

Paleocene wind-dispersed fruits and seeds from Colombia and their implications for early Neotropical rainforests

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ABSTRACT. Extant Neotropical rainforests are well known for their remarkable diversity of fruit and seed types. Biotic agents disperse most of these disseminules, whereas wind dispersal is less common. Although wind-dispersed fruits and seeds are greatly overshadowed in closed rainforests, many important families in the Neotropics (e.g., Bignoniaceae, Fabaceae, Malvaceae, Orchidaceae, Sapindaceae) show numerous morphological adaptations for anemochory (i.e. wings, accessory hairs). Most of these living groups have high to moderate levels of plant diversity in the upper levels of the canopy. Little is known about the fossil record of wind-dispersed fruits and seeds in the Neotropics. Six new species of disseminules with varied adaptations for wind dispersal are documented here. These fossils, representing extinct genera of Ulmaceae, Malvaceae, and some uncertain families, indicate that wind-dispersed fruit and seed syndromes were already common in the Neotropics by the Paleocene, coinciding with the early development of multistratal rainforests. Although the major families known to include most of the wind-dispersed disseminules in extant rainforests are still missing from the Paleogene fossil record of South and Central America, the new fossils imply that anemochory was a relatively important product and/or mechanism of plant evolution and diversification in early Neotropical rainforests.

KEYWORDS: Fossils, Malvaceae, Ulmaceae, Neotropics, Paleocene, wind dispersal syndromes

INTRODUCTION

Extant angiosperms display a remarkable diversity of morphological characters related to fruit and seed dispersal (van der Pijl 1969). Biotically dispersed fruits and seeds have developed fleshy nutritious tissue (e.g., aril and mesocarp), diverse coloration, size, odor, and varied dehiscence mechanisms for attracting dispersal agents (Howe & Smallwood 1982, Janson 1983, Gautier-Hion et al. 1985, Herrera 1989). Similarly, some abiotically dispersed disseminules are notable

for having plumes, tufts, hairs, balloon-like structures, wings, or are reduced in size and density and are dependent upon wind for dispersal (van der Pijl 1969). Wind dispersal adaptations have evolved multiple times in almost all major angiosperm clades, although such reproductive structures are most widespread in eudicots and are less common in basal groups and monocots (Janson 1992, Dallwitz et al. 2000, Lorts et al. 2008, Manchester & O’Leary 2010).

Wind-dispersed disseminules constitute 13–16% of the flowering plant species in Neotropical rainforest plots (Prance 1978, Mori & Brown 1994). This percentage is relatively low compared to estimates from savannas and dry forests in South America that contain up to 25–42% of species adapted to wind dispersal (López & Ramírez 1989, Griz & Machado 2001, Jara-Guerrero et al. 2011). The majority of wind-dispersed disseminules in Neotropical rainforests are produced by relatively few large families including Apocynaceae, Asteraceae, Bignoniaceae, Bromeliaceae, Fabaceae, Malpighiaceae, Malvaceae, Meliaceae, Orchidaceae, Rutaceae, and Sapindaceae (Mori & Brown 1994, Mirle & Burnham 1999). Remarkably, fruit and seed dispersal studies in tropical rainforests in South America, Africa, and Asia have shown that emergent trees, lianas and epiphytes, all of which are major components of the canopy, are mostly wind-dispersed, whereas understory species are predominantly biotically dispersed (Keay 1957, Prance 1978, Howe & Smallwood 1982, Augspurger 1986, Hladik & Miquel 1990, Sinha & Davidar 1992, Gentry 1993, Mori & Brown 1994).

Wind-dispersed fruits and seeds are relatively well known in Cretaceous to Neogene floras of north temperate regions (e.g., Dilcher et al. 1976, Tiffney 1984, Manchester & Donoghue 1995, Wing & Boucher 1998, Wang & Manchester 2000, Burge & Manchester 2008, Manchester & O'Leary 2010, Stults & Axsmith 2011). A survey of dispersal mechanisms for this time interval, mainly from Europe, has shown fluctuating proportions of wind-dispersed vs. animal-dispersed angiosperm taxa (Eriksson et al. 2000). Long-term climatic and vegetation changes have been hypothesized as primary selective filters creating the observed patterns of change in fossil fruit dispersal (Eriksson et al. 2000, Eriksson 2008, Kovar-Eder et al. 2012).

Little is known, however, about the fossil record of wind-dispersed fossil fruits and seeds from low-latitude assemblages. An exception comes from fossil winged seeds of *Newtonia* (Fabaceae) reported from the early Miocene (22–21 Ma) of Ethiopia (Pan et al. 2012). From northern South America only five fossil taxa of wind-dispersed disseminules are known so far. One of these was placed within Rhamnaceae from the Maastrichtian of Colombia (Correa et al. 2010), and four Neogene fossils have

been placed respectively in Anacardiaceae (Burnham & Carranco 2004), Combretaceae (Britton 1893), Fabaceae (Burnham 1995), and Malpighiaceae (Engelhardt 1895).

Here, we report six new fossil fruit and seed taxa from the middle-late Paleocene of Colombia that show distinctive morphological characters related to wind dispersal. Two of them are placed in Ulmaceae and Malvaceae respectively, whereas others represent angiosperms of uncertain familial affinity. These fossils are from assemblages previously interpreted as rainforest vegetation because of their leaf physiognomy and family-level taxonomic composition (e.g. Wing et al. 2009). We discuss the utility of these fossils for recognizing wind dispersal syndromes in middle-late Paleocene floras, and show that anemochory was more common than initially thought in early Neotropical rainforests.

MATERIAL AND METHODS

The fruits and seeds reported here were collected from two geographically separate but approximately coeval Paleocene formations from Colombia, the Cerrejón and Bogotá Formations. Three taxa from the Cerrejón Formation were collected from the middle and upper levels of a ca 700-m-thick stratigraphic sequence composed of abundant and thick coals, sandstones, and siltstones (Bayona et al. 2008). The Cerrejón strata have been dated as middle-late Paleocene (ca 58–60 Ma) based on pollen zonation, correlations with stable carbon isotopic data, and marine microfossils (Jaramillo et al. 2007, 2011).

Three additional taxa were collected from a recently discovered paleoflora in the Bogotá Formation along the eastern Cordillera of the Andes. The plant localities crop out at the Sabana de Bogotá, between 2700 and 3000 m in altitude. During the Paleocene the Andes had not been uplifted and the Bogotá Formation accumulated in the lowlands (Bayona et al. 2012). Sediments vary from extensive and thick siltstones, claystones, and paleosols to interbedded sandstones and sporadic conglomerates and breccias. 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 a middle-late Paleocene age.

The Colombian fossils are curated at the Paleontological Museum José Royo y Gomez, Geological Survey in Bogotá, Colombia. For comparative studies, we examined modern fruits representing 16 extant genera in seven families (Tabs 1–3). Plant materials were examined at herbaria of the Smithsonian Institution (U.S. National), Washington, D.C., Smithsonian Tropical Research Institute (SCZ), Panama, University of Florida (FLAS), Gainesville, Florida, Missouri Botanical Garden (MO), St. Louis, Missouri, and the

Arnold Arboretum (A and GH) at Harvard University, Cambridge, Massachusetts. The comparative data for ulmaceous fruits were assembled from herbarium specimens (Tab. 3) as well as preexisting descriptions (Minaki et al. 1988, Todzia 1989, 1992, Manchester 1989a, Wiegrefe et al. 1994, Zavada & Kim 1996, Call & Dilcher 1997, Manchester & Tiffney 2001, Denk & Dillhoff 2005, Pell et al. 2011). We reviewed 19 of 36 extant species of *Ulmus*, 9 of 12 species of *Ampelocera*, 4 of 6 species of *Zelkova*, 2 of 2 species of *Phyllostylon* and *Holoptelea*, and the monotypic genera *Hemiptelea* and *Planera*. The comparative data for fin-winged fruits in the Malvaceae and other families was assembled from herbarium specimens (Tab. 3) and preexisting descriptions (Mirle & Burnham 1999, Manchester & O'Leary 2010).

SYSTEMATICS

Family: **ULMACEAE** Mirb.

Genus: ***Ulmoidicarpum***

Herrera & Manchester gen. nov.

Generic diagnosis. Fruit a stipitate samara with an asymmetrical wing. Endocarp reniform, located at the center of the wing. Wing ciliate along the margin. Stigmatic notch located laterally with respect to the long axis of the wing, with two unequal, basally united styles. Pedicel longer than the length of the wing. Two small black scars present at the base of the wing.

Derivation of generic name. From the family Ulmaceae and the Greek word “karpos” for fruit.

Type species. *Ulmoidicarpum tupperi* Herrera & Manchester sp. nov.

Specific diagnosis. Same as generic diagnosis.

Holotype. Designated here: FH0706-STRI-9914 (Pl. 1, figs 1–4).

Paratypes. Designated here: FH0318-STRI-10413, FH0705-STRI-0917–0920, 9486, 9916, FH0706-STRI-9922, 9925, 9971, FH0708-STRI-0912, 9917, 9918, 9921, 9923, 9924, FH0709-STRI-9915, FH0711-STRI-9919 (Pl. 2, figs 1–11).

Derivation of specific epithet. In recognition of Mark Tupper for his support of the paleontological research program at STRI.

Source, age, and stratum. The nineteen specimens are middle to late Paleocene

in age (58–60 Ma). The fossils were collected at Guajira Peninsula, Ranchería Basin, Cerrejón coal mine, Cerrejón Formation, Tabaco Extensión pit. Most specimens come from localities FH0705 to FH0711 (localities placed below coal bed 175), GPS: N 11°07'49.8, W 72°34'61.5. Paratype FH0318-STRI-10413 comes from locality FH0318 (locality placed below coal bed 170), N 11.128°, W 72.555°.

Description. The samaras range from 9.8 to 16.6 mm long and from 6.9 to 8.9 mm wide ($n = 19$). The pedicel is ca 10.5 mm long, and 0.3 mm thick (Pl. 1, fig. 1). The wing completely surrounds the endocarp and is asymmetrical, being narrower on the side of the stigmatic notch (Pl. 1, fig. 2; Pl. 2, figs 4, 6, 8, 9, 11). The wing venation is obscure in most specimens except in the paratype STRI-9971 (Pl. 2, fig. 1), which shows some exmedially radiating veins. A thick marginal vein is present (STRI-9915, Pl. 2, figs 6–7). Samaras are ciliate along the margin (Pl. 2, figs 4, 6, 9, 11); the hairs are not always preserved, but when present they are densely distributed around the edge of the wing and up to 0.3 mm in length. The endocarp is positioned medially and is fed by a conspicuous vascular strand (Pl. 1, fig. 2; Pl. 2, figs 2, 11). The endocarp is reniform in the plane of bisymmetry, and ranges from 6.0 to 8.4 mm long, and 2.5 to 3.3 mm wide (measured at the widest and most basal side of the endocarp). The stigmatic notch of the wing is conspicuous and located laterally with respect to the long axis of the wing (Pl. 1, fig. 1; Pl. 2, fig. 6). The style ranges from 0.6 to 0.9 mm in length, and bears two stigmatic branches that are seemingly unequal in length and are united at their base (Pl. 1, fig. 3; Pl. 2, figs 3, 7). Remnants of perianth, observed in the holotype (Pl. 1, figs 1, 4), are positioned at the base of the narrow basal extension of the fruit, indicating that the latter represents a stipe rather than a pedicel. Thus, the fruits are strongly stipitate (Pl. 1, fig. 4); the stipe is 1.6 mm long. Two small black structures are present at the base of the wing (Pl. 1, fig. 4; Pl. 2, figs 6, 8, 11); these structures are probably scars related to abscission of the fruit from its pedicel; this may explain why the majority of the samaras are found without a pedicel.

Systematic affinity. No living angiosperm genus completely matches *Ulmoidicarpum tupperi*. However, the unique combination

Table 1. Morphological comparison of *Ulmoidicarpum* Herrera & Manchester gen. nov. and fruits of extant Ulmaceae and other unrelated genera

	Genus & Character	<i>Ampelocera</i>	<i>Hemiptelea</i>	<i>Holoptelea</i>	<i>Phyllostylon</i>	<i>Planera</i>
1.	Ovary attachment	sessile	sessile	stipitate	sessile	stipitate
2.	Fruit symmetry	symmetrical to asymmetrical	asymmetrical	symmetrical	asymmetrical	symmetrical
3.	Fruit type	drupe	samara	samara	samara	drupe
4.	Pedicel length	< 1× perianth + gynoecium	< 1× perianth + gynoecium	< 1× perianth + gynoecium	< 1× perianth + gynoecium	< 1× perianth + gynoecium
5.	Pedicel articulation	not obviously visible	not obviously visible	visible	not obviously visible	not obviously visible
6.	Mature samara margins	NA	eciliate	eciliate	eciliate	NA
7.	Fruit surface	densely pubescent over entire surface	glabrous or sparsely pubescent	glabrous or sparsely pubescent	densely pubescent over endocarp	densely pubescent over entire surface
8.	Samara venation	NA	weakly reticulate	strongly radial	subparallel	NA
9.	Samara wing width measured at equator of endocarp	NA	< seed width	> seed width	> seed width	NA
10.	Endocarp position in samara	NA	medial	distal or adjacent to notch	basal	NA
11.	Reniform-like shape endocarp seen parallel to plane of bisymmetry	absent to present	present	present	absent	absent
12.	Marginal vein in samara or main vein of pericarp (along bisymmetrical plane)	absent	present along entire samara	present along entire samara	present along one side of samara	present along bisymmetrical plane of fruit
13.	Position of two stigmatic arms with respect to long axis of fruit	apical to lateral	lateral	apical	lateral	apical
14.	Stigmatic branches united at base	present	absent	absent	absent	absent
15.	Unequal stigmatic branches	present	absent	absent	present	absent
16.	Samara develops in two separate wings	NA	absent	absent	present	NA

Notes: NA = Not applicable

of characters seen in samaras and drupes of extant Ulmaceae best supports the placement within this family. The major characters that allow us to place *Ulmoidicarpum* within Ulmaceae include (Pl. 3, figs 1–9; Tab 1): stipitate samaras (common to most genera) with ciliate margins (common in *Ulmus*), long pedicels and reniform endocarps (e.g. *Zelkova* and *Hemiptelea*), a stigmatic notch that is located laterally with respect to the long axis of the wing, and two styles that are unequal and are united at their base (as is also seen in *Ampelocera*).

Before settling on Ulmaceae as the family best accommodating these fossils, we considered fruits of other families with somewhat similar features (Tab. 1). *Smodingium* (Anacardiaceae) has samaras with asymmetrical wings, a stigmatic notch located laterally with respect to the long axis of the wing, and a centrally located endocarp that is fed by a conspicuous vascular strand (Pl. 3, figs 10–11).

These characters resemble the gross morphology of *Ulmoidicarpum*. However, major differences such as non-stipitate and non-ciliate samaras, and the presence of three styles of equal length that are not united at their base, distinguish *Smodingium* (and all morphologically similar samaras in Anacardiaceae; Pell et al. 2011) from *Ulmoidicarpum* and extant Ulmaceae. *Eucommia ulmoides* (Eucommiaceae) shows morphological similarities with Ulmaceae and therefore with *Ulmoidicarpum*. However, samaras of *Eucommia* (Pl. 3, fig. 12) are considerably larger and thicker than those of Ulmaceae and *Ulmoidicarpum*, lack hairs along the margin, and possess abundant latex strands that are commonly preserved in fossils (Call & Dilcher 1997). Lastly, affinity with *Euptelea* (Eupteleaceae) can be ruled out because its samara has a very long stipe and two stigmatic crests that strongly protrude from the cleft (Pl. 3, fig. 13).

Table 1. Continued

	<i>Ulmus</i>	<i>Zelkova</i>	<i>Ulmoidicarpum</i>	<i>Smodingium</i>	<i>Eucommia</i>	<i>Euptelea</i>
1.	stipitate	stipitate	stipitate	sessile	stipitate	long stipitate
2.	symmetrical	asymmetrical	asymmetrical	asymmetrical	symmetrical	asymmetrical
3.	samara	drupe	samara	samara	samara	samara
4.	< to >1× perianth + gynoecium	< 1× perianth + gynoecium	>1× perianth + gynoecium	< 1× perianth + gynoecium	< 1× perianth + gynoecium	< 1× perianth + gynoecium
5.	visible to not obviously visible	not obviously visible	visible	visible	visible	visible
6.	eciliate to ciliate	NA	ciliate	eciliate	eciliate	eciliate
7.	glabrous, pubescent over endocarp or entire surface	glabrous or sparsely pubescent	glabrous	glabrous	glabrous but covered with latex cells	glabrous but covered with dark spots
8.	strongly reticulate to radial	NA	strongly radial	strongly reticulate	strongly reticulate	reticulate
9.	< to > seed width	NA	> seed width	> seed width	< seed width	< seed width
10.	medial, distal to adjacent to notch	NA	medial	medial	medial	submedial
11.	absent	present	present	present	absent	absent
12.	present along entire samara	present along bisymmetrical plane of fruit	present along entire samara	absent	present along entire samara	absent
13.	apical	lateral	lateral	lateral (3 styles)	apical	lateral
14.	absent	absent	present	absent	absent	absent
15.	absent	absent	present	absent	absent	present
16.	absent	NA	absent	absent	absent	absent

Molecular phylogenetic analyses incorporating all extant genera of Ulmaceae support the recognition of two main clades (Neubig et al. 2012). One clade includes the tropically distributed genera *Ampelocera* and *Phyllostylon* from South and Central America, and *Holoptelea* from Africa and India. The other clade includes the exclusively north temperate genera *Hemiptelea* from Asia, *Planera* from the southeastern United States, *Ulmus* from Europe, Asia, and North America, and *Zelkova* from Europe and Asia. Our comprehensive review of the fruit morphology in Ulmaceae (summarized in Tab. 1; Pl. 3, figs 1–9) corroborates previous treatments of the variation of the reproductive structure (Manchester 1989a, Wiegrefe et al. 1994, Manchester & Tiffney 2001, Denk & Dillhoff 2005). We also provide new characters useful for fossil identification (Tab. 1). *Ulmoidicarpum* is more similar in gross morphology (e.g. long stipe and pedicel, well developed wings) to samaras of

Ulmus (Pl. 3, figs 1–4) and *Holoptelea* (Pl. 3, figs 5, 6), although a major difference between the fossil and these living genera resides in the position of the stigmatic notch, which is lateral rather than apical. *Ulmoidicarpum*, *Holoptelea*, and *Hemiptelea* also share a reniform endocarp (Pl. 1, fig. 1; Pl. 3, figs 6, 8). *Ulmoidicarpum*, *Ampelocera*, *Zelkova*, and *Hemiptelea* likewise present a stigmatic notch that is located laterally with respect to the long axis of the fruit (Pl. 1, fig. 1; Pl. 3, figs 709). Furthermore, *Ulmoidicarpum* and drupes of *Ampelocera* share a combination of characters that is unique to these genera within Ulmaceae: two styles that are unequal in length and that are united at their base (Pl. 1, fig. 3; Pl. 3, fig. 7).

Because none of the extant genera in Ulmaceae displays the same combination of morphological characters seen in *Ulmoidicarpum*, we propose this as a new extinct genus. No previously described fossil fruit shows the

Table 2. Morphological comparison of *Aerofructus* Herrera & Manchester gen. nov. and fruits of extant Malvaceae and other unrelated families

Family-genera & Character	<i>Burretiodendron</i>	<i>Cavanillesia</i>	<i>Maxwellia</i>	<i>Pentace</i>	<i>Aerofructus</i>	Combretaceae	Fabaceae	Onagraceae	Rutaceae
Ovary position	superior	superior	superior	superior	superior	inferior	superior	inferior	superior
Ovary attachment	long stipitate	sessile	sessile	sessile	sessile	sessile or stipe-like	medium to long stipitate	sessile or stipe-like	short stipitate
Fruit dehiscence	septicidal capsule	indehiscent capsule	indehiscent	indehiscent	indehiscent	indehiscent	indehiscent	loculicidal capsule	indehiscent
Length/Width cm	4.0/2.5	12/14	3.0/2.3	1.7/1.0	2.21/3.56	0.3–0.5 to 2.8–3.0/0.4–0.6 to 5.6	4.5–5.5 / 5.3–6.0	3.5–5.0/1.8–4.0	1.4–1.7/2.4–6.2
Wing number	5	5	3–4(–5)	3.5,10	4	2,4,5	2,4	4	2,2–3,4
Wing shape	elliptical-narrow	widely elliptical with cordate base	elliptical-narrow with cordate base and apex	elliptical-narrow with cordate base and apex	widely elliptical with cordate base	ovate, obovate, elliptical-narrow to widely elliptical, sometimes with a v-shaped notch	elliptical-narrow to widely elliptical, sometimes with emarginated or acuminate apices	elliptical to nearly circular with rounded base and apex	elliptical-narrow, circular to widely elliptical, sometimes with emarginated apex
Wing venation	main veins fan outward into the wings from the central body, and are straight to sinuous in course	strong set of subparallel veins fanning outward into the wings from the central body	subparallel veins fanning outward into the wings from the central body	subparallel veins fanning outward into the wings from the central body	strong set of subparallel veins fanning outward into the wings from the central body	mostly fine, closely spaced veins fanning outward into the wings from the central body	mostly subparallel to brochidodromous	mostly fine, closely spaced veins fanning outward into the wings from the central body	reticulate, fine and closely spaced to subparallel
Marginal vein	present	present	present	present	present	absent	absent to present	absent	present
Persistent parts	absent	bowl-shaped receptacle	remnants of perianth	remnants of perianth and two or more styles at apex	bowl-shaped receptacle	absent – stylar protrusion – calyx lobes at apex	absent – campanulate calyx at junction of pedicel and stipe – style at apex	absent	thickened area (disk-like) at the junction of fruit and pedicel beneath a very short stipe
Trichome bases	present	present	present	present	present	absent	dark spots present	absent	absent

Table 3. Extant taxa physically analyzed in this study. See Materials and Methods for supplemental literature

Species Name Ordered Alphabetically and by Family	Herbarium's or Institution's Abbreviation and No.	Collector's Name and No.	Locality
Anacardiaceae			
<i>Smodingium argutum</i> E.Mey. ex Sond.	(US) 2410495	James L Sidley, #3473	South Africa
Apocynaceae			
<i>Aspidosperma inundatum</i> Ducke	(US) 1690050	Ducke, A, #24569	Brazil
Combretaceae			
<i>Combretum schumannii</i> Engl.	(UF) 225	Unknown	Unknown
Eupteleaceae			
<i>Euptelea</i> sp.	(UF) 1331	Manchester & Chen, #3817	China
Eucommiaceae			
<i>Eucommia ulmoides</i> Oliv	(UF) 1667	Dilcher DL	Japan
Malvaceae			
<i>Burretiodendron esquirolii</i> (H.Lév.) Rehder	(UF) 0830	Chang Hung Ta	China
<i>Cavanillesia arborea</i> (Willd.) K.Schum.	(US) 704540	Curran HM, #113	Brazil
<i>Cavanillesia hylogeiton</i> Ulbr.	(US) 3583196	Kroll, #74	Peru
<i>Cavanillesia hylogeiton</i> Ulbr.	(US) 2865730	Magin RL, #55P	Peru
<i>Cavanillesia hylogeiton</i> Ulbr.	(US) 3377007	Seidel LR & Humaday M, #5510A	Bolivia
<i>Cavanillesia platanifolia</i> (Humb. & Bonpl.) Kunth	(A) 266445	Allen PH, #296	Panama
<i>Cavanillesia platanifolia</i> (Humb. & Bonpl.) Kunth	(A) 266446	Allen PH, #296	Panama
<i>Cavanillesia platanifolia</i> (Humb. & Bonpl.) Kunth	(US) 678350	Willians RS, #998	Panama
<i>Cavanillesia platanifolia</i> (Humb. & Bonpl.) Kunth	(SCZ) 15852	Perez R, #2321	Panama
<i>Cavanillesia platanifolia</i> (Humb. & Bonpl.) Kunth	(SCZ) 3399	Croat TB, #5215	Panama
<i>Craigia yunnanensis</i> W.W.Sm. & W.E.Evans	(UF) 1123	Manchester SR	China
<i>Maxwellia lepidota</i> Baill.	(A) 266449	Guillaumin & Baumann, #13129	New Caledonia
<i>Pentace laxiflora</i> Merr.	(A) 266448	Leopold, 78602	Malaysia
Ulmaceae			
<i>Ampelocera hottlei</i> (Standl.) Standl.	(UF) 0837	Gentle PH, #5291	Honduras
<i>Ampelocera macrocarpa</i> Ferero & Gentry	(MO) 4661305	Gerardo R, #1454	Costa Rica
<i>Ampelocera ruizii</i> Klotzsch	(LPB) 6046	Seidel LR, Garcia E, & Aguila M, #6046	Bolivia
<i>Ampelocera ruizii</i> Klotzsch	(FLAS) 216330	Hammond EP, #286	Bolivia
<i>Hemiptelea davidii</i> (Hance) Planch.	(UF) 0849	Dilcher DL	Germany
<i>Hemiptelea davidii</i> (Hance) Planch.	(FLAS) 139211	Judd WS, #2691	USA
<i>Holoptelea integrifolia</i> Planch.	(FLAS) 50468	West E	India
<i>Phyllostylon rhamnoides</i> (J.Poiss.) Taub.	(FLAS) 204713	Veloz JA	Dominican Republic
<i>Planera aquatica</i> J.F.Gmel.	(FLAS) 25664	West E & Arnold L	USA
<i>Planera aquatica</i> J.F.Gmel.	(FLAS) 211333	Davis SB, #258	USA
<i>Ulmus alata</i> Michx.	(FLAS) 229772	Hubbard J, # 345	USA
<i>Ulmus alata</i> Michx.	(FLAS) 154265	Kessler J	USA
<i>Ulmus americana</i> L.	(UF) 1352	Lott T,	USA
<i>Ulmus americana</i> L.	(FLAS) 210784	Davis SB, #594	USA
<i>Ulmus crassifolia</i> Nutt.	(FLAS) 118452	McDaniel S	USA
<i>Ulmus crassifolia</i> Nutt.	(FLAS) 191486	Abbott JR, # 2508	USA
<i>Ulmus parvifolia</i> Jacq.	(UF) 0852	Unknown	USA
<i>Ulmus parvifolia</i> Jacq.	(UF) 1312	Dilcher DL, #3799	Japan
<i>Ulmus rubra</i> Muhl.	(FLAS) 191489	Abbott JR, #4707	USA
<i>Ulmus rubra</i> Muhl.	(FLAS) 227327	Abbott JR, #23467	USA
<i>Zelkova crenata</i> Spach	(FLAS) 162809	Krol R	USA
<i>Zelkova serrata</i> (Thunb.) Makino	(UF) 1258	Kokawa & Manchester	Japan
<i>Zelkova serrata</i> (Thunb.) Makino	(FLAS) 221277	Abbott JR, #20812	USA

combination of characters present in *Ulmoidicarpum*. The phylogenetic position of *Ulmoidicarpum* with respect to the two major clades recognized for the family (Neubig et al. 2012) remains uncertain. We still do not know the leaves borne by this plant, and we have not yet found the pollen in direct association.

Discussion. We are unable to infer whether *Ulmoidicarpum tupperi* belongs to the tropical or temperate clade of extant Ulmaceae. Nonetheless, the occurrence of an ulmaceous samara in the Paleocene of Colombia suggests that wind-dispersed fruits may have evolved early in the history of the family.

Fossil pollen of Ulmaceae is first seen in the Maastrichtian of Japan, North America, Brazil, and India (Muller 1981). Pollen grains of *Ulmoideipites krempii* are very abundant in the late Cretaceous and Paleogene of northern South America, (Jaramillo et al. 2007, 2011) with the first appearance around 72.3 Ma and the last appearance at 33.3 Ma (Jaramillo et al. 2011). *U. krempii* grains, known from Cerrejón and Bogotá as well as various other sites in Colombia and Venezuela, are 3–5 porate, mid-sized (26–35 µm), with exine thin, tectate, and verrucate (see Jaramillo & Dilcher 2001 for additional descriptions and photographs). This morphology matches that of pollen in the family, including extant genera such as *Hemiptelea*, *Holoptelea*, *Phyllostylon*, *Planera*, *Ulmus*, and *Zelkova* described by Muller (1981), Zavada (1983), and Takahashi (1989). We do not know if some of these pollen grains correspond to extant genera, such as *Phyllostylon* which is Neotropical in its extant distribution, or to *Ulmoidicarpum*. However, the concurrent appearance of abundant ulmaceous pollen grains and samaras in Colombia suggests that the Ulmaceae became established in northern South America by the Paleocene.

Ulmoidicarpum is of interest as the earliest known fruit record for Ulmaceae. Other extinct and extant genera have only been traced to the Eocene (Manchester & Tiffney 2001). *Cedrelospermum* Saporta is another extinct ulmaceous genus with samaras that have been reported from the middle Eocene to the Oligocene in mid-latitude North America and Mexico (e.g. Manchester 1989b, Magallón-Puebla & Cevallos-Ferriz 1994), and from the middle Eocene to the Miocene in Europe (e.g. Manchester 1987, Manchester & Tiffney 2001, Hably & Thiébaud

2002, Wilde & Manchester 2003, Kovar-Eder et al. 2004). Fossil samaras that possess characters allowing them to be placed in the extant genus *Ulmus* are first seen in the early Eocene of North America and China (e.g. Manchester 1989a, Denk & Dillhoff 2005, Wang et al. 2010). Fossil fruit records also allow for recognition of extant *Zelkova* and *Hemiptelea* in Europe and Asia, but their first occurrences are younger, dating only to the Oligocene and Miocene (Manchester 1989b). Abundant isolated leaves of ulmaceous affinities first appear in the Paleocene of North America, the Arctic regions, and temperate Asia (e.g. Hickey 1977, Kvaček et al. 1994, Burnham 1986, Manchester 1989b). These leaves, usually placed in the fossil genus *Ulmites*, share characters with extant Northern Hemisphere genera (i.e. *Hemiptelea*, *Planera*, *Ulmus*, and *Zelkova*).

Family: MALVACEAE Juss
nom. cons. s.l.

Genus: ***Aerofructus*** Herrera
& Manchester gen. nov.

Generic diagnosis. Widely elliptical fin-winged fruit with at least four broad wings that form a strongly cordate base. Fruit pedicellate, with a thickened bowl-shaped receptacle. Major venation of wing subparallel with irregular higher-order veins. Abundant trichome bases present underneath the fossil cuticle.

Derivation of generic name. From the Latin words “aer” for air/wind and “fructus” for fruit, a reference to the inferred mode of dispersal.

Type species. *Aerofructus dillhoffii* Herrera & Manchester sp. nov.

Specific diagnosis. Same as generic diagnosis.

Holotype. Designated here: FH0315-STRI-9966 (Pl. 4, figs 1–5).

Derivation of specific epithet. In recognition of Richard M. and Thomas A. Dillhoff for their contributions to and generous support of paleobotanical studies.

Source, age, and stratum. The single specimen is middle to late Paleocene in age (58–60 Ma). It was collected at Guajira Peninsula,

Ranchería Basin, Cerrejón coal mine, Cerrejón Formation, Tabaco 1 pit. Locality FH0315 (locality placed below coal bed 100). N 11.135°, W 72.570°.

Description. Fin-winged fruit. At least four lateral wings aligned on the longitudinal axis of the fruit are present (Pl. 4, fig. 1). The fruit is widely elliptical with a conspicuous cordate base (Pl. 4, fig. 3), ca 22.1 mm high and 35.6 mm wide. Remnant of pedicel is 1.6 mm long and 1.4 mm wide (Pl. 4, fig. 3). A bowl-shaped thickening is observed near the fruit base and at the pedicel junction (Pl. 4, fig. 3). This structure is thicker than the surrounding wings and pedicel (1.6 mm long and 3.4 mm wide), and likely represents the floral receptacle. Each wing has a set of strong subparallel veins, ca 0.1–0.4 mm apart, that radiate from the central axis of the fruit (Pl. 4, fig. 4) and intersect with the marginal vein (Pl. 4, fig. 2). Irregular higher-order veins are present but are poorly visible due to the thickness and carbonaceous nature of the compressed tissue. Abundant, densely packed black spots, 8–10 µm in diameter, underneath the fossil cuticle of the wings represent trichome bases (Pl. 4, fig. 5). The thickness of the coalified tissue indicates that the wings were probably coriaceous.

Systematic affinity. Manchester & O’Leary (2010) identified at least 48 families and more than 140 genera containing fin-winged fruits (i.e. fruits with two or more wings aligned with the longitudinal axis). They indicated that the ovary position, wing number, texture, shape and wing venation, persistent floral parts, and dehiscence mode provided useful characters for differentiating extant families and genera, and for the identification of fossils. Using these characters, we suggest that *Aerofructus* is best placed within the Malvaceae because the fruits developed from a superior ovary, have persistent perianth parts, 4 to 5 wings, venation that fans outward from the central body and merges into a marginal vein, and abundant trichome bases (Tab 2; Pl. 4; Pl. 5, figs 1–9).

Aerofructus also presents some similarities to fin-winged fruits in Combretaceae (e.g. *Combretum*), Fabaceae (e.g. *Piscidia*), Onagraceae (e.g. *Oenothera*), and Rutaceae (e.g. *Balfourodendron*) (see Manchester & O’Leary 2010; Tab 2). Among these families, Combretaceae and Onagraceae can be ruled out

for having inferior ovaries and lacking marginal veins along the wing, unlike our fossil. Additionally, wing venation in most species in these two families consists of fine, densely spaced veins (Pl. 5, figs 10–11), in contrast to the thicker and more widely spaced veins seen in *Aerofructus*. Fabaceous fin-winged fruits can be distinguished from the Cerrejón fossil because of their long stipes, usually persistent styles, and pod-like central bodies seen in the bean family. Rutaceous fin-winged fruits differ from *Aerofructus* because they commonly have a thickened area (disk-like structure) at the junction of the fruit with the pedicel, and their wing shape and venation differ from that of the Cerrejón fossil. *Aerofructus* differs from modern Malpighiaceae fin-winged fruits in the lack of elliptical to orbicular mericarps and brochidodromous venation (Manchester & O’Leary 2010).

Among fin-winged fruits of Malvaceae, *Burretiodendron* and *Pentace* (Southeast Asia), *Maxwellia* (New Caledonia) and *Cavanillesia* (Neotropical) show the closest similarity with *Aerofructus* (Pl. 5, figs 1–8; Tab. 2). The phylogenetic position of these genera (Baum et al. 2004, Nyffeler et al. 2005, Carvalho et al. 2011) suggests that fin-winged fruits have evolved multiple times in the family. *Burretiodendron* differs from *Aerofructus* (Pl. 5, figs 7–8) by their long stipe and septicial fruits that split into 1-seeded mericarps (Manchester & O’Leary 2010). *Pentace* contrasts with the Cerrejón fossil in the general morphology of the fruit, because most of the living species are narrower than *Aerofructus*, and flowers of this genus lack the conspicuous bowl-shaped receptacle (Pl. 5, figs 4–5). *Maxwellia* fruits differ from *Aerofructus* in having thinner and narrower wings (Pl. 5, fig. 6). On the other hand, *Cavanillesia* has a fruit with widely elliptical wings, a conspicuous cordate base, a bowl-shaped receptacle, and a venation pattern that closely resembles *Aerofructus* (Pl. 5, figs 1–3). Fruits of this genus are commonly 12 cm high and 14 cm wide, making them the largest fin-winged fruits of any angiosperm (Manchester & O’Leary 2010). This contrasts with the single available specimen of *Aerofructus*, ca 2.3 cm high and 3.7 mm wide. Fruits of extant *Cavanillesia* are covered with abundant stellate trichomes, though we observed that these trichomes fall off easily from herbarium specimens, leaving noticeable bases (Pl. 5, fig. 3).

Although the stellate trichomes and stamens are commonly seen in herbarium specimens (frequently collected when immature), we noticed that they were absent from dozens of mature, fallen *Cavanillesia* fruits that we examined along a beach on the Pacific coast of the Azuero Peninsula in Panama (summer 2012; GPS: N 7°12'826, W 80°42'013). These observations imply that taphonomic factors might preclude the observation of stellate trichomes in fossil representatives of this genus.

Based on the similarities and differences seen between *Aerofructus* and the fin-winged fruits of extant representatives of Malvaceae, and considering that winged fruits have evolved multiple times across members of this family, we consider the fossil to represent an extinct genus of Malvaceae. Even though our fossil shows a greater similarity to species of *Cavanillesia* than to those of other genera, we take a conservative approach and place the fossil in a separate genus, due to marked differences in fruit size and the lack of its distinctive pollen grain in the Cerrejón palynoflora (Jaramillo et al. 2007).

Aside from *Aerofructus*, the only accepted fin-winged fossil fruits of Malvaceae are those of *Craigia* (Manchester & O'Leary 2010). This genus, today endemic to eastern Tibet and China, shows a widespread fossil record during the Cenozoic in eastern Asia, Europe, and western North America (e.g. Kvaček et al. 2005). *Craigia* fruits can be separated from *Aerofructus* based on the rounded base formed by the wing and the sparsely distributed wing veins (Pl. 5, fig. 9).

Discussion. *Aerofructus dillhoffii* augments pollen and leaf data, indicating the presence of the Malvaceae in Paleocene Neotropical floras (Jaramillo et al. 2007, Carvalho et al. 2011). Leaves of *Malvaciphyllum macondicus* and abundant pollen grains of *Bombacacidites annae* found in the Cerrejón flora indicate the Paleocene occurrence of members of the Eumalvoideae and Bombacoideae clades respectively. Given that no pollen was found to occur in situ with *A. dillhoffii*, nor was there any organic connection to leaves, it is not possible to determine whether this fossil fruit represents a new malvacean lineage in the Cerrejón flora.

Up to now, the pollen and leaf records from the Cerrejón Formation, and the winged fruit here described, remain among the earliest

known records for Malvaceae in the Neotropics, and support a minimum Paleocene age for this family in the region. No definite malvaceous fossils have been reported in a recently discovered flora from the Maastrichtian Guaduas Formation of Colombia (Martinez et al. 2014). A previous report of *Theobroma fossilium* ("Sterculiaceae") (Berry 1929, Huertas 1960) from deposits described as possibly Cretaceous of Colombia proved to lack affinities to Malvaceae *s.l.* (Brown 1946).

Incertae Sedis

Genus: ***Hickeycarpum***
Herrera & Manchester gen. nov.

Generic diagnosis. Samara pedicellate with a centrally placed seed body. Seed circular with abundant radiating ribs. Wing circular, thin, and with radiating, marginally looped venation. Thick marginal vein present.

Derivation of generic name. In honor of the paleobotanist Leo J. Hickey (1940–2013) for his remarkable legacy in the study of the plant fossil record.

Type species. *Hickeycarpum peltatum* Herrera & Manchester sp. nov.

Specific diagnosis. Same as generic diagnosis.

Holotype. Designated here: FH0903-STRI-34032 (Pl. 6, figs 1–3).

Paratypes. Designated here: FH0903-STRI-12925, 34033, 34042, 34100–34102 (Pl. 6, figs 4–9).

Source, age, and stratum. The specimens are from Cundinamarca State, Cagua town, locality FH0903, Bogotá Formation, middle to late Paleocene in age (58–60 Ma). N 5°04'36.1, W 73°57'18.9.

Description. The fruit is a samara with a circular to elliptical wing. Wing diameter ranging from 18 to 21.6 mm in circular specimens (n = 2; Pl. 6, figs 1–2) and from 12.4 to 23.1 mm high and 16.5 to 27.8 mm wide in elliptical specimens (n = 4). The fruit is peltate (i.e. pedicel is attached near the center of the fruit; Pl. 6, figs 1–2). The wing venation is brochidodromous, looping 0.5 mm away from the wing margin; veins radiating from the seed body are widely separated, from 1.3 to 2.4 mm apart. A thick marginal vein is present. The

seed is located at or near the center of the fruit (Pl. 6, figs 1–4), circular to more or less elliptical, and from 4.1 to 8.0 mm in diameter. Abundant ribs radiate from the center of the seed and appear more accentuated at its margin (Pl. 6, fig. 3). The pedicel, 6.4 to 7.6 mm long and 0.4 to 0.6 mm thick, is preserved as a narrow groove/ridge across the wing impression.

Systematic affinity. No living genus coincides fully with the morphology of *Hickeycarpum*. Extant seeds that present partial similarities in shape and size with *Hickeycarpum* include members of the genera *Anchitea* (Violaceae), *Aspidosperma* (Apocynaceae), *Dioncophyllum* and *Triphyophyllum* (Dioncophyllaceae). A major difference between these extant winged seeds and the fossil genus is the presence of radiating and looped marginal venation in *Hickeycarpum* (Pl. 6, figs 4–5). In contrast to fruits, most winged seeds in angiosperms lack conspicuous venation and in some cases venation is limited to a weak and radial pattern (e.g. *Triphyophyllum*). On the other hand, *Asteranthos* (Lecythidaceae), *Chaunochiton* (Olacaceae), *Cyclocarya* (Juglandaceae), and *Maireana* (Amaranthaceae) have fruits that partially resemble the peltate samaras of *Hickeycarpum* in size, wing shape and venation. The main dissimilarity between these extant genera and the Bogotá fossils is the occurrence of abundant radiating ribs in the central seed body of the fossils (Pl. 6, figs 2–3). We have not observed this peculiar seed character in any extant circular flat-wing samaras, thus we place the Paleocene disseminules of *Hickeycarpum* as an extinct angiosperm of unknown familial affinity.

Genus: *Anemocardium*

Herrera & Manchester gen. nov.

Generic diagnosis. Tufted fruit with persistent style, c-shaped pedicel, and ovate to elliptic in shape with more or less cordate base. Seed/endocarp with abundant ridges parallel to its longitudinal axis.

Derivation of generic name. From the Greek words “anemos” for wind (making reference to the wind-dispersed syndrome) and “kardia” for heart (making reference to the overall shape).

Type species. *Anemocardium margaritae* Herrera & Manchester sp. nov.

Specific diagnosis. Same as generic diagnosis.

Holotype. Designated here: FH0903-STRI-34103 (Pl. 7, figs 1–3).

Paratypes. Designated here: FH0903-STRI-34104–34106 (Pl. 7, figs 4–6).

Derivation of specific epithet. In honor of the student Margarita María Gómez-Gómez (1988–2011) for her passion and love of the biological and paleobotanical sciences.

Source, age, and stratum. The four specimens are from Cundinamarca State, Cogua town, locality FH0903, Bogotá Formation, middle to late Paleocene in age (58–60 Ma). N 5°04'36.1, W 73°57'18.9.

Description. Fruit with a tuft of hairs, somewhat heart-shaped, ovate to elliptic and with a cordate base (Pl. 7, figs 1–6) and 14 to 18.9 mm long and 9.6 to 13.8 mm wide (n = 4). The fruit wall is discernible from the seed body by a conspicuous furrow or layer (Pl. 7, figs 4–6), 0.7 to 1.7 mm thick. In the plane of bisymmetry the fruit wall is covered with abundant and densely distributed hairs (Pl. 7, figs 1, 4–6), up to 6.8 mm long. The style is persistent, approximately 1 mm long (Pl. 7, figs 3, 6). The pedicel is 1 to 1.5 mm long, possibly persistent, c-shaped, and thickened at the point of fruit body attachment (Pl. 7, figs 2, 5). The seed is elliptic to more or less circular and with 7 to 9 prominent ridges that run parallel to the long axis of the fruit (Pl. 7, figs 1, 4–6).

Systematic affinity. Although it clearly represents an angiosperm, the natural affinities for this genus among flowering plants remain uncertain.

***Carpolithus* sp. 1**

Diagnosis. Disseminule body central and surrounded by two lateral wings. Apex and base shape cordate. Crescent-shaped scar present.

Specimen. FHM105-106-STRI-9958 (Pl. 8, figs 1–2).

Description. Two-winged disseminule. The wings appear aligned to the longitudinal axis of the body and symmetrical with one another (Pl. 8, figs 1–2). The specimen is elliptical, about 2.9 mm high and 3.9 mm wide, with a cordate base and apex. Width of the wings

(measured from the edge of the central body to the margin) is 1.2 to 1.4 mm. The wings do not preserve venation. Central body elliptical, 2.1 mm high and 1.0 mm wide. A crescent-shaped scar appears near the apex of the central body (Pl. 8, fig. 2).

Source, age, and stratum. The single specimen is from the Guajira Peninsula, Ranchería Basin, Cerrejón coal mine, Cerrejón Formation, La Puente pit, middle to late Paleocene in age (58–60 Ma). Locality FHM105-106 (locality positioned between coal beds 105–106). N 11.5°, W 72.5°.

Systematic affinity. Uncertain.

Carpolithus sp. 2

Diagnosis. Tufted disseminule with elliptic to ovate central body. Central body with a u-shaped furrow. Two appendages diverging from the central body.

Specimens. FH0804-STRI-34107, FH0804-STRI-34109, FH0804-STRI-34110 (Pl. 9, figs 1–4).

Description. Tufted disseminule, 22.1 to 23.5 mm long (measured from edge to edge of the lateral appendages). The specimens have an elliptic to ovate central body that varies from 5.2 to 6.5 mm long and 2.6 to 3.7 mm wide. In its central body the specimens show a shallow u-shaped furrow (Pl. 9, fig. 2). Two long, lateral, and unequal appendages diverge from the central body (Pl. 9, figs 1–4). Abundant hairs are present (Pl. 9, fig. 4).

Source, age, and stratum. The three specimens are from Cundinamarca State, Nemocón locality, Checua mine (Sumicol), locality FH0804, Bogotá Formation, middle to late Paleocene in age (58–60 Ma). N 5°08'14.6, W 73°50'8.20.

Systematic affinity. Disseminules with tufted hairs and lateral appendages (e.g. bristles) are commonly seen in monocot families such as Bromeliaceae, Cyperaceae, Juncaceae, Orchidaceae, Poaceae, and Typhaceae. However, none of the genera in these families show all the morphological characters preserved in *Carpolithus* sp. 2. Seeds of Orchidaceae are usually much smaller in size and also lack strongly lignified seed walls in contrast to the Bogotá fossils (Arditti & Ghani 2000). We ruled out any affinity of *Carpolithus* sp. 2 with

the Cyperaceae, Juncaceae, and Poaceae families based on the absence of apparent bracts, lemmas, paleae, or awns in the Bogotá fossils. The Bromeliaceae (e.g., *Pitcairnia megasepala*) and Typhaceae (e.g., *Typha angustifolia*) have seeds and fruits with two prominent divergent appendages, but these structures depart from the apex and base of the disseminules, unlike the Bogotá fossils. Accordingly, we place *Carpolithus* sp. 2 as an extinct taxon of unknown affinity within angiosperms.

DISCUSSION

At least sixty fruit and seed morphotypes are recognizable from ca 300 specimens collected from the combined Cerrejón and Bogotá floras (see online appendix of Wing et al. 2009, Herrera et al. 2011), but only six are interpreted as wind-dispersed. Four are conspicuously winged: *Ulmoidicarpum*, Pl. 1, 2; *Aerofructus*, Pl. 4; *Hickeycarpum*, Pl. 6; and *Carpolithus* sp. 1, Pl. 8. Even though the abundant dispersal hairs of *Anemocardium* (Pl. 7) and *Carpolithus* sp. 2 (Pl. 9) may be suggestive of epizoochory, the absence of noticeable barb-like structures and the feathery appearance of dispersal hairs leads us to interpret these fossils as wind-dispersed. The low proportion of anemochorous taxa within these Paleocene floras (10%) is similar to that estimated from modern Neotropical and Old World rainforests (i.e. 13–16%; Prance 1978, Mori & Brown 1994), where wind-dispersed fruits are typical of canopy emergent and lianescent species. The low percentage of wind-dispersed taxa may suggest that the forest canopies represented by the Paleocene Cerrejón and Bogotá floras were already multistratal, as has been suggested before based on floristic analogs (Doria et al. 2008, Herrera et al. 2011, Stull et al. 2012). *Ulmoidicarpum* and *Aerofructus* show resemblance to fin-winged fruits of *Holoptelea* (Ulmaceae) and *Cavanillesia* (Malvaceae), respectively. These living genera grow primarily as emergent trees of the canopy in Neotropical and African rainforests (Keay 1957, Fernández-Alonso 2003).

The only pre-Cenozoic winged fruit known so far from northern South America is from the Maastrichtian Guaduas Formation of Central Colombia: *Archaeopaliurus boyacensis* Correa, which was placed as an extinct genus

of the Rhamnaceae (Correa et al. 2010). This family has a relatively low number of species in the Neotropics today (Phillips et al. 2002, Burnham & Johnson 2004) and it is commonly represented by liana or canopy tree species (Gentry 1993, Smith et al. 2004). The Guaduas Formation was deposited in sedimentary environments similar to those of the Cerrejón and Bogotá sequences; however, Maastrichtian wind-dispersed fruits appear to be very rare (one specimen out of more than 3000 plant macrofossils collected so far). The discrepancy in the abundance of wind-dispersed disseminules between floristic assemblages from similar depositional environments raises questions about the evolution of seed and fruit dispersal in Neotropical forests. Did wind-dispersed disseminules become common in Neotropical rainforests during or after the Maastrichtian? Although the answer to this question is far from certain, the rarity of wind-dispersed disseminules in this Maastrichtian Guaduas flora could suggest a Paleocene proliferation. Similarly, age-calibrated phylogenies and biogeographic analyses of living and predominantly wind-dispersed Neotropical genera in Apocynaceae, Bignoniaceae, and Orchidaceae suggest Paleocene-Eocene radiations (Ramírez et al. 2007, Rapini et al. 2007, Lohmann et al. 2013, Olmstead 2013). Eriksson & Kainulainen (2011) proposed that the evolution of “dust seeds” in extant rainforests was correlated to the development of the canopy in Paleocene rainforests. A scenario of high competition in the understory of early tropical rainforests may have favored the evolution of plants able to reach and effectively disperse from the upper layers of the rainforest during the Paleocene and Eocene (Eriksson et al. 2000, Lorts et al. 2008). Further quantitative and extensive collection of fruits and seeds from both late Cretaceous and Paleocene South American floras, as well as taphonomic studies in living tropical rainforests will be required to test these ideas.

The Cerrejón and Bogotá fossils show morphological diversity in terms of the structural adaptations for wind dispersal (i.e. disseminules with one or two well-developed wings, fin-winged fruits, and those with accessory hairs), but include an overall low proportion of anemochorous taxa, as seen in living rainforests. Although major families such as Orchidaceae, Bromeliaceae, Bignoniaceae, Apocynaceae, Asteraceae, and Sapindaceae (Mori

& Brown 1994, Mirle & Burnham 1999) are known to include most of the wind-dispersed disseminules in Neotropical rainforests today, they are still missing from the Paleogene fossil record in South and Central America. The fossils described provide a first glimpse of the variation of morphologies related to wind dispersal in the Paleocene Neotropics, and open new questions into the evolution of dispersal mechanisms in tropical rainforests.

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PLATES

Plate 1

Ulmaceous samara, *Ulmoidicarpum tupperi* Herrera & Manchester
gen. et sp. nov. Holotype, (FH0706-STRI-9914)

1. Samara showing long pedicel
2. Detail of reniform endocarp and surrounding wing
3. Detail of stigmatic notch, arrow indicates two unequal stigmatic arms united at their base
4. Detail of wing and pedicel attachment; upper arrow indicates one of the two scars, lower arrow indicates remnants of persistent perianth

Scale bars: 1 = 5 mm; 2 = 2 mm; 3, 4 = 1 mm

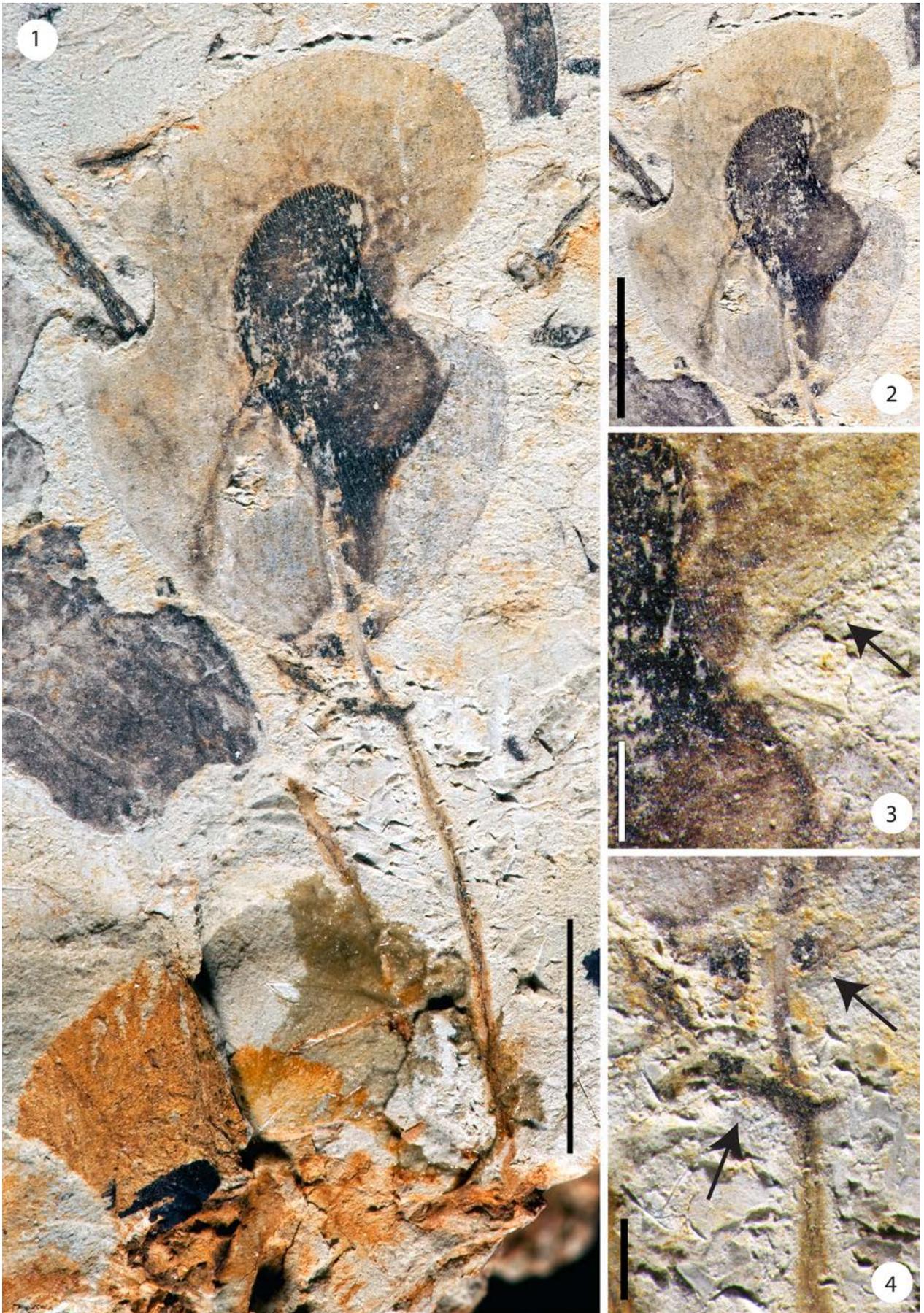


Plate 2

Ulmoidicarpum tupperi Herrera & Manchester
gen. et sp. nov.

1. Samara showing venation radiating from central endocarp (FH0706-STRI-9971)
2. Detail of wing showing minor reticulate venation (FH0705-STRI-9916)
3. Detail of stigmatic notch, arrow indicates unequal stigmatic branches (FH0708-STRI-9917)
4. Broad wing surrounding the endocarp (FH0705-STRI-0918)
5. Same as 4, arrow indicates abundant hairs along the wing margin
6. Thick vein along the wing margin (FH0709-STRI-9915)
7. Same as 6, arrow indicates two stigmatic arms united at their base
8. Samara with characteristic reniform endocarp in the center (FH0708-STRI-9918)
9. Notice lateral position of stigmatic notch with respect to the long axis of the wing (FH0705-STRI-0920)
10. Same as 9, arrow indicates high density of marginal hairs
11. One of the largest samaras of *Ulmoidicarpum*. Note that the base of the central endocarp is fed by a more or less curved vascular strand (FH0708-STRI-9921)

Scale bars: 1 = 3 mm; 2, 3, 5, 7, 10 = 1 mm; 4 = 2 mm; 6, 8, 9, 11 = 5 mm

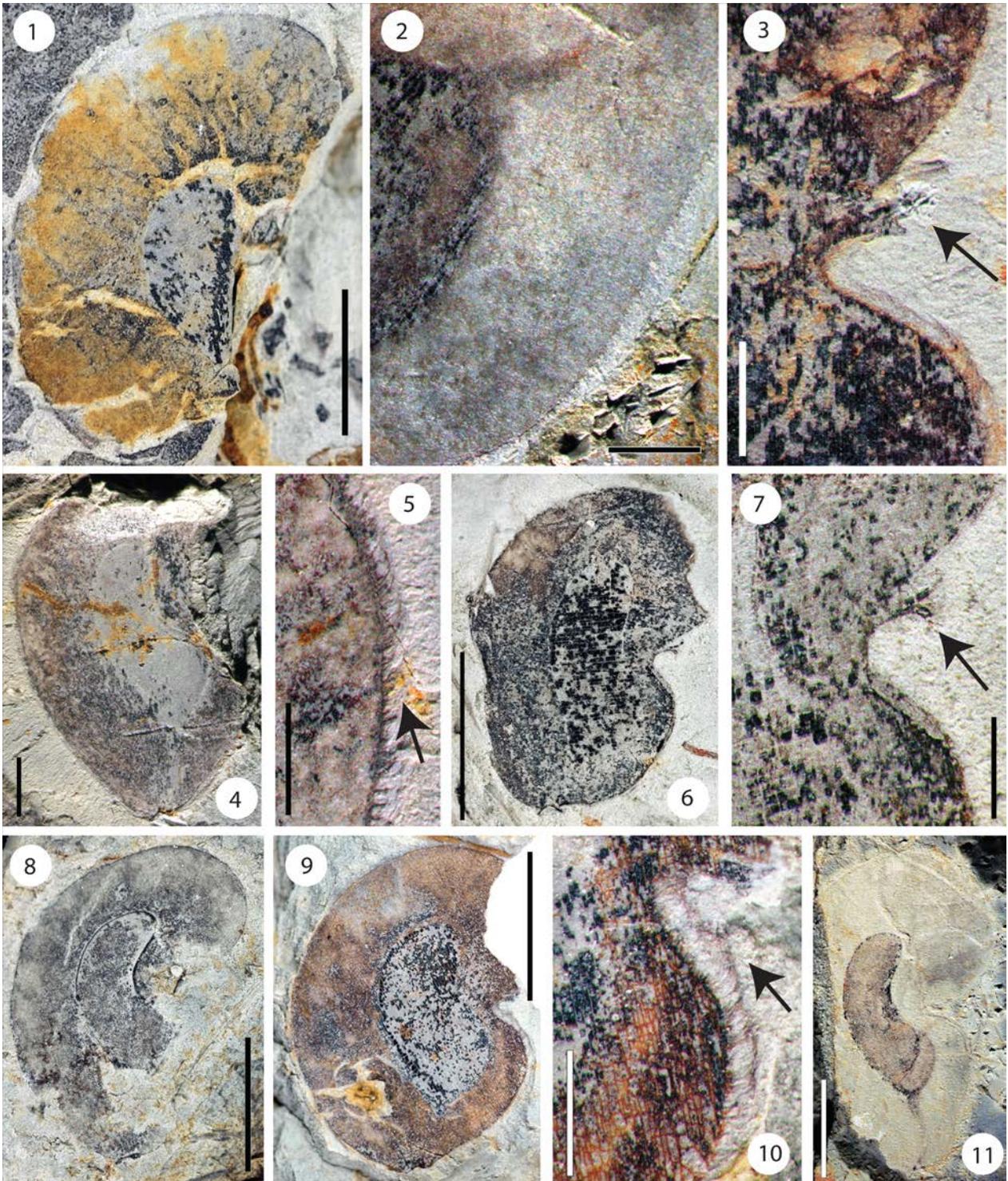


Plate 3

Extant samaras and drupes of Ulmaceae (A–J), Anacardiaceae (K–L), Eucommiaceae (M), and Eupteleaceae (N) for comparison and contrast with the fossil fruits

1. *Ulmus americana* L. (UF1352), note long pedicels (arrow) and persistent perianth parts
2. *Ulmus crassifolia* Nutt. (FLAS118452), arrow indicates ciliate margin
3. *Ulmus rubra* Muhl. (FLAS191489), note central endocarp of samara and more or less radiating venation
4. *Ulmus parvifolia* Jacq. (UF0852), note stipe and eciliate margin (arrow)
5. *Holoptelea integrifolia* Planch. (FLAS50468), see broad wing and radiating venation
6. Same as 5, showing reniform-like shape endocarp
7. *Ampelocera ruizii* Klotzsch (LPB6046), drupe, note lateral position of stigmatic notch with respect to the long axis of the fruit
8. *Zelkova serrata* (Thunb.) Makino (UF1258), showing strongly curved, reniform endocarp with strong veins on the exterior of the drupe
9. *Hemiptelea davidii* (Hance) Planch. (FLAS139211), note how the wing (arrow) surrounds partially the strongly curved endocarp
10. *Smodingium argutum* E. Mey. ex Sond. (US2410495), samara sessile (non-stipitate) (arrow) and eciliate margin
11. Same as 10, arrow indicates one of the three styles, these are of the same length and do not unite at their base
12. *Eucommia ulmoides* Oliv (UF1667), notice large size, thickness, and surficial glands of the samara
13. *Euptelea* sp. (UF1331), samara with a very long stipe and two stigmatic crests that strongly protrude the cleft (arrow)

Scale bars: 1, 3, 6, 12 = 5 mm; 2, 7, 8–10 = 2 mm; 4 = 3 mm; 5 = 1 cm; 11 = 0.5 mm; 13 = 2 cm

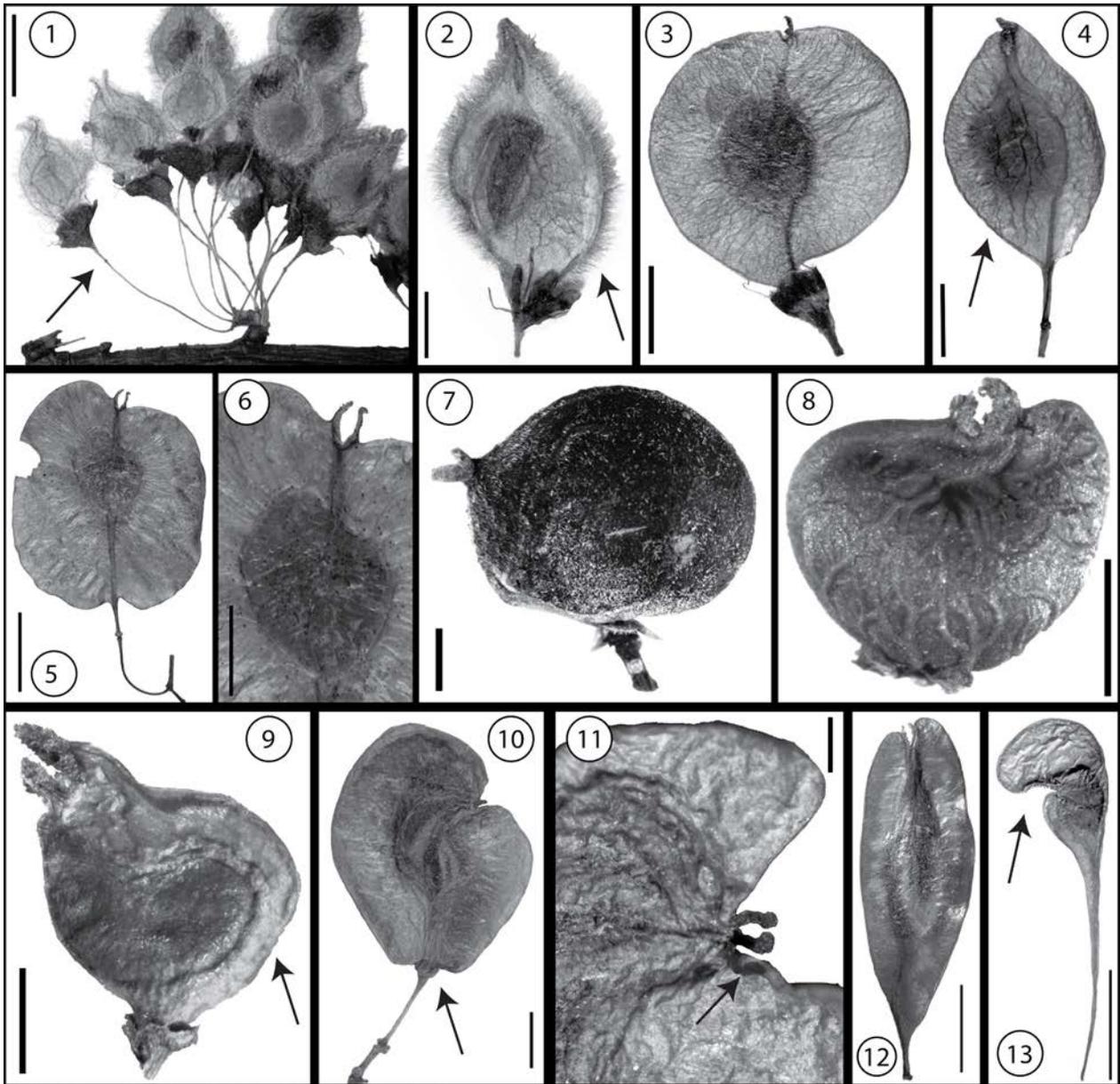


Plate 4

Malvaceous fin-winged fruit *Aerofructus dillhoffii* Herrera & Manchester
gen. et sp. nov. (Holotype, FH0315-STRI-9966)

1. Fin-winged fruit with 4 broad wings, notice wing major venation radiating from the center of the fruit in a subparallel pattern; arrow indicates close up in 3
2. Detail of wing edge and marginal vein
3. Detail of cordate base and pedicel attachment; arrows point out at a thick bowl-shaped scar, it is thicker than the surrounding wings and pedicel, thus we interpret this structure as evidence of the fruit receptacle
4. Detail of wing showing subparallel venation
5. Detail of fruit surface after removing cuticle, notice abundant and densely packed black scars or spots that we interpret as remnants of trichome bases

Scale bars: 1 = 1 cm; 2 = 1 mm; 3, 4 = 3 mm; 5 = 0.5 mm

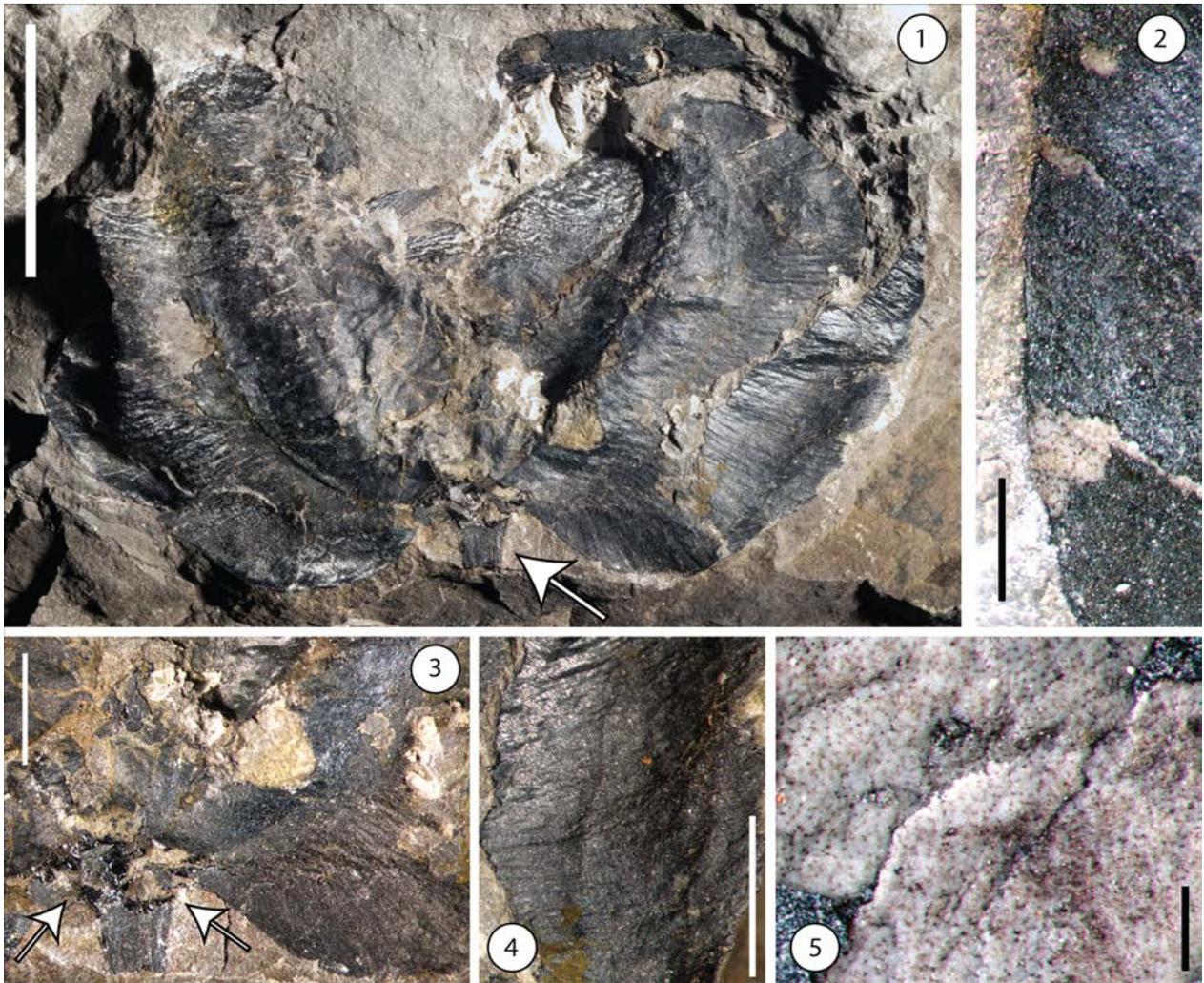


Plate 5

Extant fin-winged fruits of Malvaceae (A–I) and Combretaceae (J–K)

1. *Cavanillesia platanifolia* (Humb. & Bonpl.) Kunth (A266446), note four broad wings with venation radiating from the center of the fruit in a subparallel pattern and a cordate base
2. Same as 1, arrow indicates bowl-shaped receptacle of the fruit
3. Same as 1, note subparallel venation and abundant trichome bases
4. *Pentace laxiflora* Merr. (A266448), note narrow wings and elliptic shape of fruit
5. Same as 4, note wing venation and strongly glabrous surface
6. *Maxwellia lepidota* Baill. (A266449), strongly coriaceous and narrow wings
7. *Burretiodendron esquirolii* (H. Lév.) Rehder (UF0830), note long stipe and narrow wings
8. Same as 7, note abundant trichome bases
9. *Craigia yunnanensis* W. W. Sm. & W. E. Evans (UF1123), note elliptic wings and widely spaced venation
10. *Combretum schumannii* Engl. (UF225), fruit developed from an inferior ovary, note coriaceous wings
11. Same as 10, note the lack of a marginal vein and closely spaced and high-density veins

Scale bars: 1 = 2 cm; 2, 6 = 5 mm; 3, 8 = 2 mm; 4 = 3 mm; 5 = 0.5 mm; 7, 9, 10 = 1 cm; 11 = 1 mm

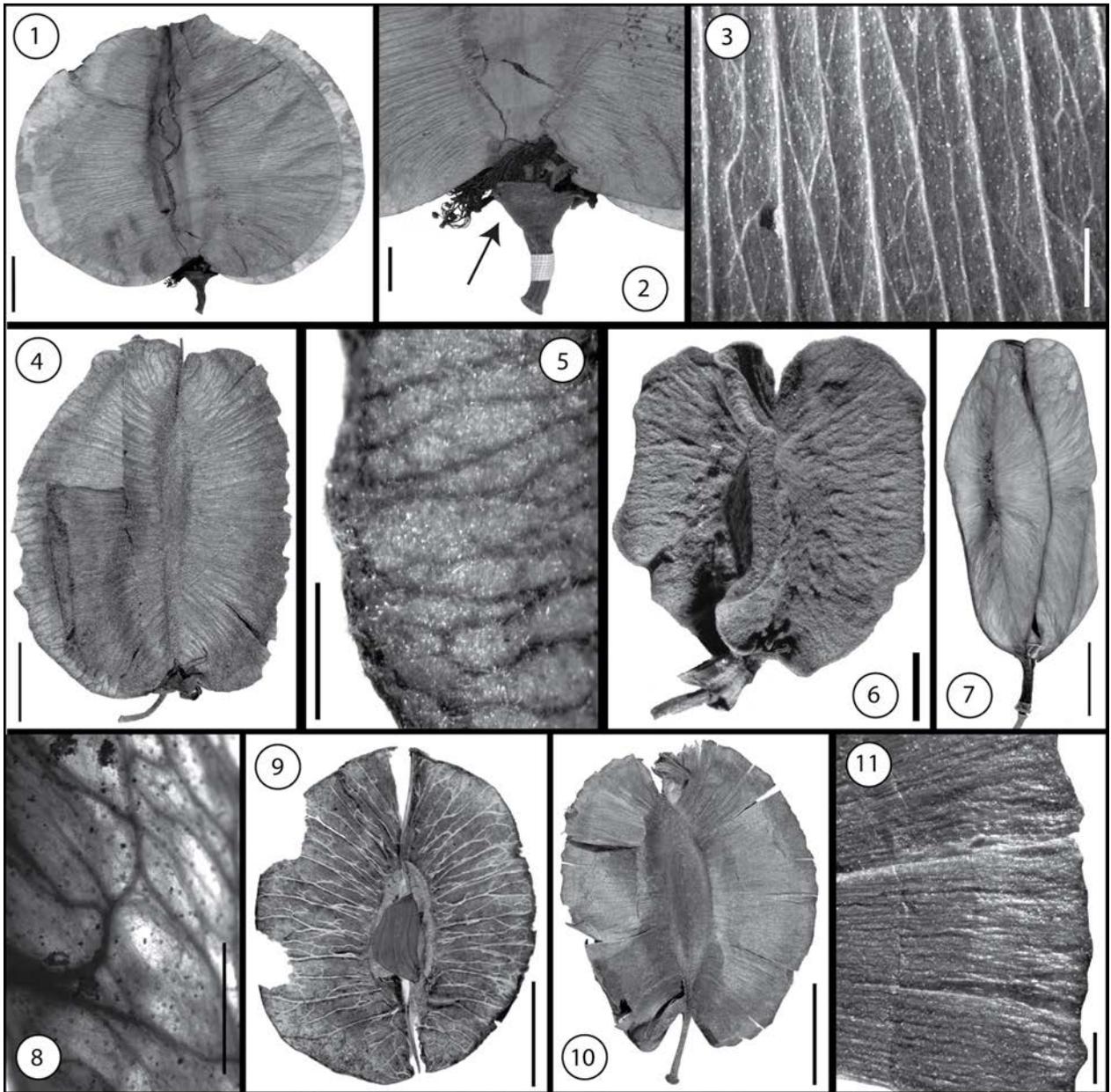


Plate 6

Samaras of *Hickeycarpum peltatum* Herrera & Manchester gen. et sp. nov.

1. Holotype (FH0903-STRI-34032), peltate samara subtended by central pedicel (arrow), note wing shape more or less circular
2. Counterpart from 1, note central seed body
3. Same as 2, note central seed body with abundant radiating ribs
4. Paratype (FH0903-STRI-34100), note wing shape elliptical, arrow points out close up in 5
5. Same as 4, arrow indicates brochidodromous wing venation
6. Paratype (FH0903-STRI-33042), arrow indicates thick marginal vein along the wing
7. Paratype (FH0903-STRI-34033), elliptical samara, arrow indicates close up in 8
8. Same as 7, arrow indicates the thickened base of the pedicel preserved just outside the wing coverage
9. Paratype (FH0903-STRI-12925), almost circular samara, central seed is not preserved

Scale bars: 1, 2, 4, 7, 9 = 5 mm; 3 = 3 mm; 5, 6, 8 = 2 mm

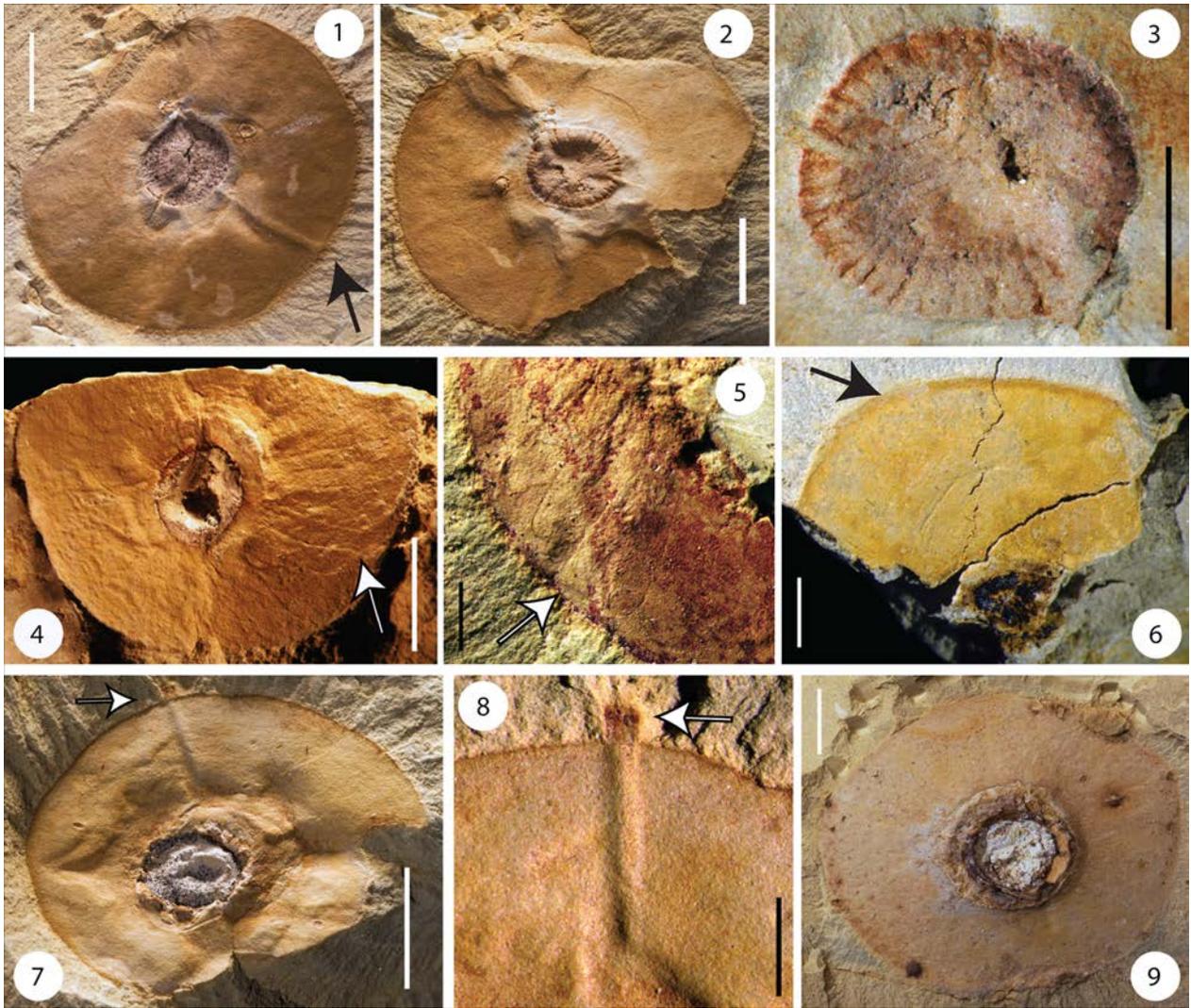


Plate 7

Anemocardium margaritae Herrera & Manchester gen. et sp. nov.

1. Holotype (FH0903-STRI-34103), note heart-shaped of a fruit, upper arrow indicates persistent style, left bottom arrow pedicel, right arrow hairs
2. Same as 1, note cordate base of fruit and pedicel (arrow)
3. Same as 1, note persistent style (arrow)
4. Paratype (FH0903-STRI-34105), note abundant hairs along the fruit pointing in the direction of the style, arrow indicates division between seed and fruit wall
5. Paratype (FH0903-STRI-34106), note abundant hairs and c-shaped pedicel, arrow indicates prominent ridges that run parallel to the long axis of the fruit
6. Paratype (FH0903-STRI-34104), lower arrow indicates that the fruit wall is discernible from the seed body by a conspicuous furrow, upper arrow indicates hairs

Scale bars: 1, 4–6 = 2 mm; 2, 3 = 1 mm

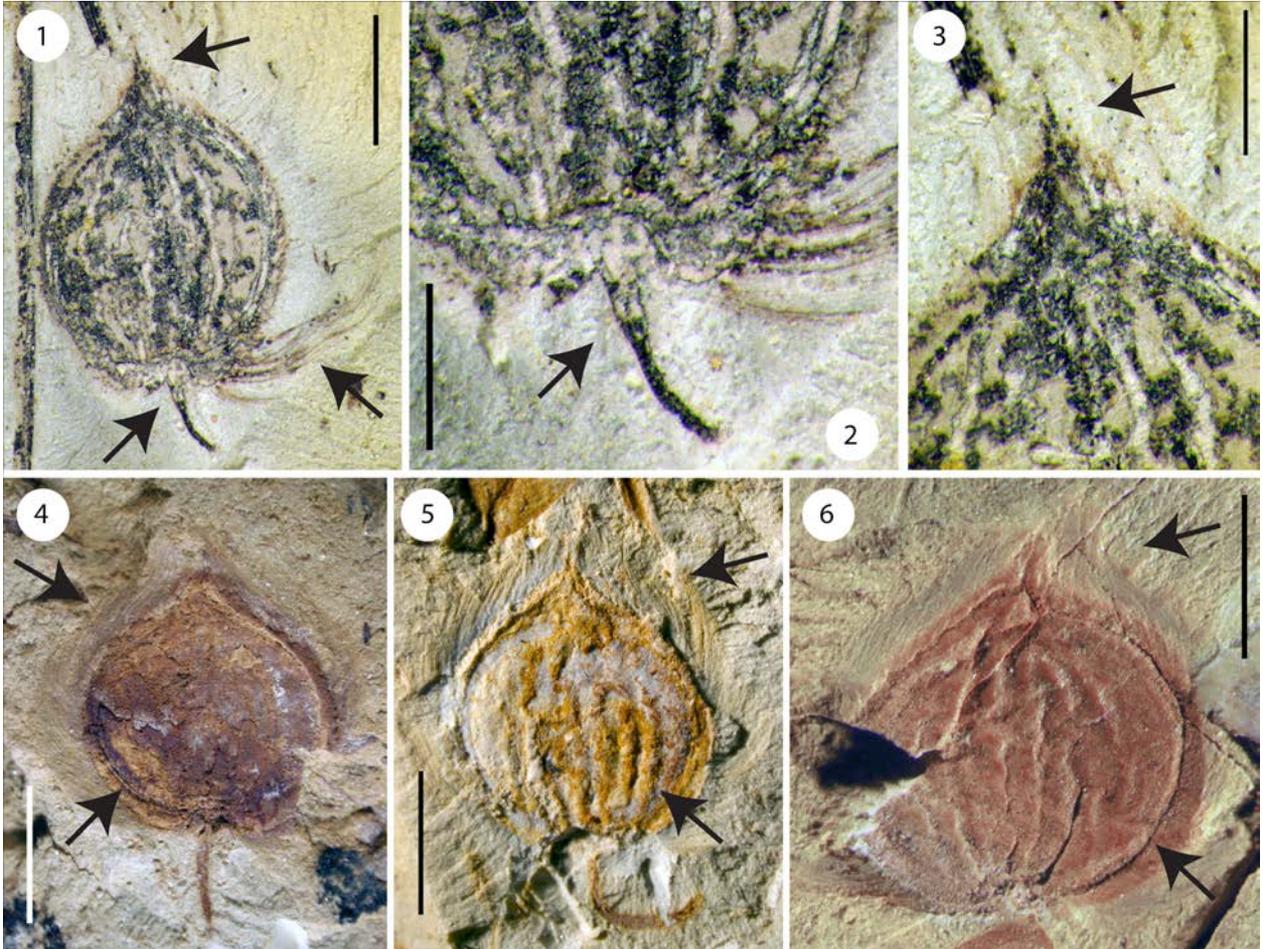


Plate 8

Carpolithus sp. 1. (FHM105-106-STRI-9958)

1. Two-winged disseminule with cordate apex and base, notice central body surrounded by lateral wings; this photo was illuminated with bulbs directed at ~45°
2. Same as 1, this photo was taken with light bulbs at very low angle, note near the apex of the fossils a crescent-shaped scar (arrow)

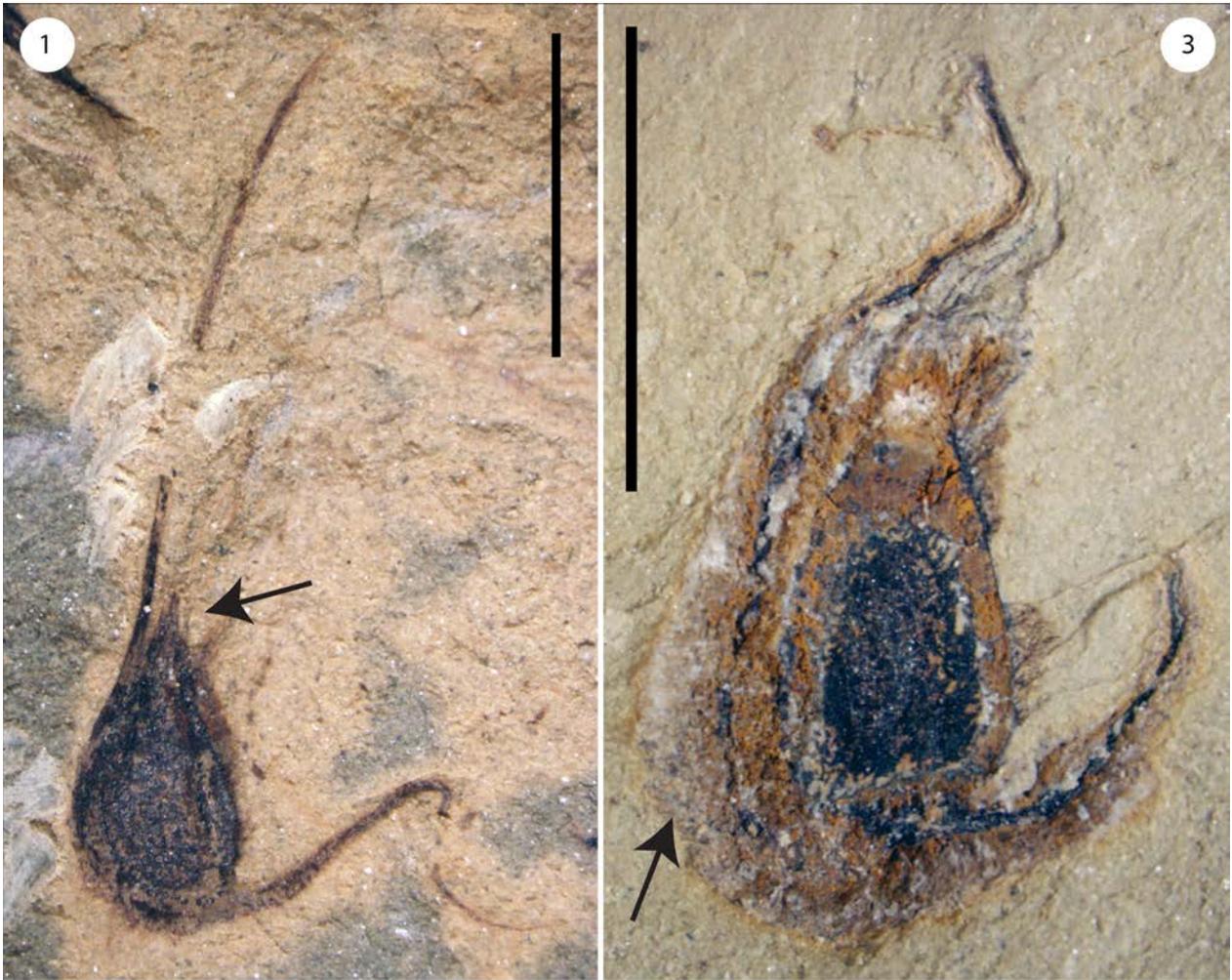
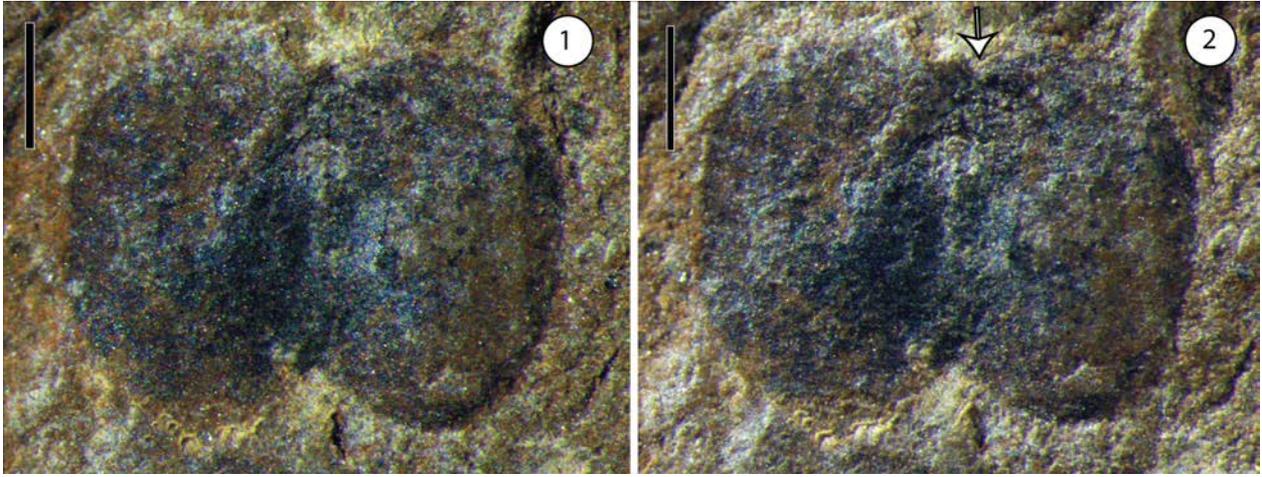
Scale bars: 1, 2 = 1 mm

Plate 9

Carpolithus sp. 2. (FH0804-STRI-34107)

1. Specimen FH0804-STRI-34107, tufted disseminule with elliptic to ovate central body, note two appendages diverging from the central body
2. Same as 1, note elliptic central body (arrow)
3. Specimen FH0804-STRI-34109, note conspicuous tuft preserved around the appendages and central body (arrow)
4. Specimen FH0804-STRI-34110, detail of central body, arrow indicates hairs

Scale bars: 1, 3, 4 = 5 mm; 2 = 2 mm



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