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MORPHOLOGY AND AFFINITIES OF *CARYA COSTATA* HICKORY NUTS FROM THE OLIGOCENE OF BOHEMIA

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Abstract: We reinvestigated type material and subsequently collected fossil nuts of *Carya costata* (C.Presl ex Unger) Unger based on type material from the Oligocene of western Bohemia. These specimens are older than most occurrences of *C. ventricosa* (C.Presl ex Brongn.) Unger which has its type locality in the Miocene of Salzhausen, Germany. Although preserved only as molds and casts in tuffaceous volcanoclastic siltstone, micro-CT scanning indicates that the morphology of *C. costata* is nearly identical to that of *C. ventricosa*. The preservation of these nuts as 3-dimensional molds retains evidence of gnawing indicating that, as today, hickory nuts were an important food source for mammals and/or birds of the Oligocene.

Key words: Hickory nuts, Juglandaceae, micro-CT scanning, molds, casts, *Alnus*, *Symplocos*

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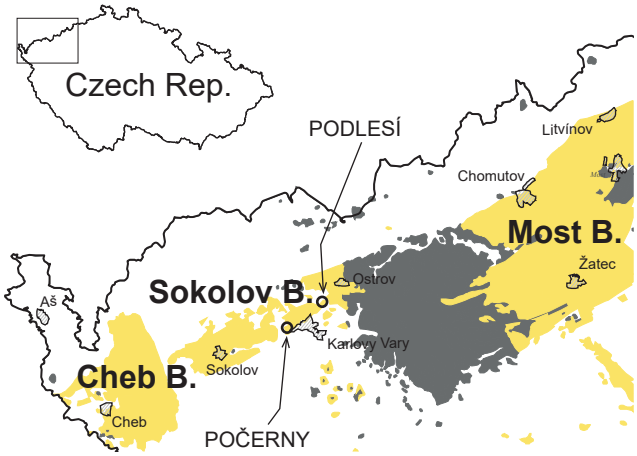
Introduction

Although hickory nuts are no longer native to Europe, the genus *Carya* has a rich European fossil record, as reviewed by Mai (1981). The development of new technologies, including micro-CT scanning, allows us to obtain more detailed morphological and anatomical data from the fossil specimens, and of the comparative extant material, providing new insights on the phylogenetic relationships. We recently reevaluated the iconic European hickory, *Carya ventricosa* (C.Presl ex Brongn.) Unger, based on type material from the Miocene of Salzhausen near Nidda, Wetterau, Germany and supported Mai's view of its close relationship to the extant tropical Asian species, *C. poilanei* (A.Chev.) J.-F.Leroy, although clearly representing an extinct species (Deng et al. 2024).

Here we revisit the species *Carya costata* (C.Presl ex Unger) Unger based on older material (Oligocene) from the volcanic complex above the coal-seam Josef of the Sokolov Basin, North Bohemia (Text-fig. 1). Unlike the *C. ventricosa* type material, which was lignitized preserving original anatomy, the type material of *C. costata* presents more challenges because it is preserved only as molds and casts in coarse sediment, precluding histological analyses. Nevertheless, the internal and external surface features of the nuts are clearly preserved, and these characters allow for confident taxonomic assessment of extant and fossil nuts within the Juglandaceae (Leroy 1955, Mai 1981, Manchester 1987, Deng et al. 2024).

The sediment containing the *Carya costata* nuts studied here also contains molds and casts of other fruits and seeds in abundance, including endocarps of *Mastixia venosa* (C.Presl) Holý, cones of *Pinus* and *Sequoia*, infructescences of *Alnus* (Text-fig. 2b–g), and fruits of *Fagus saxonica* Kvaček et H.Walther, *Liquidambar* L., and *Symplocos* Jacq. (Holý 1984). The *Symplocos* endocarps (e.g., Text-fig. 2h–m) show varied morphology and are in need of more detailed study in comparison with the Neogene



Text-fig. 1. Sketch map indicating the two sites providing the specimens treated herein, Počerny and Sadov-Podlesí. Extent of Cenozoic basins in yellow, volcanic centres in grey.

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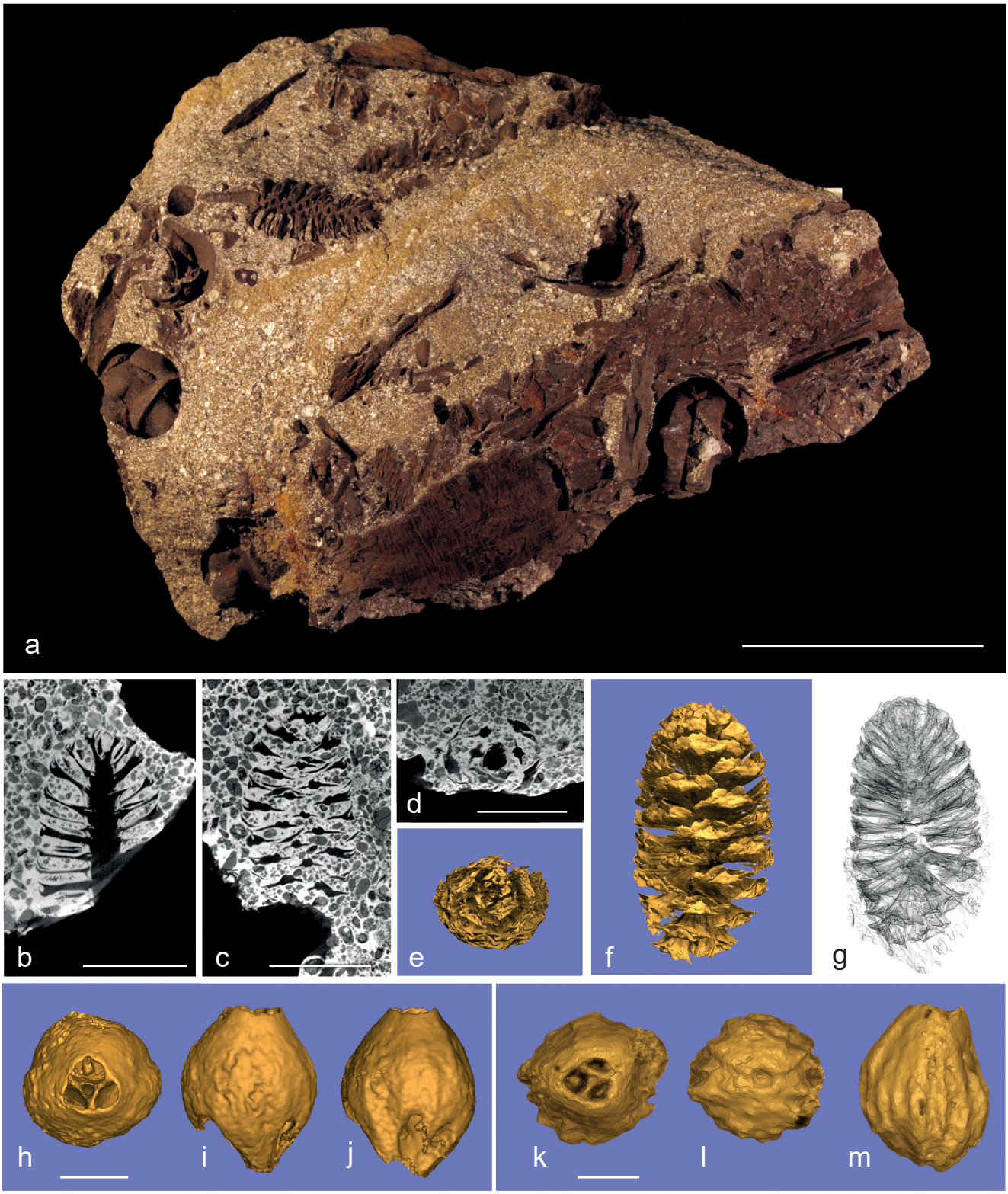
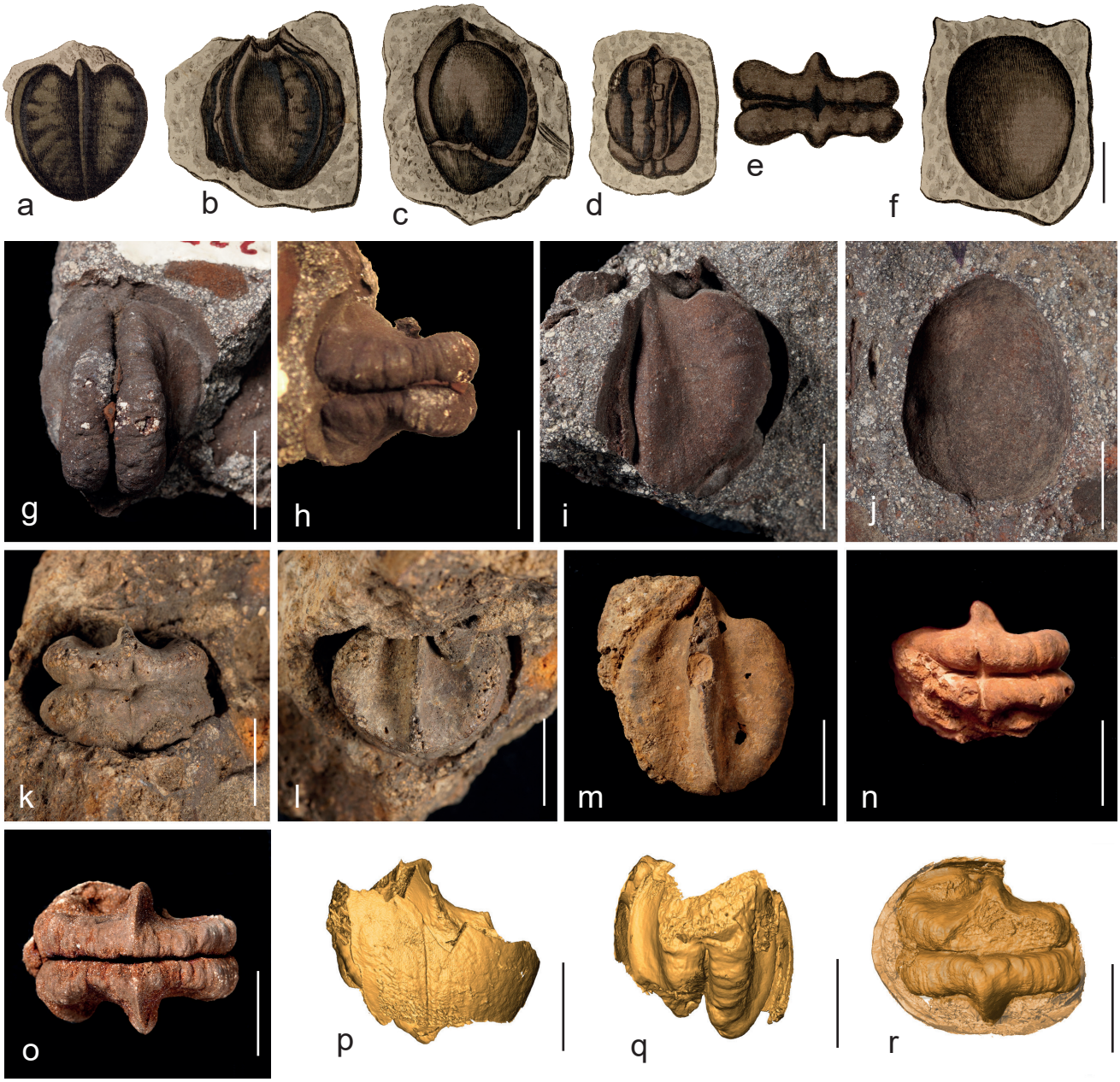


Text-fig. 2. Fossils from Sadov-Podlesí, showing the preservation of fruits and seeds as molds and casts within tuffaceous volcanoclastic sediment. a: Block of sediment showing at least three *Carya costata* nuts, and an *Alnus* infructescence. Reflected light NM-G6265. b–m: images from micro-CT scanning. b: *Alnus* in virtual longitudinal section, NM-G6265e. c–g: *Alnus* in virtual longitudinal (b, c) and transverse (d) sections, and with volume rendering in apical (e), and lateral (f, g) views, with translucency in (g), NM-G6289b. h–j: *Symplocos casparyi* R.Ludw., relatively smooth trilocular endocarp showing apical pore, and predation damage at base NM-G6033d, k–m: *Symplocos casparyi;* longitudinally ribbed trilocular endocarp, NM-G6033f. Scale bar = 5 cm (a), 1 cm (b–d), 2 mm (h–m).

species treated by Mai and Martinetto (2006). These fossils have been taken to indicate that Oligocene vegetation in the vicinity of Karlovy Vary was subtropical (Kvaček and Theodoridis 2007).

Materials and methods

The specimens of *Carya costata* that we studied are from two sites in the Sokolov Basin of northern Bohemia (Text-fig. 1). As summarized by Mai (1981), the type material

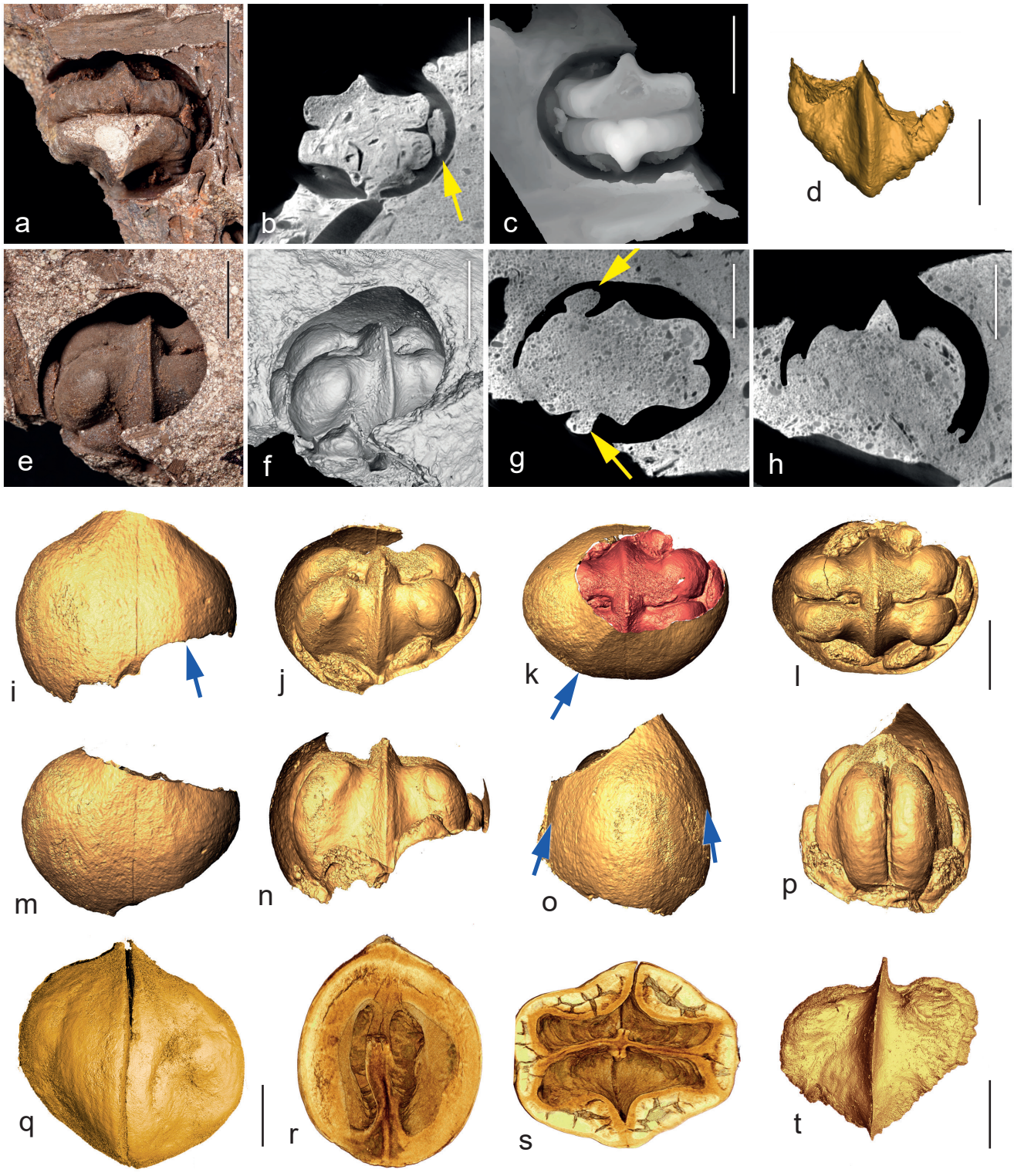


Text-fig. 3. ***Carya costata*** **(C.Presl ex Unger) Unger. a–f: Original illustrations of syntypes (Sternberg 1838: pl. 58, figs 7–12). g–o: Reflected light images. g, h: Locule cast in lateral and basal views, NM-E193, Počerny (lectotype of Mai 1981: 356, pl. 26, fig. 7). i: Locule cast and portion of surrounding nut mold, NM-E194 (same as (b), above), Počerny. j: Nut mold showing smooth, unribbed external surface, NM-E195 (same as (f), above), Počerny. k, l: Locule cast and nut mold in basal and oblique-lateral views. from the Sternberg collection, NM-G11944, Počerny. m, n: Locule cast in lateral and basal views, NM-G7151, Počerny. o: Locule cast viewed from base, NM-G7150, Počerny. p–r: Nut surface and locule cast surface images from micro-CT scanning, NM-G6265c, Sadov-Podlesí. p: Smooth nutshell surface with median vertical germination groove and predation damage at apex and base. q: Virtual locule cast in lateral view; compare with Text-fig. 2g. r: Virtual locule cast and surrounding nutshell viewed from base; primary septum oriented horizontally. Scale bars = 1 cm.**

illustrated by Sternberg (1838: 297, pl. 58, figs 7–13) came from the village of Počerny about 4 km west of Karlovy Vary (W. Bohemia). A second site, collected more recently and preliminarily studied by Holý (1984), was a kaolin quarry in Sadov-Podlesí about 4 km north of Karlovy Vary (Text-fig. 1). Nomenclatural history was clarified in part by Kvaček et al. (2021). Both localities show very similar types of volcanoclastic sediment, which are part of the Oligocene volcanic complex above the coal seam Josef of the Sokolov Basin.

The specimens are preserved as casts and molds in volcanoclastic tuff (Text-fig. 2), so the original nut morphology can be reconstructed by latex casts as was done for some fruits of other taxa from Sadov-Podlesí by Holý (1984). We prepared virtual reconstructions and digital sections from x-ray data sets obtained by micro-CT scanning of the specimens. Optical macrophotography was done using a Canon Rebel XSi dslr camera fitted with a DFS 60 mm macro lens.

Micro-CT scanning was performed on a Phoenix V|tome|xm 240 CT scanner at the Nanoscale Research Center,



Text-fig. 4. Nuts of *Carya costata* (a–p) and *C. ventricosa* lectotype (q–t). a–d: Additional images of the specimen in Text-fig. 3j, k, p, r, NM-G6265c, Sadov-Podlesí. a: Locule cast and surrounding nut mold, transverse view from base, reflected light. b: Virtual transverse section showing sediment-filled locule, black empty space of the nutshell, and surrounding sediment. Note nutshell lacuna filled with sediment (arrow). c: Depth map image of same nut viewed from base. d: Surface rendering, base of the locule cast from same specimen, showing triangular shape similar to that of *C. ventricosa*. e–p: NM-G6265a, Sadov-Podlesí. e: Oblique view showing mold of nut with locule cast inside, reflected light. f: Similar view by surface rendering from micro-CT scanning. g: Virtual equatorial section showing thin nutshell bearing lacunae, two of which are preserved (arrows). h: Longitudinal section showing damage to the basal portion of the nutshell and septum. i: Surface rendering of smooth nutshell. j: Oblique apical view of the locule cast and nutshell surface. k: Apical view of locule cast (pink), and surrounding nutshell. l: Locule cast, apical view with obscuring nutshell surface digitally removed. m: Nut rotated 180° from the view in (i). n: Lateral view of locule cast with primary septum parallel to this page. o: Nutshell in lateral view, rotated 90° from (m). p: Same view with the nutshell digitally removed to show locule cast lobes separated by groove of the primary septum. q–t: Lectotype of *Carya ventricosa*, NM-E182a, Miocene of Salzhausen near Nidda, Wetterau, Germany. q: Lateral view. r: Virtually cleaved along the natural plane of germinal separation. s: Transverse section of volume rendering. t: Virtual locule cast with triangular base similar to that in (d). Scale bars = 1 cm.

University of Florida, Gainesville. We used a Tungsten reflection target with a voltage of 210 kV, a current of 210 µA, and a voxel size of 30 µm. Resulting tiff stacks were analyzed with VG Studiomax vers. 3.1 (VolumeGraphics, Heidelberg, Germany) to generate digital slices and with Amira 6.5.0 (FEI Visualization SciencesGroup, Bordeaux, France) to produce surface and volume renderings. Amira was used to generate .ply files that were manipulated and imaged with Meshlab 2022.02 (Cignoni et al. 2008).

Systematic palaeobotany

***Carya costata* (C.Presl ex Unger) Unger, 1850**
Text-figs 2a, 3, 4a–p, 5

1838 *Juglandites costatus* C.Presl in Sternberg, vol. II, 7/8, p. 207, pl. 58, figs 7–13, nom. inval. (ICN Art. 35.1)
1845 *Juglandites costatus* C.Presl ex Unger, p. 241.
1850 *Juglans costata* (C.Presl ex Unger) Unger, p. 468.
1860 *Carya costata* (C.Presl ex Unger) Unger, p. 41.

Lectotype. NM-E193 (Sternberg 1838: pl. 58, fig. 10), selected by Mai (1981); for more details see Art. 40.3. of the Shenzhen Code (Turland et al. 2018).

Repository. Palaeobotanical Collection, National Museum, Prague, the Czech Republic.

Type locality. Počerny near Karlovy Vary, the Czech Republic (non Staré Sedlo "Altsattel"; for more details see Kvaček et al. 2021).

Type horizon. Volcanic complex above the coal seam Josef of the Sokolov Basin; Oligocene.

Nomenclatural history. This species was first described and figured as *Juglandites costatus* by C. Presl in Sternberg (1838: 207, pl. 58, figs 7–13); however the name was invalid according to Article 35.1 of ICN as noted by Kvaček et al. (2021), and subsequently validated with its publication as *Juglandites costatus* C.Presl by Unger (1845). Subsequently, Unger (1850) transferred it to the extant genus *Juglans*. A decade later, Unger (1860) transferred the species to *Carya*: as *Carya costata* (C.Presl) Unger (Unger 1860: 41, pl. 18, figs 13–17, pl. 19, fig. 16). From the original syntypes illustrated by Sternberg (1838), Mai (1981) selected NM-E173 as lectotype.

Emended diagnosis. (Mai 1981, translated, with modifications in **bold**). Nut **25–35** mm long and **20–30** mm wide, suborbicular, apical tip missing, but somewhat pointed, base rounded with a rhombic attachment point; **surface smooth with faint longitudinal grooves and four subtle longitudinal corners**. Nutshell 2.6–3 mm thick on average (inner anatomy unknown); with small, slightly high secondary septum, which extends perpendicular to and along the primary septum to, at most, half the compartment length, **but which does not extend outward to partition the locule**; **locule cast** compressed, smooth to transversely wrinkled, **2**- to 4-lobed at the base, **primary** lobes **both** of equal length**, rounded to triangular at base**, with a crest-like ridge on the dorsal side, 19–33 mm long, 17–22 mm wide, reaching up to 18 mm deep into each shell.

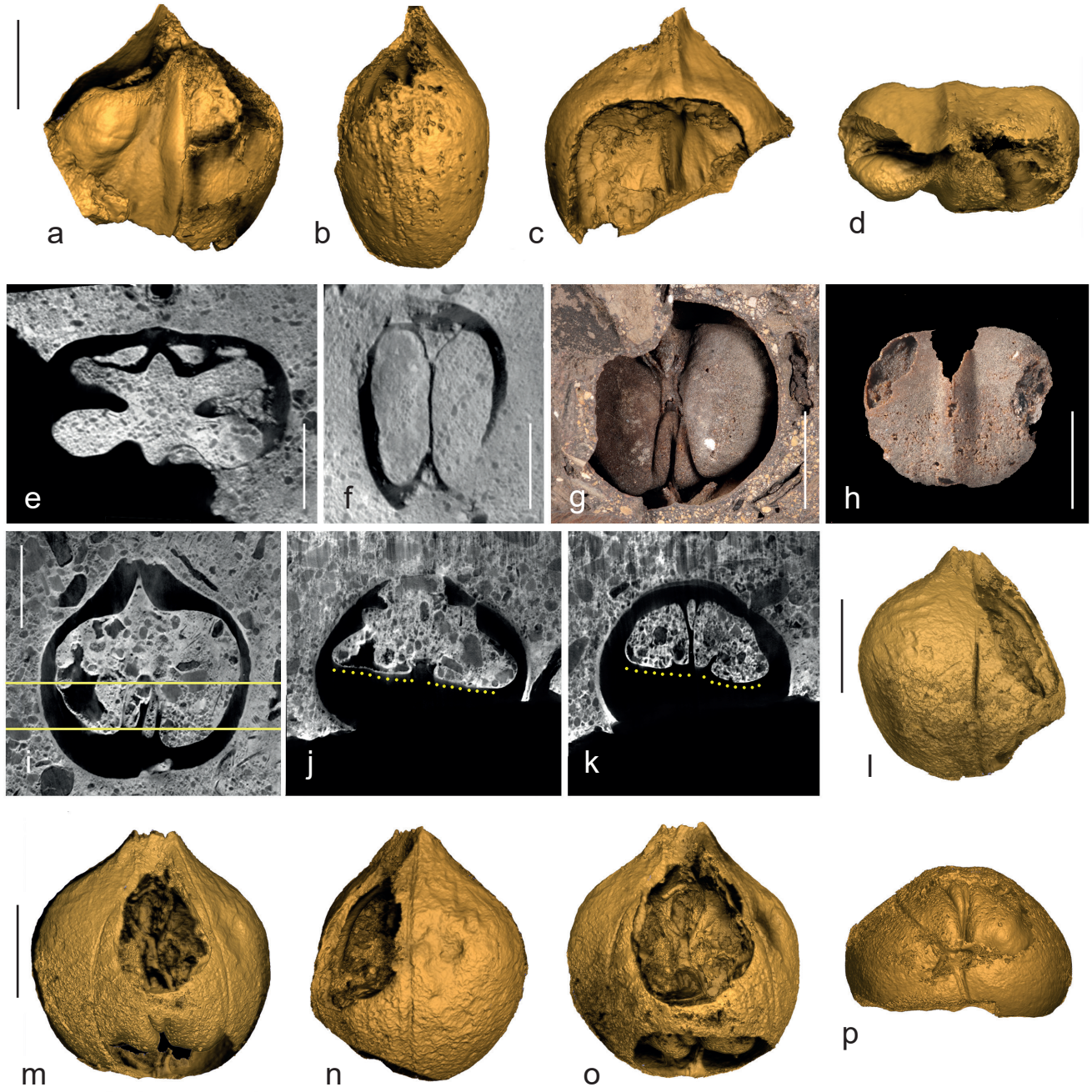
Description. The nuts are subovoid, wider in plane of the primary septum than in the plane of germinal separation. The surface is smooth to finely longitudinally grooved, with four subtle longitudinal corners (indicating margins of the shed husk valves) (arrows in Text-fig. 4i, k, o). The locule shows a prominent longitudinal cleft corresponding to the primary septum; however, the secondary septum is weak to absent, usually expressed only as a perpendicular flange on the primary septum. Lacunae within the nutshell are apparent in some specimens, where sediment has infilled (Text-fig. 4b, g, e). There is one pair of shallow inner ribs on the nutshell straddling the plane of germinal splitting. The base of the locule, as viewed in the plane of germinal separation, is rounded to cuneiform (Text-fig. 4a, i, l, m).

Discussion. Mai (1981) considered that *Carya costata* remains an unclear species, rendered heterogeneous due to later additions by other authors. He summarized other published reports of nuts attributed to *C. costata* but questioned their identification due to uncertain internal morphology. Here we focus only on material from the type area of Karlovy Vary (W. Bohemia) in anticipation that it will be helpful in re-evaluating specimens from other sites.

Our emended diagnosis differs from that of Mai (1981) mainly in the description of the base of the locule. Mai indicated that the locule cavity is basally 4-lobed, but in most of the type material it has only two lobes, separated by the primary septum; each of those lobes is rounded to triangular with no emargination of the kind seen in other species of *Carya* due to their prominent secondary septum (Text-figs 3a, l, m, d, 4h). As he described, there can indeed be a secondary septum that runs lengthwise as a flange along both sides of the primary septum, but it does not extend across the locule to form a basal partition of the locule. The secondary septum is evidenced by a groove on the ventral side of the locule casts as viewed from the basal side (e.g., Text-fig. 3n) or ventral side (e.g., Text-fig. 5g). This is much like the weak secondary septum observed in fossils of *Carya ventricosa* (Text-fig. 4s).

Nuts of *Carya costata* closely resemble those of *C. ventricosa* in the shallow inner ribs of the nutshell, weak development of secondary septum, and cuneiform base of the locule cast. The morphology of the locules is nearly identical (compare Text-fig. 4d, with Text-fig. 4t, and Text-figs 4l, 5e, with Text-fig. 4s). A distinctive feature of these nuts is that, rather than being radially symmetrical like nuts of most extant and fossil species of *Carya*, they are wider in plane of the primary septum than in the plane of germinal separation, as can be seen in apical (Text-figs 4k, l, 5d) and basal (Text-figs 3k, n, o, r, 4a, c) views as well as transverse sections (Text-figs 4g, 5e). The same feature is also apparent in nuts of *Carya ventricosa*, although it was not emphasized in earlier treatments (Text-fig. 4j).

Based on the observed similarities, it seems likely that *Carya costata* and *C. ventricosa* represent the same lineage, and perhaps the same biological species, differing mainly by the mode of preservation – lignitic in the case of *C. ventricosa*, but molds and casts in sediment in the case of *C. costata*. The older age inferred for *C. costata* (Oligocene) may indicate that the *C. ventricosa* lineage was already established in the Paleogene. We do not wish to synonymize these species because of the difference in preservational state, but it is worth noting that the name



Text-fig. 5. ***Carya costata*** **nuts from from Sadov-Podlesí. a–f: NM-G6265d, nut surface rendering in lateral (a–c) and apical (d) views, and in transverse (e) and longitudinal (f) virtual section. g–p: NM-G6033. g: Locule cast within mold of nutshell, reflected light. Casts of placentary vascular strands diverge from the base of nut. h: External view of the adjacent locule cast fragment that has broken and fallen out from the locule cast in (a). i: Virtual longitudinal section in same orientation as (g), with horizontal lines indicating the positions of sections (j, k). j, k: Digital transverse sections. The locule cast fragment of (l) had fallen out and is not included, but the other half is intact. Dotted line represents position of the primary septum. l–p: surface rendering of the nut rotated through various orientations, including lateral (l–o) and basal (p) views, with obvious gnawed holes. Scale bars = 1 cm. Bar in (a) applies to (a–d), bar in (i) applies to (i–k), bar in (m) applies to (m–p).**

Carya ventricosa would take priority over *C. costata*, because the former epithet was validated when published as *Juglans ventricosa* by Brongniart (1828: 144) whereas the latter was validated later (Unger 1845).

Deng et al. (2024) surveyed the morphology of many extant species of *Carya* by micro-CT scanning and recognized features that can distinguish extant North American species from the Asian ones. All North American species, and some of the Asian species, have strong inner longitudinal ribs in the locule on either side of the germination splitting plane; however, *C. poilanei* of Vietnam and Yunnan, China, as earlier observed by Mai (1981), has only shallow inner ribs, as is also reflected in the locule cast morphology. *Carya costata* also lacks prominent inner ribs. The *C. costata* specimens show some remnants of lacunae within the shallow ribs of the nutshell, preserved as casts (arrows in figs 3b, g, 4e).

Although not obvious from casual examination of the fossil specimens, many of the specimens we studied were

damaged by gnawing (Text-figs 3p, 4d, g-i, m, n, 5c, d, l-o), and the preservation of inner details is in part due to the fact that sediment could enter the nutshell through openings made by chewing animals prior to deposition to form casts of the locule and lacunae. Although such damage could possibly have been caused by birds or perhaps insects, the perpendicular grooves on the edges of the holes suggest the markings of rodent incisors. This is taken to indicate that hickory nuts were an important as a food source for these animals in the Oligocene.

Acknowledgements

Min Deng helped greatly in the analyses of nuts of extant and other fossil *Carya* species. Costs of micro-CT scanning were covered in part by the Dilcher-Becker paleobotanical fund of the University of Florida Foundation. Zuzana Heřmanová served as editor, Jan Sklenář improved the quality of text-figures; helpful feedback was provided by reviewers Min Deng and Edoardo Martinetto. JK was supported by the Czech Ministry of Culture (IP DKRVO 2024-2029 DKRVO/2.I.a).

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