Pollen and spores of the uppermost Eocene Florissant Formation, Colorado: a combined light and scanning electron microscopy study

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Pollen and spores of the uppermost Eocene Florissant Formation, Colorado: a combined light and scanning electron microscopy study

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Abstract

The uppermost Eocene Florissant Formation, Rocky Mountains, Colorado, has yielded numerous insect, vertebrate, and plant fossils. Three previous comprehensive palynological studies investigated sections of lacustrine deposits of the Florissant Formation and documented the response of plant communities to volcanic eruptive phases but overall found little change in plant composition throughout the investigated sections. These studies reported up to 150 pollen and spore phenotypes. In the present paper we used a taxonomic approach to the investigation of dispersed pollen and spores of the Florissant Formation. Sediment samples from the shale units containing macrofossils were investigated using light microscopy (LM) and scanning electron microscopy (SEM). The general picture of the palynoflora is in agreement with previous studies. However, the combined LM and SEM investigation provides important complementary information to previous LM studies. While a fairly large amount of previous pollen determinations could be confirmed, the purported taxonomic affinities of several pollen phenotypes need to be revised. For example, pollen referred to as *Podocarpus* or *Podocarpidites* sp. belongs to the Pinaceae *Cathaya*,

Malus/Pyrus actually belongs to Dryadoideae, pollen of the form genus *Boehlensipollis* referred to as Proteaceae/Sapindaceae/Elaeagnaceae or *Cardiospermum* belongs to Sapindaceae but not to *Cardiospermum*, and pollen of *Persicarioipollis* sp. B with previously assumed affinities to Polygonaceae actually belongs to Thymelaeaceae. *Pandaniidites* and one type of *Malvacipollis* cannot be linked with Pandanaceae and Malvaceae. A few taxa are new records for Florissant (Ebenaceae: *Diospyros*; Mernispermaceae; Trochodendraceae: *Tetracentron*). In general, SEM investigations complement the LM palynological studies and improve the identification of dispersed pollen and spores and enable integration of data from dispersed fossil pollen into a wide range of comparative morphological, taxonomic, evolutionary, biogeographic, and phylogenetic studies.

Keywords: *Colorado, dispersed pollen, late Eocene, SEM, taxonomy*

Introduction

The uppermost Eocene Florissant Formation in Colorado, USA, has yielded an exceptionally rich record of fossil organisms, of which insects are by far the dominant group (about 1500 species described). Among the vertebrates, four fish genera, four to five bird genera, and 17 mammal genera are known (Meyer, 2003; Lloyd et al., 2008; Lloyd & Eberle, 2008). Plant macrofossils from Florissant have been described since the 19th century. In his monograph on plant macrofossils from Florissant, MacGinitie (1953) recognized 120 species, about half of the ca. 250 species described in earlier works. An update of the macrofossil flora of Florissant including fruits, seeds and leaf fossils was provided by Manchester (2001). Apart from these, many taxa were described in separate papers (e.g. Hollick, 1907; Manchester & Crane 1983; Manchester, 1989a; 1992). Comprehensive palynological investigations of the Florissant Formation were carried out by Hascall (1988), Leopold and Clay-Poole (2001) and Nichols

and Wingate (2001). In these studies from 78 palynomorph types (Hascall, 1988) to about 150 pollen “phenotypes” (Leopold & Clay-Poole, 2001) were recorded based on light microscopy (LM) observations.

The aim of the present study is to investigate dispersed pollen and spores from Florissant by light microscopy (LM) and scanning electron microscopy (SEM) and to document details of pollen morphology. By this approach, detailed comparisons can be made with taxonomic studies on extant pollen and spores predominantly relying on information from SEM. The benefits of complementing LM palynological studies with SEM investigations are discussed, and the potential of such studies for broader evolutionary, phylogenetic and biogeographic investigations is outlined.

Material and methods

The sediment samples investigated for this study originate from the Florissant Fossil Beds in the Southern Rocky Mountains of Colorado. In the surroundings of Florissant, four formal rock units are distinguished, the Pikes Peak Granite, the Wall Mountain Tuff, breccias of the Thirtynine Mile Andesite, and the Florissant Formation (Evanoff et al., 2001, **Fig. 1.A**). The Florissant Formation consists of six informal units: the upper pumice conglomerate, the upper shale, the caprock conglomerate, the middle shale, the lower mudstone, and the lower shale. The paper shales of the upper, middle and lower shale unit are the main fossil-bearing strata, which yield the exquisitely preserved insect, plant, fish and bird fossils. All the age-diagnostic mammal fossils originate from the lower mudstone unit and suggest a middle to late Chadronian age (NALMA) (Lloyd et al., 2008) correlative with the Priabonum age (ICS). This corresponds with the ⁴⁰Ar/³⁹Ar weighted mean age of 34.07 ± 0.10 Ma of pumice samples obtained from the upper parts of the Florissant Formation (Evanoff et. al., 2001).

The sediment samples investigated for the present study were taken from macrofossil-bearing shale pieces of the palaeobotany and palynology collection of the Florida Museum of Natural History, Gainesville, labelled as UF15880 – 7285, the palaeobotany collection of the University of California Museum of Paleontology, Berkeley, labelled as UCMP 20778, and the palaeobotany collection of the Naturhistoriska Riksmuseet, Stockholm, labelled as S151454. UF15880 – 7285 was collected on the private property of the Stohl family, west of Florissant (**Fig. 1. B, X₁**), near the old Denver Museum Locality (MacGinitie, 1953) but this locality has not been correlated to a particular shale unit (pers. comm. Herb Meyer, 2015). S151454 was collected from the Clare Quarry locality south of Florissant (**Fig. 1. B, X₂**); this locality can be assigned to the lower shale unit (pers. comm. Herb Meyer, 2015). UCMP 20778 cannot be assigned to a collection locality, it is part of MacGinitie's collection at UCMP which was later disassociated from his original site data (pers. comm. Herb Meyer, 2015). Sedimentary rock was thoroughly washed and processed following the protocol described in Grímsson et al. (2008) and the same pollen grains were investigated with light microscopy (LM) and electron scanning microscopy (SEM; single grain method, Zetter, 1989). LM photos of sample UF15880 – 7285 were taken with a Nikon Eclipse 80i microscope equipped with a Samsung Digimax V70 digital camera; LM photos of samples UCMP20778 and S151454 were taken with an Olympus BX51 microscope equipped with an Olympus DP71 camera. Specimens were sputter coated with gold and in most cases immediately after investigated and photographed under SEM, Joel JSM 6400 scanning electron microscope and a Hitachi S-4300 cold field emission scanning electron microscope. To assess relative abundance 400 grains per sample were counted and identified. Fungal spores and algal microfossils were encountered in all samples but not considered for this study. Definition of abundance is as follows: highly abundant – average at least 10% per sample; abundant – average 9.9%–2% per sample; infrequent – average less than 2% per

sample; rare – average less than 0.5% per sample; very rare – 10 or fewer grains observed in the entire study.

The terminology for pollen morphology followed Punt et al. (2007) and Hesse et al. (2009).

The sediment samples used for this study and the SEM stubs are stored at the Swedish Museum of Natural History (specimen numbers S142992-01, 02, 03..., S142993-01, 02, 03... and S142994-01, 02, 03...).

This study is partly based on an unpublished Master's Thesis (Bouchal, 2013) using an updated taxonomy.

Systematic Palaeobotany

Divison Bryophyta

Subdivision Marchantiophytina

Class Marchantiopsida

Marchantiopsida fam.et gen. indet.

(Figures 2A, 3A–B)

Description. – Spore, spheroidal, amb circular, equatorial diameter 47–52 µm (LM), 41–47 µm (SEM); exospore 1.3–1.5 µm thick (LM); sculpturing reticulate (LM & SEM), luminae diameter 3–5 µm (SEM), supra-sculpturing verrucate (SEM); abundance: very rare.

Remarks. – This spore is corroded but strongly resembles spores found in extant Marchantiopsida (liverwort mosses) genus *Targionia* (Micheli) L. (Boros & Járαι-Komlódi, 1975, p. 61, pl. 17, figs 1–3; Zhao et al., 2011, p. 208, figs 2G–I). Marchantiopsida fam. et gen. indet. shows similarities (pitted surface) to trilete spore Type 5 of Hascall (1988, pl. 1, fig. 12). Present in sample UF15880-7285.

Divison Trachaeophyta

Subdivision Lycopodiophytina

Family Selaginellaceae Milde

Genus *Selaginella* P. Beauv

Selaginella sp. 1

(Figures 2B, 3C–D)

Description. – Spore, oblate to spheroidal, amb circular to convex triangular, equatorial diameter 38–44 μm (LM), 31–35 (SEM); exospore 2–3 μm thick (LM), trilete, laesurae $\frac{1}{2}$ to $\frac{2}{3}$ of the radius; sculpturing verrucate, rugulate (LM & SEM), sculpturing less distinct on proximal side (SEM); abundance: rare.

Remarks. – Spores of this type resemble extant *Selaginella plana* (Desv.) Hieron (Korall & Taylor, 2006). Leopold and Clay-Poole (2001, pl. 1, figs 5–6) depicted a similar spore and compared it to the extant species *Selaginella mairei* (H. Lév.) Kung, but did not provide a description of this spore type. Present in samples UF15880-7285 and S151454.

Selaginella sp. 2

(Figures 2C, 3E–F)

Description. – Spore, oblate to spheroidal, amb circular, cingulum present (LM), equatorial diameter including cingulum 37–42 μm (LM), 33–37 μm (SEM), cingulum width 4–8 μm (LM); trilete, laesurae less than $\frac{1}{3}$ of the radius (LM & SEM), trilete mark surrounded by lacunae (SEM); sculpturing verrucate (LM), microverrucate (SEM); abundance: rare.

Remarks. – Extant *Selaginella densa* Rydb., *S. sibirica* (Milde) Hieron and *S. wallacei* Hieron spores show remarkable similarities with this spore type (Heusser & Peteet, 1988). Leopold and Clay-Poole (2001, pl. 1, figs 2–3) compared this type of spores to *Selaginella densa*. Wingate and Nichols (2001, pl. 2, fig. 1) assigned this spore type to the form genus *Lusatisporis* sp. cf. *L. perinatus* Krutzsch, Sontag et Pacltová. Hascall (1988, Type 8, pl. 2,

fig. 14) depicted a similar cingulate spore with affinities to *Selaginella*. Further spores with affinities to lycophytes and/or *Selaginella* have previously been reported (Wingate & Nichols, 2001; Leopold & Clay-Poole, 2001) but were not encountered in the samples investigated for the present study. Present in samples UF15880-7285 and S151454.

Subdivision Filicophytina

Class Polypodiales

Polypodiales fam. et gen. indet.

(Figures 2D, 3G–H)

Description. – Spore, oblate, outline elliptic to renal shaped, polar axis 34–37 µm (LM), 33–35 µm (SEM), equatorial diameter 50–54 µm (LM), 44–47 µm (SEM); exospore 1–1.3 µm thick (LM), monolete; sculpturing rugulate to verrucate (LM), verrucate (SEM); abundance: rare.

Remarks. – This spore type shows an exine sculpturing typical of extant Polypodiales, e.g. Davalliaceae and Polypodiaceae, (cf. Tyron & Lugardon, 1991). Wingate and Nichols (2001, pl.1, fig. 10) assigned this spore type to the form genus *Polypodiisporites* sp. cf

Polypodiisporites secundus (Potonie) Krutzsch. Present in samples UF15880-7285 and S151454.

Incerta sedis trilete spores

Trilete spores fam. et gen. indet. 1 to 5 lack the perispore. For the distinction between bryophyte and pteridophyte spores and the determination to family or genus level the perispore is necessary, thus these spores are of uncertain origin.

Trilete spore fam. et gen. indet. 1

(Figures 2E, 3I–J)

Description. – Spore, oblate, amb circular to convex triangular, equatorial diameter 55–60 µm (LM), 50–56 µm (SEM); exospore 0.8–1.0 µm thick (LM); trilete mark, labrum present, laesurae extend nearly to the equator; sculpturing psilate (LM), microverrucate, low relief (SEM); abundance: rare.

Remarks. – Wingate and Nichols (2001, pl. 1, fig. 13) assigned this type of spore to the form genus *Biretisporites* Delcourt & Sprumont. Trilete spore fam. et gen. indet. 1 resembles trilete spore Type 7 of Hascall (1988, pl. 2, fig. 14). Present in all samples.

Trilete spore fam. et gen. indet. 2

(Figures 2F, 3K–L)

Description. – Spore, oblate, amb convex triangular, equatorial diameter 29–34 µm (LM), 27–30 µm (SEM); exospore 1–1.3 µm thick (LM); trilete, labrum present, laesurae extend nearly to the equator, single line of perforations adjacent to the laesurae (SEM); sculpturing psilate (LM), microverrucate, granulate, low relief (SEM); abundance: rare.

Remarks. – Pteridophyta fam. et gen. indet 2 shows strong morphological similarities (outline, size, length of laesurae, psilate ornamentation) to trilete spore Type 3 of Hascall (1988, pl. 2, fig. 6). Present in all samples.

Trilete spore fam. et gen. indet. 3

(Figures 2G, 3M–N)

Description. – Spore, oblate to spheroidal, amb circular to convex triangular, equatorial diameter 50–58 µm (LM), 42–48 µm (SEM); exospore 1–1.4 µm thick (LM), trilete, laesurae $\frac{1}{2}$ to $\frac{2}{3}$ of the radius, laesurae open; sculpturing psilate (LM), perforate, microrugulate, low relief (SEM); abundance: rare.

Remarks. – Trilete spore Type 6 of Hascall (1988) shows similar open laesurae but differs in a more concave triangular outline to trilete spore fam. et gen. indet 3. Wingate and Nichols (2001, pl.1, fig. 11) assigned this type of spore to *Lygodiumsporites adriennis* (Potonié & Gelletich) Potonié, Thomson, & Thiergart ex Potonié, for this form genus affinity with Pteridophyta, family Schizaeaceae has been assumed. The four extant genera of Schizaeaceae produce distinctly ornamented (rugulate, verrucate, furrowed or ridged) spores (Tryon & Lugardon, 1991), but can be smooth when the perine is lost, e.g. in *Lygodium kaulfussii* Heer, from which *in situ* spores have been studied (Manchester, 1987). Trilete spore fam. et gen. indet. 3 shows psilate exospore sculpturing, commonly found in spores, and shows morphological similarities to eg. Vittariaceae and Gleicheniaceae (Tryon & Lugardon, 1991). Present in all samples.

Trilete spore fam. et gen. indet. 4

(Figures 2H, 3O–P)

Description. – Spore, oblate, amb convex triangular, equatorial diameter 30–33 µm (LM), 24–27 µm (SEM); exospore 1.0–1.5 µm thick (LM), outer exospore thicker than inner exospore; trilete, laesurae sinuous, laesurae extending nearly to the equator; sculpturing rugulate on distal side (LM & SEM), proximal side microverrucate, perforate (SEM); abundance: rare.

Remarks. – Trilete spore fam. et gen. indet. 4 shows strong morphological similarities to trilete spore Type 2 of Hascall (1988, pl. 1, fig. 12) but differs in larger size. Present in sample UF15880-7285.

Trilete spore fam. et gen. indet. 5

(Figures 4A, 5A–B)

Description. – Spore, oblate to spheroidal, amb circular, equatorial diameter 42–50 µm (LM), 37–41 µm (SEM); exospore 1.3–1.6 µm thick (LM), trilete, labrum present, laesurae $\frac{1}{2}$ to $\frac{2}{3}$ of the radius; sculpturing psilate (LM), perforate, microrugulate to microverrucate (SEM); abundance: rare.

Remarks. – Present in all samples.

Gymnosperms

Subdivision Spermatophytina

Class Ginkgopsida

Family Ginkgoaceae Engler

Genus Ginkgo L.

Ginkgo sp.

(Figures 4B, 5C–D)

Description. – Pollen, oblate, outline circular to elliptic, equatorial diameter 28–32 µm (LM), 27–29 µm (SEM); exine 0.8–1.0 µm thick (LM); sculpturing scabrate (LM), rugulate to microrugulate (SEM), rugulae slightly crested; abundance: very rare.

Remarks. – The rugulate sculptural elements and morphological features of this pollen correspond with extant *Ginkgo biloba* L. and fossil *Ginkgo* pollen (cf. Grimsson et al., 2011; Halbritter, 2005b; Sahashi, 1997; Zetter et al., 2011). Pollen grains with this general morphology have commonly been referred to as *Monosulcites* and *Cycadopites*. From Florissant a single *Ginkgo* leaf has been recovered (Buskirk & Meyer, 2008). Present in sample UF15880-7285.

Class Coniferopsida (incl. Gnetales)

Family Cupressaceae Richard ex Bartling

Cupressaceae gen. indet. 1

(Figures 4C, 5E–F)

Description. – Pollen, spheroidal, equatorial diameter 25–30 μm (LM), 20–25 μm (SEM); leptoma; exine 1.5–2 μm thick; sculpturing scabrate (LM), sculpturing rugulate, verrucate, microechinate (SEM), leptoma microechinate, orbicule diameter 0.4–0.6 μm , orbicule with densely packed blunt microechini; abundance: common.

Remarks. – This type of pollen falls in the morphological range of several extant and fossil Cupressaceae pollen taxa (cf. Li et al., 2010; Miyoshi et al., 2011). The absence of a papilla, the distinguishing feature in Athrotaxoideae, Sequoioideae, Taiwanioideae, and Taxodioideae, would suggest affinities with apapillate Cupressaceae subfamilies. However, extant *Sequoia sempervirens* (D. Don) Endl. and fossil *Sequoia affinis* Lesquereux are known to produce both papillate and apapillate pollen (Kedves, 1985; Leopold & Clay-Poole, 2001). From Florissant two Cupressaceous genera, *Sequoia* [*Sequoioxylon pearsallii* Andrews (petrified wood), *Sequoia affinis* Lesquereux (leafy twigs)] and *Chamaecyparis* [*C. linguaeifolia* (Lesquereux) MacGinitie] have been reported (MacGinitie, 1953; Manchester, 2001; Gregory-Wodzicki, 2001). It is possible that Cupressaceae gen. et spec. indet. 1 to 3 originated from one of these fossil taxa.

Cupressaceae gen. indet. 2

(Figures 4D, 5G–H)

Description. – Pollen, spheroidal, papillate, equatorial diameter 25–30 μm (LM), 21–25 μm (SEM); exine 1.5–2 μm thick; sculpturing scabrate (LM), verrucate with microechinate sculpturing (SEM), orbicule diameter 0.4–0.6 μm , orbicule with densely packed blunt microechini; pollen ruptured, abundance: highly abundant.

Cupressaceae gen. indet. 3

(Figures 4E, 5I–J)

Description. – Pollen, spheroidal, equatorial diameter 30–40 μm (LM & SEM); sculpturing scabrate, granules (orbicule) visible (LM), verrucate with microechinate sculpturing (SEM), orbicule diameter 0.6–1 μm , orbicule with densely packed blunt microechini; pollen ruptured; abundance: highly abundant.

Remarks. – Ruptured papillate and ruptured unapillate pollen is common in all samples from Florissant (Hascall, 1988; Wingate & Nichols, 2001; Leopold & Clay-Poole, 2001), no unruptured papillate pollen was encountered in our samples. Ruptured papillate and unapillate pollen is common in extant *Sequoia sempervirens* (Kedves, 1985). The large size of the grains (van Campo, 1951) and the large orbiculae (pers. obs. J.M. Bouchal) are characteristic of extant *Sequoia*.

Family Pinaceae Lindl.

Genus Abies Mill.

Abies sp. 1

(Figures 4F, 5K–M)

Description. – Pollen, bisaccate, oblate, corpus elliptic in equatorial view, sacci nearly spherical, sacci attachment area narrow, angle between corpus and sacci 135°–145° wide (equatorial view), pollen diameter including sacci 150–170 μm (LM), 130–135 μm (SEM), pollen height including sacci 105–115 μm (LM), 85–90 μm (SEM), corpus diameter 125–140 μm (LM), 100–105 μm (SEM), corpus height 70–80 μm (LM), 55–60 μm (SEM), sacci diameter 75–90 μm (LM), 60–65 μm (SEM), sacci height 45–55 μm (LM), 40–50 μm (SEM); leptoma, exine in cappa region 3–6.5 μm thick (LM), sacci with alveolate structuring, proximal part of alveolae hexagonal; sculpturing scabrate in cappa region and psilate in

leptoma region (LM), corpus rugulate to microrugulate, scarcely perforate (SEM), sacci microrugulate, scarcely perforate (SEM); abundance: abundant.

Abies sp. 2

(Figures 4G, 5N–P)

Description. – Pollen, bisaccate, oblate, corpus elliptic in equatorial view, sacci nearly spherical, sacci attachment area narrow, angle between corpus and sacci 145°–155° wide (equatorial view), pollen diameter including sacci 130–140 µm (LM), 105–110 µm (SEM), pollen height including sacci 85–95 µm (LM), 70–80 µm (SEM), corpus diameter 90–100 µm (LM), 85–95 µm (SEM), corpus height 65–75 µm (LM), 50–60 µm (SEM), sacci diameter 60–65 µm (LM), 45–55 µm (SEM), sacci height 45–50 µm (LM), 40–45 µm (SEM); leptoma, exine in cappa region 4–8 µm thick (LM), sacci with alveolate structuring, alveolae hexagonal; sculpturing scabrate in cappa region and psilate in leptoma region (LM), corpus in sacci attachment area verrucate to microverrucate, corpus and cappa area rugulate to microrugulate, fossulate, perforate (SEM), sacci microrugulate, perforate (SEM); abundance: abundant.

Remarks. – *Abies* sp. 1 and 2 resemble extant and fossil *Abies* pollen (Beug, 2004; Stuchlik et al., 2002; Li et al., 2010; Grímsson & Zetter, 2011; Miyoshi et al., 2011; Zetter et al., 2011).

Abies sp. 2 differs from *Abies* sp. 1 in a higher abundance of perforations on cappa and saccus plus a more distinct rugulate sculpturing of the saccus attachment area and cappa, but we cannot rule out the possibility that both types originated from the same taxon reflecting its morphological range. Pollen of *Abies* has previously been reported (Hascall, 1988; Leopold & Clay-Poole, 2001; Wingate & Nichols, 2001). A single isolated winged seed determined as *Abies longiorostris* Knowlton (MacGinitie, 1953; Manchester, 2001) further corroborates the presence of *Abies* in the vicinity of the Florissant palaeolake. Present in all samples.

Genus *Cathaya* Chun et Kuang

Cathaya sp.

(Figures 6A–B, 7A–F)

Description. – Pollen, bisaccate, oblate, corpus rhombic in polar view, sacci nearly spherical, attachment area of sacci broad, pollen diameter including sacci 80–90 μm (LM), 65–80 μm (SEM), corpus width 35–55 μm (LM), 35–50 μm (SEM), sacci diameter 40–65 μm (LM), 35–55 μm (REM), sacci height 19–36 μm (LM); leptoma, sacci with alveolate structuring, sculpturing in leptoma area scabrate (LM), microechinate (SEM), cappa scabrate (LM), sacci microechinate, perforate (SEM); abundance: common.

Remarks. – Due to its microechinate sculpturing both on the corpus and the sacci (SEM) this pollen type can be securely assigned to the extant genus *Cathaya*. *Podocarpus* in Hascall (1988, pl. 3, fig. 1) shows similarities (outline, sacci attachment) and *Podocarpidites* sp. in Wingate and Nichols (2001, pl. 3, fig. 2) is virtually identical with *Cathaya* pollen depicted in Figs 6B, 7D–F. Present in all samples. *Cathaya* consists today of only one living species endemic to China, *C. argyrophylla* Chun et Kuang. Its habitat is restricted to elevations of 900–1900 m in evergreen to evergreen/deciduous broad-leaved forests on mountain slopes and ridges (Wang, 1961). During the Cenozoic *Cathaya* had a wide Northern Hemispheric distribution (cf. Liu et al., 1997; Liu & Basinger, 2000; Stuchlik et al., 2002; Grímsson & Zetter, 2011; Zetter et al., 2011). No pollen that can unambiguously be identified as *Podocarpus* has been encountered in the three investigated samples.

Genus *Larix* Mill./*Pseudotsuga* Carr.

Larix vel *Pseudotsuga* sp.

(Figures 6C, 7 G–I)

Description. – Pollen, spheroidal to oblate, circular outline in polar view, equatorial diameter 85–100 μm (LM), 70–85 μm (SEM); exine 2 μm thick; sculpturing psilate to scabrate (LM), microverrucate, perforate sculpturing (SEM), orbicule present on distal pole; circular pits are not sculptural elements but caused by erosion; abundance: very rare.

Remarks. – Size and morphological features of this pollen corresponds with that of *Larix* and *Pseudotsuga* (LM: Erdtman, 1965; Beug, 2004; SEM: Martin & Drew, 1970; Miyoshi et al., 2011; Li et al., 2011). *Larix/Pseudotsuga* type pollen has been reported by Hascall (1988, pl. 2, fig. 13) and Leopold and Nichols (2001, pl. 4, fig. 2).

Earliest unambiguous *Larix* macrofossils (vegetative axis, winged seeds, cones) in the North American fossil record are known from middle Eocene deposits (46–45 Ma) of the Thunder Mountain flora, Idaho, U.S.A (Erwin & Schorn, 2005) and the Buchanan Lake Formation, Axel Heiberg Island, Arctic Canada (LePage & Basinger, 1991). Present in sample S151454.

Genus Picea Dietrich

Picea sp.

(Figures 6D, 7 J–K)

Description. – Pollen, bisaccate, outline elliptic in equatorial view, sacchi half spherical, sacchi attachment area broad, pollen diameter including sacchi 135–150 μm (LM), 105–120 μm (SEM), pollen height including sacchi 95–105 μm (LM), 80–90 μm (SEM); leptoma, exine in cappa region 3–4 μm thick (LM), sacchi with alveolate structuring (LM), sacchi sculpturing verrucate, perforate (SEM); corpus sculpturing rugulate, fossulate (SEM); abundance: infrequent.

Remarks. – *Picea sp.* resembles extant and fossil *Picea* pollen (Beug, 2004; Stuchlik et al., 2002; Li et al., 2010; Grímsson & Zetter, 2011; Miyoshi et al., 2011; Zetter et al., 2011). Fossil seeds of *Picea magna* MacGinitie (MacGinitie, 1953; Manchester, 2001) and *Picea*

pollen have previously been reported (Hascall, 1988; Leopold & Clay-Poole, 2001; Wingate & Nichols, 2001). Present in all samples.

Genus Pinus L.

Subgenus Strobilus Lemmon (Haploxylon-pollen-type)

Pinus subgenus Strobilus sp.

(Figures 6A, 7A–C)

Description. – Pollen, bisaccate, oblate, corpus elliptic in equatorial view, sacchi half spherical, sacchi attachment area broad, angle between corpus and sacchi 135°–140° wide (equatorial view), pollen diameter including sacchi 80–95 µm (LM), 65–80 (SEM), pollen height including sacchi 55–65 µm (LM), 45–55 µm (SEM), corpus diameter 55–70 µm (LM), 45–55 µm (SEM), corpus height 40–45 µm (LM & SEM), sacchi width 40–45 µm (LM), 30–35 µm (SEM), sacchi height 20–25 µm (LM), 15–20 µm (SEM); leptoma, thickenings present in leptoma area (black spots); exine in cappa region 1.0–1.5 µm thick (LM), sacchi with alevolate structuring; sculpturing scabrate in cappa region and psilate in leptoma region (LM), corpus rugulate, fossulate (SEM), sacchi perforate, slightly rugulate relief (SEM); abundance: abundant.

Remarks. – Broadly attached, half-spherical sacchi and a leptoma with thickenings are characteristic of the Haploxylon-pollen-type (Hesse et al., 2009). Present in all samples.

Subgenus Pinus (Diploxylon-pollen-type)

Pinus subgenus Pinus sp.

(Figures 6B, 7D–F)

Description. – Pollen, bisaccate, oblate, corpus elliptic in equatorial view, sacchi nearly spherical, sacchi attachment area narrow, pollen diameter including sacchi 75–80 µm (LM), 65–

80 (SEM), pollen width including sacci 45–55 µm (LM), 40–50 µm (SEM), corpus diameter 45–55 µm (LM), sacci width 40–50 µm (LM), 40–45 µm (SEM), sacci height 25–30 µm (LM), 20–25 µm (SEM); leptoma; sacci with alveolate structuring; sculpturing scabrate in cappa region and psilate in leptoma region (LM), corpus rugulate, verrucate, perforate, fossulate (SEM), sacci slightly perforate, slightly rugulate relief (SEM); abundance: abundant.

Remarks. – Narrowly attached, spherical sacci and a leptoma with no thickenings are characteristic of the Diploxylon-pollen-type (Hesse et al., 2009). Schorn (in Manchester, 2001) identified gymnosperm macrofossils from Florissant and assigned three to *Pinus* subgenus *Strobus* (Haploxylon-type) and three to *Pinus* subgenus *Pinus* (Diploxylon-type). *Pinus* pollen belonging to both subgenera have been reported from Florissant (Hascall, 1988; Leopold & Clay-Poole, 2001; Wingate & Nichols, 2001). Present in all samples.

Genus Tsuga (Endl.) Carrière

Tsuga sp. 1

(Plate 8C, Figure 9G–H)

Description. – Pollen, monosaccate, oblate, circular in polar view, equatorial diameter 50–65 µm (LM), 40–55 µm (SEM); leptoma; sculpturing rugulate, (LM), on proximal side rugulate, fossulate (SEM); abundance: very rare.

Remarks – The rugulate, echineless proximal side sets *Tsuga* sp.1 apart from *T. sp. 2*. Echineless *Tsuga* pollen are typically found in extant *T. canadensis* (L.) Carrière and *T. caroliniana* Engelm (Sivak, 1973). Present in sample UF15880-7285.

Tsuga sp. 2

(Plate 8D, Figure 9I–M)

Description. – Pollen, monosaccate, oblate, circular in polar view, equatorial diameter 60–70 μm (LM), 55–60 μm (SEM); leptoma, sculpturing verrucate, rugulate (LM), verrucate, rugulate, fossulate, perforate (SEM), proximal side in polar area small verrucae (diameter 0.4–0.8 μm), on distal side in polar area verrucae small and sparsely microechinate (diameter 0.4–0.8 μm , SEM), in equatorial (monosaccus) area verrucae wide and sparsely microechinate (diameter 1–2 μm , SEM), proximal side in polar area verrucae medium-sized and sparsely microechinate (diameter 1.2–0.6 μm , SEM). Abundance: very rare.

Remarks – *Tsuga* sp. 2 has an echineless proximal and slightly echinate distal side, similar with extant *T. caroliniana* (Sivak, 1973). From Florissant *Zonalapollenites* sp. (Wingate & Nichols, 2001, pl. 3, fig. 3) and *Tsuga*-type pollen (Leopold & Clay-Poole 2001) have been reported. Present in samples UF15880-7285.

Order Gnetales

Family Ephedraceae Dumortier

Genus Ephedra L.

Ephedra sp.

(Figures 10A–B, 11A–D)

Description. – Pollen, inaperturate, oblate, equatorial outline elliptic, polar axis 20–28 μm (LM), 18–24 μm (SEM), equatorial diameter 45–60 μm (LM), 37–50 (SEM); exine ca. 1 μm thick, tectate; sculpturing plicate, psilate, fossulate (LM & SEM), 5–7 plicae present, sinuous pseudosulci running parallel to plicae, pseudosulci with first and second order branching (LM & SEM); abundance: abundant.

Remarks. – Pollen morphology of extant *Ephedra* has recently been studied extensively by Bolinder et al. (in press). Pollen from Florissant shares several features (number of plicae, branching of pseudosulci) with extant *E. nevadensis* S. Watson and *E. viridis* Coville (Steeves

& Barghoorn, 1959; Bolinder et al., in press). Hascall (1988) reported two types of *Ephedra* pollen, Type 1 (pl. 1, figs 5–6) with branched pseudosulci (=furrows), corresponding to the here reported *Ephedra* sp., and (very rarely) Type 2 (pl. 1, fig. 7) with unbranched pseudosulci. The grain in Fig. 10A and 11A–B shows strong similarities to *Ephedripites exiguus* (Frederiksen) Wingate et Nichols (Wingate & Nichols, 2001, pl. 3, fig. 9), while that in Fig. 10B and 11C–D is similar to *Ephedra* cf. *E. nevadensis* figured in Leopold and Clay-Poole (2001, pl. 2, fig. 4) and *E. claricristatus* (Shakhmundes) Krutzsch (Wingate & Nichols, 2001, pl. 3, fig. 8). Because pollen morphology, including number and shape of plicae, is variable in modern species of *Ephedra* El-Ghazaly and Rowley (1997) questioned the phylogenetic significance of this character in fossil *Ephedra* pollen. In a recent study on extant *Ephedra* pollen, Bolinder et al. (in press) suggested that the branching of the pseudosulci is phylogenetically significant. These authors reconstructed pollen with unbranched pseudosulci as the ancestral form, pseudosulci with first order branching as derived, and pseudosulci with first and second order branching as the most derived form. The here depicted grains correspond to the most derived type of *Ephedra* pollen according to Bolinder et al. (in press).

Angiosperms

Monocotyledone

Family Poaceae Barnhart

Poaceae gen. indet. 1 aff. Stipa/Achnatherum

(Figures 10C, 11E–F)

Description. – Pollen, spheroidal, outline circular, pollen diameter 20–25 µm (LM & SEM); eutectate, exine 0.5–1 µm thick, ulcerate; sculpturing scabrate (LM), rugulate, microechinate, perforate (SEM), micro echinae not fused; abundance: rare.

Remarks. – The echinate, perforate sculpturing of this grain resembles pollen of extant *Stipa/Achnatherum* [eg. *S. (Achnatherum) calamagrostis* Wahlenb. (Page, 1978), *S. eriocaulis* Borbás (Halbritter, 2015)]. Present in sample UF15880-7285.

Poaceae gen. indet. 2

(Plate 10D, Figure 11G–H)

Description. – Pollen, spheroidal, pollen outline circular, pollen diameter 28–36 μm (LM), 23–31 (SEM); eutectate, exine 0.8–1.2 μm thick, ulcerate, annulus present; sculpturing scabrate (LM), slightly rugulate, verrucate, microechinate (SEM), microechini fused together on rugulae/verrucae (SEM); abundance: rare.

Remarks. – Poaceae gen. indet. differs from P. gen. indet. aff. *Stipa/Achnatherum* in larger size, annulus presence and the microechinate-microrugulate sculpture. These features are common in several extant genera of Poaceae (Köhler & Lange, 1979; Page, 1978). The here depicted specimen of this rare pollen type shows pale staining and no cellular content. Nevertheless, modern contamination cannot be ruled out in this particular case.

MacGinitie (1953) assigned fossil fruits from Florissant to *Stipa florissantii* (Knowlton) MacGinitie. According to Manchester (2001) these fruits belong to Poaceae but cannot be assigned to a particular genus. The presence of Poaceae pollen was verified in previous palynological studies [Hascall, 1988, pl. 3, figs. 7 & 10; Leopold & Clay-Poole, 2001, pl. 8 figs 1–2; Wingate & Nichols, 2001; *Graminidites crassiglobolus* (Trevisan) Krutzsch, pl. 9 figs 7–8]. Present in sample S151454.

Family Typhaceae Juss.

Genus Sparganium L.

Sparganium sp.

(Plate 10E, Figure 11I–J)

Description. – Pollen, spheroidal, outline circular to elliptic, equatorial diameter 24–29 μm (LM), 20–24 μm (SEM); semitectate, exine 1.5–2 μm (LM), nexine and sexine of same thickness (LM); ulcerate, ulcus diameter 5–8 μm ; sculpturing reticulate (LM), heterobrochate reticulate (SEM), lumina elongated, lumina 0.2–1.0 μm wide, muri 0.2–0.5 μm wide, muri show blunt excrescences (SEM), freestanding columellae visible in area of ulcus; abundance: very rare.

Remarks. – In LM *Sparganium* sp. and *Typha* sp. 1 (see below) are impossible to distinguish; in SEM lumina of *Sparganium* sp. are smaller and more elongated, furthermore its muri show suprasculpturing consisting of blunt excrescences. These characteristics are also found in extant and fossil *Sparganium* pollen (Punt, 1975; Grímsson et al., 2014). Lumina of *Typha* sp. 1 are wider in size and of irregular shape; the muri show crested suprasculpturing with sharp edges. These characteristics are typically encountered in extant and fossil *Typha* pollen (Solomon et al., 1973; Punt, 1975; Hamdi et al., 2010; Stuchlik, 2009; Grímsson et al., 2015). *Typha/Sparganium*-type pollen has previously been reported from the Florissant Formation [Hascall, 1988, pl. 3, figs 12–13; Leopold & Clay-Poole, 2001, pl. 8, fig. 3; Wingate & Nichols, 2001, *Sparganiaceapollenites sparganioides* (Meyer) Krutzsch, pl. 9, fig. 10]. Present in samples UF15880-7285.

Genus Typha L.

Typha sp. 1

(Plate 10F, Figure 11K–L)

Description. – Pollen, spheroidal, outline circular to elliptic, diameter 25–30 μm (LM), 20–35 μm (SEM); semitectate, exine 1.5–2 μm (LM), nexine and sexine of same thickness (LM); ulcerate, ulcus diameter 5–8 μm ; sculpturing heterobrochate reticulate (LM & SEM), lumina

0.3–1 μm wide, muri 0.4–0.6 μm wide (SEM), muri crested with sharp ridges; abundance: abundant.

Typha sp. 2

(Plate 10G, Figure 11M–N)

Description. – Pollen, spheroidal, outline circular to elliptic, diameter 35–45 μm (LM), 30–35 μm (SEM); semitectate, exine 1.5–2 μm (LM), nexine and sexine of same thickness (LM); ulcerate, ulcus diameter 5–8 μm ; sculpturing heterobrochate reticulate (LM & SEM), lumina 0.3–1.5 μm wide, muri 0.4–1 μm wide (SEM), muri smooth; abundance: infrequent.

Remarks. – *Typha* sp. 1 and *T.* sp. 2 differ in pollen size and muri sculpturing (*T.* sp. 1, crested muri; *T.* sp. 2, smooth muri) but both fall within the morphological range (size, ulcerate aperture, reticulate ornamentation, muri ornamentation) of extant and fossil *Typha* pollen (Solomon et al., 1973; Punt, 1975; Hamdi et al., 2010; Stuchlik, 2009; Grimsson et al., 2015). Fossil leaves assigned to *Typha lesquereuxi* Cockerell (Manchester, 2001) and *Typha/Sparganium*-type pollen [Hascall, 1988, pl. 3, figs. Leopold & Clay-Poole, 2001, pl. 8 fig. 3; Wingate & Nichols, 2001, *Sparganiaceapollenites sparganioides* (Meyer) Krutzsch, pl. 9 fig. 10] are known from the Florissant Formation. Present in all samples.

Monocotyledonae pollen fam. et gen. indet.

(Figures 10H, 11O–P)

Description. – Pollen, spheroidal, outline circular, diameter 15–20 μm (LM & SEM); semitectate, exine 0.8–1 μm thick, sulcate; sculpturing psilate (LM), microreticulate to microverrucate, perforate to microfossulate (SEM); abundance: very rare.

Remarks. – A similar surface sculpturing and sulcate apertures are common in several monocot families, but occur typically within the Commelinids clade (e.g. Arecaceae,

Commelinaceae). A definite family assignment of this dispersed fossil pollen is not possible (cf. Poole & Hunt, 1980; Dransfield et al., 2008). Present in sample UF15880-7285.

Eudicotyledonae

Family Adoxaceae E.Mey./Caprifoliaceae Juss.

Adoxaceae vel Caprifoliaceae gen. indet.

(Figures 12A, 13A–B)

Description. – Pollen, prolate, outline elliptic in equatorial view, polar axis 50–55 μm (LM), 40–45 μm (SEM), equatorial diameter 40–45 μm (LM), 35–40 μm (SEM); semitectate, exine 2.5–3 μm thick, nexine thinner than sexine, tricolporate, colpus sculpturing microverrucate (SEM); sculpturing heterobrochate reticulate (LM), lumina decreasing in size to perforations in colpus area, compacted tectum with slight furrows surrounding colpus, muri smooth, muri width ca. 1 μm , collumellae width 0.3–0.6 μm , collumellae height 1.5–2 μm , footlayer of lumina with sporadic verrucae (freestanding collumellae?); abundance: common.

Remarks. – Morphological characters (tricolporate apertures, reticulate tectum, reticulum condensed in aperture areas, lumina with freestanding collumellae) of this pollen are commonly found in Dipsacales (Donoghue, 1985; Maciejewska, 1997). Adoxaceae vel Caprifoliaceae gen. indet. has morphological similarities with extant *Viburnum* L. (Donoghue, 1985; Maciejewska, 1997) and *Sambucus ebulus* L. (Punt et al., 1974; Schneider et al., 2005, Tamas et al, 2009), but differs in larger size. Pollen very similar to the one depicted here was assigned to *Viburnum* (Leopold & Clay-Poole, 2001, pl. 6, fig. 14) and resembles *Rhoipites* sp. C (Wingate & Nichols, 2001, pl. 5, fig. 21).

From Florissant *Sambucus newtoni* Cockerell (MacGinitie, 1953; Manchester, 2001) leaves and leaflets have been reported. Present in samples UCMP 20778 and UF15880-7285.

Family Amaranthaceae Juss.

Amaranthaceae gen. indet. 1

(Figures 12B, 13C–D)

Description. – Pollen, spheroidal, pollen outline circular, diameter 20–25 μm wide (LM & SEM); eutectate, exine 1.5–2 μm thick (LM), pantoporate, 36–50 pori, pori diameter 1–1.5 μm (LM & SEM), pores operculate, operculum ornamented with 4–8 microechini (SEM); sculpturing scabrate (LM), sparsely microechinate, microechini density on a 1x1 μm square 2, perforate, perforation density on a 1x1 μm square 13–16 (SEM); abundance: rare.

Remarks. – A number of studies (Dehghani & Akhane, 2009; Hamdi et al., 2009; Müller & Borsch, 2005; Olvera et al., 2006; Toderich et al., 2010) have shown that, although pollen characters are useful to distinguish species within a genus, it is impossible to reliably identify subfamilies because of substantial overlap in morphological variability.

Chenopodiaceae/Amaranthaceae Type 3 of Hascall (1988, pl. 4, fig. 31) shows similar pollen size and pore-size. Present in all samples.

Amaranthaceae gen. indet. 2

(Figures 12C, 11E–F)

Description. – Pollen, spheroidal, outline circular, pollen diameter 22–28 μm (LM); eutectate, exine 1.5–2 μm thick (LM), pantoporate, 12–17 pori, porus diameter 2–4 μm (LM & SEM), porus framed by paired microechini, pores operculate, operculum ornamented with 10–20 microechini (SEM); sculpturing scabrate (LM), microechinate, microechini density on a 1x1 μm square 4–7, perforate, perforation density on a 1x1 μm square 11–14 (SEM); abundance: rare.

Remarks. – Amaranthaceae gen. indet. 2 differs from Amaranthaceae gen. indet. 1 in slightly larger pollen size, lower number of pori and higher microechini density. Amaranthaceae gen.

indet. 2 shows strong similarities in pollen size and pore size to
Chenopodiaceae/Amaranthaceae Type 2 of Hascall (1988, pl. 4, fig. 30) and Chenopodiaceae
undetermined of Leopold and Clay-Poole (2001, pl. 9, fig. 15). Present in all samples.

Family Apocynaceae Juss.

Genus Tabernaemontana Plum. ex L.

Tabernaemontana sp.

(Figures 12I, 13M–O)

Description. – Pollen, prolate, outline elliptic in equatorial view, polar axis 18–22 μm (LM & SEM), equatorial diameter 14–18 μm (LM & SEM); eutectate, exine 1.5–2 μm , nexine thinner than sexine, tricolporate, ectoaperture colpus, colpus slightly constricted in endoaperture area, endoaperture rectangular elongated (endocingulum); sculpturing scabrate (LM), perforate to slightly microreticulate (SEM), perforations decrease in aperture area around the equator ; abundance: very rare.

Remarks. – Extant species of *Tabernaemontana* produce pollen with endocingulate colporate apertures and perforate to microreticulate sculpturing similar to the here depicted grain, which shows closest resemblance to *Tabernaemontana coronaria* (Jacq.) Willd. (Van Campo et al., 1979). The presence of Apocynaceae seeds have been confirmed by Manchester (2001) and similar pollen pollen has previously been reported by Leopold et al. (2001, *Tabernaemontana* cf. *T. coronaria* pl. 6, fig. 12–13; 2008) and Wingate and Nichols (2001, *Tetracolporopollenites* sp., pl. 6, fig. 21). The extant 15 genera, 150 species of *Tabernaemontaneae* have a pan-tropical distribution (Stevens, 2001 et seq.). Present in sample UF15880-7285.

Family Asteraceae Berchtold et J.Presl

1
2
3 *Subfamily Asteroideae (Cass.) Lindl.*

4
5 *Asteroideae gen. indet.*

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7 (Figures 12H, 13K–L)

8
9 *Description.* – Pollen, spheroidal, pollen outline circular, pollen diameter 12–17 μm (LM &
10 SEM); eutectate, exine including echine 2–4 μm thick, aperture indistinct but tricolporate;
11 sculpturing echinate (LM) echinate, perforate, slightly fossulate (SEM), echinae base 1.5–2.0
12 μm diameter (LM & SEM), upper half of echinae without perforations, base of echinae
13 slightly rugulate (SEM); abundance: very rare.

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21 *Remarks.* – *Asteroideae gen. indet.* displays indistinct apertures, short echini with perforate,
22 rugulate and slightly fossulate base, characters found in extant *Ambrosia* L. and *Iva* L.
23 (Halbritter, 2012; Jones et al., 1995; Punt & Hoen, 2009; Sam & Halbritter, 2013). Previously
24 reported Asteraceae/Compositae pollen (Hascall, 1988, pl. 4, fig 16, Wingate & Nichols,
25 2001, pl. 6 fig. 19a–19b) corresponds in size and ornamentation to the one reported here.
26 Previous palynological studies (Hascall, 1988; Wingate & Nichols, 2001; Leopold & Clay-
27 Pool, 2001) considered pollen of Asteraceae a possible modern contaminant, because of its
28 rarity and/or rather early stratigraphic appearance. Although processing of investigated
29 samples was carried out with highest diligence we cannot rule out the possibility of modern
30 contamination in this case. Present in sample UF15880-7285.
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45 *Family Betulaceae Gray*

46
47 *Subfamily Betuloideae Arnott*

48
49 *Genus Alnus L.*

50
51 *Alnus sp.*

52
53 (Figures 14B)

Description. – Pollen, oblate, outline polygonal in polar view, equatorial diameter 20–22 μm (LM); eutectate, exine 1.0–1.5 μm thick (LM); pentoporate, annulate pori, porus diameter 1.5–2 μm (LM); sculpturing scabrate (LM), arci present; abundance: single observation.

Remarks. – This grain is badly preserved but can be securely assigned to *Alnus* because of several characteristics (outline, arci presence, annulate pori) typical of pollen of this genus (Blackmore et al., 2003; Beug, 2004; Stuchlik, 2009; Zetter et al., 2011). Wingate and Nichols (2001, pl. 8, fig. 11) reported a single specimen of *Alnipollenites verus* Potonié ex Potonié; the rarity of this pollen is probably due to long distance dispersal (absence of this genus in the vicinity of the palaeolake). Modern contamination can be ruled out due to the lack of cytoplasmic content, pale staining and bad preservation of this grain. *In situ Alnus* pollen has been described from Eocene and Oligocene of Oregon, USA (Liu et al., 2014). Present in sample S151454.

Genus Betula L.

Betula sp.

(Figures 14A, 15A–B)

Description. – Pollen, oblate, convex triangular in polar view, elliptic in equatorial view, polar axis 18–20 μm (LM), equatorial diameter 18–25 μm (LM & SEM); eutectate, exine 1.0–1.5 μm thick (LM), nexine and sexine have the same thickness, nexine and sexine part in porus area forming atrium; triporate, ektoporus smaller than endoporus, annulate pori, ektoporus diameter 1.5–2 μm , endoporus diameter 3–4 μm (LM); sculpturing scabrate (LM), microrugulate, microechinate (SEM); abundance: rare.

Remarks. – The morphology of this pollen is indistinguishable from that of extant and fossil *Betula* pollen (Blackmore et al., 2003; Beug, 2004; Grimsson et al, in press; Stuchlik, 2009;

Zetter et al., 2011). This pollen resembles *Trivestibulopollenites betuloides* Pflug ex Thomson et Pflug (Wingate & Nichols, 2001, pl. 8, fig. 7). Present in all samples.

Subfamily Coryloideae

Coryloideae gen. indet. 1

(Figures 14C, 15C–D)

Description. – Pollen, oblate, circular in polar view, equatorial diameter 25–30 μm (LM), 20–25 (SEM); eutectate, exine 1.0–1.5 μm thick (LM); triporate, annulate pori, porus diameter 1.5–2 μm (LM & SEM); sculpturing scabrate (LM), microrugulate, microechinate (SEM), abundance: rare.

Remarks. – The morphology of this pollen corresponds to extant and fossil coryloid Betulaceae (Blackmore et al., 2003; Beug, 2004; Stuchlik et al., 2009; Zetter et al., 2011) with similarity to *Cranea wyomingensis* Manchester et Chen (Manchester & Chen, 1998). This grain resembles *Triatriopollenites subtriangulus* (Stanley) Frederiksen (Wingate & Nichols, 2001, pl. 8, fig. 5) and *Ostrya/Carpinus* pollen type depicted by Leopold and Clay-Poole (2001, pl. 8, figs 4–5). Present in all samples.

Coryloideae gen. indet. 2

(Figures 14D, 15E–F)

Description. – Pollen, oblate, circular in polar view, equatorial diameter 35–45 μm (LM), 25–35 (SEM); eutectate, exine 1.0–1.5 μm thick (LM); tetraporate, annulate pori, porus diameter 2.5–3 μm (LM & SEM); sculpturing scabrate (LM), microrugulate, microechinate (SEM), sculpturing shows low relief; abundance: rare.

Remarks. – The morphology of this pollen corresponds with extant and fossil coryloid Betulaceae (Blackmore et al., 2003; Beug, 2004; Stuchlik et al., 2009; Zetter et al., 2011) and

shows similarity to extant *Carpinus* L. and fossil *Palaeocarpinus dakotensis* Manchester, Pigg et Crane (Manchester et al., 2004). From Florissant fruits [*Asterocarpinus perplexans* (Cockerell) Manchester and Crane], leaves [*Paracarpinus fraterna* (Lesquereux) Manchester et Crane], and pollen of Betulaceae have been reported (MacGinitie, 1953; Manchester, 2001; Leopold & Clay-Poole, 2001; Wingate & Nichols, 2001). Present in samples UCMP20778 and UF15880-7285.

Family Cannabaceae Martinov

Genus Celtis L./Pteroceltis Maxim.

Celtis vel Pteroceltis sp.

(Figures 28B, 29C–D)

Description. – Pollen, oblate, outline circular in polar view, equatorial diameter 25–30 µm (LM), 20–25 (SEM); eutectate, exine 1–1.5 µm thick, stephanoporate (3–4), ectoporus circular, pore diameter 3–4 µm (LM), weak annulus present; sculpturing psilate to scabrate (LM), microechinate (SEM), microechini widely spaced; abundance: rare.

Remarks. – The widely microechinate exine sculpturing, slightly annulate aperture and size range of this pollen type correspond to pollen of extant *Celtis* and *Pteroceltis* (Li et al., 2010; Myoshi et al., 2011; Stafford, 1995; Takahashi, 1989; Stuchlik et al., 2009; Zavada, 1983). Morphological characters (e.g. size range, number of apertures, exine sculpturing) overlap in extant *Celtis* and *Pteroceltis* which makes it impossible to allocate dispersed pollen (compare Takahashi, 1989; Zavada, 1983). Leaves of *Celtis mccoshii* Lesquereux (MacGinitie, 1953; Manchester, 2001) and similar pollen have been reported from Florissant in previous palynological studies [Hascall, 1988, *Celtis* Type 1 & 2, pl. 3. fig 15., pl. 4. fig. 21; Wingate & Nichols, 2001, *Cricotriporites intrastructurus* (Krutzsch et Vanhoorne) Wingate et

Nichols, pl. 7, figs 16–17; Leopold & Clay-Poole, 2001, *Carpinus/Ostrya*, pl. 8, fig. 5].

Present in all samples.

Family Caprifoliaceae Juss.

Subfamily Caprifolioideae/Linnaeoideae

Caprifolioideae/Linnaeoideae gen. indet.

(Figures 14E, 15G–H)

Description. – Pollen, oblate, outline circular to convex triangular in polar view, equatorial diameter 35–45 μm (LM), 30–40 μm (SEM); eutectate, exine 1.5–2 μm thick, nexine and sexine have the same thickness, brevitricolporate; sculpturing echinate (LM), echinate to microechinate, perforate (SEM), echinae base diameter 0.4–0.6 μm (SEM); abundance: very rare.

Remarks. – This grain corresponds to extant and fossil Caprifolioideae/Linnaeoideae pollen, with strong similarity to *Abelia* R. Brown and *Lonicera* L. (Punt et al., 1974; Chia-Chi & Chao-Xin, 1988; Perveen & Qaiser, 2007; Stuchlik et al., 2014). Caprifoliaceous fruits (Manchester, 2001) and three discernible types of pollen (Wingate & Nichols, 2001) are known from Florissant. Caprifolioideae/Linnaeoideae gen. indet. corresponds to *Lonicera pollis* sp. A of Wingate and Nichols (2001, pl. 7 fig. 11). Present in samples S151454 and UF15880-7285.

Family Ebenaceae Gürke

Genus Diospyros L.

Diospyros sp.

(Figures 14F, 15I–J)

Description. – Pollen, prolate, outline elliptic in equatorial view, polar axis 40–45 µm (LM), 30–35 µm (SEM), equatorial diameter 25–30 µm (LM & SEM); eutectate, exine 0.5–1.0 µm thick, tricolporate; sculpturing scabrate (LM), microrugulate, fossulate (SEM); abundance: very rare.

Remarks. – This pollen type cannot be distinguished from other genera within Ebenaceae, Sapotaceae, and Styracaceae based on LM observations (Erdtman, 1952). The characteristic microrugulate fossulate exine ornamentation typical of *Diospyros* is only discernible when investigated under SEM (Cerceanu-Larrival et al., 1984, Grygorieva et al., 2010). Present in sample UF15880-7285.

Family Elaeagnaceae Juss.

Elaeagnaceae gen. indet.

(Figures 14H)

Description. – Pollen, oblate, outline triangular, polar axis 17–29 µm (LM), equatorial diameter 20–25 µm (LM); eutectate, exine 1.5–2.0 µm thick, nexine thinner than sexine, tricolporate to nearly syncolporate; sculpturing scabrate (LM); abundance: single observation.

Remarks. – This grain shows strong morphological similarity (size, shape, apertures) to extant Elaeagnaceae pollen (Sorsa, 1971; Li et al. 2010; Miyoshi et al., 2011; Halbritter, 2005a).

Similar pollen grains have been reported in previous studies (Wingate & Nichols, 2001,

Slowakipollis hippophaëoides Krutzsch, pl. 6, fig. 18; Leopold & Clay-Poole, 2001,

Elaeagnus cf. *Elaeagnus argentea* Pursh pl. 6, figs 8–9). Only a single grain was encountered; it could not be transferred to a SEM-stub. Present in sample UF15880-7285.

Family Ericaceae Juss.

Ericaceae gen. indet.

(Figures 14F, 15K–L)

Description. – Pollen in persistent tetrads, spheroidal, outline of monade circular, tetrad outline convex triangular, tetrad equatorial diameter 35–40 μm (LM), 30–35 μm (SEM), monade equatorial diameter 20–25 μm (LM & SEM), monade height 20–25 μm (LM); eutectate, exine 1.0–1.5 μm thick; monade tricolporate, tetrad coaperturate, tetrad hexacolpate, joined colpus length 17–19 μm , colpus membrane microechinate (SEM); sculpturing scabrate (LM), in central mesopolpium areas microverrucate, microrugulate, fossulate, in polar areas and around apertures perforate, fossulate; abundance: very rare.

Remarks. – Ericaceae gen. indet. corresponds to extant Ericaceae pollen by the presence of both microverrucate, microrugulate, and fossulate sculpturing in the mesocolpium (Sawara, 2007) but cannot be linked to a particular extant genus. From Florissant Ericaceae-type pollen have previously been reported (Leopold & Clay-Poole, 2001, pl. 7, fig. 10–11; Wingate & Nichols, 2001, *Ericipites* sp. cf. *E. longisulcatus* Wodehouse, pl. 9. Fig. 12). Present in sample UF15880-7285.

In situ pollen of persistent tetrads has also been reported from the extinct Fabaceae *Eomimosoidea* of the middle Eocene Clairborne Formation, Tennessee (Crepet & Dilcher, 1977) and *Eomimosoidea plumosa* Crepet et Dilcher of the Oligocene Catahoula sandstone, Texas (Daghlian et al., 1980). Both are superficially similar to the pollen described here in size range, aperture type and aperture position but differ in the globally distributed rugulate fossulate exine sculpturing commonly found in extant Mimosoideae pollen (e.g. Santos-Silva et al., 2013) but not in Ericaceae.

Family Eucommiaceae Engler

Genus Eucommia Oliv.

Eucommia sp.

(Figures 14H–I, 15M–P)

Description. – Pollen, prolate, triangular-lobate in polar view, elliptic in equatorial view, polar axis 20–30 μm (LM), 15–20 μm (SEM), equatorial diameter 15–25 μm (LM), 12–20 μm ; eutectate, exine 1.5–2.0 μm thick (LM), nexine and sexine have the same thickness, tricolporate to tricolporidate, colpus length 15–18 μm (LM); sculpturing psilate (LM), microechinate, perforate (SEM); abundance: infrequent.

Remarks. – This pollen corresponds in size and morphological features to extant *Eucommia ulmoides* Oliv. (Yu-Long et al., 1988; Li et al., 2010) and fossil *Eucommia* pollen (Stuchlik et al., 2014). *Eucommia* fruits (Manchester, 2001) and pollen (Leopold & Clay-Poole, 2001, pl. 5, fig. 5; Wingate & Nichols, 2001, *Tricolpopollenites parmularius* (Potonié) Thomson & Pflug, pl. 5, figs. 8–9) have previously been reported from Florissant.

Today the monotypic family Eucommiaceae, with a single extant species *Eucommia ulmoides* Oliv., is restricted to central China (Wu et al., 2003). In contrast, the Palaeogene and Neogene fossil record of *Eucommia* shows a wide Northern Hemispheric distribution (Ferguson et al., 1997; Manchester et al., 2009). Present in all samples.

Family Euphorbiaceae Marcano-Berti

aff. Euphorbiaceae gen. indet.

(Figures 16A, 17A–B)

Description. – Pollen, prolate, elliptic in equatorial view, polar axis 34–37 μm (LM), equatorial diameter 25–28 μm (LM), semitectate, exine 1.5–2.0 μm thick (LM), nexine thinner than sexine; colporate (3), sculpturing microreticulate (LM), microreticulæ funnelshaped, perforate (SEM); abundance: very rare.

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3 *Remarks.* – The funnel-shaped microreticulum and colporate apertures of this pollen suggest
4 closer affinities with Euphorbiaceae, extant tribe Epiprineae (Takahashi et al., 2000). Present
5 in sample UF15880-7285.
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11 *Family Fabaceae Lindl.*

12 *Subfamily Caesalpinioideae DC.*

13 *Caesalpinioideae gen. indet.*

14 (Figure 16B)

15
16 *Description.* – Pollen, outline circular in polar view, equatorial diameter 50–55 µm (LM);
17 semitectate, exine 1.5–2.0 µm thick (LM), nexine thinner than sexine, tricolporate;
18 sculpturing reticulate in mesocolpium and apocolpium, colpus membrane scabrate (LM),
19 microechinate, perforate (SEM); abundance: single observation.
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21
22 *Remarks.* – Caesalpinioideae gen. indet. shows strong affinities to *Margocolporites* sp. cf. *M.*
23 *vanwijhei* Germeraad, Hopping et Muller (Wingate & Nichols, 2001, pl. 6, figs 1–2), which
24 was compared with pollen of extant *Caesalpina crista* L. and *C. coriaria* (Jacq.) Willd.; to
25 this list we can add *C. echinata* Lam. (Corrêa, 2003). Only a single grain was encountered
26 that could not be transferred to a SEM-stub.
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29 From Florissant fabaceous leaflets (*Caesalpinites*, *Leguminosites*), leaves, fruits (*Cercis*) and
30 pollen have been reported (Manchester, 2001; Wingate & Nichols, 2001). Present in sample
31 UF15880-7285.
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41 *Family Fagaceae Dumortier*

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43 *Remarks* – Pollen and macrofossils of *Fagaceae* from Florissant have been reviewed by
44 Bouchal et al. (2014). *Castaneoideae*, *Fagopsis longifolia*, and *Quercus* pollen is present in
45 all samples.
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Subfamily Castaneoideae (paraphyletic)

Castaneoideae gen. indet. sp. 1

(Figures 16C, 17C–D)

Description – Pollen, prolate, elliptic in equatorial view, polar axis 14–16 μm (LM), 12–14 μm (SEM), equatorial diameter 9–11 μm (LM), 7.5–9 μm (SEM); eutectate, exine 1 μm thick (LM), tricolporate, colpus length 6–8 μm long (SEM); sculpturing scabrate (LM), microrugulate-striate, indistinctly perforate-fossulate (SEM), rugulae width 0.1–0.2 μm , microrugulae well developed, microrugulae show parallel running microstriate suprasculpturing in polar areas (SEM); abundance: infrequent.

Remarks Castanoid pollen has been reported by Hascall (1988, pl. 4, fig. 23). Further remarks on *Castaneoideae gen. indet. sp. 1* can be found in Bouchal et al. (2014).

Castaneoideae gen. indet. sp. 2

(Figures 16D, 17E–F)

Description – Pollen, prolate, elliptic in equatorial view, polar axis 14–16 μm (LM), 12–14 μm (SEM), equatorial diameter 9–11 μm (LM), 7.5–9 μm (SEM); eutectate, exine 1 μm thick (LM), tricolporate, colpus length 6–8 μm long (SEM); sculpturing scabrate (LM), microrugulate-striate, indistinctly perforate-fossulate (SEM), rugulae 0.1–0.2 μm wide, microrugulae well developed in equatorial area, most distinct in apertural region, in polar areas microrugulae are coarser and their boundaries masked by sporopollenin resulting in a weak relief (SEM); abundance: infrequent.

Remarks – Remarks on *Castaneoideae gen. indet. sp. 2* can be found in Bouchal et al. (2014).

Castaneoideae gen. indet. sp. 3

(Figures 16E, 17G–H)

Description – Pollen, prolate, elliptic in equatorial view, polar axis 11–13 μ m (LM), 8–11 μ m (SEM), equatorial diameter 8–10 μ m (LM), 5–7 μ m; eutectate, exine 1.0 μ m thick (LM), tricolporate; sculpturing scabrate (LM), microrugulate/rugulate, approaching striate (SEM), rugulae 0.1–0.2 μ m wide (SEM), groups of several parallel microrugulae forming angles of 90° to 45° to each other, “patchwork”-like; in colpus area striae parallel with colpus; abundance: infrequent.

Remarks – Remarks on *Castaneoideae* gen. indet. sp. 3 can be found in Bouchal et al. (2014).

Genus Fagopsis Hollick

Fagopsis longifolia (Lesquereux) Hollick

(Figures 16F–G, 17I–L)

Description. – Pollen, prolate to spheroidal, elliptic in equatorial view; polar axis 22–28 μ m (LM), 21–25 μ m (SEM), equatorial diameter 19–26 μ m (LM), 17–25 μ m (SEM); eutectate, exine 1–1.5 μ m thick (LM), tricolporate, bridge present, colpus length 18–22 μ m (SEM); sculpturing scabrate (LM), microrugulate (to rarely rugulate), perforate-fossulate in nonapertural region (SEM), several parallel running microrugulae forming larger rugulae, 0.5 to ≤ 1 μ m long and wide; microrugulae (“striae”) connected by short, perpendicular elements (Fig. 17K–L), in some pollen grains no such connecting elements visible between microrugulae (Fig. 17I–J); sculpturing in apertural region and bridge without fossulae, perforations can be present; abundance: common.

Remarks – Under LM the characters of this pollen (size, shape, aperture, presence of bridge) overlap with that of *Quercus*. Only in SEM the particular pattern of the sexine (rugulae formed by microrugulae), the diagnostic character of *Fagopsis longifolia* pollen, is detectable. Hascall (1988, pl. 4, fig. 18) reported *Fagopsis longifolia* pollen from Florissant, but for

unambiguous identification SEM is needed. Further remarks on *Fagopsis longifolia* can be found in Bouchal et al. (2014).

Genus Quercus L.

Quercus Group Cyclobalanopsis sp.

(Figures 16H, 17M–N)

Description. – Pollen, circular in polar view, pollen diameter 24–26 μm (LM), 21–23 μm (SEM); eutectate, exine 1.0–1.5 μm thick (LM), nexine thinner than sexine, tricolpate to tricolporoidate; sculpturing scabrate (LM), platy verrucate, perforate (SEM); abundance: very rare.

Remarks – Hascall (1988, pl. 4 figs 19, 20, 22, 26) distinguished four types of *Quercus* pollen; allocation to infrageneric groups of *Quercus* is not possible based only on LM. Further remarks on *Quercus Group Cyclobalanopsis sp.* can be found in Bouchal et al. (2014).

Quercus Group Protobalanus sp.

(Figures 16H, 17M–N) *Description.* – Pollen, prolate, elliptic in equatorial view, polar axis 20–24 μm (LM), 19–22 μm (SEM), equatorial diameter 17–20 μm (LM), 15–17 μm (SEM); eutectate, exine 1.0–1.5 μm thick (LM), tricolpate; sculpturing scabrate (LM), weakly verrucate, perforate-fossulate (SEM), suprasculpture microechinate, the microechini being the apical parts of rodlets; abundance: rare.

Remarks –Remarks on *Quercus Group Protobalanus sp.* can be found in Bouchal et al. (2014).

Quercus Group Quercus/Lobatae sp.

(Figures 18A, 19A–B) *Description.* – Pollen, prolate to spheroidal, circular to elliptic in equatorial view, polar axis 20–30 μm (LM), 18–25 (SEM), equatorial diameter 19–24 μm

(LM) 17–21 (SEM); eutectate, exine 1.0–1.5 μm thick, nexine thinner than sexine, tricolpate, colpus length 13–22 μm (LM); sculpturing scabrate (LM), rugulate-verrucate, fossulate, perforate (SEM), rugulae and verrucae show a cauliflower-like, microechinate suprasculpture (SEM); abundance: common.

Remarks – Remarks on *Quercus* Group *Quercus*/Lobatae sp. can be found in Bouchal et al. (2014).

Quercus Group *Quercus* sp.

(Figures 18B, 19C–D)

Description. – Pollen, spheroidal to prolate, circular in equatorial view, circular to elliptic in polar view, polar axis 29–32 μm (LM), 28–30 μm (SEM), equatorial diameter 28–31 μm (LM), 27–29 μm (SEM); eutectate, exine 1.0–1.5 μm thick (LM), nexine thinner than sexine, tricolpate, colpus length 18–20 μm (LM), bridge present (LM & SEM); sculpturing scabrate (LM), microverrucate, weakly perforate (SEM), microverrucae weakly sculptured, smoothly rounded (SEM); abundance: common.

Remarks – Remarks on *Quercus* Group *Quercus* sp. can be found in Bouchal et al. (2014).

Family Hamamelidaceae Brown

Subfamily Hamamelidoideae A.DC.

Hamamelidoideae gen. *indet.*

(Figures 18C, 19E–F)

Description. – Pollen, prolate to spheroidal, outline circular, diameter 22–30 μm (LM), 20–25 μm (SEM); semitectate, exine 1.0–1.5 μm thick (LM), nexine thinner than sexine, tricolpate; sculpturing microreticulate (LM & SEM), muri 0.4–0.8 μm wide (SEM), muri with

microechinate suprasculpture (SEM), footlayer microverrucate (freestanding collumellae); abundance: very rare.

Remarks. – This grain corresponds in size and morphological features (microreticulum crested by microechini, colpate aperture) to extant Hamamelidoideae (Bogle & Philbrick, 1980; Fritz & Allesch, 1999; Miyoshi et al., 2011) Present in sample UF15880-7285.

Family Juglandaceae Perleb *Form genus Momipites (Wodehouse) Nichols*

Momipites coryloides Wodehouse

(Figures 18D–E, 19G–H)

Description. — Pollen, monad, shape oblate, outline circular to convex triangular, equatorial diameter 27–33 μm (LM), 24–28 (SEM); eutectate, exine 1.0–1.5 μm thick (LM); stephanoporate (3), exine slightly thickend around porus in some specimens (LM), aperture diameter 1.5–2 μm (LM & SEM), ectopori circular; sculpturing fine scabrate (LM), microechinate (SEM), microechinimicroechini evenly spaced, microechini density on a 1x1 μm square 1.3–1.6; abundance: infrequent.

Remarks. —Pollen of this type falls within the range of *Momipites coryloides* (Nichols, 1973) and similar to previously reported specimens (Wingate & Nichols, 2001, pl. 8, fig. 1; Leopold & Clay-Poole, 2001, pl. 9, fig. 1), but slightly larger in size. Present in all samples. Strong similarities in outline, shape, exine thickness, exine sculpturing, and circular apertures are with pollen of extant *Oreomunnea* Oerst. and *Alfaroa* Standl. (Stone & Broome, 1975), but differing in slightly larger size (size range in *Oreomunnea* 17.1–26.6 μm ; *Alfaroa* 17.1–30.4 μm , Stone & Broome, 1975, table 1), microechini density, and in some cases (Fig. 18D) slightly thickened exine in pore areas. Extant *Cyclocarya paliurus* (Batal.) Iljinsk. produces predominantly tetraporate pollen (range 3 –7 pori) with thickened exine around circular pori and overlapping size range [*P. paliurus* (= *C. paliurus*) 19 –40.3 μm , Stone & Broome, 1975,

table 1). From the Paleocene Almont locality, North Dakota, USA, unambiguous *Cyclocarya* fruits have been reported (Manchester, 1987), while only triporate pollen of *Momipites* was encountered in the co-occurring pollen assemblage. Therefore, Manchester (1987) suggested the possibility that the primitive triporate condition was more prevalent in Paleocene *Cyclocarya* than in extant *C. paliurus*. The microechinate exine sculpturing of all three present *Momipites* species corresponds with extant and fossil Juglandaceae species (cf. Stone & Broome, 1975; Stuchlik et al., 2009; Grímsson et al., in press). Because of overlapping pollen morphological variability in the fossil taxa we restrain from affiliation to a subfamily within Juglandaceae and use the form genus *Momipites*.

Momipites triradiatus Nichols

(Figures 18F, 19I–J)

Description. — Pollen, monad, shape oblate, outline triangular slightly convex triangular, equatorial diameter 21–24 μm (LM), 19–22 μm (SEM); eutectate, exine 1–1.5 μm thick (LM), triradiate thickening in polar area (folds better visible in SEM); stephanoporate to xstephanobrevicolporate (3), ectoapertures meridionally elongated pores or short colpi; sculpturing psilate (LM), microechinate, perforate (SEM), microechini are evenly spaced, microechini density on a 1x1 μm square 2.1–2.4; abundance: infrequent.

Remarks. — Due to the presence of a polar triradiate thickening and corresponding size range this pollen type is assigned to *Momipites triradiatus*. Similar pollen has been reported from Florissant (Leopold & Clay-Poole, 2001, pl. 8, fig. 9; Wingate & Nichols, 2001, *Momipites triradiatus* Nichols, pl. 8, fig. 3). Present in all samples.

Except for its triradiate polar thickening, which is not found in extant Juglandaceae, pollen morphology of *Momipites triradiatus* matches extant *Engelhardia* (size range, shape, exine sculpturing, meridionally elongated pores or short colpi), and *Alfaroa* and *Oremunnea* in size

range, shape and exine sculpturing (Nichols, 1973; Stone & Broome, 1975).

Momipites microfoveolatus (Stanley) Nichols (Figures 18G, 19K–L)

Description. — Pollen, monad, shape oblate, outline triangular, equatorial diameter 24–27 μm (LM), 22–25 μm (SEM); eutectate, exine 1.0–1.5 μm thick (LM); stephanoporate, aperture diameter 1.5–2 μm (LM & SEM), ectoapertures circular; sculpturing scabrate (LM), microechinate, perforate (SEM), microechini density on a 1x1 μm square 1.4–1.8; abundance: infrequent.

Remarks. — Grains of this type are within the range of *Momipites microfoveolatus*, similar pollen have been reported in previous palynological studies from Florissant (Hascall, 1988, *Engelhardia*, pl. 3, fig. 20; Wingate & Nichols, 2001, pl. 8, fig. 2) microechini.. Present in all samples.

Due to their similarities in exine sculpturing and aperture it cannot be ruled out that *Momipites coryloides* and *M. microfoveolatus* originated from the same taxon and show the morphological variability of a single genus or species. The extant Engelhardioideae consist of four genera, including 14 species and show a South-east Asian, Central and north South American distribution (Manchester, 1987; Stone, 1993; Manos & Stone, 2001).

Subfamily Juglandoideae Eaton

Genus Carya Nuttall

Carya sp.

(Figures 18H–I, 19M–P)

Description. – Pollen, oblate, outline circular, equatorial diameter 30–40 μm (LM), 28–33 μm (SEM); eutectate, exine 1.0–1.5 μm thick (LM), nexine thinner than sexine, polar area thinned; triporate, pores sunken, pores slightly subequatorial positioned (offset towards the

distal pole, LM & SEM), aperture diameter 3–5 μm (LM & SEM); sculpturing psilate to scabrate (LM), microechinate (SEM), microechini density on a 2x2 μm square 12–18; abundance: abundant.

Remarks. – This pollen type falls within the variability of extant (Stone & Broome, 1975; Bos & Punt 1991; Jones et al., 1995) and fossil *Carya* pollen (Stuchlik et al., 2009). The grains in Figs 18H and 19O show a circular ring of exinal thinning on the proximal pole; this is also common in extant *Carya* pollen (Stone & Broome, 1975, fig. 1L; Bos & Punt, 1991, pl. 3 fig. 1). From Florissant *Carya* leaves [*C. libbeyi* (Lesquereux) MacGinitie], fruits [*C. florissantensis* Manchester (MacGinitie, 1953; Manchester, 1987; 2001], dispersed pollen [Hascall, 1988, pl. 3, fig 16, 17; Leopold & Clay-Poole, 2001, pl. 8, fig. 15; Wingate & Nichols, 2001, *Caryapollenites veripites* (Wilson et Webster) Nichols et Ott, pl. 7, fig. 13] and *in situ* pollen from a catkin (Manchester, 1987) have been reported. Present in all samples.

Genus Juglans L.

Juglans sp. 1

(Figures 20A, 21A–B)

Description. – Pollen, oblate, pollen outline circular, equatorial diameter 45–55 μm (LM), 40–45 μm (SEM); eutectate, exine 1.0–1.5 μm thick (LM), nexine thinner than sexine; stephanoporate with additional pores in distal polar area, proximal side without pores, 18–22 pores, pores slightly annulate, aperture diameter 2–3 μm (LM & SEM); sculpturing scabrate (LM), microechinate, (SEM), microechini density on a 2x2 μm square 14–18; abundance: common.

Remarks. – *Juglans sp. 1* corresponds to pollen of extant and fossil *Juglans* (Stone & Broome, 1975; Manchester, 1987; Bos & Punt, 1991; Jones et al., 1995; Stuchlik et al., 2009).

Juglans sp. 2

(Figures 20B, 21C–D)

Description. – Pollen, oblate, pollen outline circular, equatorial diameter 35–40 μm (LM), 25–30 μm (SEM); eutectate, exine 1.0–1.5 μm thick (LM), nexine thinner than sexine; stephanoporate with additional pores in distal polar area, proximal side without pores, 10–16 pores, pores slightly annulate, aperture diameter 2–3 μm (LM & SEM); sculpturing scabrate (LM), microechinate, (SEM), microechini density on a 2x2 μm square 14–18; abundance: abundant.

Remarks. – *Juglans sp. 2* differs in smaller grain size and fewer pores from *Juglans sp. 1*, but we cannot rule out the possibility that both types originated from the same species reflecting its morphological variability. *Juglans sp. 2* corresponds to pollen of extant and fossil *Juglans* (Stone & Broome, 1975; Bos & Punt, 1991; Jones et al., 1995; Stuchlik et al., 2009). Pollen aggregations comprising only pollen of this type have been encountered as well.

From Florissant possible *Juglans* leaflets, “*J. coloradensis*”, and nutshell impressions of *J. sepultus* Cockerell have been reported (Manchester, 1987). However, their affiliation with *Juglans* is debatable (Manchester, 1987). *Juglans* pollen have been reported previously from Florissant by LM (Hascall, 1988, pl. 4, fig. 17; Leopold & Clay-Poole, 2001, pl. 9, figs 8–10; Wingate & Nichols, 2001, *Juglanspollenites nigripites* (Wodehouse) Wingate et Nichols, pl. 8, figs 18–19). *Juglans* pollen is present in all samples.

*Family Malvaceae Jussieu**Subfamily Bombacaceae Burnett/Sterculioideae Beilschmied**Bombacaceae/Sterculioideae gen. indet.*

(Figures 20D, 21G–H)

Description. – Pollen, oblate, rounded triangular in polar view, equatorial diameter 30–35 μm (LM), 25–30 μm (SEM); semitectate, exine 1.5–2.0 μm thick, nexine thinner than sexine, brevicolporate (3), nexine slightly thickened around endopori (LM); sculpturing heterobrochate, reticulate (LM & SEM), brochii increase in size toward both poles; abundance: single encounter.

Remarks. – This type of pollen shows strong similarities to extant Sterculioideae (e.g. *Fremontodendron* Coville; Sharma, 1970; pers. obs.) and Bombacoideae [e.g. *Bernoullia* Oliver (Nilsson & Robyns, 1986; Tsukada, 1964)]. Manchester (1992) investigated fossil stamens of two species of the extinct malvaceous flower *Florissantia*, *F. speirii* (Lesquereux) Manchester and *F. ashwillii* Manchester, and obtained pollen with similarities to the present pollen type. Fossil flowers of *Florissantia speirii* (Manchester, 1992; 2001) and similar pollen have been reported from Florissant (Leopold & Clay-Poole, 2001, pl. 6, fig. 15; Wingate & Nichols, 2001, *Bombacacidites* sp. aff. *B. reticulatus* Krutzsch sensu Frederiksen, pl. 7, fig. 9). Leopold et al. (2001, 2008) also affiliated this pollen type with extant *Fremontodendron*. Present in sample UF15880-7285.

Subfamily Bombacoideae Burnett/Brownlowioideae Burret

Bombacoideae/Brownlowioideae gen. indet.

(Figures 20E, 21I–J)

Description. – Pollen, oblate, outline rounded triangular to circular in polar view, equatorial diameter 20–25 μm (LM), 17–20 μm (SEM); semitectate, exine 1.5–2.0 μm thick, nexine thinner than sexine, brevicolporate (3), nexine slightly thickened around endopori (LM); sculpturing scabrate (LM), microreticulate, perforate, fossulate (SEM); abundance: very rare.

Remarks. – The exine surface sculpturing of *Malvaceae* gen. indet. 2 corresponds with pollen of extant taxa found in Bombacoideae [e.g. *Aguiara* Ducke (Nilsson & Robyns, 1986;

Tsukada, 1964)] and Brownlowioideae [*Diplodiscus* Turcz., *Pentace* Hassk. (Perveen et al., 2004)]. Of the previously reported pollen, *Tilia* in Hascall (1988, pl. 4, fig. 14) and *Bombacacidites* sp. cf. *B. nanobrochatus* Frederiksen et al. sensu Frederiksen in Wingate and Nichols (2001; pl. 7 fig. 8) show morphological similarities to the here depicted specimen. Present in sample UF15880-7285.

Subfamily Malvoideae Burnett

Malvoideae gen. indet. 1

(Figures 20F, 21K–L)

Description. – Pollen, spheroidal, pollen outline circular, pollen diameter 50–60 µm (LM), 45–55 µm (SEM); eutectate, exine without echinae 2–2.5 µm thick (LM), pantocolporate, ectocolpus (SEM), endoporus (LM), endopori diameter 3–6 µm, apertures arranged in a “spiral” pattern; sculpturing echinate (LM), echinate, microbaculate, microverrucate, perforate (SEM), echinae base diameter 1.5–2.0 µm, echinae length 2.5–3.5 µm, echinae perforate and almost smooth; abundance: very rare.

Remarks. – Malvoideae gen. indet. 1 to 4 correspond to extant Malvoideae pollen (Christensen, 1986; Culhane & Blackmore, 1988; Naggar, 2004).

”Spiral” arrangement of apertures and microbaculate, microverrucate (Culhane & Blackmore, 1988 used the term nanoverrucate) exine sculpturing of Malvoideae gen. et spec. indet. sp. 1 are typical in several extant Malvoideae, for instance in extant *Malva sylvestris* L. (Culhane & Blackmore, 1988; Halbritter, 2005c). This pollen reported here is similar in size and sculpturing to *Malvacipollis* sp. C (Wingate & Nichols, 2001, pl. 9, fig 3). Present in sample UF15880-7285.

Malvoideae gen. indet. 2

(Figures 20G, 21M–N)

Description. – Pollen, spheroidal to oblate, pollen outline circular to elliptic, pollen diameter 35–40 μm (LM), 30–35 μm (SEM); eutectate, exine 1.0–1.5 μm thick, stephano- to pantoporate, pori diameter 1–3 μm (SEM); sculpturing echinate (LM), microrugulate, fossulate, perforate, echinae base diameter 1.0–1.5 μm , echinae length 1.5–2 μm ; abundance: very rare.

Remarks. – Malvaceae gen. indet. 2 shows exine sculpturing similar to extant *Malva pusilla* Smith (Culhane & Blackmore, 1988). The pollen depicted here is similar in size and sculpturing to previously reported Nymphaeaceae by Hascall (1988, pl 4, fig. 2) and *Pandaniidites* sp. by Wingate and Nichols (2001, pl. 9 fig. 9). Present in sample UF15880-7285.

Malvoideae gen. indet. 3

(Figures 20G, 21O–P)

Description. – Pollen, spheroidal to oblate, outline circular in polar view, equatorial diameter 35–45 μm (LM), 30–40 μm (SEM); eutectate, exine 1–1.5 μm thick, pantoporate, pori diameter 3.5–5 μm (SEM); sculpturing echinate (LM), echinate, microverrucate, perforate, fossulate (SEM), echinae base diameter 1–1.5 μm , echinae length 1.5–2 μm ; abundance: very rare.

Remarks. – Present in sample UF15880-7285.

Malvoideae gen. indet. 4

(Figures 22A, 23A–B)

Description. – Pollen, spheroidal to oblate, pollen outline circular to elliptic, pollen diameter without echinae 40–50 μm (LM & SEM); eutectate, exine 1.0–1.5 μm thick (LM & SEM),

stephano- to pantoporate; sculpturing echinate (LM), echinate, microverrucate, perforate (SEM), echinae base diameter 2.0–3 μm , echinae base perforate fossulate, echinae length 3.5–4.5 μm (SEM); abundance: very rare.

Remarks. – Exine sculpturing and sexine stratification of Malvoideae gen. indet. 4 is similar to extant *Malva moschata* L. (Culhane & Blackmore, 1988, *Malva alcea* type). This grain is very similar in size and sculpturing to *Malvacipollis* sp. B (Wingate & Nichols, 2001, pl. 9 fig. 2). Present in sample UF15880-7285.

Family Menispermaceae Jussieu

Menispermaceae gen. indet.

(Figures 22B, 23C–D)

Description. – Pollen, spheroidal, circular in equatorial view, polar axis 20–25 μm (LM), 15–18 μm (SEM), equatorial diameter 20–25 μm (LM), 15–18 μm (SEM); semitectate, exine 2–3 μm thick (LM), nexine thinner than sexine, tricolpate; sculpturing reticulate (LM & SEM), muri width 0.4–0.6 μm , muri suprasculpture microechinate (SEM); abundance: very rare.

Remarks. – This pollen type corresponds to extant Menispermaceae pollen. Within this family muri crested with echinae have been reported in *Burasaia* Thouars, *Chondrodendron* Ruiz et Pav., *Curarea* Barneby et Krukoff, and *Coscinium* Colebr. (Ferguson, 1975; Thanikaimoni et al., 1984; Harley, 1985). Present in sample UF15880-7285.

Family Oleaceae Hoffmannsegg et Link

Genus Fraxinus L.

Fraxinus sp.

(Figures 22C, 23E–F)

Description. – Pollen, prolate, outline circular lobate in polar view, outline elliptic in equatorial view, polar axis 23–25 μm (LM), equatorial diameter 18–20 μm (LM); semitectate, exine 1.0–1.5 μm thick, nexine thinner than sexine, tricolporate; sculpturing heterobrochate reticulate (LM & SEM), muri width 0.5–0.8 μm (SEM), muri slightly microrugulate to segmented; abundance: rare.

Remarks. – This pollen is similar in size, aperture and sculpturing to pollen of extant *Fraxinus* (Martin & Drew, 1970; Miyoshi et al., 2011; Punt et al., 1991; Renault-Miskovsky et al., 1976). Oleaceae (*Fraxinus*)-type pollen has been reported from Florissant (Leopold & Clay-Poole, 2001, not figured; Wingate & Nichols, 2001, *Fraxinopollenites medius* Frederiksen, pl. 4, fig. 5). Present in sample UCMP20778 and UF15880-7285.

Family Onagraceae Juss.

Subfamily Onagroideae Wagner et Hoch

Tribe Hauyeae Raimann in Engler et Prantl

Hauyeae gen. indet. aff. Hauya

(Figures 22E, 23J–M)

Description. – Pollen, oblate, outline convex triangular in polar view, equatorial diameter 65–85 μm (LM); eutectate, exine 2.0–2.5 μm thick (LM), nexine as thick as sexine; triporate, aperture diameter 5–7 μm , apertures with annulus, annulus with ectoporus formed by sexine, nexine only reaches endoaperture; sculpturing scabrate (LM), microverrucate (SEM), microverrucae pebblestone-like; viscin threads present, viscin threads segmented, rope-like braided; abundance: very rare.

Remarks. – Pebblestone-like verrucate exine sculpturing is commonly found in Onagraceae pollen (Pragłowski et al., 1983; 1987; 1994). Viscin threads of similar rope-like braided morphology are exclusively found in extant *Hauya* ex DC. (Skvarla et al., 1978, pl. 19–20).

Similar onagraceous pollen have been reported from Florissant and compared to extant genera [Leopold & Clay-Poole, 2001, *Semeiandra* cf. *S. grandiflora* (= *Lopezia semeiandra* Plitmann, P.H. Raven et Breedlove), pl. 6 fig. 3; Wingate & Nichols 2001, *Corsinipollenites parviangulus* Frederiksen et al., pl. 7 fig. 15]. *Semeiandra* (= *Lopezia*) pollen features beaded viscin threads (Skvarla et al., 1978); due to the rope like braided viscin threads of the pollen reported here a closer relationship with *Semeiandra* can be ruled out. Present in sample UF15880-7285.

Tribe Onagreae Dumortier/ Lopezieae Spach

Onagreae/Lopezieae gen. indet sp. 1 (Figures 22F, 23N–P)

Description. – Pollen, oblate, outline triangular in polar view, equatorial diameter 50–60 μm (LM), 40–45 μm (SEM); eutectate, exine 1.5–2.0 μm thick (LM), nexine as thick as sexine, triporate, aperture diameter 5–7 μm , apertures with prolonged annulus (dome shaped apertural protrusions), atrium present; sculpturing scabrate (LM), microverrucate microverrucae pebblestone-like, perforate (SEM), viscin threads segmented-beaded to rope-like; abundance: very rare.

Remarks. – Onagraceae/Lopezieae gen. indet. 1 differs from Onagraceae/Lopezieae gen. indet. 2 in larger size, distinctly elongated apertures protruding from the central body, more rope-like viscin threads and more widely spaced microverrucae with visible perforations. Similar onagraceous pollen with distinctly protruding apertures have previously been reported from Florissant and have been compared to extant genera [Leopold & Clay-Poole, 2001, aff. *Xylonagra*, pl. 6 fig. 4; Wingate & Nichols, 2001, *Corsinipollenites oculus-noctis parvus* (Doktorowicz-Hrebnicka) Krutzsch, affinities to *Oenothera* L. and *Epilobium* L., pl. 7 fig. 14]. Perforate exine sculpturing associated with pebblestone-like microverrucae is found in extant *Lopezia* Cav., *Oenothera* L. and *Camissonia* Link, *Epilobium* and *Xylonagra* show

densely packed microverrucae with a more elongated form compared to Onagraceae/Lopezieae gen. indet. 1 (compare Pragłowski et al., 1983; 1987; 1994; Skvarla et al., 1978). Segmented-beaded to rope like viscin threads are present in extant *Camissonia*, *Oenothera* and *Xylonagra* (compare Pragłowski, 1987; Skvarla et al., 1978). Morphological similarities are with several extant *Camissonia*, *Lopezia*, and *Oenothera* species [Skvarla et al., 1978, *C. crassifolia* (Greene) Raven, pl. 12, fig. 3; *Gaura mutabilis* (= *O. anomala* Curtis), pl. 23; *L. longiflora* (Decne) Plitmann, Raven et Breedlove, pl. 6, fig. 1; *O. hookeri* Torr. et A. Gray, pl. 29, figs 1–2; *O. texensis* P.H. Raven et D.R. Parn., pl. 31, fig. 4; Halbritter & Buchner, 2012, *O. acaulis* Lindl.; Svojtka & Halbritter, 2005, *O. glazoviana* Micheli]. It is possible that the more elongated protruding apertures of Onagraceae/Lopezieae gen. indet. 1 are more distinct because the pollen has been deformed during preservation. Present in sample UF15880-7285.

From Florissant a single fossil onagraceous flower (Manchester, 2001) has been reported.

Onagraceae/Lopezieae gen. indet sp.2

(Figures 22D, 23G–I)

Description. – Pollen, oblate, outline triangular in polar view, equatorial diameter 50–65 μm (LM), 40–50 μm (SEM); eutectate, exine 1.5–2 μm thick (LM), nexine as thick as sexine, triporate, aperture diameter 5–7 μm , apertures with protruding annulus (dome shaped apertural protrusions), atrium present; sculpturing scabrate (LM), densely microverrucate, microverrucae pebblestone-like (SEM), viscin threads beaded to segmented; abundance: very rare.

Remarks. – The protruding apertures of Onagraceae/Lopezieae gen. indet. 2 are less distinct elongated than in Onagraceae/Lopezieae gen. indet. 1. Apertures of this type are found in extant *Camissonia*, *Lopezia* and *Xylonagra*; similar segmented beaded viscin threads are

present in extant *Camissonia*, *Lopezia* and *Oenothera* (compare Skvarla et al., 1978; Praglowski et al., 1987). Present in sample UF15880-7285.

Family Platanaceae T.Lestib.

Genus Platanus L.

Platanus sp.

(Figures 24B, 25C–D)

Description. – Pollen, spheroidal, outline circular to lobate in polar view, equatorial diameter 20–24 µm (LM), 17–14 µm (SEM); semitectate, exine 1.6–2 µm thick (LM), nexine and sexine of same thickness, tricolpate, colpi broad; sculpturing scabrate (LM), microreticulate (SEM), in aperture area microreticulum breaks up, lumina open towards colpus (SEM), muri slightly crested (SEM); abundance: very rare.

Remarks. – A reticulum breaking up at the aperture margin, with open lumina towards the colpus margin and crested muri are morphological features common in extant and fossil *Platanus* pollen (Zavada & Dilcher, 1986; Denk et al., 2006; 2011; Li et al., 2010; Miyoshi et al., 2011). Pollen with affinities to Platanaceae have been reported from Florissant (Leopold & Clay-Poole, 2001; Wingate & Nichols, 2001). *Tricolpate* sp. B (Wingate & Nichols, 2001, pl. 5, fig. 5) shows strong similarities to *Platanus* sp. Fossil Platanaceae leaves (MacGintie, 1953; Manchester, 2001, *Platanus* L. or *Macginitea* Wolfe et Wehr) are known from Florissant. Present in sample UF15880-7285.

Platanaceae gen. indet aff. Macginitea

(Figures 24A, 25A–B)

Description. – Pollen, spheroidal, outline circular to lobate, diameter 20–26 µm (LM), 16–19 µm (SEM); semitectate, exine 1.6–2 µm thick (LM), nexine and sexine of same thickness,

tricolpate, colpi broad; sculpturing scabrate (LM), microreticulate (SEM), in the aperture margin area the microreticulum fuses to form an ectexine rim around the colpus (SEM), muri rounded (SEM); abundance: very rare.

Remarks. – In Cretaceous and Early Cenozoic Platanaceae a fused rim surrounding the aperture margin and a reticulum with rounded muri are commonly found (Denk & Tekleva, 2006). Platanaceae gen. indet. aff. *Macginitia* shows high similarities to pollen of *Macginitia* Wolfe et Wehr (Manchester, 1986). Present in sample UF15880-7285.

Family Rosaceae Juss.

Subfamily Spiraeoideae C.Agardh

Genus Crataegus Tournefort ex L.

Crataegus sp.

(Figures 24C, 25E–F)

Description. – Pollen, prolate, outline elliptic to rhombic in equatorial view, polar axis 24–28 μm (LM), 22–26 μm (SEM), equatorial diameter 24–26 μm (LM), 20–23 μm (SEM); eutectate, exine 1.3–1.8 μm thick (LM), nexine thinner than sexine, tricolporate, pori circular, in areas surrounding endopori sexine is forming a bridge (LM); sculpturing scabrate (LM), rugulate, rugulae are built by striae, perforate (SEM), striae are oriented parallel to the polar axis, striae densely packed, striae width 0.1–0.4 μm (SEM); abundance: very rare.

Remarks. – *Crataegus* sp. falls within the morphological range (aperture, size, exine sculpturing) of extant *Crataegus* and shows strongest similarities to extant *C. monogyna* Jacq. (Hebda et al., 1988a; Dönmez, 2008).

From the Florissant flora three different leaf species of *Crataegus* [*C. copeana* (Lesquereux) MacGinitie, *C. hendersonii* (Cockerell) MacGinitie and *C. nupta* (Cockerell) MacGinitie] can be discerned (MacGinitie, 1953; Manchester, 2001).

Present in sample UF15880-7285.

Subfamily Dryadoideae Juel

Dryadoideae gen. indet. aff. Cercocarpus/Purshia

(Figures 24H, 25O–P)

Description. – Pollen, outline circular to lobate in polar view, equatorial diameter 30–35 μm (LM), 25–28 μm (SEM); eutectate, exine ca. 1.4–1.9 μm thick, nexine thinner than sexine, tricolpate; sculpturing scabrate (LM), tuberculate, perforate (SEM); abundance: very rare.

Remarks. – Within Rosaceae tuberculate exine sculpturing similar to this grain is found in two taxa of Dryadoideae, *Cercocarpus* Kunth and *Purshia* DC. [*Cowania* (= *Purshia*) in Solomon et al., 1973; Hebda & Chinappa, 1990; 1994]. Rosaceae pollen with strong similarities to this grain has previously been reported from Florissant (Leopold & Clay-Poole, 2001, *Malus/Pyrus* type, pl. 5, fig. 11), also fossil leaves and fruits of *Cercocarpus myricafolius* (Lesquereux) MacGinitie are known (MacGinitie, 1953; Manchester, 2001). Present in sample UF15880-7285.

Rosaceae gen. indet. 1

(Figures 24D, 25G–H)

Description. – Pollen, prolate, outline elliptic in equatorial view, polar axis 24–26 μm (LM), 19–22 μm (SEM), equatorial diameter 17–19 μm (LM), 13–16 μm (SEM); eutectate, tricolporate; sculpturing scabrate (LM), striate (SEM), striae width 0.2–0.4 μm , striae densely packed, striae orientated mainly parallel to polar axis, seldom perpendicular to polar axis; abundance: very rare.

Remarks. – Striate, perforate pollen are commonly found in Rosaceae (Hebda et al., 1988a; 1988b; Hebda & Chinnappa, 1990; 1994, table 1). The lack of additional diagnostic characters makes it difficult to assign Rosaceae gen. indet. 1 to 4 to the genus level.

From the Florissant Flora leaves of *Amelanchier scudderi* Cockerell, *Cercocarpus myricafolius* (also fruits), *Crataegus copeana* (Lesquereux) MacGinitie, *C. hendersonii* (Cockerell) MacGinitie, *C. nupta* (Cockerell) MacGinitie, *Malus florissantensis* (Cockerell) MacGinitie, *M. pseudocredneria* (Cockerell) MacGinitie, *Prunus gracilis* (Lesquereux) MacGinitie, *Rosa hilliae* Lesquereux, *Vauquelinia coloradensis* (Knowlton) MacGinitie and *V. liniara* MacGinitie have been reported (MacGinitie, 1953; Manchester, 2001). Pollen with affinity to Rosaceae have been described by Wingate and Nichols (2001, pl. 6, figs 11–12) and Leopold and Clay-Poole (2001, pl. 5, fig. 11). Present in sample UF15880-7285.

Rosaceae gen. indet. 2

(Figures 24E, 25I–J)

Description. – Pollen, prolate, outline elliptic in equatorial view, polar axis 19–22 μm (LM), 14–17 μm (SEM), equatorial diameter 14–17 μm (LM), 11–13 μm (SEM); eutectate, tricolpate; sculpturing scabrate (LM), striate, perforate (SEM), striae 0.1–0.2 μm wide, striae not densely packed, “valleys” with perforations present, striae orientated mainly parallel to polar axis, seldom perpendicular to polar axis; abundance: very rare.

Remarks. – Present in sample UF15880-7285.

Rosaceae gen. indet. 3

(Figures 24F, 25K–L)

Description. – Pollen, prolate, outline elliptic in equatorial view, outline circular to lobate in polar view, polar axis 17–19 long (LM), 14–16 μm (SEM), equatorial diameter 14–16 μm (LM), 10–12 μm (SEM); eutectate, exine 1.0–1.5 μm thick, nexine thinner than sexine, tricolporate; sculpturing scabrate (LM), striate (SEM), striae densely packed, not oriented; abundance: very rare.

Remarks. – Present in sample UF15880-7285.

Rosaceae gen. indet. 4

(Figures 24G, 25M–N)

Description. – Pollen, tricolporate, prolate, outline elliptic in equatorial view, polar axis 14–16 μm (LM), 12–14 μm (SEM), equatorial diameter 7–9 μm (LM), 7–9 μm (SEM); eutectate, exine 1–1.5 μm thick, nexine thinner than sexine, tricolporate; sculpturing scabrate (LM), striate (SEM), striae densely packed, striae show no preferred orientation, only in equatorial aperture area striae run mainly perpendicular to polar axis; abundance: very rare.

Remarks. – Present in sample UF15880-7285.

Family Rutaceae Juss.

aff. Rutaceae gen. indet.

(Figures 26A, 27A–B)

Description. – Pollen, prolate to spheroidal, outline circular in equatorial view, polar axis 44–47 μm (LM), 35–38 μm (SEM), equatorial diameter 41–47 μm (LM), 35–38 μm (SEM); semitectate, exine 3–4 μm thick (LM), nexine thinner than sexine, tricolporate; sculpturing reticulate (LM), reticulate, heterobrochate, perforate to fossulate, lumina with free standing columelle, lumina decreasing in size in aperture area, colpus surrounded by a fused rim (SEM); abundance: very rare.

Remarks. – Aff. Rutaceae gen. indet. shows strong similarities to pollen of Toddalioideae, with particular similarity to *Decagonocarpus oppositifolius* Engl., from which it differs by its smaller size (Morton & Kallunki, 1993, figs 4e–f). For *Brachyruscus alleni* Cockerell from Florissant affinities to Rutaceae have been suggested by Manchester (2001) due to morphological similarities to *Ptelea*. Manchester and O’Leary (2010) reconsidered this assignment and suggested this fruit might belong to Sapindaceae. Leopold and Clay-Poole

(2001) reported pollen with affinities to *Ptelea* (not figured) and Rutaceae cf. *Euodia* (pl. 6, figs 5–6), which closely resembles pollen type 11 (Figs 32C, 33E–F).. Present in sample UF15880-7285.

Family Sapindaceae Juss.

Genus Acer L./Dipteronia Oliv.

Acer vel Dipteronia sp.

(Figures 26C, 27C–D)

Description. – Pollen, prolate, outline elliptic in equatorial view, polar axis 27–30 μm (LM), 25–27 μm (SEM), equatorial diameter 23–26 μm (LM), 21–23 μm (SEM); eutectate, exine 1.5–2 μm thick, nexine thinner than sexine, tricolporate; sculpturing striate (LM), striate, fossulate, perforate (SEM), striae running parallel to polar axis, striae smooth, striae width 0.3–0.6 μm , perforations only present in grooves between striae; abundance: rare.

Remarks. – Both extant species of *Dipteronia* produce tricolporate, prolate to subspheroidal pollen with exine ornamentation consisting of striae running parallel to the polar axis, and a size range 19.1–27 μm of the polar axis (Biesboer, 1975; Li et al., 2010; Tian, et al., 2001). In extant *Acer* pollen exine ornamentation can range from rugulate, microrugulate, microreticulate, striato-reticulate to striate, which is the predominant sexine pattern (Biesboer, 1975; Clarke & Jones, 1978; Fürstl, 2002; Jones et al., 1995; Li et al. 2010; Miyoshi et al., 2011; Tian, et al., 2001; Stuchlik, 2014). Pollen of *Acer* is of only limited infrageneric taxonomic significance due to its highly variable morphology (size, shape, aperture, ornamentation) within infrageneric clades. Only *A. negundo* L. and *A. caprinifolium* Siebold et Zucc. can be securely identified to species level (cf. Biesboer, 1975; Fürstl, 2002; Tian et al., 2001). *Acer vel Dipteronia sp.* corresponds to pollen of extant *Dipteronia* and some *Acer*

species (e.g. *A. buergerianum* Miq., *A. heptalobum* Diels, *A. robustum* Pax) by its size range, striate exine sculpturing and colporate apertures (Tian et al. 2001).

Hascall (1988) distinguished four types of *Acer/Dipteronia* pollen from Florissant of which Type 1 (pl. 4, fig. 7) corresponds in size and striation to *Acer* sp. 1, Type 2 (pl. 4, fig. 6) corresponds in size and aperture to *Acer* vel *Dipteronia* sp., Type 3 (pl. 4, fig. 8) shows similarities in size and striation to *Acer* sp. 2 and Type 4 (pl. 4, fig. 9) shows strongest morphological similarities to Pollen type 7 (Figs 30G, 31M–N) and probably does not belong to *Acer* or *Dipteronia*. Wingate and Nichols (2001) reported two types of *Acer* pollen, *Aceripollenites striatus* (Pflug) Thiele-Pfeiffer (pl. 5, fig. 2) and *Aceripollenites* sp. (pl. 5, fig. 3), which is similar to *Acer* cf. *A. glabrum* Torr. (Leopold & Clay-Poole, 2001, pl. 5, figs 8–10).

Three *Acer* species, *Acer florissantii* Kirchner (leaves), *A. mcginitiei* Wolfe et Tanai (fruits), and *A. oregonianum* Knowlton (leaves and fruits) and two *Dipteronia* organ species, *D. insignis* (Lesquereux) Brown (leaves), *D. brownii* McClain et Manchester (fruits), are known from the macrofossil record of Florissant (MacGinitie, 1953; Manchester, 2001; McClain & Manchester, 2001).

Present in all samples.

Acer sp. 1

(Figure 26B)

Description. – Pollen, prolate, outline elliptic in equatorial view, polar axis 45–48 µm (LM), 37–40 µm (SEM), equatorial diameter 27–30 µm (LM), 22–24 µm (SEM); eutectate, exine 1.5–2 µm thick, nexine thinner than sexine, tricolpate; sculpturing striate (LM), striate, fossulate, perforate (SEM), striae running parallel to polar axis, striae smooth, striae width 0.3–0.6 µm, perforations only present in grooves between striae; abundance: rare.

Remarks. – *Acer* sp. 1 shows similar parallel striation as *Acer* vel *Dipteronia* but differs in its remarkable larger size and colpate aperture, characters not found in extant *Dipteronia* (Biesboer, 1975; Li et al., 2010; Tian et al. 2001). *Acer/Dipteronia* Type 1 of Hascall (1988, pl. 4, fig. 7) and *Aceripollenites striatus* of Wingate and Nichols (2001, pl. 5, fig. 2) show similar striate ornamentation but are smaller in size. Present in all samples.

Acer sp. 2

(Figures 26D, 27E–F)

Description. – Pollen, prolate, outline elliptic in equatorial view, polar axis 40–44 μm (LM), 35–39 μm (SEM), equatorial diameter 35–40 μm (LM), 30–34 μm (SEM); semitectate, exine 1.5–2 μm thick (LM), nexine and sexine have same thickness, tricolpate; sculpturing striate (LM), striate to striato-reticulate, muri 0.4–0.8 μm wide, striae smooth, striae orientation irregular, striae branching and interweaving, (SEM), thin connections between striae present; abundance: very rare.

Remarks. – Orientation of striae in *Acer* sp. 2 is more irregular than in *Acer* vel *Dipteronia* and *Acer* sp. 1. Striae with thin connections are commonly found in extant pollen of *Acer*, e.g. *A. macrophyllum* Pursh, *A. ginnala* Maxim., *A. truncatum* Bunge, *Acer palmatum* Thunb., (Biesboer, 1975; Li et al., 2010; Miyoshi et al., 2011; Halbritter & Buchner, 2011). Present in sample UF15880-7285.

Acer sp. 3 aff. *A. negundo*

(Figures 26E, 27G–H)

Description. – Pollen, prolate, outline elliptic in equatorial view, polar axis 50–54 μm (LM), 41–44 μm (SEM), equatorial diameter 30–34 μm (LM), 26–29 (SEM); eutectate, exine 0.5–1

µm thick, tricolpate; sculpturing scabrate (LM), rugulate, fossulate, perforate (SEM);
abundance: rare.

Remarks. – This type of pollen shows strong morphological similarities (colpate aperture, rugulate ornamentation) to extant *Acer negundo* L. and *A. truncatum* Bunge pollen (Biesboer, 1975; Clarke & Jones, 1978; Tian et al, 2001) but differs in larger size. Present in all samples. An *Acer negundo*-like fruit, *Acer macginitiei* (former *A. heterodentatum*), was reported from Florissant (Wolfe & Tanai, 1987).

Unambiguous Sapindaceae fruits [*Dipteronia brownii* McClain et Manchester (with associated leaves), *Koelreuteria allenii* (Lesquereux) Edwards] and macrofossils with sapindaceous affinities [*Althayana haydenii* (Lesquereux) MacGinitie(leaves), *Brachyruscus allenii* Cockerell (fruits), *Cardiospermum terminalis* (Lesquereux) MacGinitie(leaves), *Dodonaea umbrina* MacGinitie (leaves), *Koelreuteria allenii* (Lesquereux) Edwards (leaves), *Sapindus coloradensis* Cockerell (leaves), *Thouinia straciata* MacGinitie(leaves)] have been reported from Florissant (MacGinitie, 1953; Manchester, 2001; Manchester & O’Leary, 2010).

In previous palynological studies pollen with affinities to Sapindaceae has been referred to various morphogenera and extant genera (Wingate & Nichols, 2001, *Boehlensipollis* sp. cf. *B. granulata* Frederiksen, Carr, Lowe et Wosika, pl. 6, fig. 23; *Cupanieidites* sp. A and B, pl. 7, figs 2–4; Leopold & Clay-Poole, 2001, *Cardiospermum* cf. *C. halicacabum* L., pl. 7, figs 4–7).

Family Sapotaceae Juss.

Subfamily Sapotoideae Eaton

Sapotoideae gen. indet. 1

(Figures 26F, 27I–J)

Description. – Pollen, spheroidal to subprolate, outline circular to slightly rhombic in equatorial view, polar axis 19–23 μm (LM), 15–18 μm (SEM), equatorial diameter 16–20 μm (LM), 14–16 μm (SEM); eutectate, exine 2–2.5 μm thick (LM), nexine thinner than sexine; tri- to tetracolporate, bridge present over porus (SEM), endexine thickened in aperture area (LM); sculpturing scabrate (LM), rugulate, microverrucae pebblestone-like [Harley (1991) uses the term granulate], perforate-fossulate (SEM); abundance: infrequent.

Remarks. – Harley (1991) identified twelve major pollen types (Pollen Types I–XII) with additional sub types within extant Sapotaceae. Sapotoideae gen. indet. 1 shows strong similarities (microsculpturing, aperture) to Pollen Type IA, found in several extant genera of Sapotoideae eg. *Mimusops* L., *Manilkara* Adans., *Palaquium* Blanco, and *Madhuca* J. F. Gmel. (Harley, 1991), but differs from this group by smaller size, which is common in Eocene Sapotaceae pollen (Harley, 1991; Taylor, 1989). Wingate and Nichols (2001) reported two pollen types with affinities to Sapotaceae, *Tetracolporopollenites brevis* Frederiksen (pl. 6, fig. 20) and *Tetracolporopollenites* sp. (pl. 6, fig. 21).

Sapotoideae gen. indet. 2

(Figures 26G, 27K–L)

Description. – Pollen, prolate to subprolate, outline circular to slightly rhombic in equatorial view, polar axis 21–25 μm (LM), 17–20 μm (SEM), equatorial diameter 19–22 μm (LM), 15–18 μm (SEM); eutectate, exine 2–2.5 μm thick (LM), nexine thinner than sexine; tri- to tetracolporate; sculpturing scabrate to rugulate (LM), rugulate, microverrucae pebblestone-like [granulate according to Harley (1991)], fossulate-perforate (SEM); abundance: rare.

Remarks. – Sapotoideae gen. indet. 2 shows strong similarities to Sapotaceae Pollen Type IF (Harley, 1991), but differs by its smaller size. Exine sculpturing resembles that of extant

Manilkara triflora (Allem.) Monach. pollen (Harley, 1991, fig. 9D). Sapotaceae pollen is present in all samples.

Family *Sarcobataceae* Behnke

Genus *Sarcobatus* Nees

Sarcobatus sp.

(Figures 12D–G, 13G–J)

Description. – Pollen, spheroidal, outline circular, diameter 20–30 µm (LM & SEM); eutectate, exine 1.5–2 µm thick (LM), pantoporate, 15–23 pori, porus diameter 1.5–3 µm (LM & SEM), annulus present, annulus formed by elongated collumellae (Figs 12F–G) operculum present, operculum ornamented with 35–50 microechini (SEM); sculpturing scabrate (LM), densely microechinate, microechini density on a 1x1 µm square 20–33, perforate, perforation density on a 1x1 µm square 11–15 (SEM); abundance: abundant.

Remarks. – This pollen is tentatively placed in *Sarcobatus* because of the presence of morphological features (pantoporate, microechinate operculum, microechinate perforate exine sculpturing, annulus presence) diagnostic to this genus. It differs in microechini density of tectum and opercula (compare with Nowicke, 1975, pl. 8, fig. 44; Nowicke, 1994, pl. 7.2, figs 5–6). Nowicke (1994) clarified that the annuli of extant *Sarcobatus vermicularis* (Hook.) Torr. are the result of elongated collumellae and not a locally thickened tectum. Elongated collumellae surrounding pori are visible in Figs 12F–G. In previous palynological studies this pollen type has also been compared to extant *Sarcobatus* and in particular to *S. vermiculatus* (Hascall, 1988, pl. 4, fig. 32; Leopold & Clay-Poole, 2001, pl. 9, figs 11–14; Wingate & Nichols, 2001, pl. 8, fig. 20). Present in all samples.

Family *Thymelaeaceae* Juss.

Subfamily Thymelaeoideae Burnett

Thymelaeoideae gen. indet. 1

(Figures 26H, 27M–N)

Description. – Pollen, spheroidal, pollen outline circular, equatorial diameter 29–36 μm (LM), 25–29 (SEM); semitectate, exine 2–2.5 μm thick, nexine thinner than sexine, pantoaperturate; sculpturing reticulate (LM), reticulate, echinate (SEM), echinate muri forming croton pattern, echinae with a triangular base, echinae show characteristic sculpturing of microrugulae and furrows; abundance: very rare.

Remarks. – Thymelaeoideae gen. indet. 1 is similar in exine sculpturing to pollen of several taxa within extant Thymelaeoideae, e.g. *Daphne* L., *Lachnaeae* L., and *Dirca* L. (Bredenkamp & Van Wyk, 1996; Herber, 2002). From Florissant fossil leaves of *Daphne septentrionalis* (Lesquereux) MacGinitie (MacGinitie, 1953) have been reported. Wingate and Nichols (2001) figured and described pollen (*Persicarioipollis* sp. B, pl. 8 fig. 23) with strong similarities to Thymelaeoideae gen. indet. 1 and 2. Present in sample UF15880-7285.

Thymelaeoideae gen indet. 2

(Figures 26I, 27O–P)

Description. – Pollen, spheroidal, pollen outline circular, equatorial diameter 24–28 μm (LM), 21–25 μm (SEM); semitectate, exine 1.5–2.0 μm thick, nexine thinner than sexine, pantoaperturate; sculpturing reticulate (LM), reticulate, echinate (SEM), echinate muri forming croton pattern, echinae with a round to triangular base; abundance: very rare.

Remarks. – This type of pollen is similar in size and exine sculpturing to pollen of extant *Thymelaea* Mill. (Nowicke et al., 1985; Halbritter, 2005d, T. passerina). Present in sample UF15880-7285.

Family Trochodendraceae Eichler

Genus Tetracentron Oliv.

Tetracentron sp.

(Figures 28A, 29A–B)

Description. – Pollen, prolate to spheroidal, polar axis 12–15 μm (LM), 10–13 μm (SEM), equatorial diameter 12–15 μm (LM), 10–12 μm (SEM); semitectate, exine 1–1.5 μm thick (LM), nexine thinner than sexine, tricolpate; sculpturing striate (LM), striatoreticulate (SEM); abundance: very rare.

Remarks. – Size range and exine sculpturing are nearly identical to extant and fossil *Tetracentron sinense* Oliv. (Fritz & Allesch, 1999; Manchester & Chen, 2006; Grímsson et al., 2008) differing only in smaller size of lumina, possibly due to deformation. UM 3 of Hascall (1988, pl. 4, fig. 15) shows similarities in size and exine sculpturing. Present in sample UF15880-7285.

From middle Eocene to Miocene of North America infructescences, leaves, fruits, and pollen of Trochodendraceae are known (Manchester & Chen, 2006; Pigg et al., 2007).

Today the deciduous genus *Tetracentron* is monotypic and restricted to South-East Asia.

Family Ulmaceae Mirb.

Genus Cedrelospermum (Saporta) Manchester

Cedrelospermum sp.

(Figures 28C–D, 29C–F)

Description. – Pollen, spheroidal to oblate, outline in polar view ranging from circular to convex triangular to polygonal, equatorial diameter 20–27 μm (LM), 18–22 μm (SEM); eutectate, exine 1.0–1.5 μm thick (LM), nexine thinner than sexine, tri- to pentaporate, ectoaperture ranging from circular to meridional elongated, aperture diameter 1.5–2.0 μm

(LM & SEM), sexine around porus slightly thickened (occasionally weak annulus present); sculpturing verrucate (LM), verrucate, microechinate, perforate (SEM), verrucae diameter 1–2 μm , highest density of microechini between verrucae; abundance: common.

Remarks. – The pollen of *Cedrelospermum* from Florissant corresponds to Ulmaceae by equatorial positioned apertures (annulus presence possible) and microechinate (=spinules), perforate sexine sculpturing (discernible in SEM). Furthermore, the highest density of microechini is between verrucate or rugulate sculptural elements. *Cedrelospermum* sp. shows a slightly smaller size range in equatorial diameter compared to extant Ulmaceae [equatorial diameter size range in LM: *Chaetoptelea* Liebm. 25–31 μm ; *Hemiptelea* Planch. 33–51 μm ; *Holoptelea* Planch. 23–33 μm ; *Phyllostylon* Capan. ex Benth. et Hook.f. 29–38 μm ; *Planera* J.F.Gmel. 28–40 μm ; *Ulmus* L. 23–50 μm ; *Zelkova* Spach 25–49.3 μm] and three to five pores (3–) 5 [*Chaetoptelea* : 4 (–5); *Hemiptelea*: 4 (–5–7); *Holoptelea*: (4–) 5, *Phyllostylon*: 5; *Planera* 4 (–5); *Ulmus*: (4–5–) 7, *Zelkova*: 3 (–4–) 6] (Beug, 2004; Li et al., 2010; Jones et al., 1995; Myoshi et al., 2011; Nakagawa et al., 1998; Stafford, 1995; Takahashi, 1989; Xin et al., 1993; Zavada, 1983). The distinct verrucae in *Cedrelospermum* sp. are mainly of similar diameter on an individual grain, of circular shape, and densely and evenly distributed. Extant Ulmaceae pollen is typically slightly to distinct rugulate (Takahashi, 1989). In some species of *Ulmus* exine ornamentation can show a gradual transition from rugulate to slightly verrucate, e.g. *Ulmus glabra* Huds. (Stafford, 1995; Zavada & Dilcher, 1986, fig. 54). Exine sculpturing of *Hemiptelea* is slightly rugulate, with less ornamented polar areas; exine sculpturing of *Holoptelea* is irregularly verrucate. Pollen found in *in situ* stamens of *Cedrelospermum nervosum* (Newberry) Manchester corresponds to the present pollen by its pore number (3–5) and microechinate sculpturing, but does not show distinct verrucae, possibly because of its compacted preservation and not fully mature state (Manchester, 1989a). From the middle Miocene of Austria exceptionally well preserved dispersed

Cedrelospermum pollen has been reported (Grímsson et al., in press, figs 18A–L), which are slightly larger and have 4–6 pores. Fossil leaves and fruits of *Cedrelospermum lineatum* (Lesquereux) Manchester belong to the most common plant fossils known from Florissant (Manchester, 1989a; 1989b; 2001; Meyer, 2003). Triporate sp. B of Wingate and Nichols (2001, pl.8, fig. 9) is similar to the present pollen by its circular outline, number of pori, verrucate sculpturing and annulate pori but differs by its smaller size. Hascall (1988, *Ulmus/Zelkova* Type 2, pl. 4, fig. 4) reported morphologically similar (size, triporate) pollen. Present in all samples.

Genus Ulmus L.

Ulmus sp.

(Figures 28E–F, 29I–K)

Description. – Pollen, oblate, outline rounded quadrangular to polygonal, equatorial diameter 25–40 µm (LM), 20–35µm (SEM); eutectate, exine 1.0–1.5 µm thick, nexine thinner than sexine, stephanoporate (3–6), pori diameter 2–4 µm (LM), sexine around pori slightly thickened; sculpturing rugulate (LM), rugulate, microechinate, slightly perforate (SEM); abundance: abundant.

Remarks. – *Ulmus* sp. is indistinguishable by its morphological characters (e.g. rugulate microechinate sculpturing) from extant *Ulmus* pollen (Beug, 2004; Li et al., 2010; Jones et al., 1995; Myoshi et al., 2011; Stafford, 1995; Takahashi, 1989; Xin et al., 1993; Zavada, 1983). From Florissant fruits and leaves of *Ulmus tenuinervis* Lesquereux (MacGinitie, 1953; Manchester, 1989b; 2001), ulmaceous petrified wood (Wheeler, 2001; *Zelkovoxydon chadronensis* Wheeler; cf. *Zelkova* sp.), and *Ulmus*-type pollen (Hascall, 1988, *Ulmus/Zelkova*, pl. 4, figs 3–5; Leopold & Clay-Poole, 2001, *Ulmus/Zelkova*, pl. 9, figs 2–3;

Wingate & Nichols, 2001, *Ulmipollenites undulosus* Wolff, pl. 8, fig. 14) have been reported. Present in all samples.

Ulmaceae gen. indet. cf. *Zelkovapollenites thiergartii* Nagy

(Figures 28G, 29L–M)

Description. – Pollen, oblate, outline quadrangular in polar view, equatorial diameter 22–25 μm (LM), 16–20 μm (SEM); eutectate, exine 1.0–1.5 μm thick, nexine thinner than sexine, stephanoporate (4), aperture diameter 1–1.5 μm , exine slightly thickend in aperture area; sculpturing rugulate (LM), rugulate, microechinate (SEM), high density of microechini between rugulae, presence of “pseudoarci” spanning between apertures (exine thickening or possibly an artefact); abundance: rare.

Remarks. – *Ulmaceae* gen. indet. cf. *Zelkovapollenites thiergartii* corresponds in size, presence of “pseudoarci”, and exine sculpturing to fossil *Zelkovapollenites thiergartii* (Stuchlik et al., 2009, pl. 57, figs 1–9). In previous palynological studies *Ulmus* and *Zelkova* have not been differentiated (Hascall, 1988; Leopold & Clay-Poole, 2001). Pollen morphology of extant *Zelkova* and *Ulmus* overlap in size, number and position of apertures, and exine sculpturing (Beug, 2004; Li et al., 2010; Stafford, 1995; Takahashi, 1989). Trilete foldings are present in immature pollen of *Zelkova sicula* DiPasquale, Garfi et Quézel (Nakagawa, 1998), no such folds were encountered in *Ulmaceae* gen. indet. cf.

Zelkovapollenites thiergartii. *Zelkova serrata* (Thunb.) Makino shows distinct thickened exine surrounding the apertures (Morita et al., 1998; Myoshi et al., 2011), a character which has also been reported in other *Ulmaceae* and is not diagnostic for *Zelkova* alone (Takahashi, 1989; Zavada, 1983). Wheeler (2001) reported two types of petrified wood from Florissant (cf. *Zelkova* sp., *Zelkovoxylon chadronensis* Wheeler) with morphological similarities to extant *Zelkova*. The presence of *Zelkova* in the Cenozoic of North America has been disputed

because fruits are entirely lacking from the fossil record (cf. Denk & Dillhoff, 2005). Present in all samples.

Family Vitaceae Jussieu

Vitaceae gen. indet. 1

(Figures 28H, 29N–O)

Description. – Pollen, prolate, elliptic in equatorial view, polar axis 38–42 μm (LM), 30–35 (SEM), equatorial diameter 26–28 μm (LM), 23–26 μm (SEM); semitectate, exine 1.0–1.5 μm thick (LM), nexine thinner than sexine, tricolporate; sculpturing microreticulate to reticulate (LM & SEM), nexine perforate, muri 0.5–0.8 μm wide, brochii 0.4–0.8 μm wide, brochii diameter decreases in the area surrounding the colpi; abundance: very rare.

Remarks. – Vitaceae gen. indet. 1 and 2 resemble Vitaceae pollen in size, aperture, and exine sculpturing, with strong affinities to extant and fossil *Parthenocissus* pollen (Li et al., 2010; Lu et al., 2012; Grímsson et al., 2014). From Florissant fossil leaves of *Vitis florissantellus* Cockerell have been tentatively accepted by Manchester (2001) and pollen with affinities to Vitaceae (Leopold & Clay-Poole, 2001, not figured; Wingate & Nichols, 2001, Tricolporate sp. D, pl. 6, figs 12–13) have been reported. Present in sample UF15880-7285.

Vitaceae gen. indet. 2

(Figures 28I, 29P–Q)

Description. – Pollen, prolate, elliptic in equatorial view, polar axis 40–44 μm (LM), equatorial diameter 28–30 μm (LM); semitectate, exine 1–1.2 μm thick (LM), nexine thinner than sexine, tricolporate; sculpturing microreticulate (LM), perforate to fossulate (SEM), perforations ca. 0.5 μm wide; abundance: very rare.

Remarks. – Vitaceae gen. indet. 2 differs from Vitaceae gen- indet. 1 by smaller lumina. It is possible that both represent the morphological variability of a taxon. Present in sample UF15880-7285.

Angiosperm pollen indet.

Pollen type 1

(Figures 30A, 31A–B)

Description. – Pollen, oblate to spheroidal, pollen outline circular to elliptic, pollen diameter without echinae 35–40 μm (LM), 30–35 μm (SEM); eutectate, exine 1.0–1.5 μm thick, stephanoporate, pori diameter 2–4 μm (LM & SEM), sculpturing echinate (LM), echinate, perforate (SEM), echinae base diameter 0.5–0.8 μm , echinae length 1–1.5 μm (SEM); abundance: very rare.

Remarks. – Pollen type 1 is similar in size and sculpturing to *Malvacipollis* sp. D (Wingate & Nichols, 2001, pl. 9, fig. 4); this type shows pore alignment and exine structure not found in echinate Malvaceae pollen (cf. Christensen, 1986; Culhane & Blackmore, 1988; Naggar, 2004). Present in sample UF15880-7285.

Pollen type 2

(Figures 30B, 31C–D)

Description. – Pollen, oblate, outline circular in polar view, equatorial diameter 30–40 μm (LM), 28–35 μm (SEM); eutectate, exine 1.5–2 μm thick (LM), nexine and sexine of same thickness, pento- to heptaporate, stephanoporate, pore diameter 4–6 μm (LM), 3–4 μm (SEM); sculpturing scabrate (LM), microrugulate, perforate fossulate (SEM), no perforations present in area surrounding porus; abundance: abundant.

Remarks. – In previous palynological studies this type of pollen has been referred to as UM1 by Hascall (1988, pl. 3, fig. 13) and Zonoporate sp. B by Wingate and Nichols (2001, pl. 8, fig 16), with affinities to Juglandaceae, Ulmaceae, and Nyssaceae or identified as *Pteroceltis* (Leopold & Clay-Poole, 2001, pl. 9, fig. 4, 6). Exine sculpturing in Juglandaceae is microechinate (Stone & Broome, 1975), in Ulmaceae, including extant *Pteroceltis*, slightly rugulate and microechinate (Takahashi, 1989; Li et al., 2010). Apertures in Nyssaceae are colporate (Göschl, 2008; Li et al., 2010; Stuchlik, 2014). Due to the absence of these characters in Pollen type 2, we cannot confirm previous identifications. Affinities uncertain. Present in S151454 and UCMP20778.

Pollen type 3

(Figures 30C, 31E–F)

Description. – Pollen, spheroidal, pollen outline elliptic to circular, pollen diameter excluding echinae 25–30 µm (LM), 20–25 µm (SEM); eutectate, exine 1–1.5 µm thick, inaperturate; sculpturing echinate (LM & SEM), rugulate, microverrucate, perforate (SEM), echini base diameter 0.5–0.8 µm, echini length 1.5–2 µm (SEM), microverrucae in perforations or lumina; abundance: rare.

Remarks. – Pollen types 3 and 4 share similar morphological features (echinate, perforations covered by microverrucae) but differ by their exine sculpture. Pollen type 3 has distinct perforations and lumina under the microverrucae. No such lumina are present in pollen type 4 and microverrucae are more densely spaced. Under LM both types show similarities to *Pandaniidites* sp. in size and sculpturing (Wingate & Nichols, 2001, pl. 9, fig. 9). Wingate and Nichols (2001) included in this form genus inaperturate, ulcerate and pollen with more than one pore. In pollen types 3 and 4 no aperture could be detected. Both pollen types are present in sample UF15880-7285.

Extant Pandanaceae produce ulcerate to sulcate pollen with exine sculpturing ranging from psilate, perforate, fossulate, verrucate to echinate (Erdtmann, 1952; Furness & Rudall, 2006; Hotton et al., 1994), but do not feature perforations/lumina covered by microverrucae.

Dispersed pollen of *Limnobiophyllum* sp. and *in situ* and dispersed pollen of *Limnobiophyllum scutatum* (Dawson) Krassilov (Stockey et al., 1997; Hesse & Zetter, 2007) are within the morphological range of the form genus *Pandaniidites*. Both resemble pollen types 3 and 4 by their echinate perforate exine sculpturing, but differ in aperture (ulcus with distinct annulus) and absence of microverrucae covering perforations.

Pollen type 4

(Figures 30D, 31G–H)

Description. – Pollen, spheroidal, pollen outline circular, pollen diameter without echinae 25–30 µm (LM), 20–25 µm (SEM); eutectate, exine 1.0–1.5 µm thick, inaperturate; sculpturing echinate (LM), echinate, microverrucate, microechinate, perforate (SEM), echinae base diameter 0.6–1 µm, echinae length 2.5–3.0 µm (SEM), perforations covered by microverrucae; abundance: very rare.

Pollen type 5

(Figures 30E, 31I–J)

Description. – Pollen, spheroidal, pollen outline circular, equatorial diameter 14–17 µm (LM), 10–13 µm (SEM); eutectate, exine 1.5–2.0 µm thick, nexine thinner than sexine, inaperturate; sculpturing rugulate (LM), rugulate, striate, fossulate, perforate (SEM), rugulae with striate sculpturing; abundance: very rare.

Remarks. – Affinity uncertain. Present in sample UF15880-7285.

Pollen type 6

(Figures 30F, 31K–L)

Description. – Pollen, outline circular, diameter 20–25 μm (LM & SEM); semitectate, exine 1.5–2.0 μm thick (LM & SEM), sexine thicker than nexine, pantoaperturate; sculpturing heterobrochate reticulate (LM), reticulum cristatum, heterobrochate, footlayer sculpturing microverrucate, perforate, lumina 0.5–5 μm wide, muri crested with microechinate, muri width 0.8–1.4 μm (SEM); abundance: very rare.

Remarks. – Pollen type 6 corresponds in size and sculpturing to ?*Persicarioipollis* sp. A (Wingate & Nichols 2001, pl. 8 fig. 21), affinity to Polygonaceae could not be confirmed. Present in sample UF15880-7285.

Pollen type 7

(Figures 30G, 31M–N)

Description. – Pollen, prolate to spheroidal, outline circular in equatorial view, polar axis 35–40 μm long (LM), 30–35 μm (SEM), equatorial diameter 35–40 μm (LM), 30–35 μm (SEM); eutectate, exine 1.5–2.0 μm thick, nexine thinner than sexine, tricolporate; sculpturing striate (LM & SEM), striae ribbed resembling a coiled metal wire (SEM); abundance: very rare.

Remarks. – A similar striate pollen type was described by Hascall (1988, *Acer/Dipteronia* Type 4, pl. 4, fig. 9) and Wingate and Nichols (2001, *Tricolporate* sp. E, pl. 6 fig. 14;). Affinities uncertain. Present in sample UF15880-7285.

Pollen type 8

(Figures 30H, 31O–P)

Description. – Pollen, prolate, elliptic in equatorial view, circular lobate in polar view, polar axis 20–25 μm long (LM & SEM), equatorial diameter 20–25 μm (LM & SEM); semitectate, exine 1.5–2 μm , tricolpate, colpi extending nearly from pole to pole, colpus membrane

microrugulate (SEM); sculpturing microreticulate (LM & SEM), muri are running at graded levels; abundance: very rare.

Remarks. – *Salix* Type 2 of Hascall (1988, pl. 4, fig. 10) shows strong similarities (size, aperture, reticulate ornamentation) to Pollen type 8; affinities to Salicaceae could not be confirmed. Present in sample UF15880-7285.

Pollen type 9

(Figures 32A, 33A–B)

Description. – Pollen, spheroidal, outline circular in polar view, equatorial diameter 34–38 μm (LM & SEM); semitectate, exine 2–2.5 μm thick (LM), nexine thinner than sexine, tricolporate, colpus membrane microechinate (SEM); sculpturing reticulate (LM), microreticulate, microechini at muri intersections (SEM), reticulum interwoven at different levels, muri 0.4–0.6 μm wide; abundance: very rare.

Remarks. – Pollen type 9 shows strong similarities to *Tricolporate* sp. C (Wingate & Nichols, 2001, pl. 6, fig. 7). Morphological similarities (echinate reticulum, long colpi) are with pollen of the Nyctaginaceae, genus *Neea* Ruiz et Pav. (SEM: Nowicke, 1975, pl. 2, fig. 9; LM: Roubik & Moreno, 1991, pl. 79, fig. 943). Present in sample UF15880-7285.

Pollen type 10

(Figures 32B, 33C–D)

Description. – Pollen, prolate, outline elliptic slightly rhombic in equatorial view, polar axis 17–20 μm (LM), 14–16 μm (SEM), equatorial diameter 13–16 μm (LM), 9–11 μm (SEM); semitectate, exine 1.0–1.5 μm thick (LM), nexine thinner than sexine, tricolpate, colpus length $\frac{3}{4}$ of polar axis; sculpturing scabrate (LM), microreticulate, reticulum fused in polar

area, lumina size decreasing in colpus area, reticulum interwoven on multiple levels (SEM);
abundance: very rare.

Remarks. – Affinities uncertain. Present in sample UF15880-7285.

Pollen type 11

(Figures 32C, 33E–F)

Description. – Pollen, prolate, outline elliptic in equatorial view, polar axis
23–28 μ m (LM) 22–24 μ m (SEM), equatorial diameter 14–16 μ m (LM), 10–12 μ m (SEM);
semitectate, exine 1.0–1.5 μ m thick, nexine thinner than sexine, tricolporate, aperture
membrane microverrucate to microrugulate; sculpturing reticulate (LM), striatoreticulate
(SEM); abundance: very rare.

Remarks. – Pollen type 11 resembles a pollen type figured by Leopold and Clay-Poole [2001,
Rutaceae cf. *Euodia* (= *Tetradium* Dulac), pl. 6 figs 5–6]. Morphological similarities in exine
sculpturing are with Rutaceae pollen but a definite family assignment is difficult; affinities
uncertain. Present in sample UF15880-7285.

Pollen type 12

(Figures 32D, 33G–H)

Description. – Pollen, lobate to circular outline in polar view, equatorial diameter 20–25 μ m
(LM & SEM), eutectate, exine 1.5–2 μ m thick (LM), nexine thinner than sexine, tricolpate,
sculpturing reticulate (LM), reticulate, perforate (SEM), reticulum formed by short, straight,
paired, parallel muri, muri pairs randomly orientated; lumina tetra- to pentagonally shaped,
lumina with central perforation; abundance: very rare.

Remarks. – Exine sculpturing of Pollen type 12 shows strong morphological similarities in
exine sculpturing to extant Rhamnaceae pollen, e.g. *Rhamnus crocea* Nutt., *Condalia lineata*

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3 A. Gray, *Karwinskia oblongifolia* Rusby (Schirarend & Köhler, 1993), but differs from this
4 family in having colpate apertures. Colpi of this specimen are gaping due to flattening and
5 deformation and no endoporus structure is visible in the equatorial aperture area. Present in
6 sample UF15880-7285.
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14 *Pollen type 13*

15 (Figures 32E, 33I–J)

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17 *Description.* – Pollen, outline circular to lobate in polar view, equatorial diameter 20–25 μm
18 (LM), 18–22 μm (SEM); eutectate, exine 1.0–1.5 μm thick (LM), nexine thinner than sexine,
19 tricolpate, colpi broad with rounded apex; sculpturing scabrate (LM), microechinate, perforate
20 (SEM); abundance: rare.
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27 *Remarks.* – Pollen type 13 shows strong similarities to *Tricolpate* sp. A (Wingate & Nichols,
28 2001, pl. 5, fig. 4). Affinities uncertain.
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34 *Pollen type 14/Boehlensipollis hohli* Krutzsch

35 (Figures 32F–G, 31K–N)

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37 *Description.* – Pollen, oblate, outline triangular in polar view, equatorial diameter 36–40 μm
38 wide (LM); exine 0.5–1 μm thick, eutectate, tricolp(or)ate to syncolp(or)ate, colpi can range
39 from relatively short (1/3 pollen diameter) to long, sculpturing scabrate (LM), microrugulate,
40 fossulate (SEM); abundance: rare.
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47 *Remarks.* – Pollen type 14 resembles in outline, size, aperture type and exine sculpturing
48 *Boehlensipollis hohli* (compare Sittler et al., 1975; Stuchlik, 2014), which has been associated
49 with Elaeagnaceae and Sapindaceae. Due to the bad preservation in all encountered
50 specimens it is not possible to rule out the presence of a porus. Similar triangular pollen has
51 previously been reported by Hascall (1988, Proteaceae/Sapindaceae/Elaeagnaceae, pl. 4, fig.
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1), Wingate and Nichols (2001, *Boehlensipollis* sp. cf. *B. granulata* Frederiksen et al., pl. 6, fig. 23) and Leopold and Clay-Poole (2001, *Cardiospermum* cf. *C. halicabum* L., pl. 7, figs 4–7). Present in samples UCMP30778 and UF15880-7285.

Exine sculpturing in extant Elaeagnaceae ranges from perforate, fossulate to microechinate (compare Sorsa, 1971; Li et al. 2010; Miyoshi et al., 2011; Halbritter, 2005a), but does not match Pollen type 14/ *Boehlensipollis hohli*. Pollen of extant Proteaceae *Beauprea* Brongniart et Gris, form genus *Beauprea* *elegansiformis* Cookson (Pocknall & Crosbie, 1988) and East Asian Symplocaceae, e.g. *Symplocos caudata* Wall. ex A. DC., *S. prunifolia* Sieb. et Zucc. (Namagasu, 1989; Li et al., 2010; Miyoshi et al., 2011) correspond to the present pollen by their triangular shape, size and microrugulate, fossulate ornamentation but differ from this pollen type by their brevicolpate to brevicolporate apertures. Strong morphological similarities (triangular shape, colporate to syncolporate apertures and exine sculpturing) are with pollen of extant South American Sapindaceae, *Urvillea* Kunth and *Serjania* Mill. (Ferrucci, 2006; Ferrucci & Anzotegui, 1993; Acevedo-Rodriguez et al., 2011). In Sapindaceae, apertures ranging from colporate to syncolporate have been reported within a subfamily (van der Ham, 1990). Noteworthy, Manchester and O'Leary (2010) stated after reinvestigation of the fossil fruit *Brachyruscus alleni* that it resembles most closely extant *Urviella*. Hence, among the previously suggested botanical affinities the strongest appear to be with Sapindaceae.

Pollen type 15

(Figures 32H, 33O–P)

Description. – Pollen, oblate, outline triangular in polar view, equatorial diameter 44–54 μm (LM), 32–40 μm (SEM); trichotomosulcate; sculpturing reticulate (LM & SEM), smooth muri, muri width 0.5–1 μm ; abundance: very rare.

Remarks. – The most striking character of this grain is its lack of a nexine (footlayer and endexine), only the reticulate sexine (collumellae and tectum) has been preserved. The extant Proteaceae *Leucospermum heterophyllum* (Thunb.) Rourke displays some striking morphological similarities (pollen shape and reticulum ornamentation) to Pollen type 15 but differs by the presence of a footlayer and porate apertures (Sauquet & Cantrill, 2007). Because of the presence of a trichotomosulcate aperture, affinity to Proteaceae can be ruled out.

Wingate and Nichols (2001) encountered this pollen type as well, without “inner body” [*Triporate* sp. cf. ? *Ruella laxa* (Frederiksen) Frederiksen et al., pl. 9, figs 13–14;], and concluded, Proteaceae or Acanthaceae affinity. Present in samples UF15880-7285.

Pollen type 16

(Figures 20C, 21E–F)

Description. – Pollen, prolate to spheroidal, convex triangular in polar view, outline elliptic to circular in equatorial view, polar axis 24–26 μm (LM), 18–20 μm (SEM), equatorial diameter 20–22 μm (LM), 15–18 μm (SEM); semitectate, exine 1.5–2.0 μm thick (LM), nexine and sexine have the same thickness, tricolpate; sculpturing scabrate (LM), microbireticulate (SEM); abundance: very rare.

Remarks. – The morphological characters (size, shape, exine sculpturing) of pollen type 16 resemble pollen of extant *Stachys* (Lamiaceae; Trudel et al., 1992; Salmaki et al., 2008). Present in samples UF15880-7285.

Discussion

A taxonomic approach to the investigation of dispersed pollen and spores

Three comprehensive previous studies on the spores and pollen from the Florissant Formation

have recorded a high diversity of taxa. Hascall (1988) designated 78 palynomorph types from two sections (section 8/5/84: ca. 11 m of lower mudstone unit, ca. 4 m of middle shale unit; section 8/23/84: ca. 2 m of middle shale unit, ca. 1 m of upper shale unit), Leopold and Clay-Poole (2001) reported 150 phenotypes among pollen and spores and figured about 60; Wingate and Nichols (2001) reported about 130 morphotype species from two sections of the Florissant Formation (ca. 6 m of the middle shale unit, 21 samples; ca. 3 m of the upper shale unit, 8 samples). The three sediment samples for the present study are a few randomly chosen slabs from the leaf-bearing shale units. Despite this, the diversity of pollen and spores is well comparable to that encountered in previous studies that included long stratigraphic sequences. This is not surprising as Hascall (1988) and Leopold and Clay-Poole (2001) noticed little vegetative change in their pollen diagrams. The total diversity of spores and pollen encountered in our survey is slightly lower (111 taxa) than in the studies mentioned above. However, investigating spores and pollen with the SEM in addition to conventional LM observation provides important complementary information concerning the botanical affinities of the studied palynomorphs. For example, in several cases the combined LM/SEM investigation of pollen and spores has led to significantly better taxonomic resolution. Hascall (1988) described and figured six types of Fagaceae pollen, *Castanea*, *Fagopsis longifolia* and four types of *Quercus*; Wingate and Nichols (2001) described and figured three kinds of Fagaceae pollen, *Quercoidites microhenricii* (Potonié) Potonié – “probably *Quercus*”, *Siltaria* sp. – “intermediate between *Quercus* and *Castanea*”, and *Quercipollenites* sp. – “cf. pollen of *Fagopsis*”. Leopold and Clay-Poole (2001) reported *Castanea* type pollen, *Fagopsis in situ* pollen, and two types of *Quercus* pollen. The taxonomic, phylogenetic and ecological information of these taxa is very limited since *Quercus* comprises six infrageneric groups with highly distinct evolutionary histories and ecological adaptations (e.g. Denk & Grimm, 2010; Hubert et al., 2014; Grímsson

et al., 2015). The infrageneric groups of *Quercus* have diagnostic pollen morphologies when observed by LM/SEM (Denk & Grimm, 2009; Denk & Tekleva, 2014). In contrast, pollen of “castanoid” Fagaceae is morphologically highly conservative (e.g. Praglowski, 1984), and modern *Castanea*, *Lithocarpus* and others, and extinct taxa are not readily distinguishable using pollen morphology. Hence, in a recent study on Fagaceae pollen from the Florissant Formation, Bouchal et al. (2014) using a combined LM/SEM approach recognized eight distinct pollen types referable to five genera and 4 infrageneric groups within *Quercus* (cf. Results section). Also in the family Platanaceae, close examination of tectum patterns in the colpus region allowed distinguishing two genera: *Platanus* and the extinct *Macginitiea* (Manchester, 1986; Denk & Tekleva, 2006).

In contrast, differences within another family figuring prominently in the Florissant palynological assemblage, Juglandaceae, are not very well resolved both in LM and combined LM/SEM studies. The record of *Platycarya* by Leopold and Clay-Poole (2001) is questionable. “*Platycarya*” would need to be confirmed by more and better preserved material to verify whether the two pseudocolpi on each hemisphere are present or not (cf. Stone & Broome, 1975). Apart from this, the presence of *Juglans* and *Carya* is unambiguously recorded in previous studies and in the present study. A further subdivision of Engelhardioideae pollen in an East Asian and American component is difficult if not impossible using LM/SEM. In addition, the fossil pollen may predate the split between the modern American and East Asian groups which would be in accordance with the estimated ages for the modern clade *Alfaroa/Oreomunnea* (Manos et al., 2007).

Various pollen taxa identified based on LM turn out to be misidentifications when scrutinized under the SEM.

Pollen previously identified as *Podocarpus* (Hascall, 1988) or *Podocarpidites* sp. (Wingate & Nichols, 2001) from Florissant show microechinate sculpturing when investigated with SEM

and can unambiguously be assigned to *Cathaya*. Already Wingate and Nichols (2001) stated in their remarks on *Podocarpidites* from Florissant: "..., it may not truly have affinity to extant genus *Podocarpus*." Liu and Basinger (2000) reviewed the fossil record of *Cathaya* and showed that its presence in the North American palynological record can be traced from the Late Cretaceous to the late Miocene. To date there has not been a single report of *Cathaya* macrofossils in the North American fossil record and the only convincing macrofossils of *Podocarpus* are a few leafy shoots from the Eocene of Tennessee (Dilcher, 1969). Our results suggest that *Podocarpus* should be removed from Florissant's palaeoflora list.

At the genus level, a rosaceous pollen type has been assigned to *Malus/Pyrus* by Leopold and Clay-Poole (2001; pl. 5, fig. 11). This pollen has a tuberculate sculpturing as found in two genera of subfamily Dryadoideae in the Rosaceae, *Cercocarpus* and *Purshia*, but not in *Malus/Pyrus*. The genus *Cercocarpus* has also been reported for the Florissant Formation based on fruits and leaves (Manchester, 2001).

Pollen commonly referred to as *Boehlensipollis* (Wingate & Nichols, 2001) has been recorded in previous studies and the present one. *Boehlensipollis* has been suggested to belong to Sapindaceae or Elaeagnaceae (Sittler et al., 1975; Wingate & Nichols, 2001). Hascall (1988) suggested affinity with Proteaceae, Sapindaceae or Elaeagnaceae; Leopold and Clay-Poole (2001) suggested affinity with *Cardiospermum* in the Sapindaceae. Combined LM/SEM investigation clearly shows that this pollen type cannot be linked with Elaeagnaceae based on its exinesculpturing and aperture.. Proteaceae and Symplocaceae resemble this pollen type in shape and exine sculpturing but differ in aperture form. Highest correspondence in aperture shape and variability, pollen size and exine sculpturing are with Sapindaceae, but not with the genus *Cardiospermum*.

Within the Onagraceae, "*Semeiandra*" (Leopold & Clay-Poole, 2001) differs from this extant genus by its viscin threads and is more closely related to the genus *Hauya*. Likewise,

Persicarioipollis sp. B (Wingate & Nichols, 2001) rather than being referable to Polygonaceae display exine ornamentation diagnostic of Thymelaeaceae. Furthermore, *Malvacipollis* sp. D and *Pandaniidites* (Wingate & Nichols, 2001) do not belong to Malvaceae and Pandanaceae, respectively, and *Pteroceltis* (Leopold & Clay-Poole, 2001) lacks genus diagnostic features of the tectum and thus cannot securely be assigned to Cannabaceae.

Table 1 lists taxa recognized in the present study and taxa reported in the previous studies by Leopold and Clay-Poole (2001) and Wingate and Nichols (2001) that can unambiguously be linked with pollen types encountered by us. Some taxa reported in the present study have previously only been known from the macrofossil record (*Ginkgo*, Sapotaceae, Thymelaeaceae). A few taxa are new records for Florissant (Ebenaceae: *Diospyros*; Mernispermaceae; Trochodendraceae: *Tetracentron*).

In conclusion it can be stated that while the diversity of pollen morphotypes will not necessarily increase when a combined LM/SEM approach is used, the determinations of pollen grains will certainly be more objective.

SEM investigations as a complement to conventional palynological studies

LM based palynological studies commonly cover a whole stratigraphic sequence in order to resolve vegetation/environmental changes during a certain period of time. For the Florissant Formation, Hascall (1988), Leopold and Clay-Poole (2001) and Wingate and Nichols (2001) noted a rather homogeneous pollen spectrum in which peaks of volcanic activity were expressed merely as fluctuations in the dominance of particular plant groups. As a consequence, the composition of pollen and spores in these studies and the present one are fairly similar. It has previously been stated that the strength of adding SEM to conventional LM investigations is the discrimination of small pollen grains that would otherwise be lumped in unnatural form genera or classified as undetermined (Ferguson et al., 2007).

The combined LM/SEM investigation and documentation of dispersed Cenozoic pollen and spores is of paramount importance for a wide range of evolutionary studies including biogeographic and phylogenetic studies. In addition, in some cases dispersed pollen of extinct groups can be discriminated in SEM. Examples are the extinct genera *Fagopsis* (Fagaceae; Manchester & Crane, 1983; Bouchal et al., 2014) and *Macginitiea* (Platanaceae; Manchester, 1986) originally described from reproductive structures with *in situ* pollen. In the present study, both genera are recognized among dispersed pollen, while they cannot be distinguished from modern genera/subfamilies based on LM investigation alone. Modern pollen taxonomy mainly relies on SEM characteristics (see *Remarks* in the Results section; Takahashi, 1997) and reliable comparison of dispersed fossil pollen/spores with modern taxa is only possible when fossil pollen/spores are documented with similarly high resolution. Therefore, tackling infrataxonomic relationships and tracing the evolutionary history of a group in space and time will ideally be based on a combined LM/SEM investigation of dispersed fossil pollen/spores (e.g. Liu et al., 1997; Liu & Basinger, 2000, *Cathaya*; Grímsson et al., 2008, *Tetracentron*; Grímsson et al., 2011, Wortley et al., 2012, Asteraceae; Grímsson et al., 2011, Lythraceae; Grímsson et al., 2012a, Onagraceae; Grímsson et al., 2012b, *Decodon*; Grímsson et al., 2014, *Aponogeton*; Bouchal et al., 2014, Grímsson et al., 2015, Fagaceae).

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Figures and Tables

Figure 1. (A–C) Geography, geologic setting, and stratigraphy of the Florissant Formation.

(A) Map showing the geographical position of the Florissant Fossil Beds National Monument in Colorado, USA. (B) Geological map indicating Florissant Formation and surrounding formations. X₁ = sample UF15880-7285 locality, X₂ = sample S151454 locality. Map based on and modified after U.S.G.S. Map 1-1044 (Wobus & Epis, 1978). (C) Generalized stratigraphy of the Florissant Formation, modified after Evanoff et al. (2001).

Figure 2. (A–H) LM overview micrographs of dispersed fossil spores in polar view. A.

Marchantiopsida fam. et gen. indet. B. *Selaginella* sp. 1. C. *Selaginella* sp. 2. D. Polypodiales fam. et gen. indet. E. Trilete spore fam. et gen. indet. 1. F. Trilete spore fam. et gen. indet. 2. G. Trilete spore fam. et gen. indet. 3. H. Trilete spore fam. et gen. indet. 4. Scale bars – 10 µm (A–H). Sample: UF15880-7285 (A–H).

Figure 3. SEM micrographs of dispersed fossil spores in distal (A–B) and proximal view (C–P). Overview (A, C, E, G, I, K, M, O) and detail (B, D, F, H, J, L, N, P). A–B.

Marchantiopsida fam. et gen. indet. C–D. *Selaginella* sp. 1. E–F. *Selaginella* sp. 2. G–H Polypodiales fam. et gen. indet. I–J. Trilete spore fam. et gen. indet. 1. H–L. Trilete spore fam. et gen. indet. 2. M–N. Trilete spore fam. et gen. indet. 3. O–P. Trilete spore fam. et gen. indet. 4. Scale bars – 10 µm (A, C, E, H, I, K, M, O), 1 µm (B, D, F, H, J, L, N, P). Sample: UF15880-7285 (A–P).

Figure 4. (A–G) LM micrographs of dispersed fossil spores, Ginkgoace, Cupressaceae, and Pinaceae pollen. A. Trilete spore fam. et gen. indet. 5, polar view. B. *Ginkgo* sp. C.

Cupressaceae gen. indet. 1. D. *Cupressaceae* gen. indet. 2. E. *Cupressaceae* gen. indet. 3. F. *Abies* sp 1, equatorial view. G. *Abies* sp. 2, equatorial view. Scale bars – 10 µm (A–G).

Sample: UF15880-7285 (A–D, F–G), UCMP 20778 (E).

Figure 5. (A–P) SEM micrographs of dispersed fossil spores, Ginkgoace, Cupressaceae, and Pinaceae pollen. Overview (A, C, E, G, I, K, N), detail (B, D, F, H, J), close-ups of corpus

(L, O) and saccus (M, P). A–B. Trilete spore fam. et gen. indet. 5, proximal view. C–D. *Ginkgo* sp. E–F. *Cupressaceae* gen. indet. 1. G–H. *Cupressaceae* gen. indet. 2. I–J. *Cupressaceae* gen. indet. 3. K–M *Abies* sp 1, equatorial view. N–P. *Abies* sp. 2, equatorial view. Scale bars – 10 µm (A, C, E, G, I, K, N), 1 µm (B, D, F, H, J, L, M, O, P). Sample: UF15880-7285 (A–H, K–P), UCMP 20778 (I–J).

Figure 6. (A–D) LM overview micrographs of dispersed fossil Pinaceae pollen. A–B. *Cathaya* sp., distal view. C. *Larix/Pseudotsugsa* sp., tetrad. D. *Picea* sp., equatorial view. Scale bars – 10 µm (A–D). Sample: UF15880-7285 (A, B, D), S151454 (C).

Figure 7. (A–L) SEM micrographs of dispersed fossil Pinaceae pollen. Overview (A, D, G, H, J), detail (I), close-up of leptoma (B, E), corpus (K), saccus (C, F, L). A–F. *Cathaya* sp., distal view. G–I. *Larix* sp. J–L. *Picea* sp., equatorial view. Scale bars – 10 µm (A, D, G, H, J), 1 µm (B, C, E, F, I, K, L). Sample: UF15880-7285 (A–F, J–L), S151454 (G–I).

Figure 8. (A–D) LM micrographs of dispersed fossil Pinaceae pollen. A. *Pinus* subgenus *Strobilus* sp., equatorial view. B. *Pinus* subgenus *Pinus* sp., polar view. C. *Tsuga* sp. 1, polar view. D. *Tsuga* sp. 2, polar view. Scale bars – 10 µm (A–D). Sample: UF15880-7285 (A, C, D), UCMP 20778 (B).

Figure 9. (A–M) SEM micrographs of dispersed fossil Pinaceae pollen. Overview (A, D, G, H, J), detail (H, K–M), close-ups of corpus (B, E), saccus (C, F). A–C. *Pinus* subgenus *Strobilus* sp., equatorial view. D–F. *Pinus* subgenus *Pinus* sp., distal view. G–H. *Tsuga* sp. 1, proximal view. H. Detail of proximal pole. I–M. *Tsuga* sp. 2. I. proximal view. J. Distal view. K. Detail proximal pole. L. Margin (saccus) detail. M. Distal pole detail. Scale bars – 10 µm (A, D, G, I–J), 1 µm (B, C, E, F, H, K–M). Sample: UF15880-7285 (A–C, G–M), UCMP 20778 (D–F).

Figure 10. (A–H) LM micrographs of dispersed fossil pollen of Gnetales, and Monocotyledone. A–B. *Ephedra* sp., equatorial view. C. Poaceae gen. indet. 1 aff.

Stipa/Achnatherum, equatorial view. **D.** Poaceae gen. indet. 2, top: equatorial view, bottom: polar view. **E.** *Sparganium* sp., polar view. **F.** *Typha* sp. 1, equatorial view. **G.** *Typha* sp. 2, equatorial view. **H.** Monocotyledone pollen fam. et gen. indet., equatorial view. Scale bars – 10 μm (**A–H**). Sample: UF15880-7285 (**A–C, E–H**), S151454 (**D**).

Figure 11. SEM micrographs of dispersed fossil Gnetales and Monocotyledone pollen. Overview (**A, C, E, G, I, K, M, O**) and details (**B, D, F, H, J, L, N, P**). **A–D.** *Ephedra* sp., equatorial view. **E–F.** Poaceae gen. indet. 1 aff. *Stipa/Achnatherum*. **G–H.** Poaceae gen. indet. 2. **I–J.** *Sparganium* sp., distal view. **K–L.** *Typha* sp. 1, equatorial view. **M–N.** *Typha* sp. 2, proximal view. **O–P.** Monocotyledone pollen fam. et gen. indet., equatorial view. Scale bars – 10 μm (**A, C, E, G, I, K, M, O**), 1 μm (**B, D, F, H, J, L, N, P**). Sample: UF15880-7285 (**A–F, I–P**), S151454 (**G, H**).

Figure 12. (**A–I**) LM micrographs of dispersed fossil Adoxaceae/Caprifoliaceae, Amaranthaceae, Sarcobataceae, Asteraceae, and Apocynaceae pollen. **A.** Adoxaceae vel Caprifoliaceae gen. indet., equatorial view. **B.** Amaranthaceae gen. indet. 1. **C.** Amaranthaceae gen. indet. 2. **D–G.** *Sarcobatus* sp. **G.** Porus detail. **H.** Asteroideae gen. indet. **I.** *Tabernaemontana* sp., equatorial view. Scale bars – 10 μm (**A–G**). Sample: UF15880-7285 (**A–E, H, I**), UCMP 20778 (**F, G**).

Figure 13. SEM micrographs of dispersed fossil Adoxaceae/Caprifoliaceae, Amaranthaceae, Sarcobataceae, Asteraceae, and Apocynaceae pollen. Overview (**A, C, E, G, I, K, M**) and details (**B, D, F, H, J, L, N, O**). **A–B.** Adoxaceae vel Caprifoliaceae gen. indet., equatorial view. **C–D.** Amaranthaceae gen. indet. 1. **E–F.** Amaranthaceae gen. indet. 2. **G–J.** *Sarcobatus* sp., **G–H.** same grain as in Figs 12D, **I–K.** same grain as in Fig. 12E. **K–L.** Asteroideae gen. indet. **M–O.** *Tabernaemontana* sp., equatorial view. Scale bars – 10 μm (**A, C, E, G, I, K, M**), 1 μm (**B, D, F, H, J, L, N, O**). Sample: UF15880-7285 (**A–O**).

Figure 14. (A–G) LM micrographs of dispersed fossil Betulaceae, Caprifoliaceae, Ebenaceae, Ericaceae, and Eucommiaceae pollen. **A.** *Betula* sp., top polar view, bottom equatorial view. **B.** *Alnus* sp., polar view. **C.** Coryloideae gen. indet. 1, polar view. **D.** Coryloideae gen. indet. 2, polar view. **E.** Caprifolioideae/Linnaeoidae gen. indet., polar view. **F.** *Diospyros* sp., equatorial view. **G.** Ericaceae gen. indet., polar view. **H.** Elaeagnaceae gen. indet., right equatorial view, left polar view. **I–J.** *Eucommia* sp., **I.** top equatorial view, bottom polar view. **J.** Equatorial view. Scale bars – 10 µm (A–I). Sample: UF15880-7285 (A–C, E–J), S151454 (D).

Figure 15. (A–P) SEM micrographs of dispersed fossil Betulaceae, Caprifoliaceae, Ebenaceae, Ericaceae, and Eucommiaceae pollen. Overview in polar view (A, C, E, G, K), equatorial view (I, M, O), and details (B, D, F, H, J, L, N, M). A–B. *Betula* sp. C–D. Coryloideae gen. indet. 1. E–F. Coryloideae gen. indet. 2. G–H. Caprifolioideae/Linnaeoidae gen. indet. I–J. *Diospyros* sp. K–L. Ericaceae gen. indet. M–P. *Eucommia* sp. Scale bars – 10 µm (A, C, E, G, I, K, M, O), 1 µm (B, D, F, H, J, L, N, P). Sample: UF15880-7285 (A–D, I–P), S151454 (E–F).

Figure 16. LM micrographs of dispersed fossil Fabaceae, Fagaceae and possible Euphorbiaceae pollen in equatorial (A, C–G, I) and polar view (B, H). **A.** aff. Euphorbiaceae gen. indet. **B.** Caesalpinioideae gen. indet. **C.** Castaneoideae gen. indet. 1. **D.** Castaneoideae gen. indet. 2. **E.** Castaneoideae gen. indet. 3. **F–G.** *Fagopsis longifolia*. **H.** *Quercus* Group *Cyclobalanopsis* sp. **I.** *Quercus* Group *Protobalanus* sp. Scale bars – 10 µm (A–I). Sample: UF15880-7285 (A, B, D–F, H–I), S151454 (C, F).

Figure 17. SEM micrographs of dispersed fossil Fabaceae, Fagaceae, and possible Euphorbiaceae pollen. Overview in equatorial view (A, C, E, G, I, K, O), polar view (M), and details (B, D, F, H, J, L, N, M). A–B. aff. Euphorbiaceae gen. indet. C–D. Castaneoideae gen. indet. sp. 1. E–F. Castaneoideae gen. indet. sp. 2. G–H. Castaneoideae gen. indet. sp. 3.

I–L. *Fagopsis longifolia*. M–N. *Quercus* Group *Cyclobalanopsis* sp. O–P. *Quercus* Group *Protobalanus* sp. Scale bars – 10 μm (A, C, E, G, I, K, M, O), 1 μm (B, D, F, H, J, L, N, P). Sample: UF15880-7285 (A, B, E–J, M–P), S151454 (C, D, K, L).

Figure 18. LM micrographs of dispersed fossil Fagaceae, Hamamelidaceae, and Juglandaceae pollen in equatorial (A–B) and polar view (C–I). A. *Quercus* Group *Quercus/Lobatae* sp. B. *Quercus* Group *Quercus* sp. C. Hamamelidoideae gen. indet. D–E. *Momipites coryloides*. F. *Momipites triradiatus*. G. *Momipites microfoveolatus*. H–I. *Carya* sp. Scale bars – 10 μm (A–I). Sample: UF15880-7285 (A, C–I), S151454 (B).

Figure 19. SEM micrographs of dispersed fossil Fagaceae, Hamamelidaceae, and Juglandaceae pollen. Overview in equatorial view (A, C, E), polar view (G, I, K, M, O), and details (B, D, F, H, J, L, N, P). A–B. *Quercus* Group *Quercus/Lobatae* sp. C–D. *Quercus* Group *Quercus* sp. E–F. Hamamelidoideae gen. indet. G–H. *Momipites coryloides*, micrographs of same grain depicted in Fig. 18E. I–J. *Momipites triradiatus*. K–L. *Momipites microfoveolatus*. M–P. *Carya* sp. Scale bars – 10 μm (A, C, E, G, I, K, M, O), 1 μm (B, D, F, H, J, L, N, P). Sample: UF15880-7285 (A, B, E–P), S151454 (C, D).

Figure 20. (A–H) LM micrographs of dispersed fossil Juglandaceae, Malvaceae, and unidentified pollen. A. *Juglans* sp. 1, polar view. B. *Juglans* sp. 2, polar view. C. Pollen type 16, top equatorial view, bottom polar view. D. Bombacoidae/Sterculioideae gen. et indet. E. Bombacoidae/Brownlowioideae gen. indet. F. Malvoideae gen. indet. 1. G. Malvoideae gen. indet. 2. H. Malvoideae gen. indet. 3. Scale bars – 10 μm (A–H). Sample: UF15880-7285 (B–H), S151454 (A).

Figure 21. SEM micrographs of dispersed fossil Juglandaceae, Malvaceae, and unidentified pollen. Overview (A, C, E, G, I, K, M, O) and details (B, D, F, H, J, L, N, P). A–B. *Juglans* sp. 1, polar view. C–D. *Juglans* sp. 2, polar view. E–F. Pollen type 16. G–H Bombacoidae/Sterculioideae gen. indet. I–J. Bombacoidae/Brownlowioideae gen. indet.

K–L. Malvoideae gen. indet. 1. **M–N.** Malvoideae gen. indet. 2. **O–P.** Malvoideae gen. indet. 3. Scale bars – 10 μm (**A, C, E, G, I, K, M, O**), 1 μm (**B, D, F, H, J, L, N, P**). Sample: UF15880-7285 (**C–P**), S151454 (**A, B**).

Figure 22. (**A–F**) LM micrographs of dispersed fossil Malvaceae, Menispermaceae, Oleaceae, and Onagraceae pollen. **A.** Malvoideae gen. indet. 4. **B.** Menispermaceae gen. indet., equatorial view. **C.** *Fraxinus* sp., equatorial view. **D.** Onagraceae/Lopezieae gen. indet. 2, polar view. **E.** Hauyeae gen. indet. aff. *Hauya*, polar view **F.** Onagraceae/Lopezieae gen. indet. 1. Scale bars – 10 μm (**A–F**). Sample: UF15880-7285 (**A–F**)

Figure 23. SEM micrographs of dispersed fossil Malvaceae, Menispermaceae, Oleaceae, and Onagraceae pollen. Overview (**A, C, E, G, J, K, N**) and details (**B, D, F, H, I, L, M, O, P**). **A–B.** Malvoideae gen. indet. 4. **C–D.** Menispermaceae gen. indet., equatorial view. **E–F.** *Fraxinus* sp., equatorial view. **G–I.** Onagraceae/Lopezieae gen. indet. 2, (**G**) polar view, (**H**) surface detail, (**I**) viscin thread detail. **J–M.** Hauyeae gen. indet. aff. *Hauya* sp., (**J**) proximal view, (**K**) distal view, (**L**) viscin thread detail, (**M**) surface detail. **N–P.** Onagraceae/Lopezieae gen. indet. 1, (**N**) equatorial view, (**O**) surface detail, (**P**) viscin thread detail. Scale bars – 10 μm (**A, C, E, G, J, K, N**), 1 μm (**B, D, F, H, I, L, M, O, P**). Sample: UF15880-7285 (**A–P**).

Figure 24. LM micrographs of dispersed fossil Platanaceae and Rosaceae pollen. **A.** Platanaceae gen. indet. aff. *Macginitea*, polar view. **B.** *Platanus* sp., polar view. **C.** *Crateagus* sp., equatorial view. **D.** Rosaceae gen. indet. 1, equatorial view. **E.** Rosaceae gen. indet. 2, equatorial view. **F.** Rosaceae gen. indet. 3, top equatorial view, bottom polar view. **G.** Rosaceae gen. indet. 4, equatorial view. **H.** Dryadoideae gen. indet. aff. *Cercocarpus/Purshia*, polar view. Scale bars – 10 μm (**A–H**). Sample: UF15880-7285 (**A–H**).

Figure 25. SEM micrographs of dispersed fossil Platanaceae and Rosaceae pollen. Overview (**A, C, E, G, I, K, M, O**) and details (**B, D, F, H, J, L, N, P**). **A–B.** Platanaceae gen. indet.

aff. *Macginitea*, polar view. **C–D.** *Platanus* sp., polar view. **E–F.** *Crataegus* sp., equatorial view. **G–H.** Rosaceae gen. indet. 1, equatorial view. **I–J.** Rosaceae gen. indet. 2, equatorial view. **K–L.** Rosaceae gen. indet. 3, equatorial view. **M–N.** Rosaceae gen. indet. 4, equatorial view. **O–P.** Dryadoideae gen. et indet. aff. *Cercocarpus/Purshia*, polar view. Scale bars – 10 μm (**A, C, E, G, I, K, M, O**), 1 μm (**B, D, F, H, J, L, N, P**). Sample: UF15880-7285 (**A–P**).

Figure 26. LM micrographs of dispersed fossil Sapindaceae, Sapotaceae, Thymeliaceae, and possible Rutaceae pollen. **A.** aff. Rutaceae gen. indet., equatorial view. **B.** *Acer* sp. 1, equatorial view. **C.** *Acer* vel *Dipteronia* sp., polar view. **D.** *Acer* sp. 2, equatorial view. **E.** *Acer* sp. 3 aff. *A. negundo*, equatorial view. **F.** Sapotoideae gen. indet. 1, equatorial view. **G.** Sapotoideae gen. indet. 2, equatorial view. **H.** Thymelaeoideae gen. indet. 1. **I.** Thymelaeoideae gen. indet. 2. Scale bars – 10 μm (**A–I**). Sample: UF15880-7285 (**A–I**)

Figure 27. SEM micrographs of dispersed fossil Sapindaceae, Sapotaceae, Thymeliaceae, and possible Rutaceae, pollen. Overview (**A, C, E, G, I, K, M, O**) and details (**B, D, F, H, J, L, N, P**). **A–B.** aff. Rutaceae gen. indet., equatorial view. **C–D.** *Acer* vel *Dipteronia* sp., polar view. **E–F.** *Acer* sp. 2, equatorial view. **G–H.** *Acer* sp. 3 aff. *A. negundo*, equatorial view. **I–J.** Sapotoideae gen. indet. 1, equatorial view. **K–L.** Sapotoideae gen. indet. 2, equatorial view. **M–N.** Thymelaeoideae gen. indet. 1. **O–P.** Thymelaeoideae gen. indet. 2. Scale bars – 10 μm (**A, C, E, G, I, K, M, O**), 1 μm (**B, D, F, H, J, L, N, P**). Sample: UF15880-7285 (**A–P**).

Figure 28. LM micrographs of dispersed fossil Trochodendraceae, Cannabaceae, Ulmaceae, and Vitaceae pollen. **A.** *Tetracentron* sp., equatorial view. **B.** *Celtis* vel *Pteroceltis* sp., polar view. **C–D.** *Cedrelospermum* sp., polar view. **E–F.** *Ulmus* sp., polar view. **G.** Ulmaceae gen. indet. aff. *Zelkova*, polar view. **H.** Vitaceae gen. indet. 1, equatorial view. **I.** Vitaceae gen. indet. 2, equatorial view. Scale bars – 10 μm (**A–I**). Sample: UF15880-7285 (**A–I**).

Figure 29. SEM micrographs of dispersed fossil pollen. Overview (**A, C, E, G, I, J, L, N, P**) and details (**B, D, F, H, , K, M, O, Q**). **A–B.** *Tetracentron* sp., equatorial view. **C–D.** *Celtis*

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3 vel *Pteroceltis* sp., polar view. **E–H.** *Cedrelospermum* sp., polar view. **I–K.** *Ulmus* sp., polar
4 view; **K** detail of grain in **J.** **L–M.** Ulmaceae gen. indet. aff. *Zelkova*, polar view. **N–O.**
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6 Vitaceae gen. indet. 1, equatorial view. **P–Q.** Vitaceae gen. indet. 2, equatorial view. Scale
7 bars – 10 μm (**A, C, E, G, I, J, L, N, P**), 1 μm (**B, D, F, H, K, M, O, Q**). Sample: UF15880-
8 7285 (**A–Q**).
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14 **Figure 30.** LM micrographs of unidentified dispersed fossil Angiosperm pollen. **A.** Pollen
15 type 1, polar view. **B.** Pollen type 2, polar view. **C.** Pollen type 3. **D.** Pollen type 4. **E.** Pollen
16 type 5. **F.** Pollen type 6. **G.** Pollen type 7, equatorial view. **H.** Pollen type 8, equatorial view.
17 Scale bars – 10 μm (**A–H**). Sample: UF15880-7285 (**A, C–H**), UCMP 20778(**B**).
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23 **Figure 31.** SEM micrographs of unidentified dispersed fossil pollen. Overview (**A, C, E, G,**
24 **I, K, M, O**) and details (**B, D, F, H, J, L, N, P**). **A–B.** Pollen type 1, polar view. **C–D.** Pollen
25 type 2, polar view. **E–F.** Pollen type 3. **G–H** Pollen type 4. **I–J.** Pollen type 5. **K–L.** Pollen
26 type 6. **M–N.** Pollen type 7, equatorial view. **O–P.** Pollen type 8, equatorial view. Scale bars
27 – 10 μm (**A, C, E, G, I, K, M, O**), 1 μm (**B, D, F, H, J, L, N, P**). Sample: UF15880-7285 (**A,**
28 **B, E–P**), UCMP 20778(**C, D**).
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37 **Figure 32.** LM micrographs of unidentified dispersed fossil Angiosperm pollen. **A.** Pollen
38 type 9, polar view. **B.** Pollen type 10, equatorial view. **C.** Pollen type 11, equatorial view. **D.**
39 Pollen type 12, polar view. **E.** Pollen type 13, polar view. **F–G.** Pollen type 14, polar view. **H.**
40 Pollen type 15, polar view. Scale bars – 10 μm (**A–H**). Sample: UF15880-7285 (**A–H**).
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46 **Figure 33.** SEM micrographs of unidentified dispersed fossil pollen. Overview (**A, C, E, G,**
47 **I, K, M, O**) and details (**B, D, F, H, J, L, N, P**). **A–B.** Pollen type 9, polar view. **C–D.** Pollen
48 type 10. **E–F.** Pollen type 11, equatorial view. **G–H.** Pollen type 12, polar view. **I–J.** Pollen
49 type 13, polar view. **K–N.** Pollen type 14, polar view. **O–P.** Pollen type 15, polar view. Scale
50 bars – 10 μm (**A, C, E, G, I, K, M, O**), 1 μm (**B, D, F, H, J, L, N, P**). Sample: UF15880-
51 7285 (**A–P**).
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Table 1. Taxa recognized in the present study and corresponding pollen phenotypes documented in previous studies.

Underlined taxa indicate increased taxonomic resolution as compared to previous studies.

Note that in several cases a taxon identified in the present study may be “hidden” in the morphological variability of a heterogeneous pollen taxon described in previous studies. For example, Sapotoideae sp.1 and sp. 2 cannot be distinguished from “*Quercoidites*” in LM and pollen of Sapotoideae most likely has been included with the *Quercoidites* pollen phenotype.

Abbreviations: *Acer/Dipteronia* (AC/DI); Chenopodiaceae/Amaranthaceae (CH/AM);

Proteaceae/Sapindaceae/Eleagnaceae type (PR/SA/EL); Taxodiaceae/Cupressaceae/Taxaceae type (TCT); *Typha/Sparganium* or *Sparganium/Typha* (TY/SP or SP/TY).

Figure 1. (A-C) Geography, geologic setting, and stratigraphy of the Florissant Formation. (A) Map showing the geographical position of the Florissant Fossil Beds National Monument in Colorado, USA. (B) Geological map indicating Florissant Formation and surrounding formations. X1 = sample UF15880-7285 locality, X2 = sample S151454 locality. Map based on and modified after U.S.G.S. Map 1-1044 (Wobus & Epis, 1978). (C) Generalized stratigraphy of the Florissant Formation, modified after Evanoff et al. (2001).
 173x177mm (300 x 300 DPI)

Figure 2. (A–H) LM overview micrographs of dispersed fossil spores in polar view. A. Marchantiopsida fam.et gen. indet. B. Selaginella sp. 1. C. Selaginella sp. 2. D. Polypodiales fam. et gen. indet. E. Trilete spore fam. et gen. indet. 1. F. Trilete spore fam. et gen. indet. 2. G. Trilete spore fam. et gen. indet. 3. H. Trilete spore fam. et gen. indet. 4. Scale bars – 10 µm (A–H).
239x719mm (300 x 300 DPI)

Figure 3. SEM micrographs of dispersed fossil spores in distal (A–B) and proximal view (C–P). Overview (A, C, E, G, I, K, M, O) and detail (B, D, F, H, J, L, N, P). A–B. Marchantiopsida fam. et gen. indet. C–D. *Selaginella* sp. 1. E–F. *Selaginella* sp. 2. G–H Polypodiales fam. et gen. indet. I–J. Trilete spore fam. et gen. indet. 1. H–L. Trilete spore fam. et gen. indet. 2. M–N. Trilete spore fam. et gen. indet. 3. O–P. Trilete spore fam. et gen. indet. 4. Scale bars – 10 μ m (A, C, E, H, I, K, M, O), 1 μ m (B, D, F, H, J, L, N, P). 239x340mm (300 x 300 DPI)

Figure 4. (A–G) LM micrographs of dispersed fossil spores, Ginkgoace, Cupressaceae, and Pinaceae pollen. A. Trilete spore fam. et gen. indet. 5, polar view. B. Ginkgo sp. C. Cupressaceae gen. indet. 1. D. Cupressaceae gen. indet. 2. E. Cupressaceae gen. indet. 3. F. Abies sp 1, equatorial view. G. Abies sp. 2, equatorial view. Scale bars – 10 μ m (A–G). 239x719mm (300 x 300 DPI)

Figure 5. (A–P) SEM micrographs of dispersed fossil spores, Ginkgoaceae, Cupressaceae, and Pinaceae pollen. Overview (A, C, E, G, I, K, N), detail (B, D, F, H, J, L, M, O, P), close-ups of corpus (L, O) and saccus (M, P). A–B. Trilete spore fam. et gen. indet. 5, proximal view. C–D. Ginkgo sp. E–F. Cupressaceae gen. indet. 1. G–H. Cupressaceae gen. indet. 2. I–J. Cupressaceae gen. indet. 3. K–M Abies sp 1, equatorial view. N–P. Abies sp. 2, equatorial view. Scale bars – 10 μm (A, C, E, G, I, K, N), 1 μm (B, D, F, H, J, L, M, O, P). 239x340mm (300 x 300 DPI)

Figure 6. (A–D) LM overview micrographs of dispersed fossil Pinaceae pollen. A–B. *Cathaya* sp., distal view. C. *Larix/Pseudotsugsa* sp., tetrad. D. *Picea* sp., equatorial view. Scale bars – 10 μ m (A–D).
239x719mm (300 x 300 DPI)

Figure 7. (A–L) SEM micrographs of dispersed fossil Pinaceae pollen. Overview (A, D, G, H, J), detail (I), close-up of leptoma (B, E), corpus (K), saccus (C, F, L). A–F. *Cathaya* sp., distal view. G–I. *Larix* sp. J–L. *Picea* sp., equatorial view. Scale bars – 10 μ m (A, D, G, H, J), 1 μ m (B, C, E, F, I, K, L).
239x340mm (300 x 300 DPI)

Figure 8. (A–D) LM micrographs of dispersed fossil Pinaceae pollen. A. *Pinus* subgenus *Strobilus* sp., equatorial view. B. *Pinus* subgenus *Pinus* sp., polar view. C. *Tsuga* sp. 1, polar view. D. *Tsuga* sp. 2, polar view. Scale bars – 10 μ m (A–D).
239x719mm (300 x 300 DPI)

Figure 9. (A–M) SEM micrographs of dispersed fossil Pinaceae pollen. Overview (A, D, G, H, J), detail (H, K–M), close-ups of corpus (B, E), saccus (C, F). A–C. *Pinus* subgenus *Strobilus* sp., equatorial view. D–F. *Pinus* subgenus *Pinus* sp., distal view. G–H. *Tsuga* sp. 1, proximal view. H. Detail of proximal pole. I–M. *Tsuga* sp. 2. I. proximal view. J. Distal view. K. Detail proximal pole. L. Margin (saccus) detail. M. Distal pole detail.

Scale bars – 10 μ m (A, D, G, I–J), 1 μ m (B, C, E, F, H, K–M).
239x340mm (300 x 300 DPI)

Figure 10. (A–H) LM micrographs of dispersed fossil pollen of Gnetales, and Monocotyledone. A–B. *Ephedra* sp., equatorial view. C. Poaceae gen. indet.1 aff. *Stipa*, equatorial view. D. Poaceae gen. indet. 2, top: equatorial view, bottom: polar view. E. *Typha* sp. 1, polar view. F. *Typha* sp. 2, equatorial view. G. *Sparganium* sp., equatorial view. H. Monocotyledone pollen fam. et gen. indet., equatorial view. Scale bars – 10 μ m (A–H). 239x719mm (300 x 300 DPI)

Figure 11. SEM micrographs of dispersed fossil Gnetales and Monocotyledone pollen. Overview (A, C, E, G, I, K, M, O) and details (B, D, F, H, J, L, N, P). A–D. *Ephedra* sp., equatorial view. E–F. Poaceae gen. indet. 1 aff. *Stipa*. G–H. Poaceae gen. indet. 2. I–J. *Typha* sp. 1, polar view. K–L. *Typha* sp. 2, equatorial view. M–N. *Sparganium* sp. O–P. Monocotyledone pollen fam. et gen. indet., equatorial view. Scale bars – 10 μ m (A, C, E, G, I, K, M, O), 1 μ m (B, D, F, H, J, L, N, P).
239x340mm (300 x 300 DPI)

Figure 12. (A–I) LM micrographs of dispersed fossil Adoxaceae/Caprifoliaceae, Amaranthaceae, Sarcobataceae, Asteraceae, and Apocynaceae pollen. A. Adoxaceae vel Caprifoliaceae gen. indet., equatorial view. B. Amaranthaceae gen. indet. 1. C. Amaranthaceae gen. indet. 2. D–G. Sarcobatus sp. G. Porus detail. H. Asteroideae gen. indet. I. Tabernaemontana sp., equatorial view. Scale bars – 10 μ m (A–G). Sample: UF15880-7285 (A–E, H, I), UCMP 20778 (F, G). 239x719mm (300 x 300 DPI)

Figure 13. SEM micrographs of dispersed fossil Adoxaceae, Amaranthaceae, Asteraceae, and Apocynaceae pollen. Overview (A, C, E, G, I, K, M) and details (B, D, F, H, J, L, N, O). A–B. Adoxaceae gen. indet., equatorial view. C–D. Chenopodioideae gen. indet. 1. E–F. Chenopodioideae gen. indet. 2. G–J. aff. Amaranthaceae vel Sarcobataceae gen. indet. K–L. Asteroideae gen. indet. aff. Ambrosia. M–O. Tabernaemontaneae gen. indet., equatorial view. Scale bars – 10 μm (A, C, E, G, I, K, M), 1 μm (B, D, F, H, J, L, N, O).

239x340mm (300 x 300 DPI)

Figure 14. (A–G) LM micrographs of dispersed fossil Betulaceae, Caprifoliaceae, Ebenaceae, Ericaceae, and Eucommiaceae pollen. A. *Betula* sp., top polar view, bottom equatorial view. B. *Alnus* sp., polar view. C. *Coryloideae* gen. indet. 1, polar view. D. *Coryloideae* gen. et spec. indet. 2, polar view. E. *Caprifoliaceae/Linnaeoideae* gen. indet. sp., polar view. F. *Diospyros* sp., equatorial view. G. *Ericaceae* gen. indet., polar view. H. *Elaeagnaceae* gen. indet., right equatorial view, left polar view. I–J. *Eucommia* sp., I. top equatorial view, bottom polar view. J. Equatorial view. Scale bars – 10 μ m (A–I). 239x719mm (300 x 300 DPI)

Figure 15. (A–P) SEM micrographs of dispersed fossil Betulaceae, Caprifoliaceae, Ebenaceae, Ericaceae, and Eucommiaceae pollen. Overview in polar view (A, C, E, G, K), equatorial view (I, M, O), and details (B, D, F, H, J, L, N, P). A–B. *Betula* sp. C–D. Coryloideae gen. indet. 1. E–F. Coryloideae gen. indet. 2. G–H. Caprifoliaceae/Linnaeoideae gen. indet. I–J. *Diospyros* sp. K–L. Ericaceae gen. indet. M–P. *Eucommia* sp. Scale bars – 10 μm (A, C, E, G, I, K, M, O), 1 μm (B, D, F, H, J, L, N, P).

239x340mm (300 x 300 DPI)

Figure 16. LM micrographs of dispersed fossil Fabaceae, Fagaceae and possible Euphorbiaceae pollen in equatorial (A, C–G, I) and polar view (B, H). A. aff. Euphorbiaceae gen. indet. B. Caesalpinioideae gen. indet. C. Castaneoideae gen. indet. 1. D. Castaneoideae gen. indet. 2. E. Castaneoideae gen. indet. 3. F–G. *Fagopsis longifolia*. H. *Quercus* Group *Cyclobalanopsis* sp. I. *Quercus* Group *Protobalanus* sp. Scale bars – 10 μ m (A–I). Sample: UF15880-7285 (A, B, D–F, H–I), S151454 (C, F). 239x719mm (300 x 300 DPI)

Figure 17. SEM micrographs of dispersed fossil Euphorbiaceae, Fabaceae, and Fagaceae pollen. Overview in equatorial view (A, C, E, G, I, K, O), polar view (M), and details (B, D, F, H, J, L, N, M). A–B. Euphorbiaceae gen. indet. C–D. Castaneoideae gen. indet. sp. 1. E–F. Castaneoideae gen. indet. sp. 2. G–H. Castaneoideae gen. indet. sp. 3. I–L. *Fagopsis longifolia*. M–N. *Quercus* Group *Cyclobalanopsis* sp. O–P. *Quercus* Group *Protobalanus* sp. Scale bars – 10 μm (A, C, E, G, I, K, M, O), 1 μm (B, D, F, H, J, L, N, P). 239x340mm (300 x 300 DPI)

Figure 18. LM micrographs of dispersed fossil Fagaceae, Hamamelidaceae, and Juglandaceae pollen in equatorial (A–B) and polar view (C–I). A. Quercus Group Quercus/Lobatae sp. B. Quercus Group Quercus sp. C. Hamamelidoideae gen. indet. D–E. Momipites coryloides. F. Momipites triradiatus. G. Momipites microfoveolatus. H–I. Carya sp. Scale bars – 10 μ m (A–I). Sample: UF15880-7285 (A, C–I), S151454 (B). 239x719mm (300 x 300 DPI)

Figure 19. SEM micrographs of dispersed fossil Fagaceae, Hamamelidaceae, and Juglandaceae pollen. Overview in equatorial view (A, C, E), polar view (G, I, K, M, O), and details (B, D, F, H, J, L, N, P). A–B. *Quercus* Group *Quercus/Lobatae* sp. C–D. *Quercus* Group *Quercus* sp. E–F. Hamamelidoideae gen. indet. aff. *Distylium* G–H. Engelhardioideae gen. indet. 1. I–J. Engelhardioideae gen. indet. 2. K–L. Engelhardioideae gen. indet. 3. M–P. *Carya* sp. Scale bars – 10 μ m (A, C, E, G, I, K, M, O), 1 μ m (B, D, F, H, J, L, N, P). 239x340mm (300 x 300 DPI)

Figure 20. (A–H) LM micrographs of dispersed fossil Juglandaceae, Lamiaceae, and Malvaceae pollen. A. *Juglans* sp. 1, polar view. B. *Juglans* sp. 2, polar view. C. Lamiaceae gen. indet. aff. *Stachys*, top equatorial view, bottom polar view. D. Bombacoideae/Sterculioideae gen. et indet. E. Bombacoideae/Brownlowioideae gen. indet. F. Malvoideae gen. indet. 1. G. Malvoideae gen. indet. 2. H. Malvoideae gen. indet. 3. Scale bars – 10 μ m (A–H). 239x719mm (300 x 300 DPI)

Figure 21. SEM micrographs of dispersed fossil Juglandaceae, Lamiaceae, and Malvaceae pollen. Overview (A, C, E, G, I, K, M, O) and details (B, D, F, H, J, L, N, P). A–B. *Juglans* sp. 1, polar view. C–D. *Juglans* sp. 2, polar view. E–F. Lamiaceae gen. indet. aff. *Stachys*. G–H Bombacoideae/Sterculioideae gen. indet. I–J. Bombacoideae/Brownlowioideae gen. indet. K–L. Malvoideae gen. indet. 1. M–N. Malvoideae gen. indet. 2. O–P. Malvoideae gen. indet. 3. Scale bars – 10 μ m (A, C, E, G, I, K, M, O), 1 μ m (B, D, F, H, J, L, N, P). 239x340mm (300 x 300 DPI)

Figure 22. (A–F) LM micrographs of dispersed fossil Malvaceae, Menispermaceae, Oleaceae, and Onagraceae pollen. A. Malvoideae gen. indet. 4. B. Menispermaceae gen. indet., equatorial view. C. Fraxinus sp., equatorial view. D. Oenothera sp. 1, polar view. E. Hauyeae gen. indet. aff. Hauya, polar view F. Oenothera sp. 2. Scale bars – 10 μ m (A–F).
239x719mm (300 x 300 DPI)

Figure 23. SEM micrographs of dispersed fossil Malvaceae, Menispermaceae, Oleaceae, and Onagraceae pollen. Overview (A, C, E, G, J, K, N) and details (B, D, F, H, I, L, M, O, P). A–B. Malvoideae gen. indet. 4. C–D. Menispermaceae gen. indet., equatorial view. E–F. *Fraxinus* sp., equatorial view. G–I. *Oenothera* sp. 1, (G) polar view, (H) surface detail, (I) viscin thread detail. J–M. *Hauyeae* gen. indet. aff. *Hauya* sp., (J) proximal view, (K) distal view, (L) viscin thread detail, (M) surface detail. N–P. *Oenothera* sp. 2, (N) equatorial view, (O) surface detail, (P) viscin thread detail. Scale bars – 10 μ m (A, C, E, G, J, K, N), 1 μ m (B, D, F, H, I, L, M, O, P).
239x340mm (300 x 300 DPI)

Figure 24. LM micrographs of dispersed fossil Platanaceae and Rosaceae pollen in. A. Platanaceae gen. indet. aff. Macginitea, polar view. B. Platanus sp., polar view. C. Crateagus sp., equatorial view. D. Rosaceae gen. indet. 1, equatorial view. E. Rosaceae gen. indet. 2, equatorial view. F. Rosaceae gen. indet. 3, top equatorial view, bottom polar view. G. Rosaceae gen. indet. 4, equatorial view. H. Dryadoideae gen. indet. aff. Cercocarpus/Purshia, polar view. Scale bars – 10 μ m (A–H).
239x719mm (300 x 300 DPI)

Figure 25. SEM micrographs of dispersed fossil Platanaceae and Rosaceae pollen. Overview (A, C, E, G, I, K, M, O) and details (B, D, F, H, J, L, N, P). A–B. Platanaceae gen. indet. aff. *Macginitia*, polar view. C–D. *Platanus* sp., polar view. E–F. *Crataegus* sp., equatorial view. G–H. Rosaceae gen. indet. 1, equatorial view. I–J. Rosaceae gen. indet. 2, equatorial view. K–L. Rosaceae gen. indet. 3, equatorial view. M–N. Rosaceae gen. indet. 4, equatorial view. O–P. Dryadoideae gen. et indet. aff. *Cercocarpus/Purshia*, polar view. Scale bars – 10 μ m (A, C, E, G, I, K, M, O), 1 μ m (B, D, F, H, J, L, N, P).
239x340mm (300 x 300 DPI)

Figure 26. LM micrographs of dispersed fossil Rutaceae, Sapindaceae, Sapotaceae, and Thymeliaceae pollen. A. Rutaceae gen. indet., equatorial view. B. Acer sp. 1, equatorial view. C. Acer sp. 1, polar view. D. Acer sp. 2, equatorial view. E. Acer sp. 3 aff. A. negundo, equatorial view. F. Sapotoideae gen. indet. 1, equatorial view. G. Sapotoideae gen. indet. 2, equatorial view. H. Thymelaeoideae gen. indet. 1. I. Thymelaeoideae gen. indet. 2. Scale bars – 10 μ m (A–I). 239x719mm (300 x 300 DPI)

Figure 27. SEM micrographs of dispersed fossil Rutaceae, Sapindaceae, Sapotaceae, and Thymeliaceae pollen. Overview (A, C, E, G, I, K, M, O) and details (B, D, F, H, J, L, N, P). A–B. Rutaceae gen. indet. sp., equatorial view. C–D. *Acer* sp. 1, polar view. E–F. *Acer* sp. 2, equatorial view. G–H. *Acer* sp. 3 aff. *A. negundo*, equatorial view. I–J. Sapotoideae gen. indet. 1, equatorial view. K–L. Sapotoideae gen. indet. 2, equatorial view. M–N. Thymelaeoideae gen. indet. 1. O–P. Thymelaeoideae gen. indet. 2. Scale bars – 10 μm (A, C, E, G, I, K, M, O), 1 μm (B, D, F, H, J, L, N, P).
239x340mm (300 x 300 DPI)

Figure 28. LM micrographs of dispersed fossil Trochodendraceae, Cannabaceae, Ulmaceae, and Vitaceae pollen . A. Tetracentron sp., equatorial view. B. Celtis vel Pteroceltis sp., polar view. C–D. Cedrelospermum sp., polar view. E–F. Ulmus sp., polar view. G. Ulmaceae gen. indet. aff. Zelkova, polar view. H. Vitaceae gen. indet. 1, equatorial view. I. Vitaceae gen. indet. 2, equatorial view. Scale bars – 10 μ m (A–I). Sample: UF15880-7285 (A–I). 239x719mm (300 x 300 DPI)

Figure 29. SEM micrographs of dispersed fossil pollen. Overview (A, C, E, G, I, J, L, N, P) and details (B, D, F, H, K, M, O, Q). A–B. *Tetracentron* sp., equatorial view. C–D. *Celtis* vel *Pteroceltis* sp., polar view. E–H. *Cedrelospermum* sp., polar view. I–K. *Ulmus* sp., polar view; K detail of grain in J. L–M. *Ulmaceae* gen. indet. aff. *Zelkova*, polar view. N–O. *Vitaceae* gen. indet. 1, equatorial view. P–Q. *Vitaceae* gen. indet. 2, equatorial view. Scale bars – 10 μ m (A, C, E, G, I, J, L, N, P), 1 μ m (B, D, F, H, K, M, O, Q). Sample: UF15880-7285 (A–Q).
239x340mm (300 x 300 DPI)

Figure 30. LM micrographs of dispersed fossil Angiosperm pollen. A. Pollen type 1, polar view. B. Pollen type 2, polar view. C. Pollen type 3. D. Pollen type 4. E. Pollen type 5. F. Pollen type 6. G. Pollen type 7, equatorial view. H. Pollen type 8, equatorial view. Scale bars – 10 μm (A–H).
239x719mm (300 x 300 DPI)

Figure 31. SEM micrographs of dispersed fossil pollen. Overview (A, C, E, G, I, K, M, O) and details (B, D, F, H, J, L, N, P). A–B. Pollen type 1, polar view. C–D. Pollen type 2, polar view. E–F. Pollen type 3. G–H Pollen type 4. I–J. Pollen type 5. K–L. Pollen type 6. M–N. Pollen type 7, equatorial view. O–P. Pollen type 8, equatorial view. Scale bars – 10 μm (A, C, E, G, I, K, M, O), 1 μm (B, D, F, H, J, L, N, P).
239x340mm (300 x 300 DPI)

Figure 32. LM micrographs of dispersed fossil Angiosperm pollen. A. Pollen type 9, polar view. B. Pollen type 10, equatorial view. C. Pollen type 11, equatorial view. D. Pollen type 12, polar view. E. Pollen type 13, polar view. F–G. Pollen type 14, polar view. H. Pollen type 15, polar view. Scale bars – 10 μ m (A–H).
239x719mm (300 x 300 DPI)

Figure 33. SEM micrographs of dispersed fossil pollen. Overview (A, C, E, G, I, K, M, O) and details (B, D, F, H, J, L, N, P). A–B. Pollen type 9, polar view. C–D. Pollen type 10. E–F. Pollen type 11, equatorial view. G–H. Pollen type 12, polar view. I–J. Pollen type 13, polar view. K–N. Pollen type 14, polar view. O–P. Pollen type 15, polar view. Scale bars – 10 μm (A, C, E, G, I, K, M, O), 1 μm (B, D, F, H, J, L, N, P).
239x340mm (300 x 300 DPI)

	Hascall (1988)	Wingate and Nichols (2001)	Leopold (1969); Leopold and Clay-Poole (2001)
Bryophyta			
Marchantiopsida fam. et. gen. indet.	Trilete spore type 5		
Lycopodiophytina			
<i>Selaginella</i> sp. 1			<i>Selaginella</i> cf. <i>S. mairei</i>
<i>Selaginella</i> sp. 2	Trilete spore type 8	<i>Lusatisporis</i> cf. <i>L. perinatus</i>	<i>Selaginella</i> cf. <i>S. densa</i>
Filicophytina			
Polypodiales fam. et gen. indet		<i>Polypodiisporites</i> cf. <i>P. secundus</i>	
Trilete spore fam. et gen. indet. 1	Trilete spore type 7	<i>Biretisporites</i>	
Trilete spore fam. et gen. indet. 2	Trilete spore type 3		
Pteridophyta fam. et gen. indet. 3	Trilete spore type 6?	<i>Lygodiumsporites adriennis</i>	
Pteridophyta fam. et gen. indet. 4	Trilete spore type 2?		
Pteridophyta fam. et gen. indet. 5			
Gymnosperms			
Ginkgoaceae			
<i>Ginkgo</i> sp.			
Cupressaceae			
Cupressaceae gen. indet. 1	TCT type		TCT type
Cupressaceae gen. indet. 2	TCT type	<i>Taxodiaceapollenites hiatus</i>	TCT type
Cupressaceae gen. indet. 3	TCT type	<i>Taxodiacites</i> cf. <i>T. verrucosus</i>	TCT type
Pinaceae			
<i>Abies</i> sp. 1	<i>Abies</i> type 1	? <i>Abiespollenites</i> sp.	<i>Abies</i> cf. <i>A. venusta</i>
<i>Abies</i> sp. 2	<i>Abies</i> type 3		
<i>Cathaya</i> sp.	<i>Podocarpus</i>	<i>Podocarpidites</i> sp.	
<i>Larix/Pseudotsuga</i>	<i>Larix/Pseudotsuga</i>		<i>Larix/Pseudotsuga</i>
<i>Picea</i> sp.	<i>Picea</i> type 1	<i>Piceapollis</i> sp.	<i>Picea</i> cf. <i>P. pungens</i>
<i>Pinus</i> subgenus <i>Strobus</i>	<i>Pinus</i> type 2, 3 & 4	<i>Pityosporites</i> sp.	<i>Pinus</i> sp.
<i>Pinus</i> subgenus <i>Pinus</i>	<i>Pinus</i> type 5	<i>Pityosporites</i> sp.	<i>Pinus</i> sp.
<i>Tsuga</i> sp. 1		<i>Zonalapollenites</i> sp.	<i>Tsuga</i> sp.
<i>Tsuga</i> sp. 2		<i>Zonalapollenites</i> sp.	<i>Tsuga</i> sp.
Ephedraceae			
<i>Ephedra</i> sp.	<i>Ephedra</i> type 1a & b	<i>Ephedripites exiguous</i> <i>Ephedripites claricristatus</i>	<i>Ephedra</i> sp. cf. <i>E. nevadensis</i>
Monocotyledonae			
Poaceae	Gramineae type 1 & 2	<i>Graminidites crassiglobosus</i>	Poaceae (Gramineae)
Poaceae gen. indet. 1 aff. <i>Stipa</i>			
Poaceae gen. indet. 2			
Typhaceae	TY/SP type 1 & 2	<i>Sparganiaceapollenites sparganioides</i>	SP/TY cf. <i>T. angustifolia</i>
<i>Sparganium</i> sp.			
<i>Typha</i> sp.			
Monocotyledonae pollen fam. et gen. indet.			
Eudicotyledonae			
Adoxaceae/Caprifoliaceae			
Adoxaceae vel Caprifoliaceae gen. indet.		<i>Rhoipites</i> sp. C	<i>Viburnum</i> cf. <i>V. lentago</i>
Amaranthaceae			
Chenopodiaceae gen. indet. 1	CH/AM type 3		
Chenopodiaceae gen. indet. 2	CH/AM type 2		Chenopodiaceae undet.
Apocynaceae			
<i>Tabernaemontana</i> sp.		<i>Tetracolporopollenites</i> sp.	<i>Tabernaemontana</i> cf. <i>T. coronaria</i>
Asteraceae			
Asteroidea gen. indet.	Compositae	Asteraceae sp. A	
Betulaceae			
<i>Betula</i> sp.		<i>Trivestibulopollenites betuloides</i>	
<i>Alnus</i> sp.		<i>Alnipollenites verus</i>	
Coryloideae gen. indet. 1		<i>Triatriopollenites subtriangulus</i>	<i>Ostrya/ Carpinus</i>
Coryloideae gen. indet. 2			<i>Ostrya/ Carpinus</i>
Cannabaceae			
<i>Celtis</i> vel <i>Pteroceltis</i> sp.	<i>Celtis</i> type 1 & 2	<i>Cricotriporites intrastructurus</i>	<i>Carpinus/ Ostrya</i> ,
Caprifoliaceae			
Caprifoliaceae/Linnaceoideae gen. indet.		<i>Lonicerapollis</i> sp. A	
Ebenaceae			
<i>Diospyros</i> sp.			
Elaeagnaceae			
Elaeagnaceae gen. indet.		<i>Slowakipollis hippophaeoides</i>	<i>Elaeagnus</i> cf. <i>E. argentea</i>
Ericaceae			
Ericaceae gen. indet.		<i>Ericipites</i> sp. cf. <i>E. longisulcatus</i>	Ericales, cf. Ericaceae or Pyrolaceae
Eucommiaceae			
<i>Eucommia</i> sp.		<i>Tricolpopollenites parmularius</i>	<i>Eucommia</i> sp.

Euphorbiaceae			
aff. Euphorbiaceae gen. indet.			
Fabaceae			
Caesalpinoideae gen. indet.		<i>Margocolporites</i> sp. cf. <i>M. vanwijhei</i>	
Fagaceae			
Castaneoideae gen. indet. sp. 1	<i>Castanea</i>		
Castaneoideae gen. indet. sp. 2	<i>Castanea</i>		
Castaneoideae gen. indet. sp. 3	<i>Castanea</i>		
<i>Fagopsis longifolia</i>	<i>Fagopsis longifolia</i>	? <i>Quercipollenites</i> sp. cf. <i>Fagopsis longifolia</i>	
<i>Quercus</i> Group <i>Cyclobalanopsis</i> sp.			
<i>Quercus</i> Group <i>Protobalanus</i> sp.			
<i>Quercus</i> Group <i>Quercus/Lobatae</i> sp.	<i>Quercus</i>	<i>Quercoidites microhenricii</i>	Quercoid pollen
<i>Quercus</i> Group <i>Quercus</i> sp.	<i>Quercus</i>		Quercoid pollen
Hamamelidaceae			
Hamamelidoideae			
Juglandaceae			
<i>Momipites coryloides</i>		<i>Momipites coryloides</i>	<i>Engelhardtia/Alfaroa</i>
<i>Momipites microfoveolatus</i>	<i>Engelhardtia</i>	<i>Momipites microfoveolatus</i>	<i>Engelhardtia/Alfaroa</i>
<i>Momipites triradiatus</i>		<i>Momipites triradiatus</i>	<i>Engelhardtia/Alfaroa</i>
<i>Carya</i> sp.	<i>Carya</i> type1	<i>Caryapollenites veripites</i>	<i>Carya</i> sp.
<i>Juglans</i> sp. 1	<i>Juglans</i>	<i>Juglanspollenites nigripites</i>	<i>Juglans</i> sp.
<i>Juglans</i> sp. 2			
Malvaceae			
Bombacacidoideae/Sterculioideae gen. indet.		<i>Bombacacidites</i> sp. aff. <i>B. reticulatus</i>	cf. <i>Fremontodendron</i> sp.
Bombacacidoideae/Brownlowioideae gen. indet.	<i>Tilia</i>	<i>Bombacacidites</i> sp. cf. <i>B. nanobrochatus</i>	
<i>Malvoideae</i> gen. indet. 1		<i>Malvacipollis</i> sp. C	
<i>Malvoideae</i> gen. indet. 2		<i>Pandaniidites</i> sp.	
<i>Malvoideae</i> gen. indet. 3			
<i>Malvoideae</i> gen. indet. 4		<i>Malvacipollis</i> sp. B	
Menispermaceae			
Menispermaceae gen. indet.			
Oleaceae			
<i>Fraxinus</i> sp.		<i>Fraxinipollenites medius</i>	<i>Fraxinus</i> -type
Onagraceae			
<i>Hauyae</i> gen. indet. aff. <i>Hauya</i>		<i>Corsinipollenites parviangulus</i>	<i>Semeiandra</i> cf. <i>S. grandiflora</i> (= <i>Lopezia semeiandra</i>)
Onagraceae/Lopeziae gen. indet. 1		<i>Corsinipollenites oculus-noctis parvus</i>	aff. <i>Xylona</i>
Onagraceae/Lopeziae gen. indet. 2			
Platanaceae			
<i>Platanus</i> sp.		Tricolpate sp. B	
<i>Platanaceae</i> gen. indet. aff. <i>Macginitia</i>			
Rosaceae			
<i>Crataegus</i> sp.			
<i>Dryadoideae</i> gen. indet. aff. <i>Cercocarpus/Purshia</i>			<i>Malus/Pyrus</i> type
Rosaceae gen. indet. 1 – 4			
Rutaceae			
aff. Rutaceae gen. indet.			
Sapindaceae			
<i>Acer</i> vel. <i>Dipteronia</i> sp.	AC/DI type 2		
<i>Acer</i> sp. 1	AC/DI type 1	<i>Aceripollenites striatus</i>	
<i>Acer</i> sp. 2	AC/DI type 3		
<i>Acer</i> sp. 3 aff. <i>A. negundo</i>	Salix type 2		
Sapotaceae			
Sapotoideae gen. indet. 1			
Sapotoideae gen. indet. 2			
Sarcobataceae			
<i>Sarcobatus</i> sp.	CH/AM type 1	<i>Chenopodipollis</i> sp.	<i>Sarcobatus</i> cf. <i>S. vermiculatus</i>
Thymelaeaceae			
Thymelaeoideae gen. indet. 1		<i>Persicarioipollis</i> sp. B	
Thymelaeoideae gen. indet. 2		<i>Persicarioipollis</i> sp. B	
Trochodendraceae			
<i>Tetracentron</i> sp.			
Ulmaceae			
<i>Cedrelospermum</i> sp.	<i>Ulmus/Zelkova</i> type2 ?	Triporate sp. B	
<i>Ulmus</i> sp.	<i>Ulmus/Zelkova</i> type1	<i>Ulmipollenites undulosus</i>	<i>Ulmus/Zelkova</i>
Ulmaceae gen. indet. cf. <i>Zelkovapollenites thiergartii</i>	<i>Ulmus/Zelkova</i> type3		<i>Ulmus/Zelkova</i>

Vitaceae			
Vitaceae gen. indet. 1			
Vitaceae gen. indet. 2			
Angiosperm pollen indet.			
Pollen type 1		Malvacipollis sp. D	
Pollen type 2		Zonoporate sp. B	Pteroceltis
Pollen type 3		Pandaniidites sp.	
Pollen type 4		Pandaniidites sp.	
Pollen type 5			
Pollen type 6		?Persicarioipollis sp. A	
Pollen type 7	AC/DI type 4	Tricolporate sp. E	
Pollen type 8			
Pollen type 9		Tricolporate sp. C	
Pollen type 10			
Pollen type 11			Rutaceae cf. Euodia (=Tetradium)
Pollen type 12			
Pollen type 13		Tricolporate sp. A	
Pollen type 14/ Boehlensipollis hohli	PR/SA/EL type	Boehlensipollis sp. cf. B. granulata	Cardiospermum cf. C. halicabum
Pollen type 15		Triporate sp. cf ?Ruella laxa	
Pollen type 16			