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Tufted wind-dispersed fagalean fruits, *Pogonokarydion* gen. nov., from the Upper Eocene Florissant Formation of Colorado, USA

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ABSTRACT. Wind-dispersed comose fruits from the Late Eocene of Florissant, Colorado, USA, are recognized as a new genus of fagalean affinity. *Pogonokarydion crassulum* (Cockerell) gen. et comb. nov. disseminules consist of an ellipsoidal to circular nut bearing longitudinal ribs, a persistent epigynous perianth, paired styles, and a prominent tuft of straight hairs arising from the base, which we infer to be homologous with an involucre. Prior assignments to *Juncus* (Juncaceae) and *Fagopsis* (Fagaceae) are rejected and we argue for a position within the Fagales, likely within, or close to, the Betulaceae. *Pogonokarydion* co-occurred in the Florissant flora with other fagalean genera, including some still living today, like *Quercus* and *Carya*, and others now extinct like *Fagopsis* and *Asterocarpinus*.

KEYWORDS: Comose fruits, extinct Fagales, hairy nuts, Betulaceae, impression fossils, wind dispersal

INTRODUCTION

The late Eocene flora of the Florissant Formation has attracted interest for more than a century, partly because of the aesthetically attractive impression fossils in shale, as well as huge petrified stumps highlighted in Florissant Fossil beds National Monument which was conserved following a legal battle with land developers (Leopold and Meyer, 2012). The flora preserved in the lakebed shales of Florissant has been monographed multiple times (Lesquereux, 1883; Cockerell, 1908; Knowlton, 1916; MacGinitie, 1953), and summarized by Manchester (2001) and by Meyer (2003), and has been the source of systematic treatments focused on particular taxa, including the two most abundant elements of the flora, *Fagopsis longifolia* (Lesquereux) Hollick (Hollick, 1909; Manchester and Crane, 1983) and *Cedrelospermum lineatum* (Lesquereux) Manchester (Manchester, 1989). Although those two species have been shown to be extinct genera of the Fagaceae and Ulmaceae, respectively, most of the Florissant species have been assigned to extant genera based on similarities of leaf architecture. The Florissant flora is best known from the abundant fossil leaf impressions, but also includes silicified woods (Wheeler, 2001; Wheeler and Meyer, 2012) and a diverse, well-preserved palynoflora (Bouchal et al., 2016). Analysis of the reproductive organs found along with the leaves, including flowers, fruits and seeds has been particularly helpful for resolving phylogenetic relationships.

Here we revisit the distinctive tufted nutlets found occasionally in the Florissant shales. They were originally attributed to the monocot

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family Juncaceae, as *Juncus crassulus* Cockerell (1908), and subsequently subsumed within *Fagopsis longifolia* by MacGinitie (1953). However, the fruits were excluded from *Fagopsis* Hollick 1909 in the treatment of Manchester and Crane (1983), because the cupules and fruits found in physical connection to twigs bearing *F. longifolia* leaves were shown to be distinct, and lacking the prominent dispersal hairs of "*Juncus*" *crassulus*. So, the identity of "*J.*" *crassulus* has remained in limbo. Based on new collections, as well as original material, we are now able to describe the morphology of these fruits in more detail and address their systematic position.

MATERIAL AND METHODS

Specimens were collected by splitting shales at several sites within and near the boundaries of Florissant Fossil Beds National Monument. Although at least 30 specimens are known from the Florissant beds, we have not encountered these fruits in any other Cenozoic deposits of North America or other continents. The fossils are preserved mainly as impressions although occasionally some carbonaceous material remains adhering to the impressions. Specimens were imaged with a Keyence VHX-7000N digital microscope, in some cases using the "shadow effect mode" to emphasize topographic relief. Roland Brown's informative book on etymology of scientific words (Brown, 1954) was consulted in composing the new generic name.

Specimens studied are from the collections of Florissant Fossil Beds National Monument, Florissant, Colorado (FLFO); the University of California Museum of Paleontology, Berkeley (UCMP); Florida Museum of Natural History, University of Florida, Gainesville; Sternberg Museum, Fort Hayes State University, Hayes, Kansas (FHSM); Milwaukee Public Museum (MPM), and the Smithsonian Natural History Museum, Washington DC (USNM).

Although the Florissant Beds were formerly considered to be Miocene (Cockerell, 1908) or Oligocene (Brown, 1937; MacGinitie, 1953), radiometric dating indicates that they were deposited in the Late Eocene, very close to the Eocene-Oligocene boundary, with a radiometric age ($^{40}Ar/^{39}Ar$) of 34.07 ± 0.10 Ma based on pumice samples from the upper part of the Florissant Formation (Evanovff et al., 2001).

SYSTEMATICS

Genus ***Pogonokarydion***
Manchester et Judd gen. nov.

Pogonokarydion crassulum
(Cockerell) Manchester et Judd **comb. nov.**

Figs 1, 2

Basionym.

1908 *Juncus crassulus* Cockerell 1908, p. 79, pl. 10, figs 44, 45.

1937 *Juncus*? *crassulus* Cockerell; Brown, 1937, p. 186, pl. 61, fig. 16.

Plant Fossil Names Registry Number. PFN003355 (for new genus).

Emended diagnosis. Fruit a nut with tufts of elongate simple hairs arising from its base and extending about 1.5 times the length of the nut. Nut ovoid to circular in face view, longitudinally ribbed with ~10–12 ribs in total, ribs straight and unbranched, extending from base of nut almost to the apex. Perianth epigynous, persistent and forming a collar-like protrusion ~¼ the length of the nut body. Styles two, protruding well beyond the apex of the nut with recurved tips but commonly broken at mid-length.

Holotype. Cockerell, 1908, pl. 10, figs 45, 46 (USNM 40783A, B, refigured Manchester 2001: pl. 2, fig. 9).

Additional specimens examined. FLFO 77, 3305, 3711, 3847, 3860, 3900, 3867, 3944, 4036, 4110, 4114, 4139, 4157, 4488, 4490, 6215, 9333, 9971, 8871, 10131, 11392, 11485, 11489; FHSM PB 494, 526b; MPM 2716; UCMP 3634 (MacGinitie, 1953: pl. 33, fig. 3), UCMP 3698 (MacGinitie, 1953: pl. 73, fig. 4); UF 15878-26059; USNM 39697 (Brown, 1937: pl. 61, fig. 16).

Etymology. Pogono (Gr), bearded, referring to the tuffs of hairs arising from the base, + karydion (Gr), diminutive of nut.

Description. The fruit body is elliptical to circular as seen in face view of the compressed fruits, 1.5–2.4 mm wide and 2.1–3.0 mm high. When exposed surficially, they show 10 to 12 prominent longitudinal ribs (5 to 6 visible on each counterpart of the shale impression, Fig. 1C, E, G, I). The smooth ovoid locule cast (Fig. 1B) indicates they were unilocular, and the lack of smaller ovoid impressions within the fruit body suggests that they were single-seeded. The fruits are concluded to be indehiscent because none are split or opened at maturity; hence we consider them to be nuts. A small circular scar at base of nut (Fig. 1D, E) suggests sessile attachment. A prominent tuft of hairs 2.5–4.5 mm long radiates from the base of the nut. Individual hairs are long, flexible

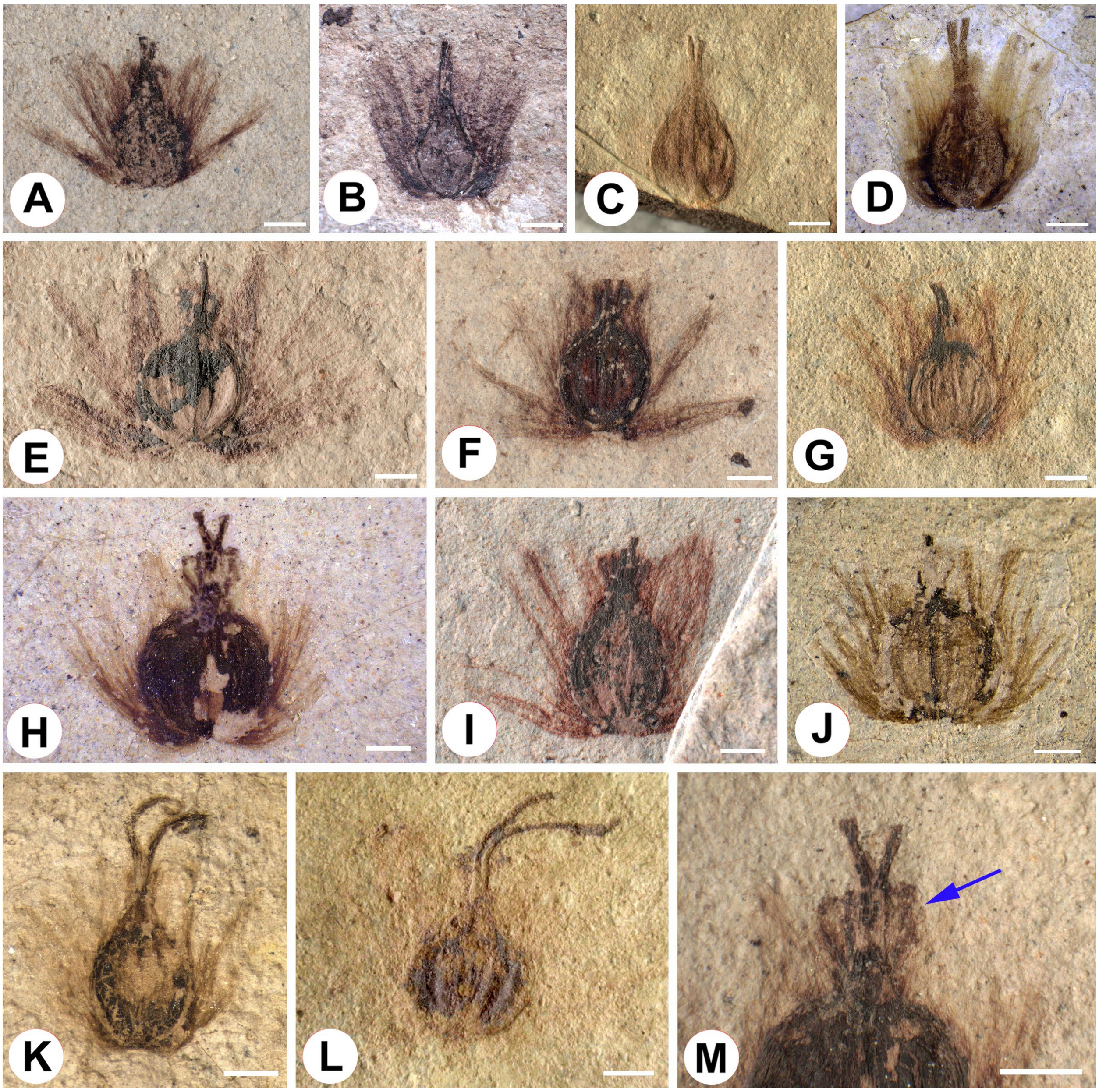

Figure 1. Disseminules of *Pogonokarydion crassulum* (Cockerell) comb. nov. from the Florissant flora, Late Eocene of Colorado, USA. **A**. Ovate nut with two styles at apex and hairs spreading from the base, FLFO 77; **B**. Fruit showing hairs spreading from the base with smooth pyriform locule cast and protruding styles, FLFO 10131; **C**. Ovate fruit showing five longitudinal ribs, faintly preserved surrounding hairs, with pair of styles protruding apically, FLFO 3944A; **D**. Ovate nut with surrounding hairs and slightly divergent styles, FLFO 3305A; **E**. Longitudinally ribbed, circular nut, with apical perianth surrounding the styles, one of which remains intact, FLFO 9971; **F**. Fruit with circular nut, dark due to adhering carbonaceous matter, FLFO 5215B; **G**. Fruit with longitudinally ribbed, circular nut, FLFO 4139B; **H**. Circular nut with persistent perianth and apically protruding pair of divergent styles, FLFO 4110; **I**. Fruit with prominent collar-like perianth, FLFO 9333; **J**. Specimen with circular nut and hairs fanning from the base, FLFO 4114; **K**. Fruit with ovate nut and complete recurved styles, FLFO 3711A, B; **L**. Nut with intact elongate styles, FLFO 4157; **M**. Enlargement of the apical portion of the fruit in H, showing persistent perianth (arrow) and styles, FLFO 4110. Scale bars = 1 mm in A–M

and unbranching (Fig. 2). We interpret this tuft to represent a derived involucre. The hairs are often clumped into 6 or more distinct bundles (e.g. Fig. 1E–G, I, J), but it is not evident whether this clumping indicates origin from separate bracteoles, or tangling in transport. A persistent epigynous perianth is preserved on many specimens and is clear for example in Fig. 1E, H, I, M. It consists of a flared, collar like structure at apex of the nut ~0.7–1.2 mm long and 1.1–1.3 mm wide. The calyx appears to have been thick-textured, because of the relatively thick layer of carbonized tissue adherent to some of the impressions (e.g. Fig. 1F, I). Lobes of the calyx are not clear – perhaps at least 3, or as many as six. Each nut bears two elongate slender styles, indicating the nuts originated from bicarpellate ovaries. The styles

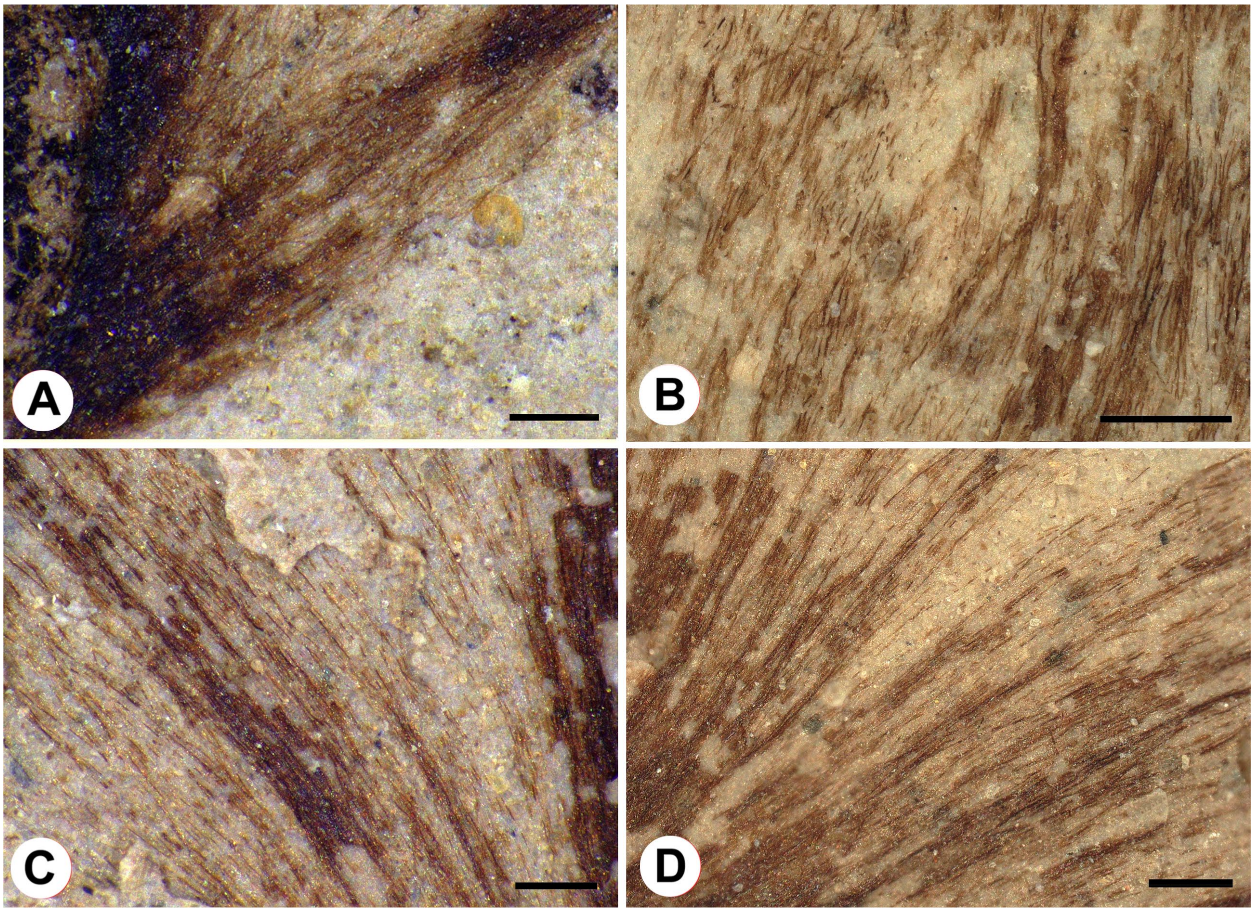

Figure 2. Details of involucral hairs arising from *Pogonokarydion crassulum* nuts as seen at surface of the shale surrounding the nut. **A**. Enlargement from the specimen in Fig. 1A, hairs arising from base of nut, FLFO 77; **B**. Hairs near periphery of the tuft from the fruit of Fig. 1I, FLFO 9333; **C**, **D**. Hairs surrounding the nut of specimen in Fig. 1E, FLFO 9971. Scale bars = 200 µm in A–D

are commonly broken off at mid-length (0.6 to 1.7 mm), but at least two specimens show complete, distally recurved styles (Fig. 1K, L). Stigmatic surfaces, whether ventral, or entirely surrounding the style arms, are not clear, but the stigmas were not capitate.

We know neither how many ovules were present per gynoecium, nor the nature of placentation. We do not know the inflorescence form, but the lack of pedicels on the fruits, and basal attachment scars (Fig. 1G), suggest that they were borne sessile.

SYSTEMATIC PLACEMENT

When the first few specimens became available, Cockerell (1908) considered them to represent capsular fruits of *Juncus* L. 1753 in the monocot family Juncaceae. This determination was later questioned by Brown (1937). The assignment to this family can be rejected because Juncaceae have three carpels rather than two, a superior rather than inferior ovary, and fruits that are dehiscent. Subsequently, MacGinitie (1953) considered these disseminules to represent dispersed fruits of *Fagopsis*, an extinct genus known from interconnected leaves, twigs, inflorescences and infructescences at the same Florissant localities. In re-assembling the *Fagopsis* plant, Manchester and Crane (1983) excluded these dispersed hairy fruits because they do not coincide with those seen attached to the *Fagopsis* twigs; hence Manchester (2001) considered their systematic affinity inconclusive. Although *Fagopsis* is considered to be of fagaceous affinity, *Pogonokarydion crassulum* differs from extant Fagaceae in having bicarpellate rather than tricarpellate fruits, as shown by the two styles seen in most specimens.

The prominent basally arising tuft of hairs consistently found on these fruits (Figs 1, 2) indicates that they were wind-dispersed. Brown (1937: p. 186) interpreted the hairs as perianth-derived: "*J. crassulus* Cockerell…. is a small spherical fruit with the remains of two styles and is surrounded at the base by a ciliated or fringed perianth twice as long as the fruit itself." However, we consider those hairs to be involucral or bract-derived, because the perianth is seen to be apical on the fruits, forming a collar around the base of the styles (e.g. Fig. 1H, I, M). The body may have been spherical as Brown inferred, but this is difficult to confirm because of the compressed state of fossils preserved in shale. They may alternatively have been lensoidal in cross section.

The combination of longitudinally ribbed ovoid to ellipsoidal nuts, basal involucre, epigynous perianth and two styles, suggests that *Pogonokarydion crassulum* belongs in the order Fagales. Fagales are well known for their diversity of fruit types with adaptive pathways for two main modes of dispersal, i.e. animal and wind dispersal (e.g. Xiang et al., 2014). In this instance the nuts are clearly suited for wind dispersal, but the involucre has developed into hairs, contrary to laminar wings which is the usual condition for wind-dispersed fruits of Betulaceae and Juglandaceae.

Among the fagalean families to which *Pogonokarydion* might correspond, we can exclude Fagaceae because the fossil lacks a well-developed cupule and the paired styles indicate two, rather than three carpels. Based on bicarpellate construction, Juglandaceae, Myricaceae, Betulaceae, Ticodendraceae and Casuarinaceae come into consideration. Nuts of Juglandaceae lack longitudinal ribs and have a basally lobed locule. Fruits of Ticodendraceae are drupes (although the pit is ribbed). *Comptonia* L'Hér. 1789 (Myricaceae) fruits are superficially similar to those of *Pogonokarydion* because of their association with bristle-like tertiary bracts, but they lack a perianth and have deciduous styles. Casuarinaceae are ruled out because they lack a perianth, have membranous samara fruits (wing derived from the ovary) that are surrounded by two woody bracteoles within indurated, cone-like catkins. The ribbed nutlets and persistent epigynous perianth of *P. crassulum* resemble the morphology of *Carpinus* L. 1753 and *Asterocarpinus* Manchester et Crane 1987 nuts and lead us to favour Betulaceae as the likely family to accommodate these fruits. The fruits bear an interesting resemblance to *Palaeocarpinus parva* Correa-Narvaez et Manchester 2021 of the Middle Eocene Clarno Formation of Oregon (Correa and Manchester, 2022), which also has a rounded nutlet, two styles and a highly dissected basal involucre that consists of radiating spines. However, those spines are thicker than the hairs of *P. crassulum*, and prominently branched. If these similarities indicate affinity, then it may suggest a coryloid affinity for *Pogonokarydion*.

The foliage of *Pogonokarydion* remains unknown. We suspect that the leaves of *Pogonokarydion* may have conformed in morphology to those of extant Betulaceae and thus would be expected to be deciduous and simple with compound marginal serration. They might be misidentified among those already documented from the Florissant. Among the previously figured leaves that might be candidates is sone of those that MacGinitie (1953) attributed to *Morus symmetrica* Cockerell 1908 (i.e. MacGinitie, 1953: pl. 24, fig. 5). It conforms in having craspedodromous secondary veins, percurrent tertiary veins and compound teeth. Leaves formerly identified as *Carpinus* from the Florissant flora, Bridge Creek, and Beaverhead Basins floras were reassigned to the fossil genus *Paracarpinus* Manchester et Crane 1987 and hypothesized to correspond with the consistently co-occurring propeller-winged nuts of *Asterocarpinus* (Manchester and Crane, 1987). However, it is also possible that the *Pogonokarydion* host plants were not close enough to the lake for their leaves to reach the site where deposition was occurring; the tufted disseminules were more likely to be wind-blown to the lake.

Other Fagales represented by megafossils in the Florissant beds include *Carya* nuts, leaves, and pollen catkins (Juglandaceae), *Asterocarpinus* fruits with *Paracarpinus* leaves (Betulaceae), *Fagopsis* leaves, flowers and fruits and *Quercus* spp. cupules and leaves (Fagaceae) (MacGinitie, 1953; Manchester, 1987; Manchester and Crane, 1983, 1987). The Florissant dispersed pollen flora, studied with both light microscopy and scanning electron microscopy (Bouchal et al., 2014, 2016), includes still more diversity of Fagales, including *Carya* Nutt. 1818, *Juglans* L. 1753, *Momipites* Wodehouse 1933 emend. Nichols 1973 (Juglandaceae), *Fagopsis*, *Quercus* L. 1753, and three indet. taxa of Castaneoideae (Fagaceae), plus several members of Betulaceae, including *Alnus* Mill. 1754 (rare grains), *Betula* L. 1753, and two unidentified taxa of Coryloideae with similarities to pollen of the Paleocene species of *Cranea* Manchester et Chen 1998 and *Palaeocarpinus* (Bouchal et al., 2016).

The late Eocene Florissant flora includes a good number of convincingly identified extant gymnosperm and angiosperm genera, e.g. *Pinus* L. 1753, *Sequoia* Endl. 1847, *Torreya* Arn. 1838, *Mahonia* Nutt. 1818, *Ulmus* L. 1753, *Acer* L. 1753, *Dipteronia* Oliv., *Koelreuteria* Lax. 1772, *Ailanthus* Desf. 1786, and *Hydrangea* L. 1753 (Meyer, 2003). However, *Pogonokarydion* joins several genera known from the same flora that are now extinct, including those cited above (*Fagopsis*, *Asterocarpinus*, *Cedrelospermum* Saporta emend. Manchester 1987), along with *Diplodipelta* Manchester et Donoghue (Caprifoliaceae; Manchester and Donoghue, 1995), *Florissantia* Knowlton emend. Manchester (Malvaceae; Manchester, 1992), *Chaneya* Wang et Manchester (Simaroubaceae; Wang and Manchester, 2000).

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ADDITIONAL INFORMATION

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