

## EVOLUTIONARY TRENDS AND ECOLOGICAL DIFFERENTIATION IN EARLY CENOZOIC FAGACEAE OF WESTERN NORTH AMERICA<sup>1</sup>

JOHANNES BOUCHAL<sup>2,3,5</sup>, REINHARD ZETTER<sup>3</sup>, FRIDGEIR GRÍMSSON<sup>3,4</sup>, AND THOMAS DENK<sup>2</sup>

<sup>2</sup>Swedish Museum of Natural History, Department of Palaeobiology, Box 50007, 10405 Stockholm, Sweden; <sup>3</sup>University of Vienna, Department of Palaeontology, Althanstraße 14 (UZA II), A-1090 Vienna, Austria; and <sup>4</sup>University of Iceland, Institute of Earth Sciences, Sturlugata 7, 101 Reykjavík, Iceland

- **Premise of the study:** The early Cenozoic was a key period of evolutionary radiation in Fagaceae. The common notion is that species thriving in the modern summer-dry climate of California originated in climates with ample summer rain during the Paleogene.
- **Methods:** We investigated in situ and dispersed pollen of Fagaceae from the uppermost Eocene Florissant fossil beds, Colorado, United States, using a combined light and scanning electron microscopy approach.
- **Key results:** Pollen types of Castaneoideae with affinities to modern *Castanea*, *Lithocarpus*, and *Castanopsis* were recognized. Pollen of the extinct genus *Fagopsis* represents a derived type of Castaneoideae pollen. Infrageneric groups of *Quercus* were well represented, including pollen of Group Protobalanus. The taxonomic diversity of Fagaceae and of the total plant assemblage indicates a mosaic of microclimates, that range from pronounced to weakly seasonal climates and depend on slope aspect and elevation. Continental climatic conditions may have triggered the evolution of sclerophyllous leaves and adaptive radiation in *Quercus* and other taxa thriving today under distinctly summer-dry and winter-dry climates.
- **Conclusions:** Vegetation types similar to modern vegetation belts of the Coastal Ranges (chaparral, nemoral conifer forest) were established in the Front Range in the late Eocene. Coeval plant assemblages from the Coastal Ranges of California indicate distinctly subtropical, moist climates. Hence, characteristic elements found today in the summer-dry and winter-dry climates of Pacific North America (*Quercus* Group Protobalanus, *Notholithocarpus*) may opportunistically have dispersed into their modern ranges later in the Cenozoic. This scenario is in contrast to the evolution and migration patterns of their western Eurasian Mediterranean counterparts (*Quercus* Group Ilex).

**Key words:** Castaneoideae; Eocene-Oligocene boundary; Front Range; mesic forest; nemoral conifer forest; origin of Mediterranean vegetation; *Quercus* Group Cyclobalanopsis; *Quercus* Group Quercus/Lobatae; *Quercus* Group Protobalanus; sclerophyllous forest.

The family Fagaceae is the most diverse tree family in the northern temperate regions and comprises about 650 to 750 (Flora of North America Editorial Committee, 1997; Wu and Raven, 1999) or 1000 species (Govaerts and Frodin, 1998). Fagaceae play an important role in broadleaved forests across the northern hemisphere and commonly form monodominant forests. Modern centers of diversity for the family are in Mexico and in Southeast Asia (Govaerts and Frodin, 1998). A number of genera or infrageneric groups that are at present confined to North America (*Quercus* Group Lobatae) or East Asia (*Castanopsis*, *Lithocarpus*, *Quercus* Group Cyclobalanopsis) were widely distributed across the northern hemisphere during the Cenozoic, and the present centers of diversity may not reflect the regions of origin of modern groups (Denk and Grimm, 2009b). The Eocene was a key epoch for the earliest appearance of modern genera of Fagaceae (e.g., *Castanea*, Crepet and Daghljan, 1980; *Fagus*, Manchester and Dillhoff, 2004; *Quercus*, Kvaček and Walther, 1989; Manchester, 1994; McIver and Basinger, 1999) while extinct lineages still played important

roles in plant communities (e.g., Manchester and Crane, 1983; Jones and Dilcher, 1988; Denk et al., 2012). For many groups within Fagaceae, however, it is difficult to establish generic affinities based on leaf imprints without preserved epidermal features (e.g., Kvaček and Walther, 1981, 1989) or based on light microscopy (LM) investigations of pollen (Denk and Grimm, 2009a). Using scanning electron microscopy (SEM) for the investigation of in situ and dispersed pollen grains has opened up new vistas in the assessment of fossil pollen grains for evolutionary and paleoecological studies (Crepet and Daghljan, 1980; Friis et al., 1988; Walther and Zetter, 1993; Kohlman-Adamska and Ziembínska-Tworzydło, 2000, 2001; Denk et al., 2010, 2011, 2012). Here, we used a combined LM and SEM investigation of in situ and dispersed pollen grains to evaluate the taxonomic diversity of Fagaceae in the uppermost Eocene of the Florissant Formation, Colorado, United States.

The Florissant fossil beds have yielded one of the most diverse fossil floras and faunas worldwide (Meyer, 2003). Fossil plants have been treated monographically by MacGinitie (1953; revised by Manchester, 2001), who described leaves, flowers, fruits, and seeds. Palynological accounts were published by Leopold and Clay-Poole (2001) and Wingate and Nichols (2001). Two genera of Fagaceae have previously been recognized on the basis of leaf fossils and partly pollen: the extinct genus *Fagopsis* (Manchester and Crane, 1983) and *Quercus* (MacGinitie, 1953). MacGinitie attributed several leaf types to white oaks (*Quercus* Group Quercus), red oaks (*Quercus* Group Lobatae), golden cup oaks (*Quercus* Group Protobalanus), and

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<sup>5</sup>Author for correspondence (e-mail: johannes.bouchal@nrm.se)

cycle cup oaks (*Quercus* Group *Cyclobalanopsis*). Furthermore, one leaf type was compared to the enigmatic European fossil taxon *Quercus cruciata* A. Braun.

In the present study, we investigated pollen of Fagaceae from the Florissant fossil beds with LM and SEM to achieve high taxonomic resolution. The observed diversity of pollen types was then compared with the previously reported diversity of leaf types. The diversity of Fagaceae in the latest Eocene of western North America was viewed in a wider northern hemispheric context. Trends of morphological/ecological adaptive radiation due to the alleged increased seasonality in parts of western North America are discussed and biogeographic links of the Fagaceae of Florissant assessed. Furthermore, we use the revised plant fossil record of Florissant to comment on the paleo-vegetation and paleoecology during the deposition of the Florissant fossil beds.

## MATERIALS AND METHODS

The plant material investigated originates from the Florissant fossil beds in the southern Rocky Mountains of Colorado (Front Range). Today, the area is located at an elevation of 2500 to 2600 m a.s.l. (Meyer, 2003) with the adjacent highest peaks to the northwest reaching more than 4000 m a.s.l. In the area of Florissant, four formal rock units can be distinguished, the Pikes Peak Granite, the Wall Mountain Tuff, the Florissant Formation, and breccias of the Thirty-nine Mile Andesite (Evanoff et al., 2001; Fig. 1A).

The Florissant Formation is a heterolithic accumulation of shale, tuffaceous mudstone and siltstone, tuff, arkosic and volcanoclastic sandstone, and conglomerate (Evanoff et al., 2001). The formation consists of six informal units: the lower shale, the lower mudstone, the middle shale, the caprock conglomerate, the upper shale, and the upper pumice conglomerate.

The paper shales of the lower, middle, and upper shale units are the main fossil-bearing strata, which yield the exceptionally well-preserved insect, plant, fish, and bird fossils. An individual of the genus *Nanodelphis* (Lloyd et al., 2008) has been recovered from these strata. All the stratigraphically relevant mammal fossils were found in the lower mudstone unit. Two species of *Lipotyphla*, six species of *Rodentia*, two species of *Lagomorpha*, four species of *Artiodactyla*, and two species of *Perissodactyla* are known to come from this unit and suggest a middle to late Chadronian age (NALMA) (Lloyd et al., 2008) or Priabonian age (ICS). This estimate corresponds with the  $^{40}\text{Ar}/^{39}\text{Ar}$  weighted mean age of  $34.07 \pm 0.10$  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 slab pieces of the paleobotany and palynology collection of the Florida Museum of Natural History, Gainesville, labeled as UF15880–7285 and the paleobotany collection of the Naturhistoriska Riksmuseet, Stockholm, labeled as S151454. UF15880–7285 was collected on the private property of the Stoll family, west of Florissant (Fig. 1, B, X<sub>1</sub>), near the old Denver Museum Locality (MacGinitie, 1953). S151454 was collected from the Clare Quarry locality south of Florissant (Fig. 1, B, X<sub>2</sub>).

Sedimentary rock was processed following the protocol described by 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). The compressed staminate inflorescence of *Fagopsis longifolia* with in situ pollen grains is from the collection of the University of California, Berkeley, Museum of Paleontology, labeled as UCMP254999. The sample was macerated in Danclor and acetolyzed; individual pollen grains were isolated with a micromanipulator.

Light micrographs were taken with a Nikon Eclipse 80i microscope equipped with a Samsung Digimax V70 digital camera. SEM micrographs were taken with a Joel JSM 6400 scanning electron microscope and a Hitachi S-4300 cold field emission scanning electron microscope. In most cases, specimens were investigated and photographed immediately after sputter coating with gold.

The terminology for pollen morphology followed that of Punt et al. (2007) and Hesse et al. (2009). The term vermiculate is used to describe winding features in a general way.

**Phylogenetic framework**—For a phylogenetic framework, the studies by Manos et al. (2001) and Denk and Grimm (2009a, 2010) were used. These studies identified six infrageneric groups and showed that the classical subdivision into *Quercus* subgenus *Quercus* and *Quercus* subgenus *Cyclobalanopsis* is unnatural. We follow the concept of Denk and Grimm (2010) who introduced informal names for the six groups within *Quercus*. The nomenclature for these groups is as follows: (1) *Quercus* Group *Cerris* (Eurasia), (2) *Quercus* Group *Cyclobalanopsis* (Asia), (3) *Quercus* Group *Ilex* (Eurasia), (4) *Quercus* Group *Lobatae* (North America), (5) *Quercus* Group *Quercus* (northern hemisphere), and (6) *Quercus* Group *Protobalanus* (western North America). For previously used partly synonymous names, see Denk and Grimm (2010). For practical reasons, we use the subfamilial name *Castaneoideae* Oersted to denote the genera *Castanea*, *Castanopsis*, *Lithocarpus*, *Chrysolepis*, and *Notholithocarpus*. These genera form a grade according to recent molecular phylogenetic studies (Manos et al., 2008; Oh and Manos, 2008; Denk and Grimm, 2010).

**Modern climatic characterization of western North America**—As a consequence of relief, sea currents, and prevailing wind directions, the climate of western North America is complex (e.g., Douglas et al., 1993). To characterize present climatic conditions, we used the Köppen-Geiger climate classification that has recently been updated (Kottek et al., 2006 [http://koeppen-geiger.vu-wien.ac.at/present.html]; Peel et al., 2007). Importantly, a number of plants that are considered Cenozoic relict taxa, e.g., *Sequoia*, *Torreya*, and *Notholithocarpus* are currently distributed in the United States portion of the Pacific Coast Ranges which are characterized by a summer-dry (Mediterranean) climate (Csa and Csb climates according to Köppen; Appendix S1, see Supplemental Data with the online version of this article). To the east, this climate is replaced by various types of dry climates (B climates according to Köppen-Geiger) in the lowlands, and by snow climates with summer rain (D climates according to Köppen-Geiger) in the Rocky Mountains. The latter climate type is present at the fossil sites of Florissant (Appendix S1). To the south, temperate, markedly seasonal winter-dry climates occur in the Sierra Madre Occidental of western Mexico (Cw climates; Walter and Lieth, 1964; Douglas et al., 1993; Peel et al., 2007; Appendix S1).

**Fossil plant assemblages and modern analogs**—The continental, intermontane setting of the depositional environment of the Florissant fossil beds along with the relatively high elevation (cf. Meyer, 2003) suggest that windward and leeward slopes may have experienced different precipitation regimes. Therefore, the fossil plant assemblages, and in particular spore and pollen assemblages, likely comprise a mixture of different vegetation types, different elevations, and may reflect different small-scale climatic conditions. For this reason, the taxa of the entire fossil plant assemblage of Florissant were subdivided into groups that are considered to represent different ecologies and correspond to particular modern vegetation types (modern analogs of particular latest Eocene vegetation types). This approach is in contrast to that used by Boyle et al. (2008) who treated the entire Florissant plant assemblage as a single (homogeneous, autochthonous) flora.

## SYSTEMATIC PALEOBOTANY

**Family**—Fagaceae Dumortier

**Genus**—*Fagopsis* Hollick

**Species**—*Fagopsis longifolia* (Lesquereux) (Figs. 2A–P, 3A–L)

**Description**—Pollen, monad, shape prolate to spheroidal, elliptic in equatorial view; in situ pollen: polar axis 22–27  $\mu\text{m}$  (LM), 19–22  $\mu\text{m}$  (SEM) (18–20  $\mu\text{m}$  according to Manchester and Crane, 1983), equatorial diameter 19–21  $\mu\text{m}$  (LM), 17–20  $\mu\text{m}$  (SEM); dispersed pollen: polar axis 22–28  $\mu\text{m}$  (LM), 21–25  $\mu\text{m}$  (SEM) equatorial diameter 19–26  $\mu\text{m}$  (LM), 17–25  $\mu\text{m}$  (SEM); eutectate, exine 1–1.5  $\mu\text{m}$  thick (LM), tricolporate, bridge present (Figs. 2I–K, 2M, 2N, 2P; 3A, 3B, 3D–F, 3H–J, 3L), colpus length 18–22  $\mu\text{m}$  (SEM); sculpturing scabrate (LM), microrugulate (to rarely rugulate), perforate-fossulate in nonapertural region (SEM), several parallel running microrugulae forming larger rugulae

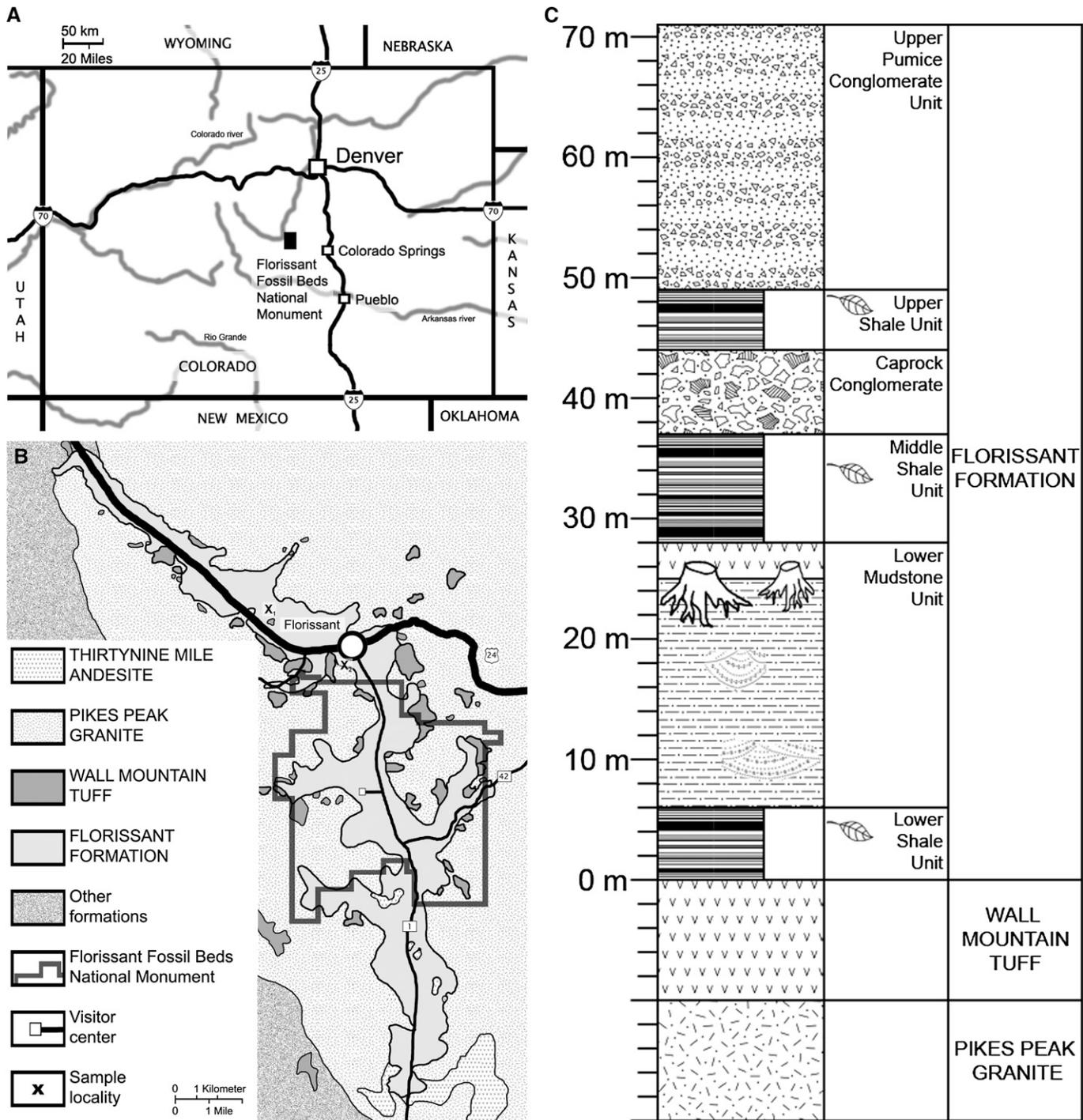


Fig. 1. (A–C) Geography, geologic setting, and stratigraphy of the Florissant Formation. (A) Map showing the geographical position of the Florissant Fossil Beds National Monument in Colorado, USA. (B) Geological map indicating Florissant Formation and surrounding formations. X<sub>1</sub> = sample UF15880–7285 locality, X<sub>2</sub> = sample S151454 locality. Map based on and modified after U.S.G.S. Map 1-1044 (Wobus and Epis, 1978). (C) Generalized stratigraphy of the Florissant Formation, modified after Evanoff (2001).

(vermiculate pattern), 0.5 to  $\leq 1 \mu\text{m}$  long and wide (Figs. 2F–H, 2K, 2L, 2O, 2P, 3C, 3D, 3G, 3H, 3K; secondary-striate sculpture according to Pragłowski, 1984); microrugulae (“striae”) connected by short, perpendicular elements (Figs. 2H, 3C), in some of the dispersed pollen grains no such connecting elements visible between microrugulae (Fig. 2K, L, O, P); sculpturing in apertural

region and bridge without fossulae, perforations can be present (Fig. 2J, K); abundance: common.

**Remarks**—The extinct fagaceous genus *Fagopsis* is known from the early Eocene Republic flora of Washington (Wolfe and Wehr, 1987), the late Eocene Florissant Formation of

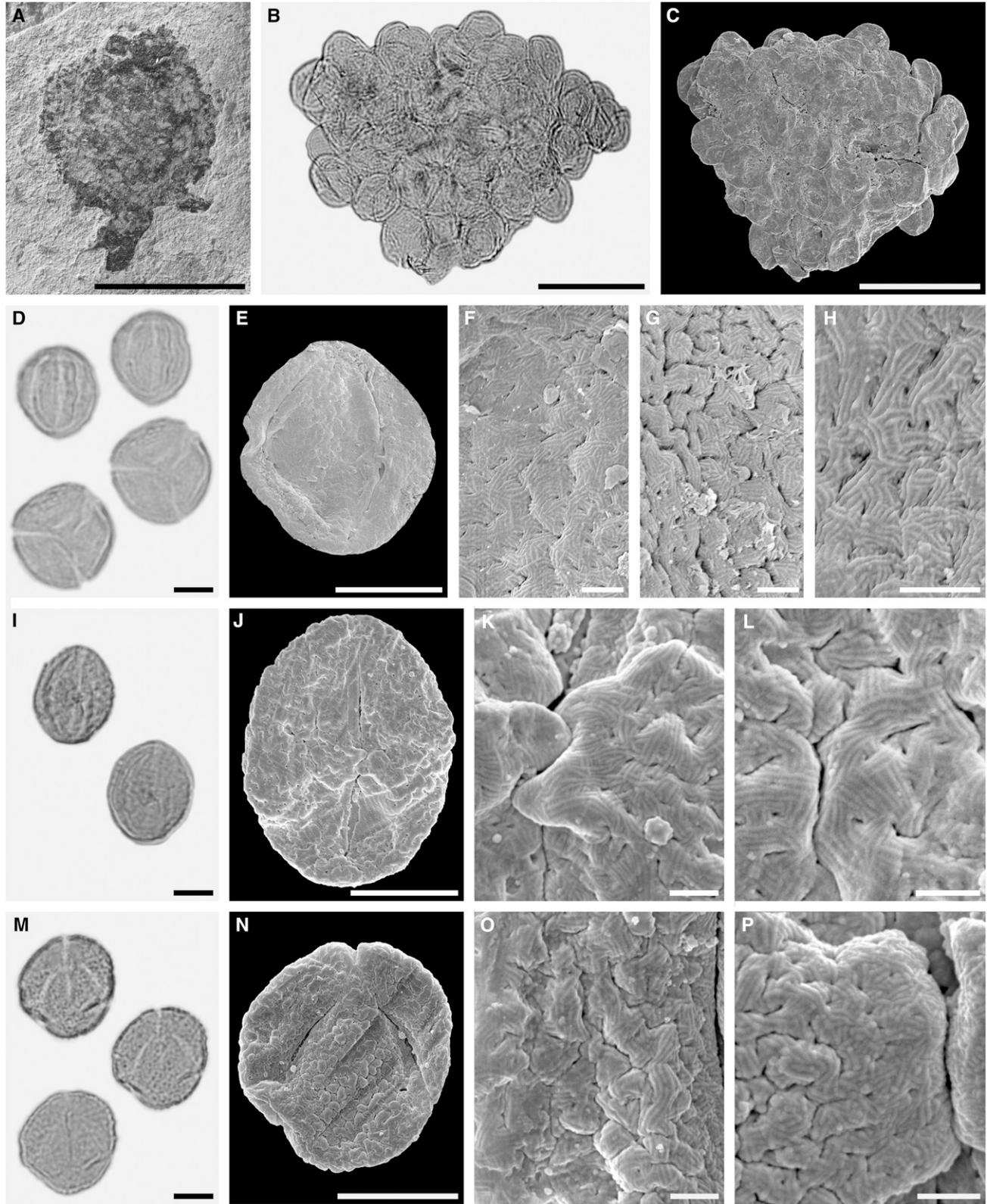


Fig. 2. (A–P) Staminate inflorescence, in situ pollen, and dispersed pollen of *Fagopsis longifolia*. (A) Staminate inflorescence (UCMP200/254999). (B, C) Pollen agglomeration from staminate inflorescence in LM and SEM. (D–H) Isolated pollen from staminate inflorescence. (D) LM, overview. (E) SEM, overview. (F–H) SEM, details. (I–P) Dispersed pollen grains. (I–L) LM and SEM micrographs from the same pollen grain. (I) LM, overview. (J) SEM, overview. (K, L) SEM, details. (M–P) LM and SEM images from the same pollen grain. (M) LM, overview. (N) SEM, overview. (O, P) SEM, details. Scale bars = 1 cm (A), 50  $\mu$ m (B, C), 10  $\mu$ m (D, E, I, J, M, N), 1  $\mu$ m (F–H, K, L, O, P).

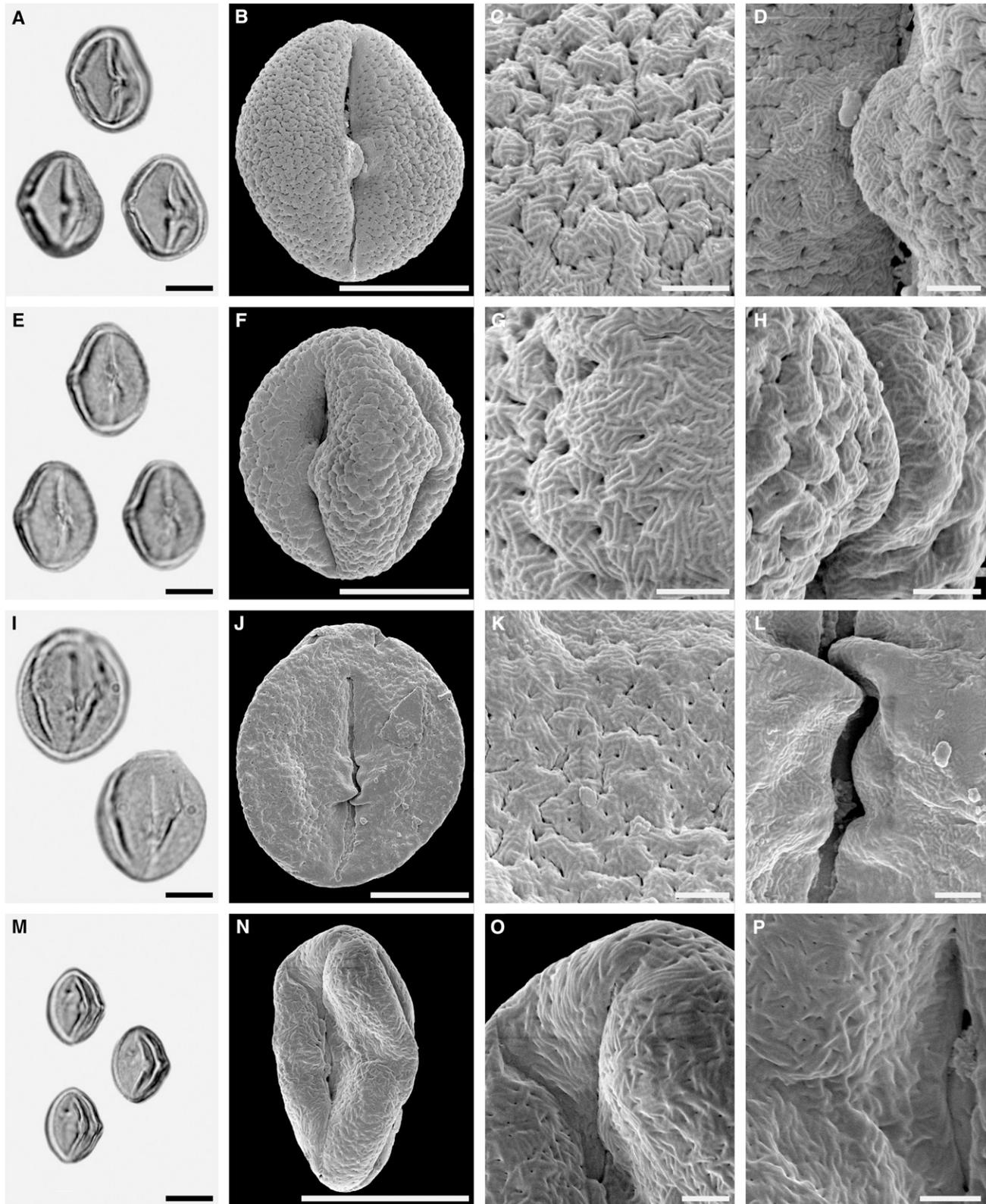


Fig. 3. *Fagopsis longifolia* and *Castaneoideae* gen. et sp. indet., sp. 1. (A–L) Dispersed *Fagopsis longifolia* pollen. (A–D) LM and SEM micrographs from the same pollen grain. (A) LM, overview. (B) SEM, overview. (C, D) SEM, details. (E–H) LM and SEM micrographs from the same pollen grain. (E) LM, overview. (F) SEM, overview. (G, H) SEM, details. (I–L) LM and SEM micrographs from the same pollen grain. (I) Pollen in equatorial view, LM. (J) Pollen in equatorial view, SEM. (K, L) Pollen details, SEM. (M–P) *Castaneoideae* gen. et sp. indet., sp. 1. LM and SEM micrographs from the same pollen grain. (M) LM, overview. (N) SEM, overview. (O, P) SEM, details. Scale bars = 10  $\mu$ m (A, B, E, F, I, J, M, N), 1  $\mu$ m (C, D, G, H, K, L, O, P).

Colorado (MacGinitie, 1953; Manchester and Crane, 1983), and Eocene/Oligocene Ruby River Basin flora of Montana (Becker, 1961; Lielke et al., 2012). Manchester and Crane (1983) described attached leaves, inflorescences, and fruits of *Fagopsis longifolia*. From staminate inflorescences, pollen was described and figured, but only to a level of magnification that did not reveal its fine ornamentation. Manchester and Crane (1983) suggested that the pollen of *Fagopsis* is most similar to *Quercus* among modern Fagaceae.

The present study shows that the tectum sculpturing is consistent with the one found in extant species of Castaneoideae. The microsculpturing in *Fagopsis* is not detectable at lower magnification (2000–5000 $\times$ ), but is crucial for fingerprinting dispersed pollen of this type. This type of microsculpturing is present in some extant and Quaternary *Castanopsis* pollen (Miyoshi, 1983; Pragłowski, 1984). In *Castanopsis*, rugulate pollen typical of Castaneoideae is found in most extant species, while a few taxa, *Castanopsis cuspidata* (Thunberg) Schottky and its varieties, have microrugulae forming larger rugulae (cf. Pragłowski, 1984, fig. 4, C) as seen in *Fagopsis*. Moreover, the same type of short perpendicular elements connecting the microrugulae in pollen of *Fagopsis* have been reported in pollen of *Castanopsis cuspidata* from modern plants and from Quaternary sediments (Miyoshi, 1983). In fully mature dispersed pollen, secondary sporopollenin can be masking the connecting elements (cf. Rowley, 1996).

Also, the pollen ultrastructure of *Fagopsis* corresponds to the pattern seen in Castaneoideae. The foot layer in genera of Castaneoideae is homogeneous and relatively thick, and the foot layer to tectum ratio is about 1. Manchester and Crane (1983) reported a footlayer to tectum ratio of 1.3 for *Fagopsis*.

**Subfamily**—Castaneoideae (paraphyletic)

**Species**—Castaneoideae gen. et sp. indet., sp. 1, aff. *Castanopsis* (Fig. 3M–P)

**Description**—Pollen, monad, shape prolate, elliptic in equatorial view, polar axis 14–16  $\mu\text{m}$  (LM), 12–14  $\mu\text{m}$  (SEM), equatorial diameter 9–11  $\mu\text{m}$  (LM), 7.5–9  $\mu\text{m}$  (SEM); eutectate, exine 1  $\mu\text{m}$  thick (LM), tricolporate, colpus length 6–8  $\mu\text{m}$  long (SEM); sculpturing scabrate (LM), microrugulate-striate, indistinctly perforate-fossulate (SEM), rugulae 0.1–0.2  $\mu\text{m}$  wide, microrugulae well developed, microrugulae show parallel running microstriate supra-sculpturing in polar areas (SEM); abundance: rare.

**Remarks**—Pollen of genera of the Castaneoideae are markedly uniform and difficult if not impossible to distinguish in LM (Pragłowski, 1984). Also in SEM, pollen morphological variability overlaps to a large degree between different genera. On account of its suprasculpturing (see above), which is similar to pollen known from extant species of *Castanopsis cuspidata* (Thunberg) Schottky (cf. Pragłowski, 1984, fig. 4, C), this pollen type resembles the genus *Castanopsis*.

**Species**—Castaneoideae gen. et sp. indet., sp. 2, aff. *Castanea* (Fig. 4A–D)

**Description**—Pollen, monad, shape prolate, elliptic in equatorial view, polar axis 14–16  $\mu\text{m}$  (LM), 12–14  $\mu\text{m}$  (SEM), equatorial diameter 9–11  $\mu\text{m}$  (LM), 7.5–9  $\mu\text{m}$  (SEM); eutectate, exine 1  $\mu\text{m}$  thick (LM), tricolporate, colpus length 6–8  $\mu\text{m}$  long (SEM); sculpturing scabrate (LM), microrugulate-striate, indistinctly perforate-fossulate (SEM), rugulae 0.1–0.2  $\mu\text{m}$  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: rare.

**Remarks**—*Castanea* differs from *Lithocarpus* and *Castanopsis* by the weak rugulation and almost smooth tectum in the polar regions. Therefore, we tentatively suggest a closer relationship of this pollen type with the genus *Castanea*. Modern species with very similar pollen are *C. dentata* (Marshall) Borkhausen and *C. floridana* (Sargent) Ashe, among others.

Earliest definite castaneoid inflorescences are known from the “middle” Eocene of Tennessee, United States (Crepet and Daghljan, 1980). Pollen produced from these inflorescences and described as *Castaneoidea puryearensis* Crepet et Daghljan, closely corresponds with the here described pollen. This pollen shows well-developed rugulate, perforate-fossulate sculpturing in the mesocolpium, which decreases in the polar areas.

Leaf fossils described as *Castanea dolichophylla* Cockerell are known from Florissant, but their generic identity is in need of review (Manchester, 2001). Although the asymmetric leaf base, dentition, and type and number of secondary veins are also found in *Castanea*, the strong intersecondary veins of *C. dolichophylla* are not encountered in extant species of *Castanea*. Such intersecondary veins are occasionally present in extinct fagaceous foliage of *Berryphyllum warmanense* J.H. Jones et Dilcher from the Eocene of the southeastern United States (Jones and Dilcher, 1988). Similarities are also encountered with the extinct European genus *Eotrigonobalanus* (Mai and Walther, 1985; Kvaček and Walther, 1989) and with the Oligocene European *Castaneophyllum lonchitiforme* (Kvaček and Walther, 2010). In addition, the leaf base, intersecondary veins, and type of dentition of *C. dolichophylla* resemble the extinct Engelhardeideae *Oreoroa* (*Engelhardia*) *orsbergensis* (P. Wessel et Weber) Dilcher et Manchester (Manchester, 1987, fig. 21). Therefore, “*Castanea*” *dolichophylla* may represent an extinct taxon in the Fagales.

**Species**—Castaneoideae gen. et sp. indet., sp. 3, aff. *Lithocarpus* (Fig. 4E–H)

**Description**—Pollen, monad, shape prolate, elliptic in equatorial view, polar axis 11–13  $\mu\text{m}$  (LM), 8–11  $\mu\text{m}$  (SEM), equatorial diameter 8–10  $\mu\text{m}$  (LM), 5–7  $\mu\text{m}$ ; eutectate, exine 1.0  $\mu\text{m}$  thick (LM), tricolporate; sculpturing scabrate (LM), microrugulate/rugulate, approaching striate (SEM), rugulae 0.1–0.2  $\mu\text{m}$  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: rare.

**Remarks**—Pollen of the extant *Lithocarpus jordanae* (Laguna) Rehder and *L. kostermansii* Soepadmo resembles the fossil pollen by its relatively long microrugulae and the patchwork-like appearance of the pollen sculpture (Pragłowski, 1984).

Possible fossil acorn cups of *Lithocarpus* are known from the Eocene Green River Formation, Colorado, United States (MacGinitie, 1969). Manchester (1994) described cupules and nuts of *Castanopsis crepetii* from the lower Lutetian Nut Beds locality of the Clarno Formation, Oregon, United States. When discussing taxonomic affinities of the fossil species, he clearly stated that the genera *Castanopsis* and *Lithocarpus* have overlapping morphological variability and cannot clearly be separated based on the cupule/nut complex. The same is true for pollen morphology.

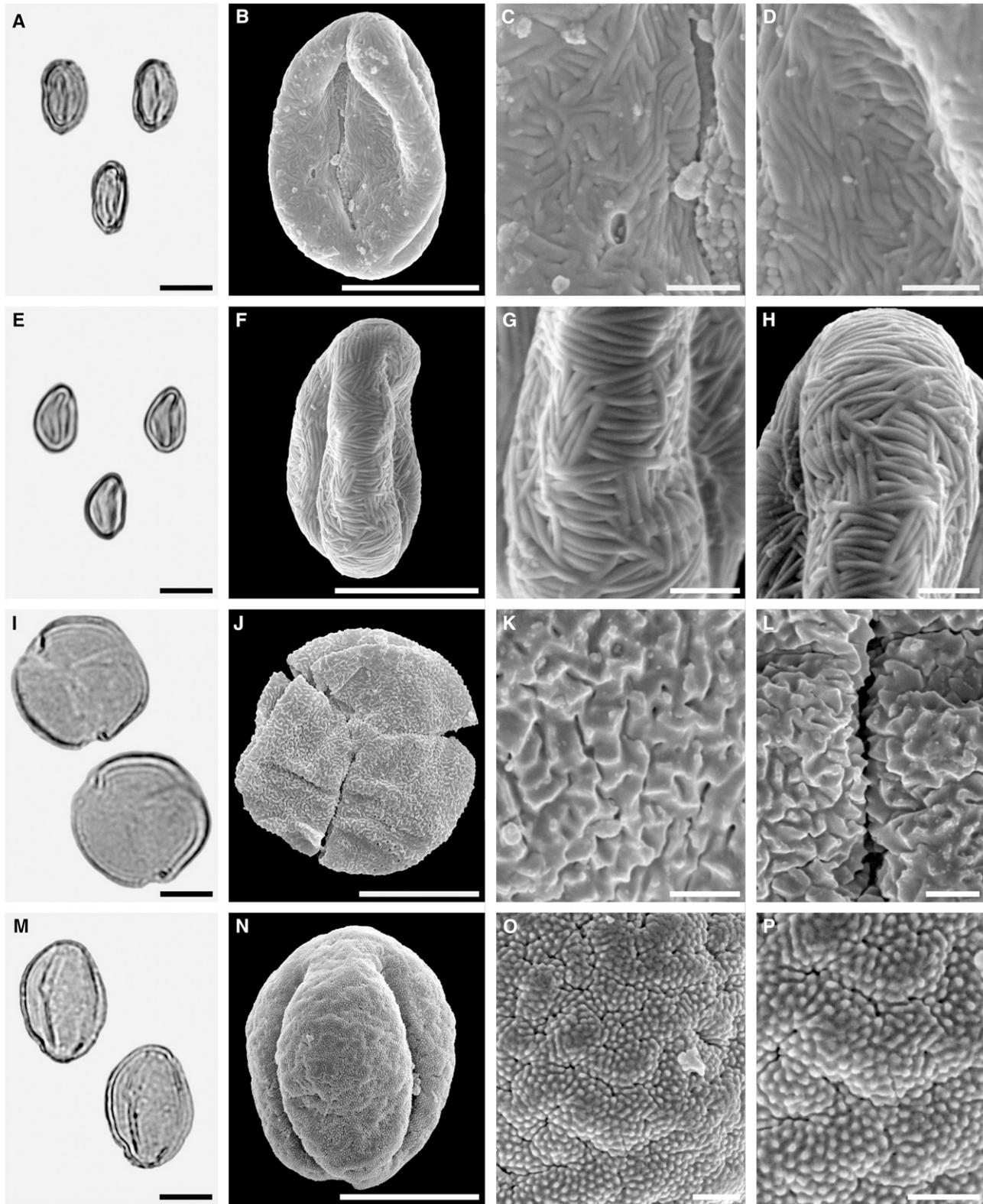


Fig. 4. Castaneoideae gen. et sp. indet., spp. 2 and 3, *Quercus* Group Cyclobalanopsis sp. and *Quercus* Group Protobalanus sp. (A–D) Castaneoideae gen. et sp. indet., sp. 2. LM and SEM micrographs from the same pollen grain. (A) LM, overview. (B) SEM, overview. (C, D) SEM, details. (E–H) Castaneoideae gen. et sp. indet., sp. 3. LM and SEM micrographs from the same pollen grain. (E) LM, overview. (F) SEM, overview. (G, H) SEM, details. (I–L) *Quercus* Group Cyclobalanopsis sp., LM and SEM micrographs from the same pollen grain. (I) LM, overview. (J) SEM, overview. (K–L) SEM, detail. (M–P) *Quercus* Group Protobalanus sp., LM and SEM micrographs from the same pollen grain. (M) LM, overview. (N) SEM, overview. (K, L) SEM, detail. Scale bars = 10  $\mu\text{m}$  (A, E, I, J, M, N), 5  $\mu\text{m}$  (B, F), 1  $\mu\text{m}$  (C, D, G, H, K, L, O, P).

**Genus**—*Quercus* Linné**Species**—*Quercus* Group Cyclobalanopsis sp. (Fig. 4I–L)

**Description**—Pollen, monad, circular in polar view, pollen diameter 24–26  $\mu\text{m}$  wide (LM), 21–23  $\mu\text{m}$  (SEM); eutectate, exine 1.0–1.5  $\mu\text{m}$  thick (LM), nexine thinner than sexine, tricolpate to tricolporoidate; sculpturing scabrate (LM), platy verrucate, perforate (SEM); abundance: rare.

**Remarks**—This type of pollen shows sculpturing corresponding to extant pollen of *Quercus glauca*, *Q. hondae*, and *Q. acuta*, figured in Makino et al. (2009), which are part of *Quercus* Group Cyclobalanopsis (Denk and Grimm, 2010).

From the early Lutetian (ca. 48 Ma) old Nut Beds Locality, Clarno Formation, Manchester (1994) described the oldest cupules and nuts of *Quercus* Group Cyclobalanopsis. Today, the evergreen small trees of Cyclobalanopsis are native from West to East Asia (Menitsky, 2005).

Leaves of *Q. scudderi* were compared with modern species of *Quercus* Group Cyclobalanopsis by MacGinitie (1953). The leaf morphology of *Q. scudderi* does not unambiguously place this fossil taxon within *Quercus* Group Cyclobalanopsis. Members of this group of oaks commonly have secondary veins that are typically bent toward the apex, secondaries are arranged more densely in the apical part of leaves, and the basal part of the lamina never is dentate.

**Species**—*Quercus* Group Protobalanus sp. (Fig. 4M–P)

**Description**—Pollen, monad, shape prolate, elliptic in equatorial view, polar axis 20–24  $\mu\text{m}$  (LM), 19–22  $\mu\text{m}$  (SEM), equatorial diameter 17–20  $\mu\text{m}$  (LM), 15–17  $\mu\text{m}$  (SEM); eutectate, exine 1.0–1.5  $\mu\text{m}$  thick (LM), tricolpate; sculpturing scabrate (LM), weakly verrucate, perforate-fossulate (SEM), supra-sculpture microechinate, the microechinae being the apical parts of rodlets; abundance: rare.

**Remarks**—The weak relief showing verrucae that unite to form a vermiculate pattern separated by fossulae is characteristic of pollen of the few modern members of *Quercus* Group Protobalanus (Denk and Grimm, 2009a). MacGinitie (1953) described the leaf taxon *Quercus predayana* and compared it with species of group Protobalanus (*Q. chrysolepis* and allies). Although members of white oaks may have very similar leaves, virtually identical leaves are encountered in the modern *Q. chrysolepis*.

**Species**—*Quercus* Group Quercus/Lobatae sp. (Fig. 5A–L)

**Description**—Pollen, monad, shape prolate to spheroidal, circular to elliptic in equatorial view, polar axis 20–30  $\mu\text{m}$  (LM), 18–25 (SEM), equatorial diameter 19–24  $\mu\text{m}$  (LM) 17–21 (SEM); eutectate, exine 1.0–1.5  $\mu\text{m}$  thick, nexine thinner than sexine, tricolpate, colpus length 13–22  $\mu\text{m}$  (LM); sculpturing scabrate (LM), rugulate-verrucate, fossulate, perforate (SEM), rugulae and verrucae show a cauliflower-like, microechinate supra-sculpture (SEM); abundance: common.

**Remarks**—This pollen belongs to *Quercus* Group Quercus/Lobatae, the white and red oaks (Denk and Grimm, 2009a, 2010). The pollen shows exine sculpturing corresponding to several extant North American oaks. Red oaks with very similar pollen ornamentation are, e.g., *Quercus myrtifolia* Willdenow,

*Q. velutina* Lamarck, *Q. nuttallii* E.J. Palmer, and *Q. marilandica* Muenchhausen (Solomon, 1983b; figs. 6c, 6d, 7b–d, 13b–d, 19b, 19c). North American members of white oaks with this type of pollen ornamentation are *Q. virginiana* Miller and its varieties *Q. virginiana* var. *minima* Sargent and *Q. virginiana* var. *geminata* (Small) Sargent (Solomon, 1983a; figs. 24b, 24c, 25a, 25b, 26a, 26b). Among Eurasian white oaks, the East Asian *Q. serrata* Murray has a highly variable pollen ornamentation that covers the one encountered in *Quercus* Group Quercus/Lobatae sp. (Makino et al., 2009).

**Species**—*Quercus* Group Quercus sp. (Fig. 5M–P)

**Description**—Pollen, monad, shape spheroidal to prolate, circular in equatorial view, circular to elliptic in polar view, polar axis 29–32  $\mu\text{m}$  (LM), 28–30  $\mu\text{m}$  (SEM), equatorial diameter 28–31  $\mu\text{m}$  (LM), 27–29  $\mu\text{m}$  (SEM); eutectate, exine 1.0–1.5  $\mu\text{m}$  thick (LM), nexine thinner than sexine, tricolpate, colpus length 18–20  $\mu\text{m}$  (LM), bridge present (LM and SEM); sculpturing scabrate (LM), microverrucate, weakly perforate (SEM), microverrucae weakly sculptured, smoothly rounded (SEM); abundance: common.

**Remarks**—This pollen type is commonly found in Eurasian species of *Quercus* Group Quercus and differs from the previous type by more clearly defined microverrucae, which appear smoother due to more embedded sporopollenin. Sculpturing of this type can be found, for example, in extant pollen of the East Asian *Quercus mongolica* var. *grosseserrata* Rehder et Wilson and *Q. aliena* Blume (Makino et al., 2009), and of western Eurasian white oaks (cf. Denk and Grimm, 2009a; fig. 3A, B).

MacGinitie (1953) reported eight oak species based on foliage, which he included within *Quercus* groups Quercus, Lobatae, Protobalanus, and Cyclobalanopsis (Table 1). Some taxa that MacGinitie (1953) compared with modern white oaks or red oaks cannot unambiguously be referred to either the one or the other group (*Q. dumosoides*, *Q. mohavensis*). A number of sclerophyllous species among red and white oaks produce similar leaves, in particular when juvenile leaves are considered.

*Quercus lyratifolia* shows similarities with modern deciduous white oaks with deeply lobed leaves, whereas *Q. peritula* most closely resembles modern sclerophyllous red oaks. *Quercus predayana* appears to be most similar to modern species of *Quercus* Group Protobalanus. The remaining three leaf taxa either belong to extinct Fagaceae or cannot be assigned unambiguously to this family. Furthermore, *Q. balaninorum* may represent oak foliage but is based on a single fragmentary specimen.

## DISCUSSION

**Systematic affinity of the extinct genus Fagopsis**—The genus *Fagopsis* has previously been placed into various families (Ulmaceae, Betulaceae, Fagaceae; reviewed by Manchester and Crane, 1983). Manchester and Crane (1983) pointed out the marked differences between the fruiting structures of *Fagopsis* and extant Fagaceae and compared this with the situation in Juglandaceae, where *Platycarya* and *Juglans* have strikingly different fruiting structures, and to Betulaceae, where the same eye-catching differences are seen in *Alnus* (many, tiny samaras dispersed per infructescence) and *Corylus* (relatively large nuts, subtended by involucre of bracts). The infructescence of *Fagopsis* is more reminiscent of the cones of *Alnus* and *Platycarya* than of extant Fagaceae and suggests that the structural diversity

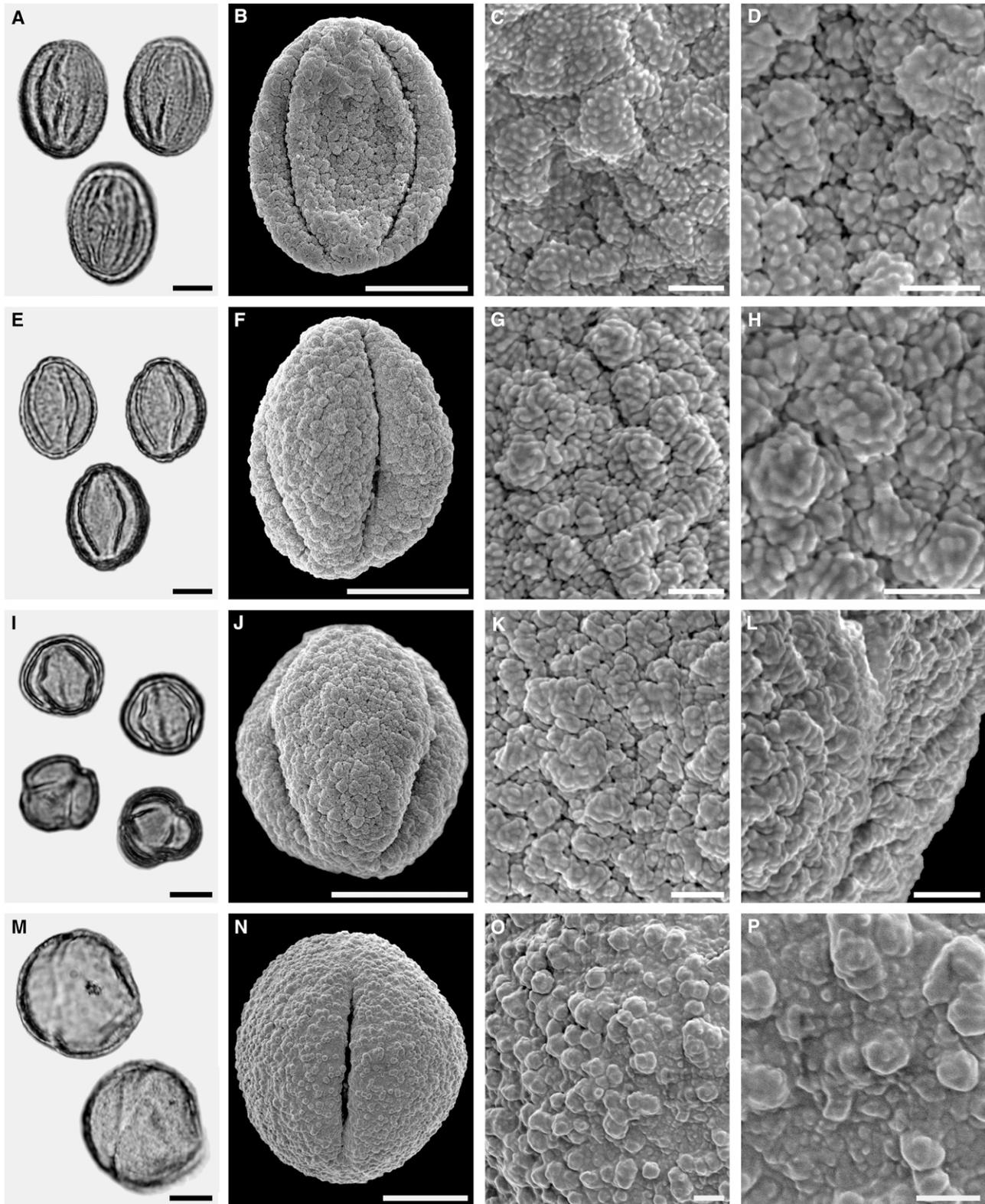


Fig. 5. (A–L) *Quercus* Group *Quercus/Lobatae* sp., and (M–P) *Quercus* Group *Quercus*. (A–D) *Quercus* Group *Quercus/Lobatae* sp., LM and SEM micrographs from the same pollen grain. (A) LM, overview. (B) SEM, overview. (C, D) SEM, details. (E–H) *Quercus* Group *Quercus/Lobatae* sp., LM and SEM micrographs from the same pollen grain. (E) LM, overview. (F) SEM, overview. (G, H) SEM, details. (I–L) *Quercus* Group *Quercus/Lobatae* sp., LM and SEM micrographs from the same pollen grain. (I) LM, overview. (J) SEM, overview. (K, L) SEM, details. (M–P) *Quercus* Group *Quercus*, LM and SEM micrographs from the same pollen grain. (M) LM, overview. (N) SEM, overview. (O, P) SEM, details. Scale bars = 10  $\mu\text{m}$  (A, B, E, F, I, J, M, N), 1  $\mu\text{m}$  (C, D, G, H, K, L, O, P).

TABLE 1. Fagaceae diversity in the latest Eocene of Florissant and potential modern analogues (PMA) of fossil taxa. PMA of previously described macrofossils are partly revised.

Pollen taxon (potential modern analogues) present study	Macro fossils (potential modern analogues) MacGinitie (1953)	Remarks to previously identified macro fossils
† <i>Fagopsis longifolia</i> Lesquereux (aff. Castaneoideae) Castaneoideae gen. et spec. indet., sp. 1 (aff. <i>Castanopsis</i> ) Castaneoideae gen. et spec. indet., sp. 2 (aff. <i>Castanea</i> ) Castaneoideae gen. et spec. indet., sp. 3 (aff. <i>Lithocarpus</i> )	† <i>Fagopsis longifolia</i> Lesquereux (Betulaceae)  “ <i>Castanea</i> ” <i>dolichophylla</i> Cockerell (leaf) ( <i>Castanea seguinii</i> Dode, <i>Castanea henryi</i> Rehder et Wilson)	Placed into Fagaceae by Manchester and Crane (1983)  Similarities with <i>Castanea</i> , extinct <i>Eotrigonobalanus</i> (Fagaceae), and extinct <i>Oreoroa</i> (Juglandaceae)
<i>Quercus</i> Group Cyclobalanopsis ( <i>Q. acuta</i> Thunberg, <i>Q. glauca</i> Thunberg, <i>Q. hondae</i> Makino) <i>Quercus</i> Group Protobalanus <i>Quercus</i> Group Quercus/Lobatae <i>Quercus</i> Group Quercus	<i>Quercus dumosoides</i> MacGinitie (leaf) ( <i>Q. dumosa</i> Nuttall)  <i>Quercus knowltoniana</i> Cockerell (reproductive structure) <i>Quercus lyratiformis</i> Cockerell (leaf) ( <i>Q. lyrata</i> Walter, <i>Q. alba</i> L.) <i>Quercus mohavensis</i> Axelrod (leaf) ( <i>Q. brandegei</i> Goldman, <i>Q. fusiformis</i> Small)  <i>Quercus peritula</i> Cockerell (leaf) ( <i>Q. incarnata</i> Trelease, syn. of <i>Q. sideroxylla</i> Bonpland, <i>Q. wislizeni</i> A.DC.) <i>Quercus predayana</i> MacGinitie ( <i>Q. wilcoxii</i> Rydberg syn. of <i>Q. chrysolepis</i> Liebmann, <i>Q. palmeri</i> Engelm.) <i>Quercus scottii</i> (Lesquereux) MacGinitie  <i>Quercus scudderii</i> Knowlton (leaf) ( <i>Q. glauca</i> Thunberg, <i>Q. cornea</i> Loureiro syn. of <i>Lithocarpus corneus</i> , <i>Q. myrsinifolia</i> Blume) <i>Quercus orbata</i> MacGinitie (leaf) ( <i>Q. undulata</i> Torrey-hybrid)	<i>Quercus</i> Group Quercus/ Lobatae ( <i>Q. agrifolia</i> Née; <i>Q. invaginata</i> Trelease; <i>Q. john-tuckeri</i> Nixon et C.H. Muller) Genus <i>Quercus</i> <i>Quercus</i> Group Quercus, deciduous  <i>Quercus</i> Group Quercus/ Lobatae ( <i>Q. depressa</i> Bonpland; <i>Q. emoryi</i> Torrey; <i>Q. galeanensis</i> C.H. Muller; <i>Q. minima</i> Small; <i>Q. peninsularis</i> Trelease) <i>Quercus</i> Group Lobatae ( <i>Q. coahuilensis</i> Nixon et C.H. Muller) <i>Quercus</i> Group Protobalanus  Extinct fagaceous leaf type aff. <i>Eotrigonobalanus</i> , <i>Castaneophyllum lonchitiforme</i> Kvaček et Walther <i>Quercus</i> -like Doubtful whether <i>Quercus</i> Group Cyclobalanopsis  Compared to extinct European “ <i>Q.</i> ” <i>cruciata</i> A. Braun No Fagaceae

in reproductive organs is as high in Fagaceae as in Betulaceae and Juglandaceae. The pollen of *Fagopsis* clearly is of the Castaneoideae type. It has recently been suggested that this pollen type based on its outer morphology and ultrastructure represents the basic type within Fagaceae (Denk and Tekleva, 2014). However, the complex vermiform sculpture formed by individual microrugulae as seen in *Fagopsis* and in a few extant taxa of *Castanopsis* clearly is derived in Castaneoideae. Most of the modern members of Castaneoideae have a simple microrugulate pollen sculpturing (Praglowksi, 1984; cf. Castaneoideae pollen types 1 to 3 of the present study). Overall, the character combination seen in *Fagopsis* suggests that it represents an extinct lineage that is distant to all modern and extinct types of Fagaceae.

**Systematic affinities of other Fagaceae in Florissant**—We found three distinct types of Castaneoideae pollen. Pollen morphology suggests that the three taxa belong to modern genera of Castaneoideae, but it is difficult to explicitly ascribe dispersed pollen to particular modern genera. Pollen of modern members of Castaneoideae shows little morphological differentiation even if some genera are conspicuously species-rich (Praglowksi, 1984;

Govaerts and Frodin, 1998). On the basis of the observation that certain pollen types are more frequent in particular genera of Castaneoideae, we tentatively assigned pollen types to modern genera (Table 1). Pollen of Castaneoideae gen. et spec. indet. 2 (aff. *Castanea*) in the present study is indistinguishable from in situ pollen of castaneoid staminate inflorescences described from the “middle” Eocene Claiborne Formation, Tennessee (Crepet and Daghl-ian, 1980). The presence of *Castanea*-like spiny cupules in the same sediments and of foliage of *Castaneophyllum tennesseense* (Berry) J.H. Jones et Dilcher further appears to support the presence of the genus *Castanea* in the middle Eocene of North America (cf. Manchester, 1999) and during the late Eocene of Florissant. Manchester (1999, p. 482) accepted the middle Eocene record from Tennessee as earliest for the genus *Castanea*. Nevertheless, Castaneoideae pollen similar to modern species of *Castanea* and foliage of “*Castanea*” *dolichophylla* from the Florissant fossil beds cannot unequivocally be attributed to *Castanea*. The same is true for foliage of “*Castanea*” from nearly contemporaneous sediments of southwestern Montana (Lielke et al., 2012). Castaneoideae gen. et spec. indet. 1 and 3 resemble particular modern species of *Castanopsis* and *Lithocarpus*, but pollen morphology cannot unequivocally

be used to discriminate between these genera and *Castanea*. Nevertheless, the pollen record demonstrates that Castaneoideae, although rare or growing at far distance from the lake, were diverse in Florissant. Virtually identical pollen of a general Castaneoideae type can be traced back until the early Late Cretaceous (early Coniacian) attached to flowers of fagalean affinity, described as *Archaeofagacea*, which are among the earliest records of Fagaceae (Takahashi et al., 2008), demonstrating how morphologically conserved pollen of Castaneoideae is. As outlined in the previous section, pollen of *Fagopsis* also displays the closest similarities with extant pollen of Castaneoideae, but the pollen of this extinct lineage is more derived within Castaneoideae.

From Florissant, nine different *Quercus* species have been distinguished based mainly on leaf fossils and in a single case on reproductive structures (MacGinitie, 1953; Manchester, 2001) (Table 1), and quercoid pollen has been reported but without further differentiation (Leopold and Clay-Poole, 2001; Wingate and Nichols, 2001). Leaf fossils are mostly sclerophyllous except for *Q. lyratiformis*, which is a lobed, deciduous type of oak strongly resembling species of *Quercus* Group Quercus. Among the remaining leaf species, *Q. peritula* shows closest similarities with modern members of *Quercus* Group Lobatae, and *Q. predayana* matches leaves of modern species of Group Protobalanus. *Quercus dumosoides* and *Q. mohavensis* resemble modern members of both Group Quercus and Group Lobatae. In addition, two species, *Q. scottii* and *Q. scudderii* cannot unambiguously be assigned to *Quercus* and probably represent extinct lineages of Fagaceae.

*Quercus orbata* was compared by MacGinitie to the European fossil species *Quercus cruciata*, which was later transferred to the genus *Pungiphylum* with unknown botanical affinities (Kvaček and Walther, 1981). The pollen types of *Quercus* partly complement the macrofossil record. *Quercus* groups Quercus, Cyclobalanopsis, Protobalanus, and Lobatae/Quercus are unambiguously recorded in the palynological record, and white and/or red oak pollen is fairly common in the counted pollen samples, while pollen of Group Cyclobalanopsis and Group Protobalanus is very rare. In contrast to Castaneoideae, pollen of *Quercus* is highly diagnostic at the intrageneric level.

**Inferred paleovegetation of Florissant**—The plant taxa recovered from the Florissant Beds are strongly indicative of three major forest/vegetation types: (1) sclerophyllous forest: mediterranean chaparral of the Californian type, pine–oak forest of northwestern Mexico, with extensions to tropical and subtropical dry woodlands, (2) nemoral coniferous forest, (3) mesic broad-leaved forest: laurel forest and broad-leaved deciduous forest according to Schroeder (1998; see table 23 in Velitzelos et al., 2014; Appendices S2, S3, see online Supplemental Data). In addition, the fossil plant assemblage includes riparian/aquatic elements and lianas (Appendix S3).

Of 151 taxa/pollen types recovered from the Florissant Beds, 54 are at present found in sclerophyllous forests and woodlands occurring in summer dry (Cs) and winter dry (Cw) climates and extending into arid BS climates (Peel et al., 2007; Appendices S1, S3); of these, 18 are not common in any other of the three vegetation types (e.g., *Athyana*, *Cercocarpus*, *Schmaltzia* [= *Rhus* sect. *Lobadium*], *Vauquelinia*). Typically, the sclerophyllous oaks of Group Protobalanus, Group Quercus, and Group Lobatae fall within this vegetation type (Cs and Cw climate types; Rzedowski, 1983; Flora of North America Editorial

Committee, 1997); they are well represented by foliage and pollen.

Today, sclerophyllous forests are closely connected to nemoral coniferous forests and replaced by them at higher elevations and at higher latitudes. Several taxa encountered from Florissant, possibly were not confined to sclerophyllous forests but also thriving in nemoral coniferous forests, often in the second tree layer (e.g., some Castaneoideae [*Notholithocarpus*], *Quercus* Group Protobalanus, Group Quercus/Lobatae). Fifty-five of the fossil taxa belong to genera that occur in nemoral coniferous forests. Of these, six are restricted to this forest type (Appendix S1) comprising several conifers (*Abies*, *Tsuga*, *Chamaecyparis*, *Sequoia*). *Chamaecyparis*, *Sequoia*, and *Torreya* probably had a wide ecological amplitude. Today, they are typical elements of the Pacific Coast Ranges. *Torreya californica* Torrey grows scattered along mountain streams and in moist canyons, commonly co-occurring with *Sequoia*, *Acer* spp., *Platanus*, and *Alnus*. Furthermore, it occurs in coastal chaparral. Its altitudinal range is from near sea level to 2500 m (Farjon, 2013). *Chamaecyparis lawsoniana* (A. Murray bis) Parlatores has a similar range but is at present absent at higher elevations (0 to 1500 m a.s.l.; Flora of North America Editorial Committee, 1993).

In addition, a relatively high number of taxa recorded from Florissant have modern analogues that are elements of fully humid mesic forests (44 taxa, of which 13 are confined to such forests; Appendix S3). Some of these taxa introduce an exotic element to the fossil flora of Florissant, represented by the East Asian Cercidiphyllaceae, Rhoipteleaceae, *Cyclocarya*, *Eucommia*, *Hovenia*, and *Tetracentron*, and possibly by some of the Castaneoideae type pollen taxa and undetermined fagaceous foliage. Humid environments are also indicated by the conifer *Cathaya*, another East Asian element with a wide northern hemispheric distribution throughout the Cenozoic (e.g., Liu and Basinger, 2000; Grímsson and Zetter, 2012), and by *Torreya* with a modern East Asian–North American disjunction. The same is true for Engelhardoideae (Miranda and Sharp, 1950; Stone, 1968).

Riparian and aquatic elements were associated with the Florissant lake and rivers and torrents flowing into the lake (39 of 151 taxa). Most prominent riparian elements of the Florissant paleoflora are the extinct Fagaceae *Fagopsis* based on the abundant occurrence of leafy branches with attached staminate and pistillate inflorescences and fruits, and *Cedrelospermum* (Manchester and Crane, 1983; Manchester, 1989, 2001). Other riparian elements are *Ginkgo*, *Ailanthus*, *Alnus*, *Fraxinus*, *Populus*, and others. The fact that *Ginkgo*, *Fraxinus*, and *Alnus* are represented by pollen and nearly absent in the leaf fossil record may indicate that these elements were not part of the riparian community in the Florissant valley dominated by *Sequoia*, *Cedrelospermum*, and *Fagopsis*, but grew along torrents flowing into the valley. Overall, from the present, revised taxon list of Florissant (Bouchal, 2013) (Table 2, Appendix S3), it appears that several of the taxa typical of and confined to broad-leaved, deciduous forests and nemoral conifer forest did not grow in close vicinity of the paleo-lake or river because they are represented by pollen only (e.g., *Cathaya*, Rhoipteleaceae, *Cercidiphyllum*, *Tetracentron*). In contrast, taxa resembling modern species growing in markedly seasonal climates are commonly represented by foliage and fruits (*Athyana*, *Cercocarpus*, *Quercus* spp.) and may have grown on slopes facing the lake, while mesic forests may have occurred higher up or in microclimatically humid areas (humid valleys and ravines, aspect-wise humid slopes). The same may have applied to moisture-loving plants such as the conifers *Cathaya* and *Torreya*.

TABLE 2. Total plant diversity in the latest Eocene of Florissant including an updated palynological record (Bouchal, 2013; this study). Plant families are listed following APG III (2009).

Class/Clade/Family	Genus	Macrofossils	Pollen	Source	Remarks
Ginkgopsida					
Ginkgoaceae	<i>Ginkgo</i>		+	5	
Coniferopsida including Gnetales					
Cupressaceae	<i>Chamaecyparis</i>	C, L		3	
	<i>Sequoia</i>	C, B, W	+	1, 2, 3, 5	
Taxaceae	<i>Torreya</i>	L		3	
Pinaceae	<i>Abies</i>	S	+	1, 2, 3, 5	
	<i>Cathaya</i>		+	5	
	<i>Picea</i>	S	+	1, 2, 3, 5	
	<i>Pinus</i> sect. <i>Strobus</i>	C, S, L	+	1, 2, 3, 5	2 spp. (MF)
	<i>Pinus</i> sect. <i>Pinus</i>	C, S, L	+	1, 2, 3	3 spp. (MF)
	<i>Tsuga</i>		+	1, 2, 5	
Ephedraceae	<i>Ephedra</i>	B	+	1, 2, 3, 5	2 types (P)
Angiosperms					
Nymphaeaceae			+	1, 2	
Magnoliids					
Lauraceae		L		3	2 spp. (MF)
Monocots					
Potamogetonaceae	<i>Potamogeton</i>	L?, Fr		3	
Dioscoreaceae	<i>Dioscorea</i>	Fr		3	
Liliaceae			+	1, 2	
Smilacaceae	<i>Smilax?</i>	L		3	
Commelinids					
Arecaceae		L	+	1, 2, 3, 5	
Cyperaceae	<i>Cyperacites</i>	L	+	2, 3	
Poaceae			+	1, 2	
	<i>Stipa</i>	Fr	+	3, 5	
Typhaceae	<i>Sparganium</i>		+	1, 2, 5	
	<i>Typha</i>	L	+	1, 2, 3, 5	
Eudicots					
Buxaceae			+	2, 5	
Platanaceae	<i>Platanus</i>	L	+	1, 2?, 3, 5	
Menispermaceae			+	5	
Berberidaceae	<i>Mahonia</i>	L		1, 3	2-3 spp. (MF)
Ranunculaceae			+	2?, 5	
Trochodendraceae	<i>Tetracentron</i>		+	5	
Core eudicots					
Amaranthaceae			+	1, 2, 5	3-4 types (P)
Cercidiphyllaceae			+	2, 5	
Grossulariaceae	<i>Ribes</i>	L		3	
Hamamelidaceae			+	2?, 3?, 5	
Polygonaceae			+	2	
Rosids					
Vitaceae	<i>Vitis</i>	L	+	1, 5	2 types (P)
			+	3	
Eurosids					
Fabaceae	indeterminable	L1	+	1, 2, 3	4 spp. (MF)
	<i>Caesalpinia</i>	L1	+	2, 3?	
	<i>Cercis</i>	L, Fr		3	
	? <i>Prosopis</i>	L		3	
	<i>Robinia</i>	L, W		3?, 4	
	<i>Vicia</i>	L		3	
Betulaceae	<i>Paracarpinus/Asterocarpinus</i> †	Fr, L	+	1, 3	
	<i>Alnus</i>		+	2	
	<i>Betula</i>		+	1, 5	
	<i>Ostrya/Carpinus</i>		+	1	
Fagaceae	Castaneoideae	L?	+	1, 2, 3, 5, 6	3 types (P)
	<i>Fagopsis</i> †	L, Fl, Fr	+	3, 6	
	<i>Quercus</i>	L, Fr	+	1, 2, 3, 5, 6	8 spp. (MF) 4 types (P)
Juglandaceae	<i>Carya</i>	L, L1, Fl, Fr	+	1, 2, 3, 5	
	<i>Cyclocarya</i>		+	1	
	Engelhardoideae			1, 2, 5	2 types. (P)
	<i>Juglans</i>	S?	+	1, 2, 3, 5	
Rhoipteleaceae			+	1, 2	
Salicaceae	<i>Populus</i>	L, Fr		3	
	<i>Salix</i>	L	+	1, 2, 3, 5	4 spp. (MF)
Euphorbiaceae		L	+	1, 2, 3, 5	

TABLE 2. Continued.

Class/Clade/Family	Genus	Macrofossils	Pollen	Source	Remarks
Elaeagnaceae			+	1, 2	
Cannabaceae	<i>Humulus</i>	L		3	
Moraceae	<i>Morus</i>	L		3	
Rhamnaceae	<i>Hovenia</i>	W		7	
Rosaceae			+	1, 2, 5	4 types (P)
	<i>Amelanchier</i>	L		3	
	<i>Cercocarpus</i>	L, Fr		3	
	<i>Crataegus</i>	L, Fr	+	2, 3, 5	3 spp.(MF)
	<i>Holodiscus</i>	L		3	
	<i>Malus</i>	L		3	
	<i>Rosa</i>	L, Ll		3	
	<i>Rubus</i>	L		3	
	<i>Vauquelin[i]a</i>	L		3	2 spp. (MF)
Ulmaceae		W	+	1, 2, 4, 5	
	<i>Celtis</i>	L		1, 3	
	<i>Cedrelospermum</i> †	L, S	+	3, 5	
	<i>Ulmus</i>	L, F	+	1, 2, 3, 5	
	<i>Zelkova</i> -type		+	1	
Malvids					
Malvaceae	indeterminable.		+	1, 2, 5	at least 6 types (P)
	<i>Florissantia</i> †	Fl, Fr	+	1, 2, 3, 5	
	<i>Tilia</i> ?	L	+	2, 3	
Thymeleaceae	indeterminable.		+	5	
	<i>Daphne</i>	L	+	2, 3, 5	
Onagraceae	indeterminable.	Fl	+	1, 2, 3, 5	2 types (P)
Sapindaceae	<i>Acer</i>	L, Fr	+	1, 2, 3, 5	3 spp. (MF)
					3 types (P)
	<i>Athyana</i>	L	+	3	
	<i>Dipteronia</i>	L, Fr		1, 3	
	<i>Koelreuteria</i>	L?, Fr, W		1, 3, 4	
Simaroubaceae	<i>Ailanthus</i>	Fr	+	2, 3	
	<i>Chaneya tenuis</i> †	Fr		3	
Meliaceae	<i>Cedrela</i> or <i>Toona</i>	S	?	2, 3	
Anacardiaceae		L	+	5	
	<i>Cotinus</i>	L		3	
	<i>Rhus</i>	L		1, 3	3 spp. (MF)
	<i>Schmaltzia</i> (= <i>Rhus</i> sect. <i>Lobadium</i> )	L		3	
Rutaceae		S?	+	1, 3, 5	
Asterids					
Cornaceae	<i>Alangium</i>		+	5	
Hydrangeaceae		L, Fl		3	
Ebenaceae	<i>Diospyros</i>		+	5	
Ericaceae			+	1, 2, 5	
Euasterids I (Lamiids)					
Apocynaceae		S		1, 3	
	<i>Tabernaemontana</i>		+	1, 5	
Eucommiaceae	<i>Eucommia</i>	Fr	+	1, 2, 3, 5	
Oleaceae	<i>Osmanthus</i> ?	L, Fr	+	1, 3	
	<i>Fraxinus</i>		+	2, 5	
Euasterids II (Campanulids)					
Asteraceae			+	1, 2, 5	
Adoxaceae	<i>Sambucus</i>	L, Ll	+	1, 2, 3	
	<i>Viburnum</i>		+	1, 5	
Caprifoliaceae	<i>Diplodipelta</i> †	Fr		3	
	<i>Lonicera</i>		+	2, 5	
Araliaceae			?	2	
	<i>Oreopanax</i>	L		3	

Notes: L, leaf; Ll, leaflet; MF, macrofossils; B, branch; C, cone; Fr, fruit; P, pollen; S, seed; W, wood; Fl, flower; +, present. Sources: 1, Leopold and Clay-Poole (2001) and Leopold et al. (2008, Table 1); 2, Wingate and Nichols (2001); 3, Manchester (2001); 4, Wheeler (2001); 5, Bouchal (2013); 6, present study; 7, Wheeler and Meyer (2012). † = extinct.

Combined evidence from macrofossils and palynological data suggest that the valley floor was dominated by riparian vegetation (*Sequoia*, *Cedrelospermum*, and *Fagopsis*). The slopes of the surrounding mountains would have been covered with sclerophyllous and pine–oak forest on edaphically or aspect-wise drier slopes, and with mesic forest on humid slopes or

in ravines. The dry and moist forest vegetation would have been followed by nemoral conifer forest with an admixture of evergreen oaks and broad-leaved deciduous elements. The inferred vegetation types are indicative of complex landscapes reflecting different vertical vegetation belts, and different aspects of slopes and canyons in an intermontane setting.

**Earlier concepts about paleoecology and climate of Florissant**—Leopold and Clay-Poole (2001) suggested close similarities with the modern vertical vegetation zonation in Tamaulipas, Mexico (El Cielo biosphere, 200 to ca. 2400 m a.s.l.; Hernández et al., 1951). Leopold and Clay-Poole (2001) estimated the paleoelevation of Florissant at ca. 1000 m a.s.l., which is similar to the vegetation belt of the cloud forest in Tamaulipas (ca. 800 to 1400 m a.s.l.). The isolated occurrence of humid temperate vegetation in Tamaulipas occurs in a montane setting situated above the winter-dry tropical lowlands and receiving plenty of humidity from the Gulf of Mexico during the growing season. Relict stands of *Fagus*, *Liquidambar*, *Illicium*, and *Magnolia* among others occur in a warm temperate, winter-dry to fully humid climate (Cwa to Cfa). *Fagus* was reported from Florissant by Leopold and Clay-Poole (2001) but not by Leopold et al. (2008), and the presence of *Fagus* could not be confirmed by the current study. *Liquidambar* has never been reported from Florissant, nor was *Magnolia* and *Illicium*. A comprehensive analysis of the historical biogeography of *Fagus* suggested that the ecology of this genus did not change much throughout the Cenozoic and that *Fagus* is strongly dependent on fully humid conditions (Denk and Grimm, 2009b). Thus, the paleoelevation of the mesic forest at Florissant may have been higher or conditions were more continental than for the modern mesic forests (cloud forests) of the Sierra Madre Oriental (cf. Miranda and Sharp, 1950; Hernández et al., 1951). Considerable effort has been used to estimate the paleoelevation of Florissant (see Meyer, 2001, for a review). Except for a few studies that suggested elevations below the present one (e.g., MacGinitie, 1953; Leopold and Clay-Poole, 2001), most paleobotanically derived estimates suggested paleoelevations between 2000 and 3000 m (cf. Meyer, 1992, 2001; Gregory and Chase, 1992; Wolfe, 1992, 1994; Gregory, 1994; Gregory and McIntosh, 1996; Forest et al., 1995, 1999; Wolfe et al., 1998).

In addition to the mesic forest reconstructed by Leopold and Clay-Poole (2001), these authors suggested the presence of desert-like scrub vegetation in drier areas more distant to the lake. However, the taxa used to infer the desert-like vegetation (e.g., *Datura*, *Semeiandra*, *Xylonagra*) could not be confirmed by Bouchal (2013).

DeVore and Pigg (2010, p. 114) interpreted the Florissant fossil assemblage as “savanna–woodland, tropical–dry”. The significant taxa listed by these authors are *Fagopsis*, *Cedrelospermum*, *Florissantia*, and Rosaceae. It is unclear how they arrived at the paleoecological interpretation based on this taxon set and the presented description of the Florissant flora (DeVore and Pigg, 2010, pp. 120, 121).

Boyle et al. (2008) used higher taxonomic composition (genus and family levels) of 241 modern forest plots exclusively from North and South America to determine a modern analog for the fossil flora of Florissant. Although they did not find a direct match, greatest similarities were calculated with three forest plots (Florida, lowland; Tamaulipas, El Cielo; northern Argentina, lower montane), which share moderately high temperatures and seasonality of precipitation. On the basis of the taxonomic composition of the Florissant plant assemblage, it is inferred that the plant assemblage (or taphocoenosis) is not derived from a homogeneous vegetation but from different vegetation types (see above). In our opinion, it would have been more meaningful to compare these subunits to modern forest/vegetation types. For example, as outlined above, the mesic component of the Florissant flora has strong similarities with the modern East Asian humid warm temperate forest flora,

whereas elements of edaphically or climatically drier stands more closely resemble western North American vegetation types thriving in distinctly seasonal climates. The continental, intermontane depositional setting of the Florissant plant assemblage lends credibility to a varied vegetation cover depending on slope aspect, soil conditions, and elevation. For modern “Tertiary relict” vegetation and for most parts of the Neogene in western Eurasia, it has been argued that sufficient amounts of precipitation that were evenly distributed throughout the year (Cfa climate according to Köppen) accounted for a blurring of vertical vegetation zonation as known today in areas with strongly seasonal (Cs and Cw) climates (Mai, 1995; Denk et al., 2001; Velitzelos et al., 2014). For example, along the northern Black Sea coast of Turkey, seemingly antagonistic elements (Mediterranean sclerophyllous oaks, humid warm temperate broadleaved deciduous and evergreen taxa, and riparian elements) co-occur without a distinctive spatial separation (Denk et al., 2001). This situation is due to the fully humid warm temperate climate and is profoundly changed on the leeward slopes of the Pontic Range (Walter, 1956). The early Cenozoic uplift of the Rocky Mountains may indeed have provided the environmental conditions that promoted ecological differentiation in plant lineages (e.g., *Quercus* Group Protobalanus) while at the same time providing niches for plant taxa requiring sufficient amount of precipitation throughout the year.

Lielke et al. (2012) suggested a pronounced summer drying trend for the Eocene-Oligocene floras of southwestern Montana. Emphasizing the presence of xeric woodland elements comprising *Quercus* spp., *Cercocarpus*, and *Mahonia* in the Eocene-Oligocene Ruby Flora of southwestern Montana along with dry conifer woodland elements of leeward slopes of mountains, these authors inferred a “highly seasonal, summer-dry climate” (Lielke et al., 2012, p. 345) for the Northern Rocky Mountains and extending further south to Florissant.

**Paleoclimatic setting**—It has been commonly assumed that ancestors of the modern western North American sclerophyllous flora evolved in seasonal summer-wet climates during the Eocene and Oligocene (Axelrod, 1973). From the tectonic history (Bryant et al., 1981; Mix et al., 2011; Frisch et al., 2011) and inferred paleoelevation for the Front Range at the Eocene-Oligocene boundary (Meyer, 2001), it can be assumed that climatic conditions in the Front Range were as complex as today. At present, because of north–south-running mountain ranges, the Rocky Mountains and their southern extensions (e.g., Sierra Blanca Peak) show a great variety of local climates (Lieth et al., 1999; Appendix S1). These include both summer-wet and summer-dry climates. It has been suggested that, locally, summer-dry climates were established during the Eocene-Oligocene boundary also in the eastern Rocky Mountains (Montana, Front Range; cf. Lielke et al., 2012). This suggestion was based on the prominent occurrence of xeric elements such as *Ephedra*, *Quercus* spp., *Cercocarpus*, and *Mahonia* among others (Lielke et al., 2012). Although indicative of pronouncedly seasonal climates, at present times these taxa occur both in summer-dry and summer-wet climates (Rzedowski, 1983; Flora of North America Editorial Committee, 1997).

At higher elevations, nemoral conifer forest flourished possibly resembling the conditions encountered today in the Coastal Range and the Cascades and Sierra Nevada (*Abies*, *Chamaecyparis*, *Torreya*, *Tsuga*). Today, these forests grow under a mild Mediterranean climate with cyclonic winter rains and considerable amounts of humidity from fog precipitation

during the summer (Dawson, 1998; Kottek et al., 2006; Peel et al., 2007). In view of the geographic position of the Front Range a summer-wet climate appears more likely, which is also supported by the fact that substantial secondary growth of *Sequoia* wood occurred during the growing season (Gregory-Wodzicki, 2001), and the prominent contribution of mesic elements to the plant assemblage.

Comparable complex climate patterns are encountered on the southern foothills of the Hindu Kush Mountains and the lower Himalayas of Kashmir (Schroeder, 1998, p. 362; Menitsky, 2005, p. 360; Kottek et al., 2006; Peel et al., 2007) where fully humid (Cf), winter-dry (Cw), and summer-dry (Cs) climates co-occur as complex mosaic. Here, sclerophyllous oaks (*Quercus* Group Ilex) and *Q. glauca* (*Quercus* Group Cyclobalanopsis) co-occur (600–1800 m), and higher up, sclerophyllous oaks are part of nemoral conifer forests (to >3500 m).

**Convergent evolution of sclerophyllous leaf traits, early adaptive radiation in *Quercus* in the Paleogene of the Northern Hemisphere**—Eocene floras in western North America comprise sclerophyllous fagaceous leaves and pollen that can unambiguously be assigned to modern groups of *Quercus* (e.g., Axelrod, 1966; MacGinitie, 1953, 1969; present study). In contrast, lobed, deciduous foliage of *Quercus* occurred in the middle Eocene floras of Arctic North America (McIver and Basinger, 1999). Eocene and early Oligocene floras of Europe and East Asia are dominated by extinct members of Fagaceae (*Eotrigonobalanus* and castanoids), which closely resemble North American (extinct) taxa, but these floras essentially lack modern genera of Fagaceae (Tanai and Uemura, 1994; Tanai, 1995; Denk et al., 2012). Sclerophyllous oaks resembling the modern (Eurasian) Mediterranean members of *Quercus* Group Ilex are not known in western Eurasia before the late early Oligocene (pollen) and the early Miocene (leaves; Mai, 1995; Denk et al., 2012) and appear to be advanced within a larger group of Eurasian sclerophyllous oaks, most of which are found in fully humid temperate Cfa climates and in (humid variants of) winter-dry monsoon climates (Cw climates; Menitsky, 2005). In general, there is no paleobotanical evidence for summer-dry, Mediterranean conditions in the Mediterranean region prior to the Pleistocene (Suc, 1984; Velitzelos et al., 2014) although many lineages comprising Mediterranean elements are phylogenetically old (e.g., *Smilax aspera* L., Qi et al., 2013; *Quercus* Group Ilex, Denk and Grimm, 2009a, 2010).

A partly contrasting picture emerges for the late Eocene of western North America. The presence of sclerophyllous oaks belonging to two to three infrageneric groups of *Quercus* (*Quercus* Group Protobalanus and Group Lobatae/*Quercus*), along with taxa belonging to genera that are today confined to seasonally dry climates of Pacific North America (summer-dry Cs climates and summer-wet Cw and BS climates) suggest that these lineages might have originated as early as the Eocene in a climatic setting similar to the modern one in the southwestern United States. For example, members of *Quercus* Group Protobalanus are at present confined to the southwestern United States and northwestern Mexico (Rzedowski, 1983; Manos, 1997) where they occur from ca. 200 to 2800 m. The presence of pollen and foliage in Florissant suggests that they were established in western North America by the late Eocene. Phylogenetically, *Quercus* Group Protobalanus is an old group, representing the ancestral lineage in one of two major clades of *Quercus* (Manos et al., 2001; Denk and Grimm, 2009a, 2010). Similarly, *Cercocarpus* (Rosaceae) foliage and fruits from

Florissant are closely similar to the modern *Cercocarpus montanus* Rafinesque species complex (southwestern USA; Manchester, 2001), and the genus is basal within all modern Spiroideae (van den Heuvel, 2002; Potter et al., 2007). Another Rosaceae, *Vauquelinia* with two modern species in the southwestern United States and northwestern Mexico, forms an early-diverging branch within subtribe Pyrinae (Campbell et al., 2007). Similarly, *Schmaltzia* (syn. *Rhus* sect. *Lobadium*, Anacardiaceae) with a modern distribution in the southwestern United States, Mexico, and northern Central America is basal within one of two major clades of the genus *Rhus* (Yi et al., 2004). In a wider biogeographic context, *Athyana*, a monotypic genus of Sapindaceae, forms an early-diverging branch within the *Paullinia* group of Sapindoideae (Buerki et al., 2009). At present, *Athyana* occurs from Peru to Argentina in seasonal BS, Cw, and Cf climates.

Two evolutionary patterns are evident from the comparison of the fossil records of Fagaceae sclerophyllous foliage in the Old World and the New World. In western Eurasia and East Asia, sclerophyllous Fagaceae are found among *Quercus* Group Ilex and Group Cerris. Mediterranean representatives of these groups are derived (Denk and Grimm, 2010). In the New World, sclerophyllous Fagaceae are found in *Quercus* Group Protobalanus, Group *Quercus*, and Group Lobatae and are taxonomically and phylogenetically unrelated to their ecological counterparts in the Old World. Second, Axelrod (1975, p. 280) assumed that “by the middle Eocene broadleaved evergreen sclerophyllous taxa occupied a subhumid belt across much of North America-Eurasia”; he termed this vegetation belt “Madrean-Tethyan sclerophyll vegetation”. Phylogenetic relationships of the constituents of this ancient vegetation clearly show that the evolutionary patterns seen in the Eurasian and North American parts of this vegetation belt were unrelated and that climate conditions in Eurasia were fully humid throughout most of the Paleogene (laurel forests with extinct Fagaceae and Lauraceae; see, e.g., Mai, 1995) in contrast to the situation in western North America (appearance of modern mediterranean lineages under, locally, markedly seasonal climates; Lielke et al., 2012; present study). In the mountains of western North America, climatic differences owing to strong topographic relief and slope aspect might have caused high niche diversity and triggered ecological radiation in Fagaceae and other plant lineages during the Paleogene.

**Conclusions**—A substantial portion of the Florissant plant assemblage represents a vegetation adapted to seasonal drought. Today, such plants typically occur in markedly seasonal winter-dry or winter-wet regions along the coast of western North America. These regions seem to have been colonized by drought-tolerant vegetation, already in place in intermontane basins and valleys of western North America, when subtropical, lowland vegetation retreated in the course of the Miocene. The modern Pacific coast region is a refugium for a number of ancestral lineages such as *Quercus* Group Protobalanus, *Notholithocarpus*, *Torreya*, and *Chamaecyparis*, which are today typical elements of the Chaparral-nemoral conifer forest succession. These lineages appear to have been adapted to distinctly seasonal climates already by the late Eocene, which demonstrates the fundamental difference between the origin of mediterranean vegetation in western North America and western Eurasia. In western Eurasia, the ecological shift from fully humid to summer-dry (mediterranean) environments is well documented in a number of plant lineages including *Quercus*

(Mai, 1995; Denk et al., 2014; Velitzelos et al., 2014) and did not happen before the end of the Pliocene.

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