A fruit and leaves of Rhamnaceous affinities from the late Cretaceous (Maastrichtian) of Colombia[1]

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Although Rhamnaceae are distributed worldwide today, the former hypothesis for its Laurasian origins may need to be reconsidered in view of recently discovered fossils from the Guaduas Formation of central Colombia (~68 Ma), including fossil leaves (*Berhamniphyllum)* and a fruit (*Archaeopaliurus boyacensis).* Recent phylogenetic studies calibrate the stem of Rhamnaceae at 64 Ma and divide the family into three groups, rhamnoid, ampeloziziphoid, and ziziphoid. Although the fruit, *Archaeopaliurus boyacensis,* resembles that of *Paliurus* and suggests a relationship to the Paliureae in the ziziphoid group, associated leaves of *Berhamniphyllum* conform in architecture to those found today only in the Rhamneae tribe. The Maastrichtian age of these fossils predates the ages previously estimated for the Rhamneae tribe (28.5 Ma) and the Paliureae tribe (31.6 Ma) using a modified clock approach. Based on the new megafossil evidence, two alternative ideas are proposed: (1) that these fossils predate the extant tribes or (2) that the family diversified into modern tribes earlier than previously proposed.

Key words: *Berhamniphyllum,* Colombia; Guaduas Formation; late Cretaceous; Maastrichtian; Paliureae; Rhamnaceae.

The presence of some fossil leaves and a fruit of rhamnaceous affinities from central Colombia are helping to unveil the natural history of the plant family Rhamnaceae, which is cosmopolitan today with about 58 genera and 900 species. The family is most common in tropical and subtropical regions, e.g., in hot tropical lowlands in all kinds of habitats, ranging from rain forests to dry forests and savannas; some species are found even in cloud forests (Heald, 2004). The most recent revision of the entire family, including detailed morphological analyses, was made by Suessenguth (1953), who recognized Hooker's (1862) five tribes: Colletieae, Gouanieae, Rhamneae, Ventilagineae, and Zizipheae. Subsequent phylogenetic analyses have demonstrated that Rhamnaceae is monophyletic and have supported some of Suessenguth's tribes (Richardson et al., 2000b). Molecular data show a division of Rhamnaceae into three clades: the ziziphoid, ampeloziziphoid, and rhamnoid (Richardson et al., 2000a). The tribe Paliureae is one of five tribes that constitute the ziziphoid group, and Rhamneae is one of the three tribes within the rhamnoid group. This family has been considered Laurasian (Gentry, 1982) although Raven and Axelrod (1974) considered the family to be so widely represented, in both tropical and temperate regions, that its biogeographic origin remains uncertain.

The rhamnoid group and particularly Rhamneae are widespread throughout the tropics, subtropics, and into temperate regions (Richardson et al., 2004). The ziziphoid group is cosmopolitan and is well distributed in the southern hemisphere, but it is thought to have had a wider distribution throughout Gondwanaland and Laurasia before the split of these land masses (Richardson et al., 2004).

There are worldwide records of megafossils of leaves from Rhamnaceae with the oldest report coming from the Albian–Cenomanian of the Russian Federation (Spicer et al., 2002). There are also reports from the Eocene of Japan (Huzioka and Takahashi 1970) and from the Miocene of Japan (Ozaki, 1991), Kazakhstan (Zhilin, 1989), Argentina (Berry, 1925b), Ecuador (Berry, 1929), and Cuba (Berry, 1939), and from the Miocene–Pliocene of Trinidad and Tobago (Berry, 1925a), but most of the reports are concentrated in North America and Europe.

Rhamnaceous affinities have been proposed for several fossil pollen occurrences including *Tricolporopollenites haanradensis*, *Rhamnus brandonensis*, *Rhamnus* sp., *Ziziphus* sp., and *Frangula* sp. (Muller, 1981). These taxa have been reported from the Eocene of Arkansas (Jones, 1961); the Oligocene to Early Miocene of Vermont, USA (Tiffney, 1994), Poland (Ziembinska-Tworzydlo, 1974), the Urals (Agranovskaya et al., 1956), and Romania (Petrescu, 1972, 1973); the Miocene of Spain (Van Campo, 1976), Poland (Stuchlik, 1964), Hungary (Simoncsics, 1969), the Netherlands (Manten, 1958), and Morocco (Bachiri Taoufiq and Barhoun, 2001); and the Pliocene of northwestern Europe and the Sahara (Muller, 1981) and Ethiopia (Bonnefille, 1976).

This report describes leaves and a fossil fruit found in Maastrichtian deposits (ca. 68 Ma) from the Guaduas Formation of central Colombia that shows affinities with Rhamnaceae. The leaves resemble some members of the tribe Rhamneae whereas the fruit resembles those of extant *Paliurus*. These are among the oldest fossils known for Rhamnaceae, and the oldest from South America.

MATERIALS AND METHODS

Four specimens, three leaves, and a fruit were found as impressions in fine-grained sandstones with abundant organic matter near the junction of the Chicamocha and Canela rivers and the Peñablanca railway station in the municipality of Paz de Río in the department of Boyacá, Colombia (5°55′44.84″N, 72°47′42.72″W) (Fig. 1). The fossils occur in the middle Guaduas Formation as

Fig. 1.   Location of Paz de Río, Boyacá, Colombia.

part of the Guaduas flora, one of the first fossil floras ever found for the Maastrichtian in the tropics (Gutierrez and Jaramillo, 2007). This formation accumulated in coastal plain environments with abundant coal deposition (Sarmiento, 1992). Two sediment samples to be dated using palynology were taken from the same level as the megafossils. The palynological preparation followed the standard procedure (Traverse, 2007). The specimens studied (GD 01-0609, GD 01-0506, GD 01-0606 20098, GD 01-0606 20100) are housed at the paleontological collection of Paleontological Museum José Royo y Gómez at the Instituto de Geología y Minería, Ingeominas, Bogotá, Colombia.

These fossils were compared with the collection of fossil and extant fruits and foliage of Rhamnaceae at the Florida Museum of Natural History in Gainesville, Florida. We also checked the descriptions of all the species of *Paliurus* with their drawings from the revision of the genus *Paliurus* Tourn. Ex Mill. (Rhamnaceae) made by Schirarend and Olabi (1994). Terminology for description of the leaves follows that of Hickey (1973) and the Leaf Architecture Working Group (1999).

AGE

The two palynological samples yielded good pollen/spore content. The assemblage includes *Echimonocolpites protofranciscoi*, *Bacumorphomonocolpites tausae*, *Buttinia andreevi*, *Crusafontites grandiosus*, *Foveotriletes margaritae*, *Periretisyncolpites giganteus*, *Zlivisporis blanensis*, and *Proteacidites dehaani*. This assemblage can be assigned to palynological zone 13 (*Proteacidites dehaani* zone of Muller et al., 1987) or 17 (*Buttinia andreevi* zone of Jaramillo and Rueda, 2004). These zones have been dated as Late Maastrichtian (ca. 68–66 Ma) based on calibration with foraminifera (Muller et al., 1987).

SYSTEMATICS

Family—Rhamnaceae Juss.

Genus—*Berhamniphyllum* sp. Jones & Dilcher (Figs. 2–4)
Specimens—GD 01-0506, GD 01-0606 20098, and GD 01-0606 20100.

Repository—Paleobotanical Collection, Ingeominas (Instituto Colombiano de Geología y Minería), Bogotá, Colombia.
Locality—GD locality 0506. Boyacá, (5°55′44.84″N, 72°47′42.72″W).

Age and stratigraphy—Upper Maastrichtian, Guaduas Formation.

Description—Leaves elliptic-oblong to ovate, lamina entire-margined, with pinnate venation; base acute; midvein of moderate thickness, straight; secondaries pinnate, eucamptodromous, 12–16 pairs, smoothly curved to the margin, entering into a marginal vein, vein spacing increasing toward base, vein angle smoothly increasing toward base. Tertiary veins percurrent, opposite, straight, thin and closely spaced, mostly perpendicular to the midvein; vein angles uniform; quaternary veins opposite percurrent (Figs. 2–4).

Comments—Three specimens are available. The petiole is lacking, but the lamina base is clearly acute; the size of the lamina ranges greatly, from 5.5 to 20 cm long and from 2.7 to 10 cm wide. These differences in size may be due to developmental stages. However, the leaf shows a venation pattern that is highly characteristic of Rhamnaceae. The uniformly curved, eucamptodromous secondaries and closely spaced, percurrent tertiaries oriented perpendicular to the midvein are known only in a few genera of Rhamnaceae.

Comparison with modern taxa—Within Rhamnaceae, there are only a few genera known with uniformly curved, eucamptodromous secondary venation and closely spaced, percurrent tertiaries oriented perpendicular to the midvein. In the case of *Rhamnidium,* the leaves are generally elliptical, with an acute base, straight midvein, eucamptodromous secondary veins whose angles of origin from the midvein increase smoothly toward the base of the lamina, and percurrent tertiaries that are perpendicular to the midvein. Variations in leaf shape like oblong or ovate forms are not found in this genus; the margin can be slightly crenate. In *Berchemia,* leaves are ovate, ovate-oblong, to elongate oblong, with a convex base, a thick and straight midvein, with eucamptodromous secondaries, whose angles of origin from the midvein increase smoothly toward the base of the lamina, and percurrent tertiaries perpendicular to midvein. Sometimes the secondaries can be straighter, not so curved to the margin (Jones and Dilcher, 1980). *Karwinskia* also shows leaves that are ovate to elliptical, with eucamptodromous secondaries and percurrent tertiary veins (Velasco de León et al., 1998), but in some species the tertiaries are oriented obtusely to the midvein. Our fossil leaves have consistent morphological similarities to these extant Rhamnaceae, and as Jones and Dilcher (1980) mentioned, this combination of characters is confined mainly to the extant genera *Rhamnidium* and *Berchemia* and, to a lesser extent, other genera within this group (tribe Rhamneae). This fossil also bears some resemblance to extant *Cornus*, which has entire-margined leaves with apex generally strongly acuminate, eucamptodromous secondary veins, and percurrent tertiary veins perpendicular to the midvein, but in *Cornus* the tertiary veins are more widely spaced. Unfortunately, the preservation of the fossil does not permit a deeper examination of the higher order venation that in *Cornus* can reach a 5th or 6th degree. There is also similarity with *Dipterocarpus;* however, although there is great variability within species of *Dipterocarpus*, the leaves tend to be very broadly oblong with a convex to truncate base, a thick midvein, secondary veins more

Figs. 2–4.   Maastrichtian leaves of *Berhamniphyllum* sp. **2.** (GD 01-0506), base incomplete, venation tertiary and quaternary clearly visible, scale 10 cm. **3.** (GD 01–0606 20100), base acute, margin entire, scale 3 cm. **4.** (GD 01–0606 20098), midvein thick, secondaries uniformly curved, scale 3 cm.

vertically oriented without curves to the margin, and tertiaries percurrent but mostly obtuse to the midvein. These characteristics, especially the secondary and tertiary venation, are conclusive for the differentiation of this fossil leaf from *Dipterocarpus.*

Morphogenus—*Archaeopaliurus* Correa, Manchester, Jaramillo et Gutierrez gen. nov.

Generic diagnosis—Same as for type species (described later)

Etymology—Archae- (Gr = ancient) + *Paliurus*, referring to the similarity with fruits of extant *Paliurus.*

Type species—*Archaeopaliurus boyacensis* Correa, Manchester, Jaramillo et Gutierrez sp. nov. (Figs. 5, 9–11)

Species diagnosis—Winged fruit with a nearly circular wing 3.5 cm wide surrounding a prominent domed central fruit body, 12 mm wide, with a height of 4 mm (measured from the impression; original thickness estimated ~8 mm). Fruit body with 10 meridional vascular bundles. The wing is slightly entire-margined, without lobes. The veins of the wing apparently radiate in subparallel fashion (somewhat like wood rays) from the margin of the fruit body, anastomosing, and dichotomizing once up to four times before reaching the margin (Fig. 5 and close-up details in Figs. 9–11).

Holotype—GD 01–0609.

Etymology—The epithet *boyacensis* denotes the locality where it was found, in the department of Boyacá, Colombia.

Repository—Paleobotanical Collection, Ingeominas (Instituto Colombiano de Geología y Minería), Bogotá, Colombia.

Locality—GD locality 0506. Boyacá, (5°55′44.84″N, 72°47′42.72″W).

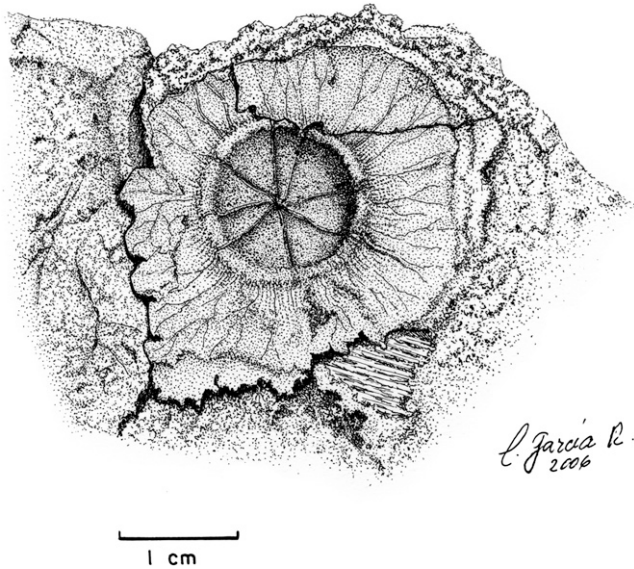*Age and stratigraphy*—Upper Maastrichtian, Guaduas Formation.

Fig. 5. Illustration of *Archeopaliurus boyacensis* (by Consuelo García) with details of the venation of the wing and vascular bundles.

Comments—Only one specimen is available, and some segments of the wing are missing due to rock fractures. Only the base of the fruit body and the wing seem to be represented in the shale impression; the counterpart impression, which would have shown the opposite (apical?) surface of the fruit, was not recovered. It is not completely clear whether it shows the base or the apex, but as shown in Figs. 6–8 the base of the receptacle of *Paliurus* has strong venation with 10 vascular bundles, and probably those are the structures that arise from the center of the concavity visible within the fossil (two of them not obvious but visible with magnification). Table 1 summarizes the characters shared with other species and indicates the affinity to *Paliurus*.

Affinities of *Archaeopaliurus boyacensis* sp. nov.—Winged fruits with a circular wing, that completely surrounds a globose endocarp, and with radiating dichotomous and anastomosing venation are encountered today in the genera *Cyclocarya* (Juglandaceae) and *Paliurus* (Rhamnaceae). These unrelated genera are closely convergent in their morphology, and there has been some confusion in the assignment of fossil remains (Manchester, 1987). When the central body and seeds are structurally preserved, it is easy to distinguish these genera, because *Paliurus* has 2–3 distinct locules, whereas *Cyclocarya* has a single locule partitioned at its base into 2 or 4 compartments. However, our

specimen has preserved only the impression of the base of the fruit surface, without internal structure.

There are additional characters that help to differentiate *Cyclocarya* fruits from *Paliurus*, mainly the venation pattern, the shape of fruit bodies, and the floral-fruit structure.

In *Cyclocarya*, the pattern of venation of the wing is mainly subparallel (radiating) and does not dichotomize before the medial part. This character is present in fossils as well as in the extant species. Although *Cyclocarya* has both pyramid-shaped and rounded fruit bodies, the species of the latter shape are mostly Oligocene and younger, distributed in Europe and Asia (Manchester, 1987). The only exception is *C. minuta* Manchester with rounded fruit bodies from the Paleocene of Wyoming (Manchester, 1987), but its notably smaller size (10–16 mm vs. 35 mm) is enough to separate it from *A. boyacensis*. Our specimen could be confused also with *C. brownii* Manchester & Dilcher but it has a marked pyramidal fruit body. When the fruit body is lost, it leaves a square mark at the level of the wing that narrows to the bottom of a depression, and a cross mark is also prominent even if the fruit body is not present.

The fruit bodies of *Paliurus* are typically globose or lenticular, leaving a rounded mark at the level of the wing. When the fruit body is lost, a concave depression, sometimes with numerous vascular bundles of the receptacle or hypanthium can be seen radiating from the concavity (Figs. 9–11), but never with that characteristic cross shape of *Cyclocarya*. Some characteristics that differentiate *Paliurus* from *Cyclocarya* are summarized in Table 2. (For more details on morphology and relationships of *Paliurus*, see Burge and Manchester, 2008).

On the other hand, there are some characteristics that may be confusing in the identification of this specimen. For example, our specimen lacks a receptacle rim or disc, which is present in other *Paliurus* and would be very useful to confirm more precisely the relationship with extant species, but this may be due to the way the fruit was deposited with the base buried. The pattern of venation of the wing also differs in being more conspicuous and with thicker veins than in all extant and fossil *Paliurus*. Overall size is another difference: the diameter of the fruit body of *Archaeopaliurus boyacensis* is 12 mm, and the total diameter including the wing is 35 mm; in the other fruits observed, the diameter of the fruit body was 4–7 mm, and the total diameter including the wing ranged between 10 mm and 25 mm. However, fossil fruits tend to be highly variable in size, spanning and even exceeding the entire range of sizes of modern species (Burge and Manchester, 2008).

We propose that the fruit is closely related to extant *Paliurus*, which is an extant genus of deciduous trees and shrubs with

Figs. 6–8. *Paliurus spina-christi* Mill. Details of the vascular bundles (photographed by Lionel Roux).

TABLE 1.   Characters in common shared by *Paliurus* species and *Archaeopaliurus boyacensis*.

Characters	*Archaeopaliurus boyacensis*	*P. favonii* UF18049–26117	*P. clarnensis* UF0262–17703	*P. spina-christi*	*Cyclocarya* sp.
Fruit body shape	Hemispheric to lensoidal	Hemispheric to lensoidal	Hemispheric to lensoidal	Hemispheric to lensoidal	Pyramidal to slightly hemispheric
Vascular bundles of hypanthium	8–10	8–10	8–10	8–10	None
Shape of wing	Circular to ellipsoidal	Circular to ellipsoidal	Circular to ellipsoidal	Circular to ellipsoidal	Circular to ellipsoidal
Venation of wing	Subparallel (radiating) anastomosing	Subparallel (radiating)	Subparallel (radiating)	Subparallel (radiating)	Subparallel (radiating) anastomosing

stipules usually modified into spines, and bisexual, 5-merous, flowers with a superior ovary (Schirarend and Olabi, 1994). The genus has five extant species restricted to Europe and Eastern Asia: *Paliurus ramosissimus* (Lour.) Poir., *P. hirsutus* Hemsl., *P. spina-christi* Mill., *P. hemsleyanus* Rehd., and *P. orientalis* (French.) Hemsl.

Co-occurrence of the fruit and leaves—Although no fossil leaves that could correspond to *Paliurus* have been found in association with the fruit of *Archaeopaliurus*, the leaves of extant *Paliurus* are readily distinguishable from those of the Rhamneae and would be recognized if recovered as fossils. Leaves are chartaceous, ovate to elliptic, with base obtuse to acute base and apex, and a densely crenate margin with minute apical glands at the tooth apices. Venation is brochidodromous with a pair of basal secondaries (Schirarend and Olabi, 1994). It is intriguing that the three leaves of *Berhamniphyllum* and the fruit of *Archaeopaliurus* were collected from the same locality. Both have clear affinities to the Rhamnaceae, but they have characters found in different modern genera of the family clades, Rhamneae and Paliureae, respectively. If the same species actually produced both these organs, then it would represent an extinct genus with a mosaic of characters now found in separate clades. Alternatively, the organs may have been produced by different species, in which case, the occurrence of two different taxa of Rhamnaceae in the Late Cretaceous of Colombia would be of additional biogeographic significance.

BIOGEOGRAPHY

Leaves with architecture similar to our *Berhamniphyllum* sp. occur in members of the rhamnoid clade that today is widely distributed in Southeast Asia, India, Africa, and North and South America. This clade is subdivided into three tribes, and all the genera with these similarities in leaf architecture (uniformly curved, eucamptodromous secondaries, and closely spaced, percurrent tertiaries oriented perpendicular to the midvein) belong to the tribe Rhamneae. These genera are *Karwinskia,* with Central American distribution from the southern United States to northern Colombia and the Antilles (Velasco de León et al., 1998, Tapia-Pastrana et al., 2004); *Rhamnidium,* distributed in tropical South America, Cuba, and Jamaica (Woodson et al., 1971); and *Berchemia,* which is in not only South America, but also Africa and Asia (Lee et al., 2003). Fossils with this kind of architecture are known from the middle Eocene in Tennessee and Kentucky (Jones and Dilcher, 1980). Some other reports incorrectly assigned to *Rhamnus marginatus* from the Eocene of Texas (Ball, 1931) and Oregon (Sanborn, 1935) seem to belong to this genus, as does *Rhamnus eolignicious* (Ball, 1931) as observed by Jones and Dilcher (1980). Fossil leaves of *Rhamnidium* have been reported from California, Middle–Late Eocene (MacGinitie, 1941); Loja Ecuador, Early–Late Miocene (Berry, 1929) and Argentina, Early–Late Miocene (Berry, 1925b). There is a single occurrence of this group in Europe represented by a fossil from the Miocene of Switzerland, which was assigned to *Berchemia* (Bollinger, 1992). *Karwinskia axamilpense* Velasco de León et al., reported from the Eocene–Oligocene of Mexico, also resembles *Berhamniphyllum* (Velasco de León et al., 1998). The overall pattern suggests a tropical South American origin for this clade during the Late Cretaceous with a later migration to North America during the Eocene (Fig. 12), perhaps related to the Early Eocene global warming.

Paliurus is distributed today in Asia and Eastern Europe (Schirarend and Olabi, 1994) but had a broader distribution in the Tertiary including North America as well as Europe and Asia (Burge and Manchester, 2008). For example, fruits have been reported from the Middle Eocene Clarno Formation of Oregon (Burge and Manchester, 2008); the Upper Eocene Ube flora of Japan (Huzioka and Takahashi, 1970); the Upper Oligocene of the Czech Republic (Bůzek, 1971); the Miocene of Austria (Kirchheimer, 1957), Germany (Mai, 2001), Washington

Figs. 9–11.   *Archaeopaliurus boyacensis* sp. nov. from Guaduas Formation. (GD 01-0609), scale = 1 cm. **9.** Complete view showing nearly circular wing structure. **10.** Detail of the vascular bundles radiating from the center of the concavity. **11.** Detail of subparallel venation of the wing.

Table 2.   Differences between the fossil fruits of *Paliurus* and *Cyclocarya*

Character	*Paliurus* (Rhamnaceae)	*Cyclocarya* (Juglandaceae)
Venation dichotomization	Starts near base of wing	Not before medial part of wing
When the fruit body is preserved		
No. locules	2–3	1 partitioned at its base into 2–4 compartments
When the fruit body is not preserved		
Depression	Hemispheric	Square or pyramidal
	Numerous vascular bundles radiating from the depression	Cross mark shape in the depression, also present when nut is preserved
Mark at level of wing	Rounded	Squared

(Berry, 1928), and Florida (Alum Bluff; Burge and Manchester, 2008); the Middle Miocene of China (WGCP, 1978); and the Upper Miocene of Kazakhstan (Zhilin, 1989) and Japan (Northeast Honshu; Tsukagoshi and Suzuki, 1990). These fossil occurrences, like the extant species, show a northern temperate distribution pattern. In contrast, the Guaduas fossils are from northern South America (Fig. 13), where the paleoclimatic data (mean annual temperature 22.1 ± 3.4°C and mean annual precipitation 2400 mm/year) indicate a lowland forest, (Gutierrez and Jaramillo, 2007).

Because Rhamnaceae is cosmopolitan in distribution today, it has been difficult to determine its place of origin (Raven and Axelrod 1974). On the basis of the present distribution, Gentry (1982) proposed a probable Laurasian derivation because the taxa are proportionally better represented in the temperate North America than in the neotropics (e.g., *Rhamnus*). From the molecular perspective, the family was widespread before Gondwanan breakup (Richardson et al., 2004) and kept its cosmopolitan character, and now the diversity is higher in the southern hemisphere (Richardson et al., 2000a). Some closely related

members within the tribe Rhamneae (*Karwinskia*, *Rhamnidium*, and *Berchemia*) that constitute the complex including *Berhamniphyllum* could have appeared in the tropics since the Late Cretaceous and then spread mainly to North and South America and later on to other continents, diverging in the Eocene as the presence of *K. axamilpense* in southern Mexico suggests.

Many of the genera and families of tropical South America are shared more with Malaysia and Southeast Asia than with Africa (Thorne, 1973). Several genera of Menispermaceae and Icacinaceae are shared only with tropical America and tropical Southeast Asia. (Pennington and Dick, 2004). *Meliosma* (Sabiaceae) has a similar disjunction today (van Beusekom, 1971). Floral affinities between North America and Asia have been recognized ever since the studies of Asa Gray in the mid-1800s (Graham, 1972). The 57 genera of vascular plants that show this pattern (Qian and Ricklefs, 2004) belong to families like Rhamnaceae, Juglandaceae, Lauraceae, Styracaceae, and Nyssaceae, among others. The genus *Paliurus* exhibits this pattern of distribution, and although the ziziphoid group is suggested to be of Gondwanan origin, the tribe Paliureae is thought to be
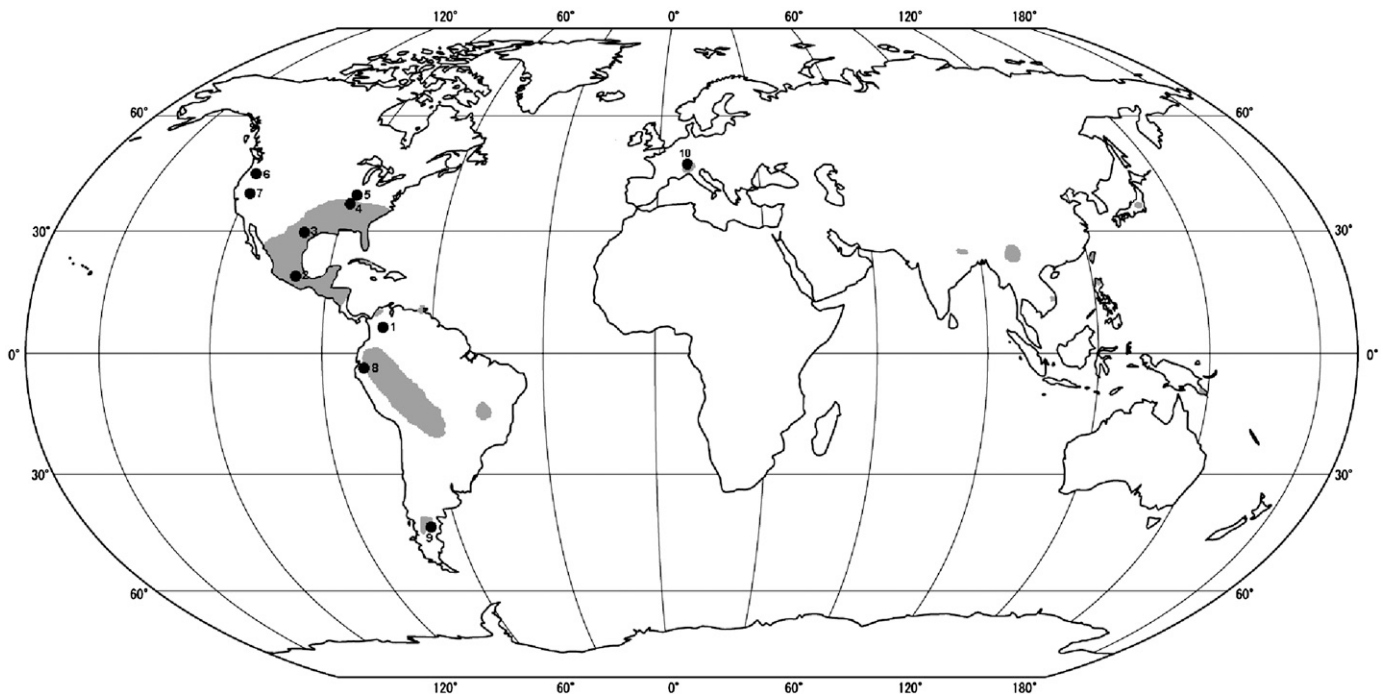

Fig. 12.   Shaded areas with modern distribution of some members of the Rhamneae tribe (*Berchemia, Rhamnidium* and *Karwinskia*), numbers corresponding to fossil leaf occurrences of members of the Rhamnae tribe. 1, Colombia (Maastrichtian); 2, Mexico (Eocene-Oligocene); 3, Texas, USA (Eocene); 4, Tennessee, USA (Eocene); 5, Kentucky, USA (Eocene); 6, Oregon, USA (Eocene); 7, California, USA (Middle Miocene); 8, Ecuador (Miocene); 9, Argentina, (Miocene); 10, Switzerland (Miocene).
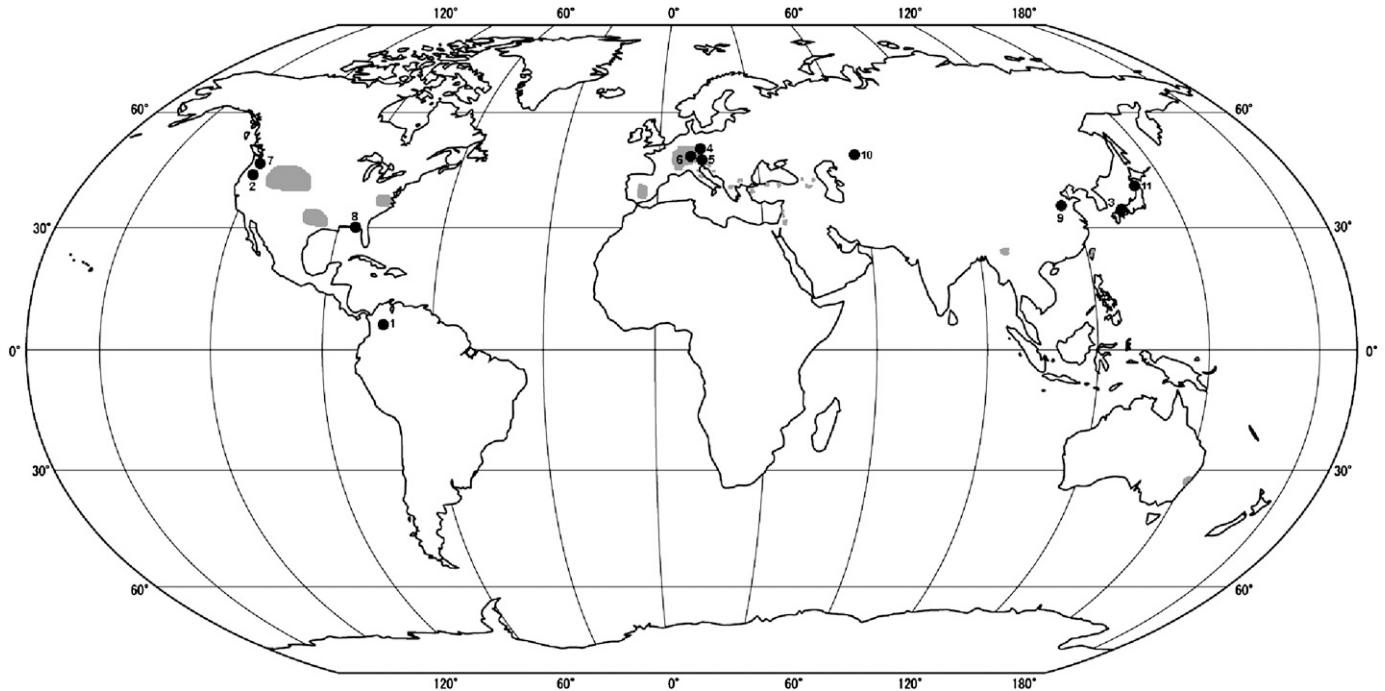
Fig. 13.   Shaded areas with modern distribution of *Paliurus,* numbers corresponding to fossil occurrences. 1, *Archaeopaliurus* Colombia Maastrichtian; 2–8, fossil *Paliurus* species known in the fossil record. 2, Oregon, USA (Eocene); 3, Japan (Eocene); 4, Czech Republic (Oligocene); 5, Austria (Miocene); 6, Germany (Miocene); 7, Washington, USA (Miocene); 8, Florida, USA (Miocene); 9, China (Miocene); 10, Kazakhstan (Miocene); 11, Japan (Miocene).

Laurasian because some of its members are well represented in the Late Eocene–Miocene of North America and Eurasia (Richardson et al., 2004; Burge and Manchester, 2008). This could be a biased observation, however, due to less thorough exploration in the tropics. On the basis of this phylogeny, Pennington and Dick (2004) proposed *Colubrina*, *Rhamnidium*, and *Ziziphus* to be immigrants from the north, but this is not yet convincingly established; it conflicts with ages of origination of some of the groups discussed earlier and minimizes the importance of the South American flora in the present tropical distribution as supported by a supposedly good fossil record and defined phylogenies. Fossils considered to be members of derived angiosperm lineages are being documented from increasingly older geological deposits (Wikström et al., 2001), such as the reproductive structures of Rhamnaceae from the Late Cretaceous of Mexico reported by Calvillo-Canadell and Cevallos-Ferriz (2007).

The occurrence of older fossils in northern South America should be taken into consideration, because the possibility of a Gondwanan origin for some of the groups previously considered of Laurasian origin cannot be dismissed.

PHYLOGENY

The most recent phylogenetic analysis made by Richardson et al. (2004) sets the Rhamnaceae stem in 64 Ma, based on estimates made by Wikström et al. (2001). The crown of the tribe Rhamneae is estimated at $27.6–28.5 \pm 2.7$ Ma, established by the Rhamneae-Maesopsis split with a penalized likelihood date of 27.7 Ma, and the crown of the tribe Paliureae at $30.6–31.6 \pm 3.1$ Ma based on the oldest fossil of *Hovenia,* the sister taxon

of *Paliurus* and *Ziziphus*. Our Maastrichtian records would suggest a much earlier split both of the Rhamneae tribe and of *Paliurus* from *Hovenia*—a minimum of 68 Ma—and a minimum age for the origin of the family that is older than presently believed. Calvillo-Canadell and Cevallos-Ferriz (2007) proposed a minimum age of 72 Ma for the origin of the family. Reports of derived groups far back in the geological past imply that the timing for early angiosperm diversification is still being underestimated (Wikström et al., 2001). Consequently, the new evidence suggests two alternative ideas. First, the tribes Paliureae and Rhamneae are older than recent interpretations of phylogeny have indicated (Middle Oligocene and Late Oligocene, respectively). Or second, the family Rhamnaceae underwent a rapid diversification before the Maastrichtian, but extant tribes did not exist in the Cretaceous, and the Maastrichtian fossils exhibits a mosaic of characters found later in separated tribes.

In conclusion, the plant megafossil record of tropical regions (especially the neotropics and Africa) is very poorly documented. Because the record holds the clues to understanding the biogeographic and phylogenetic history of many extant tropical lineages, we need to intensify the search and study of these ancient tropical floras.

LITERATURE CITED

AGRANOVSKAYA, I. A., A. D. BACHARINIKOVA, AND Z. I. MARTYNOVA. 1956.   Short description of spores and pollen from Lower Oligocene deposits of the Northern and Central Urals. VSEGEI, New Series. Atlas of Oligocene spore–pollen complexes of various regions of the USSR, 16, 141–173.

BACHIRI TAOUFIQ, N., AND N. BARHOUN. 2001.   La végétation, le climat et l'environnement Marin au Tortonien Supérieur dans le bassin de

Taza-Guercif (Corridor Rifain, Maroc Oriental) d'après la palynologie. *Geobios* 34: 13–24.

Ball, O. M. 1931. A contribution to the Paleobotany of the Eocene of Texas. *Bulletin of the Agricultural and Mechanical College of Texas* 2: 1–173.

Berry, E. W. 1925a. The Tertiary flora of the Island Trinidad, B.W.I. *John Hopkins University Studies in Geology* 6: 71–161.

Berry, E. W. 1925b. A Miocene flora from Patagonia. *John Hopkins University Studies in Geology* 6: 183–251.

Berry, E. W. 1928. A Miocene *Paliurus* from the state of Washington. *American Journal of Science, Series 5* 16: 39–44.

Berry, E. W. 1929. The fossil flora of the Loja Basin in southern Ecuador. *John Hopkins University Studies in Geology* 10: 79–135.

Berry, E. W. 1939. A Miocene flora of from the gorge of the Yumuri River, Matanzas, Cuba. *John Hopkins University Studies in Geology* 13: 95–135.

Bollinger, T. H. 1992. Kleinsäugerstratigraphie in der miozänen Hörnlischüttung (Ostschweiz). *Documenta Naturae* 75: 1–296.

Bonnefille, R. 1976. Palynological evidence for an important change in the vegetation of the Omo Basin between 2.5 and 2 million years ago. *In* Y. Coppens [ed.], Earliest man and environments in the Lake Rudolf Basin: Stratigraphy, paleoecology and evolution, 421–431. University of Chicago Press, Chicago, Illinois, USA.

Burge, D. O., and S. R. Manchester. 2008. Fruit morphology, fruit history and biogeography of *Paliurus* (Rhamnaceae). *International Journal of Plant Sciences* 169: 1066–1085.

Bůzek, È. 1971. Tertiary flora from the northern part of the Pĕtispy area (North-Bohemian Basin). *Edice Rozpravy Ustředního Ustavu Geologikého* 36: 1–118 Praha.

Calvillo-Canadell, L., and S. Cevallos-Ferriz. 2007. Reproductive structures of Rhamnaceae from Cerro del Pueblo (Late Cretaceous, Coahuila) and Coatzingo (Oligocene, Puebla) Formations, Mexico. *American Journal of Botany* 94: 1658–1669.

Gentry, A. H. 1982. Neotropical floristic diversity: Phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden* 69: 557–593.

Graham, A. 1972. Outline of the origin and historical recognition of floristic affinities between Asia and eastern North America. *In* A. Graham [ed.], Floristics and paleofloristics of Asia and eastern North America, 1–18. Elsevier, Amsterdam, Netherlands.

Gutierrez, M., and C. Jaramillo. 2007. Maastrichtian paleotemperature and paleoprecipitation from the Guaduas Formation, Colombia. *Palynology* 32: 260.

Heald, S. V. 2004. Rhamnaceae, buckthorn family. *In* N. Smith, S. A. Mori, A. Henderson, D. W. Stevenson, and S. V. Heald [eds.], Flowering plants of the neotropics, 323–324. Princeton University Press, Princeton, New Jersey, USA.

Hickey, L. J. 1973. Classification of the architecture of dicotyledoneous leaves. *American Journal of Botany* 60: 17–33.

Hooker, J. D. 1862. Rhamnaceae. *In* G. Bentham and J. D. Hooker [eds.], Genera plantarum, vol. 1, 371–386. Reeve and Co., London, UK.

Huzioka, K. and E. Takahashi, 1970. The Eocene flora of the Ube coal-field, southwest Honshu, Japan. *Journal of the Mining College, Akita University, series A* 4(5): 1–88, 21 pl.

Jaramillo, C., and M. Rueda. 2004. Impact of biostratigraphy on oil exploration. III Convención Técnica Asociación Colombiana de Geólogos y Geofísicos del Petroleo [ACGGP]. La inversión en el conocimiento geológico, P4 [CD-ROM]. ACGGP, Bogotá, Colombia.

Jones, E. L. 1961. Plant microfossils of the laminated sediments of the Lower Eocene Wilcox Group in south-central Arkansas. Ph.D. dissertation, University of Oklahoma, Norman, Oklahoma, USA.

Jones, J.. H., and D. L. Dilcher. 1980. Investigations of angiosperms from the Eocene of North America: *Rhamnus marginatus* (Rhamnaceae) reexamined. *American Journal of Botany* 67: 959–967.

Kirchheimer, F. 1957. Die laubgewäsche der Braun-kohlenzeit. Veb Wilhelm Knapp Verlag, Halle (Saale), Germany.

Leaf Architecture Working Group. 1999. Manual of leaf architecture: Morphological description and categorization of dicotyledonous and net-veined monocotyledonous angiosperms. Smithsonian Institution, Washington D.C., USA.

Lee, S-W., Y-M. Kim, and W-W. Kim. 2003. Lack of allozyme and ISSR variation in the rare endemic tree species, *Berchemia berchemiaefolia* (Rhamnaceae) in Korea. *Annals of Forest Sciences* 60: 357–360.

MacGinitie, H. D. 1941. A Middle Eocene flora from the central Sierra Nevada. Carnegie Institution of Washington Publication no. 534. Carnegie Institution of Washington, Washington, D.C., USA.

Mai, D. H. 2001. Die mittlemiozänen und obermiozäenen floren aus der Meuroer und Raunoer Folge in der Lausitz. III Fundstellen und Paläobiologie. *Palaeontographica Abteilung B* 258: 1–85.

Manchester, S. R. 1987. The fossil history of the Juglandaceae. *Monographs in Systematic Botany from the Missouri Botanical Garden.* 21: 1–137.

Manten, A. A. 1958. Palynology of the Miocene Browncoal mined at Haanrade (Limburg, Netherlands). *Acta Botanica Neerlandica* 7: 445–488.

Muller, J. 1981. Fossil pollen records of extant angiosperms. *Botanical Review* 47: 1–141.

Muller, J., E. Di Giacomo, and A. van Erve. 1987. A palynologic zonation for the Cretaceous, Tertiary and Quaternary of northern South America. *American Association of Stratigraphic Palynologists Contribution Series* 19: 7–76.

Ozaki, K. 1991. Late Miocene and Pliocene floras in central Honshu, Japan. Bulletin of the Kanagawa Prefectural Museum of Natural Science, Special Issue, 1–244. Kanagawa Prefectural Museum, Yokohama, Japan.

Pennington, R. T., and C. W. Dick. 2004. The role of immigrants in the assembly of the South American rainforest tree flora. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* 359: 1611–1622.

Petrescu, J. 1972. Caracterele generale Ale Spectrului sporo-Polinic din Oligocenul Partii de Nv a Transilvaniei. Studia Universitatis Babes-Bolyai. *Geologia-Geographia* 17: 65–69.

Petrescu, J. 1973. Paleobiologie de la forêt Oligocene du NO de la Roumanie, après les études palinologiques, The palynology of the cenophyte. *In* Proceedings of the III International Palynological Conference, 132–138, USSR. Nauka, Moscow, USSR.

Qian, H., and R. E. Ricklefs. 2004. Geographical distribution and ecological conservatism of disjunct genera of vascular plant in eastern Asia and eastern North America. *Journal of Ecology* 92: 253–265.

Raven, P. H., and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539–637.

Richardson, J. E., L. W. Chatrou, J. B. Mols, R. H. J. Erkens, and M. D. Pirie. 2004. Historical biogeography of two cosmopolitan families of flowering plants: Annonaceae and Rhamnaceae. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* 359: 1495–1508.

Richardson, J. E., M. F. Fay, Q. C. B. Cronk, D. Bowman, and M. W. Chase. 2000a. A phylogenetic analysis of Rhamnaceae using *rbcL* and *trnL-F* plastid DNA sequences. *American Journal of Botany* 87: 1309–1324.

Richardson, J. E., M. F. Fay, Q. C. B. Cronk, and M. W. Chase. 2000b. A revision of the tribal classification of Rhamnaceae. *Kew Bulletin* 55: 311–340.

Sanborn, E. I. 1935. Comstock flora of west central Oregon. Carnegie Institution of Washington Publication No. 465. Carnegie Institution of Washington, Washington, D.C., USA.

Sarmiento, G. 1992. Estratigrafía y medio de deposición de la Formación Guaduas. *Boletín Geológico Ingeominas* 32: 3–44.

Schirarend, C., and M. N. Olabi. 1994. Revision of the genus *Paliurus* Tourn. ex Mill. (Rhamnaceae). *Botanische Jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie* 116: 333–359.

Simoncsics, P. 1969. Sporen-Pollen-Und Moortypen aus dem Miozanen Braunkohlen-Gebiet von Nograd. 1. *Acta Biologica* 15: 37–49.

Spicer, R. A., A. Ahlberg, A. B. Herman, S. P. Kelley, M. I. Raikevich, and P. M. Rees. 2002. Palaeoenvironment and ecology of the

middle Cretaceous Grebenka Flora of northern Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 184: 65–105.

STUCHLIK, L. 1964.   Analiza pylkowa osadu Miocenskiego z Rypina. *Acta Palaeobotanica* 5: 3–111.

SUESSENGUTH, K. 1953.   Rhamnaceae. *In* A. Engler and K. Prantl [eds.], Die Naturlichen Pflanzenfamilien 20d: 7–145. Duncker and Humboldt, Berlin, Germany.

TAPIA-PASTRANA, F., R. FERNÁNDEZ, S. GÓMEZ-ACEVEDO, and P. MERCADO-RUARO. 2004.   Estudio cromosómico en tres especies de *Karwinskia* (Rhamnaceae) endémicas de México. Anales del Instituto de Biología. *Universidad Nacional Autónoma de México, Serie Botánica* 75: 1–10.

THORNE, R. 1973.   Floristic relationships between tropical Africa and tropical America. *In* B. J. Meggers and W. D. Duckworth [eds.], Tropical forest ecosystems in Africa and South America: A comparative review, 27–47. Smithsonian Institution Press, Washington, D.C., USA.

TIFFNEY, B. H. 1994.   Re-evaluation of the age of the Brandon Lignite (Vermont, USA) based on plant megafossils. *Review of Palaeobotany and Palynology* 82: 299–315.

TRAVERSE, A. 2007.   Paleopalynology, 2nd ed., 813–814, Springer, Dordrecht, Netherlands.

TSUKAGOSHI, M., AND K. SUZUKI. 1990.   On the late Miocene *Cinnamomum* and *Paliurus* from the lower part of the Takamine Formation, western mountainous region of the Yonezawa Basin, northeast Honshu, Japan. *Bulletin of the Misunami Fossil Museum.* 17: 71–78.

VAN BEUSEKOM, C. F. 1971.   Revision of Meliosma (Sabiaceae), section Lorenzanea excepted, living and fossil, geography and phylogeny. *Blumea* 9: 355–529.

VAN CAMPO, E. 1976.   La flore sporopollenique du gisement Miocene terminal de Venta del Moro (Espagne). Ph.D. dissertation, University of Montpellier, Montpellier, France.

VELASCO DE LEÓN, P., S. CEVALLOS-FERRIZ, AND A. SILVA-PINEDA. 1998.   Leaf of *Karwinskia axamilpense* n. sp. (Rhamnaceae) from Oligocene sediments, near Tepexi de Rodriguez, Puebla, Mexico. *Canadian Journal of Botany* 76: 410–419.

WGCPC [WRITING GROUP OF CENOZOIC PLANTS OF CHINA]. 1978.   The Cenozoic plants from China, fossil plants of China, vol. 3. Science Press, Beijing, China.

WIKSTRÖM, N., V. SAVOLAINEN, AND M. W. CHASE. 2001.   Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London, B, Biological Sciences* 268: 2211–2220.

WOODSON, R. E., R. W. SCHERY, AND J. W. NOWICKE 1971.   Flora of Panama, part VI, Family 111. Rhamnaceae. *Annals of the Missouri Botanical Garden* 58: 267–283.

ZHILIN, S. G. 1989.   History of the development of the temperate forest flora in Kazakhstan, U.S.S.R. from the Oligocene to the Early Miocene. *Botanical Review* 55: 205–330.

ZIEMBINSKA-TWORZYDLO, M. 1974.   Palynological characteristics of the Neogene of Western Poland. *Acta Palaeontologica Polonica*19: 309–432.