Palms (Arecaceae) from a Paleocene rainforest of northern Colombia[1]

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Palms are a monophyletic group with a dominantly tropical distribution; however, their fossil record in low latitudes is strikingly scarce. In this paper, we describe fossil leaves, inflorescences, and fruits of palms from the middle to late Paleocene Cerrejón Formation, outcropping in the Ranchería River Valley, northern Colombia. The fossils demonstrate the presence of at least five palm morphospecies in the basin ca. 60 Ma. We compare the morphology of the fossils with extant palms and conclude that they belong to at least three palm lineages: the pantropical Cocoseae of the subfamily Arecoideae, the monotypic genus *Nypa*, and either Calamoideae or Coryphoideae. The fossil fruits and inflorescences are among the oldest megafossil records of these groups and demonstrate that the divergence of the Cocoseae was more than 60 Ma, earlier than has previously been thought. These fossils are useful in tracing the range expansion or contraction of historical or current neotropical elements and also have profound implications for the understanding of the evolution of neotropical rainforests.

Key words: Arecaceae; Arecoideae; Attaleinae; Cerrejón; *Cocos*; Colombia; neotropics; *Nypa*; Paleocene.

Arecaceae, the palm family, is a monophyletic group including 183 genera and 2364 species (Govaerts and Dransfield, 2005; Dransfield et al., 2008). At present, most palms are distributed in the tropics with a few species reaching subtropical areas (Henderson et al., 1995). Fossil records from the tropics are less common, however, than those from middle latitudes (Harley and Morley, 1995; Dransfield et al., 2008). The palm fossil record reflects a broader latitudinal distribution of palms in the late Mesozoic and early Cenozoic because of warmer global climate, but also lack of study in the tropics.

Palms are hypothesized to have originated in Australasia (including New Guinea, New Caledonia, and New Zealand) and their crown node is estimated to be ca. 110 Myr old (late Aptian) (Janssen and Bremer, 2004; Bremer and Janssen, 2005).

However, the oldest unequivocal macrofossil records are stems (not assignable below the family level) from the lower Upper Cretaceous (Turonian, 95 Ma) of France (Dransfield et al., 2008). After their first appearance, palms underwent an important radiation during the Paleocene–Eocene period (Harley, 2006; Dransfield et al., 2008), coinciding with long-term global warming (Zachos et al., 2001).

The family has been placed in recent studies within the commelinid clade of the monocotyledons (Chase et al., 2006; Davis et al., 2006). Arecaceae is composed by five strongly supported subfamilies: Arecoideae, Calamoideae, Ceroxyloideae, Coryphoideae, and Nypoideae with Calamoideae as sister group to the rest of the palms and Nypoideae as the next branch (Asmussen et al., 2006; Dransfield et al., 2005, 2008; Baker et al., in press). The oldest fossils reported for the most basal subfamilies (Nypoideae and Calamoideae), however, are pollen of Maastrichtian age, while the oldest palm fossil assignable below family level is 20 Ma older (Berry, 1914) and belongs to the more derived subfamily Coryphoideae (Dransfield et al., 2008).

In this paper, we describe five palm morphospecies from a Paleocene (ca. 60–58 Ma) rainforest (Herrera et al., 2005) in northeastern Colombia. The fossils are inflorescences, fruits and leaves related to three out of the five palm subfamilies (Arecoideae, Nypoideae, and either Calamoideae or Coryphoideae). Thus, by the Paleocene, the family was represented in northern South America by more than half of the major extant palm lineages.

The inflorescences collected have affinities with the subfamily Arecoideae, as does one of the fruit morphotypes, which we assign to cf. *Cocos*, a pantropical genus in the tribe Cocoseae. The other fruit type we assign to the monotypic genus *Nypa* (Nypoideae). Palm leaves were separated into pinnate and palmate morphospecies with uncertain subfamilial affinity, although the palmate type belongs to either Calamoideae or Coryphoideae. The fossils described here provide information

about the previous distribution ranges and minimum ages of extant palm lineages. In particular, the inflorescences and fruits are among the oldest megafossil records of the modern groups to which they are assigned.

MATERIALS AND METHODS

Cerrejón Formation—The fossil palms were recovered from six localities at the Cerrejón open-pit coal mine, Ranchería Basin, Guajira Department, northeastern Colombia (Fig. 1). The sampled strata are in the middle and upper part of the Cerrejón Formation, a sedimentary sequence dominated by mudstone, sandstone, and coal, and deposited in a fresh water-influenced coastal plain (Jaramillo et al., 2007). The six fossil localities are: 0317 (11°14′N; 72°57′W), 0318 (11°13′N; 72°55′W), 0319 (11°66′N; 73°31′W), 0323 (11°64′N; 73°33′W), 0324 (11°62′N; 73°32′W), and La Puente M105–106 (11°90′N; 72°30′W) (Fig. 2). The formation is middle to late Paleocene (ca. 60–58 Ma) based on pollen and carbon isotope studies (Van der Kaars, 1983; Jaramillo et al., 2007).

Fossil material—The megafossils are compressions of reproductive and vegetative organs of palms preserved with external morphological details. The collections are deposited at Ingeominas (Instituto Colombiano de Geología y Minería) in Bogotá, Colombia. Fossil cuticles were prepared using Schulze's solution and other standard techniques (Kerp and Krings, 1999). Fossil cuticles obtained by maceration were extremely fragmented even with the gentlest treatment. Cuticle description follows Tomlinson (1961). Cuticles from modern palm leaves, prepared for comparison, were isolated with commercial bleach, and then stained in 1% aqueous safranin-O. The cellular patterns displayed by the tissues isolated from the fossil fruits were compared with impressions in a transparent resin of the surface of modern palm fruits. Modern material was examined from the Universidad de Antioquia Herbarium (HUA), Herbario Nacional Colombiano (COL), New York Botanical Garden Herbarium (NY) and Fairchild Tropical Botanic Garden (FTBG). The plant fossils were examined with a Nikon SMZ-2T stereomicroscope (Nikon, Tokyo, Japan) and an Olympus BH-2 optical microscope (Olympus, Tokyo, Japan), and photographed with a Nikon D70 digital camera. The background of the pictures was subtracted and/or black-replaced with Photoshop CS software (Adobe Systems, San Jose, California, USA). The drawings of the fossils were made using photographs as a template with CorelDRAW software (Corel, Ottawa, Ontario, Canada).

Cerrejón fossil floral assemblage—The Cerrejón megaflora was first collected over forty years ago (Doubinger and Pons, 1970) and represents one of the very few known fossil floral assemblages from the neotropics (Burnham and Johnson, 2004). An analysis of leaf morphological characters shows a high proportion of entire margins and large leaves, which point to a wet tropical climate with a mean annual temperature and precipitation of ca. >24°C and ~4000 mm, respectively (Wing et al., 2004; Herrera et al., 2005). Another estimate of paleotemperature based on the size of fossil snake vertebrae from the same strata suggested a minimum mean annual temperature of 30–34°C (Head et al., 2009). Wing et al. (2004) and Herrera et al. (2005) found affinities of the Cerrejón flora with typical tropical rainforest families such as Anacardiaceae, Araceae, Arecaceae, Euphorbiaceae, Fabaceae, Lauraceae, Malvaceae, Menispermaceae, and the order Zingiberales (Doria et al., 2008; Herrera et al., 2008).

Based on a palynological study of the Cerrejón Formation strata, Jaramillo et al. (2007) concluded that the composition and diversity of the Cerrejón flora did not change significantly through the formation. They also found three fossil palynomorph species that have been assigned to palms, including *Arecipites regio*, *Mauritiidites franciscoi*, and *Psilamonocolpites medius*, all of which are abundant. However, a detailed morphological study to assess their natural affinities within Arecaceae has not been carried out yet. *Spinizonocolpites echinatus*, a fossil pollen species that is related to *Nypa* (Germeraad et al., 1968) was only found below coal seam 100 (Fig. 2).

RESULTS

Fossil Nypa sp.—*Order*—Arecales

Family—Arecaceae Schultz Sch. 1832

Subfamily—Nypoideae Griffith 1850

Genus—*Nypa* Steck 1757

Species—*Nypa* sp.

Specimens—ING-337 (Fig. 3A–E), ING-338, ING-339.

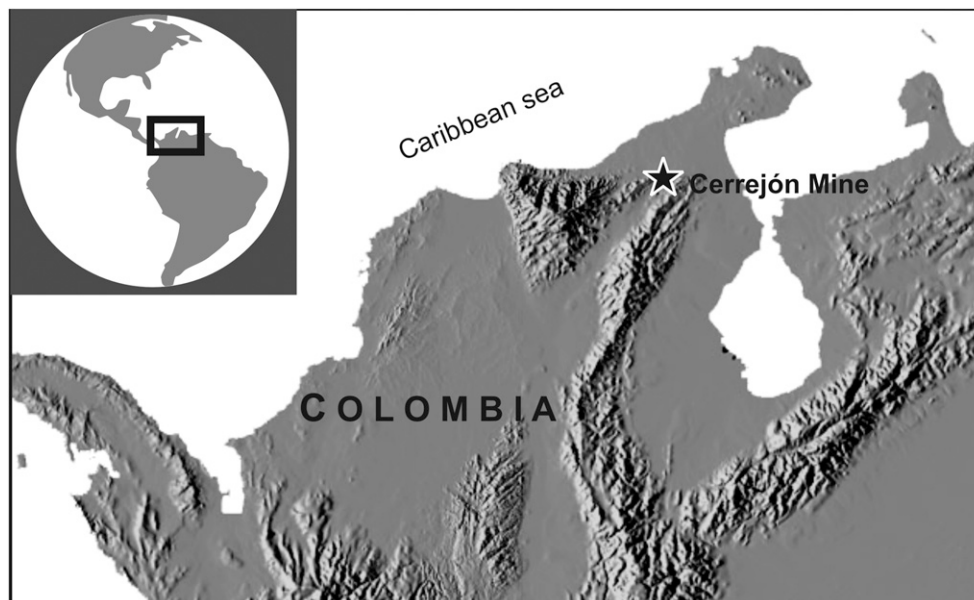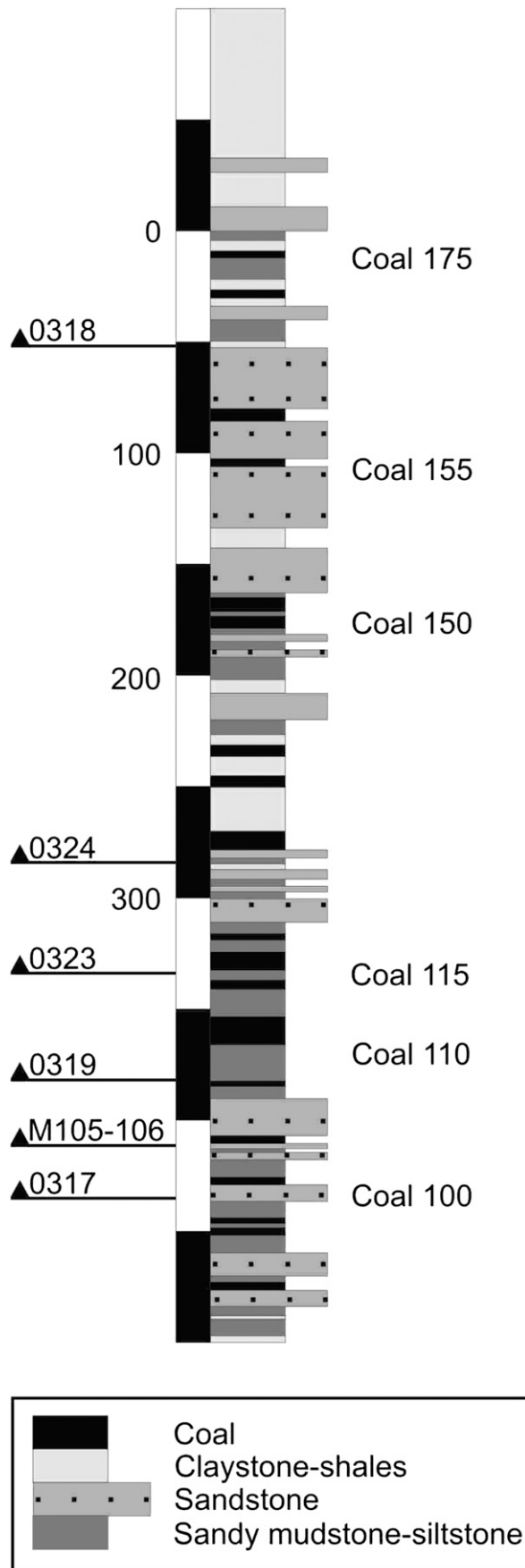*Repository*—Paleobotanical Collection, Ingeominas (Instituto Colombiano de Geología y Minería), Bogotá, Colombia.

Fig. 1.   Geographic location of the Cerrejón coal mine in northeastern Colombia. The map is courtesy of NASA/JPL-Caltech.

Fig. 2. Middle to upper section of the Cerrejón Formation stratigraphic column showing the fossil localities on the left side (0317, 0318, 0319, 0323, 0324, M105–106) and the coal seams on the right side of the depth scale. Depth scale in meters.

Locality—ING-337 from 0319 (11°66′N; 73°31′W) in Tabaco High Dip-pit. ING-338 and ING-339 collected in La Puente M105–106 (11°90′N; 72°30′W), La Puente-pit (Table 1). Cerrejón coal mine, Ranchería River Basin, northern Colombia.

Age and stratigraphy—Middle to late Paleocene, Upper Cerrejón Formation, between coal seams 105 and 106.

Description—Compressed fruits, obovoid in shape, asymmetrical, 80–92 mm wide and 170 mm long (Fig. 3A). The apex has a truncated pyramid-shaped protuberance 7–9 mm long and 9–11 mm wide at its base (Fig. 3B, C). The whole surface is covered by longitudinal fiber scars and has 1–2 longitudinal ridges 4.5–13 mm high on its wider part (Fig. 3D). The base of the fruit is 45 mm wide and truncated (Fig. 3E). Cuticle and other tissue could be isolated from only one specimen, but the material was extremely fragmented and did not help in the determinations.

Comparisons—Fruits with an obovoid shape, conspicuous longitudinal ridges, a truncated base, and an apical truncated-pyramidal protuberance are not present in other families besides Arecaceae. All these characters suggest an affinity to the genus *Nypa* (see Fig. 3F for comparison with modern *Nypa* fruit). Dispersed fruits of *Barringtonia asiatica* (L.) Kurz (Lecythidaceae) are similar to those of *Nypa* in overall size and shape, but have net-like fibers interwoven in the mesocarp, differing from the longitudinally oriented fibers in *Nypa*. Additionally, in *Barringtonia* the widest part of the mesocarp is at least half the width of the seed, whereas in *Nypa* the widest part of the mesocarp is less than half the width of the seed.

The fruit is different from members of other palm subfamilies because of the combination of longitudinal ridges, pyramidal stigmatic remains on the apex, truncated base, and a large size (90 × 170 mm). Some species included in Attaleinae can have similar fruits, but they have a terminal beak, they do not have prominent longitudinal ridges, the base is normally obtuse, and the overall shape is ellipsoidal, ovoid, or globose (except in *Allagoptera*, which has small fruits). Palmate and pinnate leaves were found in the localities where *Nypa* sp. was collected (Table 1). Modern *N. fruticans* has pinnate leaves with distinct epidermal features. However, as explained later, the fossil cuticles are very fragmented, and the affinities of the leaves could not be determined. Jaramillo and Dilcher (2001) found *Spinizonocolpites,* a palynomorph that has been related to *Nypa,* in the Upper Paleocene and Middle Eocene of Colombia. In the Cerrejón Formation, *Spinizonocolpites echinatus* was found by Jaramillo et al. (2007), but in older strata.

Fossil fruits, endocarps, or seeds comparable to *Nypa,* have been named *Burtinia*, *Castellinia*, *Fracastoria*, *Nipa*, *Nipadites*, and *Nypa* (Tralau, 1964). Rendle (1894) and Tralau (1964) recognized that the differences used to separate those fossil genera are similar to variations found within a single infructescence of living *Nypa fruticans* Wurmb. Rendle (1894) included *Burtinia*

TABLE 1.   Localities where fossil palm fragments were collected, type and relative abundance of fragments.

Locality	*Nypa* sp. fruit	cf. *Cocos* sp. fruit	Arecoideae sp. inflorescence	Arecaceae sp.1 pinnate leaf	Arecaceae sp.2 fan-shaped leaf
0317	—	—	Rare	Common	—
0318	—	—	—	Common	—
0319	Rare	—	—	–	Common
0323	—	—	—	Rare	—
0324	—	Common	—	—	—
La Puente M105–106	Rare	—	—	Rare	—

Notes: absent: —; rare: 1–3 specimens, common: one of the two most abundant morphotypes at the locality.

in the genus *Nipadites*, and then Reid and Chandler (1933), synonymized *Nipadites* with *Nypa burtini*. Thereafter, Tralau (1964), included *Castellinia* and *Fracastoria* in *N. burtini* (Brongniart) Ettinghausen. *Nypa burtini* differs from *N. fruticans* by the faint or absent sulcus in the seed that in modern *N. fruticans* is conspicuous. Details of internal layers or seeds could not be seen in the compressed fruits collected in this study, so a detailed comparison with *N. burtini* cannot be made. *Nypa australis* is separated from living *N. fruticans* based on epidermal leaf features (Pole and Macphail, 1996) (Table 2). The characters of the fruits here collected agree with those of *N. sahnii* Lakhanpal (1952) and the specimens described by Mehrotra et al. (2003).

Fossil cf. Cocos sp.—*Order*—Arecales

Family—Arecaceae Schultz Sch. 1832

Subfamily—Arecoideae Griffith 1850

Tribe—Cocoseae Mart. 1837

Subtribe—Attaleinae Drude 1887

Species—cf. *Cocos* sp.

Specimens—ING-870 (Fig. 4A–E), ING-871, ING-872, ING-873, ING-874, ING-875, ING-876, ING-877, ING-878, ING-879, ING-880, ING-881.

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

Locality—0324 (11°62′N; 73°32′W) in Tabaco High Dip-pit (Table 1). Cerrejón coal mine, Ranchería River Basin, northern Colombia.

Age and stratigraphy—Middle to late Paleocene, Upper Cerrejón Formation, between coal seams 125 and 130.

Description—Compressed fruits, ovoid, 150 mm wide, 250 mm long, and 4–8 mm thick; apex acute, asymmetrically located, with a scar perpendicular to the longer axis of the fruit, at 8–10 mm from the apex (Fig. 4A–E); base and the whole surface covered by longitudinal fiber scars; inconspicuous ridge longitudinally oriented.

Comparisons—Characters exhibited by the fossil fruits including the ovoid shape, the parallel, longitudinally oriented fibers, the inconspicuous longitudinal ridges, and the very large size, can only be found in Arecaceae. Within Arecaceae, those

characters suggest a relation with the well-supported subtribe Attaleinae (Dransfield et al., 2005; Asmussen et al., 2006) of the Cocoseae. Among the modern genera of the Attaleinae, only *Cocos* is similar to the fossils in being large and having inconspicuous longitudinal ridges (Fig. 4C). We ascribe the perpendicular scar in the apex (Fig. 4D, E) to the stigmatic remains. Due to compaction of the fruits during preservation, the fruit internal layers are not distinguishable, and thus it is not possible to determine whether they had the three pores in the endocarp characteristic of the tribe Cocoseae.

Fossils assigned to Attaleinae such as those reported by Berry (1926, considered as cocosoid-like by Dransfield et al., 2008), Kaul (1951), Ballance et al. (1981), Patil and Upadhye (1984), Rigby (1995), and Campbell et al. (2000, cited by Dransfield et al., 2008) are preserved endocarps and cannot be compared with the whole compressed fruits of cf. *Cocos* sp., where only surface morphology is visible. *Cocos nucifera*-like fruits from the Tertiary of India (Tripathi et al., 1999) are smaller in size than cf. *Cocos* sp. (Table 3). Berry (1929) describes a fruit (*Attalea gunteri*) from the Upper Eocene of Florida. The fruit is subspherical, 25 × 36 mm in size, with longitudinally oriented fibers and its affinity with *Attalea* is rather doubtful.

Fossil Arecoideae sp.—*Order*—Arecales

Family—Arecaceae Schultz Sch. 1832

Subfamily—Arecoideae Griffith 1850

Species—Arecoideae sp.

Specimens—ING-321, ING-322 (Fig. 5A–D, F–I).

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

Locality—0317 (11°14′N; 72°57′W) in Tabaco 1 pit (Table 1). Cerrejón coal mine, Ranchería River Basin, northern Colombia.

Age and stratigraphy—Middle to late Paleocene, Upper Cerrejón Formation, between coal seams 100 and 102.

Description—Inflorescences, branched to one order, peduncle not preserved, rachis 23 mm wide (Fig. 5A, D), bearing spirally arranged rachillae, 3–30 mm apart, lacking bracts subtending them. Rachillae erect, 2.2–3.5 mm wide in the central part and 7.0–8.0 mm wide in the basal part (Fig. 5B, C), with flower insertion scars starting at 43–56 mm from the insertion into the rachis. The scars are 0.6–1.1 mm long and 0.6–1.2 mm wide, spirally arranged, separated by 0.2–10 mm, circular
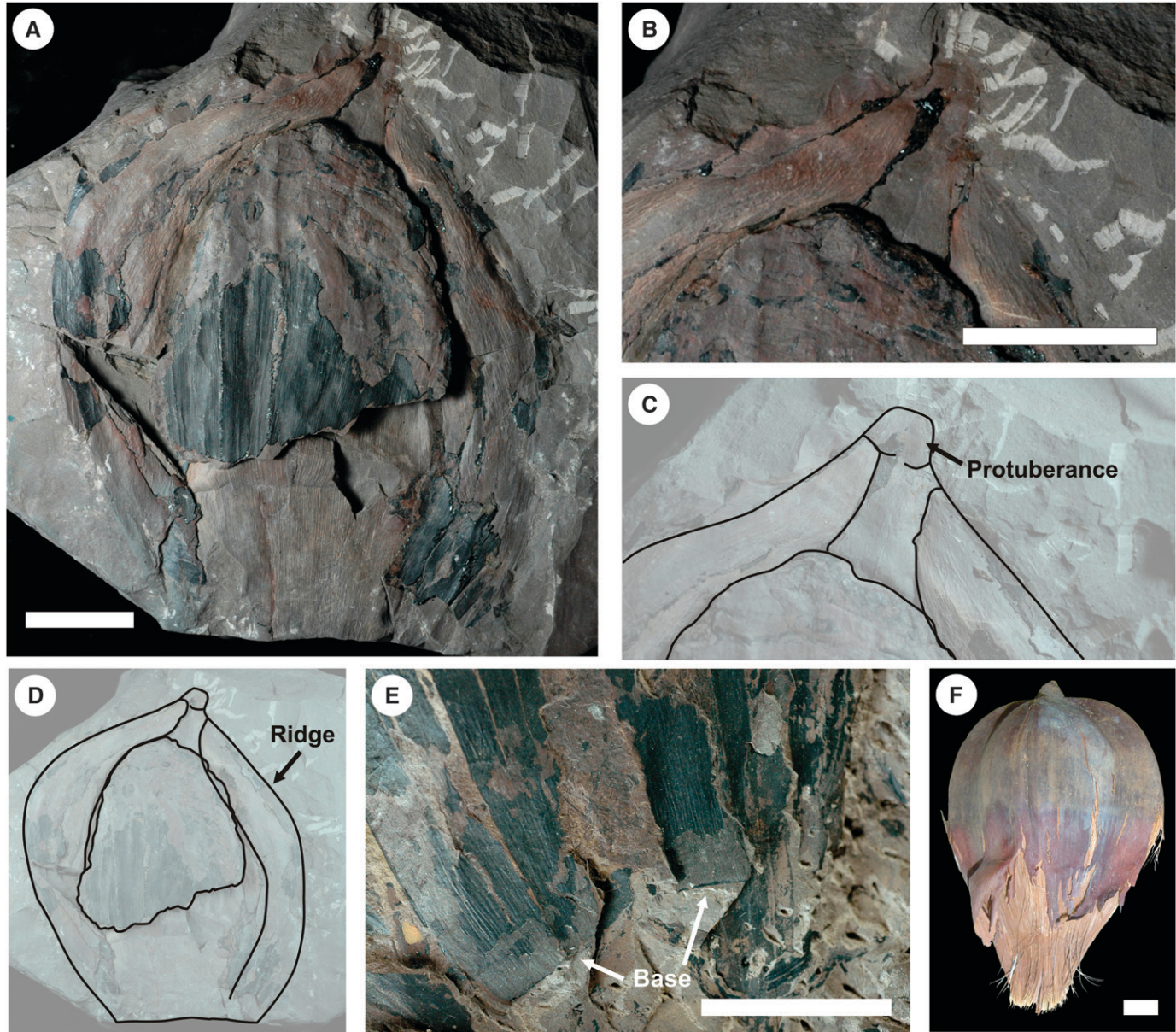
Fig. 3.   *Nypa* sp. and extant *Nypa fruticans* Wurmb. A–E. *Nypa* sp. (A) Fruit, incomplete in the basal part. ING-337. (B) Fruit apex. ING-337. (C) Drawing of fruit apex, showing the apical protuberance. (D) Drawing of fruit, showing the longitudinally oriented ridges. (E) Truncated base of fruit. ING-337. (F) Extant *N. fruticans* fruit (*Tomlinson s.n.*, FTG). A, B, E and F: bar = 20 mm.

to truncated pyramid-shaped, slightly concave, and protruding in the basal half; lacking floral bracteoles or bracts subtending the flower insertions (Fig. 5F, G). Lateral and distal to each floral scar, there are two scars of flower insertions, 0.2–0.3 mm wide, and 0.3–0.4 mm long (Fig. 5H, I).

Comparisons—The fossil inflorescences are assigned to Arecaceae because the flowers exhibit an organization in triads (with the central insertion larger than the lateral ones) that is only present in this family. Several inflorescence characters suggest an affinity with the Arecoideae (see Fig. 5E, J for comparison with an extant inflorescence): inflorescence branched to one order, rachillae thin and straight (Fig. 5A, D), proximally with a 4–5 cm bare portion, triads spirally arranged along the

rachillae, pistillate flower insertions slightly concave, not forming deep pits, with a smaller diameter than the rachilla, rachis much wider (about 10 times) than the rachillae (Fig. 5F–I). Pinnate leaves were common at the locality where this species was collected (Table 1). However, the leaf cuticles are very fragmented, and their affinity with modern palms could not be determined.

Within the Arecaceae, the fossil can be excluded from the subfamily Nypoideae, which has an inflorescence formed by a pistillate head with lateral staminate spikes. The inflorescences of the subfamily Coryphoideae are highly branched, their bracts are sometimes tubular, and the flowers are either solitary or in cincinni. Inflorescences of Ceroxyloideae are also highly branched. Calamoideae differ from the fossil in having highly

TABLE 2.   Comparison of reported *Nypa* sp. fossils and the extant and fossil *Nypa* species.

Characters	Modern *Nypa fruticans*	*Nypa* sp.	*Nypa* aff. *fruticans*	*Nypa australis*	*Nypa fruticans*	*Nypa sahnii*
Reference	Tralau, 1964; Collinson, 1993	Gómez-N. et al., present study	Tralau, 1964	Pole and Macphail, 1996	Mehrotra et al., 2003	Lakhanpal, 1952
Locality	—	Northern Colombia	Europe	Tasmania	NE India	India
Geological time	—	Paleocene	Eocene	Early Eocene	Oligocene and early Miocene	Miocene
Organs recovered	—	Fruits	Fruits, seeds	Leaves, fruits, pollen	Fruits, leaves	Fruits
Fruit breadth (mm)	20–85	45–92	35–145	10–50	25–58	65
Fruit length (mm)	50–120	84–119	40–150	40–110	30–95	110
Fruit ridges	Evident to inconspicuous	Evident to inconspicuous	Evident to inconspicuous	?	Evident to absent	Evident
Apical fruit umbo	Present	Present	Present to absent	?	Present	Present

branched inflorescences, with tubular bracts, and with flowers in dyads (Dransfield et al., 2008). The fossil inflorescences have features of subfamily Arecoideae, but none that support assignment to a particular genus or even to a well-supported group of tribes. Some tribes, however, can be excluded for the following reasons: flower sunken in pits (as in Geonomateae, Pelagodoxeae), inflorescences highly branched (Leopoldinieae, Roystoneeae), spicate inflorescences (Podococceae, Scleropermeae), inflorescences enclosed by the prophyll and peduncular bract during anthesis (Manicarieae), flowers arranged in acervuli (Chamaedoreae), or nonwoody inflorescences (Reinhardtieae). The rest of the tribes included in the subfamily that are potentially related with the fossil inflorescence (Areceae, Cocoseae, Euterpeae, Iriarteae, and Oranieae) do not form a monophyletic group (Dransfield et al., 2008). These tribes all have characters similar to the ones we observe in the fossil inflorescence.

Inflorescences are uncommon in the palm fossil record, and they are usually difficult to assign to genera (Dransfield et al., 2008). Bonde (1996) described *Arecoidostrobus*, a fossil rachilla from the Deccan Intertrappean beds of India. Bonde ascribed this fossil either to Caryoteae, Areceae, Cocoseae, or Geonomateae based on rachilla characters such as flowers arranged in triads, male flowers immersed in pits in the rachilla, and structures of the perianth lobes and of the gynoecium. Arecoideae sp. reported here has flowers arranged in triads but differs from *Arecoidostrobus* in the shallow insertions of the flowers in the rachillae. Also from the Deccan Intertrappean beds of India Mahabalé (1950) assigned a fossil inflorescence to either *Bactris* or *Hyphaene*. However, the fossil was not described, and it is not possible to compare it with Arecoideae sp. Lakhanpal et al. (1982) described *Monocotylostrobus bracteatus*, and Bonde (1996) assigned it to Arecoideae based on its woody axis, well developed-bracts and bracteoles, and flowers arranged in triads along the rachillae. In contrast, Arecoideae sp. lacks conspicuous bracts in the flower insertions. There are other records of inflorescences compiled by Harley (2006) for which the affinities have not been determined.

***Fossil Arecaceae sp. 1.**—Order*—Arecales

Family—Arecaceae Schultz Sch. 1832

Species—Arecaceae sp. 1.

Specimens—ING-822 (Fig. 6A), ING-323, ING-324, ING-334, ING-336 (Fig. 6B–H), ING-869, ING-886, ING-887.

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

Locality—ING-323 and 324 collected in 0317 (11°14′N; 72°57′W, Tabaco 1-pit). ING-886 and 887 from La Puente M105–106 (11°90′N; 72°30′W, La Puente-pit). ING-334 and ING-336 from 0318 (11°13′N; 72°55′W, Tabaco High Dip-pit). ING-822 and ING-869 collected in 0323 (11°64′N; 73°33′W, Tabaco High Dip-pit) (Table 1). Cerrejón coal mine, Ranchería River Basin, northern Colombia.

Age and stratigraphy—Middle to late Paleocene, Upper Cerrejón Formation, between coal seams 100 and 102 (0317), 105 and 106 (La Puente M105–106), 115 and 120 (0323), 160 and 161 (0318).

Description—Fragments of pinnate leaves (Fig. 6A). Rachis 23 mm wide at the base and 7–17 mm wide in more apical fragments, with a longitudinal ridge. Leaflets are plicate, with entire margins, regularly arranged in one plane, opposite to semialternate, separated by 8–42 mm at their insertions. Each leaflet has a prominent midrib 0.5–0.7 mm wide and two orders of parallel veins separated by 1–2.3 mm. Transverse veinlets are not evident. Small cuticle fragments were extracted from two specimens and consisted of two types. (1) Cuticles with stomata, cells isodiametric to rectangular (mainly), with straight walls of 4–6 sides, 13.4–29.0 μm long and 10.8–16.1 μm wide, longitudinally to diagonally extended (near to the stomata); trichomes absent; stomata in irregular lines (Fig. 6B). Guard cells 21.78–25.52 μm long and 5.72–8.58 μm wide; lateral subsidiary cells 25.96–32.56 μm long and 2.64–10.56 μm wide; terminal subsidiary cells without lobes, 9.46–14.96 μm long and 12.54–17.38 μm wide (Fig. 6C, D). (2) Cuticles without stomata, cells with 4–6 sides, rectangular (Fig. 6E, G) to isodiametric (Fig. 6F, H), with straight walls, 10.12–34.32 μm long and 8.14–20.02 μm wide.

Comparisons—Arecaceae sp. 1 displays characters that clearly indicate it is a palm. It is pinnate in shape and has plicate leaflets with a strong midvein (Fig. 6A) bounded on either side by at least two orders of parallel veins, as is observed in palms (Read and Hickey, 1972). Because of the great similarity in leaf morphology between nonrelated genera in palms (Read and Hickey, 1972), the affinities of this species with living genera are difficult to determine. Additionally, we cannot determine whether the insertion of the leaflets on the rachis is reduplicate or induplicate because we did not find complete leaves with the apex preserved. Also cuticles are so fragmented that we cannot
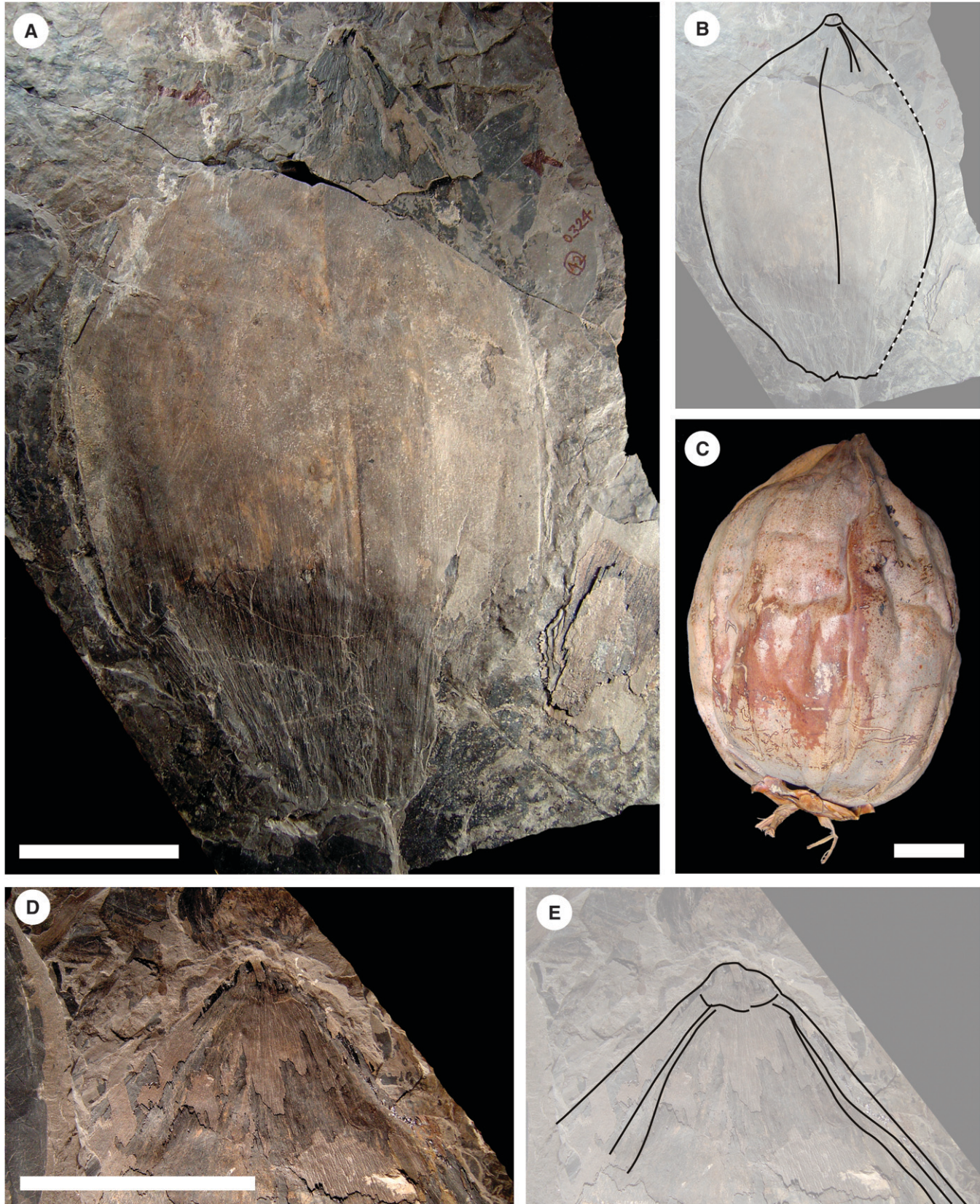
Fig. 4.   cf. *Cocos* sp. and extant *Cocos nucifera* L. (A) Whole fruit. of cf. *Cocos* sp. ING-870. and (B) drawing of whole fruit. (C) Extant *C. nucifera* fruit. (D) Counterpart of cf. *Cocos* sp. apex. ING-870 and (E) drawing showing scar perpendicular to the longer axis and inconspicuous longitudinal ridges. Bar = 50 mm.

TABLE 3.   Comparison of cf. *Cocos* sp. with modern *Cocos nucifera* L. and fossil fruits of Attaleinae species.

Characters	Modern *Cocos nucifera*	cf. *Cocos* sp.	*Cocos nucifera*-like
Reference	Dransfield et al., 2008; Henderson et al. 1995	Gómez-N. et al., present study	Tripathi et al., 1999
Locality	—	Northern Colombia	Madhya Pradesh, India
Geological time	—	Paleocene	Tertiary
Fruit shape	Ellipsoidal to broadly ovoid	Ovoid, asymmetric	Ovoid
Maximum fruit breath (mm)	120–200	150	60–100
Fruit length (mm)	200–300	250	130
Longitudinal fruit ridges	3	1 observable	Present
Fruit apex	Acute, with stigmatic remains	Acute, with stigmatic remains	?

tell whether the isolated pieces belong to the upper or lower epidermis. Thus, it is difficult to assign Arecaceae sp. 1 to a palm subfamily or to assign it to any of the form genera (*Phoenicites*, with reduplicate pinnae and *Phoenix*, with induplicate pinnae) proposed by Read and Hickey (1972).

Fossil Arecaceae sp. 2.—*Order*—Arecales

Family—Arecaceae Schultz Sch. 1832

Species—Arecaceae sp. 2.

Specimens—ING-817, ING-818 (Fig. 6H, I).

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

Locality—0319 (11°66′N; 73°31′W) in Tabaco High Dip-pit (Table 1). Cerrejón coal mine, Ranchería River Valley, northern Colombia.

Age and stratigraphy—Middle to late Paleocene, Upper Cerrejón Formation, between coal seams 105 and 106.

Description—Fragments of costapalmate or palmate leaves (Fig. 6I); segments 51.6–112 mm wide, with entire margins, and a midvein 1.5 mm wide. Parallel to the midvein, there are veins of four orders: first order veins 1.17–1.6 mm wide, separated by 38–38.29 mm; second order veins 0.8–1.1 mm wide; primary and secondary veins separated by 0.2 mm approximately; tertiary veins 0.1–0.2 mm wide, separated by 2.0–3.44 mm; tertiary veins or tertiary and secondary veins separated by 6–8 mm; quaternary veins very thin, almost indiscernible, separated by 0.2 mm and approximately seven in number between two tertiary veins. Crossveins 0.10–0.12 mm wide, strikingly sinuous, with an irregular course, percurrent, spaced 1–5 mm apart and joining the middle or primary veins decurrently at a 45° angle (Fig. 6J). Away from their decurrent junction with thicker veins, the crossveins bend to cross the secondary veins at an almost straight angle; they can connect two primaries or a primary and a lesser order vein. Crossveins are visible only in the leaf fragments that were partly decomposed prior to preservation.

Comparisons—The leaves can be recognized as palm because of the palmate or costapalmate shape, segments with a strong midvein, at least two orders of parallel veins (Read and Hickey, 1972), and crossveins with an irregular course (Tomlinson, 1961). The costapalmate or palmate leaves here described (Fig. 6I) are not assignable below the family level. Owing to their incompleteness, it cannot be determined whether they have a costa nor how their segments are inserted (induplicate or reduplicate). Also, the cuticles could not be isolated. However, within the palms only the subfamilies Coryphoideae and Calamoideae include species either with palmate or costapalmate leaves. Arecaceae sp. 2 should belong to one of these two subfamilies, and the distinctive pattern of venation could lead to a more specific placement within these subfamilies once the systematic distribution of these characters is known.

DISCUSSION

Biogeographic implications of the Nypa sp. report—*Nypa fruticans* is the lone species included in the subfamily Nypoideae, and currently it is restricted to mangrove habitats of southeastern Asia (India, Malasia, Solomon Islands, Ryukyu, and Australia; Tomlinson, 1986), although it has been introduced to western Cameroon, Panama, and Trinidad (Dransfield et al., 2008). *Nypa* was widespread globally in the Maastrichtian and Paleogene (Morley, 2000; Harley, 2006), reaching its maximum range during the Eocene (Europe, Australia, Tasmania, tropical Africa and Asia, North America, Central and South America; Tralau, 1964; Germeraad et al., 1968; Haseldonckx, 1972; Muller, 1981; Collinson, 1993; Pole and Macphail, 1996; Gee, 2001; Jaramillo and Dilcher, 2001; Mehrotra et al., 2003; Pan et al., 2006) (Fig. 7). After the Eocene, *Nypa* records gradually decline, and by the early Miocene, its range contracted to southeastern Asia, probably in response to continental movement and more seasonal and drier climate (Rull, 1998; Harley, 2006). Maastrichtian *Nypa* records are all from pollen, with the oldest megafossils being the Paleocene fruits reported here and those from Brazil (Harley, 2006).

Biogeographic implications of the cf. Cocos report—Molecular phylogenetic analysis of the tribe Cocoseae (Dransfield et al., 2005, 2008) found three well-supported subtribes, the Bactridinae, Elaeidinae, and Attaleinae with the groups Bactridinae and Elaeidinae resolved as sister clades. After calibrating the divergence times of the tribe using the fossil record, Gunn (2004) suggested the divergence of the Bactridinae-Elaeidinae from the Attaleinae occurred between 50 and 60 Ma ago. The Paleocene (ca. 60 Ma) fruits of Attaleinae reported here demonstrate that these two clades must have diverged at an earlier time.

Besides the pantropical *Cocos*, the Attaleinae is composed of seven genera restricted to the neotropics and three distributed in Africa and Madagascar. The three non-neotropical genera have been resolved as sister to the rest of Attaleinae (Hahn, 2002; Gunn, 2004; Asmussen et al., 2006). This phylogenetic reconstruction and their distribution may imply that the early radiation of the Attaleinae occurred outside the Americas, probably
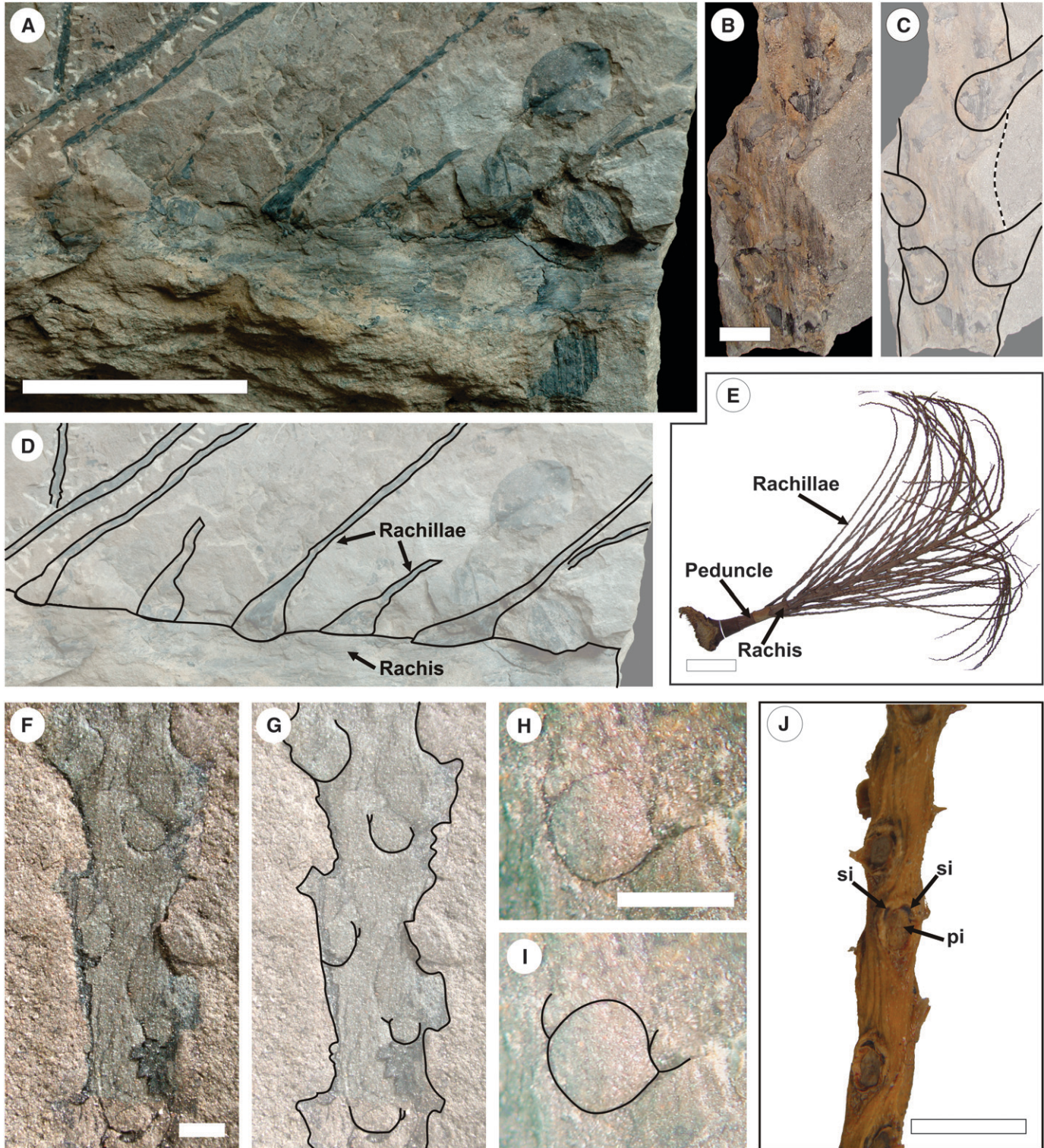
Fig. 5. Arecoideae sp. fossil inflorescence and extant Euterpeae inflorescence. A–D, F–I. Arecoideae sp.; Figs. E, J. Extant Euterpeae inflorescence and rachilla. (A) Fossil inflorescence. ING-322. (B) Rachis and spirally inserted rachillae. (C) Drawing of rachis and spirally inserted rachillae. (D) Drawing of fossil inflorescence showing the main rachis and rachillae. (E) Extant *Prestoea acuminata* (Willd.) H. E. Moore inflorescence (*Gómez-N. et al. 2*, HUA). (F) Rachilla detail. ING-322. (G) Rachilla drawn to show the insertion scars. (H) Zoom into the rachilla, showing an individual insertion composed by three scars; the central and two smaller lateral insertions. ING-322. (I) Drawing of the triad. (J) Rachilla with spirally arranged triads of modern *Prestoea decurrens* (H. Wendl. ex Burret) H. E. Moore (*Rentería et al. 5294*, HUA). pi, pistillate insertion; si, staminate insertion. Bars: A, E = 50 mm, B = 10 mm, F, H = 1 mm, J = 5 mm.
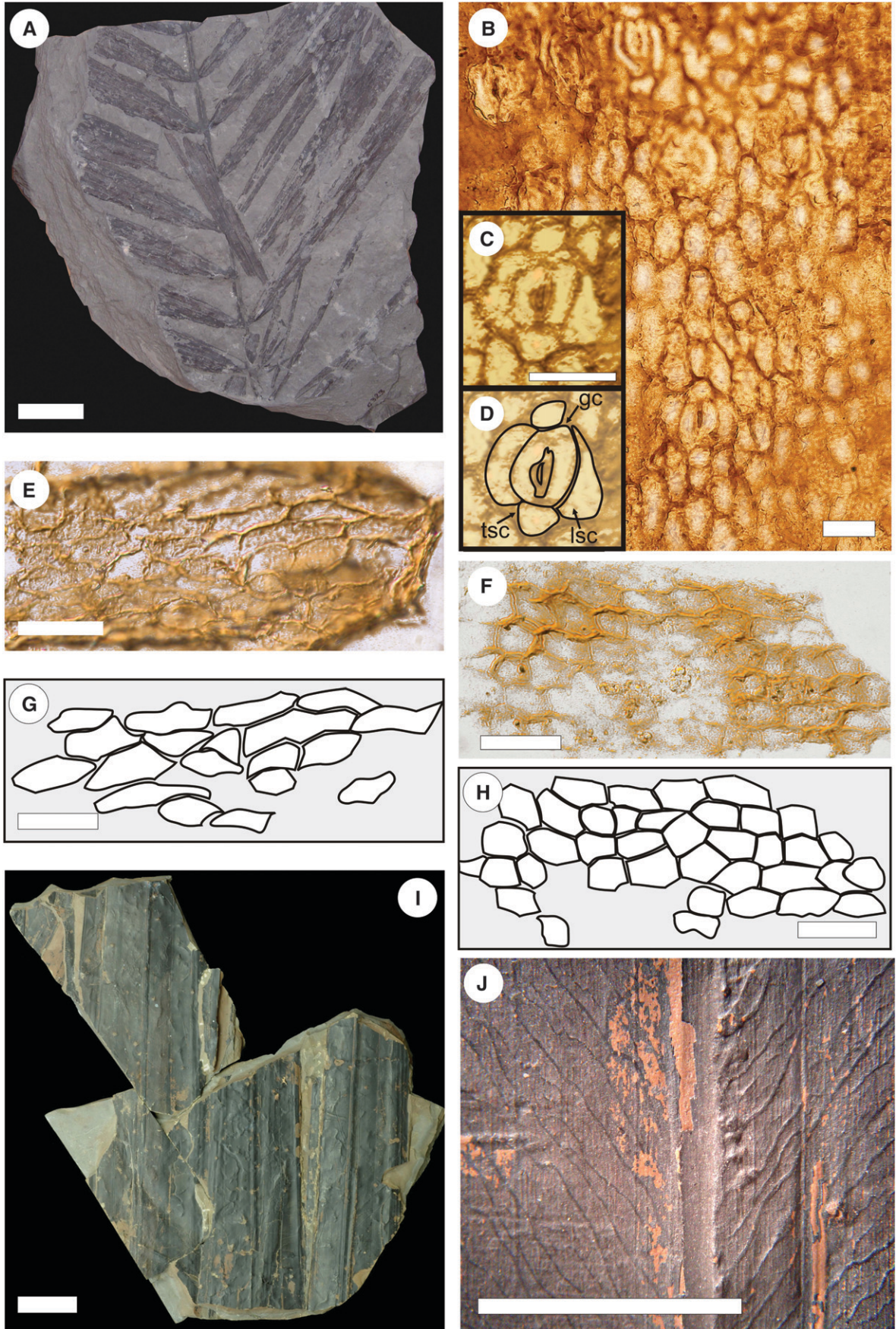
Fig. 7.   Previous reports of fossil fruits and pollen of Attaleinae and *Nypa*. The pollen records are indicated by a white dot in the middle of the symbol.

in Africa, Madagascar or elsewhere, and that a single colonization resulted in the great diversity of the group in the Americas (Dransfield et al., 2008). Finding a member of the Attaleinae (cf. *Cocos* sp.) in South America at 60 Ma implies the subtribe colonized America earlier than estimated by Gunn (2004) (ca. 50 Ma).

The fossil record of Attaleinae by the Eocene is composed only by an endocarp recorded from Jodhpur, India (*Cocos sahnii*; Kaul, 1951). The cf. *Cocos* reported here shows that the subtribe was also present in America since the Paleocene. More recent *Cocos*-related fruits or endocarps are those reported by Rigby (1995) from the Late Pliocene of Queensland, Australia and those of Ballance et al., (1981) and Berry (1926) reported from the Miocene-Pliocene of Auckland, New Zealand, beyond the modern range of the Attaleinae. There are also records with inaccurate dating including those of Patil and Upadhye (1984), Tripathi et al. (1999), Campbell et al. (2000, cited by Dransfield et al., 2008) from the Tertiary of Madhya Pradesh (India) and Canterbury (New Zealand) (Fig. 7).

Cocos is currently cultivated throughout the tropics and some warm subtropical areas, and its origin has been very controversial. For a long time, it was accepted to have an origin in the western Pacific (Harries, 1978), tropical Asia, Polynesia (Beccari, 1963; Corner, 1966), or Melanesia (Moore, 1973). Other authors proposed a South American origin and a later range extension to the Indo-Pacific region (Guppy, 1906; Cook, 1910; Hahn, 2002; Gunn, 2004) based on its ability to disperse long distances over the water. If the fossil here described belongs to the genus *Cocos,* this would be consistent with a neotropical origin. The nesting of *Cocos* within the neotropical Attaleinae also suggests that its immediate ancestors were American (Dransfield et al., 2008)

Biogeographic implications of the Arecoideae sp. report—Arecoideae is the largest and most diverse subfamily of the Arecaceae. It has a worldwide distribution in both the tropics and the subtropics. It has been resolved as a monophyletic

group in the majority of studies (Dransfield et al., 2008); in recent phylogenies, it has been positioned as the most derived clade of the family and sister to the subfamily Ceroxyloideae. The Arecoideae fossil record is substantial but, in most of the cases, inconclusive (Dransfield et al., 2008). The oldest fossils are Maastrichtian in age, but the age estimates need to be reassessed. These include fossils from the Deccan Intertrappean beds of India (e.g., Mahabalé, 1950; Kulkarni and Mahabalé, 1971; Lakhanpal et al., 1982; Patil and Upadhye, 1984; Bonde, 1996; Tripathi et al., 1999) and from Mexico (Weber, 1978, cited in Harley, 2006). Later records are Eocene, Oligocene, or Miocene (see Dransfield et al., 2008 for details). The fossil arecoid inflorescence described here is together with the cf. *Cocos* sp., the first and also the oldest report of the subfamily in South America. Based on its nested placement within the neotropical subfamily Ceroxyloideae, it has been hypothesized that the Arecoideae originated in the Americas (Dransfield et al., 2008).

Biogeographic implications of the fan-shaped leaf report—The presence of Arecaceae sp. 2 in the Paleocene of northern Colombia is significant if it is either a member of the subfamily Calamoideae or a member of the Coryphoideae. As a fossil of Coryphoideae, this would be the first report of the subfamily for South America. Berry (1921) assigned to *Sabalites* a leaflet from the Tertiary of Venezuela, but Dransfield et al. (2008) noticed instead a resemblance with *Iriartea* (subfamily Arecoideae). As a Calamoideae, the leaf we describe here would be the first macrofossil report of the subfamily for America, although *Mauritiidites franciscoi*, a palynomorph related to *Mauritia,* was reported for the Paleocene to Middle Eocene of northern South America (Jaramillo and Dilcher, 2001). *Mauritiidites franciscoi* was also reported by Jaramillo et al. (2007) for the Cerrejón formation.

Implications of the findings for Paleocene neotropical rainforest—Lithofacies, sedimentary structures, and the preservation

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Fig. 6.   Arecaceae sp. 1 leaf and tissues and Arecaceae sp. 2 leaf. A–H. Arecaceae sp. 1 tissues and whole leaf. (A) Arecaceae sp. 1 pinnate leaf. ING-822. (B) Cuticle with stomata and (C) leaf stomata. ING-336. (D) Drawing of leaf stomata. gc, guard cells; lsc, lateral subsidiary cells; tsc, terminal subsidiary cells. Tissue without stomata with (E) rectangular cells and with (F) isodiametric cells. ING-336. Drawing of tissue without stomata with (G) rectangular cells and with (H) isodiametric cells. I, J. Arecaceae sp. 2 leaf and venation. (I) Palmate or costapalmate leaf. ING-818. (J) Venation pattern at juncture with the main vein of a segment to show the irregular course of crossveins. Bars: A, I = 50 mm, B–F = 25 μm, J = 10 mm.

of large palm leaves, inflorescences, and fruits suggest that these specimens were part of a local flora in a coastal flood-plain, rather than being transported from long distances. The high abundance of palm leaves, pollen, and fruits found at Cerrejón implies that the plants were abundant elements along river margins, lakes, swamps, and mangroves during the Paleocene, similar to the ecology of some extant members of the family. The presence of at least three (Arecoideae, Nypoideae, and either Calamoideae or Coryphoideae) of the five palm subfamilies clearly indicates that by the Paleocene (ca. 60 Ma) the family was well represented in northern South America by more than half of the extant palm lineages. The Cerrejón flora at the family level is very similar to extant neotropical rainforest in family composition and leaf traits (Wing et al., 2004). It is interesting that at lower ranks such as subfamily, tribe or genus, the Paleocene neotropical rainforests had already evolved important components of these extant ecosystems (Herrera et al., 2008).

Conclusions—The palm megafossil record of the Cerrejón Formation (middle to late Paleocene, ca. 60 Ma) in northern Colombia contains five palm morphospecies: an inflorescence related to the subfamily Arecoideae, a fruit belonging to the subtribe Attaleinae in the same subfamily (possibly the oldest record of *Cocos*), one of the two oldest megafossil records of *Nypa* in South America, and two fossil leaf types, a palmate or costapalmate leaf, and a pinnate leaf. The presence of cf. *Cocos* sp. (subfamily Arecoideae) indicates that the divergence of this lineage was older than 60 Ma, earlier than previously estimated divergence times. The inflorescence of Arecoideae also supports the hypothesis of an earlier divergence of this lineage. The report of the Southeast Asian genus *Nypa* helps reconstruct the changes in the range of the genus over geological time. These early megafossil records of extant lineages of palms demonstrate the importance of studying the fossil record of tropical latitudes to understand the evolution of tropical plant families.

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