Int. J. Plant Sci. 180(3):220–231. 2019.
1058-5893/2019/18003-0005$15.00 DOI: 10.1086/701468

EOCENE FOSSIL LEGUME LEAVES REFERABLE TO THE EXTANT GENUS *ARCOA* (CAESALPINIOIDEAE, LEGUMINOSAE)

Patrick S. Herendeen[1],* and Fabiany Herrera*

*Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, Illinois 60022, USA

Editor: Michael T. Dunn

Premise of research. Fossil leaves from the early Eocene Green River Formation of Wyoming and late Eocene Florissant Formation of Colorado have been studied and described here as two species in the monospecific extant genus *Arcoa* (Leguminosae, subfamily Caesalpinioideae). The single living species of *Arcoa* is endemic to the Caribbean island of Hispaniola. The species from Florissant has been known since the late 1800s but has been incorrectly treated as several different legume genera.

Methodology. The compression fossils were studied using standard methods of specimen preparation and microscopy. Fossils were compared with extant taxa using herbarium collections at the Field Museum and Smithsonian Institution.

Pivotal results. The fossil bipinnate leaves exhibit an unusual morphological feature of the primary rachis, which terminates in a triad of pinnae, one terminal flanked by two lateral pinnae, all of which arise from the same point at the apex of the rachis. This feature, combined with other features that are diagnostic of the family Leguminosae or subgroups within it, allows the taxonomic affinities of the fossil leaves to be definitively determined as representing the extant genus *Arcoa*, which is restricted to the Caribbean island of Hispaniola today.

Conclusions. The fossil leaves described in this article demonstrate that the monospecific genus *Arcoa* was more diverse and had a much more widespread distribution in the past than it has today. Although the two fossil species are clearly referable to the same genus, differences between them in leaf size are consistent with differences in climate that are inferred for the more tropical Fossil Lake flora of the Early Eocene Green River Formation as compared with the warm temperate Late Eocene Florissant flora.

Keywords: Arcoa, Caesalpinioideae, Caribbean, fossil, Hispaniola, Leguminosae.

Introduction

The legume family (Leguminosae, Fabaceae) is the third-largest family of flowering plants (ca. 768 genera, 19,600 species) and is ecologically very important in almost all terrestrial habitats (Lewis et al. 2005; G. P. Lewis, personal communication). The family has an abundant fossil record, beginning in the late Paleocene and diversifying rapidly through the Eocene (Herendeen et al. 1992). By the late Eocene the fossil record of the family is diverse, with numerous caesalpinioid, mimosoid, and papilionoid taxa documented from many fossil localities around the world. The fossil record of the family was reviewed in the book *Advances in Legume Systematics*, Part 4 (Herendeen and Dilcher 1992), and subsequently expanded on by numerous additional contributions (e.g., Burnham 1995; Herendeen and Jacobs 2000; Calvillo-Canadell and Cevallos-Ferriz 2002, 2005; Wang et al. 2006, 2007, 2014; Bruneau et al. 2008; Wing et al. 2009; Collinson et al. 2012; Pan et al. 2010, 2012; Jia and Manchester 2014). While many fossil legume leaves, flowers, and fruits have been identified to genus, many more remain unidentified (Herendeen et al. 1992). In most cases, the unidentified dispersed fossil leaves or fruits lack distinctive or diagnostic features (Lewis et al 2005; LPWG 2017) that would allow them to be referred to one or more particular groups within the family; they are clearly legumes but not distinctive in any way that would aid identification. In other cases, the fossils may exhibit distinctive features (e.g., winged fruits, bipinnate leaves terminating in a triad of pinnae, etc.), but in such a diverse family with ca. 768 genera it can take considerable time to determine which clades within the family share these characters. The latter situation applies to the fossils described in this article.

In this article, we describe two species of bipinnate legume leaves from the Eocene of Colorado (early Eocene Green River Fossil Lake flora, late Eocene Florissant flora) and discuss their systematic relationships within the family. The species from Florissant was previously described, first as a species tentatively assigned to the extant genus *Caesalpinia* by Lesquereux (1874) and subsequently as a species in the fossil genus *Mimosites* Bowerbank (Lesquereux 1878) and later transferred by MacGinitie

---

[1] Author for correspondence; email: pherendeen@chicagobotanic.org.

ORCIDs: Herendeen, https://orcid.org/0000-0003-2657-8671; Herrera, https://orcid.org/0000-0002-2412-672X.

Manuscript received July 2018; revised manuscript received October 2019; electronically published February 5, 2019.

(1953) to the extant genus *Prosopis* L. (Mimosoideae). The fossil leaves from Green River and Florissant are unusual in that they are bipinnate and terminate with a triad of pinnae, a central terminal pinna, and a pair of lateral pinnae, all attached at the apex of the primary rachis. This is in contrast to most taxa with bipinnate leaves, in which the leaf terminates with a pair of pinnae. Although the leaves and leaflets have a stereotypical mimosoid appearance, and many extant mimosoid genera have bipinnate leaves, no extant mimosoid genus is characterized by the presence of bipinnate leaves that terminate with a triad of pinnae. Leaves with this architecture do occur in two distinct clades within the Caesalpinioideae. Although it is straightforward to make a list of all genera and species known to have bipinnate leaves, the distinctive feature that characterizes the fossils described here is not so easily investigated because it is not always mentioned in genus or species descriptions. Thus, specimens often need to be examined in herbarium collections to document this feature.

The fossil plants are from two Eocene age localities, the Fossil Lake flora from the Fossil Butte Member of the Green River Formation (lower Eocene of Wyoming) and the Florissant Formation (upper Eocene of Colorado). The fossils from the Green River Formation described here occur in limestone deposits from Fossil Lake in southwestern Wyoming. Fossil Lake was the smallest of three lakes that make up the Green River Formation. Fossil Lake is the source of a diverse biota of fossil animals and plants, which have been studied for many years. Grande (2013) provides a history of Fossil Lake and descriptions of the animals and plants that have been documented from the rich fossil deposits of this basin. The fossils from the Florissant Formation were collected in the later 1800s and early 1900s and described in several publications, including Lesquereux (1874, 1878, 1883), Knowlton (1898), and MacGinitie (1953). The Florissant fossil locality is now preserved at the Florissant Fossil Beds National Monument in Florissant, Colorado. Fossil plants, insects, and vertebrates are preserved in lacustrine sediments of a relatively small lake that formed during the early stages of uplift of the Rocky Mountains. Veatch and Meyer (2008) provides a history of paleontological research on the Florissant deposit. These fossil leaves are interesting because they demonstrate that *Arcoa* was more diverse and had a much more widespread distribution during the Eocene. *Arcoa* today includes a single living species endemic to Hispaniola. The genus belongs to the *Umtiza* clade, which includes seven genera, four of which are monospecific and narrowly distributed (Herendeen et al 2003). The *Umtiza* clade exhibits a number of unusual morphological features and biogeographic distribution patterns.

Material and Methods

Fossils from the Green River Formation have been collected from multiple quarries, and the specimens described here come from Fossil Butte Member Locality A (Lewis Ranch site no. 1) and Locality D (Lewis Ranch site no. 4) near Fossil Ridge, ca. 20 km west of Kemmerer, Wyoming (Grande 2013, app. A). The Green River specimens have been prepared using an air scribe to expose portions of the specimens that were covered with sediment. Specimens are deposited in the paleobotanical collections of the Field Museum of Natural History (PP) and Fossil Butte National Monument (FOBU). The fossils described here from Florissant, Colorado, are housed in the Paleobotanical Collections of the US National Museum of Natural History, Smithsonian Institution. The specimens have been cited in Lesquereux (1874, 1878) and Knowlton (1898) and described in some detail in MacGinitie (1953).

Fossil specimens were studied using light microscopy and photographed using a Canon Rebel camera with 100-mm macrolens attached to a Stackshot system, and digital images were merged using Helicon Focus software. Herbarium specimens from the Field Museum (F) and National Museum of Natural History, Smithsonian Institution (US), were used for comparison with the fossils.

Results

The two species treated here share a number of morphological features in common, including bipinnate leaf structure, opposite pinnae and leaflets, essentially sessile leaflets, and a fleshy transversely wrinkled pulvinus at the petiole base, at the bases of pinnae, and on the leaflet bases. The most distinctive and diagnostic feature exhibited by both of these species is that the leaf terminates with three pinnae, of which two are lateral and one is central or terminal. The number of pairs of pinnae and number of leaflets per pinna differ between the two species, as do leaflet size and overall size of the leaves. As a consequence, we recognize these fossils as two species belonging to the same genus.

Systematics

Family—Leguminosae

Subfamily—Caesalpinioideae

*Genus—*Arcoa *Urb.*

*Type—*Arcoa gonavensis *Urb.*

The genus *Arcoa*, with its single living species, is composed of small trees with two types of leaves, bipinnate leaves that terminate in a triad of pinnae, and once-pinnate leaves. Both leaf types are often found on the same branch. Flowers are unisexual (plants dioecious). Leaves and flowers are borne on short shoots. Fruits are fleshy, indehiscent, and more or less cylindrical.

Arcoa lindgreni *Herendeen et Herrera, sp. nov.*

Holotype. PP55447, Field Museum of Natural History (figs. 1*A*, 2*C*–2*E*).

Figures. 1, 2.

Description. Leaves bipinnate, with at least 8 pairs of opposite pinnae; leaf terminates in triad of pinnae, with a pair of pinnae plus a single terminal pinna. Petiole incomplete, base not preserved; leaf length 230 mm, maximum width 255 mm. Primary rachis 110 mm long (distance from first pair of pinnae to terminal triad of pinnae), ca. 2 mm wide, no evidence observed of foliar glands on the petiole or rachis; pinnae 35–131 mm long, 8–20 mm wide, pinna rachis ca. 1 mm wide, pulvinus pronounced, ca. 2 mm long; pinnae bear ca. 35–75 pairs of opposite leaflets; leaflets pinnate, linear, straight, sessile, base obtuse to truncate, slightly asymmetric, apex obtuse to rounded, symmet-

Fig. 1 *Arcoa lindgreni* Herendeen et Herrera, sp. nov. Holotype, PP55447. *A*, Bipinnate leaf with eight pairs of opposite pinnae, including a terminal pair of pinnae and a central third pinna. Each pinna bears numerous small sessile leaflets. Scale bar = 1 cm.

rical, margin entire; 6–12 mm long, ca. 1–1.5 mm wide near the center of the pinna, smaller near the pinna apex and base; venation poorly preserved, only primary vein near leaflet base is sometimes evident, centrally positioned.

Etymology. The new species is named in honor of Thomas Lindgren, who generously donated the holotype to the Field Museum.

Additional material. FOBU specimens figured in this article: FOBU13377 (fig. 2*A*), FOBU11603a (fig. 2*B*).

Comments. Three specimens of this species are known, two isolated pinnae and a single nearly complete leaf. One of the isolated pinnae appears to be immature (fig. 2*B*), based on its more delicate texture and smaller size. One isolated pinna with numerous leaflets (fig. 2*A*) was identified as *Parvileguminophyllum coloradensis* in Grande (2013, p. 324), and the bipinnate leaf was figured in Grande (2013, p. 325) but not identified to species.

Arcoa linearifolia *(Lesquereux) Herendeen et Herrera, comb. nov.*

Neotype. USNM 40563, National Museum of Natural History, Smithsonian Institution (figs. 3, 4*C*).

Figures. 3, 4.

Caesalpinia (?) *linearifolia* Lesquereux, Ann. Rept. U.S. Geol. and Geogr. Surv. Terr., Part II, pp. 390, 417. [1873] 1874, Neotype, designated here, USNM 40563, National Museum of Natural History, Smithsonian Institution.

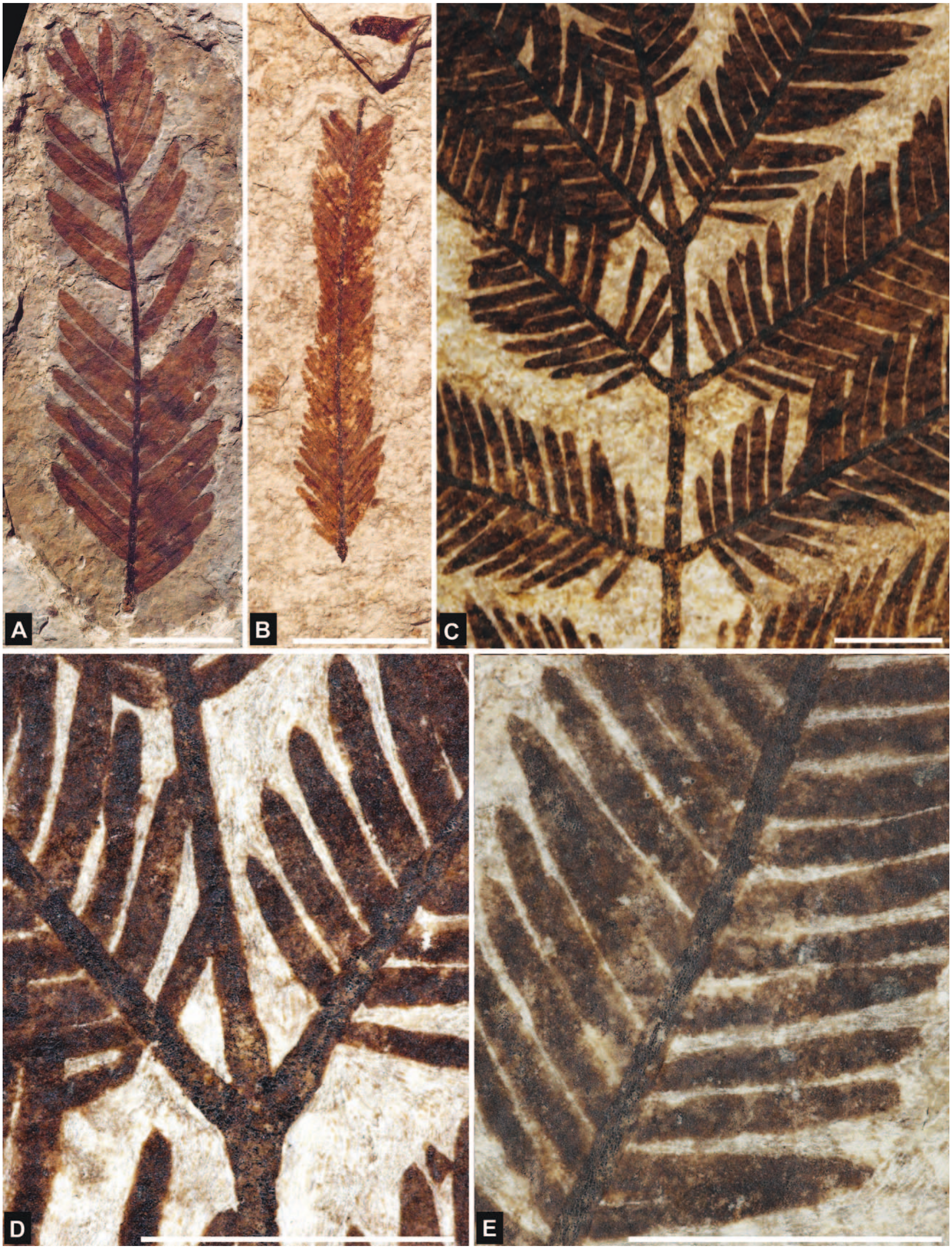

Fig. 2 *Arcoa lindgreni* Herendeen et Herrera, sp. nov. *A*, Disarticulated pinna, FOBU13377, bearing numerous small opposite leaflets. *B*, Disarticulated pinna, FOBU11603a, bearing numerous small opposite leaflets. Specimen is interpreted to be immature based on small size and delicate texture. *C*, Apex of holotype (PP55447) to show opposite pairs of pinnae and terminal triad of pinnae. *D*, Enlargement to show attachment of three pinnae at apex of rachis. *E*, Enlargement of pinna to show details of narrow, sessile, opposite leaflets. All scale bars = 1 cm.

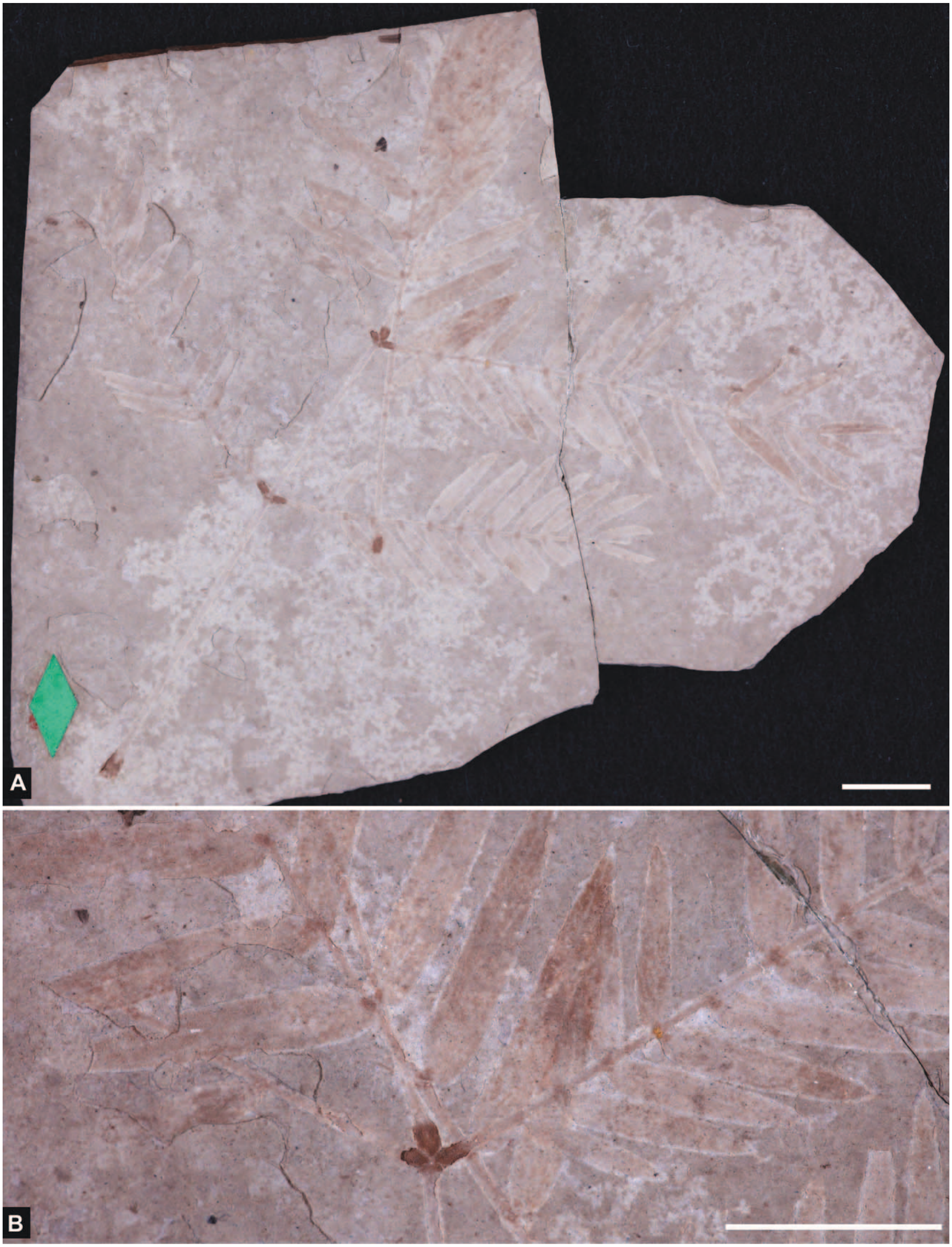

Fig. 3 *Arcoa linearifolia* (Lesquereux) Herendeen et Herrera, comb. nov. *A*, Neotype, USNM 40563. Complete bipinnate leaf showing opposite pairs of pinnae and terminal pinna pair with central third pinna. Note the darkly colored pulvinus at base of pinnae and base of petiole. *B*, Close-up of apex of leaf showing attachment of pair of pinnae plus a single terminal pinna. Note the additional detached pinna crossing obliquely. Scale bars = 10 mm.

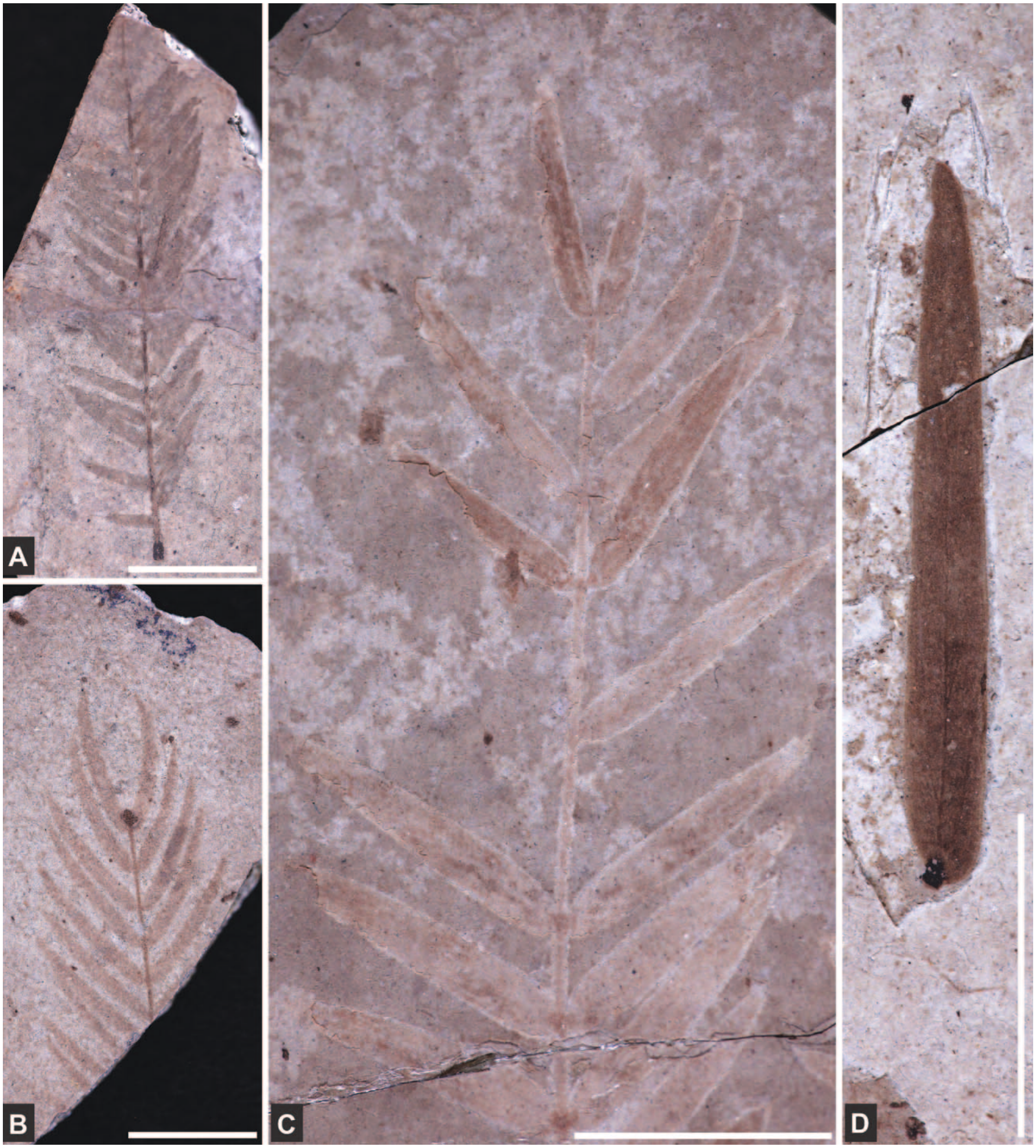

Fig. 4 *Arcoa linearifolia* (Lesquereux) Herendeen et Herrera, comb. nov. *A*, Isolated pinna with numerous opposite leaflets and well-developed pulvinus at base of rachis, USNM 332422. *B*, Incomplete isolated pinna with opposite, slightly falcate leaflets, USNM 332421. *C*, Apex of pinna from neotype showing details of opposite leaflets, USNM 40563. *D*, Single dispersed leaflet showing poorly preserved venation, USNM 332423. Scale bars = 10 mm.

Mimosites linearifolius (Lesquereux) Lesquereux. Rept. U.S. Geol. Survey Terr. Vol. 7, Part II, p. 300, pl. 59, fig. 7. 1878. [the figured specimen is missing].

Mimosites linearis (Lesquereux) Knowlton, nom. Illeg. Bull. U.S. Geol. Surv. No. 152, p. 144. 1898. [non *M. linearis* Engelh. 1894].

Prosopis linearifolia (Lesquereux) MacGinitie, nom. illeg. Carnegie Inst. Wash. Pub. 599: 126, plate 46, Figs. 1, 5. 1953; Plate 73, Fig. 7 (fruit) excluded.

Description, here emended. Leaves bipinnate, with 2 pairs of opposite pinnae; leaf terminates in triad of pinnae, with a third pair of pinnae plus a single terminal pinna. Petiole 36 mm long, ca. 1 mm wide, pulvinus well developed; leaf length 103 mm, maximum width 106 mm. Primary rachis 23 mm long, ca. 1 mm wide, no evidence observed of foliar glands on the petiole or rachis; pinnae 50–100 mm long, 30–40 mm wide, pinna rachis 0.5 mm wide, pulvinus pronounced, ca. 1.8 mm long; pinnae bear 13–26 pairs of opposite leaflets; leaflets pinnate, linear, straight, or falcate, sessile, base rounded, slightly asymmetric, apex acute, symmetrical, margin entire, 20–25 mm long, ca. 2 mm wide near the center of the pinna; venation poorly preserved, only primary vein is evident, centrally positioned, finer venation not observed.

Additional material. USNM specimens figured in this article: USNM 332421 (fig. 4*B*), 332422 (fig. 4*A*), 332423 (fig. 4*D*). Additional specimens originally deposited at Princeton University are now located at USNM and Yale Peabody Museum (YPM).

Nomenclatural considerations. Lesquereux (1874) used two spellings of the epithet (*linearis*, *linearifolia*) for a new species that he tentatively assigned to the extant genus *Caesalpinia*. It is clear from the context that only a single species was being described; therefore, they can be regarded as validly published alternative names (Turland et al 2018, Art. 36.3). Subsequently, Lesquereux (1878) used the epithet *linearifolius* in making the new combination *Mimosites linearifolius* (Lesquereux) Lesquereux, and he cited *C. linearis* in synonymy, thereby establishing priority for the epithet *linearifolia*. Knowlton (1898) erroneously selected the epithet *linearis* to make the new combination *Mimosites linearis* (Lesquereux) Knowlton, which is a later homonym of *Mimosites linearis* Engelh. (1894). MacGinitie (1953) attempted to publish the new combination *Prosopis linearifolia*, but the name was not validly published because he failed to cite a full and direct reference to the basionym (Lesquereux 1874, not 1878).

Neotype selection. No specimen is known to correspond to *Caesalpinia* (?) *linearifolia* Lesquereux (1874). No specimens were cited or figured in the original publication. The description of *Caesalpinia* (?) *linearifolia* corresponds closely to the description for *Mimosites linearifolius* (Lesquereux) Lesquereux (1878), which is accompanied by an illustration. Unfortunately, that specimen has not been located and remains unknown (H. Meyer, Florissant Fossil Beds National Monument, Colorado, personal correspondence). MacGinitie (1953) cited several specimens as syntypes and hypotypes, but this designation was in error because no specimens were cited or figured in the protolog (Lesquereux 1874). Furthermore, the single specimen illustrated in Lesquereux (1878) is missing, so it is not possible to make the case that this specimen likely represents Lesquereux's original material. Because no specimen from the protolog is available, a neotype must be designated. We have selected as neotype the most informative specimen known, which is USNM 40563, the bipinnate leaf that is figured in MacGinitie (1953, plate 46, fig. 5 and fig. 3 of this article).

Discussion

Systematic Relationships

Arcoa lindgreni and *Arcoa linearifolia* share a number of morphological features that support treating them as two species within the same genus. These include bipinnate leaf structure with a triad of pinnae at the apex; opposite pinnae; and opposite leaflets that are pinnate, small, linear, and sessile. The two species differ in overall size of the leaves (230 mm long and 255 mm wide in *A. lindgreni* vs. 103 mm long and 106 mm wide in *A. linearifolia*) and leaflets (6–12 mm long and ca. 1–1.5 mm wide vs. 20–25 mm long and ca. 2 mm wide), and number of leaflets per pinna (35–75 pairs vs. 13–26 pairs). Both species are characterized by pinnate leaflets with an entire margin, and the presence of a fleshy pulvinus at the base of the leaflets and at the base of each pinna and the base of the petiole. These features are characteristic of the family Leguminosae. The bipinnate leaf organization and terminal triad of three pinnae are most important for determining relationships within the family. This is a very unusual feature in leaves of the legume family.

Two specimens of bipinnate leaves of *A. linearifolia* have been figured in previous publications (Lesquereux 1883, plate 37, Fig. 10; MacGinitie 1953, plate 46, Fig. 5), but it is only the latter that shows the apex of the leaf, which is critical in evaluating relationships within the Leguminosae. The single bipinnate specimen of *A. lindgreni* exhibits this feature. No genus of subfamily Papilionoideae has bipinnate leaves (LPWG 2017). The caesalpinioid subfamilies Duparquetioideae, Cercidoideae, Detarioideae, and Dialioideae also lack bipinnate leaves (Lewis et al. 2005; LPWG 2017). All taxa with bipinnate leaves are included within subfamily Caesalpinioideae, which includes the mimosoid clade (formerly subfamily Mimosoideae; LPWG 2017). The mimosoid clade can be eliminated because although many mimosoid legumes have bipinnate leaves, no extant mimosoid genera have a bipinnate leaf that terminates with a triad of pinnae. Within the non-mimosoid Caesalpinioideae, two clades exhibit bipinnate leaves that terminate in a triad of pinnae, a subset of the *Umtiza* clade (*Tetrapterocarpon*, *Acrocarpus*, *Arcoa*; Herendeen et al. 2003; Lewis 2005; Manzanilla and Bruneau 2012) and a subset of the Caesalpinia group (*Haematoxylum*, *Hoffmannseggia*, *Stenodrepanum*, *Pomaria*, *Libidibia*, *Cenostigma*, *Erythrostemon*, *Arquita*; Lewis 2005; Gagnon et al. 2016).

The eight genera of the Caesalpinia group with this structure can be eliminated based on other vegetative morphological features, including the presence of petiolulate leaflets, differences in venation patterns, and the presence of a diverse range of multicellular glands on the abaxial surface or margins of the leaflets. In addition, in some taxa the pinnae are alternate to subopposite (see appendix for details).

The leaves of the three genera of the *Umtiza* clade (*Tetrapterocarpon*, *Acrocarpus*, *Arcoa*) are quite different in gross morphology. Leaves of *Acrocarpus* (single species in south and southeast Asia) are large with ovate, petiolulate leaflets. Leaves of *Tetrapterocarpon* (single species endemic to Madagascar) are relatively large with petiolulate oblong leaflets that are variably opposite to alternate on the pinnae. Leaves of *Arcoa* (endemic to Hispaniola) are very similar to the two fossil species described here (fig. 5). The bipinnate leaves are of approximately similar size to the fossils, and they bear opposite pinnae and leaflets. The leaflets are sessile, with similar narrow linear shape. The secondary venation is obscure and not easily seen on either surface of the leaflet, which is consistent with the obscure secondary venation in the fossils.

Although only leaves are known for these two fossil species, all morphological features preserved in the fossil leaves are consistent with only one extant legume taxon, the monospecific

Fig. 5 Leaves of *Arcoa gonavensis* Arb. *A*, Single pinna; *B*, bipinnate leaf; *C*, bipinnate leaf; *D*, enlargement of primary rachis showing three pairs of opposite pinnae and apical triad of pinnae; *E*, enlargement of primary rachis showing three pairs of opposite pinnae and apical triad of pinnae. A, B, D. *W.J. Eyerdam 598* (F), C, E. *T. Zanoni 32164* (US). Scale bars = 10 mm.

genus *Arcoa*. Furthermore, there are no structural details, other than leaf size, that are contradictory with the single living species, *Arcoa gonavensis*. Unfortunately, associated fossil flowers and fruits are unknown for these fossil leaves, which is not surprising given the rarity of the fossil leaves. This situation raises a general philosophical problem that often arises in taxonomy (both paleobotanical and neobotanical): make the taxonomic decision based on the available information or be safe and establish a new taxon because of the missing information. In this case, based on the available evidence, which includes distinctive, diagnostic, and unique structural features of the leaves, we have decided that there is no justification to establish a new genus for these fossils based simply on the absence of information. Thus, we assign these species to the extant genus *Arcoa*. This decision can always be revisited in the future if additional information becomes available. If our taxonomic decision is correct, we predict that the flowers would be unisexual (plants dioecious) and the fruits would be fleshy, indehiscent, and cylindrical, somewhat like the fruits of *Tamarindus*. Furthermore, *Arcoa* is distinctive in that leaves and inflorescences are borne on short shoots that are very similar to those of *Ginkgo* (short shoots of *Arcoa* are distinguished from *Ginkgo* by the presence of stipule remnants associated with the leaf scars).

The *Umtiza* clade was studied by Herendeen et al (2003). In addition to *Tetrapterocarpon*, *Acrocarpus*, and *Arcoa*, the clade also includes *Gleditsia*, *Gymnocladus*, *Umtiza*, and *Ceratonia*, all of which lack the leaf apex structure with a triad of pinnae. Subsequent studies have been inconsistent in the resolution of this group as a clade or paraphyletic grade. For example, Manzanilla and Bruneau (2012) found that the group formed a grade at the base of a large clade that included the *Caesalpinia*, *Peltophorum*, *Cassia*, and mimosoid clades. Although there remains uncertainty about whether this group forms a clade or a grade, the genera *Arcoa*, *Tetrapterocarpon*, and *Acrocarpus* are potentially united by this morphological feature, although only leaves of *Arcoa* are found to be comparable to the fossils in all morphological features.

The biogeography of the *Umtiza* clade/grade is interesting, and the new fossils add to the disjunct distribution patterns that characterize the group. Four genera are monospecific with narrow distributions in different parts of the world: *Umtiza* is restricted to South Africa, *Tetrapterocarpon* is restricted to Madagascar, *Acrocarpus* is found in southeast Asia, and the single living species of *Arcoa* is restricted to Hispaniola. *Ceratonia* includes two species native to northeastern Africa and perhaps the eastern Mediterranean (*Ceratonia siliqua* native range is uncertain due to a long history of cultivation). *Gymnocladus* includes approximately five species disjunct between eastern North America and Asia. *Gleditsia* is the most diverse genus with ca. 12 species, with a disjunct distribution in North America, South America, Asia, and around the Caspian Sea (Herendeen et al. 2003).

Green River and Florissant Legume Floras

The early Eocene Fossil Lake flora of the Green River Formation and the late Eocene Florissant flora are quite different in composition and leaf physiognomy (e.g., Brown 1934, 1937, 1956; MacGinitie 1953, 1969; Grande 1984, 2013; Manchester 2001; Meyer 2003; Leopold et al. 2008). The Fossil Lake and Florissant floras provide a unique view of the flora of North America as the Rocky Mountains were rising. However, the early Eocene Fossil Lake Green River flora grew under subtropical conditions, whereas the late Eocene Florissant flora likely grew under a more temperate setting and at higher elevation (MacGinitie 1969; Wolfe 1994)

One of the families present in both floras is the Leguminosae (Fabaceae). Extant genera such as *Mezoneuron* (formerly *Caesalpinia* subg. *Mezoneuron*), *Cercis*, *Arcoa*, and *Cladrastis* are known from one or both of these floras (Herendeen and Dilcher 1991; Herendeen et al. 1992; Meyer 2003; Jia and Manchester 2014). In addition, several other legume leaf and fruit morphotypes that are not referable to any extant or fossil genus are also known from Green River and Florissant.

The Green River Formation is geographically more widespread than Florissant, with three depositional basins in Colorado, Utah, and Wyoming that range in age from late Paleocene to middle Eocene (Brown 1934; MacGinitie 1969; Grande 1984, 2013; Smith et al. 2008). Several fossil legumes are known from the various Green River localities, but only one has been studied in detail. Herendeen and Dilcher (1991) described fossil fruits as *Caesalpinia flumen-viridensis* Herendeen & Dilcher (now known as *Mezoneruon flumen-viridensis* (Herendeen & Dilcher) R. Clark & E. Gagnon since the segregate genus *Mezoneuron* has been resurrected as being distinct from *Caesalpinia* (Clark and Gagnon 2015; Gagnon et al. 2016). The fossil fruits are from the Lake Gosiute Little Mountain locality in southwestern Wyoming (Wilkins Peak Member of the Green River Formation; Herendeen and Dilcher 1991). The Green River fossil leaves described in this article are one of several legumes known from Fossil Lake, west of Lake Gosiute. Grande (2013) illustrated two specimens of this leaf taxon: a complete bipinnate leaf and one dispersed pinna bearing ~25 pairs of small leaflets.

Florissant is a well-known fossil assemblage from the late Eocene of Colorado (Lesquereux 1874, 1878; Cockerell 1908; Knowlton 1916; MacGinitie 1953; Leopold and Clay-Poole 2001; Leopold et al. 2008; Meyer and Smith 2008; Veatch and Meyer 2008). Florissant was previously regarded to be of early Oligocene age, but that has been revised to late Eocene based primarily on recalibration of the Eocene-Oligocene boundary rather than new knowledge about the Florissant deposit (Evanoff et al. 2001). Multiple legume taxa are known from the Florissant assemblage, several of which are of unknown affinity within the family. Two taxa have been studied in detail, *Cercis* (Jia and Manchester 2014) and the fossil leaf species described here. Lesquereux (1874) originally described the leaf with a tentative assignment to the extant genus *Caesalpinia* and subsequently transferred to the form genus *Mimosites* (Lesquereux 1878). MacGinitie (1953) attempted to transfer the species to the extant mimosoid genus *Prosopis* (see nomenclatural notes above). Although Lesquereux (1874) based the species on fossil leaves, MacGinitie (1953) also referred a fossil fruit to this species, but there is no evidence that the leaves and fruit were produced by the same plant species.

The bipinnate leaf from Green River (*A. lindgreni*) is nearly twice as large as the species from Florissant (*A. linearifolia*) and bears a greater number of pairs of opposite pinnae. This size difference may be reflective of the climatic differences between the early and late Eocene in this part of North America. The early Eocene Fossil Lake plant assemblage includes many tropical and subtropical plant taxa, and the leaf size is relatively large

(Grande 2013). In contrast, the late Eocene Florissant assemblage includes many more taxa of warm temperate climates, and the leaf size is considerably smaller. The single extant species of *Arcoa*, *Arcoa gonavensis*, occurs in seasonal dry forest vegetation in Hispaniola (Cano Ortiz et al. 2017). *Arcoa lindgreni* and *A. linearifolia* demonstrate that the genus *Arcoa* was more diverse and widely distributed geographically in the Eocene as compared with today. No *Arcoa* fossils have been reported from the Caribbean region and, considering that during most of the Eocene Hispaniola was predominantly underwater (based on the widespread occurrence of limestone deposits in that area; Bowin 1975; Mann et al. 1991), it is very likely that *Arcoa* arrived to the island sometime after the Eocene.

Acknowledgments

We thank two anonymous reviewers for constructive comments on the manuscript. We thank Herb Meyer and Sarah Allen (Florissant National Monument), Shusheng Hu (Peabody Museum, Yale University), and Jonathan Wingerath (National Museum of Natural History) for assistance in searching for early Florissant specimens. We thank Fred Barrie (Missouri Botanical Garden) for assistance with nomenclatural questions. We thank Lance Grande (Field Museum) for access to the Green River fossil specimens. Finally, we thank Thomas Lindgren for generously donating the magnificent bipinnate leaf specimen of *Arcoa lindgreni* to the Field Museum.

Appendix

Umtiza Clade Genera with Bipinnate Leaves Terminating with a Triad of Pinnae

Arcoa Urb.

Leaves clustered on ginkgolike short shoots, once-pinnate or bipinnate on same plant; bipinnate leaves terminating in a triad of pinnae; pinnae opposite, 2–6 pairs; leaflets opposite, small, sessile, linear, apex obtuse to acute, base truncate, slightly asymmetrical. Pinnae of bipinnate leaves bear leaflets very close to the basal pulvinus, whereas the rachis of once-pinnate leaves has a greater distance between the basal pulvinus and the first pair of leaflets. Venation is obscure with just the primary vein visible.

Acrocarpus Wight ex Arn.

Leaves large, bipinnate, ending in a triad of pinnae; pinnae opposite, typically 3–4 pairs including the terminal triad of pinnae; leaflets opposite, 5–7 pairs, elliptical, up to 10 cm long, apex acute, base rounded, petiolulate. Differs from the fossils in the much larger leaves and leaflets and pronounced petiolule.

Tetrapterocarpon Humbert.

Leaves bipinnate, ending in a triad of pinnae; pinnae opposite to subopposite, 2–5 pairs including the terminal triad of pinnae; leaflets alternate to subopposite, obovate to oblong, 15–30 mm long, 6–15 mm wide, apex truncate to shallowly notched, base rounded to cuneate, petiolulate. Differs from the fossils in the alternate to subopposite organization of pinnae and leaflets, leaflet shape, and pronounced petiolule.

Caesalpinia Group Genera with Bipinnate Leaves Terminating with a Triad of Pinnae (from Gagnon et al. 2016)

Haematoxylum L.

Leaves pinnate and/or bipinnate, sometimes on same plant, bipinnate leaves ending in a triad of pinnae; pinnae opposite, 1–3 pairs; leaflets opposite, obcordate to obovate, apex emarginate to obtuse, base cuneate to attenuate, short petiolulate. Differs from the fossils in leaflet morphology and venation, which is quite different, plus the presence of a short petiolule on the leaflets.

Hoffmannseggia Cav.

Leaves bipinnate, ending in a triad of pinnae (except *H. aphylla*); pinnae opposite, 1–13 pairs; leaflets small and numerous, 2–15 (–18) pairs per pinna, glabrous to pubescent, and glandular. Differs from the fossils in smaller, glandular, petiolulate leaflets.

Stenodrepanum Harms.

Leaves bipinnate, ending in a triad of pinnae; pinnae opposite, 1–3 pairs, 4–10 cm long; leaflets 5–9 pairs per pinna, obtuse, with a crenulate, glandular margin, and embedded glands on the lower surface. Differs from the fossils in the small petiolulate leaflets with marginal and embedded glands.

Pomaria Cav.

Leaves bipinnate, ending in a triad of pinnae; pinnae opposite, 1–8 (–11) pairs; leaflets small, in 2–16 (–27) pairs per pinna, always with multiple sessile glands on the lower surface. Differs from the fossils in having smaller leaves, petiolulate leaflets, and glandular abaxial epidermis.

Libidibia (DC.) Schltdl.

Leaves bipinnate, rarely pinnate (*L. monosperma*); bipinnate leaves ending in a triad of pinnae; pinnae opposite, 2–10 pairs; leaflets opposite, 3–31 pairs, ovate, elliptic to oblong, apex rounded, mucronate or acute, base often oblique, subcordate, rounded or obtuse, eglandular or with subsessile gland dots on the undersurface. Differs from the fossils in leaflet shape, presence of petiolule, and in some species presence of abaxial glands.

Cenostigma Tul.

Leaves pinnate or bipinnate; bipinnate leaves ending in a triad of pinnae; pinnae opposite to alternate; 1–11 pairs, 3–29 alternate to subopposite (occasionally opposite) leaflets; leaflets vary greatly in size, 0.5–15 × 0.1–7 cm, ovate-elliptic, lanceolate with an acute to acuminate apex, obovate, oblong-elliptic or suborbicular, apex rounded or emarginate, mucronate, base cuneate, cordate or truncate, the blade often inequilateral at the base; glabrous to densely pubescent, sometimes with stellate hairs or various types of sessile or stalked glands. Differs from the fossils in the alternate to subopposite, petiolulate glandular leaflets. In some species, the pinnae are alternate to subopposite.

Erythrostemon Klotzsch.

Leaves bipinnate, usually ending in a triad of pinnae; pinnae alternate, subopposite or opposite, 1–6 (–15) pairs; leaflets opposite, 2–13 (–20) pairs, size variable, blades eglandular or with conspicuous black sessile or sunken glands along the margin. Differs from the fossils in leaflet morphology and presence of petiolule. Some species also differ in the alternate to subopposite organization of pinnae and presence of glandular epidermis.

Arquita E. Gagnon, G. P. Lewis & C. E. Hughes.

Leaves bipinnate, usually ending in a triad of pinnae; pinnae opposite, 1–5 pairs of pinnae; leaflets in 4–12 opposite pairs, oblong-obovate, often with maroon/black glands in depressions on crenulated leaflet margins, and sometimes with occasional sessile black glands on the undersurface of leaflet blades. Differs from the fossils in the small, petiolulate, glandular leaflets.

Literature Cited

Bowin C 1975 The geology of Hispaniola. Pages 501–552 *in* The Gulf of Mexico and the Caribbean. Springer, Boston.

Brown RW 1934 The recognizable species of the Green River flora. US Geol Surv Prof Pap 185-C:45–77.

——— 1937 Additions to some fossil floras of the western United States. US Geol Surv Prof Pap 186-J:163–206.

——— 1956 New items in Cretaceous and Tertiary floras of the western United States. J Wash Acad Sci 46:104–108.

Bruneau A, M Mercure, GP Lewis, PS Herendeen 2008 Phylogenetic patterns and diversification in caesalpinioid legumes. Botany 86:697–718.

Burnham R 1995 A new species of winged fruit from the Miocene of Ecuador: *Tipuana ecuatoriana* (Leguminosae). Am J Bot 82:1599–1607.

Calvillo-Canadell L, SRS Cevallos-Ferriz 2002 *Bauhcis moranii* gen. et sp. nov. (Cercideae, Caesalpinieae), an Oligocene plant from Tepexi de Rodríguez, Puebla, Mexico, with leaf architecture similar to *Bauhinia* and *Cercis*. Rev Palaeobot Palynol 122:171–184.

——— 2005 Diverse assemblage of Eocene and Oligocene Leguminosae from Mexico. Int J Plant Sci 166:671–692.

Cano Ortiz, A, CM Musarella, E Cano Carmona 2017 Biogeographical areas of Hispaniola (Dominican Republic, Republic of Haiti). Pages 165–189 *in* Plant ecology: traditional approaches to recent trends. InTech. doi: http://dx.doi.org/10.5772/intechopen.69081.

Clark R, E Gagnon 2015 A revision of *Mezoneuron* (Leguminosae: Caesalpinioideae) in New Caledonia, with perspectives on vegetation, geology, and conservation. Phytotaxa 207:68–92. doi: http://dx.doi.org/10.11646/phytotaxa.207.1.3.

Cockerell TDA 1908 The fossil flora of Florissant, Colorado. Bull Am Mus Nat Hist 24:71–110.

Collinson ME, SR Manchester, V Wilde 2012 Fossil fruits and seeds of the Middle Eocene Messel biota, Germany. Abh Senckenb Natforsch Ges 570:1–249.

Evanoff E, WC McIntosh, PC Murphey 2001 Stratigraphic summary and 40Ar/39Ar geochronology of the Florissant Formation, Colorado. Proc Denver Mus Nat Sci 4:1–16.

Gagnon, E, A Bruneau, CE Hughes, L Paganucci de Queiroz, GP Lewis 2016 A new generic system for the pantropical *Caesalpinia* group (Leguminosae). PhytoKeys 71:1–160.

Grande L 1984 Paleontology of the Green River Formation, with a review of the fish fauna, 2nd ed. Geol Surv Wyoming 63:1–334.

——— 2013 The lost world of Fossil Lake: snapshots from deep time. University of Chicago Press, Chicago.

Herendeen PS, WL Crepet, DL Dilcher 1992 The fossil history of the Leguminosae: phylogenetic and biogeographic implications. Pages 303–316 *in* PS Herendeen, DL Dilcher, eds. Advances in legume systematics. Pt 4. The fossil record. Royal Botanic Gardens, Kew.

Herendeen PS, DL Dilcher 1991 *Caesalpinia* subgenus *Mezoneuron* (Leguminosae, Caesalpinioideae) from the Tertiary of North America. Am J Bot 78:1–12.

——— 1992 Advances in legume systematics. Pt 4. The fossil record. Royal Botanic Gardens, Kew.

Herendeen PS, BF Jacobs 2000 Fossil legumes from the Middle Eocene (46.0 Ma) Mahenge Flora of Singida, Tanzania. Am J Bot 87:1358–1366.

Herendeen PS, GP Lewis, A Bruneau 2003 Floral morphology in caesalpinioid legumes: testing the monophyly of the "*Umtiza* clade." Int J Plant Sci 164(suppl):S393–S407.

Jia H, SR Manchester 2014 Fossil leaves and fruits of *Cercis* L. (Leguminosae) from the Eocene of western North America. Int J Plant Sci 175:601–612.

Knowlton FH 1898 A catalogue of the Cretaceous and Tertiary plants of North America. Bull U S Geol Surv 152.

——— 1916 A review of the fossil plants in the United States National Museum from the Florissant lake beds at Florissant, Colorado, with descriptions of new species and list of type-specimens. Proc U S Natl Mus 51:241–297.

Leopold EB, ST Clay-Poole 2001 Florissant leaf and pollen floras of Colorado compared: climatic implications. Proc Denver Mus Nat Sci 4:17–69.

Leopold EB, SR Manchester, HW Meyer 2008 Phytogeography of the late Eocene Florissant flora reconsidered. Pages 53–70 *in* HW Meyer, DM Smith, eds. Paleontology of the Upper Eocene Florissant Formation, Colorado. Geol Soc Am Spec Pap 435. Geological Society of America, Boulder, CO.

Lesquereux L 1874 The Lignitic formation and its fossil flora. Pages 365–425 *in* Seventh Annual Report of the United States Geological and Geographical Survey of the Territories for the year 1873. Government Printing Office, Washington, DC.

——— 1878 Contributions to the fossil flora of the Western Territories. Pt 2. The Tertiary flora. Report of the United States Geological and Geographical Survey of the Territories. Government Printing Office, Washington, DC.

——— 1883 Contributions to the fossil flora of the Western Territories. Pt 3. The Cretaceous and Tertiary floras. Report of the United States Geological and Geographical Survey of the Territories. Government Printing Office, Washington, DC.

Lewis GP 2005. Tribe Caesalpinieae. Pages 127–161 *in* GP Lewis, BD Schrire, B Mackinder, M Lock, eds. Legumes of the world. Royal Botanic Gardens, Kew.

Lewis GP, BD Schrire, B Mackinder, M Lock 2005 Legumes of the world. Royal Botanic Gardens, Kew.

LPWG (Legume Phylogeny Working Group) 2017 A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. Taxon 66:44–77.

MacGinitie HD 1953 Fossil plants of the Florissant beds, Colorado. Carnegie Institution of Washington publication 599: contributions to paleontology, Carnegie Institution of Washington, Washington DC. 198 pp.

——— 1969 The Eocene Green River flora of northwestern Colorado and northeastern Utah. University of California publications in geological sciences. Vol 83. University of California Press, Berkeley, CA.

Manchester SR 2001 Update on the megafossil flora of Florissant, Colorado, USA. Proc Denver Mus Nat Sci Ser 4:137–161.

Mann P, G Draper, JF Lewis 1991 An overview of the geologic and tectonic development of Hispaniola. Geologic and tectonic development of the North America-Caribbean plate boundary in Hispaniola. Geol Soc Am Spec Pap 262:1–28.

Manzanilla V, A Bruneau 2012 Phylogeny reconstruction in the Caesalpinieae grade (Leguminosae) based on duplicated copies of the sucrose synthase gene and plastid markers. Mol Phylogenet Evol 65:149–162. https://doi.org/10.1016/j.ympev.2012.05.035

Meyer HW 2003 The fossils of Florissant. Smithsonian, Washington, DC. 258 pp.

Meyer HW, DM Smith 2008 Paleontology of the Upper Eocene Florissant Formation, Colorado. Paleontology of the Upper Eocene Florissant Formation, Colorado. Geol Soc Am Spec Pap 435.

Pan, AD, ED Currano, BF Jacobs, M Feseha, N Tabor, PS Herendeen 2012 Fossil *Newtonia* (Fabaceae: Mimoseae) seeds from the early Miocene (22–21 Ma) Mush Valley in Ethiopia. Int J Plant Sci 173:290–296.

Pan AD, BF Jacobs, PS Herendeen 2010 Detarieae sensu lato (Leguminosae) from the Late Oligocene (28–27) Ma Guang River flora of northwestern Ethiopia. Bot J Linn Soc 163:44–54.

Smith ME, AR Carroll, BS Singer 2008 Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, western United States. Geol Soc Am Bull 120:54–84.

Turland NJ, JH Wiersema, FR Barrie, W Greuter, DL Hawksworth, PS Herendeen, S Knapp, et al 2018 International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code). Regnum Vegetabile, no. 159, Koeltz Botanical Books, Oberreifenberg, Germany.

Veatch SW, HW Meyer 2008 History of paleontology at the Florissant fossil beds, Colorado. Pages 1–18 *in* HW Meyer, DM Smith, eds. Paleontology of the Upper Eocene Florissant Formation, Colorado. Geol Soc Am Spec Pap 435.

Wang Q, DL Dilcher, TA Lott 2007 *Podocarpium* A. Braun ex Stizenberger 1851 from the middle Miocene of eastern China, and its palaeoecology and biogeography. Acta Palaeobot 47:237–251.

Wang Q, DL Dilcher, X-Y Zhu, Y-L Zhou, TA Lott 2006 Fruits and leaflets of *Wisteria* (Leguminosae, Papilionoideae) from the Miocene of Shandong Province, eastern China. Int J Plant Sci 167:1061–1074.

Wang Q, Z Song, Y Chen, S Shen, Z Li 2014 Leaves and fruits of *Bauhinia* (Leguminosae, Caesalpinioideae, Cercideae) from the Oligocene Ningming Formation of Guangxi, South China and their biogeographic implications. BMC Evol Biol 14:88.

Wing SL, F Herrera, CA Jaramillo, C Gómez–Navarro, P Wilf, CC Labandeira 2009 Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest. Proc Natl Acad Sci USA 106:18627–18632.

Wolfe JA 1994 Tertiary climatic changes at middle latitudes of western North America. Palaeogeogr Palaeoclimatol Palaeoecol 108:195–205.