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Evolutionary Trends and Ecological Differentiation in Early Cenozoic Fagaceae of Western North America

Johannes Bouchal[2,3,5], **Reinhard Zetter**[3], **Friðgeir Grímsson**[3,4], and **Thomas Denk**[2]

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

Abstract

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 Mediterranean climate of California originated in climates with summer rain during the Paleogene.

Methods—We investigated *in situ* and dispersed pollen of Fagaceae from the uppermost Eocene Florissant Fossil Beds, Colorado, using a combined light and scanning electron microscopy approach (single grain method).

Key results—Pollen types of Castaneoideae with affinities to modern *Castanea*, *Lithocarpus*, and *Castanopsis* are recognized. Pollen of the extinct genus *Fagopsis* represents a derived type of Castaneoideae pollen. Infrageneric groups of *Quercus* are well represented, including pollen of Group Protobalanus. The flora indicates a climatic setting for Florissant, located in the Front Range of the Rocky Mountains, which corresponds with the modern-day situation in the Coastal Ranges. Continental climatic conditions and seasonality may have triggered the evolution of sclerophyllous leaves and adaptive radiation in *Quercus* and other taxa confined today to Mediterranean vegetation of California and Mexico.

Conclusions—The Florissant plant assemblage indicates that modern vegetation belts of the Coastal Ranges (Chaparral, nemoral conifer forest) were established in the Front Range by the late Eocene. The constituent taxa demonstrate that typical elements found in the Mediterranean climate of Pacific North America (Group Protobalanus, *Notholithocarpus, Torreya*, and *Calocedrus*) did not undergo dramatic ecological shifts. They opportunistically migrated into their modern ranges. This is in stark contrast to the evolution and migration patterns of their western Eurasian Mediterranean counterparts (*Quercus* Group Ilex).

Keywords

Castaneoideae; Eocene-Oligocene boundary; Front Range; laurel forest; nemoral conifer forest; origin of Mediterranean vegetation; *Quercus* Group Cyclobalanopsis; *Quercus* Group Quercus/Lobatae; *Quercus* Group Protobalanus; sclerophyllous forest

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[5]Author for correspondence: johannes.bouchal@nrm.se.

Introduction

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 mono-dominant 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 Daghlian, 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, 1988) 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 Daghlian, 1980; Friis et al, 1988; Walther and Zetter, 1993; Kohlmann-Adamska and Ziembínska-Tworzydło, 2000, 2001; Denk et al., 2010; 2011, 2012). Here, we use a combined LM and SEM investigation of *in situ* and dispersed pollen grains in order to evaluate the taxonomic diversity of Fagaceae in the uppermost Eocene of the Florissant Formation, Colorado, USA. 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 cycle cup oaks (*Quercus* Group Cyclobalanopsis). Furthermore, one leaf type was compared to the enigmatic European fossil taxon *Quercus cruciata*.

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 to 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 paleovegetation and paleoecology during the deposition of the Florissant Fossil Beds.

MATERIAL AND METHODS

The plant material investigated for the present study 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 Thirtynine Mile Andesite (Evanoff et al., 2001; Fig. 1.A).

The Florissant Formation is a heterolithic accumulation of shale, tuffaceous mudstone and siltstone, tuff, arkosic and volcaniclastic 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 unit are the main fossil-bearing strata, which yield the exceptionally well-preserved insect, plant, fish and bird fossils. An individual of the genus *Herpetotherium* (an extinct small opossum) 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 Priabonium age (ICS). This corresponds with the ^{40}Ar/^{39}Ar 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 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 family Stoll, west of Florissant (Fig. 1. B, X_1), near the old Denver Museum Locality (MacGinitie, 1953). S151454 was collected from the Claire Quarry locality south of Florissant (Fig. 1. B, X_2) Sedimentary rock was 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). The compressed staminate inflorescence of *Fagopsis longifolia* with *in situ* pollen grains is from the collection of the University of California Museum of Paleontology in Berkeley, labelled as UCMP200/254999. The sample was macerated in Danclor™ and acetolysed; individual pollen grains were isolated with a micromanipulator.

LM 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 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 (2009, 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 in recent molecular phylogenetic studies (Manos et al., 2008; Oh and Manos, 2008; Denk and Grimm, 2010).

SYSTEMATIC PALEOBOTANY

Family

Fagaceae Dumortier

Genus

Fagopsis Hollick

Species

Fagopsis longifolia (Lesquereux) (Fig. 2 A-P, 3 A-L)

Description

Pollen, monad, shape prolate to spheroidal, elliptic in equatorial view; *in situ* pollen: polar axis 22-27 µm (LM), 19-22 µm (SEM) [18-20 µm according to Manchester and Crane, 1983], equatorial diameter 19-21 (LM), 17-20 µm (SEM); dispersed pollen: polar axis 22-28 µm (LM), 21-25 (SEM) equatorial diameter 19-26 µm (LM), 17-25 µm (SEM); eutectate, exine 1-1.5 µm thick (LM), tricolporate, bridge present (Fig. 2 I-K, M, N, P. 3 A, B, D-F, H-J, L), colpus length 18-22 µm (SEM); sculpturing scabrate (LM), micro-rugulate (to rarely rugulate), perforate-fossulate in non-apertural region (SEM), several parallel running micro-rugulae forming larger rugulae (vermiculate pattern), 0.5-≤1 µm long and wide (Fig. 2 F-H, K, L, O, P, 3 C, D, G, H, K; secondary-striate sculpture according to Praglowski, 1984); micro-rugulae ("striae") connected by short perpendicular elements (Fig. 2 H, 3 C), in some of the dispersed pollen grains no such connecting elements visible between micro-rugulae

(Fig. 2 K, L, O, P); sculpturing in apertural region and bridge without fossulae, perforations can be present (Fig. 2 J, 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 Colorado (MacGinitie, 1953; Manchester and Crane, 1983), and the Oligocene Ruby River Basin flora of Montana (Becker, 1961). 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 micro-sculpturing in *Fagopsis* is not detectable at lower magnification (2000-5000 x), but is crucial for fingerprinting dispersed pollen of this type. This type of micro-sculpturing is present in some extant and Quaternary *Castanopsis* pollen (Miyoshi, 1983; Praglowski, 1984). In *Castanopsis*, rugulate pollen typical of Castaneoideae is found in most extant species, while a few species, *Castanopsis cuspidata* (Thunberg) Schottky and *C. sieboldii* (Makino) Hatusima have micro-rugulae forming larger rugulae (cf. Praglowski, 1984, fig. 4, C) as seen in *Fagopsis*. Moreover, the same type of short perpendicular elements connecting the micro-rugulae 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 pollen ultrastructure of *Fagopsis* corresponds to the pattern seen in Castaneoideae. The foot layer in genera of Castaneoideae is homogeneous, relatively thick and the ratio foot layer to tectum is about 1. Manchester and Crane (1983) reported a footlayer:tectum ratio of 1.3 for *Fagopsis*.

Subfamily

Castaneoideae (paraphyletic)

Species

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

Description

Pollen, monad, shape 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), micro-rugulate-striate, indistinctly perforate-fossulate (SEM), rugulae 0.1-0.2 µm wide, micro-rugulae well developed, micro-rugulae show parallel running micro-striate suprasculpturing in polar areas (SEM); abundance: rare.

Species

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

Description

Pollen, monad, shape 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), micro-rugulatestriate, indistinctly perforate-fossulate (SEM), rugulae 0.1-0.2 μm wide, micro-rugulae well developed in equatorial area, most distinct in apertural region, in polar areas micro-rugulae are coarser and their boundaries masked by sporopollenin resulting in a weak relief (SEM); abundance: rare.

Remarks

Pollen of genera of the Castanoideae are markedly uniform and difficult if not impossible to distinguish in LM (Praglowski, 1984). Also in SEM pollen morphological variability overlaps to a large degree between different genera. *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, USA (Crepet and Daghlian, 1980). Pollen produced from these inflorescences and described as *Castaneoidea puryearensis* Crepet et Daghlian, 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* are known from Florissant but their generic identity is in need of review (Manchester, 2001). Although the asymmetric leaf base, dentition, 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 southeastern USA (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 Engelhardoideae *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. 4 E-H)

Description

Pollen, monad, shape prolate, elliptic in equatorial view, polar axis 11-13 μm (LM), 8-11 μm (SEM), equatorial diameter 8-10 μm (LM), 5-7 μm; eutectate, exine 1.0 μm thick (LM), tricolporate; sculpturing scabrate (LM), micro-rugulate/rugulate, approaching striate (SEM), rugulae 0.1-0.2 µm wide (SEM), groups of several parallel micro-rugulae 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 micro-rugulae and the patchwork-like appearance of the pollen sculpture (Praglowski, 1984).

Possible fossil acorn cups of *Lithocarpus* are known from the Eocene Green River Formation, Colorado, USA (MacGinitie, 1969). Manchester (1994) described cupules and nuts of *Castanopsis crepetii* from the lower Lutetian Nut Beds locality of the Clarno Formation, Oregon. 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.

Genus

Quercus Linné

Species

Quercus Group Cyclobalanopsis sp. (Fig. 4, I-L)

Description

Pollen, monad, circular in polar view, pollen diameter 24-26 µm wide (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: 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 to 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 towards 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. 4, M-P)

Description

Pollen, monad, shape 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 micro-echinate, the micro-echinae 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 to 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. 5, A-L)

Description

Pollen, monad, shape 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, micro-echinate suprasculpture (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-d, 7b-d, 13b-d, and 19b-c). 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 var. *geminata* (Small) Sargent (Solomon, 1983a; figs. 24b-c, 25a-b, and 26a-b). 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. 1 and sp. 2 (Makino et al., 2009).

Species

Quercus Group Quercus sp. (Fig. 5. M-P)

Description

Pollen, monad, shape 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 and SEM); sculpturing scabrate (LM), micro-verrucate, weakly perforate (SEM), micro-verrucae 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 micro-verrucae, 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 to 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 lyratiformis* shows similarities with modern deciduous white oaks with deeply lobed leaves, whereas *Q. peritula* resembles most closely 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 are cannot unambiguously be assigned 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 in 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 to 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 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 ultra-structure represents the basic type within Fagaceae (Denk and Tekleva, in press). However, the complex vermiform sculpture formed by individual micro-rugulae 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 micro-rugulate pollen sculpturing (Praglowski, 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 (Praglowski, 1984; Govaerts and Frodin, 1998). Based on 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 Daghlian, 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 would appear 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 *Archaefagacea*, which are among the earliest records of Fagaceae (Takahashi et al., 2008). This demonstrates how morphologically conserved pollen of Castaneoideae is. As outlined in the previous section, pollen of *Fagopsis* also displays 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. scudderi* 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* A.Braun, which was later transferred to the genus *Pungiphyllum* with unknown botanical affinities (Kvaček and Walther, 1981). The pollen types of *Quercus* partly complement the macro fossil record. Quercus Group 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 four major forest/vegetation types: (1) Sclerophyllous forest (Mediterranean chaparral of the Californian/Mexican type) with extensions to tropical and subtropical dry woodlands, (2) nemoral coniferous forest, (3) laurel forest, and (4) broad-leaved deciduous forest according to Schroeder (1998; see table 23 in Velitzelos et al., 2014; Appendix S1). In addition, the fossil plant assemblage includes riparian/aquatic elements and lianas (Table 2, Appendix S1). Of 155 taxa/pollen types recovered from the Florissant Beds, 52 are at present found in summer dry Mediterranean sclerophyllous forests and woodlands extending to BS and Cw climates with summer rain; of these, 16 are not common in any other of the four vegetation types (e.g. *Athyana*, *Cercocarpus*, *Schmaltzia* [=*Rhus* sect. *Lobadium*], *Vauquelinia*). Typically, the sclerophyllous oaks of Group Protobalanus, Quercus and Lobatae fall within this vegetation type; they are well represented by foliage and pollen.

Mediterranean 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, therefore, are not confined to sclerophyllous forests but are also thriving in nemoral coniferous forests, often in the second tree layer (e.g. some Castaneoideae [*Notholithocarpus*], *Quercus* Group Protobalanus, Quercus/Lobatae). Fifty-five taxa belong to genera that occur in nemoral coniferous forests, of which six are restricted to this forests type (Appendix S1). Naturally, most of the conifer taxa recorded for Florissant are characteristic elements of nemoral coniferous forests at present (*Tsuga*, *Chamaecyparis*, *Sequoia*, *Torreya*). Of these, *Chamaecyparis*, *Sequoia*, and *Torreya* probably had a wide ecological amplitude. Today, they are typical element 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) Parlatore has a similar range but is at present absent at higher elevations (0 to 1500 m; Flora of North America Editorial Committee, 1993).

The succession from Mediterranean vegetation to nemoral conifer forest encountered in the fossil plant assemblage of Florissant matches perfectly the modern situation in the Mediterranean climate of California. Major constituents of these vegetation types are well represented in modern-day California and the Eocene Florissant flora, despite the considerable geographic distance between the Coastal Ranges and the Front Range.

In addition, a relatively high number of taxa recorded from Florissant are elements of fully humid laurel forests (24 taxa, of which four are confined to laurel forests; Appendix S1). Today, comparable vegetation is found in the northern parts of the Coastal Ranges. Eocene taxa typical of this vegetation type introduce an exotic element to the fossil flora of Florissant, represented by the East Asian Rhoipteleaceae, *Cyclocarya*, *Tetracentron*, *Eucommia*, *Cercidiphyllaceae*), 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* (see above). Elements of laurel forests are commonly also found in broad-leaved deciduous forests (Appendix S1).

A relatively large number of riparian and aquatic elements were associated with the Florissant lake and rivers and torrents flowing into the lake. Most prominent riparian element 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, 1984; Manchester, 2001). Other riparian elements are *Ginkgo*, *Ailanthus*, *Alnus*, *Fraxinus*, *Populus*, and others.

From the present, revised taxon list of Florissant (Bouchal, 2013; Table 2, Appendix S1) it appears that several of the taxa typical of and confined to laurel forest, nemoral conifer forest and broadleaved deciduous forests did not grow in close vicinity of the paleo-lake because they are represented by pollen only. In contrast, taxa resembling modern Mediterranean species are commonly represented by foliage and fruits (*Athyana*, *Cercocarpus*, *Quercus* spp.) and may have grown on slopes facing the lake, while laurel forest and broad-leaved deciduous forest may have grown higher up or in micro-climatically 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*. This mosaic of 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 western slopes of the central Cascades, Oregon, support vegetation comprising *Tsuga*, *Taxus*, *Acer*, *Mahonia nervosa* which can serve as a modern analogue to the plant assemblage from Florissant. These forests grow under a mild Mediterranean climate with cyclonic winter rains plus considerable amounts of humidity from fog precipitation (Dawson, 1998).

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. According to Meyer (2003) the succession from the valley floor to the slopes of the surrounding volcano involved riparian vegetation and groves of *Sequoia* and *Chamaecyparis* and deciduous trees, followed by dry vegetation and upland coniferous forests.

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; Hernández et al., 1951). 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* and *Liquidambar* among others occur in a warm temperate, winter-dry to fully humid climate. *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 present study. *Liquidambar* has never been reported from Florissant. This suggests that the coastal range of northeastern Mexico may not be a suitable analogue to the situation in Florissant.

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).

In contrast, Lielke et al. (2012) suggested a pronounced summer drying trend (Mediterranean climate) for the Eocene-Oligocene floras of southwestern Montana and Florissant. Correctly 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, origin of the modern Mediterranean flora of western North America

The paleovegetation of Florissant is in conflict with traditional views that ancestors of the modern western North American sclerophyllous flora evolved in summer wet climates (Axelrod, 1973; Leopold and Clay-Poole, 2001). Based on the modern distribution of regional climates when moving from the southeastern to the southwestern USA (Appendix S2) and assuming topographic barriers similar to today during the late Eocene, it is likely that the climate in the Florissant valley was a boundary climate between Cs and BS (see Appendix S2, climate station Pocatello and Salt Lake City). From the tectonic history (Bryant et al., 1981; Mix et al., 2011; Frisch et al., 2011) it can be assumed that climatic conditions in the Front Range at the Eocene-Oligocene boundary were as complex as today. Today, summer rain decreases from Atlantic North America to the west. Therefore, the fully humid climates of the east (Cfa climate according to Köppen; Kottek et al., 2006) are replaced by dry climates with summer rain in the Great Plains (BS climates). Western North America receives cyclonic rains during the winter months and is characterized by a summer dry Mediterranean climate (Cs climates). To the north and at higher elevations, snow climates occur (Df climates). Because of complex north south running mountain ranges, the Rocky Mountains show a great variety of local climates (Lieth et al., 1999; Appendix S2). These include both summer rain and winter rain climates and it is well possible that, locally, Mediterranean climates were established during the Eocene-Oligocene boundary also in the eastern Rocky Mountains (Montana, Front Range). 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) where fully humid (Cf), summer dry (Cs), and winter dry (Cw) climates co-occur as complex mosaic. Here, sclerophyllous oaks and *Q. glauca* (*Quercus* Group Cyclobalanopsis) co-occur (600 to 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 Takahashi, 1994; Tanai, 1995; Denk et al., 2012). Sclerophyllous oaks resembling the modern 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 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, 2009, 2010).

A 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*, along with taxa belonging to genera that are today confined to seasonally dry climates of Pacific North America (summer dry Cs climates and winter dry BS climates) suggest that these lineages might have originated as early as during Eocene times in a climatic setting similar to the modern one in the southwestern U.S. For example, members of *Quercus* Group Protobalanus are at present confined to southwestern USA and NW Mexico (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, 2009, 2010). *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 southwestern USA 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 southwestern USA, 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. 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. This is an example of convergent evolution. 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 entirely 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 markedly seasonal climates; Lielke et al., 2012). 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. The major climate types (Cs, Bs, Df) and vegetation types were essentially the same in the Paleogene as today. Old lineages (*Quercus* Group Protobalanus) occur from 200 to 2800 m in different altitudinal vegetation belts. The same is true for *Notholithocarpus*.

Conclusions

The Florissant paleoflora represents the earliest record of proto-Mediterranean vegetation, a vegetation adapted to seasonal drought, in North America. Thus, it challenges the traditional view by Axelrod (1973, 1975) that “sclerophyllous plants that now typify the area [i.e. California, Pacific Coast Range] are survivors of a richer flora that persisted here as summer rainfall gradually disappeared in the late Cenozoic.” In contrast, this area must have been colonized by drought-tolerant vegetation, already in place in intermontane basins and valleys of western North America, after tropical, lowland vegetation retreated. The modern-day Pacific coast region functions as a refuge for a numbers of ancestral lineages such as *Quercus* Group Protobalanus, *Notholithocarpus, Torreya*, and *Calocedrus*, which are typical elements of the Chaparral–nemoral conifer forest successions. This demonstrates the fundamental difference between “Mediterranean” vegetation in western North America and western Eurasia. In western Eurasia, the ecological shift from fully humid to summer-dry environments is well documented in a number of plant lineages including *Quercus* (Mai, 1995; Denk et al., 2014; Velitzelos et al., 2014).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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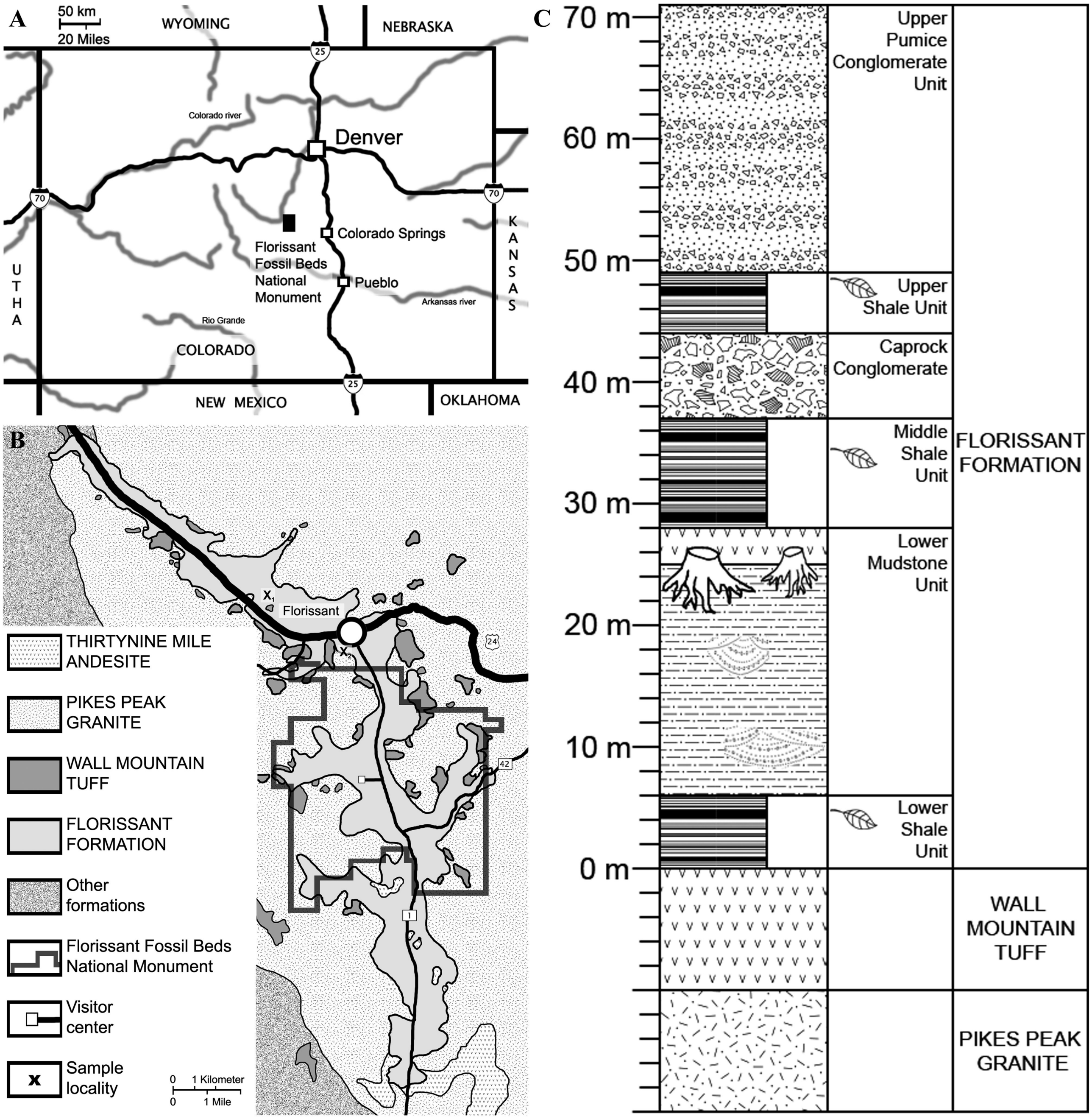

Figure 1.

A-C. Geography, geologic setting, and stratigraphy of the Florissant Formation A. Map showing the geographical position of the Florissant Fos sil Beds National Monument in Colorado, USA. B. Geological map indicating Florissant Formation and surrounding formations. X_1 = sample UF15880–7285 locality, X_2 = sample S151454 locality. Map based upon 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).

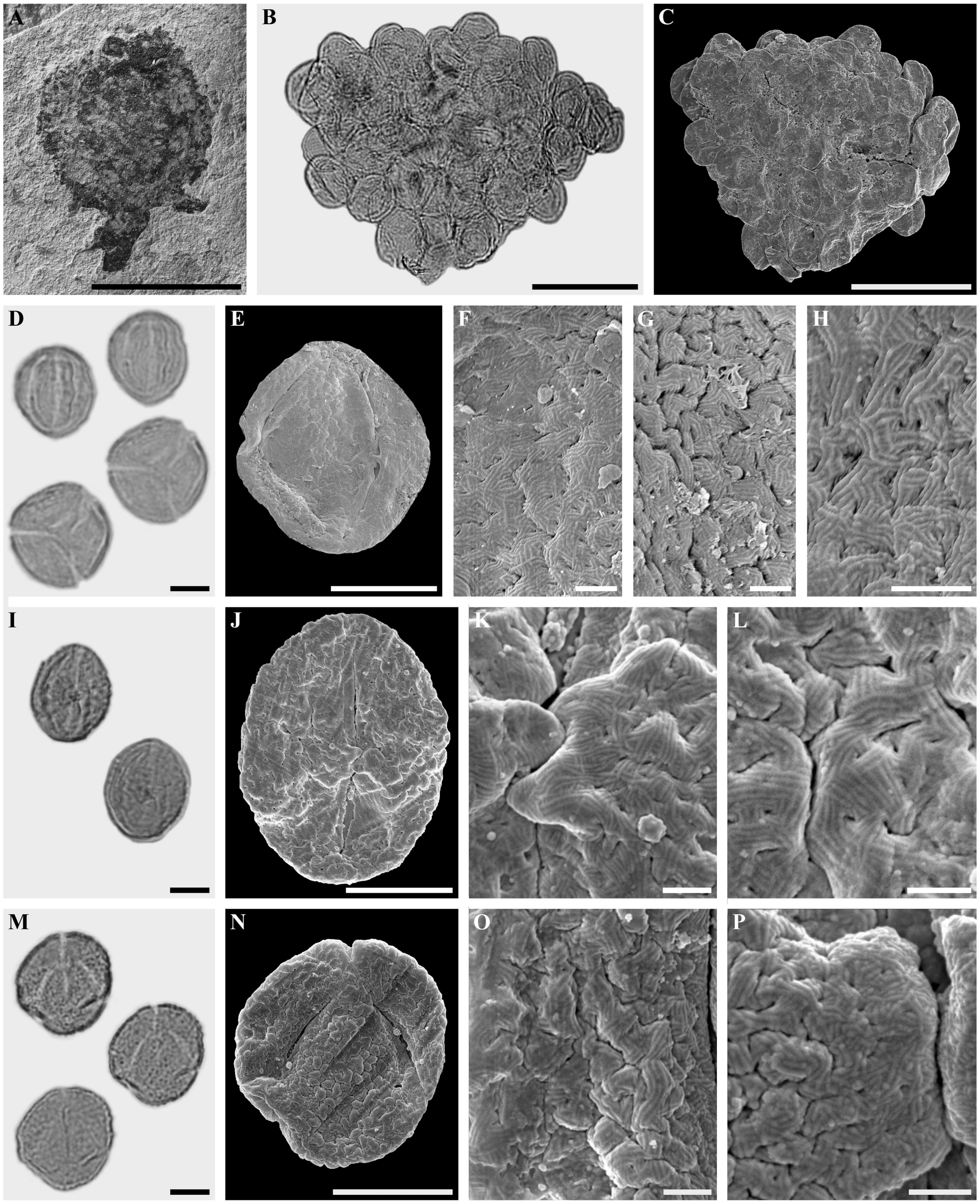

Figure 2.

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 pictures from the same pollen grain. M. LM, overview. N. SEM, overview. O-P. SEM, details.

Scale bars = 1 cm in Fig. A. 50 µm in Figs. B, C. 10 µm in Figs D, E, I, J, M and N. 1 µm in Figs. F-H, K, L, O and P

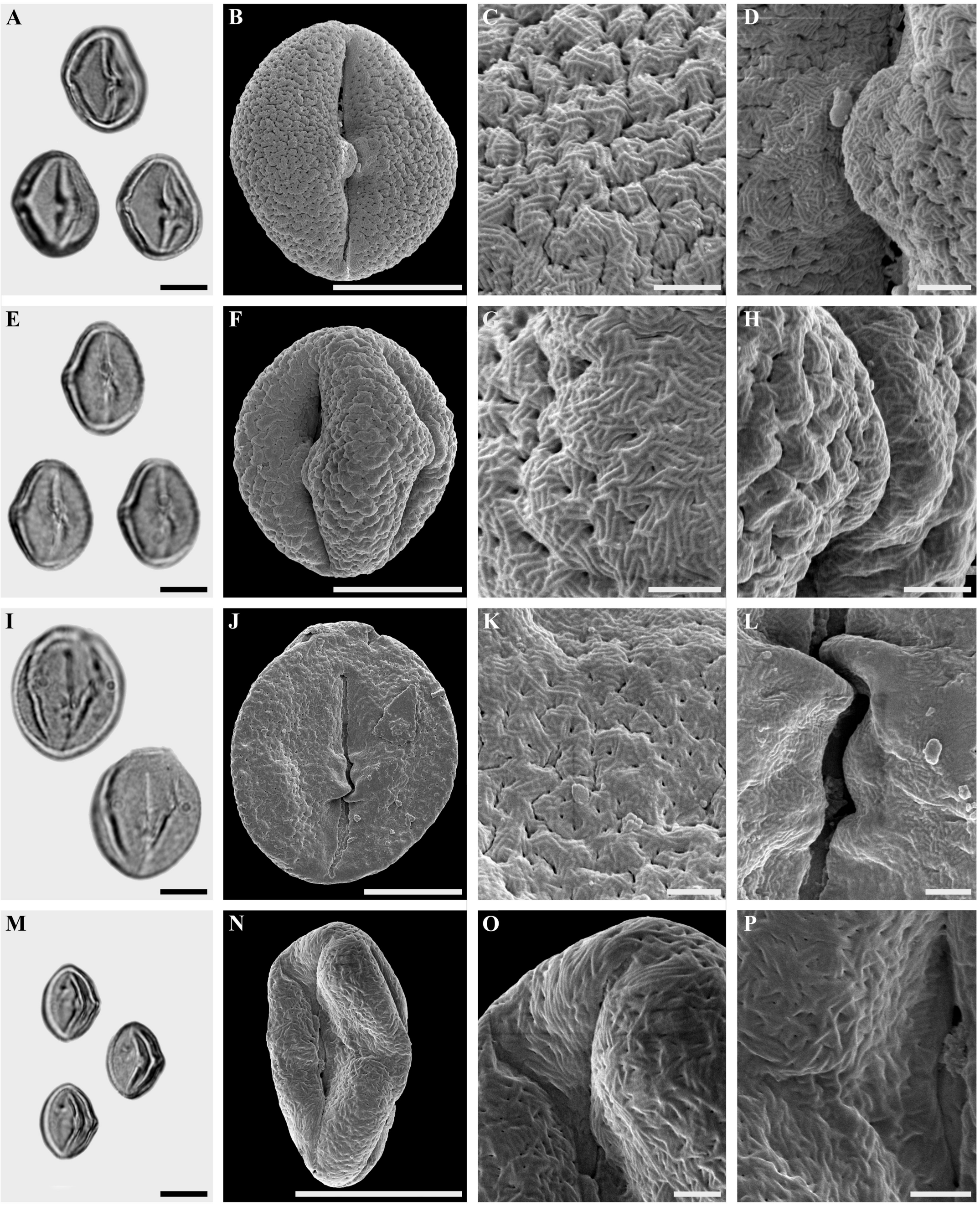

Figure 3.

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 μm in Figs A, B, E, F, I, J, M and N. 1 μm in Figs. C, D, G, H, K, L, O and P

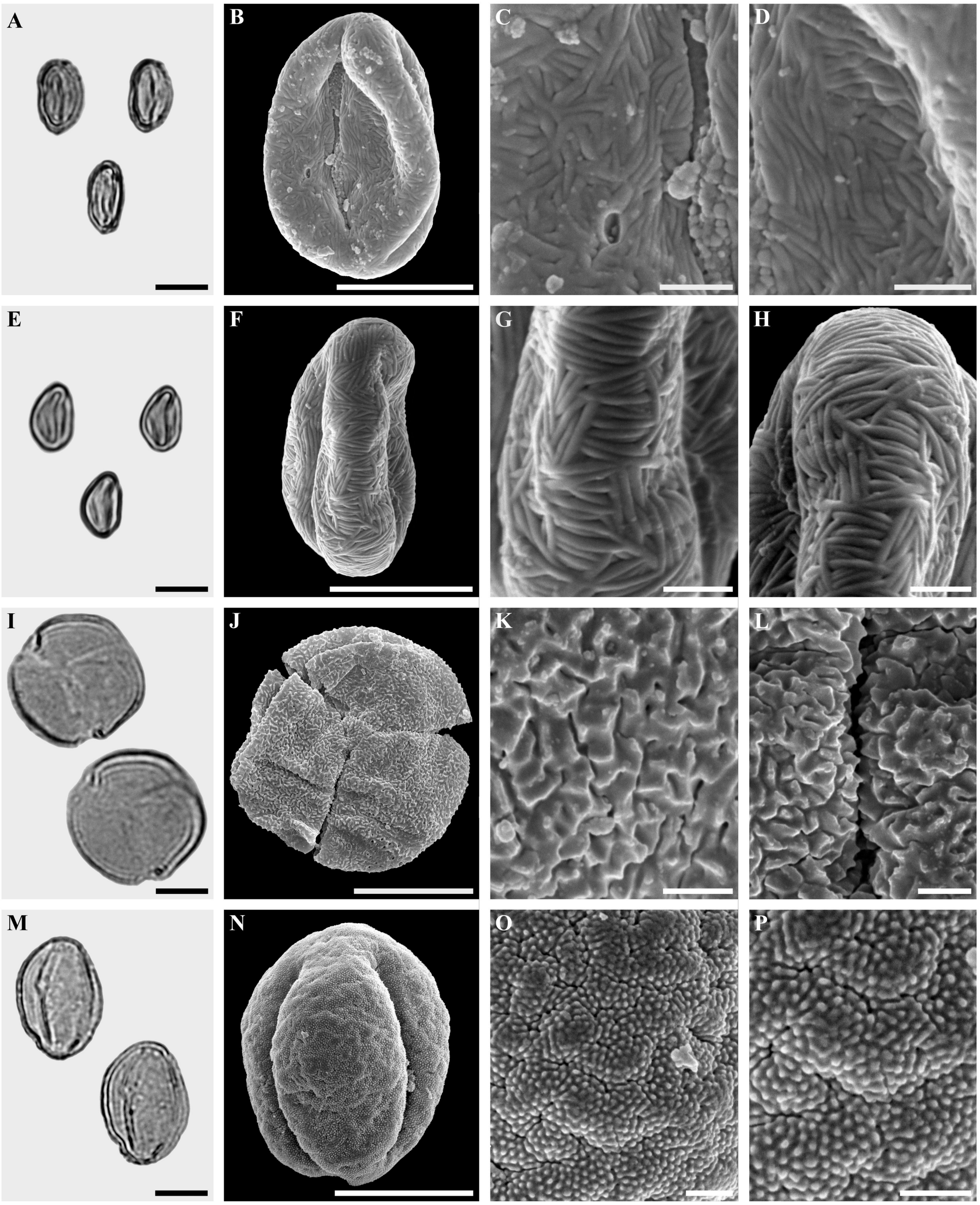

Figure 4.

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. J. SEM, overview. K-L. SEM, detail.

Scale bars = 10 µm in Figs A, E, I, J, M and N. 5 µm in Figs. B and F. 1 µm in Figs. C, D, G, H, K, L, O and P

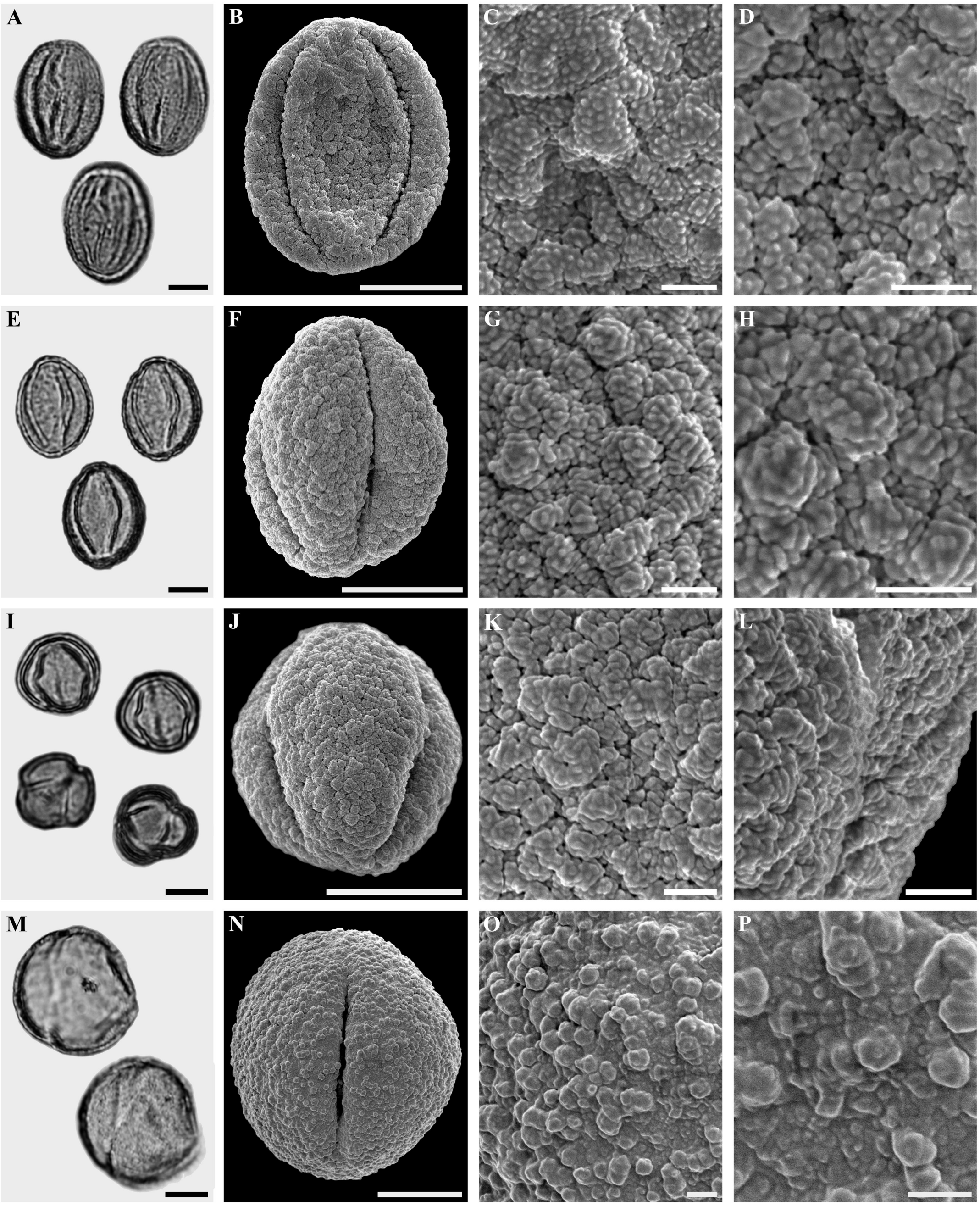

Figure 5.

A-H *Quercus* Group Quercus/Lobatae sp., and *Quercus* Group Quercus †I-P.

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 µm in Figs A, B, E, F, I, J, M and N. 1 µm in Figs. C, D, G, H, K, L, O and 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**
†***Fagopsis longifolia*** **Lesquereux** [aff. Castaneoideae]	†***Fagopsis longifolia*** **Lesquereux** [Betulaceae]	Placed into Fagaceae by Manchester and Crane (1983)
Castaneoideae gen. et spec. indet., sp. 1 [aff. *Castanopsis*]		
Castaneoideae gen. et spec. indet., sp. 2 [aff. *Castanea*]		
Castaneoideae gen. et spec. indet., sp. 3 [aff. *Lithocarpus*]		
	“Castanea” dolichophylla Cockerell [*Castanea seguinii* Dode *Castanea henryi* Rehder et Wilson]	Similarities with *Castanea*, extinct *Eotrigonobalanus* (Fagaceae), and extinct *Oreoroa* (Juglandaceae)
Quercus **Group Cyclobalanopsis** [*Q. acuta* Thunberg, *Q. glauca* Thunberg, *Q. hondae* Makino]		
Quercus **Group Protobalanus**		
Quercus **Group Quercus/Lobatae**		
Quercus **Group Quercus**		
	Quercus dumosoides **MacGinitie** (L) [*Q. dumosa* Nutall]	***Quercus*** **Group Quercus/Lobatae** [*Q. agrifolia* Née; *Q. invaginata* Trelease; *Q. john-tuckeri* Nixon et C.H. Muller]
	Quercus knowltoniana **Cockerell** (R)	**Genus *Quercus***
	Quercus lyratiformis **Cockerell** (L) [*Q. lyrata* Walter, *Q. alba* L.]	***Quercus*** **Group Quercus, deciduous**
	Quercus mohavensis **Axelrod** (L) [*Q. brandegei* Goldman, *Q. fusiformis* Small]	***Quercus*** **Group Quercus/Lobatae** [*Q. depressa* Bonpland; *Q. emoryi* Torrey; *Q. galeanensis* C.H.Muller; *Q. minima* Small; *Q. peninsularis* Trelease]
	Quercus peritula **Cockerell** [*Q. incarnata* Trelease, syn. of *Q. sideroxyla* Bonpland, *Q. wislizeni* A.DC.]	***Quercus*** **Group Lobatae** [*Q. coahuilensis* Nixon et C.H. Muller]
	Quercus predayana **MacGinitie** [*Q. wilcoxii* Rydberg syn. of *Q. chrysolepis* Liebmann, *Q. palmeri* Engelmann]	***Quercus*** **Group Protobalanus**
	Quercus scottii **(Lesquereux) MacGinitie**	Extinct fagaceous leaf type aff. *Eotrigonobalanus, Castaneophyllum lonchitiforme* Kvaček et Walther
	Quercus scudderi **Knowlton** [*Q. glauca* Thunberg, *Q. cornea* Loureiro syn. of *Lithocarpus corneus*, *Q. myrsinifolia* Blume]	*Quercus*-like Doubtful whether *Quercus* Group Cyclobalanopsis
	Quercus orbata **MacGinitie** [*Q. undulata* Torrey-hybrid]	Compared to extinct European “*Q.*” *cruciata* A.Braun No Fagaceae

(L), leaf; (R), reproductive structure

Table 2

Total plant diversity in the latest Eocene of Florissant including an updated palynological record (Bouchal, 2013; this study).

Class/Clade/Family	Genus	Macro Fossils	Pollen	Source	Remarks
Ginkgopsida					
Ginkgoaceae	*Ginkgo*		x	5	
Coniferopsida incl. Gnetales					
Cupressaceae	*Chamaecyparis*	C, L		3	
	Sequoia	C, B, W	x	1, 2, 3, 5	
Taxaceae	*Torreya*	L		3	
Pinaceae	*Abies*	S	x	1, 2, 3, 5	
	Cathaya		x	5	
	Picea	S	x	1, 2, 3, 5	
	Pinus sect. *Strobus*	C, S, L	x	1, 2, 3, 5	2 spp. (MF)
	Pinus sect. *Pinus*	C, S, L	x	1, 2, 3	3 spp. (MF)
	Tsuga		x	1, 2, 5	
Ephedraceae	*Ephedra*	B	x	1, 2, 3, 5	2 types (P)
Angiosperms					
Nymphaceae			x	1, 2	
Magnoliids					
Lauraceae		L		3	2 spp. (MF)
Monocots					
Potamogetonaceae	*Potamogeton*	L?, Fr		3	
Dioscoreaceae	*Dioscorea*	Fr		3	
Liliaceae			x	1, 2	
Smilacaceae	*Smilax*?	L		3	
Commelinids					
Arecaceae		L	x	1, 2, 3, 5	
Cyperaceae	*Cyperacites*	L	x	2, 3	
Poaceae			x	1, 2	
	Stipa	Fr	x	3, 5	
Typhaceae	*Sparganium*		x	1, 2, 5	
	Typha	L	x	1, 2, 3, 5	
Eudicots					
Buxaceae			x	2, 5	
Platanaceae	*Platanus*	L	x	1, 2?, 3, 5	
Menispermaceae			x	5	
Berberidaceae	*Mahonia*	L		1, 3	2-3 spp. (MF)
Ranunculaceae			x	2?, 5	
Trochodendraceae	*Tetracentron*		x	5	
Core Eudicots					
Amaranthaceae			x	1, 2, 5	3-4 types (P)

Class/Clade/Family	Genus	Macro Fossils	Pollen	Source	Remarks
Cercidiphyllaceae			x	2, 5	
Grossulariaceae	*Ribes*	L		3	6
Hamamelidaceae			x	2?, 3?, 5	
Polygonaceae			x	2	
Rosids					
Vitaceae			x	1, 5	2 types (P)
	Vitis	L	x	3	
Eurosids					
Fabaceae	indet.	Ll	x	1, 2, 3	4 spp. (MF)
	Caesalpinia	Ll	x	2, 3?	
	Cercis	L, Fr		3	
	?*Prosopis*	L		3	
	Robinia	L, W		3?, 4	
	Vicia	L		3	
Betulaceae	*Paracarpinus*/*Asterocarpinus* †	Fr, L	x	1, 3	
	Alnus		x	2	
	Betula		x	1, 5	
	Ostrya/Carpinus		x	1	
Fagaceae	Castaneoideae	L?	x	1, 2, 3, 5, 6	3 types (P)
	[a]*Fagopsis* †	L, Fl, Fr	x	3, 6	
	Quercus	L, Fr	x	1, 2, 3, 5, 6	8 spp. (MF) 4 types (P)
Juglandaceae	*Carya*	L, Ll, Fl, Fr	x	1, 2, 3, 5	
	Cyclocarya		x	1	
	Engelhardoideae			1, 2, 5	2 types. (P)
	Juglans	S?	x	1, 2, 3, 5	
Rhoipteleaceae			x	1, 2	
Salicaceae	*Populus*	L, Fr		3	
	Salix	L	x	1, 2, 3, 5	4 spp. (MF)
Euphorbiaceae		L	x	1, 2, 3, 5	
Elaeagnaceae			x	1, 2	
Cannabaceae	*Humulus*	L		3	
Moraceae	*Morus*	L		3	
Rosaceae			x	1, 2, 5	4 types (P)
	Amelanchier	L		3	
	Cerocarpus	L, Fr		3	
	Crataegus	L, Fr	x	2, 3, 5	3 spp.(MF)
	Holodiscus	L		3	
	Malus	L		3	
	Rosa	L, Ll		3	
	Rubus	L		3	
	Vauquelin[i]a	L		3	2 spp. (MF)

Class/Clade/Family	Genus	Macro Fossils	Pollen	Source	Remarks
Ulmaceae		W	x	1, 2, 4, 5	
	Celtis	L		1, 3	
	Cedrelospermum †	L, S	x	3, 5	
	Ulmus	L, F	x	1, 2, 3, 5	
	Zelkova-type		x	1	
Malvids					
Malvaceae	indet.		x	1, 2, 5	at least 6 types (P)
	Florissantia †	Fl, Fr	x	1, 2, 3, 5	
	Tilia?	L	x	2, 3	
Thymeleaceae	indet.		x	5	
	Daphne	L	x	2, 3, 5	
Onagraceae	indet.	Fl	x	1, 2, 3, 5	2 types (P)
Sapindaceae	*Acer*	L, Fr	x	1, 2, 3, 5	3 spp. (MF) 3 types (P)
	Athyana	L	x	3	
	Dipteronia	L, Fr		1, 3	
	Koelreuteria	L?, Fr, W		1, 3, 4	
Simaroubaceae	*Ailanthus*	Fr	x	2, 3	
	Chaneya tenuis †	Fr		3	
Meliaceae	*Cedrela* or *Toona*	S	x?	2, 3	
Anacardiaceae		L	x	5	
	Cotinus	L		3	
	Rhus	L		1, 3	3 spp. (MF)
	Schmaltzia [=*Rhus* sect. *Lobadium*]	L		3	
Rutaceae		S?	x	1, 3, 5	
Asterids					
Cornaceae	*Alangium*		x	5	
Hydrangeaceae		L, Fl		3	
Ebenaceae	*Diospyros*		x	5	
Ericaceae			x	1, 2, 5	
Euasterids I (Lamiids)					
Apocynaceae		S		1, 3	
	Tabernaemontana		x	1, 5	
Eucommiaceae	*Eucommia*	Fr	x	1, 2, 3, 5	
Oleaceae	*Osmanthus?*	L, Fr	x	1, 3	
	Fraxinus		x	2, 5	
Euasterids II (Campanulids)					
Asteraceae			x	1, 2, 5	
Adoxaceae	*Sambucus*	L, Ll	x	1, 2, 3	
	Viburnum		x	1, 5	
Caprifoliaceae	*Diplodipelta* †	Fr		3	

Class/Clade/Family	Genus	Macro Fossils	Pollen	Source	Remarks
	Lonicera		x	2, 5	
Araliaceae			x?	2	
	Oreopanax	L		3	

[a] The wood taxon *Chadronoxylon* possibly belongs to the plant that produced foliage and reproductive structures of *Fagopsis* (Meyer, 2003).

Macro fossils: L-leaf, Ll-leaflet, B-branch, C-cone, Fr-fruit, S-seed, W-wood, Fl-flower.

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.

† = extinct; Remarks: MF-macro fossils, P-pollen.