

FOSSIL ARACEAE FROM A PALEOCENE NEOTROPICAL RAINFOREST IN COLOMBIA¹

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Both the fossil record and molecular data support a long evolutionary history for the Araceae. Although the family is diverse in tropical America today, most araceous fossils, however, have been recorded from middle and high latitudes. Here, we report fossil leaves of Araceae from the middle-late Paleocene of northern Colombia, and review fossil araceous pollen grains from the same interval. Two of the fossil leaf species are placed in the new fossil morphogenus *Petrocardium* Herrera, Jaramillo, Dilcher, Wing et Gomez-N gen. nov.; these fossils are very similar in leaf morphology to extant *Anthurium*; however, their relationship to the genus is still unresolved. A third fossil leaf type from Cerrejón is recognized as a species of the extant genus *Montrichardia*, the first fossil record for this genus. These fossils inhabited a coastal rainforest ~60–58 million years ago with broadly similar habitat preferences to modern Araceae.

Key words: *Anthurium*; Araceae; Colombia; fossils; monocotyledons; *Montrichardia*; Paleocene; systematics.

Araceae is one of the most diverse monocotyledonous families, comprising nine subfamilies, 106 genera, and ~3300 species (Croat, 1979; French et al., 1995; Mayo et al., 1997; Govaerts and Frodin, 2002; Keating, 2003a, 2004). It is most diverse in the tropics, with the Pacific slopes of the northern Andes home to the greatest number of species (Croat, 1992b; Vargas et al., 2004; Mora et al., 2006). Growth forms include herbs, vines, hemiepiphytes, epiphytes, lithophytes, rheophytes, and helophytes (Croat, 1990, 1992a; Mayo et al., 1997; Bown, 2000). Despite high species diversity, a large range of life forms, and a wide geographical distribution, the origin and evolution of the Araceae is poorly known. Its fossil record is sparse and controversial, possibly because the herbaceous habitat of most members of the family makes them unlikely to fossilize (Herendeen and Crane, 1995).

The oldest reported fossils of Araceae are inaperturate, striate pollen grains from the late Barremian–early Aptian

(~124–117 million years ago [Ma]) of Portugal (Fig. 1; Friis et al., 2004, 2006), but this age has been questioned and remains problematic (Heimhofer et al., 2007). Those pollen grains, assigned to the fossil genus *Mayoa*, may be related to the subfamily Pothoideae, tribe Monstereae according to the classification of Araceae by Keating (2003b, 2004). Fossils of Araceae have been reported from a number of Late Cretaceous localities (Fig. 2), including several from the Coniacian of Eastern Asia (Krassilov, 1973), the Campanian of Central Europe (Kvaček and Herman, 2004) and North America (Bogner et al., 2005), and the Maastrichtian of India and South America (Herngreen, 1974; Sarmiento, 1994; Bonde, 2000; Hesse and Zetter, 2007).

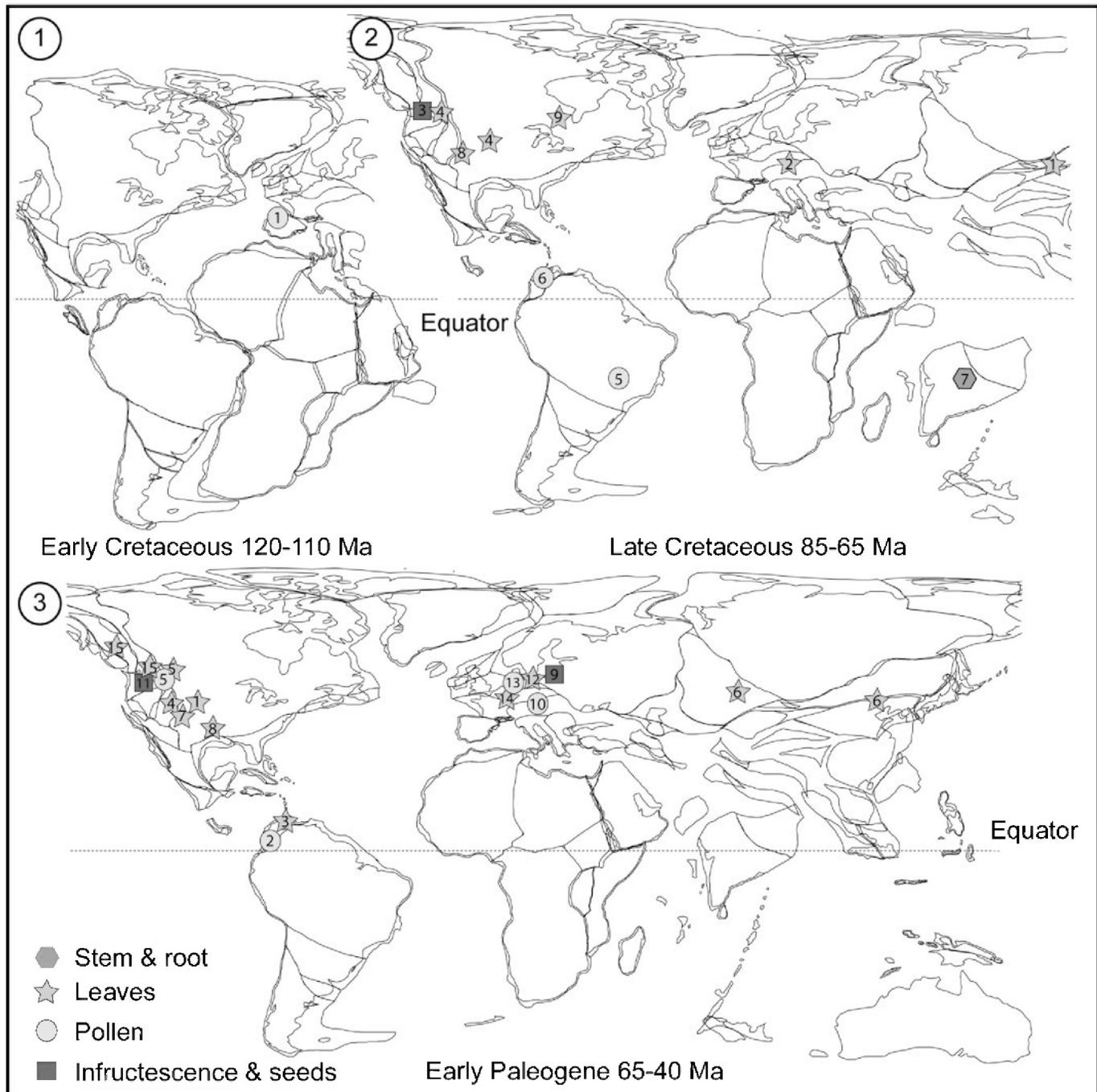
The minimum age estimated for the origin of the family, using molecular analysis calibrated with fossils, is 105–128 million years (Bremer, 2000; Janssen and Bremer, 2004). The extant diversity and subfamilial structure of Araceae is complex and predominantly tropical (Croat, 1979; Mayo, 1993), suggesting that low latitudes were an area of origin and radiation. The fossil record of tropical Araceae has remained nearly unexplored, however (Figs. 1–3). In tropical South America, the only araceous records are dispersed pollen grains from the Maastrichtian and Paleocene, that have been referred to *Spathiphyllum* and *Proxapertites operculatus* (Van der Hammen, 1954; Van der Hammen and García de Mutis, 1966; Sarmiento, 1994; Jaramillo and Dilcher, 2001; Hesse and Zetter, 2007).

Here, we describe new species of Araceae from the Cerrejón flora (Wing et al., 2004; Herrera et al., 2005) based on fossil leaves preserved in Paleocene sediments in northern South America. One species belongs to the modern neotropical genus *Montrichardia*, two other species were assigned to the new fossil morphogenus *Petrocardium* Herrera, Jaramillo, Dilcher, Wing et Gomez-N gen. nov. The three new fossil leaves and the three pollen grains from the Cerrejón flora suggest a moderate diversity and similar habitat preferences to modern Araceae. Also, the fossil leaves and its closest living relatives raise important questions about how some genera may have reached or kept the levels of diversity seen today.

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Figs. 1–3. Paleogeographic distribution of Araceae. Maps are based on Scotese (2001). Locality numbers on the maps correspond to numbers in italics after the respective citation(s). **1.** Barremian-Aptian in age, Pothoideae subfamily suggested (according to the most recent classification of Araceae by Keating [2003b, 2004]) (Friis et al., 2004: locality no. 1). **2.** Coniacian, Lemnoideae (Krassilov, 1973: 1). Campanian, Orontioideae (Kvaček and Herman, 2004: 2; Bogner et al., 2005: 3); Aroideae? (Stockey et al., 2007: 4). Maastrichtian, Pothoideae (Herngreen, 1974: 5; Sarmiento, 1994; Hesse and Zetter, 2007: 6); Bonde, 2000: 7); Orontioideae (Bogner et al., 2007: 8–9). **3.** Paleocene, Orontioideae (Bogner et al., 2007: 1); Philodendroideae and/or Pothoideae (Van der Hammen, 1956; Van der Hammen and García de Mutis, 1966; Jaramillo and Dilcher, 2001; Hesse and Zetter, 2007: 2); Philodendroideae (fossil leaf, this paper: 3); Lemnoideae (McIver and Basinger, 1993: 4; Stockey et al., 1997: 5); Unknown subfamily (Van Hoeken-Klinkenberg, 1966; Jaramillo et al., 2007: 2). Paleocene-Eocene, Aroideae (Fedotov, 1975: 6). Eocene, Aroideae (Hickey, 1977: 7; Dilcher and Daghljan, 1977: 8); Philodendroideae and/or Pothoideae (Bogner, 1976: 9; Zetter et al., 2001; Hesse and Zetter, 2007: 10). Middle Eocene, Lasioidae (Cevallos-Ferriz and Stockey 1988; Smith and Stockey, 2003: 11); Pothoideae and Aroideae (Wilde et al., 2005: 12); Lemnoideae (Hesse and Zetter, 2007: 13); Late Eocene, Aroideae, (Wilde et al., 2005: 14); Orontioideae (Bogner et al., 2007: 15).

MATERIALS AND METHODS

The fossil leaves described in this study were collected from the Cerrejón Formation, exposed in the Cerrejón mine, a large open-pit coal mine located in northeastern Colombia (11°9'14.58"N, 72°36'30.43"W). The Cerrejón Formation has been correlated with the middle to late Paleocene (60–58 Ma) using fossil pollen (Jaramillo et al., 2007). The 700-m-thick stratigraphic sequence, composed of thick coals, fluvial sandstones, and lacustrine siltstones was deposited in a rapidly subsiding basin (Bayona et al., 2004). The seven specimens of fossil leaves reported here were found ~380 m above the base of the formation.

The specimens ING-0902 and ING-0804 were recovered from a lens-shaped deposit of laminated, gray-black, fine-grained sandstone approximately 50 cm thick and ~6 m in lateral extent (locality 0315). A total of 239 leaf specimens have been found in this locality. Most leaf specimens are complete and well preserved; sizes range from microphyll to macrophyll with mesophyll leaves being dominant. The specimen ING-0808 came from a brown, fine-grained lithic sandstone with inclined heterolithic strata. These araceous fossils were deposited in fluvial channel sediments. The fine-grained sandstones with laminations and heterolithic stratification suggest overbank deposits, such as crevasse splays and forebanks (Bayona et al., 2004). These deposits grow by accumulation of fine-grained sediment during episodes of flooding (Reading and Levell, 1996).

The specimen ING-0903 was found at the same stratigraphic level as locality 0315, between coal beds 100 and 102, in a dark gray siltstone. The specimens ING-0904, -0905, and -0906 were recovered from an extensive gray siltstone bed approximately 60–90 cm thick (localities 0705 and 0708). The gray siltstone underlies one of the thickest coal beds at the top of the Cerrejón Formation (~7 m). These siltstones were deposited in a swampy-lacustrine environment.

We performed an exhaustive comparison of the fossils with collections of extant Araceae in the United States National Herbarium, Washington D.C.; the Smithsonian Tropical Research Institute, Republic of Panama; and the University of Florida Herbarium, Gainesville, Florida. We studied 90% (95 of the 106) of the extant genera, and all the tribes and subfamilies. Araceae leaf morphology is extremely variable and diverse; it has not been commonly used as a taxonomic tool. Nevertheless, recent morphological work by Keating (2003b) considers leaf venation to have useful taxonomic characteristics. Here we follow Keating's classification of Araceae (2003b, 2004). We use leaf terminology adapted from LAWG (1999) to avoid the inconsistent terminology for leaf venation that has been used in many previous Araceae descriptions (see Keating, 2003b for a discussion). Consequently, the term primary lateral vein is here called secondary vein. The term midrib (or mid-vein) is used to describe the primary vein, which is the thickest vein of the lamina; secondary veins are the next narrower class of veins after the midrib (and originate from it). The term collective veins is kept for its widespread use in araceous descriptions, referring to those intramarginal veins that closely parallel the leaf margin; the terms anterior division and posterior division were taken from Mayo et al. (1997) and refer to divisions of the leaf blades; we use these terms to clarify the systematic description of the fossils.

Leaves of fossil and extant Araceae were photographed for comparison using Nikon D70 and DXM1200F cameras. Leaves of *Montrichardia arborescens* Schott were cleared and mounted using the techniques of Hickey (1973) and Dilcher (1974). Fossil leaf tracings were made using Adobe (San Jose, California, USA) Photoshop and Adobe Illustrator CS2.

The fossil material is stored in the paleontological collections of the Colombian Geological Institute (INGEOMINAS) in Bogotá, Colombia.

SYSTEMATICS

Although two of the species described in this paper are more similar in leaf features to extant *Anthurium* than to any other living Araceae, we have placed them in a form genus that is incertae sedis with respect to Araceae, rather than in *Anthurium*. This placement is due to the fossils also sharing some characters with the subfamily Lasioideae and our not having identified foliar synapomorphies for *Anthurium* and Pothoeae. (Such a comprehensive phylogenetic analysis of leaf characters is beyond the scope of this paper.) In contrast,

the third fossil species described here is placed within the modern genus *Montrichardia* because the fossils possess a unique combination of leaf characters found only in the two living species of *Montrichardia*.

Family—Araceae Juss.

Morphogenus—*Petrocardium* Herrera, Jaramillo, Dilcher, Wing et Gomez-N gen. nov.

Generic fossil diagnosis—Leaves ovate, margin entire, apex acuminate, base cordate or sagittate, naked basal veins, midrib multistranded, secondary veins eucamptodromous, one or two collective veins of secondary gauge, one or two intersecondary veins per intercostal region with courses parallel to those of the secondaries, tertiary veins mixed opposite/alternate percurrent and reticulate.

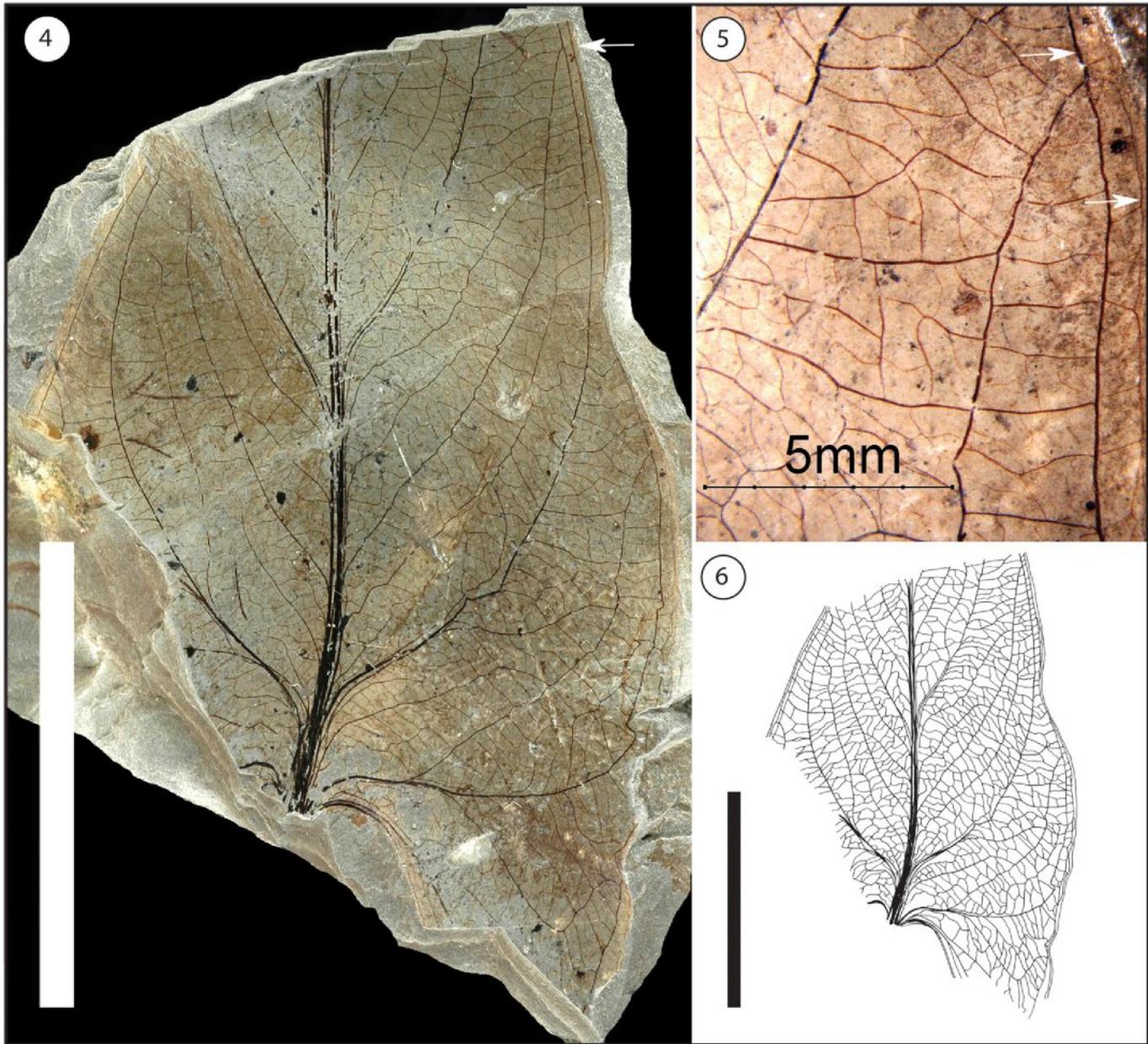
Derivation of generic name—From the Greek, petro for rock and cardium for heart. Resembling a heart-shaped fossil leaf in a rock.

Type species—*Petrocardium wayuuorum* Herrera, Jaramillo, Dilcher, Wing et Gomez-N sp. nov.

Species diagnosis—*Petrocardium wayuuorum* Herrera, Jaramillo, Dilcher, Wing et Gomez-N. Lamina shape ovate, margin entire, base incompletely preserved, but either cordate or sagittate, naked basal veins, midrib multistranded, two collective veins running near the margin, secondary veins eucamptodromous, intersecondary veins present and parallel to secondaries, most tertiary veins mixed opposite/alternate percurrent, but exmedially they merge perpendicularly with the innermost collective vein, higher order veins irregular polygonal to orthogonal reticulate.

Holotype hic designatus—ING-0902, only one specimen found. Figures 4–6.

Species description—Holotype incomplete; lamina shape ovate, length 6.2 cm, width 3.8 cm (Figs. 4, 6); margin entire; posterior division of the blade not completely preserved, but the presence of lamina tissue proximal to the petiole attachment means the base is cordate or sagittate; naked basal veins form part of the margin near the petiole, this character is expressed when the exmedial side of the most basal secondaries, forms part of the leaf margin; anterior division of the blade longer than posterior division; midrib multistranded; the holotype preserves six pairs of secondary veins on the right side of the blade (Appendix S1, see Supplemental Data with online version of this article). The most basal secondary vein curves in a proximal direction and feeds the basal lobe. The next most basal secondary is oriented almost perpendicular to the midrib for much of its course, forms the middle collective vein (Fig. 5), and displaces toward the margin a minor and outer collective vein that arises from the posterior division of the blade. The third secondary vein curves distally to parallel the margin, forming the inner collective vein. The rest of the secondary veins are strongly eucamptodromous and ascend from the midrib at angles from 29° to 35°; one or two intersecondary veins are present between each pair of secondaries and have courses almost parallel to the secondaries. Both secondary and intersecondary veins are strongly decurrent on the midrib and



Figs. 4–6. *Petrocardium wayuorum* gen. nov. sp. nov. Holotype (ING-0902). **4.** Whole leaf; the arrow indicates the location of Fig. 5; bar = 3 cm. **5.** The arrows point out the two collective veins; notice that the opposite percurrent secondary veins dominate exmedially; higher order veins from irregular polygonal to orthogonal reticulate; bar = 5 mm. **6.** Drawing of veins; bar = 3 cm.

follow a course that curves toward the margin distally. The tertiary veins are mixed opposite/alternate percurrent, but exmedially most tertiaries are opposite percurrent and are oriented perpendicular to the midrib (Fig. 5), except for those developed in the basal lobe, which tend to be parallel to the midrib. Higher order veins are irregular polygonal to orthogonal reticulate.

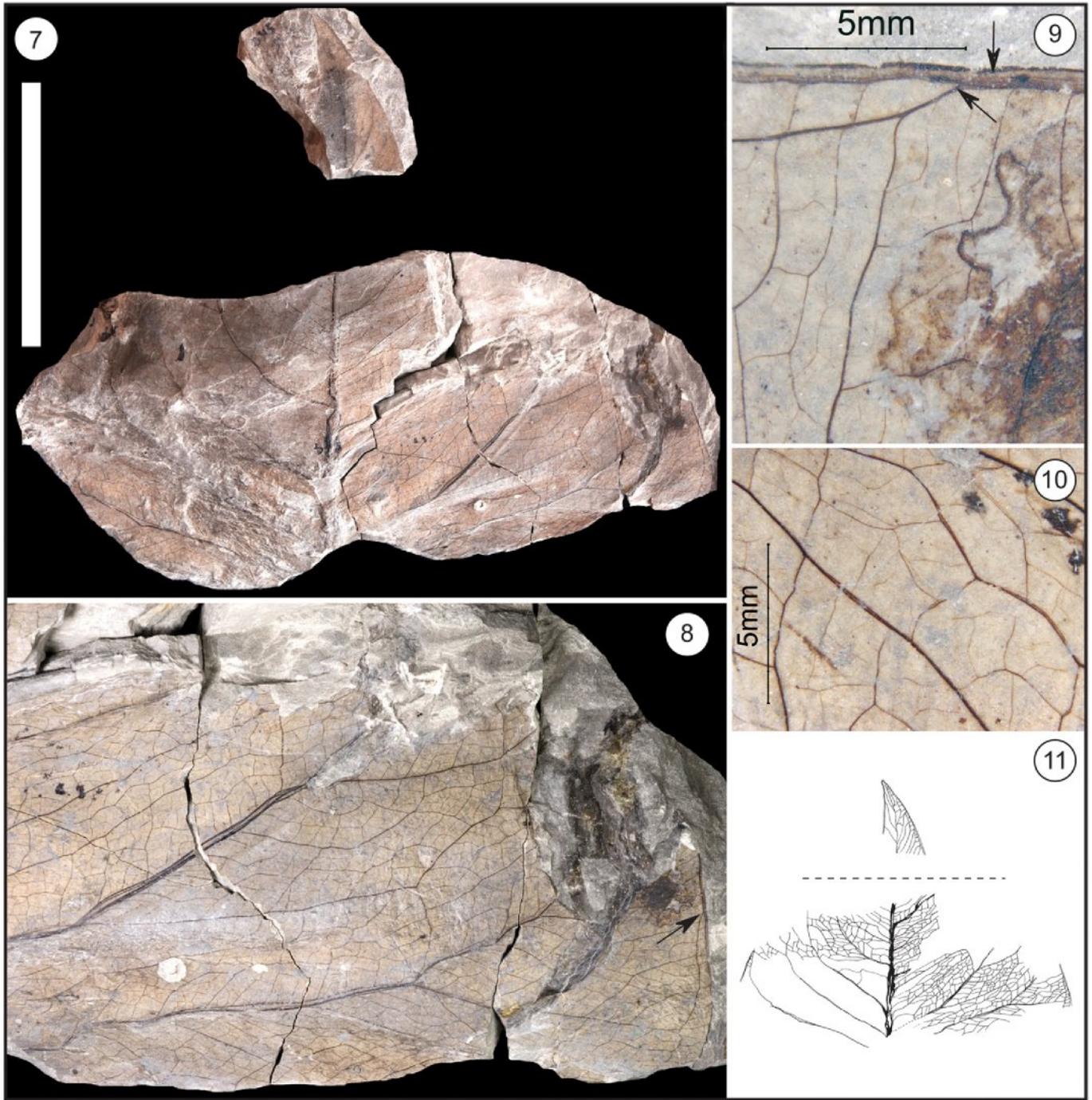
Derivation of specific epithet—From the Wayuu, an Amerindian group of La Guajira Peninsula, Rancheria Basin.

Source, age, and stratum—Colombia, Rancheria Basin, Cerrejón Formation, Cerrejón coal mine, locality 0315, Pit

Tabaco 1, locality placed between coal beds 100 and 102, middle to late Paleocene, coordinates 11.13°N, 72.57°W.

Second fossil species—*Petrocardium cerrejonense* Herrera, Jaramillo, Dilcher, Wing et Gomez-N sp. nov.

Species diagnosis—*Petrocardium cerrejonense* Herrera, Jaramillo, Dilcher, Wing et Gomez-N. Margin entire; leaf apex acuminate; midrib stout and multistranded; secondary veins eucamptodromous with basal pairs forming agrophic veins; one collective vein running very close to margin; intersecondary veins present; tertiary and higher order veins reticulate, fimbrial vein present.



Figs. 7–11. *Petrocardium cerrejonense* gen. nov. sp. nov. Holotype (ING-0804). **7.** Fossil leaf preserves part of the middle and the apex of the leaf; bar = 10 cm. **8.** Right side of the blade, secondary veins running toward margin; tertiary and higher orders veins showing reticulate patterns; the arrow shows the region where the margin is preserved and the location of Fig. 9. **9.** The diagonal arrow points to a secondary vein merging with the collective vein, which runs very close to the margin; the vertical arrow shows the fimbrial vein running along the margin; bar = 5 mm. **10.** Close up of reticulate higher order veins; bar = 5 mm. **11.** Drawing of veins, dashed line indicates that apex and middle fragments were not attached so their positions relative to one another are uncertain.

Holotype hic designatus—ING-0804, only one specimen found. Figures 7–11.

Species description—Holotype incomplete, blade is >9.5 cm long and >24.3 cm wide (Figs. 7 and 11); margin entire; leaf apex

acuminate; midrib stout and multistranded; five pairs of secondary veins (preserved on the anterior division of the blade), which depart the midrib at about $\sim 50^\circ$ proximally, shifting to $< 20^\circ$ near the apex (Appendix S1, see online Supplemental Data); secondary veins branch at $\sim 45^\circ$ and arch apically (Fig. 8); one or two

TABLE 1. Comparative table of morphological features of fossil leaf taxa and extant Araceae.

Taxon	Blade	Apex	Base	Naked basal veins	2° vein type	2° vein crowding	No. posterior 2°s	No. anterior 2°s
<i>Caladium bicolor</i> (Aiton) Vent	Ovate	Convex	Cordate-peltate	Absent	Straightened CV	Present	4	6-8
<i>Xanthosoma mexicanum</i> Liebm	Ovate	Acute	Cordate	Present	Straightened CV	Present	4	4-5
<i>X. sagittifolium</i> Schott	Elliptic	Acute	Cordate	Present	Curved CV	Present	4	5-6
<i>X. robustum</i> Schott	Ovate	Obtuse	Cordate	Present	Straightened CV	Present	4	7
<i>X. undipes</i> (K.Koch & C.D.Bouché) K.Koch	Ovate	Acute	Cordate	Present	Straightened CV	Present	4	6-7
<i>X. violaceum</i> Schott	Elliptic	Acute	Cordate	Absent	Straightened CV	Absent	4	7
<i>Colocasia esculenta</i> (L.) Schott	Ovate	Acute	Cordate-peltate	Absent	Straightened CV	Present	8	5-6
<i>Syngonium llanoense</i> Croat	Elliptic	Acute	Cordate	Absent	Straightened CV	Present	6	15-17
<i>S. schottianum</i> H.Wendl. ex Schott	Elliptic	Acute	Hastate	Absent	Straightened CV	Present	6	11-13
<i>Montrichardia arborescens</i> (L.) Schott	Ovate	Acute	Cordate	Present	Brochidodromous	Present	4	6-11
<i>M. linifera</i> (Arruda) Schott	Ovate	Acute	Cordate	Present	Brochidodromous	Present	4	6-11
<i>M. aquatica</i> ^a	Ovate	Rounded	Cordate-sagittate	Present	Brochidodromous	Present	4	10-11
<i>Caladiosoma messelense</i> Wilde, Z. Kvaček & Bogner ^b	Ovate	Acute	Cordate	?	Straightened CV	Present	?	8-9
<i>C. miocenicum</i> Berry ^b	?	?	?	?	?	?	?	?
<i>Anthurium oxybelium</i> Schott	Ovate	Acute	Lobate	Present	Eucamp-brochido	Absent	6	7-9
<i>A. variegatum</i> Sodiro	Ovate	Acute	Lobate	Present	Eucamptodromous	Absent	4	7-9
<i>A. subsagittatum</i> (Kunth) Kunth	Ovate	Acute	Cordate	Present	Eucamptodromous	Absent	4	7-8
<i>A. nigrescens</i> Engl	Ovate	Acute	Cordate	Present	Eucamp-brochido	Absent	6	8-9
<i>A. marmoratum</i> Sodiro	Ovate	Acute	Cordate	Present	Eucamptodromous	Absent	6	7-9
<i>A. karstenianum</i> Engl	Ovate	Acute	Hastate	Absent	Eucamp-brochido	Absent	4	6-7
<i>A. concinatum</i> Schott	Ovate	Acute	Lobate	Present	Eucamp-brochido	Absent	4	8-9
<i>A. brownii</i> Mast	Ovate	Acute	Cordate	Present	Eucamptodromous	Absent	4	8
<i>A. rzedowskii</i> Croat	Ovate	Acute	Cordate	Absent	Eucamptodromous	Present	8	6-7
<i>A. coripatense</i> N.E.Br. ex Engl	Ovate	Acute	Lobate	Present	Eucamptodromous	Absent	4	10-11
<i>A. hoffmannii</i> Schott	Ovate	Acute	Lobate	Present	Eucamptodromous	Absent	6	5-8
<i>A. cotobrusii</i> Croat & R.Baker	Ovate	Acute	Lobate	Present	Eucamptodromous	Present	4	7-8
<i>A. capevatum</i> Croat & R.Baker	Ovate	Acute	Cordate	Present	Eucamptodromous	Absent	6	9-10
<i>A. obtusifolium</i> (W.T.Aiton) G.Don in R.Sweet	Ovate	Acute	Cordate	Present	Eucamptodromous	Absent	6	8-9
<i>A. ochranthum</i> K.Koch	Ovate	Acute	Cordate	Present	Eucamptodromous	Absent	6	9-10
<i>A. ravenii</i> Croat & R.Baker	Ovate	Acute	Cordate	Present	Eucamptodromous	Absent	4	8-10
<i>A. roseospadix</i> Croat	Ovate	Acute	Cordate	Present	Eucamptodromous	Absent	6	11-12
<i>A. sanctifidense</i> Croat	Ovate	Acute	Cordate	Present	Eucamptodromous	Absent	7	9-10
<i>Urospatha friedrichsthalii</i> Schott	Ovate	Acute	Deeply sagittate	Present	Eucamptodromous	Present	4	1-2
<i>U. sagittifolia</i> (Rudge) Schott	Ovate	Acute	Deeply sagittate	Present	Eucamptodromous	Present	6	1-3
<i>U. somnolenta</i> R.E.Schult	Ovate	Acute	Deeply sagittate	Present	Eucamptodromous	Present	6	1
<i>Petrocardium wayuuorum</i> ^a	Ovate	?	Cordate/sagittate	Present	Eucamptodromous	Absent	4	>4
<i>P. correjonense</i> ^a	?	Acute	?	?	Eucamptodromous	?	?	>5

2° veins angle	No. inter-secondaries	Fimbrial vein	No. intra-marginals	3° vein type	3° vein exmedial angle	Higher order veins	Glands
90°-60°		1	2	Colocasioid		Regular polygonal ret.	Absent
90°-30°		1	2	Colocasioid		Regular polygonal ret.-squarish	Hairs
90°-30°		1	2	Colocasioid		Squarish	Hairs
90°-45°		1	2	Colocasioid		Regular polygonal ret.	Hairs
90°-60°		0	2	Colocasioid		Regular polygonal ret.	Absent
90°-60°		1	1	Colocasioid		Several	Present
90°-30°		1	1-2	Colocasioid		Regular polygonal ret.-squarish	Absent
90°-30°		1	3	Colocasioid		Irregular polygonal ret.	Present
90°-30°		1	3	Colocasioid		Irregular polygonal ret.	Present
90°-40°		0	1-4	"Colocasioid"		Irregular polygonal ret.	Present
90°-40°		0	1-4	"Colocasioid"		Irregular polygonal ret.	Present
90°-45°		0	1-4	"Colocasioid"		Irregular polygonal ret.	?
80°-40°		?	Several	Colocasioid		Regular polygonal ret.-elongate	?
?		?	?	Colocasioid		Irregular polygonal ret.-elongate	?
45°-40°	1-2	0	2	Mixed opp/alt	~90° to midrib	Regular polygonal ret.	Absent
45°	1-2	1	2	Mixed opp/alt	~90° to midrib	Regular polygonal ret.	Absent
45°-30°	1-2	1	2	Mixed opp/alt	~90° to midrib	Regular polygonal ret.	Present
40°-30°	1-2	0	2	Mixed opp/alt	~90° to midrib	Regular polygonal ret.	Present
45°-40°	1-2	0	2	Mixed opp/alt	~90° to midrib	Regular polygonal ret.	Absent
45°	1-2	1	2	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Present~
50°-45°	1-2	0	2	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Present
45°	2-3	1	2	Regular poly. ret.		Regular polygonal ret.	Present
40°-30°	1-2	1	2	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Absent
45°-40°	1-2	1	1	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Present

TABLE 1. Continued.

2° veins angle	No. inter=secondaries	Fimbrial vein	No. intra-marginals	3° vein type	3° vein exmedial angle	Higher order veins	Glands
40°–30°	1–2	1	1–2	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Present
60°–40°	1–2	1	1	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Absent
45°–40°	1–2	0	2	Regular poly. ret.		Regular polygonal ret.	Present
50°–45°	1–2	1	1	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Absent
50°–45°	1–2	0	2	Regular poly. ret.		Regular polygonal ret.	Present
45°–30°	1–2	0	2	Mixed opp/alt		Regular polygonal ret.	Absent
40°–30°	1–2	1	2	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Present
45°–30°	1–2	0	2	Mixed opp/alt	~90° to midrib	Regular polygonal ret.	Present
30°–15°	0–1	1	1	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Present
35°–20°	0–1	1	1	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Present
35°–20°	0–1	1	1	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Present
35°–30°	1–2	0	2	Mixed opp/alt	~90° to midrib	Regular polygonal ret.	Absent
50°–20°	1–2	1	1	Regular poly. ret.	~90° to midrib	Regular polygonal ret.	Absent

Notes: Taxa in boldface correspond to araceous fossil leaves. CV = collective veins; Mixed opp/alt = M. opposite/alternate percurrent; Regular poly. ret. = R. polygonal reticulate; Eucamp-brochido. = eucampitodromous-brochidodromous)

^aCorrejón fossils

^bWilde et al., 2005

pairs of intersecondary veins are present for each pair of secondaries, and their courses are more or less parallel to the secondaries; secondary and intersecondary veins are strongly decurrent on midrib; agrophic veins present, a collective vein runs very close (~0.5 mm) to margin (Fig. 9); tertiary veins form polygons of different shapes and sizes (Figs. 8–10); higher order veins also form irregular polygons measuring between 5 and 8 mm in length and width; a fimbrial vein runs along the margin (Fig. 9).

Derivation of specific epithet—From the Correjón Formation, where the fossil was found.

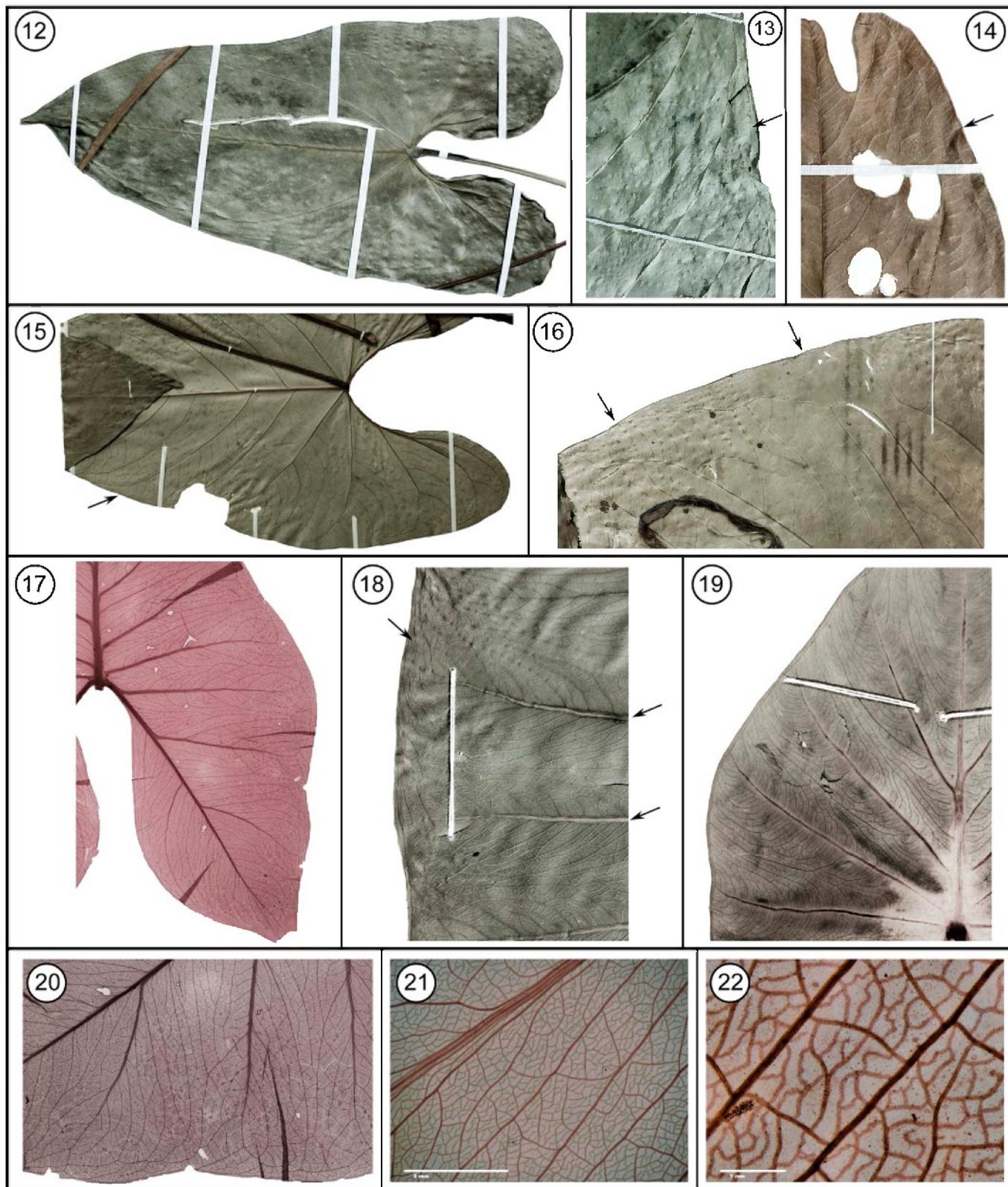
Source, age, and stratum—Colombia, Rancheria Basin, Correjón Formation, Correjón coal mine, locality 0315, Pit Tabaco1, locality placed between coal beds 100 and 102, middle to late Paleocene, coordinates 11.13°N, 72.57°W.

Systematic affinity within angiosperms—The family Araceae is placed in the Alismatales, an order of 14 families that are predominantly aquatic herbs (APG II, 2003). Most Alismatales have basic monocot leaves: oblong and entire-margined with parallel major veins and short, perpendicular cross veins. Araceae leaves are unusual in the order, however, for having a venation pattern that is strongly similar to that of dicots (Keating, 2003b). Some Alismataceae, Limnocharitaceae, and Potamogetonaceae (and outside of Alismatales, Dioscoreaceae in the Dioscoreales) have predominantly ovate to elliptic blades with cordate to sagittate bases and acrodromous or campylodromous venation that resemble Araceae. (See Riley and Stockey [2004] for a discussion of leaf morphology in these families.) However, the combination of leaf characters in the fossils of *Petrocardium* are not seen in these families. Also, *Petrocardium* lacks acrodromous or campylodromous primary veins running in strong convergent arches toward the leaf apex and the dominantly opposite percurrent tertiary veins seen in many species of Alismataceae, Limnocharitaceae, Potamogetonaceae, and Dioscoreaceae.

Systematic affinity within Araceae—*Petrocardium wayuorum* and *P. correjonense* closely resemble the leaf morphology in the extant neotropical genus *Anthurium* Schott. *Anthurium* is placed in the tribe Pothoeae Engler (Keating, 2003b; 2004) with

Pothos (~70 spp., from South-Southeast Asia, and Madagascar), *Pedicellarum* (1 sp., from Indonesia and Malaysia), and *Pothoidium* (1 sp., Southeast Asia). Keating (2003b) recognized different types of leaf morphologies within the tribe, with primary and secondary veins ranging from slightly acrodromous to brochidodromous or eucampitodromous, and higher vein orders reticulate. *Anthurium* is the most diverse genus in the tribe (~1200 sp.) and varies greatly in leaf shape, size, and venation. *Petrocardium wayuorum* and *P. correjonense* do not resemble the three other genera of Pothoeae, which have linear-lanceolate to ovate or narrowly elliptic blades. Furthermore, the other three genera lack the cordate or sagittate bases seen in *Petrocardium* and extant *Anthurium*.

Anthurium, *Philodendron* (tribe Philodendreae), and *Monstera* (tribe Monstereae) are perhaps the most variable genera of Araceae in leaf morphology (Grayum, 1990; Ray, 1990). In spite of this variability, there is a combination of leaf characters typical for the genus *Anthurium*: the secondary veins form collective veins, leaf bases are cordate or sagittate, and higher order veins are opposite/alternate percurrent and reticulate (Croat and Bunting, 1979). *Petrocardium wayuorum* and *P. correjonense* have similar venation patterns to many modern species of *Anthurium* in terms of collective venation, and secondary and higher order veins types (Table 1). *Petrocardium wayuorum* is comparable to modern species that have two collective veins (Figs. 12–14, Table 1; Appendices S2, S3 in online Supplemental Data). In contrast, *P. correjonense* is similar to extant *Anthurium* species that possess only a single collective vein (Figs. 15, 16, Table 1; online Appendices S2, S4) running about ~0.5 mm from the leaf margin (Fig. 9). Although, these differences in submarginal vein patterns are distinctive characters used to discriminate between species, in some very rare cases, we found both types of submarginal veins present in extant species of *Anthurium* (Fig. 14), although this morphological variation changes only a small part of the margin and involves only one secondary vein. The fossils described here are thought to represent two distinct species based on differences in tertiary vein pattern, the presence or absence of dichotomy in secondary veins and agrophic and fimbrial veins, and the dissimilarity in departure angles of the secondary veins (Table 1; online Appendix S2 in Supplemental Data).



Figs. 12–22. Extant aroid leaves. **12.** *Anthurium lucens* Standl (National Herbarium, #2980121); the species has two collective veins. **13.** *A. rotundistigmatum* Croat (NH #3113554); arrow points to a secondary vein merging with the inner collective vein. **14.** *A. ravenii* Croat & R.Baker (NH #1793970); arrow points to a secondary vein ending on the main collective vein and then merging on a secondary collective vein very close to margin. **15.** *A. rubrinervium* (Sims) G.Don in R.Sweet (NH #2025269); secondary veins merging on a collective vein that runs very close to margin. **16.** *A. cerrypelonense* Matuda (NH #3093115); the arrows point to secondary veins merging with an collective vein that runs very close to margin. Notice dominance of opposite

Although several good leaf characters (secondary veins forming collective veins and cordate or sagittate bases and higher order veins variables) are recognizable and useful for many species in *Anthurium*, these characters are not unique to the genus. Keating (2003b) distinguished the reticulate high order veins as those found in the tribe Pothoideae and the subfamily Lasioideae. There is no way, however, to differentiate members of this tribe and subfamily based only on the higher order veins. Both species reported here share similar higher order veins to those found in the tribe Lasioideae. Also *P. cerrejonense* has comparable secondary vein types that end in a single collective vein. However, extant members of Lasioideae have other leaf venation patterns that are unique for that subfamily and that are present neither in the Cerrejón fossils nor in the genus *Anthurium*. For example, in the genus *Urospatha* (Table 1) and all other genera of Lasioideae leaves with pinnate venation have the posterior division of the blade longer than the anterior division. This character is combined with deeply sagittate bases, few apical secondary veins (usually 1–3), acute secondary vein angles with the midvein, and secondary courses running in strong convergent arches toward the leaf apex. *Petrocardium* does not have these leaf venation patterns and therefore is more similar to *Anthurium* than to any other extant genus.

Subfamily—Philodendroideae Engler

Tribe—Philodendreae Schott

Genus—*Montrichardia* Crüger

Generic leaf description—Leaf apex rounded, margin entire, cordate or sagittate base, each basal lobe fed by a secondary vein that branches several times, naked basal veins, midrib and secondary veins stout and multistranded, secondary veins crowded basally and attached to the midrib at very obtuse angles basally (~90–100°) and decreasing apically to ~45°, secondaries merging into several collective veins in a complex brochidodromous pattern, tertiary veins attached to the midrib and secondaries at angles between 20° and 45° to form a network of intercostal venation, higher order veins strongly irregular polygonal reticulate with wandering courses and vein junctions at variable angles.

Fossil species—*Montrichardia aquatica* Herrera, Jaramillo, Dilcher, Wing et Gomez-N sp. nov.

Holotype hic designatus—ING-0904. Figures 23–26.

Paratypes—ING-0808, Figs. 27–30; ING-0903, Fig. 31–33; ING-0905 and ING-0906, Appendix S5 (see Supplemental Data with online version of this article).

Species diagnosis—*Montrichardia aquatica* Herrera, Jaramillo, Dilcher, Wing et Gomez-N. Same as for the genus *Montrichardia*.

Species description—Maximum length measured on the holotype (Fig. 23) is ~56 cm, and maximum width measured at the

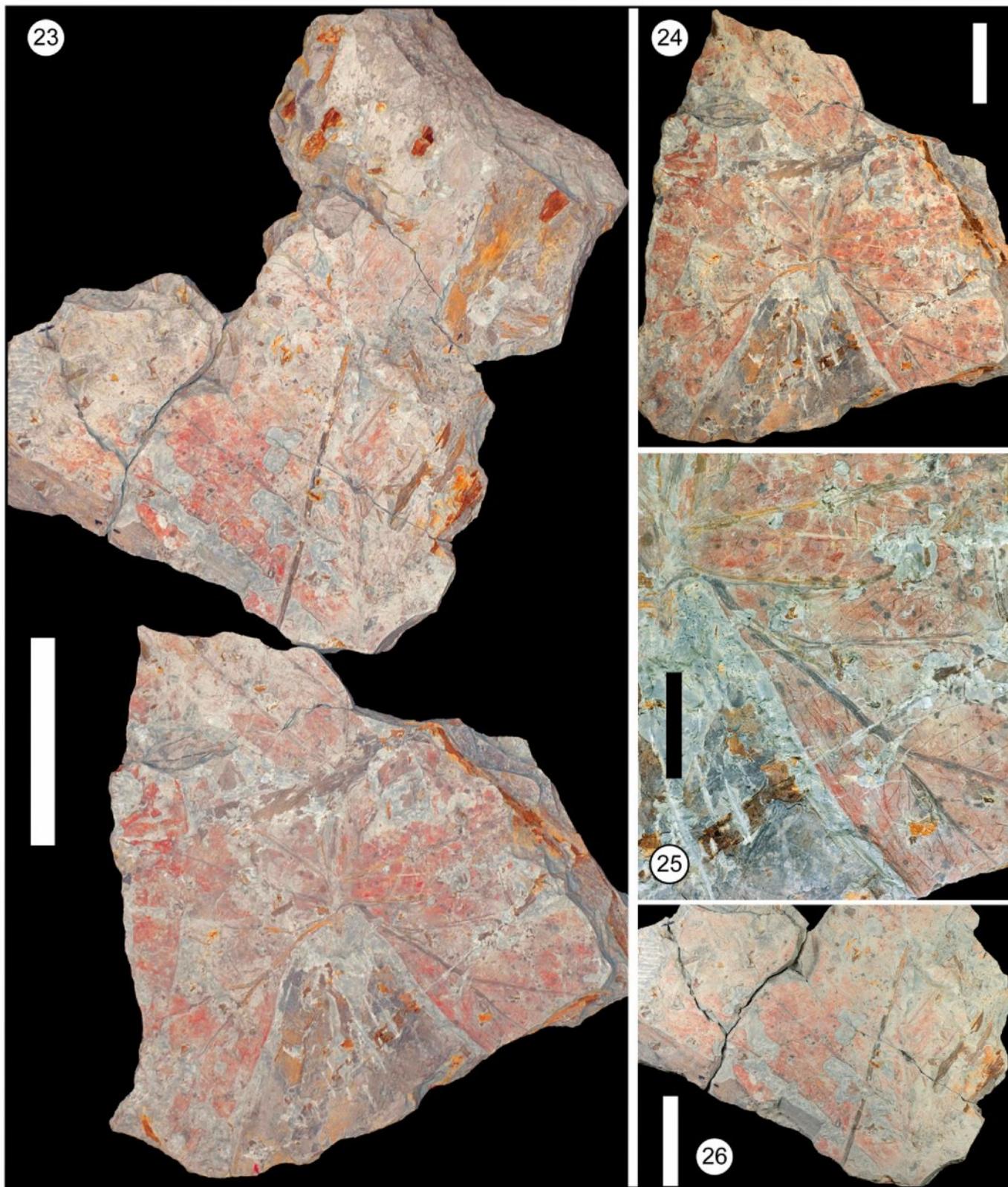
posterior division ~26 cm. Margin entire; leaf apex rounded; midrib multistranded and up to 1.5 cm wide; leaf base cordate or sagittate (Figs. 24, 25; online Appendices S5C and S6), the basal lobes are fed by the most basal secondary veins; these secondary veins are very well developed and form part of the leaf margin at the base as naked basal veins (Fig. 25; Appendix S6), the two basal secondary veins also dichotomize within the lobes several times to form minor secondaries that have perpendicular courses with respect to the midrib and very obtuse angles basally (Figs. 24, 25; Appendix S6); secondary veins are multistranded, very thick and decurrent on the midrib; the holotype and the paratypes ING-0808 and ING-0905 (Fig. 26; Appendix S5A) preserve up to 10 and 11 secondary veins on the anterior division of the blade, secondary veins crowded basally and four veins depart from the petiole insertion, secondary veins branch in a complex brochidodromous pattern, never reaching the margin (Fig. 31; Appendix S5B); secondary veins on the anterior division are attached to the midrib at very obtuse angles, basally ~90–100° but decreasing apically to ~45°, the course of the secondary veins is straight to slightly up curved exmedially; tertiary veins are very decurrent on the midrib and secondary veins at angles between 20° and 45° (Figs. 29, 30; Appendix S5B), tertiary vein spacing is 1–6 mm (Figs. 30, 32); tertiary veins join to form an intercostal vein network and are joined exmedially to the secondaries by higher order veins, forming a system of collective veins very close to margin (Fig. 31; Appendix S5B); the course and spacing in between the collective veins are very irregular; higher order veins are irregular polygonal reticulate with wandering courses (sinuous, angular, or straight) and connections at variable angles (Figs. 32, 33).

Derivation of specific epithet—From the Latin *aquaticus*, living in or near water.

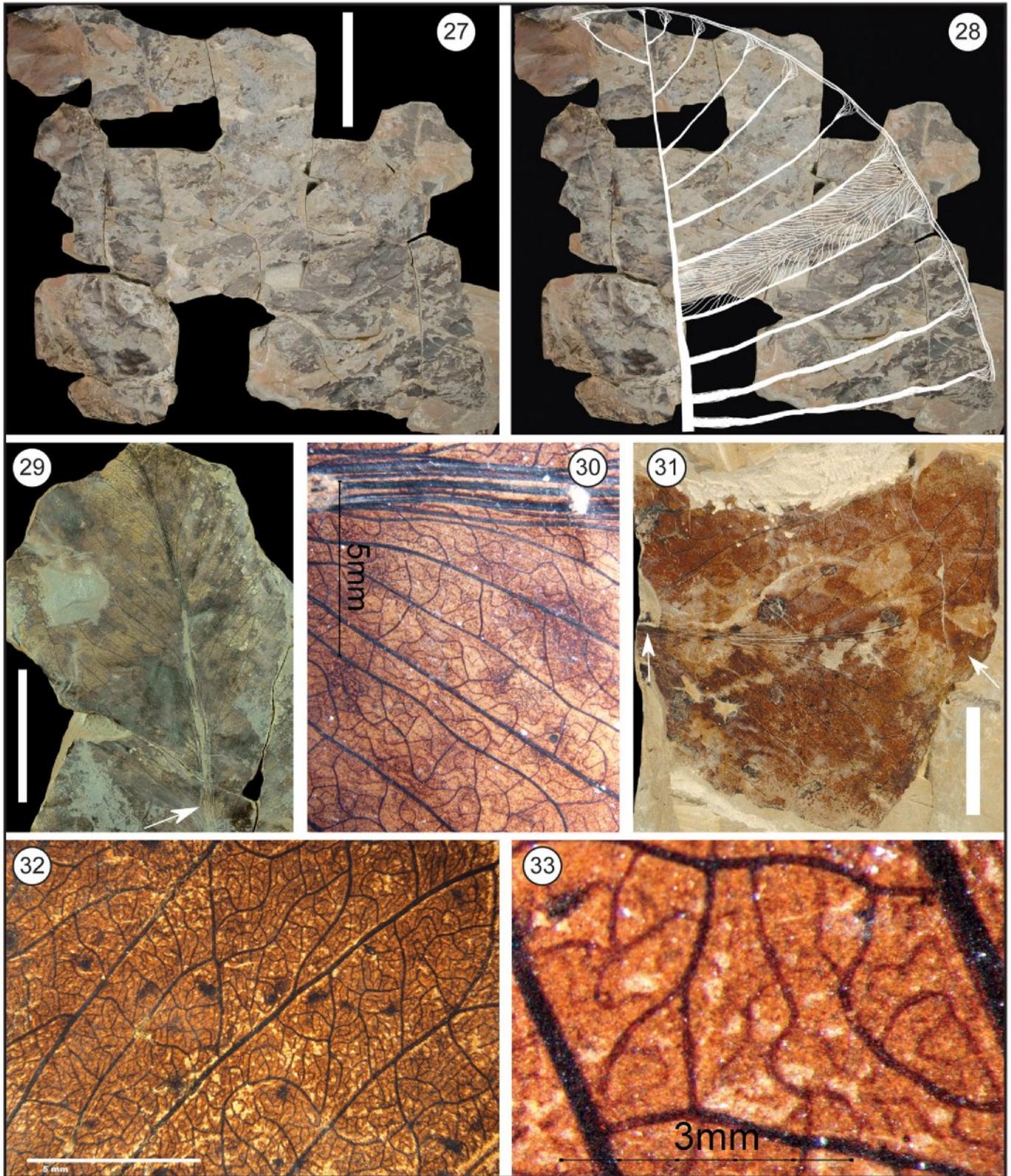
Source, age, and stratum—Colombia, Rancheria Basin, Cerrejón Formation, Cerrejón coal mine, ING-0904, ING-0905, and ING-906 were found at Pit Tabaco Extension, locality 0708 and 0705, localities placed between coal beds 165 and 170, coordinates 11.07°N, 72.34°W; ING-0808 and ING-0903 were found at pit Tabaco 1, locality placed between coal beds 100 and 102, coordinates 11.15°N, 72.55°W, age middle to late Paleocene.

Systematic affinity within angiosperms—Outside of Araceae, the only families that share these leaf architectural characters with *Montrichardia aquatica* are Nymphaeaceae and Nelumbonaceae. These two families may have leaves similar in size and base shape to those of *Montrichardia*, but they are very distinct in venation. (See Upchurch et al. [1994], and Wang and Dilcher [2006] for a complete revision of the leaf morphology in these families.) Nymphaeaceae and Nelumbonaceae lack collective veins, a network of intercostal venation, naked basal veins, and the higher order veins that characterize the Cerrejón fossil and all araceous leaves. There are no extant monocot families other than Araceae that have all the characters seen in *M. aquatica*.

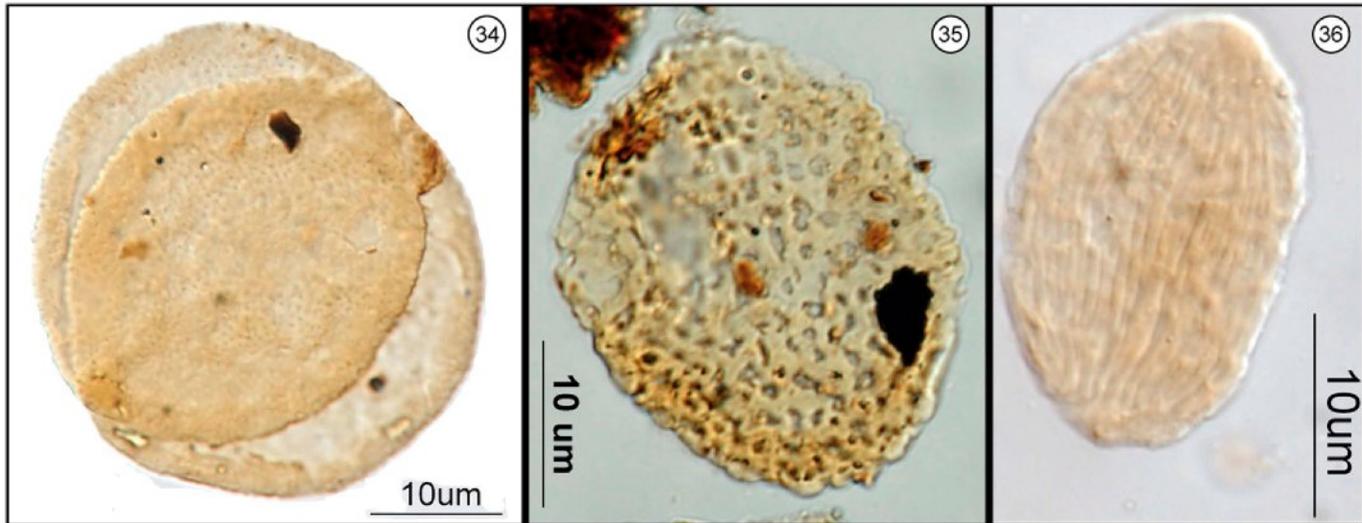
←
percurrent secondary veins exmedially. **17.** *Montrichardia arborescens* (L.) Schott (NH #3307839). **18.** *M. linifera* (Arruda) Schott (NH #2174078); arrows on the right side point to two secondary veins, arrow on left points to the collective venation pattern. Notice that the secondary veins branch toward margin and form several collective veins. **19.** *Colocasia esculenta* (L.) Schott (NH #3290213), notice that the secondary veins merge bluntly with a straight collective vein. **20–22.** Cleared leaf of *M. arborescens* (L.) Schott (NH #3307839). **20.** Secondary veins branch toward margin and form several collective veins. **21.** Tertiary veins decurrent on a secondary vein, higher order veins strongly irregular polygonal reticulate that have wandering courses and connections at variable angles, bar = 5 mm. **22.** Close up of higher order veins, bar = 1 mm.



Figs. 23–26. *Montrichardia aquatica* gen. nov. sp. nov. Holotype (ING-0904). 23. Fossil leaf preserves partially the base and the anterior division, bar = 10 cm. 24. Close up of leaf base, bar = 5 cm. 25. Close up of right lobule, notice naked basal veins, bar = 3 cm. 26. Close up of anterior division, margin preserved on the left side of the blade, bar = 5 cm.



Figs. 27–33. *Montrichardia aquatica* gen. nov. sp. nov. Paratypes (Figs. 27–30, ING-0808; Figs. 31–33, ING-0903). **27.** Fossil leaf incomplete, bar = 10 cm. **28.** Drawing of veins. **29.** The arrow shows a secondary vein, notice intercostal venation, bar = 3 cm. **30.** Tertiary veins merging with a multistranded secondary vein, notice higher order veins strongly irregular polygonal reticulate that have wandering courses and connections at variable angles, bar = 5 mm. **31.** Arrow on the left side marks a secondary vein branching toward margin; arrow on the right side shows several collective veins, bar = 2 cm. **32.** Close up of tertiary veins and higher order veins, bar = 5 mm. **33.** Close up of higher order veins, bar = 3 mm.



Figs. 34–36. The three pollen grains present in the Cerrejón palynoflora. **34.** *Proxapertites operculatus* (Van der Hammen, 1954) Van der Hammen, 1956, plate WRV04774–112.9-J30/4. **35.** *Proxapertites cursus* Van Hoeken-Klinkenberg, 1966, plate WRV04774–216.9-K16/2. **36.** *Spathiphyllum vaneensis* (Van der Hammen and García de Mutis, 1966) Hesse and Zetter 2007, plate WR04774–151.82-F36/4.

Systematic affinity within Araceae—The leaf form and venation patterns of the fossil leaves are extremely similar to those found in the extant genus *Montrichardia* Crüger (Figs. 17, 18; Appendix S6, see online Supplemental Data), which has two species *M. arborescens* and *M. linifera*. This genus is restricted to tropical America and the West Indies and is placed in the tribe Philodendreae Schott (Keating, 2003a, 2004) with *Anubias* (8 subsp., from tropical Africa), *Furtadoa* (2 spp., from Indonesia and Malaysia), *Philodendron* (~500 subsp., from Mexico to Argentina), and *Homalomena* (~110 spp. from tropical America and Southeast Asia). Keating (2003b) recognized several leaf venation patterns for the tribe Philodendreae. Primary and secondary veins range from acrodromous to brochidodromous or eucamptodromous, and tertiary veins are generally closely spaced and parallel to one another. The characters indicate this subfamily is the most varied anatomically in the Araceae (Keating, 2004). *Montrichardia* is genetically isolated with respect to the other four genera within the tribe Philodendreae (Cabrera et al., 2003; Keating, 2004). This isolation is also seen in terms of leaf venation; *Montrichardia* is easily separated from the other four genera for having colocasiod venation, which Mayo et al. (1997, p. 310) defined as “a type of higher order leaf venation in which the finer veins branch almost at right angles from the primary lateral veins and then arch strongly towards the leaf margin, often fusing along the way to form a more-or-less sinuous interprimary collective vein between the primary lateral veins, and finally joining within the margin to form an intramarginal collective vein.”

Colocasiod venation is known in the extant tribes Caladieae (New World, except for *Hapaline* from Southeast Asia and Brunei) and Colocasieae (Old World); both tribes are part of the subfamily Aroideae and seem to be very well separated genetically from each other (Keating, 2004). Colocasiod venation has been reported in the fossil genus *Caladiosoma* Berry from the Neogene of Trinidad and the Eocene of Germany (Berry, 1925; Wilde et al., 2005, Table 1). *Montrichardia aquatica* has a leaf shape and intercostal venation similar to Caladieae and Colocasieae (Fig. 19), but the collective vein and higher order

vein patterns differ. In Caladieae and Colocasieae, the secondary veins (secondary veins are called primary lateral veins by Mayo et al., 1997) merge bluntly with one to three straightened collective veins (Fig. 19, Table 1; online Appendix S7), while the secondary veins in the fossil and extant *Montrichardia* branch very close to the margin and are subsidized by higher order veins that finally form several collective veins. Also the spacing and course of these collective veins are very irregular compared to tribes Caladieae and Colocasieae, in which the collective veins run parallel to the margin and each other, and the vein spacing is kept constant (Figs. 18, 20, 31; Appendix S7). Higher order veins and areolation in Colocasieae and Caladieae are dominated by cross venation and elongated polygons of similar shape and size, while living *Montrichardia* and the fossil leaves have higher order veins that anastomose irregularly with wandering courses, connections at variable angles, and poorly developed areolation (Figs. 21, 22, 30, 32, 33, Table 1). Because the collective venation pattern and higher order veins characterize the extant genus *Montrichardia* and the fossil *M. aquatica*, we do not relate the Cerrejón fossil leaves to the fossil morphogenus *Caladiosoma* Berry, nor to its living relative tribes Caladieae and Colocasieae.

DISCUSSION

Paleobiogeography—The Araceae fossil record is sparse, and most specimens belong to taxa that inhabited ponds, lakes, or flooded areas (e.g., Kvaček, 2003). A complete revision of the Araceae macrofossil record was recently made by Wilde et al. (2005); previous revisions include Grayum (1990), Mayo et al. (1997), and Keating (2003a). It seems clear that the geographic distribution of Araceae in the past was driven largely by the global climate (Figs. 1–3).

From the early Cretaceous (~120 Ma) to the early Paleogene (~65–40 Ma) for about 60 million years, the climate was warmer than today (Zachos et al., 2001; Bralower et al., 2006), thereby, permitting migration and evolution of megathermal plants in

current temperate latitudes (Morley, 2003). By the end of the Cretaceous, three or four Araceae subfamilies were present, including Pothoideae, Lemnoideae, Orontioideae, and perhaps Aroideae? (subfamily names according to Keating, 2003b, 2004) (Figs. 1, 2). During the early Paleogene, the Cretaceous subfamilies expanded their fossil record and three new subfamilies appeared: Philodendroideae, Aroideae, and Lasiodeae (Fig. 3).

Paleoecology—Leaf margin and leaf area analysis of the entire Cerrejón flora suggest a mean annual precipitation of ~4 m and a mean annual temperature $\geq 24^{\circ}\text{C}$ (Herrera et al., 2005). Apart from Araceae, the most abundant families and orders recognized in the Cerrejón flora are Leguminosae, Araceae, Malvales, Lauraceae, Menispermaceae, and Zingiberales. The Cerrejón paleoclimate and its floristic composition suggest the presence of a rainforest during the middle–late Paleocene in northern South America (Wing et al., 2004; Herrera et al., 2005; Doria et al., 2008).

Lithofacies, sedimentary structures, and the preservation of complete large leaves within the associated paleoflora suggest that *Petrocardium wayuuorum* and *P. cerrejonense* were part of a local flora in a coastal floodplain, rather than being transported from far away. It has been estimated that in some Amazonian floodplain forests ~90% of trees carry epiphytic Araceae (Leimbeck and Balslev, 2001); such common epiphytes might have been preserved as fossils. The sedimentary environment also raises the possibility that the fossils were rheophytes, but this life form is rarely found in tropical American Araceae (Croat, 1990).

Extant *Montrichardia* species possesses a strict helophytic life form (Croat, 1990; Mayo et al., 1997) and grow in freshwater habitats, especially fluvial to coastal plain areas, along river margins and adjacent swamps subject to seasonal changes in water level (Croat, 1990; Bown, 2000). The foliage generally remains above the water level, forming dense colonies that trap sediment; it is a primary colonist in swamp forest areas (Bown, 2000). *Montrichardia* is found throughout tropical America, but it is dominant along large rivers of central Amazonia and deltaic zones where it grows even under tidal influence (Mayo et al., 1997; Bown, 2000). Lithofacies and sedimentary structures suggest that *M. aquatica* grew along river margins (forebanks), and swamps, where it coexisted in palm-dominated environments, similar to the ecology of extant *Montrichardia*.

Araceous pollen grains from the Cerrejón flora—The fossil pollen record shows interesting aspects of the paleobiogeography and paleoecology of Araceae. Recently, Hesse and Zetter (2007) made a complete review of the pollen record, recognizing three fossil pollen types attributable to Araceae: *Limnobiophyllum* sp. (Lemnoideae), *Spathiphyllum vanegensis* and *S. elsikii* (Pothoideae), and *Proxapertites operculatus* (Philodendroideae/Pothoideae). The Cerrejón palynoflora has a high abundance of araceous pollen (Jaramillo et al., 2007; for a complete morphological description of the pollen grains, see associated references). The three fossil pollen grains present in the Cerrejón palynoflora are *P. operculatus* (Fig. 34) (Van der Hammen, 1954, 1956), *P. cursus* (Fig. 35) (Van Hoeken-Klinkenberg, 1966), and, *S. vanegensis* (Fig. 36) (Van der Hammen and Garcia de Mutis, 1966; Hesse and Zetter 2007). *Proxapertites operculatus* is one of the most abundant pollen types in both coal and noncoal samples. On the other hand, *P. cursus* and *S. vanegensis* are present only in noncoal samples. This distribution by depositional environment for fossil pollen

grains and leaves suggests that Araceae occupied more than one floodplain habitat by the Paleocene in the tropics.

Diversity—Six fossil morphospecies are recognized from Cerrejón flora so far. Although this number may increase in the future, in recent sampling from plant localities at the coal mine, more specimens seem to be related to Araceae (F. Herrera, personal observation). Although, the number of araceous fossil species from Cerrejón flora is not significant compared to the modern diversity for Araceae in the neotropics (Vargas et al., 2004), it may be significant in terms of the diversity of tribes and genera during the Paleocene; the Cerrejón fossil may belong to at least three different modern tribes or genera.

It is also interesting that the extant relatives of the araceous fossil leaves we describe here show a strong contrast in diversity between two lineages that have lived in tropical South America since the late Paleocene. *Anthurium*, which we think is closely related to and possibly descended from *Petrocardium*, is extremely diverse along the wet, Pacific side of the Andes in Colombia and Ecuador (Croat, 1992b; Vargas et al., 2004; Mora et al., 2006). In contrast, *Montrichardia* has only two species, each of which is widespread in the neotropics (Bown, 2000; Mayo et al., 1997). If the two lineages have been present in the neotropics for roughly the same period of time, why is one so much more diverse than the other?

We suggest that differences in diversity may be the result of population structure. Living *Montrichardia* tends to occur in large, dense populations and to be water dispersed, consistent with the depositional environment of the fossil species. These attributes may have reduced the chance of forming genetically isolated populations, with the result that speciation within the genus has been slow. In contrast, living *Anthurium* species are generally epiphytic and terrestrial, and the species tend to have local endemism and small ranges of distribution (Croat, 1990, 1992b). Many ecological and biological adaptations in *Anthurium* populations such as specific pollination and dispersion syndromes (Croat, 1980) and historical events like the rise of the Andes must have influenced the evolution of diversity seen in *Anthurium* today.

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