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Middle to Late Paleocene Leguminosae fruits and leaves from Colombia

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Abstract. Leguminosae are one of the most diverse flowering-plant groups today, but the evolutionary history of the family remains obscure because of the scarce early fossil record, particularly from lowland tropics. Here, we report ~500 compression or impression specimens with distinctive legume features collected from the Cerrejón and Bogotá Formations, Middle to Late Paleocene of Colombia. The specimens were segregated into eight fruit and six leaf morphotypes. Two bipinnate leaf morphotypes are confidently placed in the Caesalpinioideae and are the earliest record of this subfamily. Two of the fruit morphotypes are placed in the Detarioideae and Dialioideae. All other fruit and leaf morphotypes show similarities with more than one subfamily or their affinities remain uncertain. The abundant fossil fruits and leaves described here show that Leguminosae was the most important component of the earliest rainforests in northern South America *c*. 60–58 million years ago.

Additional keywords: diversity, Fabaceae, fossil plants, legumes, Neotropics, South America.

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Introduction

Leguminosae, the third-largest family of flowering plants with ~770 genera and ~19 600 species, has a cosmopolitan distribution and an extraordinary ecological (e.g. symbiosis with nitrogen-fixing bacteria) and economic importance (e.g. Doyle and Luckow 2003; Lewis *et al*. 2005; Legume Phylogeny Working Group 2013*a*, 2013*b*; Epihov *et al*. 2017). The family is one the most dominant plant groups in the Neotropics (Phillips *et al*. 2002), from lowland rainforests to deciduous and semi-arid forests and savannas (Schrire *et al*. 2005*a*, 2005*b*; Yahara *et al*. 2013).

Six subfamilies are currently recognised within Leguminosae on the basis of plastid *mat*K gene sequences obtained from a large number of genera (~91.2% of all currently recognised genera; Legume Phylogeny Working Group 2017) and include the following: Caesalpinioideae, Cercidoideae, Detarioideae, Dialioideae, Duparquetioideae and Papilionoideae. The relationships among the three early branching subfamilies (i.e. Cercidoideae, Detarioideae and Duparquetioideae) are still unresolved, whereas the other three subfamilies form a strongly supported clade (i.e. Caesalpinioideae, Papilionoideae and Dialioideae; Lavin *et al*. 2005; Bruneau *et al*. 2008; Legume Phylogeny Working Group 2017). Stem-group Leguminosae has been inferred to originate *c*. 92.1 million years ago (Magallón *et al*. 2015) and many other studies have inferred dates for the crown clades ranging from the Cretaceous to the Early Paleogene, *c*. 90–50 million years ago (e.g. Wikström *et al*. 2004; Lavin *et al*. 2005; Bruneau *et al*. 2008; Bell *et al*. 2010). Tremendous efforts have been made to understand the relationships and rates of molecular evolution within Leguminosae. Although these studies have been very helpful in understanding the origin and patterns of relationships of extant legumes, the only direct evidence we have of diversity through time and evolutionary history comes from the fossil record.

Here, we report abundant and well preserved Middle to Late Paleocene fossils from Colombia on the basis of fruits and leaves that can be confidently assigned to the Leguminosae. The purposes of this study are to present the descriptions of legume diversity observed in the Paleocene of northern South America, and to assess their overall phylogenetic affinity to the extent possible. This report on fossil legumes from Colombia is significant because there are very few records of fossil plants from low-latitude tropics, where the family is most diverse today. The fossils document important additional evidence about three extant legume subfamilies, diversity and abundance in Paleocene Neotropical rainforests.

Materials and methods

The fossil fruits and leaves reported here were collected from the Cerrejón and Bogotá Formations in Colombia. These two

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stratigraphic sequences are geographically separated but they are approximately coeval. The Cerrejón Formation crops out in the open cast Cerrejón coalmine, near the base of the Guajira Peninsula, ~1000 km north-east of Bogotá (GPS: ~11.1°N, 72.5°W; see also Wing *et al*. 2009). The Bogotá Formation is exposed in open clay pits of central Colombia, Sabana de Bogotá (GPS: Nemocón locality: ~5°08′146″N, 73°50′820″W; Cogua locality: ~5°04′605″N, 73°57′318″W), between 2700 and 3000 m above sea level along the Eastern Cordillera.

Approximately 300 legume specimens (fruits and leaves) were collected from the middle and upper levels of the Cerrejón Formation, a ~700-m-thick stratigraphic sequence composed of abundant and thick coals, sandstones and siltstones (Bayona *et al*. 2008). This formation was deposited in a complex system of coastal to fluvial floodplains. The Cerrejón strata have been dated as Middle to Late Paleocene (*c*. 60–58 million years ago) on the basis of pollen zonation, correlations with stable carbon isotopic data, and marine microfossils (Jaramillo *et al*. 2007, 2011).

Approximately 200 legume specimens (fruits and leaves) were collected from the Bogotá Formation. The stratigraphic sequence is composed of extensive and thick siltstones, claystones, paleosols, inter-bedded sandstones, sporadic conglomerates and breccias (Morón *et al*. 2013). This formation was deposited predominantly in fluvial environments, and characteristically lacks coal deposits. During the Paleocene, the Andes had not been uplifted and the Bogotá Formation was deposited in lowland settings (Bayona *et al*. 2010). Pollen assemblages from the same sites where the megafossils were collected belong to the zone T-03b-*Foveotricolpites perforatus* of Jaramillo *et al*. (2011), indicating Middle to Late Paleocene age (*c*. 60–58 million years ago).

Fossil specimens are deposited at the paleontological collections of the Colombian Geological Survey (SGC) and the Colombian Petroleum Institute (ICP). Additional information about samples and localities can be accessed through the Smithsonian Tropical Research Institute (STRI) sample database (http://biogeodb.stri.si.edu/jaramillosdb/web/login, accessed 30 April 2019). The leaf morphological descriptions are based on the terminology of shape and venation characters of Ellis *et al*. (2009). The terminology of the fruit morphological descriptions is mostly based on Gunn (1984, 1991), Kirkbride *et al*. (2003) and Legume Phylogeny Working Group (2017).

Results

All fossil fruits and leaves are described here as 'morphotypes', an informal taxonomic category, rather than identified to formal taxonomic groups. Eight fruit and six leaf morphotypes referable to the Leguminosae are recognised from the Cerrejón and Bogotá Formations (Table 1).

Fruit morphotype 1

(Fig. 1A–C.)

Fruits incomplete, ~14 cm long and ~6 cm wide. Placental margin conspicuously winged, ~0.7–1.1 cm wide. Non-placental margin inconspicuous, not winged. Fragment of pedicel ~2.2 cm long. Base outline obtuse, rounded; apex not preserved. Seeds 6–10+, attached along the placental margin. Seed chambers distinct, strongly septate, more or less symmetrical near the centre (arranged in a columnar-like pattern) of the fruit to asymmetrical near the base, ~0.7–1.8 cm wide, transverse to slightly oblique near the base of the fruit.

Remarks

Both specimens are from the Cerrejón Fm. (locality SW0317). This is the largest legume fruit morphotype described here. The fruits appear to have been thin and membranous, not woody, and were probably indehiscent wind-dispersed samaras.

Comments on affinity

Broadly winged fruits are known from several legume genera, including *Mezoneuron* (Caesalpinioideae), *Barnebydendron* (Detarioideae), *Zenia*, *Storckiella* and *Dicorynia* (Dialioideae). This type of samara has evidently evolved multiple times within the family. Venation patterns on the valves and wing can be useful in distinguishing among the genera (Herendeen and Dilcher 1990); however, venation details are not preserved in these fossil fruits. The fruits are perhaps most similar to those of *Barnebydendron* (occurs today in Central and South America) in their overall size and presence of multiple seeds; however, without venation details, it is not possible to investigate relationships beyond the superficial resemblance.

Fruit morphotype 2

(Fig. 1D.)

Fruit nearly complete, ~2.2 cm long and 1.3 cm wide. Placental margin narrowly winged, ~1.7–2.1 mm wide. Non-placental margin prominent, ~0.5 mm thick. Fragment of pedicel ~2.4 mm long. Base obtuse, rounded; apex not preserved. Seeds 2–3(?), attached along the placental margin. Seed chambers indistinct, ~5.0–5.7 mm wide, and oblique. Fruit margin slightly constricted near the centre.

Remarks

Only one specimen has been found in the Cerrejón Fm. (locality SW0318). This is the smallest legume fruit morphotype from the Cerrejón flora discovered so far. The fruit is likely to be indehiscent because the coalified matter in the compression seems to indicate complete closed valves.

Comments on affinity

Similar to Fruit morphotype 1, but it is distinguished by its small size, presence of a narrow wing on the placental margin, a well-developed non-placental margin, indistinct seed chambers, and a slightly constricted margin. Narrowly winged fruits are known from numerous legume genera in multiple subfamilies. No venation details are preserved, which precludes evaluation of possible relationships.

Fruit morphotype 3

(Fig. 2–4.)

Fruits ~3.0–7.9 cm long and 0.9–1.7 cm wide. Placental and non-placental margins conspicuously winged, ~1.0–3.8 mm wide. Fragment of pedicel ~5 mm long. Base outline acute to

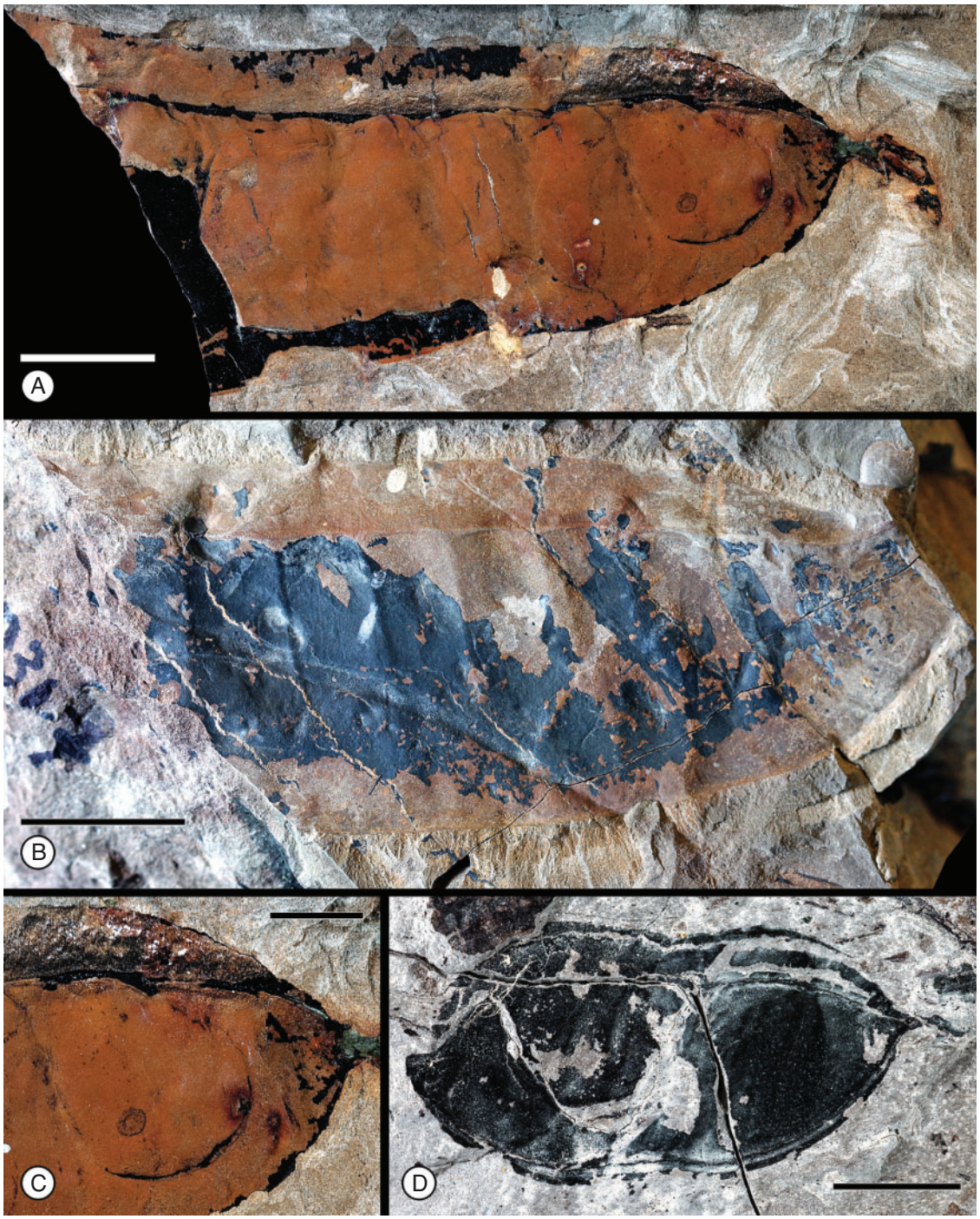

Fig. 1. A–C. Fruit morphotype 1. D. Fruit morphotype 2. A. Large one-winged fruit, note conspicuous placental margin wing and distinct seed chambers (#13001). B. Fragmentary specimen; note at least 10 seed chambers and broad placental wing (#0834). C. Detail from A; note distinct seed chamber, placental wing and fragment of pedicel. D. Note placental margin narrowly winged and fruit margin slightly constricted near the centre (#13002). All specimens from the Cerrejón Formation. Scale bars: 2 cm (A, B), 1 cm (C), 5 mm (D).

obtuse, sometimes tapered; apex obtuse, rounded. Seeds 3–9, ~4.0–9.0 mm wide and 1.5–4.0 mm high, attached along the placental margin, oriented parallel to the margin or longest axis of the fruit; seed outlines somewhat reniform, ovate to elliptical; funiculus thin and short. Seed chambers indistinct, ~0.6–1.0 cm wide, transverse to slightly oblique. Margin straight to slightly constricted between the seeds. In some specimens, the constriction corresponds to the presence of an abortive ovule (Fig. 2A, 3A). Outer and inner surfaces of the two valves with faint, oblique striations.

Fig. 2. Fruit morphotype 3. All specimens are two-winged and from the Bogotá Formation. A. Specimen with two broad wings; note at least eight seed chambers, detail of fruit in Fig. 3A (#12895). B. Large specimen with several constrictions along the margin (#12916). C. Specimen with at least six seed chambers and a more or less straight margin, detail of fruit in Fig. 3B (#12868). D. Specimen with at least six seed chambers; fruit appears more or less distorted in the sediment; note abundant ferruginous deposits along both wings (#12825). All scale bars: 1 cm.

Remarks

This is the most abundant fruit morphotype recovered in the Bogotá flora (locality FH0903). It co-occurs with Fruit morphotype 8. Only one specimen (Fig. 3G) of this fruit morphotype has been collected from the Cerrejón flora (locality FH0711). One immature (likely abortive) ovule is present in the specimen shown in Fig. 2A and 3A, which corresponds to the position of the constriction in the fruit valves. The fruit is likely to be indehiscent because most recovered impressions seem to indicate complete closed valves.

Comments on affinity

Legume fruits bearing wings on both margins are quite uncommon in the family. They are known in *Cladrastis platycarpa* (Papilionoideae), and *Acrocarpus* and *Peltophorum* (Caesalpinioideae). This morphology is also present in, for example, *Derris*, *Paraderris* and *Xeroderris*

Fig. 3. Fruit morphotype 3. All specimens are two-winged and from the Bogotá Formation, except G from the Cerrejón Formation. A. Detail from Fig. 2A; note aborted ovule with thin short funiculus (left arrow) and ovate seed outline oriented parallel to the margin (right arrow). B. Detail from Fig. 2C; note elliptical outline of seed chamber. C. Detail from Fig. 2D; note two large somewhat reniform outlines of seeds, oriented more or less parallel to the fruit margin. D. Specimen with at least three seed chambers; note faint, oblique striations (#13003). E. Specimen with conspicuous central constriction between the seeds (#13004). F. Specimen more or less elliptical in outline; note thick fruit base–pedicel area (#12764). G. Fragment of fruit with at least three seed chambers; note thick fruit base–pedicel area (#9932). All scale bars: 1 cm.

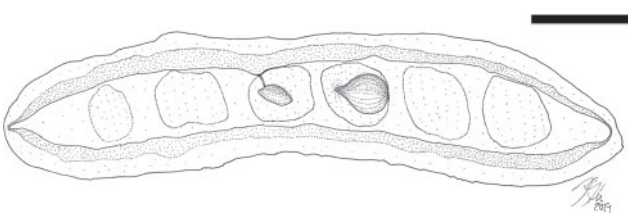

Fig. 4. Line drawing of fruit morphotype 3. Detail of specimen from Fig. 2A; two winged fruit; note reniform seed and abortive ovule. Scale bar: 1 cm.

(Papilionoideae), although the seed outline is clearly reniform. Orientation of the seeds parallel to the long axis of the fruit is unusual in legumes, but does occur for example in *C. platycarpa* and several species of *Peltophorum*, however, these extant fruits posses distinct venation patterns that are not present in the Bogotá fossils. Fruit morphotype 3 is likely to be indehiscent, similar to *C. platycarpa* and *Peltophorum* fruits (like most samaroid legume fruits).

Fruit morphotype 4
(Fig. 5A–C.)

Fruits ~3.3–4.1 cm long and 0.8–1.1 cm wide. Placental and non-placental margins distinct, narrow and non-winged; approximately of equal thickness, ~0.7 mm wide. Fruits stipitate, stipe ~0.4 mm long. Fragment of pedicel ~5 mm long. In one specimen remnants of the calyx are present. Base outline acute, tapering; apex obtuse, slightly asymmetrical and with a short remnant of the style. Seeds 2+, attached along the placental margin; seed outline poorly preserved, possibly rounded. Seed chambers not evident. Margin straight to slightly constricted between the seeds.

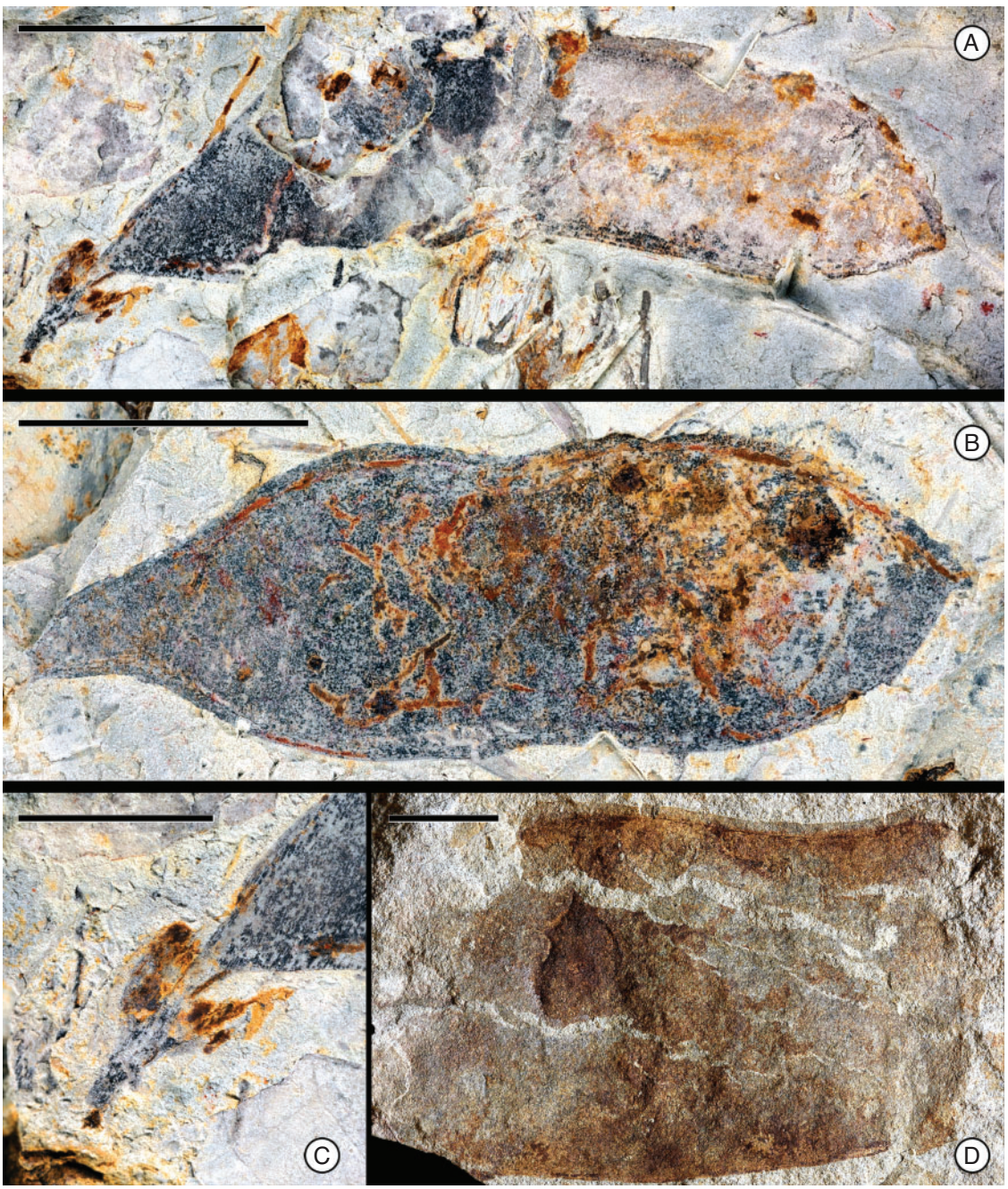

Fig. 5. A–C. Fruit morphotype 4 (Cerrejón Formation). D. Fruit morphotype 5 (Bogotá Formation). A. Fruit stipitate with distinct, narrow and non-winged placental and non-placental margins; note remnants of calyx (#9931). B. Fruit slightly constricted between the seeds, with short remnant of style, and tapered base (#9930). C. Detail from A; note short stipe and remnants of calix. D. Large fragmentary specimen; note inconspicuous placental and non-placental margins and one seed outline with a thin and long funiculus (#13071). Scale bars: 1 cm (A, B, D), 5 mm (C).

Remarks

Only two specimens have been recovered from the Cerrejón flora (locality FH0708). The fruit is likely to be indehiscent because the thick coalified matter in the compressions seems to indicate complete closed valves.

Affinity

The fossils are distinct from other fruit morphotypes, but characteristic features that would help identify relationships within the family must await additional specimens. Unfortunately, the calyx remnants are not adequately preserved to help in assessing relationships.

Fruit morphotype 5

(Fig. 5D.)

Fruit incomplete, ~5.6 cm long and 3.4 cm wide. Placental and non-placental margins inconspicuous and non-winged; placental margin slightly wider than the non-placental one, ~2.0 mm *v.* 1.0 mm wide. Base and apex not preserved. Seeds 1+, ~1.0 cm long and 0.7 cm wide, attached along the placental margin; seed outline more or less elliptical; funiculus thin and long, ~7.0 mm, apically attached to the seed; Seed chambers not evident. Margin straight to slightly constricted between the seeds.

Remarks

Only one specimen has been recovered from the Bogotá flora (locality FH0918).

Affinity

This incomplete fossil fruit is different from the other fruit morphotypes, but distinctive features that would help identify relationships within the family must await additional specimens. Fruits of many extant legume genera are similarly non-distinctive and are very difficult to identify to genus- or higher-level taxon without additional information from leaves, flowers or other organs.

Fruit morphotype 6

(Fig. 6–8.)

Incomplete branching infructescence bearing opposite fruits. The infructescence is composed of bifurcating axes; only a small portion of a central 'primary' axis is preserved (~0.8 cm long), this central axis bifurcates into two long and diverging 'secondary' axes (~9.2 cm long and 0.2 cm wide) that bifurcate two more times into 'tertiary' (~2.1 cm long) and 'quaternary' axes. Fruits ~4.5–13 cm long and 0.9–2.0 cm wide. Placental and non-placental margins very narrow and non-winged, approximately of equal thickness, ~1 mm wide. Pedicel ~1.0–1.6 mm long. Base outline convex to slightly cuneate (tapered); apex not preserved. Seeds 6+, occupying most of the seed chamber, attached along the placental margin; seed outline elliptical. Seed chambers possibly septate, ~0.7–0.9 cm wide. Margin straight. Surface of outer valves with faint, oblique striations.

Remarks

The most common fruit morphotype in the Cerrejón flora (localities SW0318, FH0705, FH0708). Fruit is likely to be dehiscent because most recovered specimens seem to be impressions and compressions of only one valve.

Affinity

This is a very 'generic' fruit morphology lacking distinctive features, which is seen in many extant groups of legumes. However, the incomplete but distinctive organisation of the infructescence is very similar to the branched thyrsoid inflorescences and infructescences that characterise the subfamily Dialioideae (Legume Phylogeny Working Group 2017).

Fruit morphotype 7

(Fig. 9.)

Fruits nearly complete, ~3.8–4.1 cm long and 2.0–2.2 cm wide; strongly asymmetrical. Placental and non-placental margins very narrow and non-winged; approximately of equal thickness, ~1.0 mm wide. Pedicel short and stout, ~4.0–5.0 mm long, perpendicular to long axis of fruit. Base outline obtuse, rounded; apex not preserved. Number of seeds unclear. Seed chambers not evident. Margins straight. Fruit venation transverse to oblique, veins closely spaced, evenly distributed (~1–2 mm apart), more or less recurved at the margins.

Remarks

Three specimens have been recovered from the Cerrejón flora (locality SW0318).

Affinity

There is some similarity to some members of Detarioideae (e.g. *Macrolobium*, *Peltogyne*), but diagnostic features that would place it in a subfamily are lacking.

Fruit morphotype 8

(Fig. 10–11.)

Fruits small, ~10–18 mm long and 3–5 mm wide; strongly asymmetrical. Placental and non-placental margins narrow and non-winged; approximately of equal thickness, ~0.5 mm wide. Fruits stipitate, stipe ~0.4 mm long. Pedicel short, ~1.8–2.0 mm long. Base outline acute, tapered; apex obtuse to acute with a prominent persistent style base. Seeds 1(2?), oblique, transverse, to more or less parallel to the margin or longest axis of the fruit. Seed chambers not evident. Placental margin straight to slightly concave, non-placental margin curved, convex. Fruit venation straight and oblique, veins equally distant (~80–140 µm apart). Fruit surface covered with small, rounded resinous bodies (~65–96 µm in diameter).

Remarks

The second most common and smallest fruit morphotype from the Bogotá flora (locality FH0903). It co-occurs with Fruit morphotype 3. The fruit is likely to be indehiscent because the thick impressions seem to indicate complete closed valves.

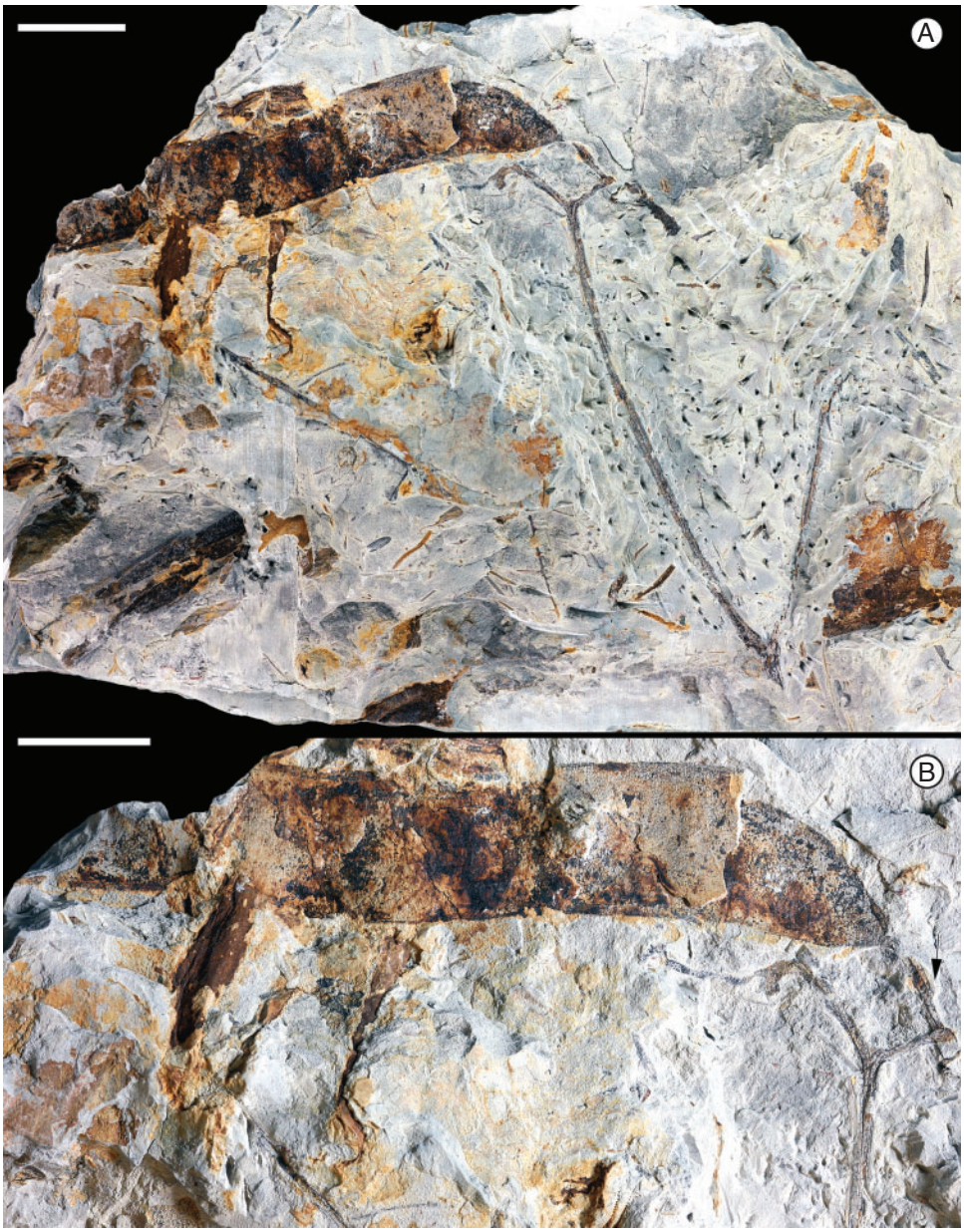

Fig. 6. Fruit morphotype 6. A. Incomplete branching thyrsoid infructescence, with one associated fruit; note bifurcating pattern of axes (#9927; Cerrejón Formation). B. Detail from A, showing large elongate fruit; note pedicel of fruit in organic attachment (arrow) and at least seven seed chambers. Scale bars: 2 cm (A), 1 cm (B).

Affinity

Detarioideae. Several genera of Detarioideae produce resin and have resin bodies present in the fruit walls (e.g. *Hymenaea*, *Peltogyne*, *Guibourtia*, *Copaifera*).

Leaf morphotype 1

(Fig. 12.)

Leaf bipinnate, incomplete; largest leaf fragment ~5.4 cm long and 3.5 cm wide; petiole base and pulvinus not preserved, apex even pinnate (ending with two opposite pinnae). Primary rachis incomplete, ~2.5 cm long. Pinnae opposite, at least 3 pairs; interval between pinnae is 1–1.3 cm. Pinnae ~3.5–3.9 cm long, rachis ~0.8 mm wide at base, first pair of leaflets ~1.4 mm from base, with well-developed basal pulvinus at base of pinna (~1 mm long), pulvinus with transverse striations. Pinnae bear at least 62 pairs of small leaflets; apex of pinnae ending with two opposite leaflets. Leaflets opposite, ~2.4–5.8 mm long and 0.8–1.7 mm wide (leptophyll to nanophyll); petiolule and pulvinus at base of leaflet very short, ~0.2–0.3 mm long; interval between leaflets is ~1.2–2.5 mm. Leaflet margin entire. Leaflet shape elliptical to ovate; apex acute,

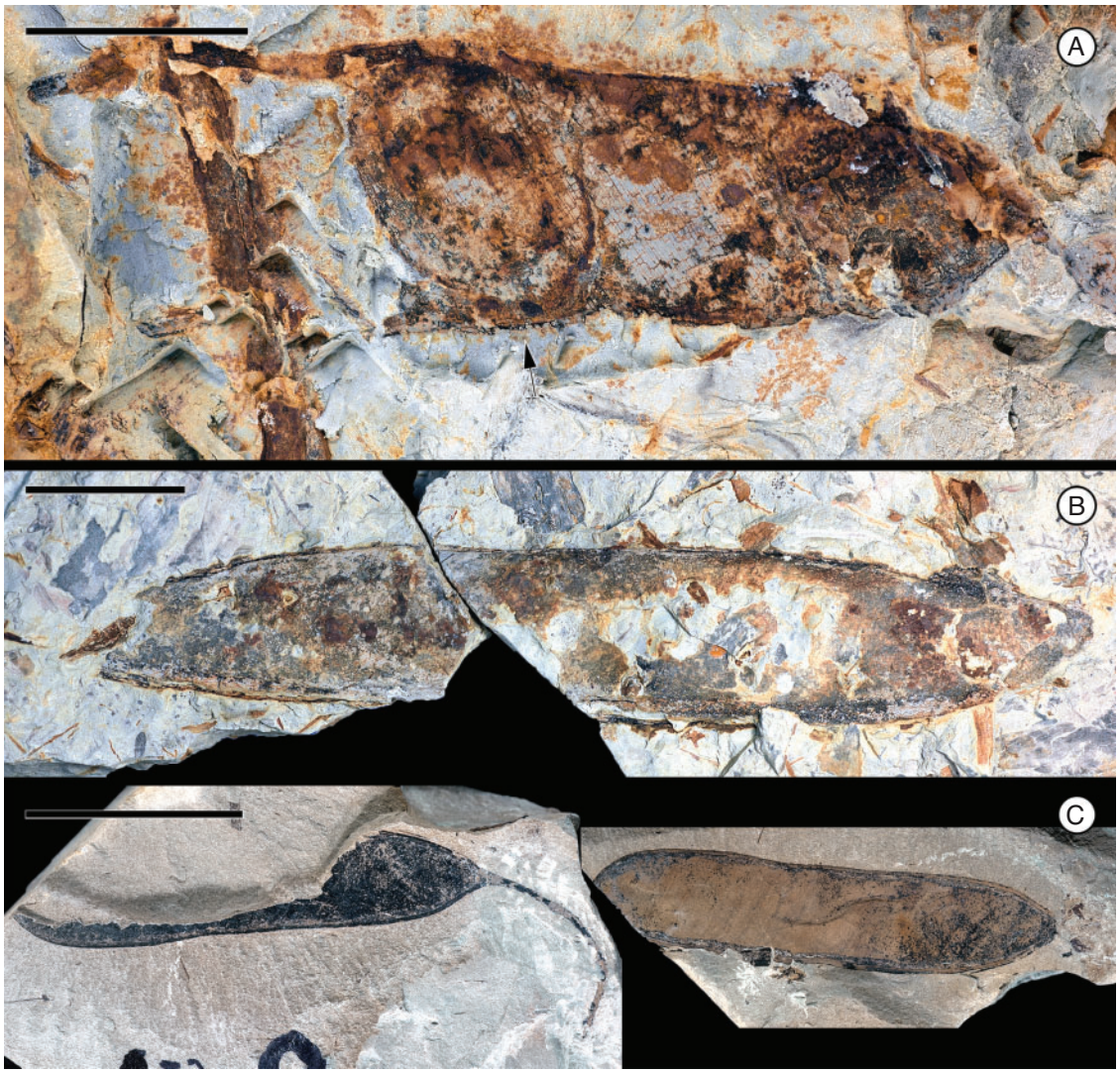

Fig. 7. Fruit morphotype 6. All specimens from Cerrejón Formation. A Fragment of fruit showing three large and possibly septate seed chambers, one of them with a probable elliptical seed outline (arrow) (#9933). B. Large fruit with very narrow, non-winged placental and non-placental margins (#9929). C. Part and counterpart of specimen; note surface of outer valves with faint, oblique striations and long pedicel (#13005). Scale bars: 2 cm (B, C), 1 cm (A).

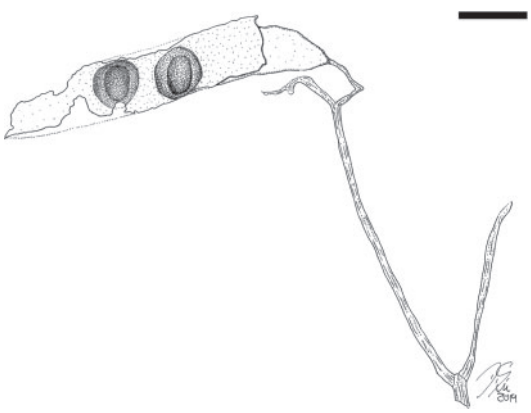

Fig. 8. Line drawing of fruit morphotype 6. Detail of specimen from Fig. 6A; incomplete branching infructescence bearing opposite fruit; note two seeds and bifurcating axes. Scale bar: 2 cm.

convex to rounded; base asymmetrical (slightly broader on the proximal side than on the distal side of the primary vein). Leaflet venation pinnate, primary vein ~0.1 mm thick; secondary venation not preserved. Extrafloral nectaries apparently absent.

Remarks

This fossil leaf morphotype is known from the Cerrejón flora (localities FH075, FH0708, FH0711). Most specimens are represented by isolated leaflets.

Affinity

Bipinnate leaves are restricted to the Caesalpinioideae (Legume Phylogeny Working Group 2017). They are found in several clades including the mimosoid clade, *Dimorphandra* group genera, the *Umtiza* clade (or grade), and the *Caesalpinia*

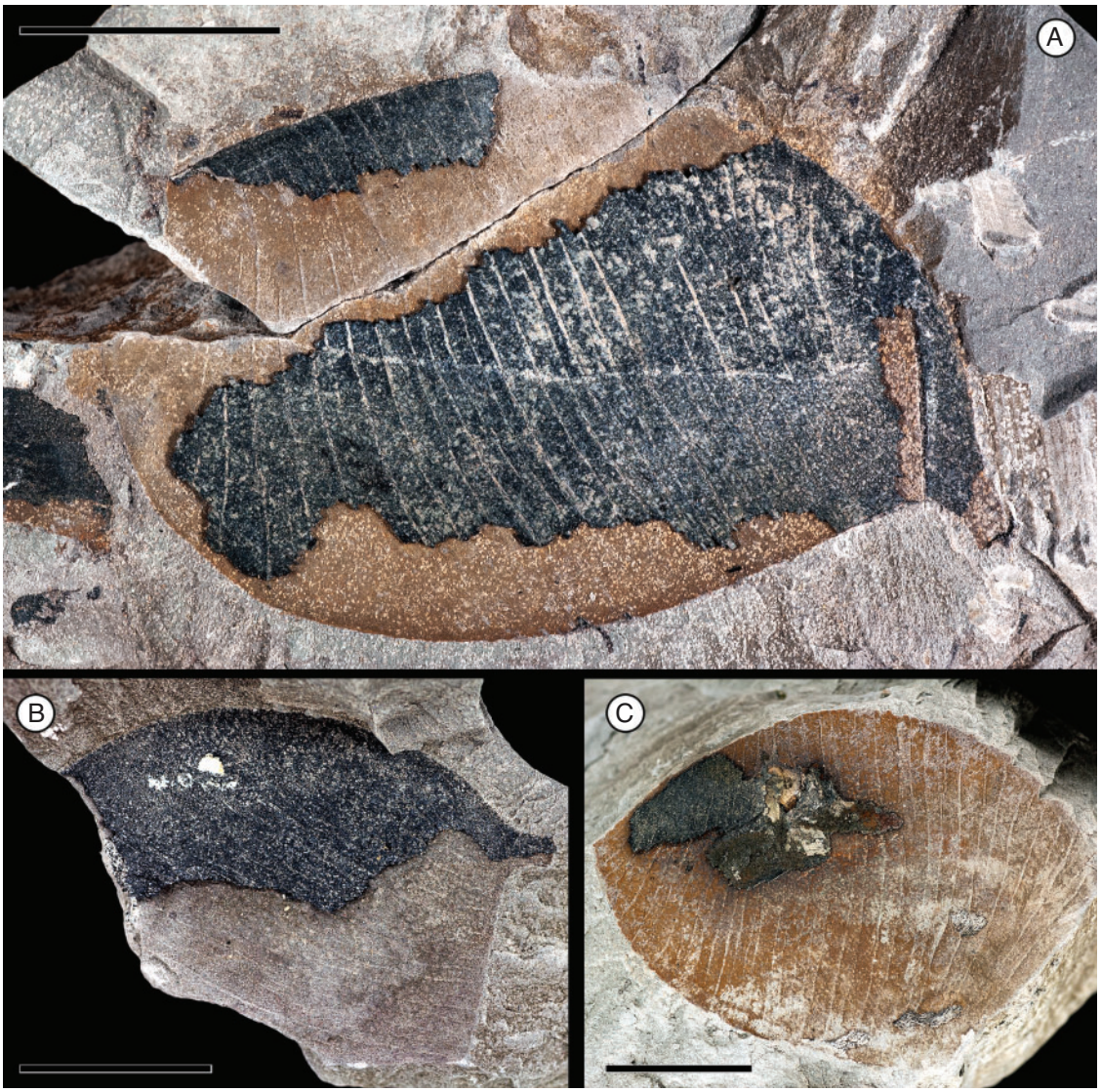

Fig. 9. Fruit morphotype 7. All specimens from Cerrejón Formation. A. Fruit nearly complete, strongly asymmetrical, non-winged (#13006). B. Fragment of specimen; note short, stout pedicel (#9913). C. Fragment of specimen; note fruit venation with transverse to oblique closely spaced parallel veins. All scale bars: 1 cm.

group. Extrafloral nectaries are present on the leaves of most members of the mimosoid clade, whereas they appear to be lacking in the fossil. Similarities seem to be greatest with the Dimorphandra group genera with bipinnate leaves, but preservation of morphological details is not adequate to make detailed comparisons.

Leaf morphotype 2

(Fig. 13–14.)

Leaf bipinnate; largest leaf fragment ~2.5 cm long and 3.0 cm wide; basal pulvinus and petiole not preserved, apex even pinnate (ending with two opposite pinnae). Primary rachis incomplete, ~1.7 cm long. Pinnae opposite, at least 4 pairs; interval between pinnae is ~1.0 cm. Pinnae at least ~4.4 cm long, rachis ~0.8 mm wide at base, with well-developed basal pulvinus at base of pinna (~2 mm long), pulvinus with transverse striations. Pinnae bear at least 20 pairs of small leaflets; apex of pinnae ending with two opposite leaflets. Leaflets opposite, ~5.5–7.9 mm long and 1.0–1.6 mm wide (leptophyll to nanophyll); petiolule and pulvinus at base of leaflet very short, ca. 0.4 mm long; interval between leaflets is 2.6–3.5 mm. Leaflet margin entire. Leaflet shape oblong, elliptical to ovate; apex acute, convex to rounded with a mucronate tip; base asymmetrical (slightly broader on the proximal side than on the distal side of the primary vein). Leaflet venation pinnate, primary vein ~1.0 mm thick. Secondary venation eucamptodromous, 10–15 pairs of veins. Tertiary venation opposite percurrent. Extrafloral nectaries apparently absent.

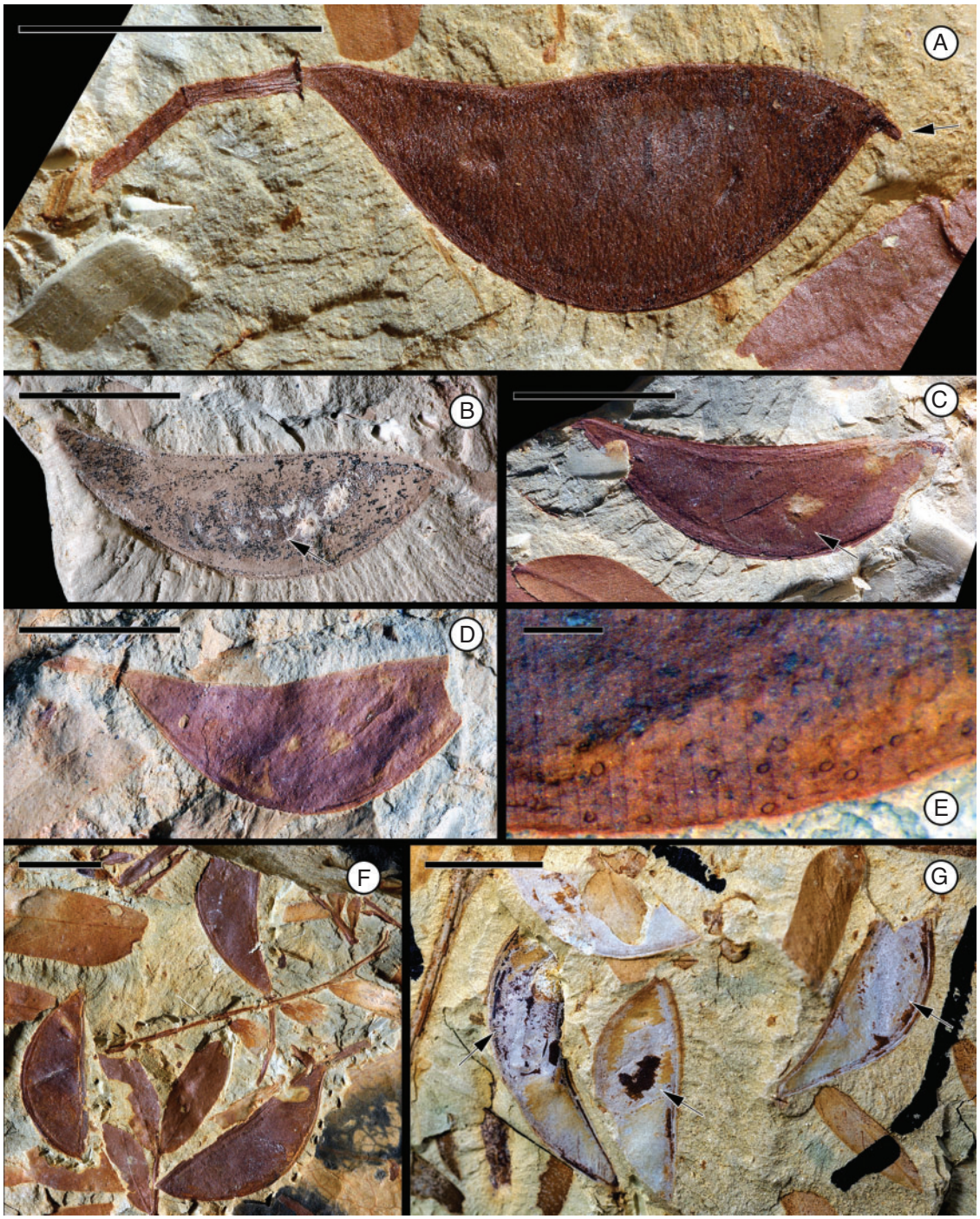

Fig. 10. Fruit morphotype 8. All specimens from Bogotá Formation. A. Stipitate and strongly asymmetrical fruit; note one seed outline and remnant of style (arrow) (#12740). B. Fruit non-winged, note one seed outline (arrow) (#13007). C. Fruit nearly complete, with one large seed outline (arrow). D. Fragmentary specimen missing apex; note pedicel (#12913). E. Detail from C; note fruit venation with straight and oblique veins and small, rounded resinous bodies. F. Specimen with at least three isolated fruits and associated leaflets (Leaf morphotype 2) (#13008). G. Specimen with at least four isolated fruits and associated leaflets (Leaf morphotype 2); note three fruits with single seed outlines (arrows) (#12764). Scale bars: 5 mm (A–D, F, G), 500 µm (E).

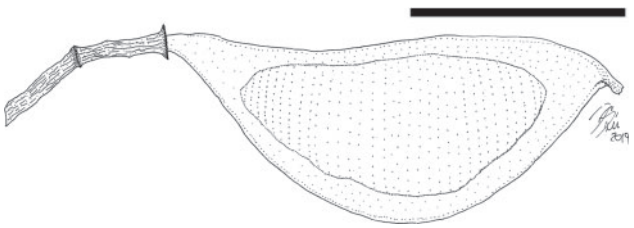

Fig. 11. Line drawing of fruit morphotype 8. Detail of specimen from Fig. 10A; note seed outline. Scale bar: 5 mm.

Remarks

Most abundant leaf morphotype recovered in the Bogotá flora (locality FH0903). It co-occurs with Fruit morphotypes 3 and 8. Leaf morphotype 2 can be distinguished from Leaf morphotype 1 by the smaller number of leaflets per pinna (20 pairs *v*. 62), the more oblong and asymmetrical shape of leaflets, their larger size (up to 7.9 mm long *v*. 5.8 mm long), and the greater interval between leaflets (up to 3.5 mm *v*. 2.5 mm).

Affinity

Bipinnate leaves are restricted to the Caesalpinioideae (Legume Phylogeny Working Group 2017).

Leaf morphotype 3

(Fig. 15.)

Once-pinnately compound leaves, whether paripinnate or imparipinnate unknown (apex not preserved). Largest leaf fragment ~5 cm long and 5.3 cm wide. Apex, pulvinus and petiole not preserved. Rachis incomplete, ~4.6 cm long and 0.16 cm wide, with central groove and two parallel longitudinal ridges running close to the edge of the rachis on the adaxial surface. Leaflets opposite, ~1.3–5.4 cm long and 0.9–1.8 cm wide (microphyll to notophyll). Pulvinus at base of leaflet well developed, ca. 2.3–2.7 mm long and 0.8–1.1 mm wide. Leaflet base asymmetrical with lamina on inferred proximal side attached near base of petiolule, creating a nearly 'sessile' attachment. At least 6 pairs of leaflets; interval between leaflets is 0.6 to 1.3 cm. Leaflet margin entire. Leaflet shape oblong, elliptical to slightly ovate; apex convex, sometimes emarginate; base cordate and strongly asymmetrical (broader on the proximal side than on the distal side of the primary vein). Leaflet venation pinnate, primary vein ~0.8 mm thick. Secondary venation strongly brochidodromous, a few basal veins eucamptodromous; 13–16 pairs of secondary veins, with ~4–6 basal veins strongly crowded on the asymmetrical proximal side of the leaflet blade. Marginal secondary vein present. One to two inter-secondary veins present that run parallel to major secondaries. Tertiary and quaternary veins reticulate.

Remarks

This leaf morphotype is known from the Bogotá flora (localities FH0806, FH0808, FH0914). Specimens show diverse insect damage marks.

Affinity

The strongly unequal leaflet base, multiple eucamptodromous basal veins, and well developed secondary and tertiary venation are characteristic of many Detarioideae genera.

Leaf morphotype 4

(Fig. 16.)

Once-pinnately compound leaves, likely imparipinnate. Largest leaf fragment ~4.7 cm long. Petiole and basal pulvinus not preserved. Rachis incomplete, ~1.1. mm wide. Leaflets opposite, ~1.8–9.5 cm long and 1.0–4.6 cm wide (microphyll to mesophyll). Pulvinus at base of leaflet well developed, ca. 1.0 mm long and 1.6 mm wide. Leaflet base asymmetrical with lamina on inferred proximal side attached near base of petiolule, creating a nearly 'sessile' attachment. At least 4 pairs of leaflets; interval between leaflets is ~2.3–2.6 cm. Leaflet margin entire. Leaflet shape elliptical to slightly ovate; apex not well preserved; base asymmetrical, strongly unequal (broader on the proximal side than on the distal side of the primary vein). Leaflet venation pinnate, primary vein ~2 mm thick. Secondary venation eucamptodromous becoming brochidodromous distally; 8–12 pairs of secondary veins, with ~2 or 3 basal veins strongly crowded on the asymmetrical proximal side of the leaf blade. Marginal secondary vein absent. One to three inter-secondary veins present which run parallel to major secondaries. Tertiary and quaternary veins reticulate.

Remarks

This leaf morphotype is known from the Cerrejón flora (localities SW0317, FH0410). Specimens show diverse insect damage marks.

Affinity

Possibly Detarioideae. The strongly unequal leaflet base with two or three veins originating at the apex of the petiolule on the proximal side of the leaflet is characteristic of several genera in the Detarioideae.

Leaf morphotype 5

(Fig. 17.)

Isolated leaflets, ~9.3–17 cm long and 3.0–5.4 cm wide (microphyll to mesophyll). Petiolule and pulvinus at base of leaflet well developed, ~5.1 mm long and 3.4 mm wide. Leaflet margin entire. Leaflet shape ovate to oblong; apex and base symmetrical, apex acute; base rounded to convex. Leaflet venation pinnate, primary vein ~3–5 mm thick. Secondary venation eucamptodromous becoming brochidodromous distally; 13–15 pairs of crowded secondary veins; secondaries strongly decurrent on mid-vein. Marginal secondary vein absent. One to two inter-secondary veins present, which run parallel to major secondaries. Tertiary and quaternary veins reticulate.

Remarks

This leaf type is known from the Cerrejón flora (localities SW0315, SW0318, FH0708).

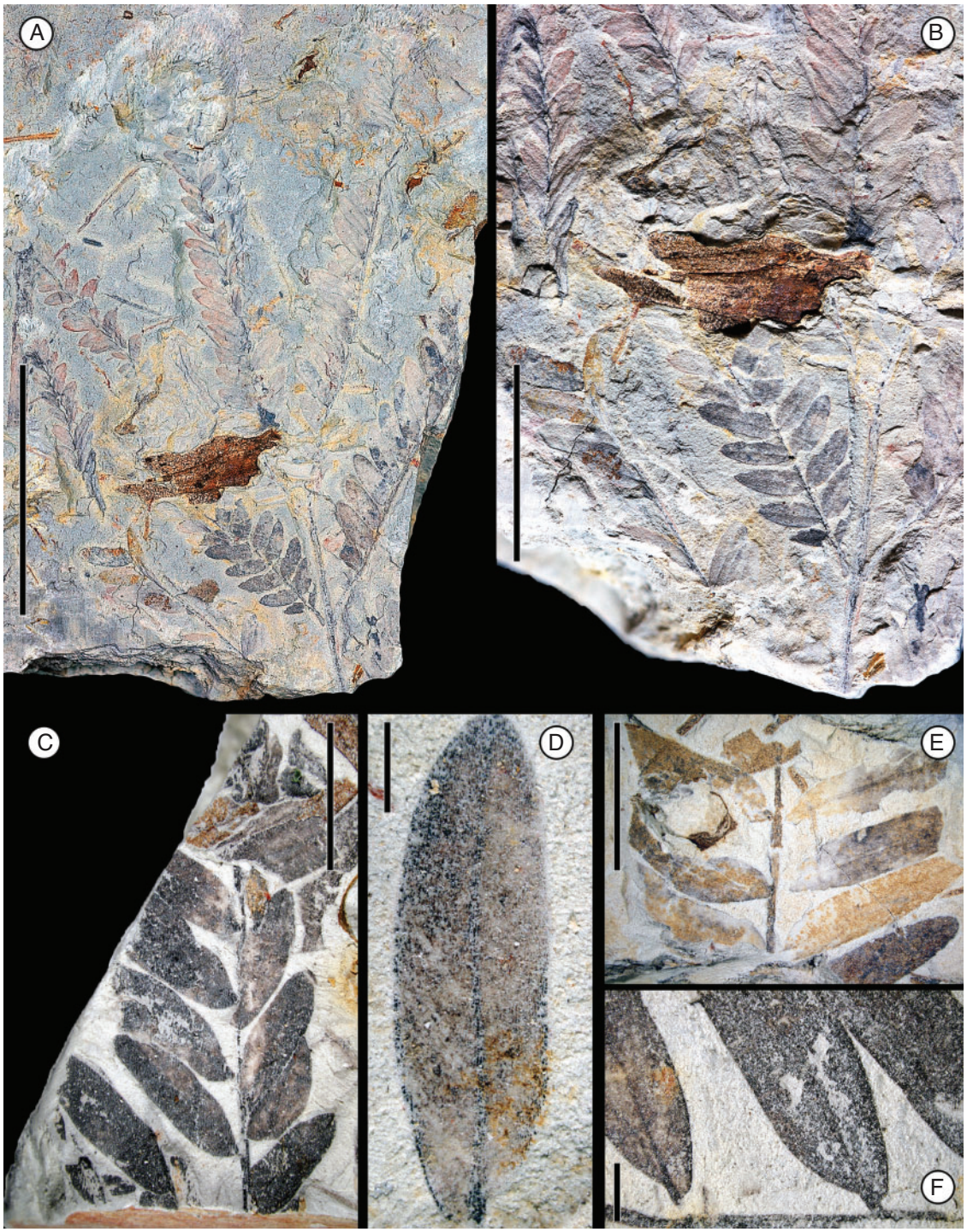

Fig. 12. Leaf morphotype 1. All specimens from Cerrejón Formation. A. Fragment of bipinnate leaf with at least three pairs of opposite pinnae; note even pinnate apex (#11873). B. Detail from A, showing primary rachis, pinnae, and opposite leaflets. C. Fragment of pinna showing at least six pairs of opposite leaflets; note that several leaflets appear slightly disarticulated, giving the appearance of subopposite arrangement (#9696). D. Isolated leaflet showing entire margin, pinnate venation, asymmetrical base, and small petiolule (#9712). E. Detail of fragment of pinna with at least four pairs of opposite leaflets (#9680). F. Detail of pinna showing three leaflets; note articulated leaflet with small petiolule (#9687). Scale bars: 2 cm (A), 1 cm (B), 5 mm (C, E), 1 mm (D, F).

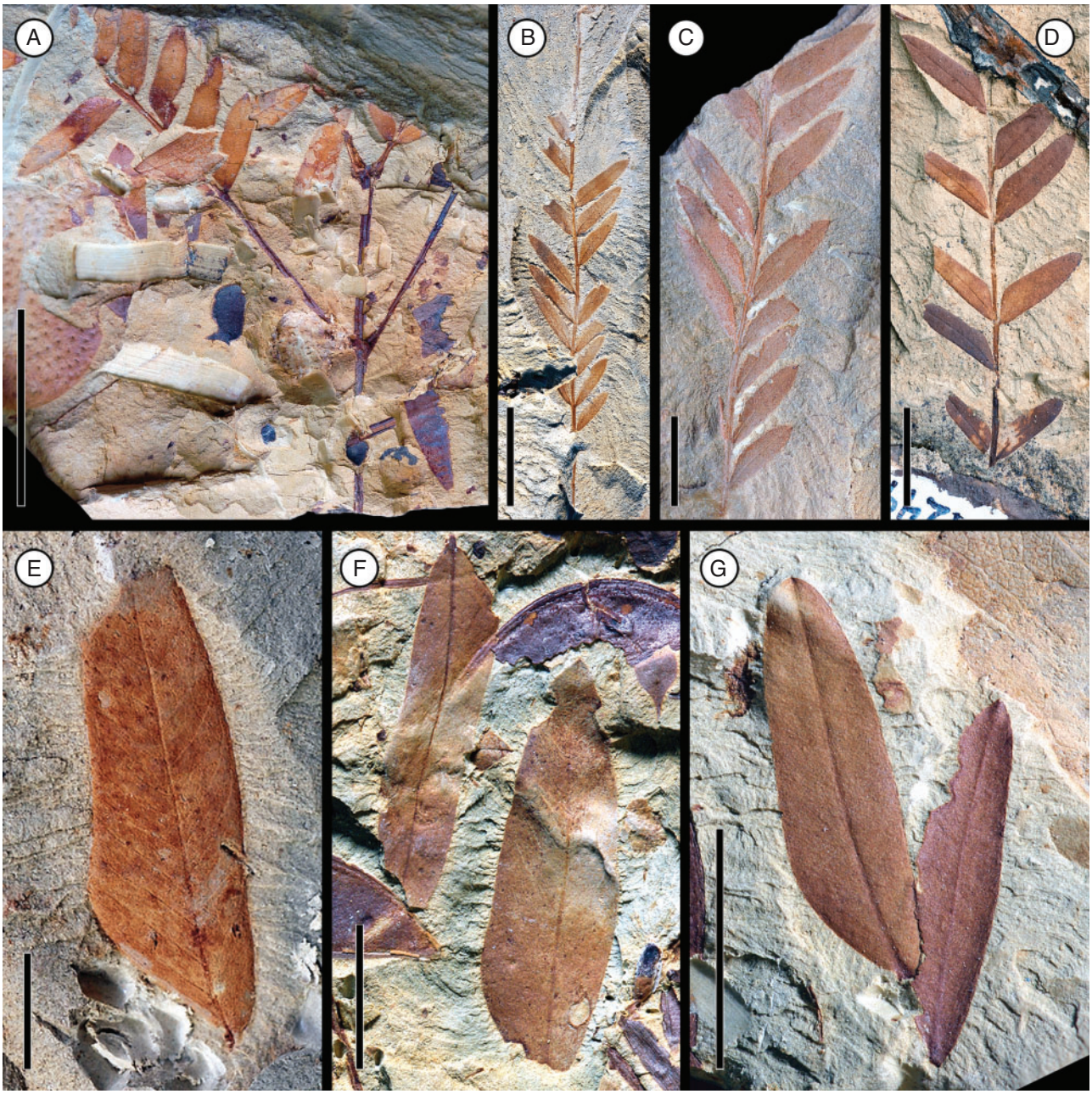

Fig. 13. Leaf morphotype 2. All specimens from Bogotá Formation. A. Fragment of bipinnate leaf with at least two pairs of opposite pinnae; note even pinnate apex and conspicuous pulvini; see also Fig. 14A (#12478). B. Fragment of the pinna with at least 11 pairs of opposite leaflets; note that most leaflets are indicated by scars near base and apex of pinna; see also Fig. 14B (#13009). C. Fragment of pinna with at least nine pairs of opposite leaflets (#12338). D. Fragment of pinna with at least six pairs of opposite leaflets (#12496). E. Isolated leaflet showing entire margin, pinnate venation, eucamptodromous secondary venation, asymmetrical base, and small petiolule; see also Fig. 14C (#12477). F. Two isolated leaflets; note insect leaf damage (#13008). G. Two isolated leaflets; note diminutive mucronate tip and insect leaf damage (#12879). Scale bars: 1 cm (A, B, D), 5 mm (C, F, G), 2 mm (E).

Affinity

The leaflet morphology is very generalized within the family and can be observed in numerous extant legume genera. There are no distinctive features that would help narrow possible relationships.

Leaf morphotype 6

(Fig. 18–19.)

Mostly isolated leaflets; one specimen with a leaflet still attached to a fragment of a rachis. Fragment of rachis ~1.5 cm long and 6 mm wide. Leaflets ~13–28 cm long and 5–10 cm wide

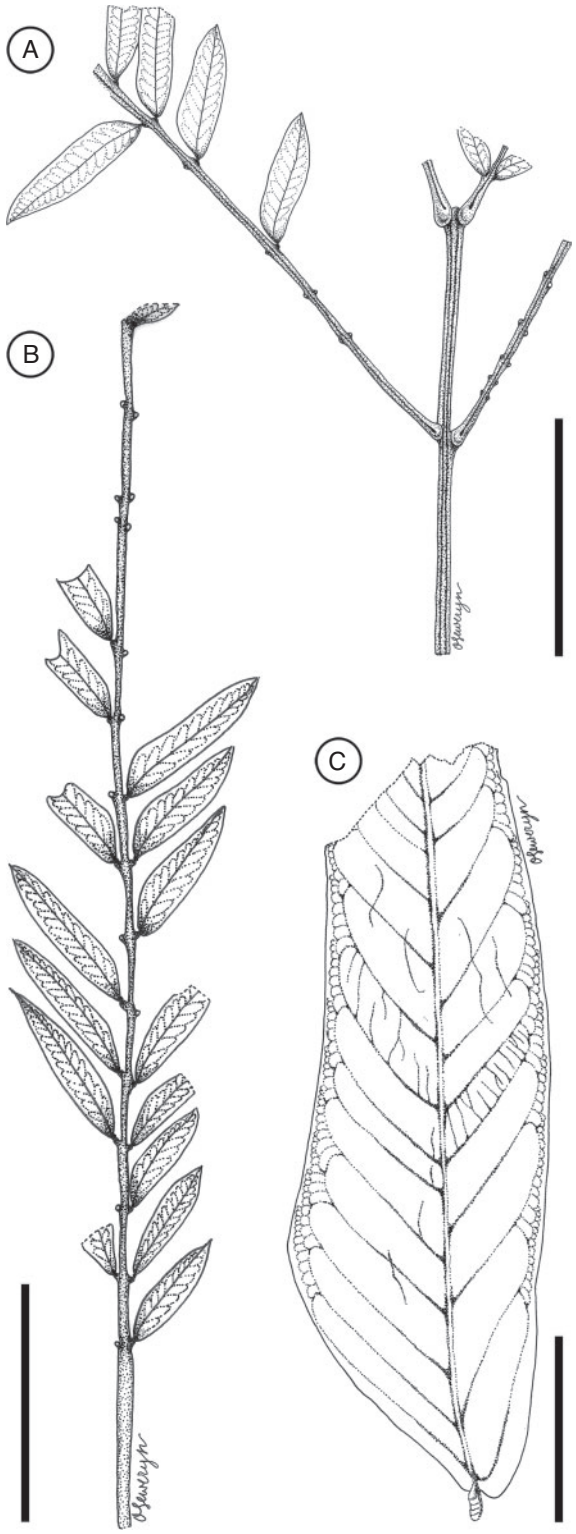

Fig. 14. Line drawings of Leaf morphotype 2 from Bogotá Formation. A. Detail of specimen from Fig. 13A; note conspicuous pulvini and leaflet scars along rachis of pinnae. B. Detail of specimen from Fig. 13B; note at least 11 pairs of opposite leaflets and leaflet scars along rachis of pinna. C. Detail of specimen from Fig. 13E; note pulvinus and at least 15 pairs of eucamptodromous secondary veins. Scale bars: 1 cm (A, B), 2 mm (C).

(notophyll to macrophyll). Pulvinus on petiolule well developed, strongly transversely striated, ~9.5–15 mm long and 4–8 mm wide. Leaflet margin entire. Leaflet shape elliptic, obovate to oblong; apex and base symmetrical, apex acuminate (with and without drip tip) to rounded; base obtuse to rounded. Leaflet venation pinnate, primary vein ~4–6 mm thick. Secondary venation eucamptodromous becoming brochidodromous distally; 19–22 pairs of secondary veins; secondaries excurrent on mid-vein; minor secondary veins simple brochidodromous, looping at low angles near the leaf margin. Marginal secondary vein absent. Inter-secondary veins absent. Tertiary veins percurrent, opposite straight to opposite convex. Quaternary veins alternate percurrent. Quinternary veins irregular reticulate. Areolation present.

Remarks

The most abundant leaf morphotype recovered in the Cerrejón flora (localities SW0315, SW0317, SW0319, SW0322, FH0410).

Affinity

Legume genera with large leaflets are known from the Dialioideae, Detarioideae, Caesalpinioideae, and Papilionoideae. The symmetrical, equal base is more frequently found in the latter two groups, whereas the leaflet base is typically asymmetrical in Detarioideae. Insufficient details are preserved to evaluate relationships more precisely.

Discussion

Comparison with other Paleocene fruits

A few reliable legume fossils of Paleocene age have been reported from southern South America, North America, Europe and India (Fig. 20). Although some of these fossils show similarities with the Cerrejón and Bogotá fruits and leaves, those described here are distinct from all other Paleocene records.

From the Early Paleocene (~63–64 million years) of Patagonia, Argentina, a medium-size leaflet from the Salamanca Formation (Palacio de los Loros; Iglesias *et al*. 2007; Brea *et al*. 2008) slightly resembles three of the leaf morphotypes from Colombia, Morphotypes 3–5 (Fig. 15–17). Leaf morphotypes 3 and 4 differ from the Salamanca specimen because of their strongly asymmetrical bases, whereas Morphotype 5 has a large amount of inter-secondary veins that appear to be absent in the Patagonian fossil.

Four morphotypes of fossil leaflets and a similar number of fossil fruits of Leguminosae have been reported from Paleocene–Eocene Thermal Maximum (PETM) strata in Wyoming (~56 million years ago; Wing *et al*. 2005; Wing and Currano 2013). Among those leaflets are some that are similar to Leaf morphotypes 1 and 2 (Fig. 12–14), although no bipinnate leaves have been recovered from Wyoming. One Wyoming leaflet type of similar size has strongly eucamptodromous venation unlike Morphotypes 1 and 2 described here, and the other has larger (1.9–2.3 cm), more symmetrical leaflets. Other PETM fabaceous leaflet morphotypes from Wyoming have venation that is distinctly different from the larger leaflets described here. Fossil fruits and leaves from the Late

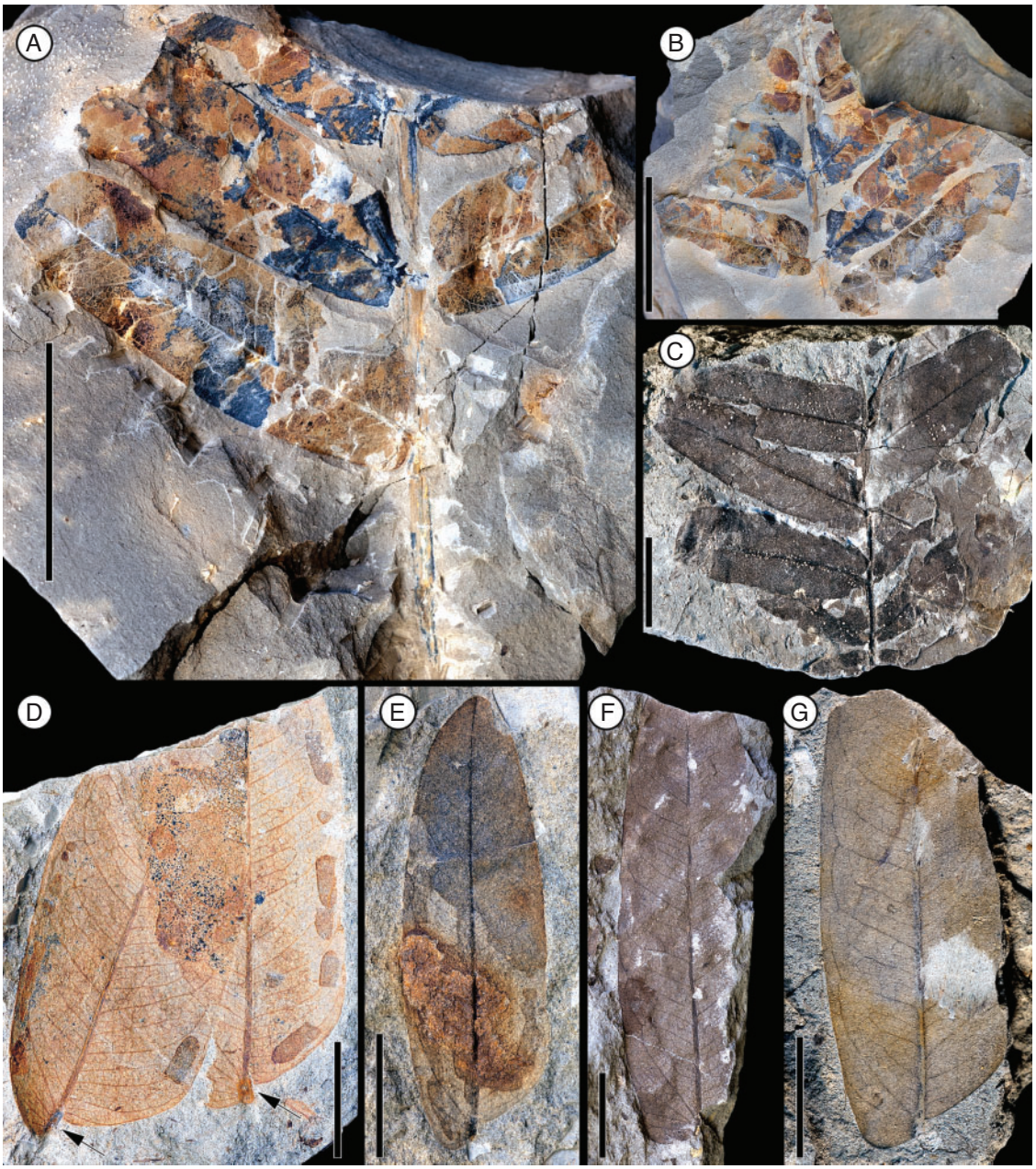

Fig. 15. Leaf morphotype 3. All specimens from Bogotá Formation. A. Fragment of once-pinnately compound leaf; note at least three pairs of opposite leaflets articulated along rachis (#12504). B. Counterpart from A. C. Fragment of once-pinnately compound leaf; note at least four pairs of opposite leaflets articulated along rachis (#12344). D. Two isolated leaflets without preserved apices; note strongly asymmetrical bases; conspicuous pulvini (arrows) and insect damage near their margins (#12349). E. Isolated leaflet showing pinnate venation and asymmetrical base; note insect damage in the proximal half of the lamina (#12378). F. Isolated leaflet showing strongly brochidodromous secondary venation (#12341). G. Isolated leaflet showing strongly asymmetrical base and brochidodromous secondary venation (#12366). Scale bars: 2 cm (A, B), 1 cm (C–G).

Paleocene Willwood Formation in the Bighorn Basin of Wyoming are referable to the Papilionoideae (P. S. Herendeen and S. L. Wing, unpubl. data). The fruits are samaras with a narrow wing on the placental margin that are clearly distinct from the fruit morphotypes from Cerrejón and Bogotá floras. Likewise, the associated pinnately compound leaves are distinct from the leaf morphotypes described in the present paper.

Fruits of *Leguminocarpon gardneri* (Chandler) Herendeen & Crane from the Late Paleocene Reading Formation of England are to some extent similar to Fruit morphotypes 7

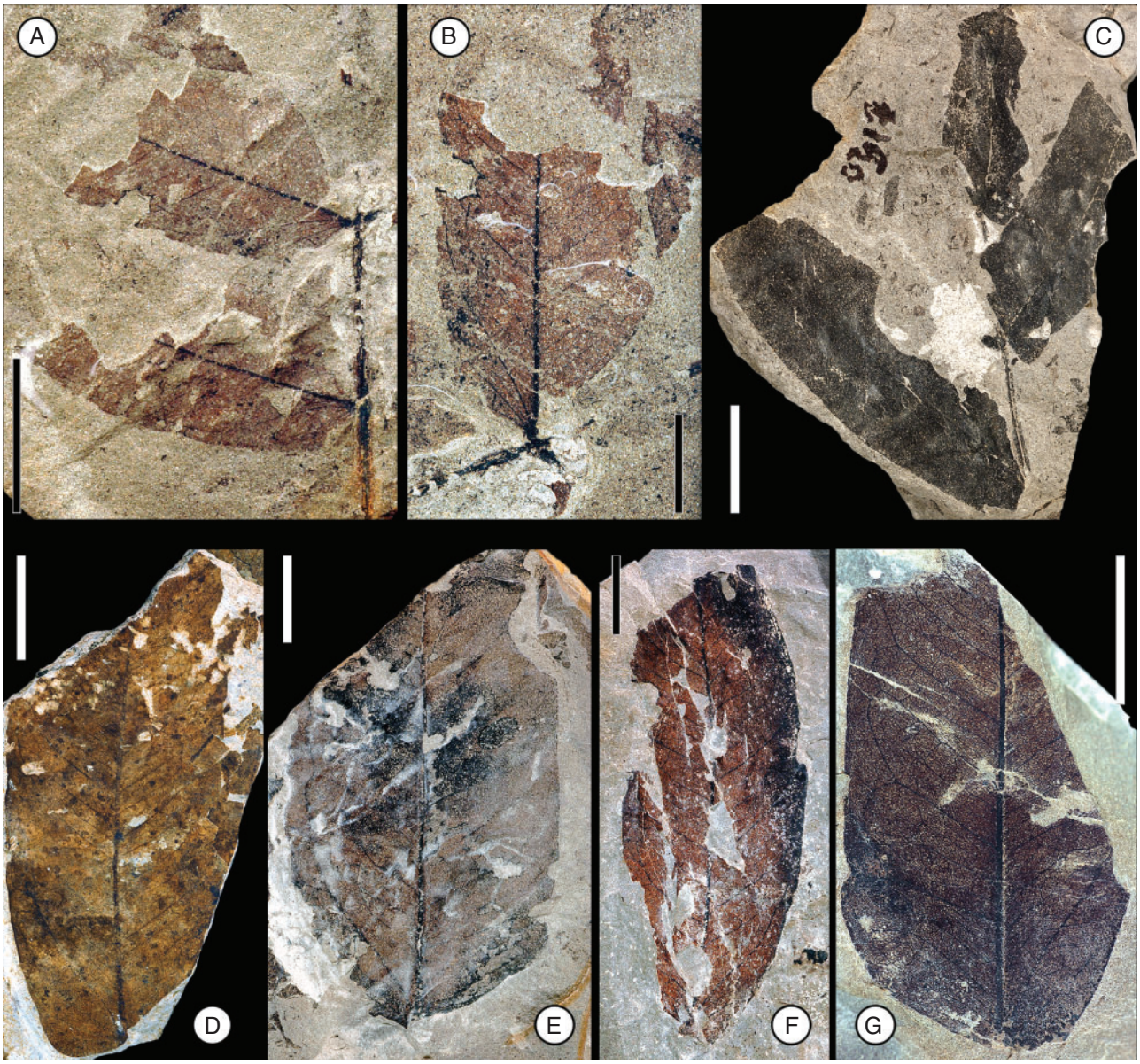

Fig. 16. Leaf morphotype 4. All specimens from Cerrejón Formation. A. Fragment of once-pinnately compound leaf; note two articulated leaflets with remnants of corresponding opposite pulvinus (#13010). B. Detail of leaflet from A; note asymmetrical base and short pulvinus. C. Apical fragment of likely imparipinnate, once-pinnately compound leaf (#13011). D–G. Isolated leaflets showing asymmetrical bases, pinnate venation, and details of the secondary venation (#13012). Scale bars: 2 cm (A, B), 1 cm (C–G). Scale bars: 2 cm (A, D), 1 cm (B, C, E–G).

and 8 (Fig. 9–11; Herendeen and Crane 1992). Those fossils range from symmetrical to asymmetrical, ~8–22 mm long and 7–13 mm wide, are stipitate with a narrow wing along the placental margin, and the valve venation appears transverse and strongly reticulate (Herendeen and Crane 1992). However, fruits of Morphotype 7 are wingless, not stipitate, and the valve venation is not reticulate (Fig. 9). The pods of Fruit morphotype 8 are stipitate, but differ from the England fossils by the lack of a wing along the placental margin and the absence of reticulate venation (Fig. 10). Fruits of Morphotype 8 are also much smaller (~10–18 mm long and 3–5 mm wide) than those of *L. gardneri*.

Five species of *Leguminocarpon* were described from compression fossils of the Tura Formation in the Garo Hills, Meghalaya, India (Bhattacharyya 1985). The age of the Tura Formation was initially reported as Early Eocene (Bhattacharyya 1985; Tripathi *et al*. 2000), but it is now considered Late Paleocene on the basis of several palynological studies in the Garo Hills region (Saxena *et al*. 1996; Ambwani and Kar 2000; Mehrotra 2000; Agarwal 2008; Monga *et al*. 2014). From the

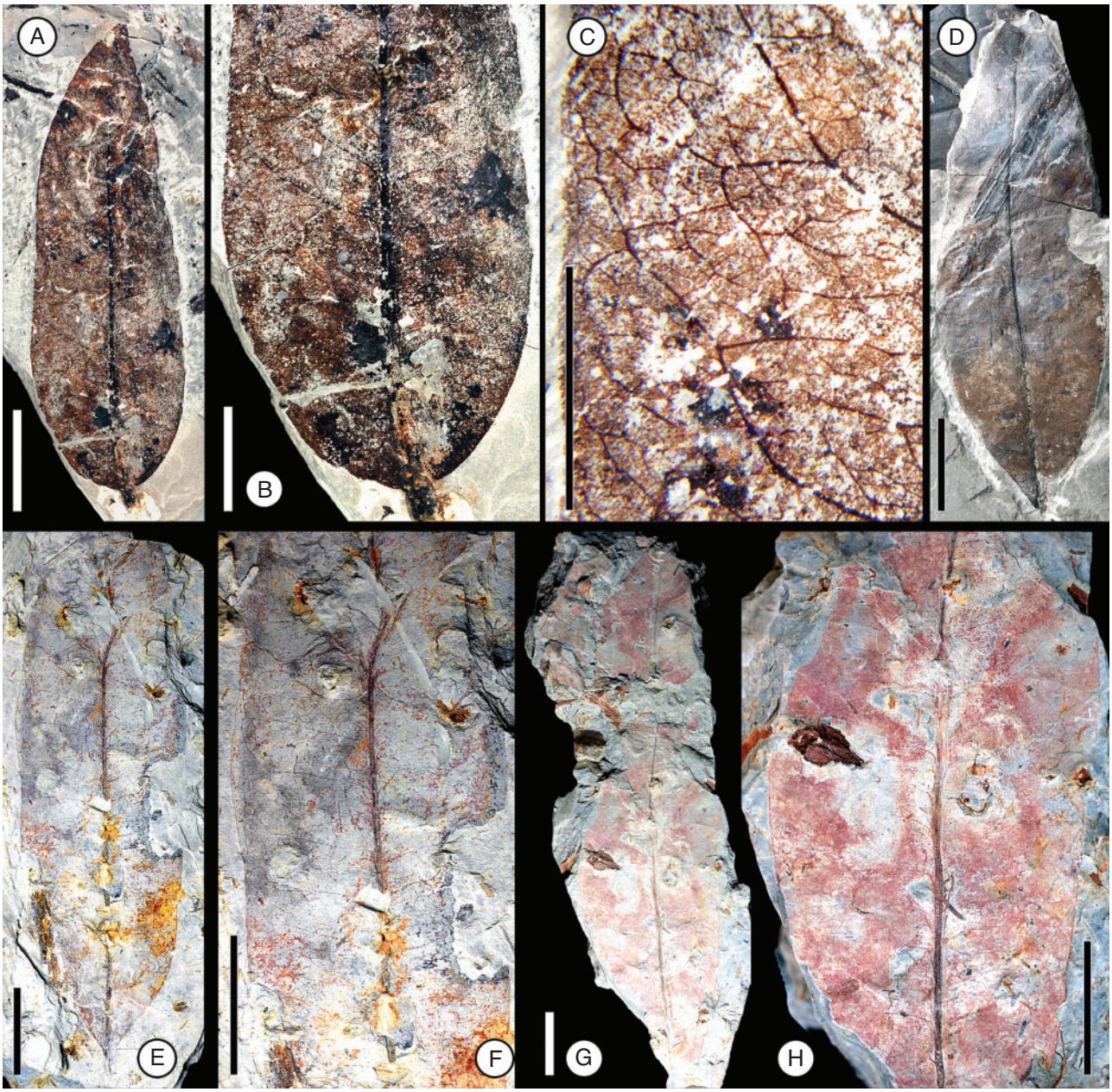

Fig. 17. Leaf morphotype 5. All specimens from Cerrejón Formation. A. Isolated leaflet showing well developed pulvinus, pinnate venation, and acute apex (#13013). B. Detail from A, showing pulvinus and basal eucamptodromous secondary venation. C. Detail from A; note reticulate tertiary and quaternary veins. D. Isolated leaflet (#10206). E. Isolated leaflet; note pinnate venation and secondary veins becoming brochidodromous distally (#9431). F. Detail from E. G. Isolated leaflet; note pinnate venation and secondary veins becoming brochidodromous distally. H. Detail from G. Scale bars: 2 cm (A, D–H), 1 cm (B), 5 mm (C).

Indian fossils, fruits of *L. desmodioides* and *L. albizioides* are more or less similar to Fruit morphotype 6 (Fig. 6–8), but they differ from the Colombian fossils because of the strongly segmented pods and apparent two series of alternate seeds respectively. Pods of *L. derrisoides* appear to be inconspicuously winged on the placental side, being, to some extent, similar to Fruit morphotypes 1 and 2 (Fig. 1), but the placental wing in the Colombian fossils is much wider and the fruits are also larger in size. Other potential legume fruits and wood have been reported from the Late Cretaceous to the

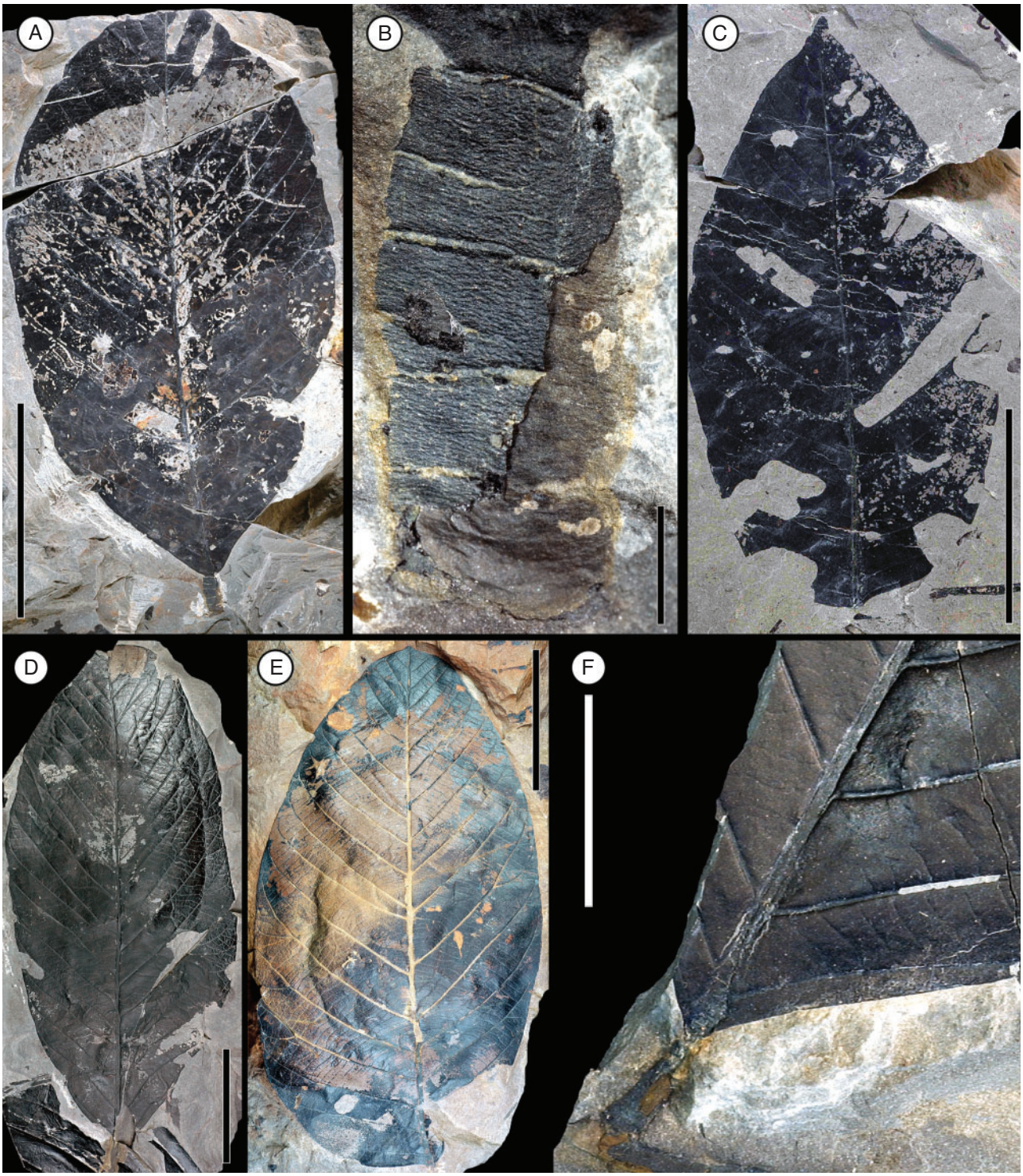

Fig. 18. Leaf morphotype 6. All specimens from Cerrejón Formation. A. Isolated leaflet showing conspicuous pulvinus and pinnate venation; see also Fig. 19 (#13014). B. Detail from A, showing strongly transversely striated pulvinus. C. Isolated leaflet showing short acuminate apex and abundant insect damage (#13015). D. Large isolated leaflet showing pinnate venation and at least 22 pairs of secondary veins (#10173). E. Isolated leaflet showing eucamptodromous secondary venation becoming brochidodromous distally (#11916). F. Detail of leaflet near the base showing conspicuous pulvinus articulated to fragmentary rachis (#13016). Scale bars: 5 cm (A, C–E), 2 cm (F), 2 mm (B).

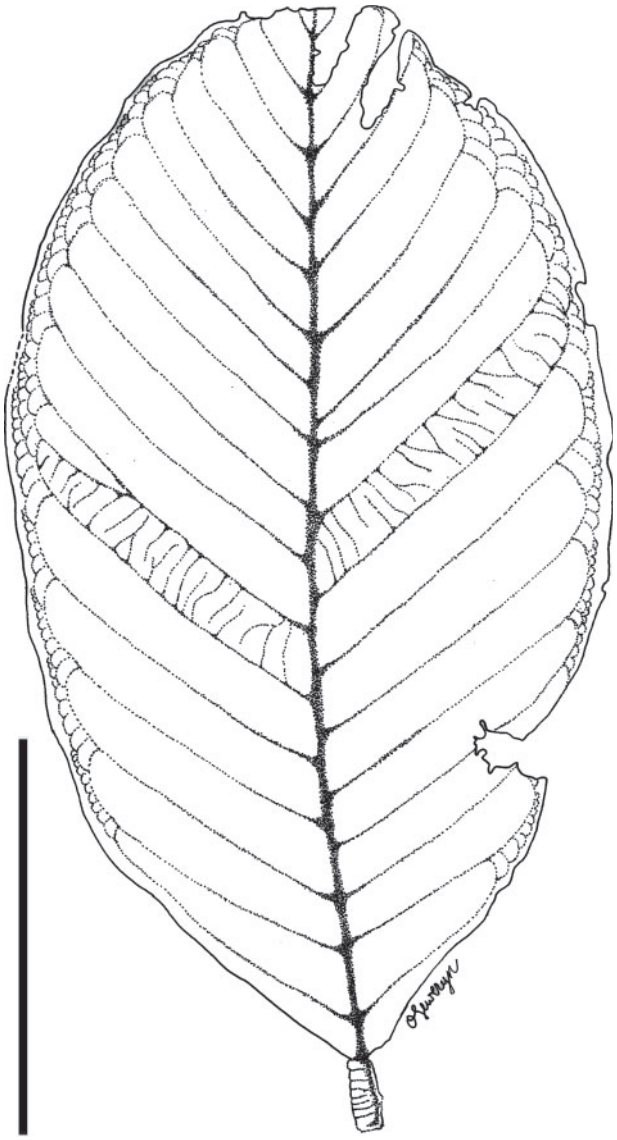

Fig. 19. Line drawing of Leaf morphotype 6 from Cerrejón Formation. Detail of specimen from Fig. 18A; note conspicuous, transversely striated pulvinus and eucamptodromous secondary venation becoming brochidodromous distally. Scale bar: 5 cm.

Paleocene of the Deccan Intertrappean beds in India (e.g. Srivastava 2011); however, the legume affinity and age of those fossils remain poorly documented.

Implications for legume evolution

The Cerrejón and Bogotá floras preserve a remarkable assemblage of fruits and leaves of the legume family from the Middle to Late Paleocene of northern South America. The morphological variety of these fossil fruits and leaves is also a reflection of the floristic legume diversity seen in the earliest Neotropical rainforests of Colombia. Two morphotypes of bipinnate leaves (Morphotypes 1 and 2; Fig. 12–13) can be placed with confidence in the Caesalpinioideae subfamily. Fruit morphotype 6, with its branching thyrsoid inflorescence, is placed in the subfamily Dialioideae (Fig. 6–8), and the resinous Fruit morphotype 8 (Fig. 10–11) shows a strong similarity with several genera in the resin-producing clade of Detarioideae. Although all other Cerrejón and Bogotá fruits and leaves show clear and definitive legume characteristics, most of those fossils show morphological similarities with more than one subfamily (e.g. Fruit morphotypes 1, 2, 3 and 7; Leaf types 3, 4 and 6; Table 1) and cannot be placed confidently within any single group. Nevertheless, sufficient details are preserved to compare these fossil taxa with previously published fossils. All Cerrejón and Bogotá leaves and fruits can be clearly distinguished from other Paleocene records from southern South America, North America, Europe and India.

The Cerrejón and Bogotá floras represent the earliest lowland rainforests in the Neotropical region (Wing *et al*. 2009; Herrera *et al*. 2011) and the new abundant fossils described here also show that the Leguminosae was the most important component of this biome (Wing *et al*. 2009). Like extant lowland rainforests in the Neotropics, these fossil floras were also composed of Annonaceae, Araceae, Arecaceae, Lauraceae, Malvaceae, Menispermaceae, Ulmaceae, Zingiberales, and several unidentified ferns, among others (Jaramillo *et al*. 2007; Doria *et al*. 2008; Herrera *et al*. 2008, 2014; Gomez-Navarro *et al*. 2009; Wing *et al*. 2009; Carvalho *et al*. 2011). These forests also included families and genera that are characterised by lianas and woody climbers that have been extirpated from the Neotropical region, such as Icacinaceae and *Stephania* in Menispermaceae (Herrera *et al*. 2011; Stull *et al*. 2012). The Cerrejón and Bogotá fossils contribute to our understanding of the extraordinary diversification of Leguminosae during the Middle to Late Paleocene tropics of South America. Contrary to most molecular-dating analyses that suggest a Cretaceous age for the family (e.g. Wikström *et al*. 2004; Lavin *et al*. 2005; Bruneau *et al*. 2008; Bell *et al*. 2010; Magallón *et al*. 2015), no reliable legume fossils have been discovered prior to the Paleocene.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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Table 1. Comparative table of fossil fruits and leaves from Cerrejón and Bogotá floras

Sizes are given in centimetres for fruits, and as size categories for leaflets. Additional comments on the affinity of the fossils are presented in the systematic section

Morphotype	Diagnostic feature	Size	Affinity	Occurrence
Fruit morphotype 1	One-winged, seeds 6–10+, septate	+14 cm length, 6-cm width	Uncertain; similar to fruits in Caesalpinioideae, Detarioideae, & Dialioideae	Cerrejón flora only
Fruit morphotype 2	One-winged, seeds 2 or 3(?), slightly septate	2.2-cm length, 1.3-cm width	Uncertain; similar to fruits in Caesalpinioideae, Detarioideae, & Dialioideae	Cerrejón flora only
Fruit morphotype 3	Two-winged, seeds 3–9, septate	3.0–7.9-cm length, 0.9–1.7-cm width	Uncertain; similar to fruits in Papilionoideae & Caesalpinioideae	Dominant in Bogotá flora; one specimen from Cerrejón flora
Fruit morphotype 4	Non-winged, stipitate seeds 2+, non-septate	3.3–4.1-cm length, 0.8–1.1-cm width	Uncertain	Cerrejón flora only
Fruit morphotype 5	Non-winged, seeds 1+, non-septate	+5.6-cm length, 3.4-cm width	Uncertain	Bogotá flora only
Fruit morphotype 6	Infructescence, non-winged, seeds 2+, septate	4.5–13-cm length, 0.9–2.0-cm width	Dialioideae	Cerrejón flora only
Fruit morphotype 7	Non-winged, strongly asymmetrical	3.8–4.1-cm length, 2.0–2.2-cm width	Uncertain, similar to fruits in Detarioideae	Cerrejón flora only
Fruit morphotype 8	Non-winged, stipitate, seeds 1(2?), resinous	10–18-mm length, 3–5-mm width	Detarioideae	Bogotá flora only
Leaf morphotype 1	Bipinnate leaves	Leptophyll to nanophyll	Caesalpinioideae	Cerrejón flora only
Leaf morphotype 2	Bipinnate leaves	Leptophyll to nanophyll	Caesalpinioideae	Bogotá flora only
Leaf morphotype 3	Paripinnate or imparipinnate	Microphyll to notophyll	Uncertain, similar to leaves in Detarioideae	Bogotá flora only
Leaf morphotype 4	Imparipinnate	Microphyll to mesophyll	Uncertain, similar to leaves in Detarioideae	Cerrejón flora only
Leaf morphotype 5	Isolated leaflets, pulvinus strongly striated	Microphyll to mesophyll	Uncertain	Cerrejón flora only
Leaf morphotype 6	Isolated leaflets, pulvinus strongly striated	Notophyll to macrophyll	Uncertain, similar to leaves in Detarioideae, Dialioideae Caesalpinioideae and Papilionoideae	Cerrejón flora only

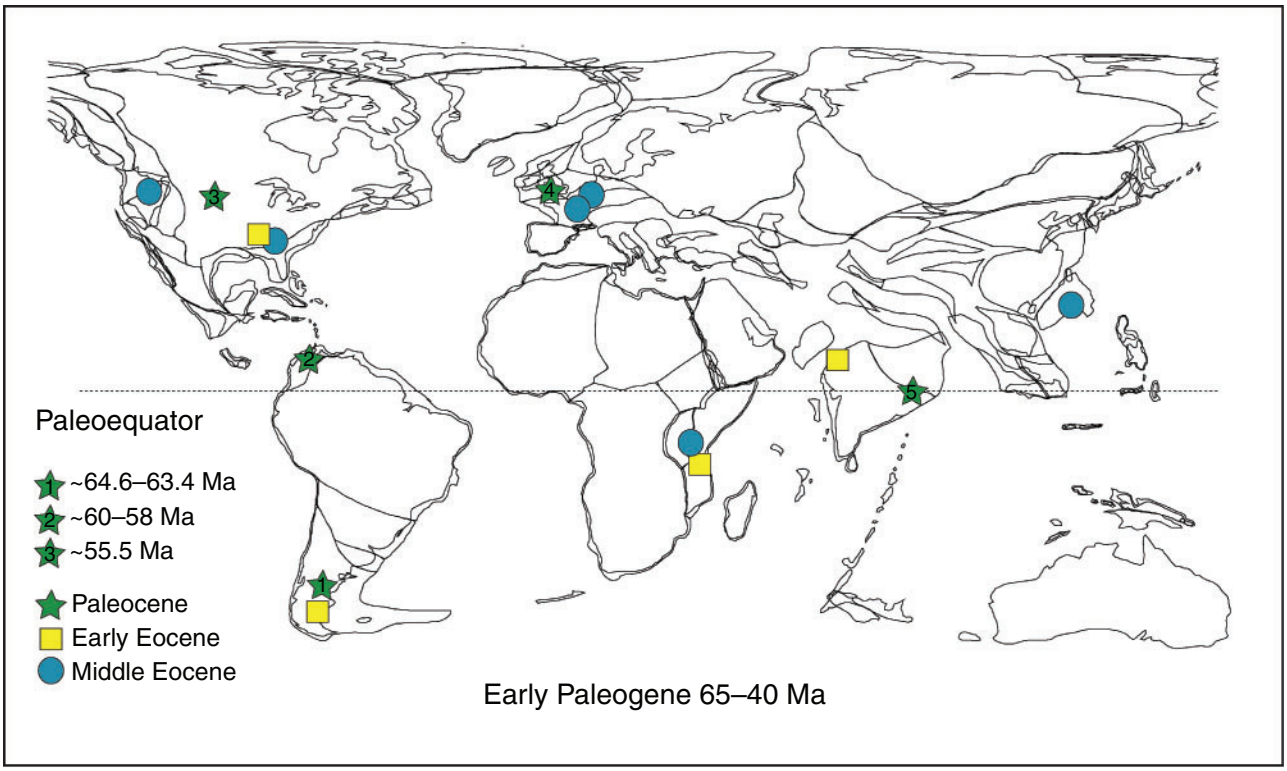

Fig. 20. Paleogeographic distribution of the Leguminosae fossil record during the Paleogene. Map is based on Scotese (2001). Paleocene reliable records: (1) Iglesias *et al*. (2007); Brea *et al*. (2008). (2) This paper; Wing *et al*. 2009. (3) Wing *et al*. (2005). (4) Herendeen and Crane (1992). (5) Bhattacharyya (1985); Saxena *et al*. (1996). Selected Early to Middle Eocene floras. South America: Wilf *et al*. (2003). North America: Crepet and Taylor (1985, 1986); Herendeen (1992); Herendeen *et al*. (1992); Crepet and Herendeen (1992); Jia and Manchester (2014); Dilcher *et al*. (2014). Europe: Senesse and Gruas-Cavagnetto (1990); Collinson *et al*. (2012). Africa: Cantrill *et al*. (2013); Herendeen and Jacobs (2000); Jacobs and Herendeen (2004). India: Shukla and Mehrotra (2016). China: Xu *et al*. (2015).

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