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MENISPERMACEAE FROM THE CERREJÓN FORMATION, MIDDLE TO LATE PALEOCENE, COLOMBIA[1]

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The origin and processes creating the high diversity of plant species in neotropical rain forests and their floristic composition and multistratitified forest structure are still uncertain. Here, we studied one of the most common leaf morphotypes of the Cerrejón flora (middle-late Paleocene, ca. 60-58 Ma), Guajira, Colombia, that contains one of the oldest records of neotropical rain forest floras. Fifty-seven leaf specimens were carefully examined with a focus on general morphology, venation patterns, and cuticular characteristics. The analysis allowed us to recognize four new species that were assigned to the fossil-leaf genus *Menispermites* on the basis of an ovate leaf shape with cordate to truncate bases, actinodromous primary venation, brochidodromous secondary venation, percurrent tertiary venation, regular polygonal reticulate fourth and fifth venation, well-developed polygonal areoles, entire margin, and the presence of a fimbrial vein. This set of characters suggests a possible affinity with the pantropical angiosperm family Menispermaceae. The predominantly climbing habit of this family suggests that the Cerrejón Paleocene tropical rain forest was already multistratified. These findings represent the earliest record for the family in northern South America.

Key words: Colombia; leaf morphology; lower eudicots; Menispermaceae; paleobotany; Ranunculales.

The plant diversity in the tropics of South America is one of the greatest in the world; nevertheless, the evolutionary patterns of the neotropical floras across geologic time, the climatic conditions in which they appeared, and the mechanisms that explain such variation are still poorly known (Burnham and Johnson, 2004). The record of pollen and spore diversity from the Paleogene to early Neogene in the neotropics shows that plant diversity in the tropics has been variable through time and seems to correlate with long-term global climatic changes (Jaramillo et al., 2006). The Paleocene Cerrejón flora of northern Colombia has been investigated in the last couple of years with more than 1500 specimens (mostly leaves) collected and about 57 morphotypes identified (Wing et al., 2004; Herrera et al., 2005). The Cerrejón flora, according to leaf margin and area analysis, corresponded to a rain forest that grew in coastal areas (Herrera, 2004; Herrera et al., 2005). Here, we studied one of the most common morphotypes of the Cerrejón flora, that is related to Menispermaceae. The study of this morphotype can give us clues about the evolution of neotropical forests because lianas, which are common in Menispermaceae, are a key component of multistratified forests (Gentry, 1991).

Menispermaceae is a diverse family in the order Ranunculales (Cronquist, 1981; APG II, 2003) whose species are distributed mainly in tropical lowlands and grow in low altitudes (Kessler, 1993). The family is primarily composed of herbaceous or woody climbers with dioecious and small inconspicuous flowers. The fruits are drupes, probably dispersed by birds (Kessler, 1993), and the common name of the family, the moonseed family, is derived from their curved endocarp and embryo. The basic type of pollen is tricolpate, lacking operculum and costae, with perreticulate tectum, a collumellate infratectal layer, and a granular endexine (Thanikaimoni, 1984).

Extant Menispermaceae include ~500 species grouped into 70 genera (Ortiz et al., 2007). The classification is principally based upon fruit and seed characters, and the most important differences between the genera concern the endocarp (Diels, 1910; Kessler, 1993). Several molecular phylogenetic analyses have confirmed the monophyly of the family (Hoot et al., 1999; APG II, 2003; Ortiz et al., 2007), but the intrafamiliar classification has been controversial (Barneby, 1970; Forman, 1986; Kessler, 1993; Ortiz et al., 2007). Different intrafamiliar classifications have been proposed (Miers, 1851; Hooker and Thomson, 1855; Bentham and Hooker, 1862; Miers, 1864; Prantl, 1888; Diels, 1910; Kessler, 1993); however, the traditional and most accepted one (Diels, 1910) divides the family into eight tribes based on a combination of characters from the seeds, flowers, and endocarps. The only phylogenetic hypothesis for Menispermaceae to date, based on molecular data (Ortiz et al., 2007), provides evidence for the monophyly of four of the eight tribes circumscribed by Diels and shows that the four remaining tribes are polyphyletic.

Modern biogeographic distribution of Menispermaceae shows predominance in West Gondwanaland (Raven and Axelrod, 1974; Gentry, 1982). However, the cradle of the family is unknown, and different hypotheses have been proposed. Most authors think that the group has a Laurasian origin, as for many other Ranunculales, because the most basal species of the family occurs in the West Pacific and the fossil records to date come mainly from the northern hemisphere (Diels, 1910; Takhtajan,

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1969; Raven and Axelrod, 1974; Wolfe, 1977; Kessler, 1993). In contrast, Thanikaimoni (1984) hypothesized that because the primitive characters of Menispermaceae are found in African species, the family may have originated in the lowlands of Africa during the Cretaceous, when South America, Africa, Madagascar, and India were close to one another. The recently published phylogeny (Ortiz et al., 2007) recovers two major clades within Menispermaceae, with *Tinomiscium petiolare*, an Indo-Malaysian centered taxon, as sister to the remainder of the family; however, no biogeographic interpretations have been drawn from this basis.

Although Menispermaceae has an extensive fossil record that includes both extant and extinct genera (Tables 1–3), the present study reports and describes for the first time fossil leaves from northern South America. The oldest record identified with some confidence is an endocarp from the Turonian (Upper Cretaceous, 91 Ma) of central Europe (Knobloch and Mai, 1984, 1986), but fossil leaves found in North America (Fontaine, 1889; Berry, 1916; Hollick, 1927; Seward, 1927; Hollick and Martin, 1930; Bell, 1956; Doyle and Hickey, 1976) and Asia (Takhtajan, 1974; Spicer et al., 2002) suggest that the family can be traced to the Early Cretaceous. Fossil pollen has been widely reported since the Early Cretaceous in many different geographic areas (Table 3).

The tropical fossil record of Menispermaceae is very sparse and consists of endocarps (Chesters, 1957) and leaves (Jacobs and Kabuye, 1987) from the Miocene of Kenya, leaves from the Eocene of Borneo (Andrews, 1970), and pollen from the Miocene of Tunisia (Méon and Tayech, 1986) and Taiwan (Huang, 1980; Song et al., 2004) and Pleistocene of Ethiopia (Bonnefille et al., 1987).

In South America the fossil record of the family is reduced to fossil leaves from the Paleocene of Argentina (Iglesias et al., 2007) and the Eocene (De Lima and Salard-Cheboldaeff, 1981)

Table 1. Seeds and endocarps of Menispermaceae in the fossil record.

Age	Area	Locality	References
Paleocene	Europe	Czech Republic	Knobloch, 1971
Eocene	Europe	Belgium	Fairon-Demaret and Smith, 2002
		England	Chandler, 1925, 1962, 1963, 1964, 1978; Reid and Chandler, 1933; Scott, 1954; Eyde, 1970
		Germany	Collinson, 1988
		France	Jacques and De Franceschi, 2005
	North America	Oregon	Scott, 1954; Manchester, 1994
		Virginia	Tiffney, 1999
		Washington	Pigg and Wehr, 2002
Oligocene	Europe	Czech Republic	Kvacek and Walther, 1998
		Germany	Kirchheimer, 1957
		Russia	Szafer, 1938; Dorofeev, 1963; Tralau, 1963; Takhtajan, 1974
Miocene	Africa	Kenya	Chesters, 1957
	Asia	Russia	Dorofeev, 1969; Takhtajan, 1974
Pliocene	Europe	Netherlands	Reid and Reid, 1910; Zagwijn, 1963
Neogene	Australia	New South Wales	Mueller, 1876; Andrews, 1970

Table 2. Leaves of Menispermaceae in the fossil record.

Age	Area	Locality	References
Early Cretaceous	Asia	Russia	Takhtajan, 1974; Spicer et al., 2002
	North America	Alaska	Hollick and Martin, 1930
		British Columbia	Hollick, 1927; Bell, 1956
		Louisiana	Berry, 1916
		Virginia	Fontaine, 1889; Doyle and Hickey, 1976
		Greenland	Seward, 1927
Late Cretaceous	Asia	Russia	Kryshtofovich and Baikovskaia, 1960; Budantsev, 1968; Takhtajan, 1974
	Europe	Czech Republic	Velenovsky, 1889; Hughes, 1976
	North America	Alaska	Hollick and Martin, 1930
		Alberta	Bell, 1962
		British Columbia	Bell, 1957
		New Mexico	Robison et al., 1982
		Wyoming	Dorf, 1942; Van Boskirk, 1998
Paleocene	Asia	Russia	Ablaev, 1971; Takhtajan, 1974
	North America	Alaska	Wolfe, 1966, 1972; Hickey, 1977
		British Columbia	Wolfe, 1966, 1972; Hickey, 1977
		Colorado	Barclay et al., 2003
		Greenland	Wolfe, 1966, 1972; Hickey, 1977
		High Arctic	McIver and Basinger, 1999
		Louisiana	Berry, 1922a
		North Dakota	Hickey, 1977
		Rocky Mountains and Great Plains	Brown, 1962; Rüffle, 1968
	South America	Argentina	Iglesias, et al., 2007
Eocene	Asia	Borneo	Andrews, 1970
	North America		Diels, 1910
		Alaska	Wolfe, 1972, 1977
		California	Potbury, 1935; MacGinitie, 1941
		Kentucky	Berry, 1922b
		Sierra Nevada Central	Wolfe, 1968
		Utah	MacGinitie, 1969
		Washington	Wolfe, 1968, 1977; Wolfe and Tanai, 1978
		Wyoming	Hickey, 1977; Wing et al., 1995; Wilf, 2000
	South America	Brazil	De Lima and Salard-Cheboldaeff, 1981
Oligocene	Asia	Russia	Iljinskaja, 1972
Miocene	Africa	Kenya	Jacobs and Kabuye, 1987
	Asia	Japan	Ozaki, 1991
		Russia	Takhtajan, 1974
	North America	Alaska	Wolfe, 1966
		Nebraska	MacGinitie, 1962
Pliocene	Europe	France	Hollick, 1927
	South America	Brazil	Dolianiti, 1949; Mello, Sant'Anna, and Bergqvist, 2000

TABLE 3. Pollen of Menispermaceae in the fossil record

Age	Area	Locality	References
Lower Cretceous	Asia	Russia	Papulov and Ediger, 1973; Srivastava, 1978
Upper Cretaceous	Asia	Russia	Zaklinskaya, 1953; Boytsova and Pokrovskaya, 1954; Agranovskaya et al., 1960; Sedova, 1960; Samsonov, 1964; Andreeva et al., 1966; Grigoreva, 1966; Fradkina, 1967; Markova et al., 1967; Golbert and Markova, 1968; Chlonova, 1971; Pogodayeva, 1973; Laukhin and Kulkova, 1974; Blyakhova, 1976; Fradkina and Kiseleva, 1976; Aleksandrova et al., 1977; Boytsova et al., 1980; Samoilovich, 1980; Mikhelis, 1982; Levina et al., 1983; Markova and Skuratenko, 1983; Kalmeneva et al., 1986; Kruchinina et al., 1990
	North America	Delaware, Maryland	Graham, 1964
Paleocene	Asia	Russia	Pokrovskaya, 1960b; Blyakhova, 1966; Pelipenko, 1966; Brattseva, 1969; Grinenko and Kiseleva, 1971; Kulkova and Laukina, 1975; Fradkina and Kiseleva, 1976; Tomskaya, 1981; Mikhelis, 1982; Zharikova et al., 1982; Teslenko, 1990; Fradkina, 1996
Eocene	Asia	Russia	Zaklinskaya, 1953; Agranovskaya et al., 1960; Pokrovskaya, 1960a; Andreeva et al., 1966; Barbashinova, 1966; Shakhmundes, 1966; Krayenva et al., 1967; Barbashinova, 1968; Rzhanikova, 1968; Brattseva, 1969; Barbashinova, 1971; Pulatova, 1973; Bykadorov et al., 1974; Oleynik and Oleynik, 1979; Zosimovich and Mikhelis, 1979; Korallova, 1981; Akhmeteev et al., 1996; Davidzon et al., 1996; Turdukulov and Fortuna, 1996
	Europe	France	Gruas-Cavagnetto et al., 1980
	North America	Wyoming	Leopold and MacGinitie, 1972
Oligocene	Asia	Russia	Boytsova and Pokrovskaya, 1954, 1956; Blom, 1960; Andreeva et al., 1966
	South America	Guyana	Van der Hammen and Wijmstra, 1964
Miocene	Africa	Tunisia	Méon and Tayech, 1986
	Asia	Taiwan	Huang, 1980; Song et al., 2004
	Asia	Russia	Shchekina, 1954; Pokrovskaya, 1956; Sedova, 1956; Dzhabarova, 1959; Manykin, 1960; Mchedlishvili, 1963; Andreeva et al., 1966; Ramishvili, 1969; Leye, 1980
	Europe	Hungary	Istvan, 1964
		France	Bessedik, 1982; Bessedik et al., 1984; Méon et al., 1989
		Spain	Durand-Delga et al., 1989
	South America	Surinam	Amstelveen, 1971
Pliocene	Asia	Russia	Mchedlishvili, 1963
	Europe	France	Suc, 1978, 1980, 1981; Michaux and Suc, 1981
		Portugal	Diniz, 1984
		Romania	Drivaliari et al., 1999
		Netherlands	Zagwijn, 1963
Pleistocene	Africa	Ethiopia	Bonnefille et al., 1987
	Europe	France	Suc, 1978, 1980, 1981; Michaux and Suc, 1981
		Polland	Stachurska et al., 1973
Quaternary	Asia	China	Li and Wu, 1978

and Pliocene of Brazil (Dolianiti, 1949; Mello et al., 2000), one liana fossil wood probably related to Ranunculales from the Miocene of Argentina (Lutz and Martínez, 2007), and fossil pollen from the Oligocene to recent of British Guiana (Van der Hammen and Wijmstra, 1964) and the Miocene of Suriname (Amstelveen, 1971).

Here, we studied one of the most common morphotypes of the Cerrejón flora. We describe it in detail and compare it with modern floras and fossil taxa to assess its phylogenetic affinity.

MATERIALS AND METHODS

Fossil leaves were collected from six localities (0315, 0317, 0318, 0319, 0322 and 0323) at the Cerrejón Formation, an outcrop at El Cerrejón coal mine on the northern side of the Cesar-Rancheria basin, Guajira peninsula, Colombia (11°1′ N, 72°45′ W; Fig. 1). The Cerrejón coal mine is bounded to the north by the Oca Fault, to the west by the eastern foothills of the Sierra Nevada de Santa Marta, and to the east by northwest-verging thrust faults of the Perijá Range (Jaramillo et al., 2007). Lithofacies, sedimentary structures, and palynological associations in the ~700-m-thick Paleocene succession in the Cerrejón coal mine suggest that a mixed platform was covered and buried by coal-bearing siliciclastic strata, which accumulated on coastal plains (Jaramillo et al., 2007).

Sedimentation was characterized by deltas toward the base of the formation and continental environments dominated by channel systems, floodplains, swamps, and lagoons upward (Jaramillo et al., 2007). The Cerrejón Formation has been dated using mollusks (Etayo-Serna, 1979) and pollen (Van der Kaars, 1983; Bayona et al., 2004; Jaramillo et al., 2007) as middle to late Paleocene (~60–58 Ma), following the time scale of Gradstein et al. (2004).

The fossil remains consist of whole or fragmented leaf impressions and compressions. Sixty-eight specimens were collected from the morphotype informally named CJ6. Fifty-seven specimens were examined: four specimens from locality 0315, 24 from 0317, 21 from 0318, four from 0319, three from 0322, and one from 0323 (Fig. 2). The CJ6 morphotype was described following

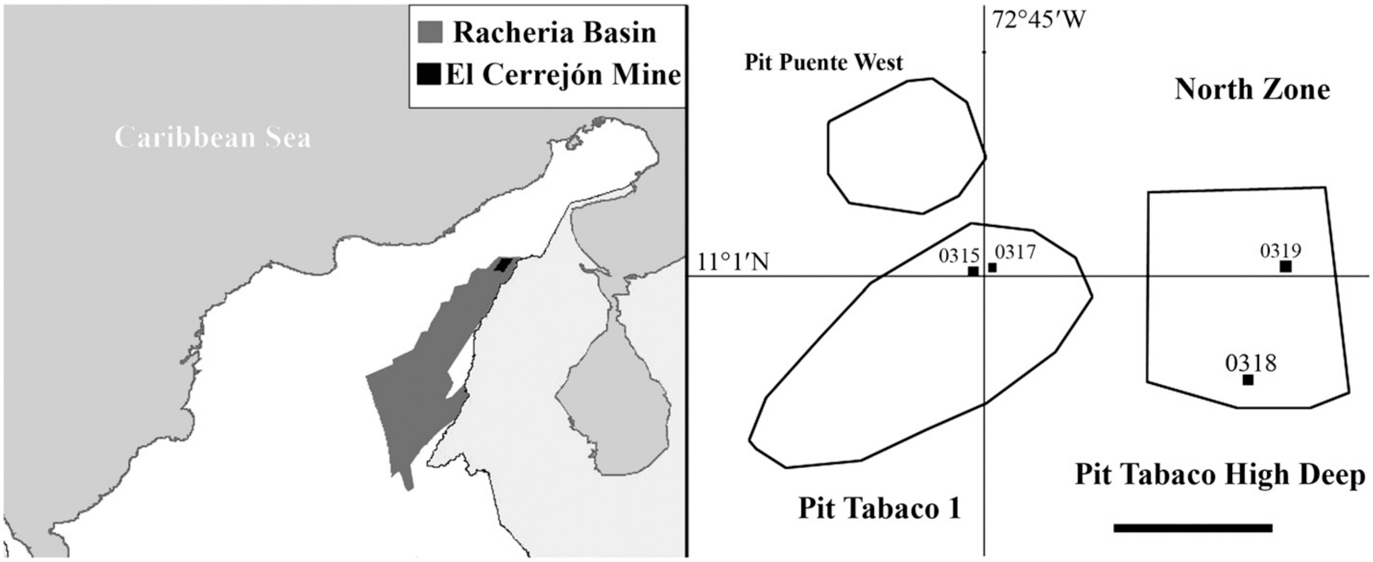


Fig. 1. Map of location of the Cerrejón coal mine, northern Colombia.

the parameters of the Leaf Architecture Working Group (LAWG, 1999), which focus on general morphology and venation patterns. Terminology of fossil taxa previously described was modified following LAWG terminology when necessary, to make the comparison easier. Specimens were analyzed using a stereomicroscope and photographed using a Nikon (Washington, D.C., USA) D70s digital camera with low-angle lighting to reveal venation details. The drawings of veins were traced from the photographs. Cuticles were prepared using a modified Schulze (1855) method. The better-preserved cuticles were isolated from the matrix with fine needles and treated with a saturated solution of potassium chlorate in 65% nitric acid for 1–24 h. The cuticles were rinsed three times with distilled water when they turned clear, upon which they were submerged in 10% NaOH for 15 min. Finally, cuticles were rinsed again, and the two surfaces were separated, one from the other, with needles when possible. The cuticles were mounted in glycerol on glass slides. Anatomical features were photographed using a Nikon digital camera DXM1200 in a Nikon Eclipse 80i microscope. All specimens are housed at the paleobotanical collections of INGEOMINAS (Instituto Colombiano de Geología y Minería) in Bogota, Colombia. The leaves were compared with living and fossil taxa through consultation of the literature (Troupin, 1962; Barneby, 1970; Krukoff and Barneby, 1970a, b, 1974; Barneby and Krukoff, 1971; Ott, 1997), observation of specimens from herbarium collections at Herbario Nacional Colombiano (COL) and Herbario de la Universidad de Antioquia (HUA), and direct observation of extant species in the field. Several angiosperm families with similar gross morphology (i.e., Aristolochiaceae, Dioscoreaceae, Euphorbiaceae, Malvaceae, Passifloraceae), were examined to establish the natural affinities of the morphotype. Exemplars of 12 extant neotropical genera (*Abuta* Aubl., *Anomospermum* Miers., *Borismene* Barneby, *Chondrodendron* Spreng., *Cissampelos* L., *Curarea* Barneby & Krukoff, *Disciphania* Eichl., *Hyperbaena* Miers ex Benth., *Odontocarya* Miers, *Orthomene* Barneby & Krukoff, *Sciadotenia* Miers, *Telitoxicum* Moldenke) were examined in the herbaria. Descriptions and illustrations by Ott (1997) were used as the main source for the neotropical taxa not found in the visited herbaria (e.g., *Elephantomene* Barneby & Krukoff). Comparisons including non-neotropical taxa were made with photographs from the C. V. Starr Virtual Herbarium, Neotropical Herbarium Specimens (http://sciweb.nybg.org/VirtualHerbarium.asp).

RESULTS

Four different kinds of leaves constitute the CJ6 morphotype. They are assigned here to four new species of *Menispermites* Lesquereux. Common characters for the leaf forms are as follows: blades simple; lamina ovate symmetrical; base cordate to truncate; apex acute; margin entire, unlobed; first venation actinodromous basal; lateral primaries ascending toward apex; secondaries brochidodromous, one to several ascending secondaries merging from the midvein; tertiary veins alternate percurrent, opposite percurrent or mixed alternate-opposite percurrent; higher-order veins regular polygonal reticulate; polygonal areoles well developed; and ultimate marginal venation fimbrial.

Systematic description*—Family*—Menispermaceae

Genus—*Menispermites* Lesquereux.

*Species****—****Menispermites cerrejonensis Doria, Jaramillo & Herrera sp. nov.* Diagnosis—Simple notophyllous to mesophyllous leaves. Ovate symmetrical lamina, 11.0 (8.5–14) cm (4 specimens measured), 8 (5.4–11.3) cm wide (8 specimens measured). Base truncate to slightly cordate, base angle obtuse; apex acuminate, apex angle acute. Margin entire and unlobed. First vein category actinodromous basal, 5–9 veins departing from the petiole insertion; central primary slightly wider than lateral primaries; first pair of lateral primaries extending about two-thirds the distance to apex into apical half of lamina. Secondary venation brochidodromous; one or few pairs of ascending secondaries from the midrib, with the lowermost pair merging above the middle of the blade; central secondaries alternate or subopposite. Simple agrophic veins. Weak intersecondaries. Third vein category alternate percurrent. Fourth vein category regular polygonal reticulate, sometimes alternate percurrent; fifth vein category regular polygonal reticulate. Areoles well developed, 4–5 sided; free-ending veinlets absent, unbranched, or 1-branched. Fimbrial vein conspicuous.

Holotype—ING-CJ6–0145–0318, Fig. 3A, B.

Paratypes—ING-CJ6–0907–0318, Fig. 3C, D; ING-CJ6–0137–0318.

Type locality—0318, Pit Tabaco High Deep, Cerrejón coal mines, northern Cesar-Rancheria basin, Guajira peninsula, northern Colombia, located at 11°13′ N, 72°55′ W.

Horizon—Upper part of the Cerrejón Formation. Between coal seams 160 and 170.

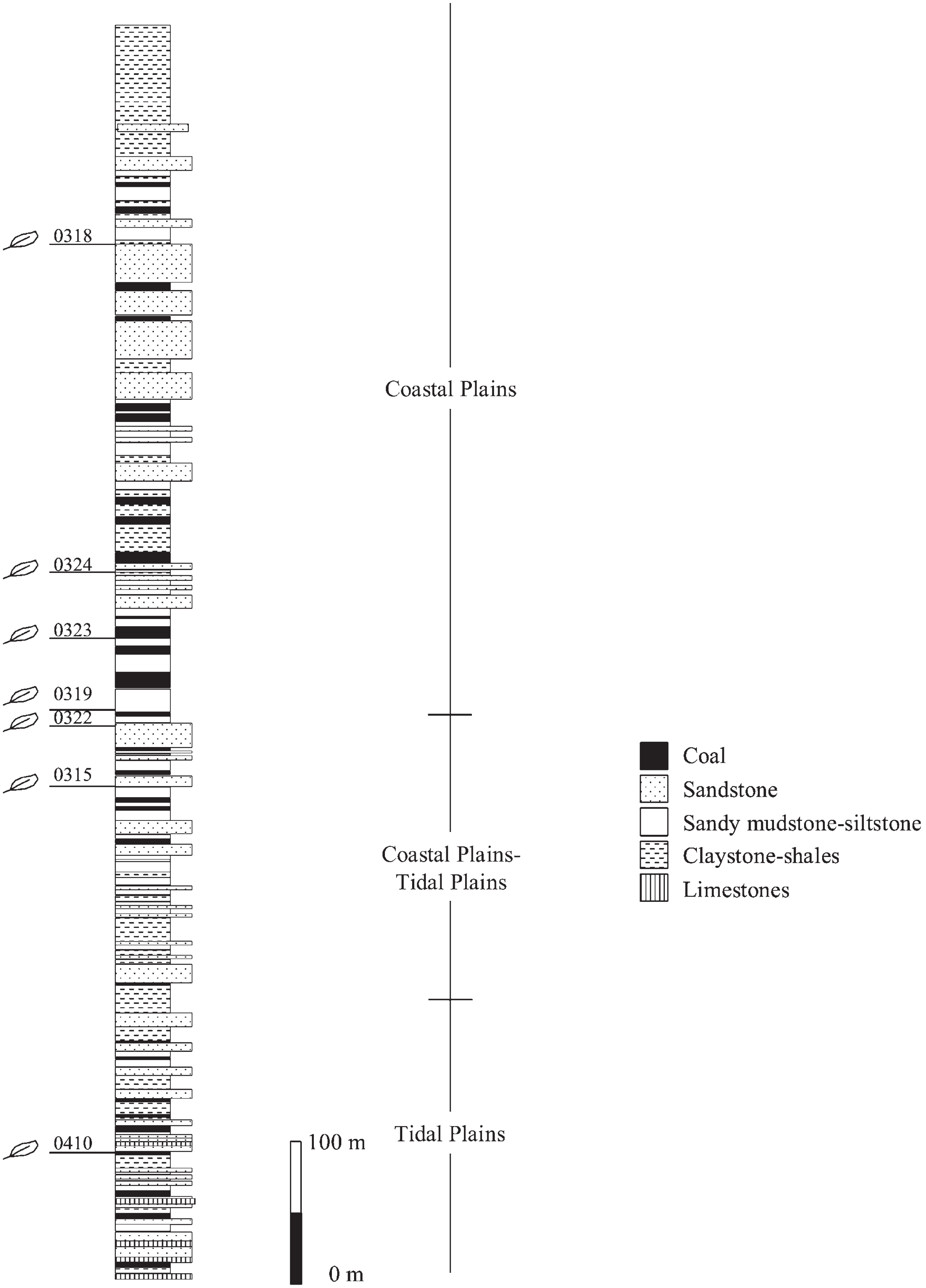


Fig. 2. Stratigraphical section of the Cerrejón Formation. Numbers indicate fossil plant localities. (Adapted from Bayona et al., 2004).

Derivatio nominis—The specific epithet refers to the type locality at the Cerrejón Formation.

Studied material—ING-CJ6–0135–0318 to ING-CJ6–0154–0318, ING-CJ6–0606–0318, ING-CJ6–0908–0318.

Description—Specimens assigned to this morphotaxon were found in locality 0318. Leaf shape is ovate with the base rounded, truncate, or slightly cordate. Length to width ratio varies from 1 : 1–2 : 1. The apex is rarely preserved. Central primary with straight course; central secondaries alternate, sometimes subopposite. The first pair of lateral primaries merge at a narrow acute angle (20–50°) from the midrib, with a moderately curved course upward reaching to the distance to the apex, branching exmedially at the length of the vein and forming loops with the central secondaries; second pair of lateral primaries merging at a wide acute angle (40–90°), slightly curved reaching one-third the distance to apex, looping with lateral secondaries, with several secondaries merging distally (simple agrophic veins), each one joining superadjacent at an acute angle (Fig. 3). Third venation mostly alternate percurrent (Fig. 4). Shape of epidermal cells is irregular, with sinuous anticlinal walls at the areoles, and rectangular, with straight anticlinal walls at the veins (Fig. 5A); anomocytic stomata, with four cells adjacent to the guard cells not differentiated in any way from the normal epidermal cells (Fig. 5B, C), and a diffuse pattern of distribution, probably only present at the abaxial surface. Leaf texture membranaceous, cuticle well preserved.

Comparisons—*Menispermites cerrejonensis* differs from *M. guajiraensis* sp. nov. and *M. horizontalis* sp. nov. in having absent or few central secondary veins from the midrib, with the lowermost vein pair originating above the middle of the blade, instead of having several pairs of central secondaries with the lowermost pair originating below the middle of the blade. *Menispermites cordatus* sp. nov. also presents similar venation patterns in the central secondaries; however, *M. cordatus* can be distinguished from *M. cerrejonensis* by having deeply cordate bases vs. rounded, truncate, or slightly cordate, concave primaries vs. straight or slightly curved primaries, and tertiary venation opposite percurrent vs. alternate percurrent.

Chondrodendron brasiliense Dolianiti from the Pliocene of Brazil (Dolianiti, 1949) is similar in base shape and in the patterns of primaries and central secondaries. However, in *C. brasiliense* the uppermost secondaries loop near the margin, fusing with the fimbrial vein, whereas in *M. cerrejonensis* they loop far from the margin. Moreover, third venation is opposite percurrent in *Chondrodendron brasiliense*, not alternate percurrent as in *M. cerrejonensis*.

Menispermites cerrejonensis presents several characteristics present in the neotropical Menispermaceae genera *Curarea* Barneby & Krukoff (clade II, Tiliacorae, Ortiz et al., 2007) and *Disciphania* Eichler (clade I, expanded Tinosporeae, Ortiz et al., 2007). This resemblance is particularly strong in *M. cerrejonensis* having (1) few central secondaries, alternate or subopposite, with the lowermost pair arising above the middle of the blade; (2) first pair of lateral primaries branching once or few times exmedially along the length of the vein; and (3) membranaceous leaf texture.

Epidermal characters provide useful systematic information in the Menispermaceae (Ferguson, 1974; Cutler, 1975; Wilkinson, 1978; Hong et al., 2001). However, irregular epidermal cells with sinuous anticlinal walls and anomocytic stomata are widely represented within Menispermaceae (Hong et al., 2001). Thus, *Menispermites cerrejonensis* cannot be related to a single taxonomic group on the basis of these characters. In many species of Menispermaceae, different types of indumenta are present; in the fossil cuticles, however, indument was not detected.

Species—Menispermites cordatus Doria, Jaramillo & Herrera sp. nov.

Diagnosis—Simple mesophyllous leaves. Ovate symmetrical lamina, 14.1 (8.5–24) cm long (11 specimens measured), 12.63 (6.7–22) cm wide (10 specimens measured). Base cordate to deeply cordate, base angle obtuse; apex acuminate when preserved, apex angle acute. Margin entire and unlobed. First vein category actinodromous basal; 5–7 veins from the base; central and lateral primaries homogeneous. Secondary venation brochidodromous; one or few ascending secondaries from the midrib, with the lowermost pair merging above the middle of the blade; central secondaries alternate to subopposite. Main first and second veins concave. Compound agrophic veins present. Third vein category mostly opposite percurrent, but alternate percurrent and mixed opposite-alternate types also present. Fourth vein category regular polygonal reticulate. Fifth vein category regular polygonal reticulate. Areolation well developed, areoles 4–5 sided. Free-ending veinlets unbranched to 1–2 branched. Fimbrial vein conspicuous. Leaf texture chartaceous.

Holotype—ING-CJ6–0128–0317, Fig. 6A, B

Paratypes—ING-CJ6–0154–0317, Fig. 6C, D

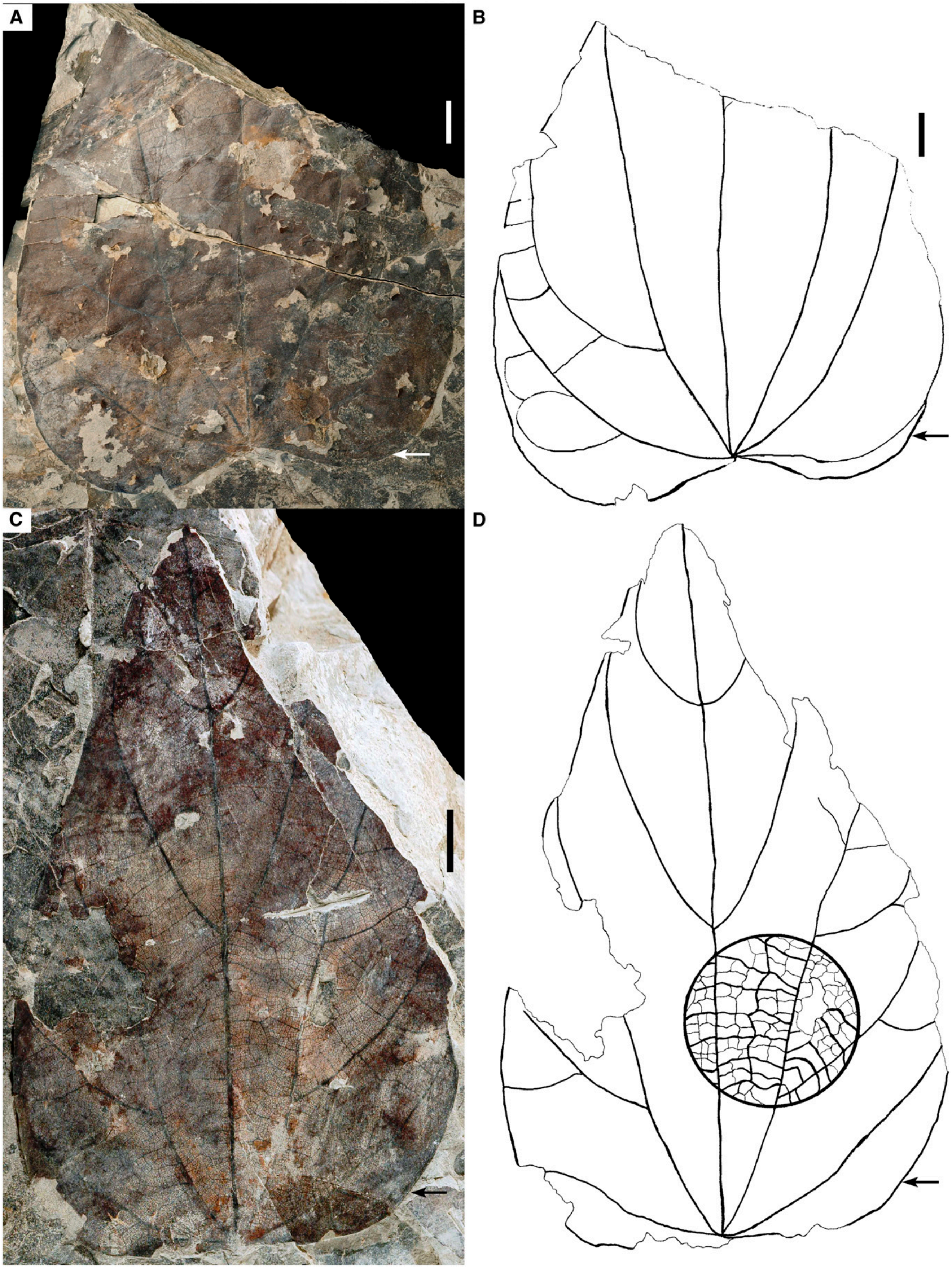
Type locality—0317, Pit Tabaco, Cerrejón coal mines, northern side of the Cesar-Rancheria basin, Guajira peninsula, northern Colombia, located at 11°14′ N. 72°57′ W.

Horizon—Upper part of the Cerrejón Formation. Between coal seams 100 and 102.

Derivatio nominis—The specific epithet refers to the characteristic cordate base shape.

Studied material—ING-CJ6–0120–0317, ING-CJ6–0121–0317, ING-CJ6–0125 to ING-CJ6–0134–0317, ING-CJ6–0155–0317, ING-CJ6–0156–0317, ING-CJ6–0158–0317 to ING-CJ6–0160–0317, ING-CJ6–0162–0317 to ING-CJ6–0164–0317, ING-CJ6–0167–0317, ING-CJ6–0176–0315, ING-CJ6–0177–0317, ING-CJ6–0179–0315.

Description—Specimens assigned to this morphotaxon were found at localities 0315 and 0317. It is the most common form in the localities, with 25 specimens. Leaf shape is ovate with the base wide and cordate. Marginal petiole has been detected in four specimens (ING-CJ6–0121–0317, ING-CJ6–0156–0317, ING-CJ6–0159–0317, ING-CJ6–0132–0317), which showed it as either stout and straight or thin and curved (Fig. 6C, D). Central primary is slightly curved toward the apex, and central secondaries are subopposite or alternate. First pair of lateral primaries merge at an acute to perpendicular (40–90°) angle from the central, reaching 2/3–1/4 the distance to the apex, looping with the central secondaries. The second pair of lateral primaries and subsequent pairs emerge at a wide acute to obtuse (70–120°) angle; all primaries with concave ascending course toward the apex. First and second pairs of lateral primaries branching distally at 1/2 the length. Several tertiaries merging distally from the exmedial pairs of primaries (simple or compound agrophics) at an obtuse to perpendicular angle, joining superadjacent vein at an acute angle. In many of the specimens, conspicuous opposite percurrent third venation occurs, with the angles of the tertiaries becoming more obtuse with respect to the midrib, away from the axis


A
B
C
D

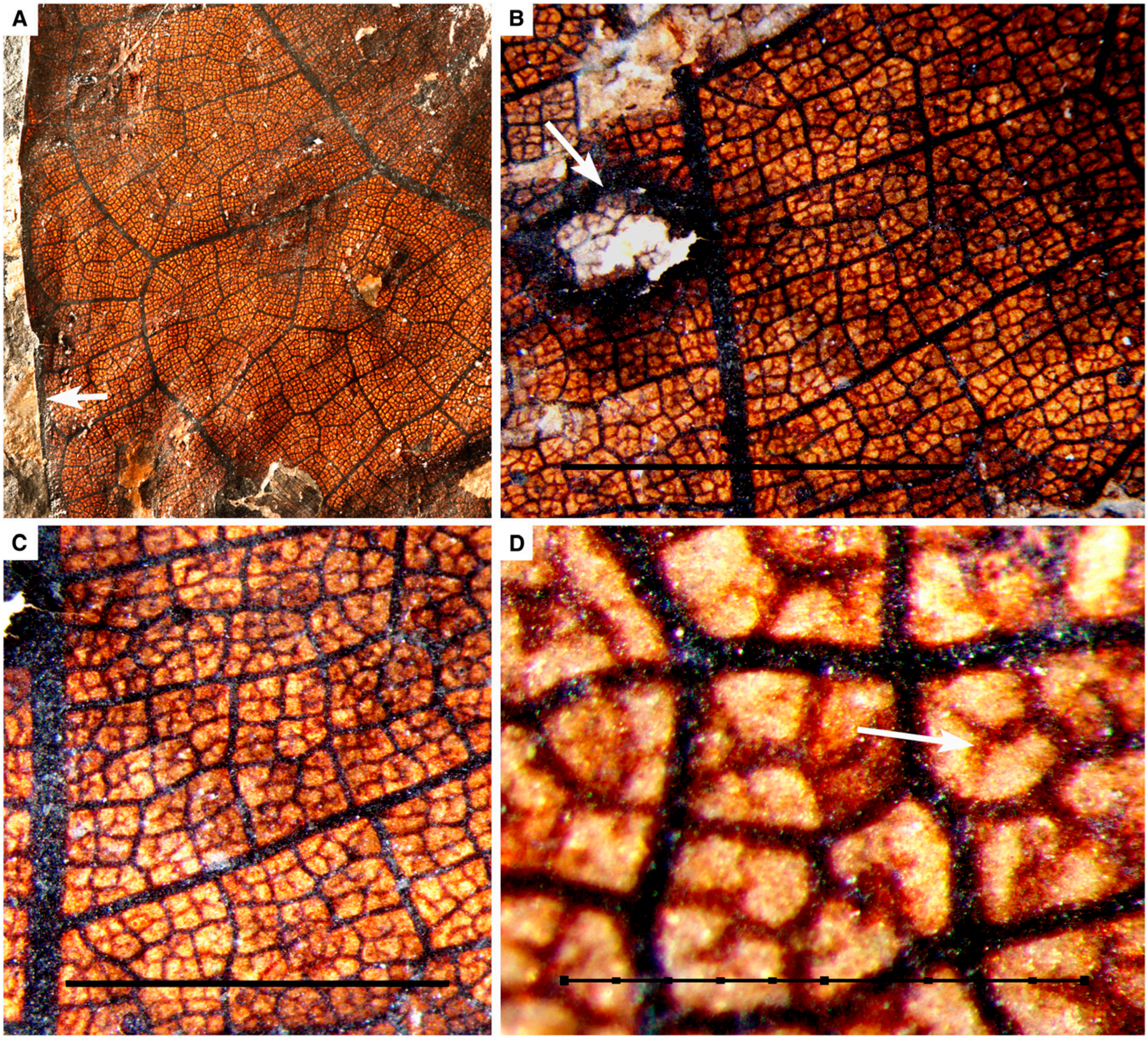


Fig. 4. Venation patterns of *Menispermites cerrejonensis* Doria, Jaramillo & Herrera sp. nov. (A) Secondary brochidodromous venation. Arrow: fimbrial vein, ING-CJ6–0137–0317. (B–D) ING-CJ6–0908–0318. (B) Tertiary, fourth and fifth orders of venation. Arrow: sign of herbivory. (C) Close up of (B). (D) Areolation. Arrow: branched free ending veinlets. Scale bars: B = 5 mm, C = 3 mm, D = 1 mm.

of symmetry, forming almost continuous concentric semicircles of tertiary veins; this pattern is not evident where the third venation is alternate percurrent or alternate-opposite percurrent (Fig. 6). Highest venation orders and fimbrial vein are well preserved in many specimens, but it was not possible to prepare cuticles.

Comparisons—*Menispermites cordatus*, like *M. cerrejonensis*, presents one or few pairs of secondaries merging from the midrib with the lowermost pair arising above the middle of the blade; however, *M. cordatus* presents deeply cordate bases, concave ascending principal veins, and tertiary venation mostly opposite percurrent, whereas *M. cerrejonensis* presents rounded to truncate bases, straight or slightly curved ascending secondaries and mostly alternate percurrent tertiary venation.

The combination of characters found in *M. cordatus* is also found in the neotropical genus *Abuta* Aublet (clade II-A,

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Fig. 3. Leaf architecture of *Menispermites cerrejonensis* Doria, Jaramillo & Herrera sp. nov. (A, B) ING-CJ6–0145–0318 (holotype). (C, D) ING-CJ6–0907–0318 (paratype). Arrows in A, B and C: fimbrial veins. Circle in D shows third and fourth orders of venation. Scale bars = 10 mm.

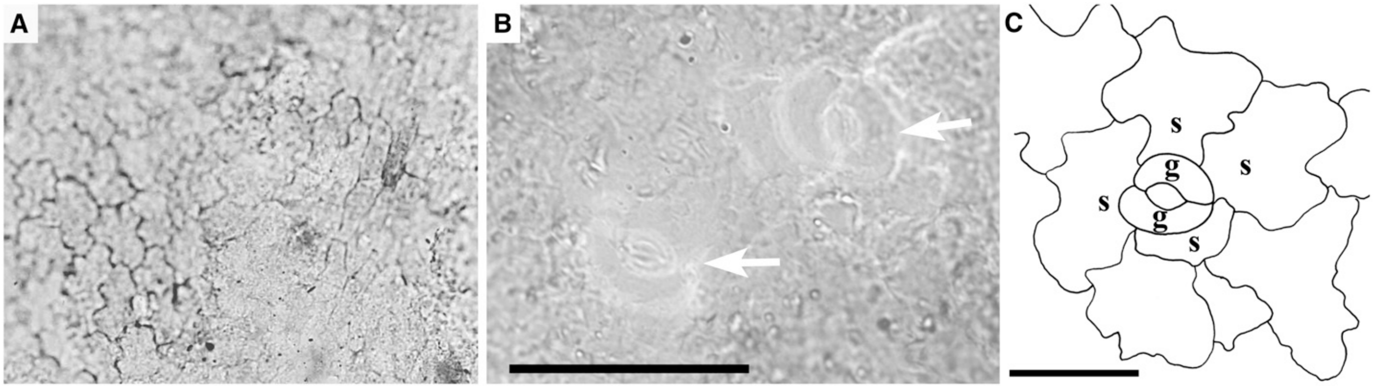

Fig. 5. Cuticular features of *Menispermites cerrejonensis* Doria, Jaramillo & Herrera sp. nov. (A) Epidermal cells. (B, C) Stomata in the areole area. Arrows in (B): guard cells. g = guard cell, s = subsidiary cell. Scale bars= 25 µm.

Anomospermae, Ortiz et al., 2007). Conspicuous opposite percurrent tertiaries, forming concentric semicircles, are also present in many *Abuta* species [e.g., *A. rufescens, A. mycetandra* Krukoff & Barneby, and *A. pahni* (Mart.) Krukoff & Barneby]. *Menispermites cordatus* differs from *Abuta* species with broadly ovate leaves in having secondaries and tertiaries looping far from the margin in rounded arches, whereas extant species of *Abuta* have veins looping conterminous to the fimbrial vein occur, at least at the basal part of the blade.

Species—Menispermites guajiraensis Doria, Jaramillo & Herrera sp. nov.

Diagnosis—Simple mesophyllous to megaphyllous leaves. Ovate symmetrical lamina, 18 (13–30) cm long and 18.5 (11–28) cm wide (3 specimens measured); base cordate, base angle obtuse; apex not preserved. Margin entire and unlobed. First vein category actinodromous basal, 5–7 veins from the base; central primary wider than the lateral primaries. Secondary venation brochidodromous; several pairs of ascending secondaries from the midrib, with the lowermost pair merging below the middle of the blade; central secondaries opposite to subopposite. Third vein category opposite percurrent. Fourth and fifth venation orders regular polygonal reticulate. Areolation well developed. Fimbrial vein not observed, but probably present.

Holotype—ING-CJ6–0169–0319 (Fig. 7A, B)

Paratype—ING-CJ6–0868–0319

Type locality—0319, Pit Tabaco High Deep, Cerrejón coal mines, northern side of the Cesar-Rancheria basin, Guajira peninsula, northern Colombia, 11°66′ N, 73°31′ W.

Horizon—Middle part of the Cerrejón Formation. Between coal seams 105 and 106.

Derivatio nominis—The specific epithet refers to the collection area at Guajira Department.

Studied material—ING-CJ6–0122–0317, ING-CJ6–0154–0317, ING-CJ6–0170–0319, ING-CJ6–0171–0319.

Description—Specimens were collected from localities 0317 and 0319. The largest specimens of the morphotype CJ6, reaching the megaphyll size category, are included in this morphotaxon. Petiole, where present, is marginal and stout. Central primary markedly wider than the lateral ones, with straight course. Central secondaries emerging at an acute angle, with straight to smoothly curved course toward the margin. The innermost pair of lateral primaries emerging at an acute (30–60°) angle from the central primary, with straight course, ascending 3/4 of the total length, looping with central secondaries, branching exmedially several times, each secondary merging at an acute angle joining with the superadjacent vein at an obtuse angle; second pair of primaries merging at a wide acute to obtuse (70–106°) angle, with slightly curved course toward the margin reaching 1/4 of the total length of the blade, subparallel to the secondaries from the first lateral primaries, looping with the lowermost secondary; several tertiaries merging distally at an acute angle, each one joining with the superadjacent at an acute angle (Fig. 7A, B). Leaf texture is chartaceous to coriaceous. Highest orders of venation are not easily recognizable.

Comparisons—*Menispermites guajiraensis* differs from *M. cerrejonensis* and *M. cordatus* in having several pairs of secondaries merging from the midrib, with the lowermost pair arising below the middle of the blade, not one to few central secondaries merging above the middle of the blade. *Menispermites horizontalis* presents a pattern of central secondaries distribution similar to that of *M. guajiraensis*, but the secondaries in this taxon are horizontal and not with straight to smoothly curved course toward the margin. Thus, the characters that allow us to differentiate *M. guajiraensis* from the other taxa here described are the number of secondary veins and their angle and course.

Among extant Menispermaceae, the fossils present some similarities with *Elephantomene* Barneby & Krukoff (clade II-A, Anomospermae, Ortiz et al., 2007). This resemblance is particularly strong in the following characters: (1) several regularly spaced medial secondary veins, departing from the midrib at an acute angle with straight course toward the margin; (2) first pair of lateral primaries merging at an acute angle, branching exmedially in a series of straight parallel secondaries regularly spaced; and (3) exmedial pair of primaries merging at an obtuse angle reaching 1/4 or less the distance to the apex. In *Elephantomene eburnea* Barneby & Krukoff, the only extant species of the genus, the leaves are broadly ovate to suborbicular, and the bases are rounded to truncate (Ott, 1997), not cordate as in *M. guajiraensis*. Both *E. eburnea* and *M. guajiraensis* have major secondaries that form a narrow acute angle with the central primary, thus forming a fan (Ott, 1997). Establishing the affinities of this taxon is rather difficult because the highest orders of venation—reliable characters for confirming affinities within Menispermaceae—were not well preserved.

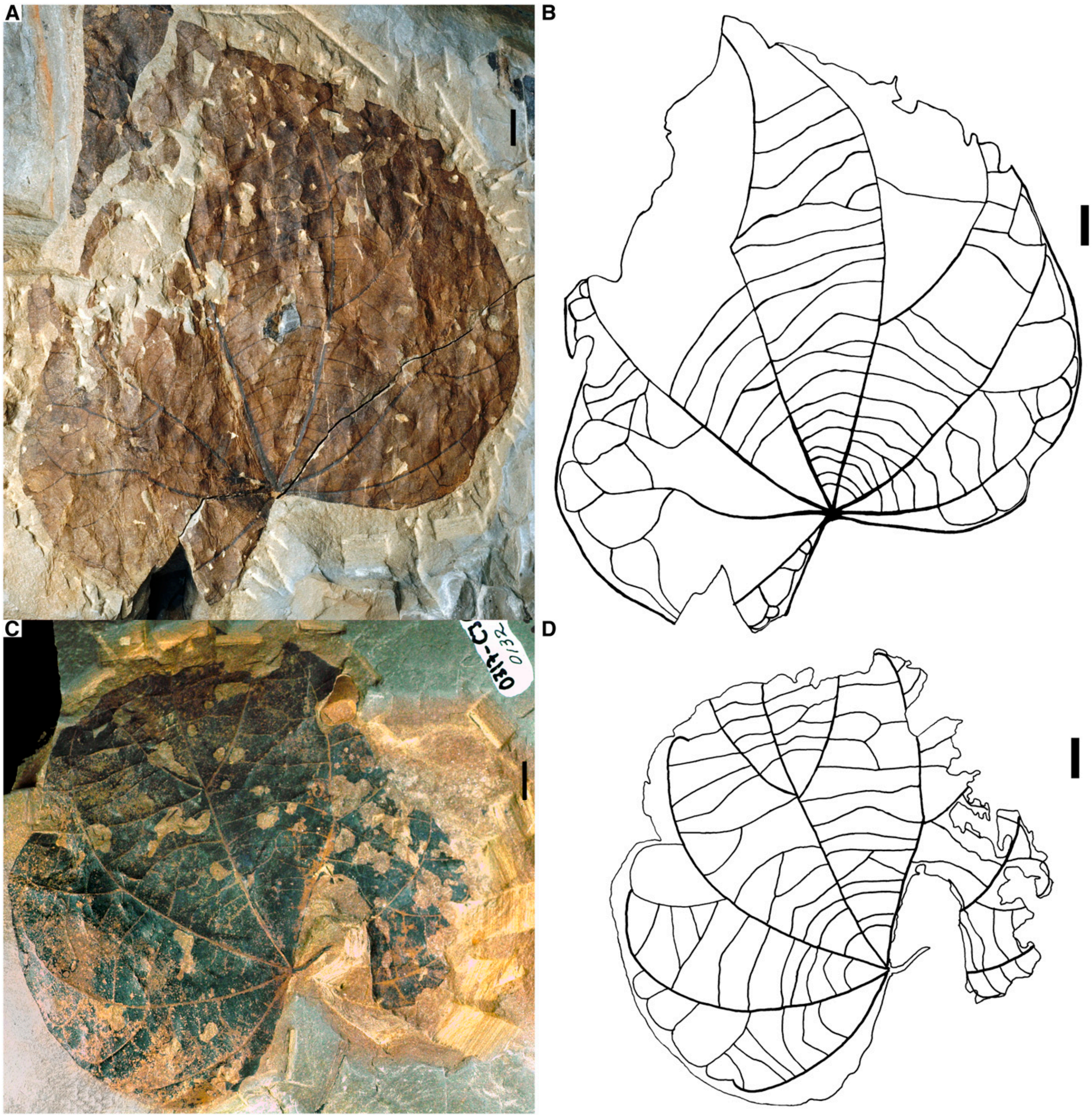

Fig. 6. Leaf architecture of *Menispermites cordatus* Doria, Jaramillo & Herrera. (A, B) ING-CJ6–0128–0317 (holotype). (C, D) ING-CJ6–0154–0317. Scale bars = 10 mm.

Species—Menispermites horizontalis Doria, Jaramillo and Herrera sp. nov.

Diagnosis—Simple megaphyllous leaves. Ovate symmetrical lamina; base not preserved; apex acute, apex angle acute. Margin entire and unlobed. First vein category probably actinodromous basal, 3 (probably 5) veins from the base; central primary wider than the lateral primaries. Secondary venation brochidodromous; several pairs of horizontal secondaries from the midrib, with the lowermost pair merging below the middle of the blade; central secondaries opposite. Third vein category opposite percurrent. Fourth and fifth venation orders regular polygonal reticulate. Areolation well developed. Fimbrial vein present.

Holotype—ING-CJ6–0166–0317 (Fig. 8)

Type locality—0317, Pit Tabaco, Cerrejón coal mines, northern side of the Cesar-Rancheria basin, Guajira peninsula, northern Colombia, located at 11°14′ N, 72°57’′W.

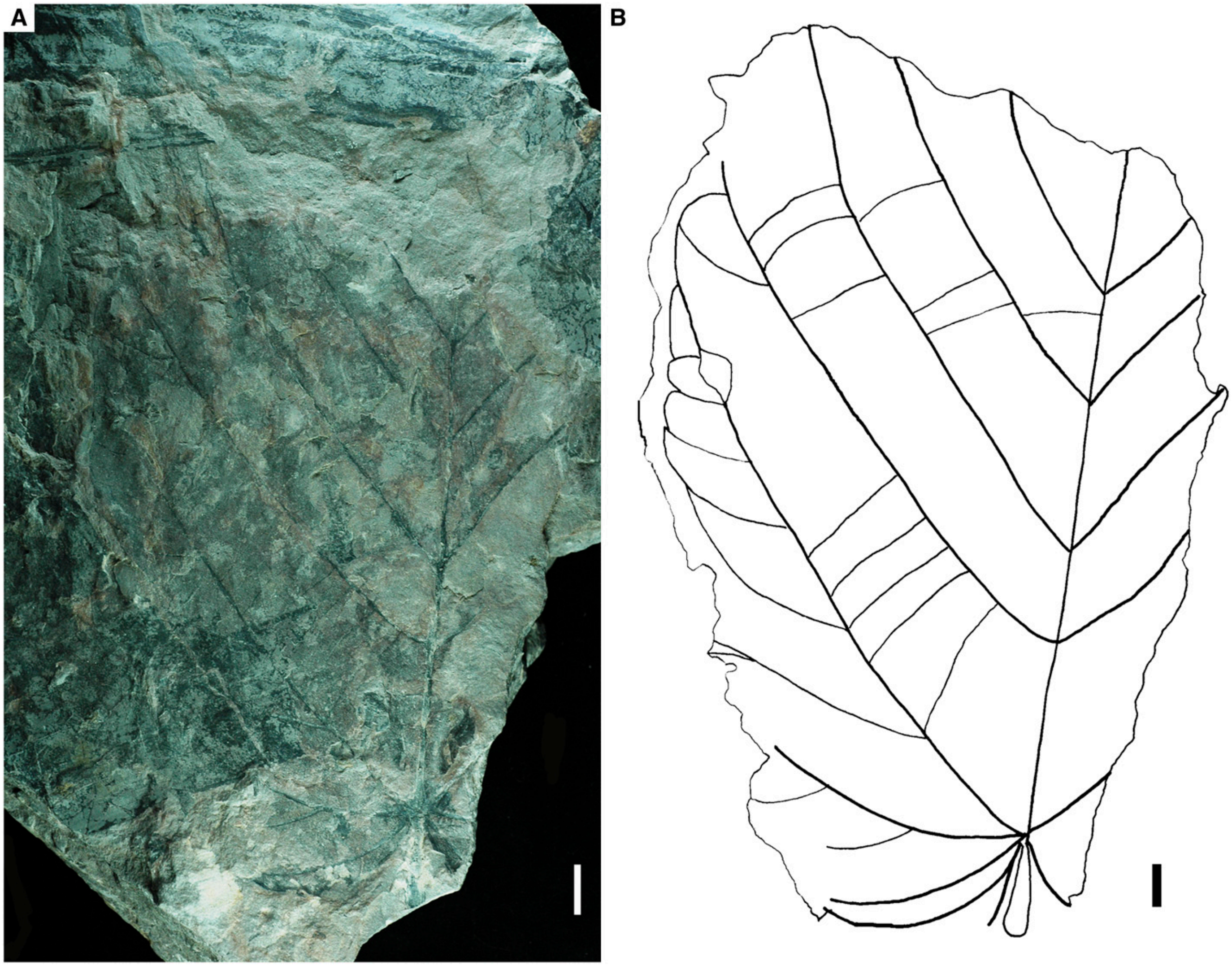

Fig. 7. Leaf architecture of *Menispermites guajiraensis* Doria, Jaramillo & Herrera sp. nov. ING-CJ6–0169–0319 (holotype). Scale bars = 10 mm.

Horizon—Upper part of the Cerrejón Formation. Between coal seams 100 and 102.

Derivatio nominis—The specific epithet refers to the characteristic horizontal secondary venation.

Studied material—ING-CJ6–0166–0317

Description—Specimen was collected in locality 0317. It is a fragmentary leaf that has a marginal vein, apparently palmate venation (the base is missing), two pairs of conspicuous presumed lateral primaries with slightly curved course toward the apex (Fig. 8A). Numerous pairs of secondaries merging from the midrib at a perpendicular angle, the lowermost arising below the middle of the blade, medial secondaries opposite with horizontal course (Fig. 8A, B). Exmedial secondaries departing from lateral primaries at a wide acute to perpendicular angle, also with horizontal course, looping with the superadjacent at an acute angle (Fig. 8C). All secondaries (medial and exmedial) regularly and closely spaced. Tertiary veins opposite percurrent, perpendicular to secondaries (Fig. 8C). Leaf texture chartaceous.

Comparisons—*Menispermites horizontalis*, like *M. guajiraensis*, presents several medial secondaries with the lowermost merging below the middle of the blade, but differs in having numerous horizontal instead of ascending medial secondaries. Moreover, the number of medial secondaries is higher in *M. horizontalis*. As in *M. cordatus*, *M. guajiraensis* has third venation opposite percurrent, but the two differ in the position and number of medial secondaries.

Among extant Menispermaceae, several characters are similar to those of the neotropical *Sciadotenia* (clade II, Tiliacoreae, Ortiz et al., 2007), including (1) the presence of numerous horizontal secondaries, (2) tertiary venation opposite percurrent, and (3) exmedial secondaries joining with the uppermost in an acute angle. In *Sciadotenia* usually the innermost pair of primary veins are plinerved (i.e., suprabasal actinodromous venation), diverging 0.3–1 cm above the base (Ott, 1997; G. Doria, personal observation); however; this character is not preserved in this specimen.

DISCUSSION

The general morphology observed in the four species described suggests a relationship to the angiosperm family

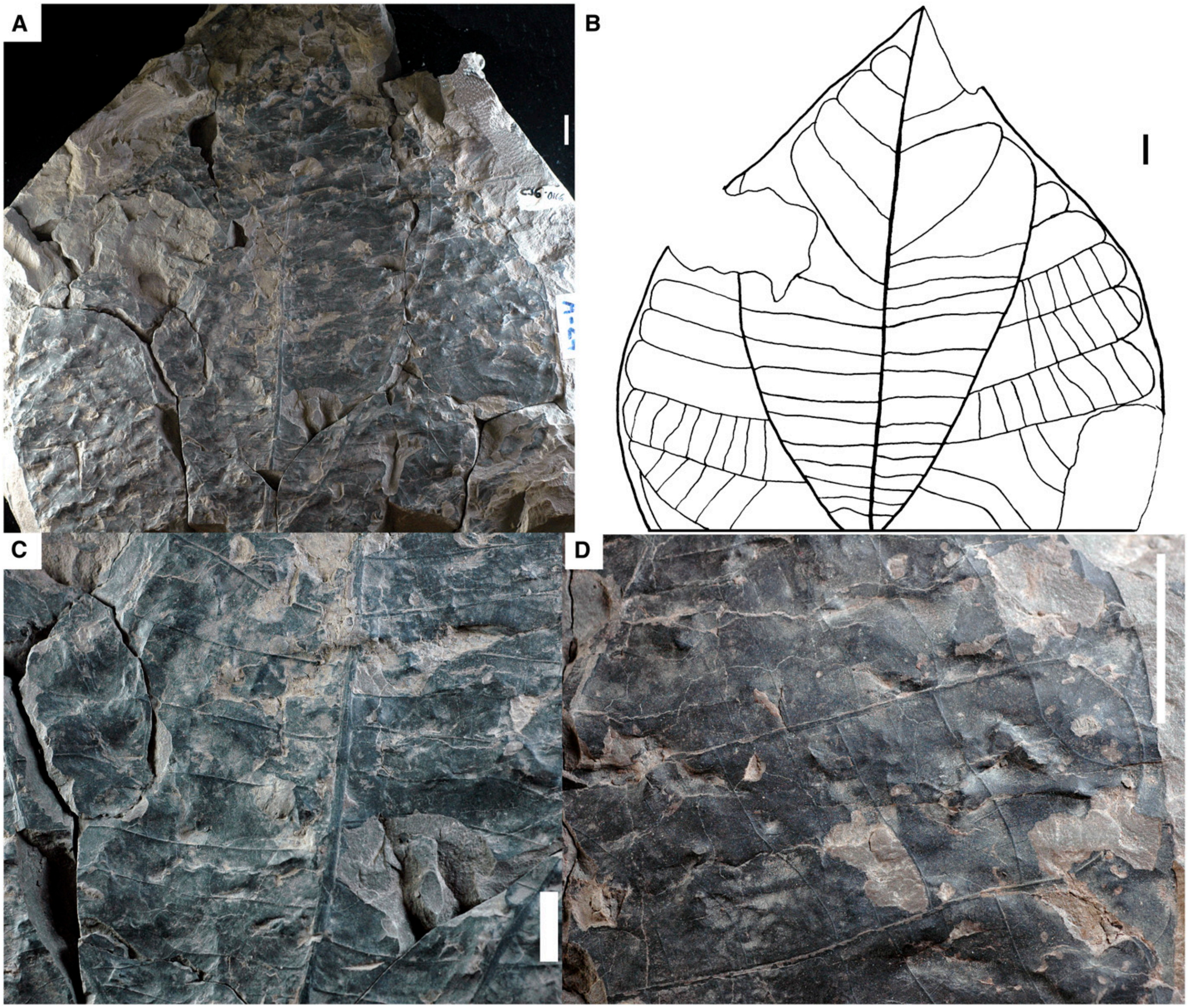

Fig. 8. Leaf architecture of *Menispermites horizontalis* Doria, Jaramillo & Herrera sp. nov. (A–D) ING-CJ6–0166–0319 (holotype). (C) Medial secondaries. (D) Exmedial secondaries and perpendicular tertiaries. Scale bars = 10 mm.

Menispermaceae (basal eudicots, Ranunculales, APG II, 2003). Similar characteristics are pointed out by Wolfe (1968, 1977) as diagnostic for fossil leaves of Menispermaceae. The principal features of the new morphotaxa indicating a relationship with this family are (1) primary venation actinodromous; (2) secondary veins brochidodromous with conspicuous rounded loops; (3) tertiary veins opposite percurrent, alternate percurrent, or mixed opposite-alternate percurrent; (4) fourth and fifth venations polygonal reticulate; (5) areolation well developed; (6) margin entire; and (7) fimbrial vein present.

Other unrelated families, Aristolochiaceae and Malvaceae, also present the first four characters, but they do not have a fimbrial vein. The fimbrial vein results from the fusion of higher vein orders into a vein running just inside the margin, and it is almost a constant character in the fossil specimens, except in the specimens of *M. guajiraensis*. Conspicuous loops formed by the fusion of primary and secondary veins are present in Aristolochiaceae and Malvaceae as well; however, in Aristolochiaceae these arcs correspond to a brochidodromous festooned type of venation, whereas in Menispermaceae the venation is brochidodromous simple. In Malvaceae the arcs are mainly angular and sharp, not well rounded as in Menispermaceae.

The generic name here adopted for the four new taxa, *Menispermites* Lesquereux (Lesquereux, 1874), was originally proposed to describe broadly deltoid, peltate, or subpeltate, trilobed fossil leaves with actinodromous first venation, from the Upper Cretaceous of North America, presumably related to Menispermaceae (e.g., Hickey and Wolfe, 1975). The genus is used now to encompass a wider morphological range including taxa with wide ovate to orbicular, peltate, subpeltate, or basifixed, unlobed to 3- or 5-lobed leaves with actinodromous or acrodromous first venation (Table 4). Several species have been

Table 4. Comparative table of morphological features of fossil leaf taxa, presumably related to Menispermaceae.

Taxon	Leaf shape	Lobation	Petiolar attachment	Margin	Base shape	Apex	1st Venation	No. of primaries	2nd Venation	No. pairs of central secondaries	3rd Venation	Marginal ultimate venation	Time	Literature
Menispermites acerifolia Lesquereux	Deltoid	3–5 Lobate	Not peltate (marginal?)	Entire	Nearly truncate to cuneate	Lobed acute apex	Actino	3–5	?	1–2	?	?	Cretaceous	Lesquereux, 1874
M. acutilobus Lesquereux	Deltoid	Lobate	?	Dentate	Broadly rounded-nearly truncate	Lobed acute apex	Actino	5	Craspe	?	Open inosculating network		Late Cretaceous	Bell, 1957
M. americanus Berry	Slightly cordate (Ovate)	Unlobed	Marginal	Entire	Broadly truncate or slightly cordate	Bluntly pointed	Pinnate	1	Campto (Brochi.)	4–5	?	?	Eocene	Berry, 1930
M. belli Berry	Ovate	Unlobed	?	Entire	Cordate	Rounded	Actino	5	Campto	?	?	?	Late Cretaceous	Dorf, 1942
M. cockerelli (Knowlton) Dorf	?	Unlobed	Subpeltate	Entire–undulate	?	?	?		Campto	?	Opposite percurrent	?	Late Cretaceous	Dorf, 1942
M. hardemanensis Berry	Ovate	Unlobed	Marginal	Entire	Broadly truncated to slightly cordate	?	Actino	3 (5?)	Campto–brochi?	2–3	?	?	Eocene	Berry, 1930
M. knightii Knowlton	Orbicular	Lobed	?	Lobed-undulate	Cordate	Rounded	Actino	7	Campto	?	?	?	Late Cretaceous	Dorf, 1942
M. limaciodes MacGinitie	Ovate	Unlobed	Marginal	Entire	Cuneate	Acuminate	Acro		Looping near the margin	?	Opposite percurrent	Fimbrial	Eocene	MacGinitie, 1969
M. obtusiloba Lesquereux	Reniform-deltoid	Obscurely 3-lobate	Peltate	Deeply undulate	Obtuse, peltate, enlarged and truncate	?	Actino	5	Subcraspe	None–few	?	?	Cretaceous	Lesquereux, 1874
M. parvareolatus Hickey	Very wide ovate	Unlobed	Marginal	Shallowly lobed	Obtuse (Concave)	Rounded-emarginate	Acro	3	Looping near the margin	?	High acute angles	Fimbrial	Paleocene	Hickey, 1977
M. potomacensis Berry	Orbicular to oval, ovate	Unlobed	Marginal	Crenate-undulate	Cuneate	Rounded	Actino	7–13	?	?	?	?	Late Cretaceous	Bell, 1956, Doyle and Hickey, 1976
M. reniformis Dawson	Semiorbicular to Semielliptical	Unlobed	Marginal	Entire-slightly undulate	Cordate	Rounded	Actino	7	Campto	?	?	?	Late Cretaceous	Bell, 1956
M. salinensis Lesquereux	Broadly triangular	Obscurely 5-lobed or Deeply undulately lobed	Not peltate (marginal?)	Deeply undulately lobed	Nearly truncate or attenuated cuneiform	?	Actino	5	Brochi	?	?	?	Cretaceous	Lesquereux, 1874
Menispermites sp. Bell	?	Lobed?	?	?	Asymmetrical-cordate	?	Actino	5	?	?	?	?	Late Cretaceous	Bell, 1962
Menispermites sp. (Knowlton) n. comb. Bell	Ovate	Unlobed	?	Entire	Cordate	?	Actino	?	?	?	Opposite percurrent	?	Late Cretaceous	Bell, 1962, (plate 20, fig. 3)
M. tenuinevis Fontaine	Ovate		?		Truncate to obtuse		Actino	?	?	?	?	?	Late Cretaceous	Doyle and Hickey, 1976
M. torosus Bell	Ovate-orbicular	Unlobed	?	Entire?	Truncate-slightly cordate	?	Actino	5(−7)	Brochi–campto	Few, remote from the base	Percurrent, fairly strong	?	Late Cretaceous	Bell, 1957
M. virginiensis Fontaine	Orbicular	Unlobed	?	Crenulate	Cordate	?	Actino	10	?	?	?	?	Late Cretaceous	Doyle and Hickey, 1976

TABLE 4. Continued.

Taxon	Leaf shape	Lobation	Petiolar attachment	Margin	Base shape	Apex	1st Venation	No. of primaries	2nd Venation	No. pairs of central secondaries	3rd Venation	Marginal ultimate venation	Time	Literature
Anamirta milleri Wolfe	Ovate	Unlobed	Marginal	Entire	Cordate	Acuminate	Actino	7	Brochi	?	?	Fimbrial vein	Eocene	Wolfe, 1977
Calkinsia frankliniensis Wolfe	Obovate	Unlobed	Marginal	Entire	Cuneate	Abruptly acute	Actino	3	Campto or craspe	2–4	?	Fimbrial vein	Eocene	Wolfe, 1968
Calkinsia plafkerii Wolfe	Elliptical	Unlobed	Marginal	Entire	Acute	Acuminate	Actino	5	Craspe	3–4	?	Fimbrial vein	Eocene	Wolfe, 1977
Chondrodendron brasiliense Dolianiti	Ovate	Unlobed	Subpeltate	Entire-undulate	Slightly cordate	Retuse	Actino	7	Craspedodromous	Few, above the middle of the blade	?	Fimbrial vein	Pliocene	Dolianiti, 1949
Cissampelos rotundifolia Potbury	Widely ovate	Unlobed	Marginal	Entire	Deeply cordate-peltate	Rounded-slightly retuse	Actino	3	Brochi	4?	?	?	Late Eocene	Potbury, 1935
”*Cocculus*” *flabella* (Newberry) Wolfe	Elliptical to obovate	Unlobed	Marginal	Entire, crenate or shallowly lobate	Acute to obtuse	Rounded-mucronate	Acro	3	Campto	0–4	Regular polygonal reticulate	?	Paleocene	Wolfe, 1966, 1972; Hickey, 1977
Cocculus rotunda MacGinitie	Circular	Unlobed	Marginal	Entire	Broadly rounded-slightly cordate	Rounded	Actino	5	Brochi–craspe	3?	?	?	Miocene	MacGinitie, 1962
Cocculus sp.	?	Unlobed	?	Entire	Rounded	?	Actino	3	Campto	?	?	?	Eocene	Wolfe, 1977 (plate 26, fig. 5)
Cocculus sp. Ozaki	Oval to elliptical	Shallowly 3-lobed	Marginal	Entire	Cordate	?	Acro	3	Campto	?	Weakly percurrent	?	Miocene-Pliocene	Ozaki, 1991
Hyperbaena diforma Potbury	Ovate to obovate	Unlobed	Marginal	Entire	Cuneate to cordate	Acute or acuminate	Actino	5	Brochi	1–2 above the middle of the blade	Opposite percurrent	?	Late Eocene	Potbury, 1935
Hypserpa cashmanensis Wolfe	Elliptical	Unlobed	Marginal	Entire	Narrowly rounded	Rounded	Actino	5	Brochi	Several	?	Fimbrial vein	Eocene	Wolfe, 1968
H. frankliniensis Wolfe	Elliptical	Unlobed	Marginal	Entire	Narrowly rounded	Acute	Actino	5	Brochi	Several	?	Fimbrial vein	Eocene	Wolfe, 1968
Limacia stenophylla Wolfe	Ovate	Unlobed	Marginal	Entire	Narrowly rounded	Acute	Actino	3	Campto	?	Alternate percurrent	Fimbrial vein	Eocene	Wolfe, 1977
Menispermum dauricumoides Bell	Subpentagonal to subhexagonal	Unlobed-lobate	Peltate	Entire-dentate	?	?	Actino	6–8	Craspe	1–2	Loose network	?	Late Cretaceous	Bell, 1957
Paratinomiscium conditionalis Wolfe	Ovate	Unlobed	Marginal	Entire	Broadly rounded	Acute	Actino	5	Campto (forming loops)	?	?	Fimbrial vein	Eocene	Wolfe, 1977
Pycnarrhena sp.	Elliptic	Unlobed	?	Entire	Rounded?	Rounded?	Actino	5	Brochi	?	?	?	Eocene	Wolfe, 1977

Notes: Acro, acrodromous; Actino, actinodromous; Brochi, brochidodromous, Campto, Camptododromous; Craspe, craspedodromous proposed under this generic name from the Upper Cretaceous to Eocene of North America (Fontaine, 1889; Berry, 1916, 1922a, b; Seward, 1927; Hollick and Martin, 1930; Dorf, 1942; Bell, 1956, 1957, 1962; MacGinitie, 1969; Doyle and Hickey, 1976; Hickey, 1977; Wing et al., 1995), Asia (Kryshtofovich and Baikovskaia, 1960; Budantsev, 1968; Takhtajan, 1974; Spicer et al., 2002), and Europe (Hughes, 1976). The four species described here fit into the broad diagnosis for the genus. *Menispermites* species cannot be assigned to a tribe within Menispermaceae, but they have many characteristics of leaf morphology and venation patterns that suggest an affinity with Menispermaceae.

Leaf characters are thought to be highly homoplasious within Menispermaceae (Ortiz et al., 2007). Examination of the morphological transitions in the molecular phylogeny of the family shows that the typically simple leaf with actinodromous venation is the plesiomorphic condition in the family (Ortiz et al., 2007). Leaf characters in Menispermaceae have been reported as useful for identification (Ott, 1997), but the full variation of leaf morphology, including cuticles, among all 70 genera of Menispermaceae remains to be studied.

Although similar to the leaves of several modern menispermaceous taxa, each species of *Menispermites* described here has a unique combination of features not found in living Menispermaceae or other fossil leaves. However, some characters could be used to relate the fossils to extant groups. In *Menispermites cerrejonensis* the membranaceous leaf texture is notable, suggesting a herbaceous habit, and the venation pattern of secondaries (Figs. 3, 4) resembles that of several species of *Disciphania*, tropical American climbers currently centered in Amazonia (Kessler, 1993). Leaf texture is hardly recognizable in the other three fossil taxa because of the type of fossilization (impressions vs. compressions in *M. cerrejonensis*). In *Menispermites cordatus*, the most conspicuous characters are the strongly curved primaries and medial secondaries, and the opposite percurrent third venation (Fig. 6A–D). This species resembles some species of the extant *Abuta*, the most speciose genus of Menispermaceae in the neotropics with ~32 species (Kessler, 1993). *Menispermites guajiraensis* resembles *Elephantomene*, a monospecific genus from the South American tropics, in the pattern of first and second venation, where the major secondaries form a narrow acute angle with the central primary, forming a fan (Fig. 7A, B). The presence of horizontal secondaries in *M. horizontalis* (Fig. 8) is characteristic of the extant *Sciadotenia*, a genus of ~20 species of climbers from tropical Central and South America (Kessler, 1993). However, a megaphyllous leaf size is not common in the extant *Sciadotenia*.

Most of the extant species of Menispermaceae are lianas or vines. Woody habit probably is the ancestral condition in the group (Kim et al., 2004; Ortiz et al., 2007). Lianas are an important component in neotropical floras (Gentry, 1991) and influence the dynamics of many forests (Schnitzer et al., 2000; Schnitzer and Bongers, 2002; Londré and Schnitzer, 2006). The presence of extant families of lianas as Menispermaceae, Icacinaceae, and Vitaceae, has been suggested as an indicator of the multilayered structure of Cenozoic forests in contrast with Late Cretaceous forests (Muller, 1981, 1984; Upchurch and Wolfe, 1987). This multilayered structure is also indicated by the fossil record of families during the Eocene that form tall canopy trees in megathermal rain forests (e.g., Anacardiaceae, Sapotaceae) (Reid and Chandler, 1933; Wolfe, 1977). Upchurch and Wolfe (1987) proposed that many of the patterns of diversification seen in extant families during the Early Cenozoic are explained by canopy closure coupled with an increase in forest height and canopy stratification. Our study suggests that Menispermaceae was present very early in the Cenozoic, being the earliest record for this family of lianas in the South American tropics. There are very few records of fossil floras from the Late Cretaceous of tropical South America. However, preliminary analysis of a new Maastrichtian flora (ca. 70 Ma) from central Colombia, the Guaduas flora, indicates the absence of Menispermaceae (Gutierrez and Jaramillo, 2007). The Paleocene Cerrejón paleoflora could then be the oldest record of a multistratified tropical rain forest in the neotropics, suggesting that multistratification is an ancient characteristic of South American rain forests, one that evolved following the Cretaceous–Paleocene transition.

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