Central Europe and Banks Island were considered separate entities (e.g. *J. megacinerea* Miki ex Chaney, *J. hanamakiensis* Nirei and *J. mikii* Nirei in Japan; *J. dorofeevii* Iljinskaja in Siberia; *J. eocinerea* Hills, Klovan & Sweet on Banks Island, Canada; *J. tephrodes* Unger in Germany). Van der Ham (2015) considered that these species show too much morphological overlap to justify maintaining them as distinct; accordingly, he assigned all scabrate fossil nuts of the *Cardiocaryon* morphology to *J. bergomensis* (Balsamo Crivelli) Massalongo, noting that this is the earliest available valid binomial for the fossil. A neotype based on a specimen from the type locality was designated recently to substitute for the missing holotype (Martinetto et al. 2015).

A newly investigated permineralized nut from a mid-Miocene calcareous concretion from a site near Brady, Grays Harbor County, Washington, preserves external and internal features consistent with assignment to *J. bergomensis*. This fossil, studied by physical sectioning and nano-CT scanning, was compared with extant and previously described fossil *Cardiocaryon* specimens. This new occurrence adds to the recurring pattern of widespread Northern Hemispheric biogeographic history of plants and specifically to that of sect. *Cardiocaryon*, which contrasts with its modern restricted ranges. The new occurrence also helps reconstruct the floristic environment of the Pacific Northwest's mid-Miocene coast. Furthermore, nano-CT scans from this study facilitate a more detailed comparison of its three-dimensional morphology and internal structure with other fossil and extant members of the genus.

MATERIALS AND METHODS

The fossil, embedded in a concretion, was found at a site near Brady, Washington, by Jim Goedert (Affiliate Researcher, Burke Museum, University of Washington) along the west side of a road cut 400 m north of a junction between log road #A2700 and the A Line d south of the Chehalis River between Montesano and Satsop, 5.5 km due south of the community of Brady, Grays Harbor County, Washington, USA (46.94186°N, 123.52004°W) (Fig. 1; Pl. 1, figs 1–9). It is archived at the Burke Museum of Natural History and Culture, at the University of Washington, Seattle, Washington.

The concretion is a dark grey, calcareous, silty, fine-grained sandstone and comes from a layer of poorly sorted conglomerates ca 15 cm thick containing the bivalve *Anadara devincta* and shark teeth. Starting with Etherington (1931), many authors have speculated that the rocks there correspond to the Astoria Formation in Oregon, due to their similar sedimentology, foraminiferal and molluscan assemblages (Snavely et al. 1958, Moore 1963, Fowler 1965, Rau 1967). The Astoria Formation has its type area to the south in Astoria, Oregon, and is traced through better-known localities in Lincoln and Tillamook Counties in Oregon (Moore 1963) but extends from Montesano, Washington (Etherington 1931), to just south of Cape Blanco, Oregon (Durham 1953, Moore 1963). Because the Astoria Formation cannot be traced continuously from its type area in Astoria, Oregon, into this part of Washington, these rocks have been tentatively referred to as the "Astoria (?) Formation" in the literature

Fig. 1. Map of *J. bergomensis* localities based on van der Ham (2015), using azimuthal projection from GISGeography (https://gisgeography.com/azimuthal-projection-orthographic-stereographic-gnomonic/). Circles represent previously known localities or groups of localities, and the square is the Brady, Washington, locality

(Moore 1963). The Grays Harbor County exposures are considered to be mid-Miocene based on foraminiferal studies (Etherington 1931) and molluscan studies (Moore 1963). Paleomagnetic data from the Astoria Formation of Oregon provide dates ranging from 20.7 to 15.1 Ma (Prothero et al. 2001) but diatom fossils from the Astoria (?) of Washington are thought to correlate with an age between 14.5 and 13 Ma (Barron 1981). To complicate the matter, the Cape Foulweather Basalt, overlying the Astoria Formation in Newport, Oregon, was correlated with the Ginkgo Basalt, both of which are Columbia River Flood Basalts, giving it an upper limit of 15.4 ± 0.3 Ma (Wells et al. 1989). However, because this flow does not extend up to the Brady locality it is possible that deposition occurred afterward. The Astoria Formation has been also correlated with the Clallam Formation (Arnold 1906) and Wahkiakum Formation (Weaver 1912) in Washington, with type localities to the north of the Brady locality. In Grays Harbor County, the Astoria (?) is positioned unconformably over the Lincoln Creek Formation of Late Eocene through Early Miocene age (Moore 1963, Beikman et al. 1967, Rau 1967) and below the Montesano Formation, considered to be from the early part of the Late Miocene (Weaver 1912, Moore 1963, Gower & Pease 1965, Rau 1967).

Invertebrate fossils preserved in silty sandstone from the Astoria Formation indicate a warm-temperate ocean in moderate to shallow depths (Moore 1963). Foraminiferal studies in Grays Harbor County by Rau (1967) confirm a near-shore neritic environment and also suggest a shallowing sequence.

The Brady specimen was initially cut with a thin diamond blade (Microslice II annular saw) into three wafers to reveal internal structure and was photographed. A subsequent nano-CT scan of the reassembled fossil nut was performed on a GE Phoenix V|tome|xm240 CT Scanner at the Nanoscale Research Center, University of Florida, Gainesville, Florida. We used a Tungsten reflection target, with a voltage of 210 kV and current of 210 µA, with 1550 images of a single specimen for voxel size of 30 µm. Datasets from nano-CT were analyzed with Avizo 9.0 Lite (FEI Visualization Science Group, Bordeaux, France) to provide volume renderings, isosurface renderings and virtual sections in transverse and longitudinal orientations. Virtual sections are available at www.morphosource.org (doi: 10.17602/M2/M63198). A supplemental video of the fossil nut's lacunae was made in VGStudio Max 3.1.1 (Volume Graphics, Heidelberg, Germany). The fossil was virtually sectioned transversely from apex to base and laterally in views parallel and perpendicular to the primary septum. Comparable nano-CT images were obtained for modern and other fossil butternuts housed at the Florida Museum of Natural History, University of Florida, Gainesville, Florida, with settings adjusted to lower voltages to accommodate unpermineralized specimens. These included extant material of *Juglans cinerea* (UF 327, Bloomington, Indiana, USA; UF 1957 Greene Co., Indiana), *J. mandshurica* (UF 325, Magarita, Iwate Pref., NE Honshu, Japan) and fossils including *J. lacunosa* Manchester (UF 18751-4788, Eastgate, Washington; UF 18752-4789, mouth of Jansen Creek, Washington) and *J. bergomensis* (UF 19366-4370, 4371, Tagebau Frechen, Germany).

SYSTEMATICS

Order FAGALES (Engl.)

Family JUGLANDACEAE DC. ex Perleb

Genus *Juglans* L.

Section *Cardiocaryon* Dode

Juglans bergomensis (Balsamo Crivelli) Massalongo

Pl. 1, figs 1–9

D e s c r i p t i o n. The unilocular nut is ca 2.2 cm tall (Pl. 1, fig. 2) and 1.6 by 1.8 cm in equatorial diameter. Perpendicular to the primary septum the nut is obovate and tapers towards the base (Pl. 1, fig. 2). Parallel to the primary septum the nut is also obovate (Pl. 1, fig. 3). This orientation also reveals an asymmetric base (Pl. 1, fig. 3). Eight primary ribs run along the exterior of the shell down to the base, giving rise to two to four secondary ribs, each forming a bladed to scabrate texture with large concavities (Pl. 1, fig. 1). The ribs are rounded and in places contain lacunae (Pl. 1, fig. 1). In cross section the nut is rectangular, measuring 1.8 cm perpendicular to the primary septum by 1.6 cm along the primary septum measuring from rib tip to rib tip (Pl. 1, fig. 1). Two placental strands run longitudinally through the primary septum between the pair of lacunae of the primary septum.

In transverse section near the apex, two rectangular lacunae (one and a half visible, two inferred from symmetry) are seen to be positioned on either side of the apical keel of the locule. The inner margin of the lacunae have three angular protrusions directed towards the center and surrounding the elliptical apical keel of the locule (Pl. 1, fig. 4). These two lacunae divide and connect at various vertical levels in the nut, forming a continuous, complex hollow network (see 3D view in supplemental material). It should be noted that there are only two true lacunae, one within each nutshell half (each with multiple lobes), so the multiple lacunae described elsewhere in the literature refer to the *apparent* number of lacunae intercepted in particular planes of section. Transverse sections closer to the equator show that
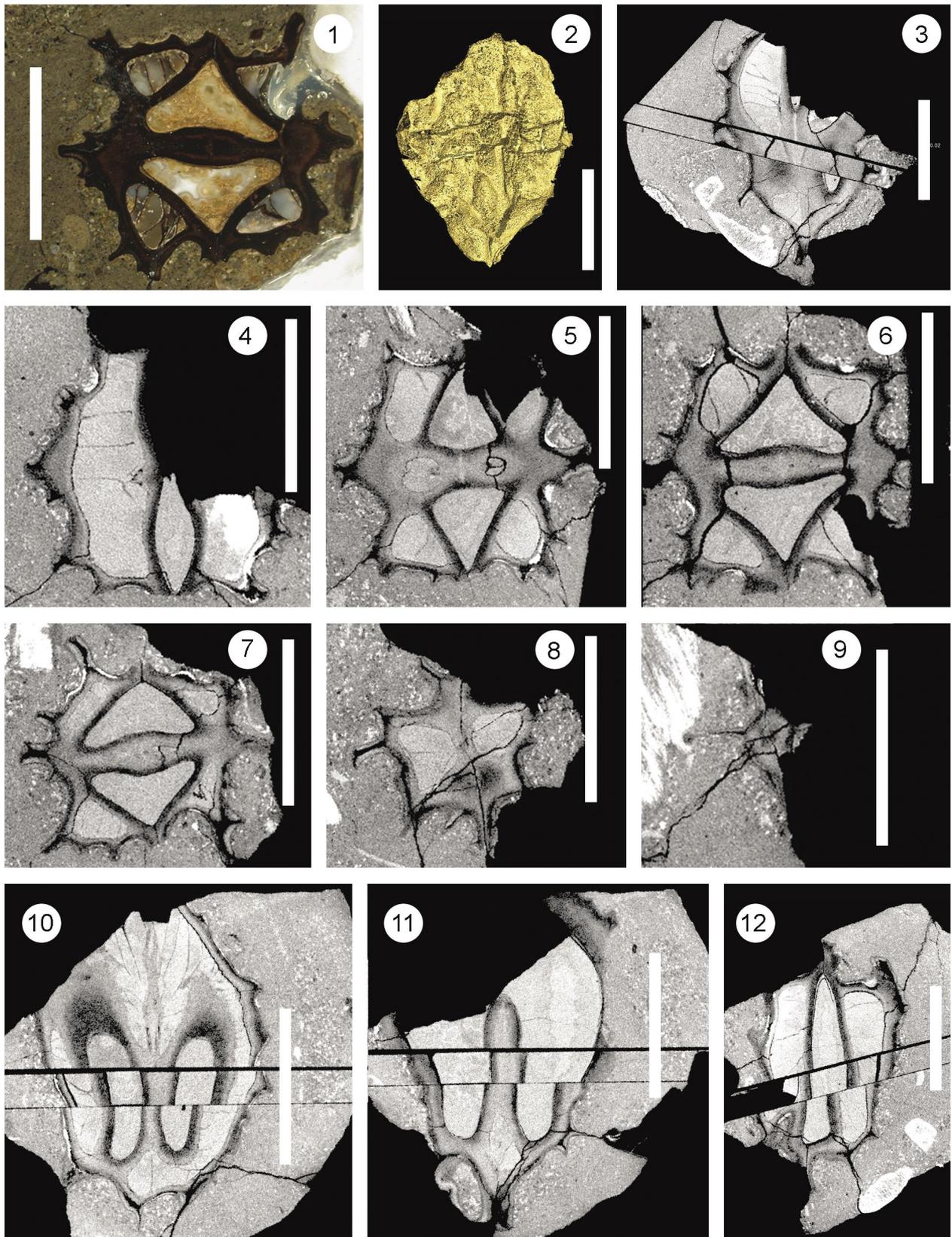
Plate 1. *Juglans bergomensis* (Balsalmo Crivelli) Massalongo UWBM 36885-B5585, from Brady, Washington; **1**. Slide of oblique cross section on slide looking from base to apex, showing two lobes of seed separated by primary septum and four lacunal lobes within the nutshell; **2**. Isosurface rendering of nut, digitally extracted from matrix; **3**. Median longitudinal section of nut parallel to primary septum; **4–9**. Successive digital transverse sections from near apex to near base, each separated by ca 3.7 mm. Cross sections starting near apex; **10**. Longitudinal section perpendicular to primary septum ca 8 mm in from periphery; 11. Median longitudinal section perpendicular to primary septum; **12**. Longitudinal section of nut parallel to primary septum ca 5 mm in from periphery. Scale bar = 1 cm

each lacuna splits into three lobes: a central one that is circular with a wedge missing, facing the axis in the primary septum; and two on either side that are triangular or rectangular, each with a flat or concave face adjacent to the seed lobes (Pl. 1, fig. 5). In total, there are four triangular outer lacunal lobes in the nutshell visible in all sections at and near the equator plus two smaller lacunal lobes within the primary septum visible in some equatorial sections (Pl. 1, figs 5–7). In sections approaching the base of the nut, the lacunal lobes of the primary septum disappear but four triangular marginal lacunae are still visible, one at each corner of the nut. The point opposite the shortest side of each triangular lacuna always points counterclockwise (Pl. 1, figs 5–7. Note that Pl. 1 fig. 1 is a section of the nut mounted on a slide and photographed upside down, therefore showing a clockwise pattern). Proceeding from apex to base, the two seed lobes become triangular in transverse section and the proximal edges of the seed lobes are nearly parallel but slightly concave (Pl. 1, figs 1, 5–7). The combined space of two lacunae is nearly equal to the volume of one seed lobe in cross section (Pl. 1, figs 1, 6, 7). Still closer to the base, the overall structure persists but two lacunal lobes reappear in the primary septum (Pl. 1, fig. 7). They merge with the two adjacent marginal lacunae, forming two lacunae in total (Pl. 1, fig. 8). Both have a "peak" where the lacuna in the primary septum was and two "wings" as a result of connection with the peripheral lacunae (Pl. 1, fig. 8). The lacunae become polygonal and extend beyond the seed lobes (Pl. 1, fig. 8). In successively lower transverse slices, eventually all that remains is the basal protuberance (Pl. 1, fig. 9).

In longitudinal section, perpendicular to the primary septum, the locule has an inverted, broad U-shape with rounded, blunt ends that flare slightly outwards (Pl. 1, figs 10, 11). Due to the rugose exterior, the thickness of the nutshell varies from 2 to 3 mm (Pl. 1, figs 1, 3–12). Lacunae are well seen at the top and bottom of the primary septum but are absent in the middle portion (Pl. 1, figs 1, 6). Lacunal lobes at the basal end are larger and elliptical in shape and connect peripherally with those higher in the nutshell (Pl. 1, figs 4, 8).

Looking longitudinally in the plane of the primary septum, the base of the nut appears to be asymmetrical (Pl. 1, figs 3, 12). The

seed lobe (tall and elliptical) and two bordering lacunae (tall and rectangular) can be seen (Pl. 1, fig. 12). The seed lobe bulges outwards in the center, with the lacunae fitting around them (Pl. 1, fig. 12).

DISCUSSION

SYSTEMATIC PLACEMENT

This specimen is a unilocular nut that separates along a plane perpendicular to its primary septum, a feature consistent with all nuts of Juglandaceae (Manning 1978, Manchester 1987). Additionally, the subglobose rather than flattened aspect of the nut supports its placement in the subfamily Juglandoideae Manning (Manning 1978). The rugose, ribbed shell and the appearance of four lacunae inside the wall, as seen in equatorial cross section of the nut, places it within the tribe Juglandeae Nakai (Manning 1978). The absence of fruit wings and of ribbing on the seed lobes, as well as the rough exterior and axial placental strands in the primary septum all help to identify the fossil as a member of the genus *Juglans* L. and distinguish it from the somewhat similar nuts of *Carya* (see discussions of Scott 1954, Manchester 1987).

The elongated shape of the nut, the prominent blade-like ridges, the presence of a primary septum that is both thick and lacunose, and the lack of a well-developed secondary septum justify its placement in section *Cardiocaryon* (Manchester 1987). *Juglans* has two other sections: *Rhysocaryon* and *Juglans*. Members of sect. *Rhysocaryon* are more globose and have a thick secondary septum that, along with the primary septum, results in a four-lobed seed, contrasting with the two-lobed seeds of sect. *Cardiocaryon* (Manchester 1987). Likewise, members of sect. *Juglans* are globose to ellipsoid, have a smooth to rugose shell, and thin, non-lacunose primary and secondary septa that, as in sect. *Rhysocaryon*, divide the base of the seed into four lobes (Manchester 1987).

The Brady butternut matches descriptions of *Juglans bergomensis* in external features including shape (obovate), base (pointed) and texture (bladed and scabrate) differing from the smooth-walled nuts of the fossil *J. lacunosa* (Pl. 2, figs 1–3). In terms of size, the Brady nut falls within the known range of *J. bergomensis*
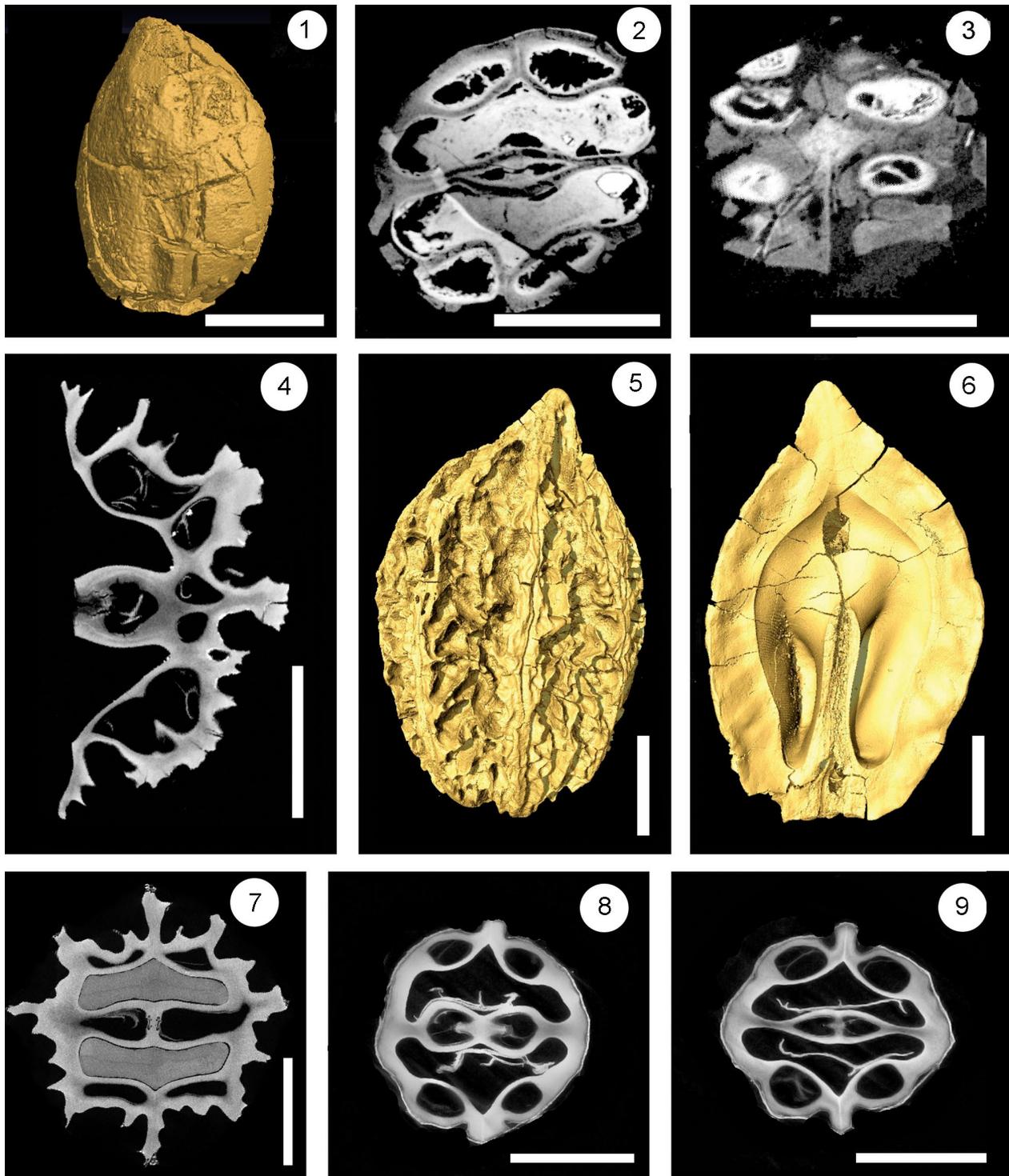
Plate 2. 1–3. *Juglans lacunosa* Manchester UF 18751-4788, from Early Oligocene Eastgate locality, Washington; **1**. Isosurface rendering of nut, digitally extracted from matrix; **2**. Section showing smooth wall of nut, two lobes of seed separated by primary septum, and large lacunae within nutshell; **3**. Cross section near base showing secondary septum and four seed lobes; **4–6**. *Juglans bergomensis* (Balsalmo Crivelli) Massalongo UF 19366-4791, Pliocene of Frechen, Germany; **4**. Cross section showing scabrate surface and lacunae within nutshell; **5**. External view showing sculptured surface; isosurface rendering; **6**. Same specimen rotated 180 degrees, opened along plane of dehiscence, showing smooth outline of locule and medial primary septum; isosurface rendering; 7. Extant *Juglans cinerea* L. UF 1957 Greene Co., Indiana. Cross section showing rugose surface with eight primary ribs, four outer lacunal lobes, two lacunal lobes in primary septum and two seed lobes with three protrusions each along primary septum; **8**, **9**. *Juglans mandschurica* Maxim. UF 0325 from Araya, Iwate, Japan; **8**. Cross section showing smooth outer surface, with three lobes along the locule parallel to the primary septum (two concave surfaces per lobe along primary septum); **9**. Cross section below the level of Figure 8, showing smooth surface and smooth, concave, triangular locule lobes. Scale bar = 1 cm. Supplementary Material 3D rendering of both lacunae from the Brady fossil nut, from nano-CT scan done in VGStudio Max 3.1.1. – http://bomax.botany.pl/filmy/Acta_Palaeobot_58_2_Smith&Manchester_Suppl_Juglans.wmv

and is one of the two smallest nuts found (Hills et al. 1974, van der Ham 2015). Some features of this fossil may have been eroded in transport or in situ (ribbing and apex), giving a more rounded appearance to some of the ridges as compared with fossils from other sites (e.g. Pl. 2, figs 4, 5). Internally, the seed has an inverse U shape, as in other sect. *Cardiocaryon* nuts (Pl. 2, fig. 6), and the nut has a rectangular cross section which has not been described previously from fossil material attributed to *J. bergomensis* but can be seen in both *J. cinerea* (Pl. 2, fig. 7) and the horticultural variety *J. ailantifolia* var. *cordiformis* (Manchester 1987). CT scans of complete *J. bergomensis* nuts from other localities are needed to better document variation of the shape of locules and lacunal lobes at different vertical levels of sectioning.

In his description of extant *Juglans cinerea*, van der Ham (2015) wrote that "All lacunae can be easily observed in a cross-section of the nut," and that the lacunae in the primary septum connect with those in the apex and base of the nut. Our observations of the butternuts with CT scans confirm that the lacunae in the apex, primary septum and base are interconnected. Each nut has two lacunae, one for each side of the shell. However, a single cross section does not reveal the relationship of the lacunae, nor show the depth of the lacunae or the variability of the number of lacunal lobes between successive cross sections. This is demonstrated, for example, in the Brady specimen of *J. bergomensis*, which at middle levels of transverse sections do not show lacunae in the primary septum. Some specimens that Hills et al. (1974) treated as *J. eocinerea* and *J. tephrodes* may hint at the possibility that other butternuts presently considered to be *J. bergomensis* also contain non-continuous lacunae in the primary septum, based on longitudinal views perpendicular to the primary septum, though these observations from the publication figures may be an artifact of the field of view or the orientation of the plane in which the nuts were physically sectioned.

The Brady butternut has a pair of locule lobes that are each triangular in cross section, with a flat side along the primary septum, in contrast to other specimens which have a concave side along the plane of the primary septum; this is best documented in the segmentation movie (supplement). However, this character has not received any attention in the literature. The triangular shape of the locule lobe viewed in cross section is seen in other fossil butternuts from North America such as in *J. lacunosa* (Pl. 2, figs 2, 3), *Juglans eocinerea* Hills et al. (now in *J. bergomensis*) from Banks Island, and some but not all transverse sections of the Asian butternut *J. mandshurica* (Pl. 2, figs 8, 9). In contrast to the triangular shape, the European fossil *J. bergomensis* and the extant *J. cinerea* from eastern North America have locules that are trident-shaped in cross section, with a portion in the center of the lobe along the plane of the primary septum pointing inward. Once again, the taxonomic utility of this character is poorly known; possibly it varies intraspecifically.

The *J. bergomensis* specimen we investigated from Tagebau Frechen, Germany (Pl. 2 figs 4–6), and those treated by Van der Ham (2015) are more strongly sculptured than the Brady nut, closely resembling nuts of modern *J. cinerea* (Pl. 2, fig. 7). Additionally, the lacunae in the primary septum are non-continuous and those adjacent to the outer margin of the nut are more dissected. The locule lobes also flare inward. However, both are scabrate and have only a primary septum.

The large population of fossil butternuts from Banks Island described as *J. eocinerea* by Hills et al. (1974) includes nuts ranging in size from 2.48 to 6.16 cm tall and 1.42 to 2.96 cm wide. This kind of large size variability was later reaffirmed by van der Ham (2015), who also showed that lacuna size and the presence and number of secondary marginal lacunae can vary greatly in both fossil and modern *Cardiocaryon* species. These traits not only vary between nuts from different trees but between nuts from the same tree (van der Ham 2015). Accordingly, he synonymized all of the fossil species except for *J. lacunosa* (Pl. 2, figs 1–3), which was distinguished by its smooth surface (van der Ham 2015).

Hills et al. (1974) and subsequent authors noted the high variability of features in butternuts and attributed this to low selection pressure. Some of this variation could be due to hybridization. Extant *J. cinerea* is known to hybridize with Asian butternuts (*J. ailantifolia* and *J. mandshurica*). Intersectional hybrids also occur. When crossed, black walnuts such as *Juglans microcarpa* Berland. (sect. *Rhysocaryon*) and the Persian walnut *Juglans regia* L. (sect. *Juglans*) and different cultivars

of *J. ailantifolia* can have nut morphological features different from those of pure bred or wild individuals (Funk 1979, McDaniel 1979, Manchester 1987, Ross-Davis et al. 2008, Farlee et al. 2010, Rink n.d.). The amount of natural morphological variation within pure populations has rarely, if ever, been documented. A combination of low selection pressure and high hybridization potential may contribute to this variation.

Juglans lacunosa is known from late Eocene and early Oligocene sediments of Alaska and Washington (also marine but from an older formation) and the middle Miocene of Clarkia, Idaho (Manchester 1987). The original investigation was based on physical sections and naturally fractured specimens. In our examination of the CT scans of *J. lacunosa* (e.g. Pl. 2, figs 1–3) we also found evidence of a secondary septum, with the seed being split into four lobes at the base (Pl. 2, fig. 3). Extant butternuts are characterized by seeds that are only two-lobed at the base (to the extent that they have been surveyed). This raises the question of whether *J. lacunosa* should remain in *Cardiocaryon* or be placed in another section of *Juglans* and/or whether this is a pleisiomorphic character retained in the Paleogene but lost in extant members of the clade.

Because the Brady nut shares most of its features with *J. bergomensis* and the continuity of lacunae within the primary septum has not been examined in detail for most other occurrences, we consider that this nut is assignable to *J. bergomensis*.

BIOGEOGRAPHY

Juglans bergomensis is also known from Europe and Asia (Russia and Japan) (reviewed as *J. tephrodes* Unger in Manchester 1987; van der Ham 2015). Given that no modern species in Juglandaceae has such a broad geographic range, it is possible that *J. bergomensis* nuts form a species complex. It is suspected that some tree species such as *Ailanthus confucii* may have had a broader Northern Hemisphere distribution during parts of the Cenozoic than their modern relatives do today (Corbett & Manchester 2004). *Metasequoia occidentalis* lived from Arctic Canada through the Caucasus region (LePage et al. 2005). Perhaps a boreal distribution was more common during the Oligocene through Miocene, before major vicariance and climate change events leading

to extinction and speciation. The section is relatively young and low selection pressure hypothesized by Hills et al. (1974) may also account for the broad geographic range. As we do not know the details of the other organs of the plant that bore *J. bergomensis* nuts, it is not possible to discriminate fossil species from each other with the resolution we expect when determining modern species.

The new occurrence documented here, along with the Banks Island material, might indicate a North American origin for the species. Spread must have occurred quickly because middle Miocene *J. bergomensis* fossils are known from Germany (Czaja 2003, van der Ham 2015). The timing of the Bering Land Bridge makes it a more likely route than the Atlantic land bridge (see van der Ham 2015). Radiation to modern Asian species may have occurred during Pleistocene glacial and interglacial transitions.

Although *Juglans* sect. *Rhysocaryon* occurs in western North America today (e.g. Arizona, California), sect. *Cardiocaryon* is restricted to eastern North America and Eastern Asia. However, this is now the third fossil *Cardiocaryon* occurrence from western North America where no extant species exist today. The others are *J. lacunosa* from Alaska, Washington and Idaho and what was described as *J. eocinerea* (now *J. bergomensis*) from Banks Island, Canada (Hills et al. 1974). The Brady specimen is the westernmost and southernmost example of *J. bergomensis* in North America. Its occurrence in shallow marine sediments leads to some uncertainty about whether the nut was transported by current or was deposited from a tree growing near the coast of modern-day Washington. Local and global climatic changes during the Miocene probably resulted in its extinction.

PALEOECOLOGICAL IMPLICATIONS

The southwestern Washington occurrence of *Juglans bergomensis* nut is one of the few formally recognized plant species records from sediments affiliated with the Astoria Formation. Some plant fossil remains are known from the outcrops of the Astoria Formation in Oregon. Charred petrified wood (often preserved as *Toredo* wood) is the most common, although some leaves have also been found (Moore 1963). Miller (1992) described a permineralized pine cone from the Astoria Formation, naming it *Pinus berglundii* Miller. Other specimens of

P. berglundii were subsequently found by the first author and by amateur collectors. It is uncertain if these plants were all from the local coastline or rather drifted in from other directions. Paleopalynological studies may help clarify this. If in fact these plants are local, they would help reconstruct the forest ecosystem. If transported, the nut would attest to the direction of transport and to taphonomic rigidity.

CONCLUSIONS

This nut represents the southernmost and westernmost occurrence of *Juglans bergomensis* in North America and augments the occurrences of this species known from Europe and Asia. Such a large intercontinental geographical range attributed to a single species is striking. It seems unlikely that all of the fossils attributed to *J. bergomensis* are really a single species; they might represent a species complex. Other morphological characters that might allow finer species distinctions, such as foliar and floral features, remain unknown for these fossils. Unless full plant reconstructions can be done we are left to treat the *J. bergomensis* complex as one fossil species. CT scanning has proved useful as it is less invasive and enables observation of features at multiple levels of the fossil that traditional methods would not reveal.

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