

FRUITS OF *OREOMUNNEA* (JUGLANDACEAE) IN THE EARLY MIOCENE OF PANAMA

Fabiany Herrera, Steven R. Manchester, Rebecca Koll, and Carlos Jaramillo*

ABSTRACT

Permineralized fruits of Juglandaceae have been recovered from the Early Miocene Cucaracha Formation exposed in excavations of the Panama Canal. Transverse sections and peels reveal that the nuts are subdivided into eight chambers at the base, and the nutshell and septa are composed mainly of fibers. Together, these features are found only in the Neotropical juglandaceous clade composed of extant *Alfaroa* Standl. and *Oreomunnea* Oerst. Based on the small nut size and relatively thin wall and septa, these nuts are assigned to *Oreomunnea*, which is distinguished from extant *Alfaroa* by its winged fruits adapted for wind dispersal. A. Graham first reported pollen grains of the *Alfaroa/Oreomunnea* type from the Miocene of Panama. The new fossil fruits of the Cucaracha Formation are the earliest macrofossil record of *Oreomunnea*, enhancing our understanding of the phytogeographic history of Juglandaceae in Central America. If this newly described fossil species, *O. grahamii* Manch. & Herrera, grew in similar ecological settings to those of its modern counterparts, the fossils may be an indicator of the medium-high paleotopographic relief of Panama during the Early Miocene.

Key words: *Alfaroa*, fossils, fruits, Juglandaceae, Miocene, *Oreomunnea*.

The Juglandaceae have an excellent fossil record in the Northern Hemisphere, well represented by pollen, leaves, wood, catkins, and fruits. This record includes most of the extant genera, plus a few extinct ones in the Paleogene (Manchester, 1987, 1989; Elliot et al., 2006). Some extinct upper Cretaceous genera based on flowers containing Normapolles pollen from Europe may belong on the stem lineage of Juglandaceae (Friis, 1983; Friis et al., 2006). However, the modern

Neotropical genera *Alfaroa* Standl. and *Oreomunnea* Oerst. have mostly eluded detection in the macrofossil record.

Ten genera in two subfamilies are recognized for the Juglandaceae (Manos & Stone, 2001; Manos et al., 2007), although a broader circumscription of the family that includes *Rhoiptelea* Diels & Hand.-Mazz. (traditional Rhoipteleaceae) has gained some acceptance (APG, 2009). *Rhoiptelea* appears as sister to Engelhardioideae (*Alfaroa*,

*Author for correspondence: steven@fjmnh.ufl.edu

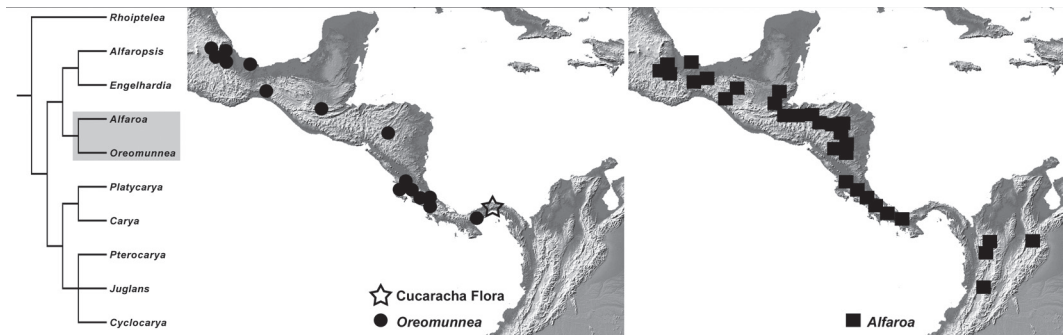


FIGURE 1. Left: phylogenetic relationships of genera in Juglandaceae (modified from Manos et al., 2007; Sauquet et al., 2012). Center: occurrence of extant *Oreomunnea* and location of Early Miocene Cucaracha flora. Right: occurrence of extant *Alfaroa* (data accessed through GBIF Data Portal, Global Biodiversity Information Facility, data.gbif.org, accessed 9 April 2013). Base maps courtesy of National Aeronautics and Space Administration Jet Propulsion Laboratory, California Institute of Technology.

Alfaropsis Iljinsk., *Engelhardia* Lesch. ex Blume, *Oreomunnea*) and Juglandoideae (*Carya* L., *Cyclocarya* Iljinsk., *Juglans* L., *Platycarya* Siebold & Zucc., *Pterocarya* Kunth) (Manos et al., 2007; Sauquet et al., 2012). There are about 60 species, distributed mainly in the Northern Hemisphere of both the Old and New World, although some genera reach the Southern Hemisphere and tropical latitudes (Stone, 1989, 1993). *Oreomunnea* and *Alfaroa* are usually components of mountain forests. *Oreomunnea* is distributed from Mexico to Panama (Fig. 1), with two living species. It was formerly considered to be congeneric with the Asian genus *Engelhardia* (including *Alfaropsis*), because of similar winged nuts with a prominent trilobed wing developed from a persistent inflorescence bract (Fig. 2). However, Stone (1972) built a strong case for retaining generic status for *Oreomunnea*, noting in particular that its two species share more in common morphologically with *Alfaroa* than with *Engelhardia*. Distributed from southern Mexico to northern Colombia (Fig. 1), *Alfaroa* has five extant species (Stone, 2010). It has wingless fruits (Fig. 2), but retains an inconspicuous 3-lobed inflorescence bract at the base of the developed fruit. Subsequent molecular work (Manos & Stone, 2001; Manos et al., 2007; Sauquet et al., 2012) indicates that *Oreomunnea* and *Alfaroa* form a clade that is sister to

the Asian clade composed of *Alfaropsis* (former *Engelhardia roxburghiana* Wall.) and *Engelhardia* (Fig. 1).

Although no macrofossils of *Oreomunnea* and *Alfaroa* had been identified yet in the Neotropics, Graham (1988b) noted the occurrence of triporate juglandaceous pollen, which he referred to as *Alfaroa/Engelhardia* from several sites in the Neogene of Panama, including the Early Miocene Cucaracha and La Boca formations (Graham, 1989), and the Eocene Gatuncillo Formation (Graham, 1985). He also reported *Alfaroa/Engelhardia* pollen grains from the Oligocene of Puerto Rico (Graham & Jarzen, 1969) and Haiti (Graham, 1990). With subsequent acceptance of extant *Oreomunnea* as a genus distinct from the Old World *Engelhardia*, Graham (1991) revised the identification of this pollen morphotype to *Alfaroa/Oreomunnea*, while noting that in the stratigraphic literature this pollen type is generally known as *Momipites*. Although some of the extant genera of Juglandaceae are readily distinguished from one another by features of pore number and distribution and patterns of exinous thickening and thinning, the four genera of subfamily Engelhardioideae are very similar in pollen morphology, each having triporate isopolar grains. With transmission electron microscopy, Stone and Broome (1975) found a way to distinguish the two New

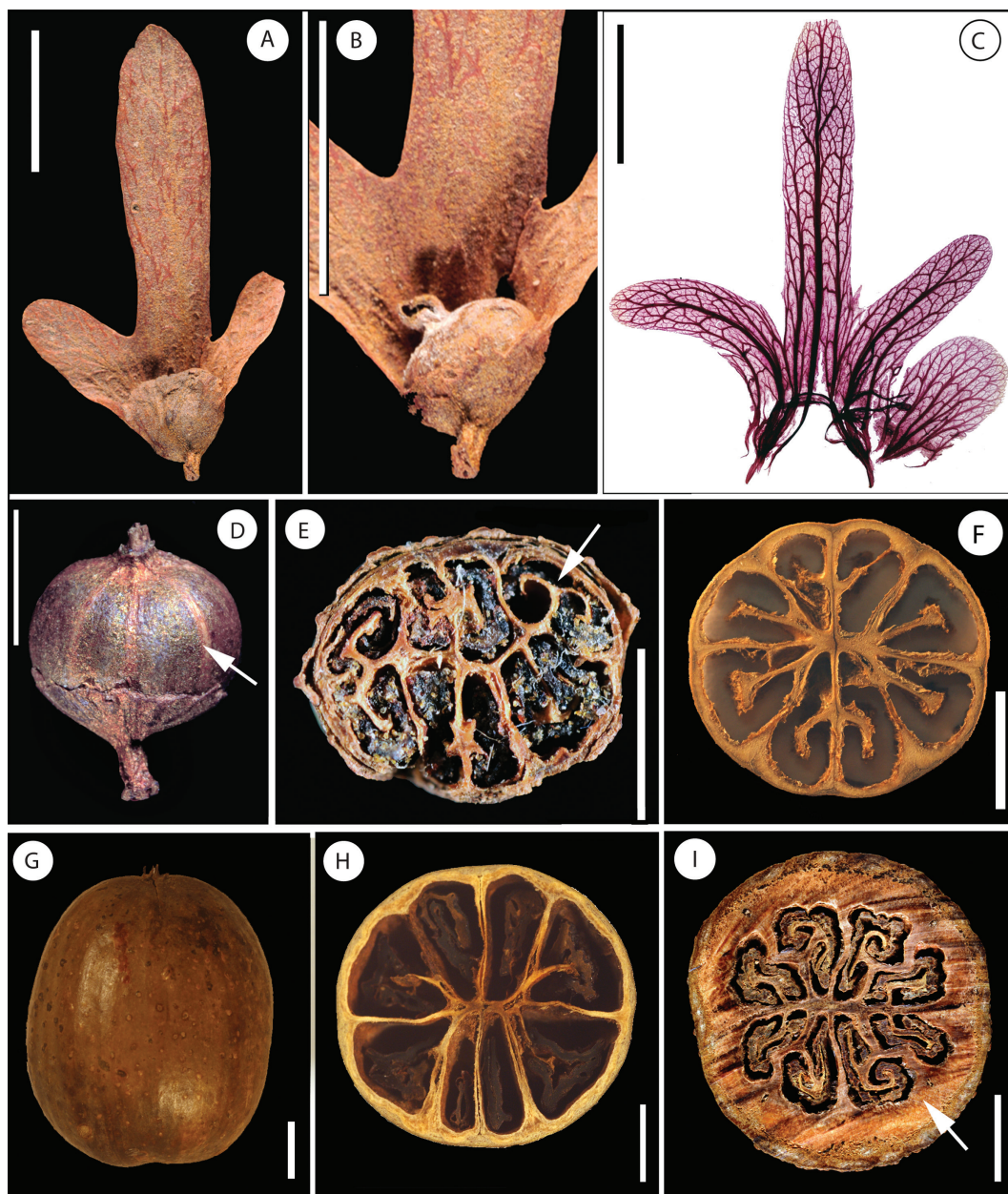


FIGURE 2. Extant fruits of *Oreomunnea* and *Alfara*. A–E. *Oreomunnea mexicana*. —A. Three-lobed wing for fruit dispersal. —B. Close-up from A; nut with two short styles. —C. Cleared wing with three major veins in lobes. —D. Lateral view of nut showing strands of fibers (arrow). —E. Equatorial cross section of nut; locule divided by primary and secondary septa into eight compartments, four on each side of the straight primary septum, and Y-shaped bifurcated septum (arrow). —F. *Oreomunnea pterocarpa*, equatorial cross section of nut; locule with eight compartments. G, H. *Alfara williamsii*. —G. Lateral view of nut. —H. Equatorial cross section of nut; locule with eight compartments and inconspicuous bifurcations of septa. —I. *Alfara guatemalensis*, equatorial cross section of large nut; locule with eight compartments and conspicuous bifurcations of septa. A, B, D, E, Stone 2141; C, UFI 312; F, Stone 134; G, H, Stone 2210; I, Stone 2999. Scale bars: A–C, G–I = 1 cm; D–F = 0.5 cm.

World genera from the Asian clade, in that *Engelhardia* and *Alfaropsis* pollen have walls with significantly thinner nexine than those of *Oreomunnea* and *Alfaroa*. The pollen grains recovered by Graham could be either *Alfaroa* or *Oreomunnea*, but without additional data we could not identify which of these genera was present.

Renewed excavations of the Panama Canal created exposures of the Cucaracha Formation, including a new rich fruit and seed permineralized flora (Herrera et al., 2010). Inventory of this carpoflora has revealed the presence of *Oreomunnea* fruits, providing the first confirmation of this genus in the megafossil record. We describe this as a new species, *O. grahamii* Manch. & Herrera (Fig. 3), honoring the contributions of Alan Graham to the study of Neotropical floristic history.

MATERIALS AND METHODS

The fossil nuts reported in this study were collected from the Gaillard Cut section (Lirio East outcrop) of the southeastern part of the Panama Canal (9°3'20"N, 79°39'40"W; Fig. 1). The fossils were found in March 2007 while exploring new temporary exposures created during the expansion of the canal (Herrera et al., 2010). The locality is in the lowermost part of the Cucaracha Formation. This formation was deposited in a succession grading from nearshore shallow marine environments at the base to terrestrial facies in upper levels, and it is reconstructed as a coastal delta plain consisting of abundant paleosols, channel, levee, floodplain, marsh, and volcanic deposits (Retallack & Kirby, 2007; Kirby et al., 2008). The Cucaracha Formation overlies the Culebra Formation, also exposed in the canal, which includes a distinct marine succession ranging from neritic environments at the base (coral reef, coastal lagoon) to delta and prodelta fronts at the top (Woodring & Thompson, 1949; Kirby et al., 2008). The ages of these two formations have

been inferred from mammals, pollen, marine invertebrates, magnetostratigraphy, and radiometric dating (Woodring, 1957–1982; Bold, 1973; Graham, 1988a, 1988b; MacFadden & Higgins, 2004; Johnson & Kirby, 2006; MacFadden, 2006; Kirby et al., 2008). These sources indicate an age of ca. 19.5–14 Ma for the Cucaracha Formation and 23–19 Ma for the underlying Culebra Formation (Kirby et al., 2008). Recent palynological, magnetostratigraphic, and uranium-lead (U-Pb) dating provide an age estimate of ca. 19.5–19 Ma for the Culebra and ca. 19–18.5 Ma for the Cucaracha Formation (Montes et al., 2012a, 2012b; MacFadden et al., 2012). These data suggest an age of ca. 19 Ma (Early Miocene) for the Juglandaceae fossils at the Lirio East site.

For comparative study we examined fruits of extant taxa deposited in the modern fruit and seed reference collection of the Paleobotanical Division of the Florida Museum of Natural History, including juglandaceous specimens collected and donated by Donald A. Stone. Transverse sections of fossil and extant fruits were made using a microslice II annular diamond saw. Anatomical details of the fossil fruits were obtained by preparing acetate peels after etching the slices with hydrochloric acid using the technique of Joy et al. (1956). Specimens are deposited in the Paleobotanical Collection of the Florida Museum of Natural History, University of Florida (UF), Gainesville, Florida, U.S.A.

SYSTEMATICS

Family: Juglandaceae DC. ex Perleb

Genus: *Oreomunnea* Oerst.

Species: *Oreomunnea grahamii* Manch. & Herrera sp. nov.

Holotype: designated here: UF00621-59109 (Fig. 3A–C).

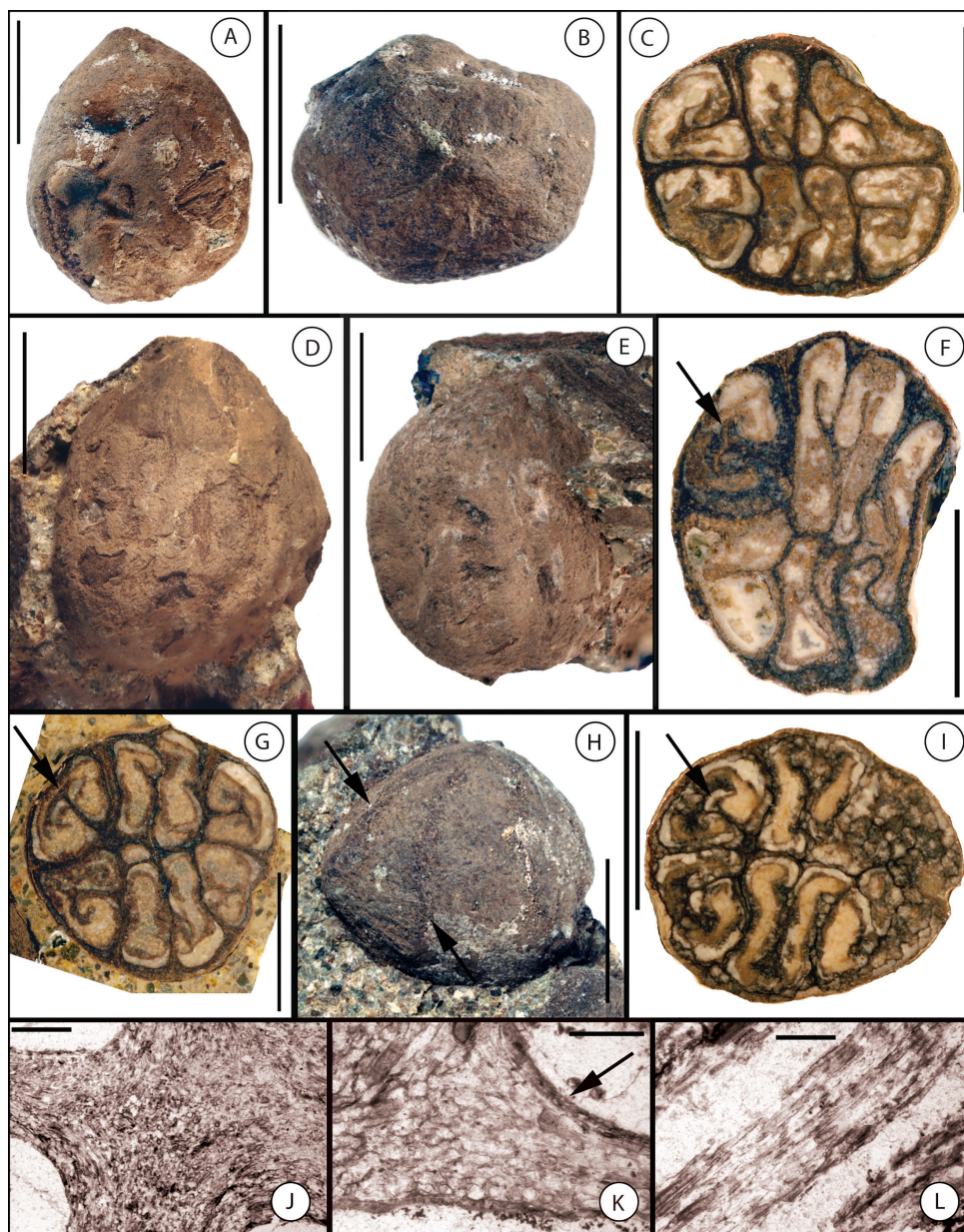


FIGURE 3. *Oreomunnea grahamii* Manch. & Herrera. A–C. Holotype UF621-59109. —A. Lateral view of nut. —B. Apical view of nut. —C. Equatorial cross section of nut; locule divided by primary and secondary septa into eight compartments, four on each side of the straight primary septum. —D. Paratype UF621-59110, lateral view of nut. E, F. Paratype UF621-59111. —E. Lateral view of nut. —F. More or less compressed specimen showing equatorial cross section and conspicuous Y-shaped bifurcated septum (arrow). —G. Paratype UF621-59108, more or less circular nut in cross section; arrow showing one of the eight compartments of the locule. H, I. Paratype UF621-59112. —H. Lateral view of nut showing strands of thick and dark fibers (arrows). —I. Equatorial cross section showing conspicuous Y-shaped bifurcated septum (arrow). J–L. Peel acetates from paratype UF621-59108. —J. Primary septum showing anisodiametric cells and abundant strands of fibers. —K. Close-up of secondary septum; fiber cells appear darker and thicker near the edge of septum (arrow). —L. Strand of long fiber cells. Scale bars: A–I = 0.5 cm; J–L = 200 μ m.

Paratypes: designated here: UF00621-59110 (Fig. 3D), UF00621-59111 (Fig. 3E, F), UF00621-59108 (Fig. 3G, J–L), UF00621-59112 (Fig. 3H, I).

Type locality: Lirio East Outcrop, Gaillard Cut, southeastern Panama Canal (9°3′20″N, 79°39′40″W).

Stratigraphy and age: Lower Cucaracha Formation, Early Miocene.

Etymology: This species is named in honor of Alan Graham for his research contributions on the study of Neotropical floristic history.

Diagnosis: Nuts ovoid, elliptical in cross section, 8.3–10.1 mm long, 8.2–9.6 mm wide, 6.6–7.8 mm deep, rounded basally, pointed apically (Fig. 3A, B, D, E, H), smooth at the surface but with more or less conspicuous bands of dark and thick fibers (Fig. 3H), these bands separated from each other by 0.35–0.45 mm near the equator. In equatorial cross sections, the nut appears divided by primary and secondary septa, creating 8 compartments, 4 on each side of the straight primary septum (Fig. 3C, F, G, I). Each compartment intruded by an additional partial septum, straight or curved, often bifurcated in the shape of a Y in the 4 exterior compartments as seen in cross section. Nutshell 0.11–0.56 mm thick, septa 0.10–0.89 mm thick, composed of anisodiametric cells (13–71 μm in diameter; Fig. 3J, K) and abundant strands of fibers (>900 μm long and 13–19 μm thick; Fig. 3L), fiber cells appear darker and thicker near the edge of the septa (Fig. 3K).

Taxonomic affinity of the fossil: The subdivision of the nut by primary and secondary septa into eight compartments is a feature found only in *Oreomunnea* and *Alfaroa*. Other Juglandaceae have two main compartments divided by a primary septum, or four subcompartments formed by the intersection of secondary and primary septa.

In Juglandaceae, the primary septum arises from the base of the ovary and extends nearly but not completely to the apex. The single seed is thus deeply lobed from the base. The secondary septa also arise from the base and are usually oriented at right angles to the primary septum. In some taxa secondary septa do not develop, and in most genera they extend only about half of the distance to the apex; however, in *Oreomunnea* and *Alfaroa* they extend half or more the distance to the apex. The predominantly fibrous composition of the septa and nutshell is a feature shared by members of the Engelhardioideae subfamily that distinguishes them from other Juglandaceae, in which the septa and nutshell are mostly composed of isodiametric sclereids. The extinct engelhardioid genus, *Beardia* Elliott, Stockey & Mindell, from the Middle to Late Eocene of Vancouver Island, British Columbia, had a thick husk and a nutshell composed of fibers (Elliott et al., 2006). It appears to have been wingless, like *Alfaroa*, but transverse sections of that fossil show that the fruit was divided into four compartments at the base and two at the equatorial section, contrasting with the eight-compartmented nuts of *Alfaroa* (Elliott et al., 2006).

One of the main characters separating *Oreomunnea* and *Alfaroa* is the presence of dispersal wings on the former (Fig. 2A–C). The Panamanian fossils lack evidence of attached wings (Fig. 3), but this does not mean that they were wingless in life. The coarse, high-energy sediments in which these fossils are preserved are suitable for preservation of wood, fruits, and seeds, but they rarely preserve leaves and other laminar organs. Size and shape of nuts is another feature that helps to distinguish these two genera. Lengths and widths of the fruits in extant *Alfaroa* species (Fig. 2G–I) range from 2.0×1.5 cm in *A. williamsii* Ant. Molina to 6.5×3.35 cm in *A. guatemalensis* (Standl.) L. O. Williams & Ant. Molina (D. E. Stone, unpublished data). On the other hand, *Oreomunnea* nuts (Fig. 2D–F) range from 0.5 cm in *O. mexicana* (Standl.) J.-F. Leroy to 1.1×1.3 cm

in *O. pterocarpa* Oerst. The size of the Cucaracha fossils, 0.8–1 cm long, and 0.7–0.9 cm in equatorial diameter, is significantly smaller than those of extant *Alfaroa* species and consistent with the range in extant *Oreomunnea*. In addition, the thickness of the nutshell and septa highly contrast between the two extant genera. In *Oreomunnea*, nutshell and septa thickness varies from ca. 0.1–0.5 mm, while in *Alfaroa* thickness varies from ca. 0.5–7.3 mm (Fig. 2E, F, H, I). Based on nut size and nutshell and septa thickness, the Panamanian fossils thus conform to *Oreomunnea*.

DISCUSSION AND IMPLICATIONS

Dilcher et al. (1976) described a winged fruit from the Eocene of Tennessee as *Paraoreomunnea* Dilcher, Potter & Crepet, which showed wing venation similar to that of *Oreomunnea* fruits and fragmentary carbonized fruit remains that were possibly eight-compartmented (Dilcher et al., 1976: fig. 22), but those fossils are not permineralized and the compression material is too fragmentary to be sure about the number and position of septa. Manchester (1987) transferred this and other fossil winged fruits with *Engelhardia*- and *Oreomunnea*-like trilobate wings from the North American, European, and Asian Tertiary to *Palaecarya* Saporta, because many of the fossil occurrences show a combination of characters that is not completely confined to one modern genus or the other. In Europe, and in most North American localities, the venation of the bracts (with three strongly ascending veins in each lobe) resembles that of *Oreomunnea*, but the associated nutlets are only two- to four-celled (Manchester, 1987). The Tennessee fossil *Palaecarya puryearensis* (Berry) Manchester appears to represent the closest extinct taxon to *Oreomunnea* (assuming that the eight-compartment interpretation of the nutlet is correct), or it may belong on the stem lineage of the *Oreomunnea*–*Alfaroa* clade. The fossil fruits of *P. puryearensis* have a bilobed prophyllum (Manchester, 1987: fig. 24A, B) unlike

the rounded, unlobed prophyllum of extant species of *Oreomunnea*. Dilcher and Manchester (1986) studied associated compound juglandaceous leaves from the Eocene of western Tennessee and concluded that they showed similarity both to *Oreomunnea* and *Alfaroa*, and therefore assigned them to a fossil genus, *Oreoroa* Manch. & Dilcher.

The pollen records of Graham indicate that the Engelhardioideae clade was present already in the Eocene Gatuncillo Formation and extended to the Miocene of the Culebra (formerly treated as La Boca by Graham, 1989) and Cucaracha formations, but we do not know if those Eocene populations corresponded to one of the extant genera, or to an extinct related genus. In the Eocene of Tennessee, four distinct genera of winged engelhardioid fruits were present, all of which are thought to have had triporate, isopolar pollen similar to that of the extant genera. These were *Paraengelhardtia* Berry, with a small nut and shallowly trilobed wing; *Paleooreomunnea* Dilcher, Potter & Crepet, with a very large bilobed nut and shallowly trilobed wing; *Engelhardia mississippiensis* Berry, with a deeply trilobed wing having venation similar to that of extant *Engelhardia*; and *Palaecarya*.

The *Oreomunnea grahamii* fruits considered here provide resolution to the generic level, permitting recognition of *Oreomunnea* in the Central American fossil record for the first time. It is possible that *Alfaroa* and *Oreomunnea* represent a radiation that was confined to the Neotropics. Although we still do not have unequivocal fossil evidence for the genus *Alfaroa*, this fossil confirms that the eight-celled condition, regarded here as a synapomorphy of the *Alfaroa*–*Oreomunnea* clade, was present about 20 Ma in Panama.

The *Oreomunnea* fruits are just one component of the permineralized Cucaracha fruit and seed flora currently under study (Herrera et al., 2012). Other disseminule elements include Anacardiaceae (*Spondias* L., *Pentoperculum* Manch.), Annonaceae, Arecaceae, Cannabaceae, Chrysobalanaceae (cf. *Parinari* Aubl.), Euphorbiaceae, Fabaceae, Hu-

miriaceae (*Sacoglottis* Mart.; Herrera et al., 2010), Icacinaceae (Phytocreneae tribe), Lauraceae, Menispermaceae, Myristicaceae, Passifloraceae, and Vitaceae (*Cissus* L.). Silicified woods from the same level include Annonaceae and Malvaceae (Rodríguez-Reyes & Falcon-Lang, 2011). This megafossil flora indicates a strong representation by angiosperms and emphasizes the woody component of the flora—mainly trees, shrubs, and lianas, contrasting with the Cucaracha palynoflora (Graham, 1988b), which included a high proportion of fern spores. As comparative studies of the fossil and extant fruits continue, we expect to expand our understanding of the vegetation to which *O. grahamii* belonged. Extant *Oreomunnea* grows in forests of medium to high elevation in Central America; if *O. grahamii* grew in similar ecological settings, the new fossils may be an indicator of the Early Miocene topographic relief in Panama, which is also suggested by recent exhumation using Zircon thermochronology (Farris et al., 2011; Montes et al., 2012a, 2012b).

ACKNOWLEDGMENTS

We thank A. Graham for his inspiration over the years, P. Raven for inviting this contribution, T. Lott for help with manuscript processing, and H. Wang for curatorial assistance. We thank M. Carvalho, E. Correa, B. MacFadden, R. Portell, L. Londoño, and M. I. Barreto for their assistance in the Panama field trips. F. Herrera thanks B. Himschoot for his constant support. This research was made possible through funding from NSF-DEB-1210404 (Dissertation Research Improvement Grant), PCP PIRE (Partnerships for International Research and Education, NSF grant 0966884, OISE, EAR, DRL), Evolving Earth Foundation, Geological Society of America Foundation, Asociación Colombiana de Geólogos y Geofísicos del Petróleo-ARES, Smithsonian Institution, the Gary S. Morgan Student Research Award, and the Lewis & Clark Foundation-American Philosophical Society to F. Herrera;

funding from BSR-0743474 to S. R. Manchester; and funding from NSF DEB-0733725, M. Tupper, and R. Pérez S.A. to C. Jaramillo.

LITERATURE CITED

- APG (Angiosperm Phylogeny Group). 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161: 105–121.
- Bold, W. A. 1973. Ostracoda of the La Boca Formation, Panama Canal Zone. *Micropaleontology* 18: 410–442.
- Dilcher, D. L. & S. R. Manchester. 1986. Investigations of angiosperms from the Eocene of North America: Leaves of the Engelhardieae (Juglandaceae). *Bot. Gaz.* 147: 189–199.
- Dilcher, D. L., F. W. Potter & W. L. Crepet. 1976. Investigations of angiosperms from the Eocene of North America: Juglandaceous winged fruits. *Amer. J. Bot.* 63: 532–544.
- Elliott, L. L., R. A. Mindell & R. A. Stockey. 2006. *Beardia vancouverensis* gen. et sp. nov. (Juglandaceae): Permineralized fruits from the Eocene of British Columbia. *Amer. J. Bot.* 93: 557–565.
- Farris, D. W., C. Jaramillo, G. Bayona, S. Restrepo-Moreno, C. Montes, A. Cardona, A. Mora, R. J. Speakman, M. D. Glasscock, P. Reiners & V. Valencia. 2011. Fracturing of the Panamanian Isthmus during initial collision with South America. *Geology* 39: 1007–1010.
- Friis, E. M. 1983. Upper Cretaceous (Senonian) floral structures of juglandalean affinity containing *Normapolles* pollen. *Rev. Palaeobot. Palynol.* 39: 161–188.
- Friis, E. M., K. R. Pedersen & J. Schönenberger. 2006. Normapolles plants: A prominent component of the Cretaceous Rosid diversification. *Pl. Syst. Evol.* 260: 107–140.
- Graham, A. 1985. Studies in Neotropical paleobotany. IV. The Eocene communities of Panama. *Ann. Missouri Bot. Gard.* 72: 504–534.
- Graham, A. 1988a. Studies in Neotropical paleobotany. V. The Lower Miocene communities of Panama: The Culebra Formation. *Ann. Missouri Bot. Gard.* 75: 1440–1466.
- Graham, A. 1988b. Studies in Neotropical paleobotany. VI. The Lower Miocene communities of Panama: The Cucaracha Formation. *Ann. Missouri Bot. Gard.* 75: 1467–1479.
- Graham, A. 1989. Studies in Neotropical paleobotany. VII. The Lower Miocene communities of Panama:

- The La Boca Formation. *Ann. Missouri Bot. Gard.* 76: 50–66.
- Graham, A. 1990. Late Tertiary microfossil flora from the Republic of Haiti. *Amer. J. Bot.* 77: 911–926.
- Graham, A. 1991. Studies in Neotropical paleobotany. IX. The Pliocene communities of Panama: Angiosperms (Dicots). *Ann. Missouri Bot. Gard.* 78: 201–223.
- Graham, A. & D. M. Jarzen. 1969. Studies in Neotropical paleobotany. I. The Oligocene communities of Puerto Rico. *Ann. Missouri Bot. Gard.* 56: 308–357.
- Herrera, F., S. R. Manchester, C. Jaramillo, B. MacFadden & S. A. Da Silva-Caminha. 2010. Phyto-geographic history and phylogeny of the Humiriaceae. *Int. J. Plant Sci.* 171: 392–408.
- Herrera, F., S. R. Manchester, M. R. Carvalho, E. Correa & C. Jaramillo. 2012. Paleobiogeographical and paleoclimatical implications from a permineralized fruit and seed flora of the Middle Miocene of Panama. *Geol. Soc. Amer. Abstracts with Programs* 44(7): 163.
- Johnson, K. G. & M. X. Kirby. 2006. The Emperador limestone rediscovered: Early Miocene corals from the Culebra Formation, Panama. *J. Paleontol.* 80: 283–293.
- Joy, K. W., A. J. Willis & W. S. Lacey. 1956. A rapid cellulose peel technique in palaeobotany. *Ann. Bot. (Oxford)* 20: 635–637.
- Kirby, M. X., D. S. Jones & B. J. MacFadden. 2008. Lower Miocene stratigraphy along the Panama Canal and its bearing on the Central American peninsula. *PLoS ONE* 3(7): e2791. doi: 10.1371/journal.pone.0002791.
- MacFadden, B. J. 2006. North American Miocene land mammals from Panama. *J. Vertebr. Paleontol.* 26: 720–734.
- MacFadden, B. J. & P. Higgins. 2004. Ancient ecology of 15-million-year-old browsing mammals within C³ communities from Panama. *Oecologia* 140: 169–182.
- MacFadden, B. J., D. A. Foster, A. F. Rincon, G. S. Morgan & C. Jaramillo. 2012. The New World Tropics as a cradle of biodiversity during the Early Miocene: Calibration of the Cenenario fauna from Panama. *Geol. Soc. Amer. Abstracts with Programs* 44(7): 163.
- Manchester, S. R. 1987. The Fossil History of the Juglandaceae. *Monogr. Syst. Bot. Missouri Bot. Gard.* 21: 1–137.
- Manchester, S. R. 1989. Early history of the Juglandaceae. *Pl. Syst. Evol.* 162: 231–250.
- Manos, P. S. & D. E. Stone. 2001. Evolution, phylogeny, and systematics of the Juglandaceae. *Ann. Missouri Bot. Gard.* 88: 231–269.
- Manos, P. S., P. S. Soltis, D. E. Soltis, S. R. Manchester, S.-H. Oh, C. D. Bell, D. L. Dilcher & D. E. Stone. 2007. Phylogeny of extant and fossil Juglandaceae inferred from the integration of molecular and morphological data sets. *Syst. Biol.* 56: 412–430.
- Montes, C., G. Bayona, A. Cardona, D. M. Buchs, C. A. Silva, S. E. Morón, N. Hoyos, D. A. Ramírez, C. Jaramillo & V. Valencia. 2012a. Arc-continent collision and orocline formation: Closing of the Central American seaway. *J. Geophysical Res.* 117: B04105. doi: 10.1029/2011JB008959.
- Montes, C., A. Cardona, R. R. McFadden, S. Morón, C. A. Silva, S. Restrepo-Moreno, D. A. Ramírez, N. Hoyos, J. Wilson, D. W. Farris, G. Bayona, C. Jaramillo, V. Valencia, J. Bryan & J.-A. Flores. 2012b. Evidence for Middle Eocene and younger emergence in Central Panama: Implications for Isthmus closure. *Geol. Soc. Amer. Bull.* 124: 780–799. doi: 10.1130/B30528.1.
- Retallack, G. J. & M. X. Kirby. 2007. Middle Miocene global change and paleogeography of Panama. *Palaios* 22: 667–679.
- Rodriguez-Reyes, O. & H. Falcon-Lang. 2011. A 16-million-year-old (Middle Miocene) fossil forest from the Cucaracha Formation, Panama: Wood systematics. *Newsletter 25*, Linnean Soc. Meeting. Burlington House, London, 2 November.
- Sauquet, H., S. Y. W. Ho, M. A. Gandolfo, G. J. Jordan, P. Wilf, D. J. Cantrill, M. J. Bayly, L. Bromham, G. K. Brown, R. J. Carpenter, D. M. Lee, D. J. Murphy, J. M. K. Sniderman & F. Udovicic. 2012. Testing the impact of calibration on molecular divergence times using a fossil-rich group: The case of *Nothofagus* (Fagales). *Syst. Biol.* 61: 289–313.
- Stone, D. E. 1972. New World Juglandaceae. III. A new perspective of the tropical members with winged fruits. *Ann. Missouri Bot. Gard.* 59: 297–321.
- Stone, D. E. 1989. Biology and evolution of temperate and tropical Juglandaceae. Pp. 117–145 in P. R. Crane & S. Blackmore (editors), *Evolution, Systematics and Fossil History of the Hamamelidae*, Vol. 2. 'Higher' Hamamelidae. Systematics Association Special Volume 40B. Clarendon Press, Oxford.
- Stone, D. E. 1993. Juglandaceae. Pp. 348–359 in K. Kubitzki, J. G. Rohwer & V. Bittrich (editors), *The Families and Genera of Vascular Plants*, Vol. II. Flowering Plants-Dicotyledons. Springer, Berlin.

-
- Stone, D. E. 2010. Review of New World *Alfaroa* and Old World *Alfaropsis* (Juglandaceae). *Novon* 20: 215–224.
- Stone, D. E. & E. C. R. Broome. 1975. Juglandaceae. *World Pollen Spore Fl.* 4: 1–31.
- Woodring, W. P. & T. F. Thompson. 1949. Tertiary formations of Panama Canal Zone and adjoining parts of Panama. *Bull. Amer. Assoc. Petrol. Geologists* 33: 223–247.
- Woodring, W. P. 1957–1982. *Geology and Paleontology of Canal Zone and Adjoining Parts of Panama*. U.S. Geol. Survey Prof. Paper 306. U.S. Govt. Print. Off., Washington, D.C.