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## PHYTOGEOGRAPHIC HISTORY OF THE HUMIRIACEAE (PART 2)

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**Premise of research.** Humiriaceae occupy predominantly Neotropical lowland rainforests, with only a single Old World species in western Africa. Molecular divergence time estimates suggest that the family might have originated during the middle Cretaceous; however, fossil occurrences are lacking prior to the Paleocene. Here we provide new fossil evidence that expands our understanding of the paleobiogeographic history and evolution of this family.

**Methodology.** Fossil endocarps and wood were compared with extant relatives of the family. Transverse and longitudinal sections of fossil and modern fruits were studied anatomically and morphologically.

**Pivotal results.** Fruits of the new species, *Duckesia berryi* sp. n., from the Oligocene of Pacific coastal Peru (ca. 30–28.5 Ma), provide the earliest fossil evidence of *Duckesia*—the genus is now confined to Amazonia. We also document the earliest fossil fruit record for *Sacoglottis tertiaria*, from the early Oligocene (ca. 33.9–28.4 Ma) of Puerto Rico, and a new occurrence of *Vantanea cipaconsensis* fruits, from the late Miocene of Panama (ca. 9–8.5 Ma). The new fossil wood, *Humiriaceoxylon ocuensis* gen. et. sp. n., from the late Eocene (ca. 37.2–33.9 Ma) of Ocú, Panama, confirms that this family was represented by large trees anatomically consistent with the extant genera.

**Conclusions.** Humiriaceae originated in the Neotropics, with the oldest-known occurrences being fruits of *Lacunofructus cuatrecasana* and wood of *H. ocuensis* from the late Eocene of Panama. The family was generically diverse and widely distributed geographically across northern South America and Central America by the early Miocene. The new fossils also provide further evidence of regional extinctions within the Neotropics; extirpation of particular genera from Central America, the Caribbean, and coastal Peru indicate that Neogene orogenic and climatic events had an important effect on the modern-day distribution of the family.

**Keywords:** endocarps, fossils, Malpighiales, Neotropics, paleobiogeography, Panama, Peru, Puerto Rico, wood.

### Introduction

Humiriaceae are mostly woody and evergreen plants including very tall canopy trees to medium shrubs that occupy primarily the lowland rainforests of the Neotropics. A few species, mostly of the genus *Humiria*, are also found in montane areas and savannas. The family includes ~50 extant species (and a dozen subspecies) in tropical America (Cuatrecasas 1961; Sabatier 2002), plus a single species native to west coastal Africa (i.e., *Sacoglottis gabonensis*). Seven or eight living genera have been recognized in the Humiriaceae, including *Vantanea*, *Humiria*, *Duckesia*, *Hylocarpa*, *Endopleura*, *Humirium*, *Sacoglottis*, and *Schistostemon* (Cuatrecasas 1961). However, *Schistostemon* was restored to subgeneric status within *Sacoglottis* based on the similarity of their endocarps and other characters (Herrera et al. 2010). A previous phylogenetic analysis based on morphological characters

yielded two most parsimonious trees indicating *Vantanea* as sister taxon to all genera within Humiriaceae (Herrera et al. 2010). *Duckesia*, the only monotypic genus of the family, grows as a large tree in the terra firma rainforests of central Amazonia in Brazil (Cuatrecasas 1961).

The Humiriaceae have a rich fossil record exclusive to the Neotropics that includes wood, pollen, and fruits (Herrera et al. 2010). The 15 reported fossil occurrences of humiriaceous endocarps have been placed in four different genera ranging from the late Eocene to the Pleistocene of Peru, Colombia, Bolivia, Brazil, Panama, and Costa Rica (Herrera et al. 2010, 2012). Humiriaceous fossil woods were recently reported from the Miocene of Amazonia (Pons and De Franceschi 2007; Klotter et al. 2012). Pons and De Franceschi (2007) suggested an affinity of their Peruvian fossils with extant *Humirium* and *Humiria*. Previously, Stern and Eyde (1963) identified woods from a deposit of uncertain age near Ocú (Panama), including some that they identified as *Vantanea*. However, a thorough investigation of the wood anatomy of extant genera of Humiriaceae has not been published, so the question remains whether wood characters provide resolution to the generic level

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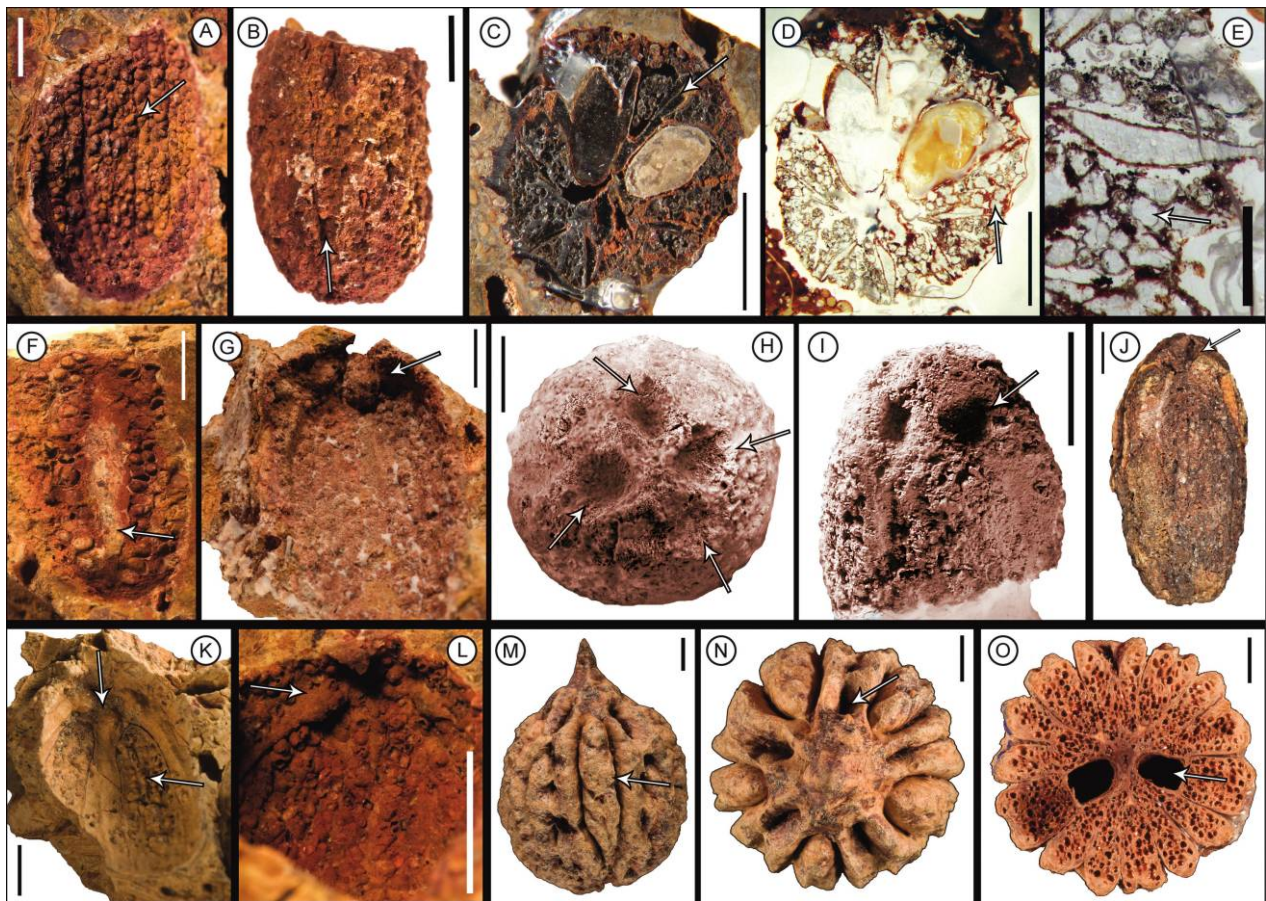
**Table 1**  
**Wood Characters of Extant and Fossil Humiriaceae**

Taxa	Growth rings	Porosity	Vessel/mm <sup>2</sup>	PP (no. bars)	Vessel-ray pitting	Vessel MTD (μm)	Fibers with bordered pits	Nonseptate fibers	Fiber wall	AAP	PAP	Parenchyma strand	Ray width	Ray cell comp.
<i>Duckesia:</i>														
<i>D. verrucosa</i> (Ducke) Cuatrec.	A	DP	6–10	S (5–9)	RB	150	Yes	Yes	Thick	A	Short wings	8–14	2	Procumbent
<i>Endopleura:</i>														
<i>E. uchi</i> (Huber) Cuatrec.	A	DP	2–6	S (6–9)	RB; pits horizontal	150–160	Yes	Yes	Thick	A-D	Scanty		2	Procumbent
<i>Humiria:</i>														
<i>H. balsamifera</i> Aubl.	A	DP	6–15	S (10–15)	DB; pits horizontal, rounded, angular	120–150	Yes	Yes	Thick	A	Scanty		1–2	Procumbent mixed
<i>H. balsamifera</i> var. <i>floribunda</i> (Mart.) Cuatrec.	A	DP	18–24	S (10–20)	DB-RB; pits horizontal, rounded, angular	110–160	Yes	Yes	Thick	A-D	Short wings		1–2	Procumbent mixed
<i>Humiria balsamifera</i> var. <i>guianensis</i> (Benth.) Cuatrec.	A	DP	15–22	S (10–20)	DB-RB; pits horizontal, rounded, angular	90–140	Yes	Yes	Thick	A-D	Short wings		1–2	Procumbent mixed
<i>Humirastrum:</i>														
<i>H. excelsum</i> (Ducke) Cuatrec.	A	DP	10–15	S (12)	DB	160–170	Yes	Yes	Thick	A	Scanty		1–2	Procumbent mixed
<i>Hylocarpa:</i>														
<i>H. heterocarpa</i> (Ducke) Cuatrec.	A	DP	10–13	S (10–13)	DB	120–140	Yes	Yes	Thick	A-D	Short wings	6–8	1–2	Procumbent mixed
<i>Sacoglottis:</i>														
<i>S. amazonica</i> Mart.	A	DP	5–10	S (10–15)	DB-RB; pits horizontal, rounded, angular	140–180	Yes	Yes	Thick	D	Short wings	6–8	1–2	Procumbent mixed

<i>S. cydonioides</i> Cuatrec.	A	DP	5–10	S (10–15)	RB	140–180	Yes	Yes	Thick	D	Short wings	6–8	1–2	Procumbent mixed	
<i>S. gabonensis</i> (Baill.) Urb.	A	DP			DB-RB; pits horizontal, rounded, angular	100–200	Yes	Yes	Thick	D	Short wings	6–8	1–2	Procumbent mixed	
<i>S. guianensis</i> Benth.	A	DP	5–10	S (10–15)	DB-RB; pits horizontal, rounded, angular	140–180	Yes	Yes	Thick	D	Short wings	6–8	1–2	Procumbent mixed	
<i>S. mattogrossensis</i> Malme	A	DP	5–10	S (10–15)	RB	140–180	Yes	Yes	Thick	D	Short wings	6–8	1–2	Procumbent mixed	
<i>Vantanea:</i>															
<i>Vantanea barbourii</i> Standl.	A	DP	U	S (5–10)	RB; pits horizontal, rounded, angular	80–110	Yes	Yes	Thick	D	Short wings	?	1–2	Procumbent mixed	
<i>V. compacta</i> (Schnizl.) Cuatrec.	A	DP	U	S (3–16)	RB	80–110	Yes	Yes	Thick	D	Short wings	?	1–2	Procumbent mixed	
<i>V. guianensis</i> Aubl.	A	DP	U	S (2–14)	RB; pits horizontal, rounded, angular	110–160	Yes	Yes	Thick	D	Short wings	?	1–2	Procumbent mixed	
<i>V. macrocarpa</i> Ducke	A	DP	U	S (5–18)	RB; pits horizontal, rounded, angular	110–130	Yes	Yes	Thick	D	Short wings	?	1–2	Procumbent mixed	
<i>V. paraensis</i> Ducke	A	DP	6–8	S (5–10)	RB	130–170	Yes	Yes	Thick	A	Short wings	8–10	1–2	Procumbent	
<i>V. parviflora</i> Lam.	A	DP	6–8	S (5–10)	RB	130–170	Yes	Yes	Thick	A	Short wings	8–10	1–2	Procumbent	
<i>Humiriaceoxylon</i> <i>ocuensis</i> <sup>a</sup>	A	DP	4–12	S (5–13)	DB	102–145	Yes	Yes	Thick	A-D	Scanty		1–2	Procumbent	

Note. A, absent; AAP, apotracheal axial parenchyma; comp., composition; D, diffuse; DB, distinct borders; DP, diffuse porous; MTD, mean tangential diameter; PAP, paratracheal axial parenchyma; PP, perforation plates; RB, reduced borders; S, scalariform.

<sup>a</sup> Fossil taxon.



**Fig. 1** Extinct *Duckesia berryi* Herrera sp. n. (A–L) and extant *Duckesia verrucosa* Cuatr (M–O). A–E, Holotype (UF 603-54944). A, Lateral view of counterpart of endocarp mold; arrow indicates boundary of germination valve. B, Permineralized endocarp; arrow shows delimitation of germination valve. C, Transverse section from B; note two locules and bilobed septa (arrow). D, Peel from C; arrow shows abundant lacunae, transmitted light. E, Detail from D; arrow indicates one of the numerous lacunae. F, Paratype (UF 603-54937); arrow shows lateral view of locule; note abundant lacunae in the endocarp layer. G, Paratype (UF 603-56001), fossil mold of endocarp; arrow shows four radially arranged intrusions into the endocarp layer. These structures are interpreted as evidence of apical pores (foramina). H, Apical view of silicone internal cast from G; note radially arranged foramina (arrows). I, Detail of lateral view of silicone internal cast from G; note foramina (arrow). J, Paratype (USNM 317942), apical view of endocarp; arrow shows apical foramen. K, Paratype (UF 603-54936), fossil mold; upper arrow indicates foramina, lower arrow germination valve. L, Paratype (UF 603-54947), fossil mold; arrow shows foramina. M, *D. verrucosa* (US 2517928), lateral view of extant endocarp, showing prominent apex and germination valve (arrow). N, Apical view of endocarp; arrow denotes one of the five apical foramina. O, Transverse section at equator of endocarp, showing two well-developed locules (arrow); note bilobed septa and abundant lacunae. Scale bars = 5 mm in A–D, F–O; 2 mm in E.

in this family. A comparative survey of extant and fossil woods of Humiriaceae is crucial for the understanding of the evolution of the family.

Since our earlier review of the fossil record of Humiriaceae (Herrera et al. 2010) based largely on Berry's collections at the Smithsonian (USNM, Washington, DC), we have relocated and made new collections from Berry's (1927, 1929a, 1929b) original Belén plant locality, leading to a revised assessment of the geologic age and taxonomic composition (early Oligocene age rather than Eocene; Manchester et al. 2012). The larger collection of Belén specimens now available permits a fuller description of *Vantanea cipaconensis* (Berry) Herrera and leads us to recognize a second genus of Humiriaceae, which constitutes the first-known fossil record of the extant genus *Duckesia*. In addition, we present a new occurrence of

*Vantanea* from the late Miocene Gatun Formation of Panama and the earliest occurrence of the fossil taxon *Sacoglottis tertiaria* (Berry) Herrera from the early Oligocene of Puerto Rico. Finally, we reviewed the wood anatomy of the eight extant genera and the fossil woods of Humiriaceae. The review and new reports of humiriaceous fossils in this study suggest that the family was more widely distributed across the Neotropics in the Oligocene than previously recognized.

### Material and Methods

We collected permineralized fruits from the Belén locality of Berry (1927, 1929a, 1929b) in the desert coastal area of northwestern Peru (Manchester et al. 2012). The fossiliferous strata are located ~13 mi south of Talara, Piura Region, ~0.4 mi



east of the old road that connects Talara and the city of Piura, outcropping at the base of some hills rising above the local plane of Quaternary saline deposits (locality 602: lat. 4°44.946'S, long. 81°14.137'W; locality 603: lat. 4°44.966'S, long. 81°14.219'W). The age of the Belén strata has been recently revised based on a diatom assemblage recovered from the fossil-fruit-bearing sediments (Manchester et al. 2012); the new data suggest a latest early Oligocene age (ca. 30–28.5 Ma). More than 150 new specimens of humiriaceous endocarps and isolated seeds were collected from Belén. They are preserved variously as permineralizations in both calcium carbonate and silica and sometimes as sedimentary casts and molds. Transverse and longitudinal sections were cut through the equatorial plane of permineralized endocarps, and acetate peels of the internal anatomy were prepared using the technique of Joy et al. (1956). Internal casts of the endocarp molds were prepared with silicone rubber (Silicones, GI-1220), initially under vacuum, and cured for about 10 d.

An additional endocarp of Humiriaceae comes from the early Oligocene (ca. 33.9–28.4 Ma) San Sebastian Formation of Puerto Rico. The fossil locality is found at the Río Guatemala, near the town of San Sebastián (lat. 18°21'24.6"N, long. 66°59'41.8"W). The plant fossil layer is ~1.5 m above the type locality of the gavialoid crocodylian *Aktiogavialis puertoricensis* (Vélez-Juarbe et al. 2007). The San Sebastián stratigraphic sequence near the plant locality is composed of soils interbedded with marine mudstones and siltstones grading up into deltaic sands (Vélez-Juarbe et al. 2007, 2014).

Two endocarp specimens were recovered from the Gatun Formation, in the new excavations of the Panama Canal at the Gatun Third Lock locality (nos. 290372 and 470045, Colon State, lat. 9°26.847'N, long. 79°91.235'W). The stratigraphic sequence of the Gatun, which was deposited in shallow marine conditions (Coates 1996; Collins et al 1996; Hendy 2013), ranges from 12 to 7.8 Ma (Hendy 2013), but the specimens are from the middle part of the formation, dated as ca. 8.5–9 Ma (Hendy 2013).

Humiriaceous fossil wood from Panama was first reported by Stern and Eyde (1963). The single specimen was collected by John E. Ebinger in 1961, 2 mi northwest of Ocu, Los Santos State, in the Azuero Peninsula. We revisited Ocu and collected abundant large silicified wood fragments. The wood specimens are not found in situ but instead appeared scattered in pastures, without evidence of the parental rock (lat. 7°55.476'N, long. 80°47.959'W; UF locality 606). The abundance of the fossil wood chunks near Ocu is remarkable, and the local people use them as decorative building stones. Near Ocu we found siltstones from a small quarry (lat. 7°54.790'N, long. 80°47.085'W; UF locality 607). This new locality yielded impressions of elliptical fruits resembling Humiriaceae and fragments of carbonized wood. Fossil invertebrates from the siltstones indicate a late Eocene age for these sediments (A. Hendy, personal communication). Recent mapping of the north-central part of the Azuero Peninsula suggests that sediments exposed near the town of Ocu and surrounding areas belong to the late Eocene–late Oligocene Tonosi Formation (Buchs et al. 2011). Based on our observations near Ocu and the recent geological mapping, we tentatively consider the fossil wood of Stern and Eyde (1963) to be Late Eocene (ca. 37.2–33.9 Ma) in age.

We compared the fossils with collections of extant Humiriaceae fruits and wood in the US National Herbarium (US) at the Smithsonian Institution in Washington, DC; the Smithsonian Tropical Research Institute (STRI) in Panama; the University of Florida Herbarium (FLAS) in Gainesville, Florida; the Missouri Botanical Garden Herbarium (MO); and the US National Arboretum Herbarium (BARC). The wood observations were supplemented by consideration of available descriptions and images (Metcalfe and Chalk 1950; D tienne and Jacquet 1983; Araujo and Mattos-Filho 1985; Miller and D tienne 2001; InsideWood 2004–; Wheeler 2011). Descriptions from table 1 are based entirely on mature samples, but we also examined small-diameter stems of *Endopleura*, *Humiria*, and *Sacoglottis*. *Hylocarpa* and fossil wood sections were prepared by standard petrographic grinding methods with a Buehler thin-sectioning machine. The specimens were embedded with Devcon epoxy and 2 Ton Crystal Clear Epoxy resin prior to sectioning.

## Results

### Systematics of Fossil Endocarps

#### *Humiriaceae* Juss

#### *Duckesia* Cuatrecasas

#### *Duckesia berryi* Herrera, Manchester, V lez-Juarbe et Jaramillo sp. n.

**Diagnosis.** Endocarp ellipsoidal. Septa and valves five, radially arranged. Septa strongly bilobed. Germination valves long and conspicuous. Seeds one per locule. Four to five apical foramina present. Wall cavities abundant.

**Holotype.** UF 603-54944. Figure 1A–1E.

**Paratypes.** USNM 317942 (Berry 1929a, plate I, fig. 14, refigured in fig. 1J); UF 603-54936; 603-54937; 603-54947; 603-56001 (fig. 1F, 1G, 1K, 1L).

**Occurrence and age.** The fossiliferous strata located ~13 mi south of Talara, locality 602: lat. 4°44.946'S, long. 81°14.137'W; locality 603: lat. 4°44.966'S, long. 81°14.219'W. Latest early Oligocene age (~30–28.5 Ma).

**Description.** Shape ellipsoidal (fig. 1B, 1F, 1J); length ~17 to ~35 mm, width ~15 to ~20 mm ( $n = 12$ ). Septa and valves five, alternating with one another, radially arranged (fig. 1C, 1D). Septa strongly bilobed and enlarging outward, as seen in transverse section (fig. 1C, 1D). Germination valves conspicuous, long, lingulate, without a median furrow on the surface, extending lengthwise but never reaching the top or the base of the endocarp, sometimes observed in the internal molds as longitudinal lines (fig. 1A, 1K). Placentation axile. Seeds one per locule, ~15 mm in length (measured in three specimens). Up to two fertile seminal cavities per fruit; more or less pentagonal as viewed in transverse section, from ~4 to 5 mm in length and ~1.7–2.3 mm wide (fig. 1C, 1D). Endocarp with four or five apical foramina (fig. 1G–1L); these are observed in three molds as intruding bulbs that are located in between the valves near the apex of the endocarp (fig. 1G, 1K, 1L); silicone rubber molds prepared for three specimens show the presence of four apical foramina; although a portion is missing,

a fifth foramen is inferred from the symmetry (fig. 1I, 1J). Rounded cavities abundant in the endocarp wall and septa, ranging from ~0.3 to ~1.3 mm in diameter (fig. 1A–1F). Vascular strand present along the central axis of the endocarp.

**Comments.** Most of the specimens are internal molds of the endocarps (fig. 1G, 1K, 1L), but in a few cases the endocarps have been permineralized, with anatomical preservation of tissues (fig. 1A–1E).

**Derivation of specific epithet.** In honor of the paleobotanist Edward W. Berry who reported and studied the Belén flora.

**Systematic affinity.** Fruits of Humiriaceae have woody endocarps with a central vascular axis, up to 10 carpels, and one or two seeds per locule and are easily recognizable by their distinctive dorsal germination valves (Herrera et al. 2010). No other family among flowering plants presents this set of characters. *Duckesia berryi* preserves the combination of characters diagnostic for Humiriaceae, along with additional characters supporting the generic assignment.

*Duckesia* is a monotypic genus now native to the Amazon region of Brazil (Cuatrecasas 1961), with drupes distinguished by their corrugated endocarp, strongly bilobed septa (fig. 1M–1O), five long germination valves, five apical foramina that alternate with the valves, and abundant and small cavities in the septa and endocarp wall (fig. 1M–1O). The new fossil species preserves the main characters diagnostic for extant *Duckesia*. Two differences are the prominent apex and larger endocarps (up to ~7 cm in length) observed in living *Duckesia verrucosa*.

Among Humiriaceae, *Humiriastrum*, *Endopleura*, and *Humiria* also have apical foramina (Herrera et al. 2010); however, they are distinguished from *Duckesia* by additional characters. In *Humiria*, the endocarps usually do not exceed ~1.6 cm in length, have two seeds per locule rather than one, and lack cavities. *Endopleura* also has bilobed septa, but they appear much thinner, giving a 10-radiate asterisk appearance in transverse section (Herrera et al. 2010), and the endocarps lack internal cavities. *Humiriastrum*, which also has similar endocarp wall cavities, shows the closest similarity with *Duckesia*; however, it has very short germination valves that are located near the apex, the septa do not appear bilobed, and the endocarp tissue is strongly fibrous (Herrera et al. 2010).

*Duckesia berryi* endocarps also resemble, superficially, those of the *Sacoglottis-Schistostemon* clade (Herrera et al. 2010). However, the internal cavities of the endocarp in that clade are twice as big as those in *Duckesia*, their endocarps lack apical foramina, and their germination valves occupy most of the locule area, leaving the septa as thin exterior lines in the endocarp.

The only previously described fossil species that resembles *D. berryi* is *Sacoglottis tertiaria* (Berry) Herrera, a widespread species known from the middle Miocene of Colombia and Panama; the Pliocene-Pleistocene of Bolivia, Costa Rica, and Colombia (Herrera et al. 2010); and the Oligocene of Puerto Rico (see below). Their endocarps are similar in the presence of abundant cavities; however, *S. tertiaria*, like modern species of *Sacoglottis*, lacks apical foramina and the bilobed septa, and the valves are much wider than in *D. berryi*.

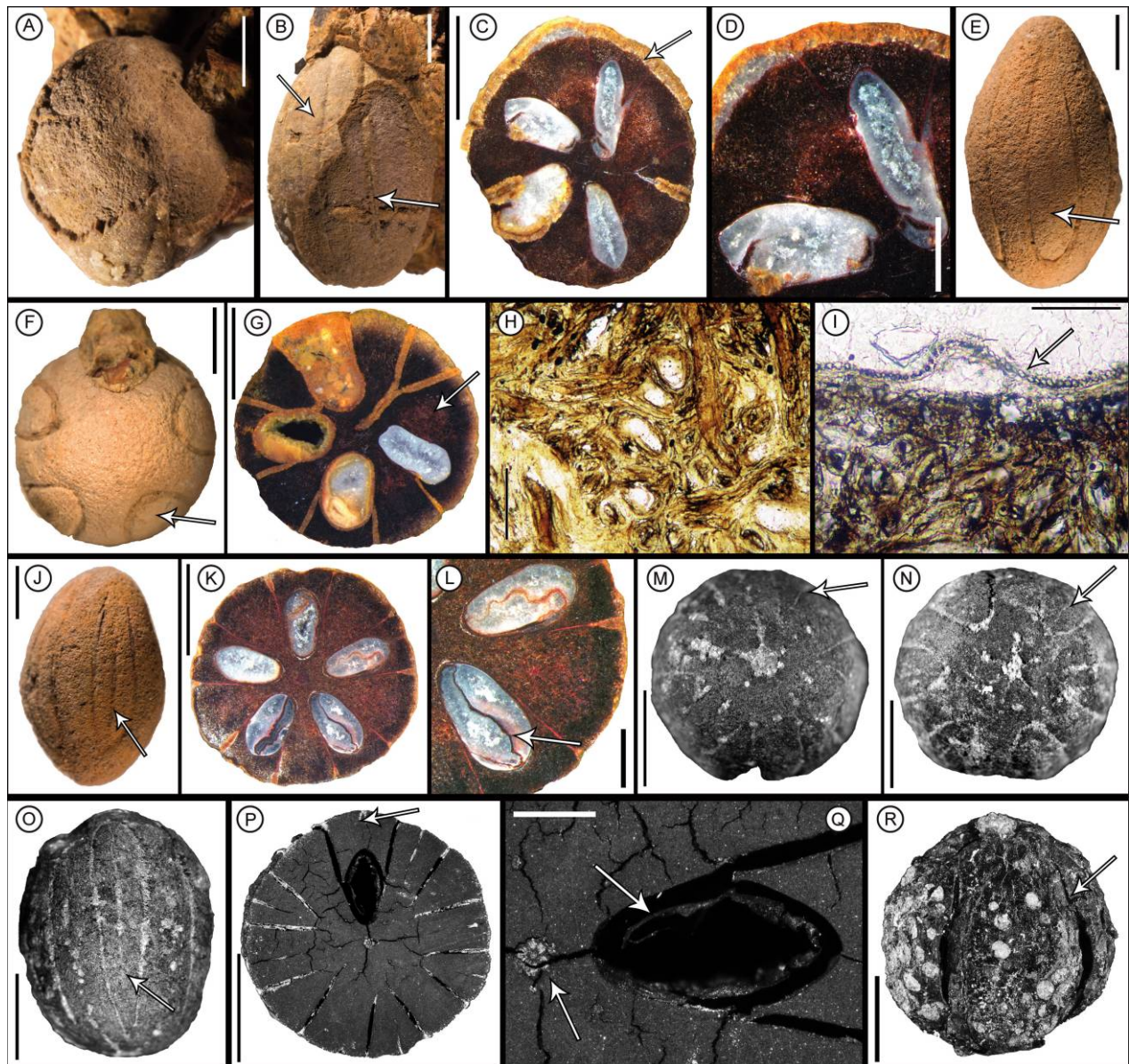
Berry (1927) reported abundant endocarp specimens of Humiriaceae from Belén. Initially, those endocarps were classified

as *Sacoglottis cipaconensis*, but after collecting additional specimens, he gave them subspecific status, *S. cipaconensis* subsp. *peruvianus* (Berry 1929a). The species was more recently transferred to the extant genus *Vantanea* (Herrera et al. 2010), but we now recognize that one of the specimens photographed by Berry (1929a; plate I, fig. 14; USNM 327942, refigured in fig. 1J) is distinguished from the other specimens by a larger size and shows cavities, apical foramina, and valves, indicating that this specimen belongs to *D. berryi*. Among the two species of Humiriaceous fruits found in the Belén deposits, the *D. berryi* specimens are more poorly preserved, usually not well permineralized, and represented by molds of the endocarp with casts of the wall cavities rather than fully permineralized fruits. The *Vantanea* specimens are usually smaller but commonly are permineralized, with excellent preservation of anatomical details (fig. 2). These differences in preservation between the two Belén taxa could be explained by disparity of surface porosity of the original endocarps.

#### **Revisions and Additions to the Distribution, Age, and Morphological Characterization of *Vantanea cipaconensis* (Berry) Herrera and *Sacoglottis tertiaria* (Berry) Herrera**

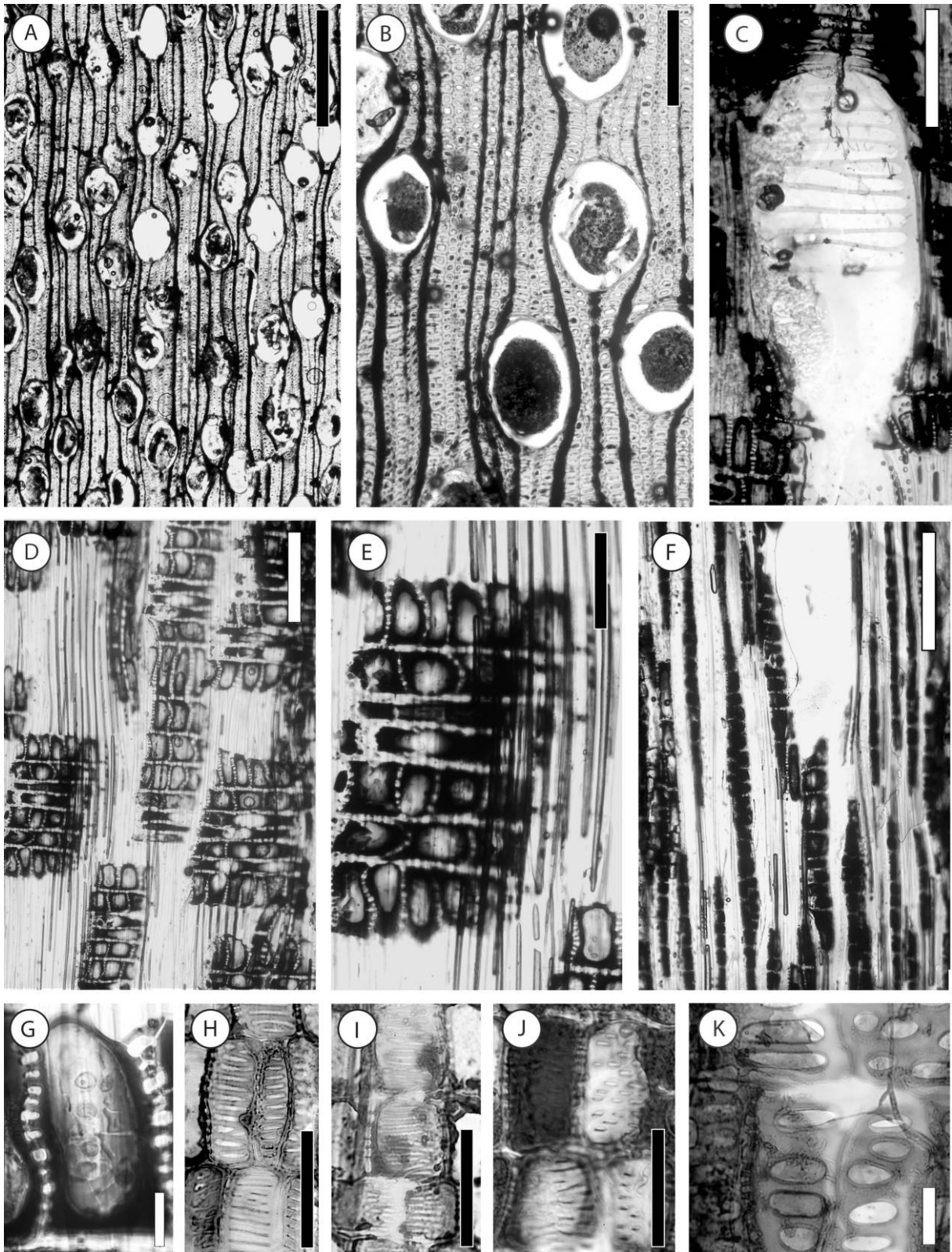
*Vantanea cipaconensis* is the most abundant (>100 specimens) fossil species from the two recently recollected localities at Belén (fig. 2A–2L; Manchester et al. 2012). The new collection allowed us to describe its morphological variation and anatomical features. The endocarps range from ~7 to ~30 mm in length and from ~4 to ~15 mm in width. The shape of the endocarps is usually ellipsoidal, although ovoidal endocarps are also present (fig. 2B, 2E, 2J). The number of valves varies from two to four for the smallest specimens and increases to five or six in the largest specimens. Endocarp length range shows a normal distribution, supporting the treatment as a single fossil species. We did not find any difference in cell size and shape for small and large endocarps. The endocarp wall and septa are composed of elongate fibers up to 10  $\mu\text{m}$  wide (fig. 2D, 2H, 2I, 2L). These cells, seen in transverse and longitudinal sections, form a twisted and messy network with very high density, giving the endocarps a woody-like texture (fig. 2D, 2L). This contrasts with most of the endocarps of *Duckesia berryi*, which do not preserve evidence of the endocarp tissue (except for three specimens). Cells of the seed coat are isodiametric and less than 1  $\mu\text{m}$  in diameter as measured in transverse section (fig. 2I); the seed coat varies between ~5 and 10  $\mu\text{m}$  thick. Transverse and longitudinal sections of the specimens reveal the presence of only one seed cavity for smaller endocarps (<10 mm); however, for larger endocarps, no correlation was found between size and the number of locules, ranging from two to five (fig. 2A, 2F, 2K). Two cotyledons are observed in the seed, divided by a sinuous median plane (fig. 2D, 2L). One specimen (fig. 2A–2D) was found preserving a thin external bilayer, interpreted as an infilling of the space left by the mesocarp (~0.5 mm wide) and the exocarp (~0.3 mm wide); this is the only fossil specimen of Humiriaceae so far recovered that preserves evidence of the outer layers of the pericarp. Endocarps of *V. cipaconensis* from Belén have been referred to in the literature as early to middle Eocene,





**Fig. 2** *Vantanea cipaconensis* (Berry) Herrera (Peru, A–L; Panama, M–Q) and *Sacoglottis tertiaria* (Berry) Herrera (Puerto Rico, R). A–L, UF 603-54950. A, Apical view of endocarp. B, Lateral view of fruit; upper arrow shows evidence of mesocarp, lower arrow germination valve. C, Transverse section from B, showing four well radially arranged locules; arrow indicates layer of infilling of the space left by the mesocarp and the exocarp. D, Close-up from C. E–I, UF 603-54932. E, Lateral view of elliptic endocarp; arrow shows external germination valve. F, Apical view of endocarp; arrow shows one of the five germination valves. G, Transverse section from E; notice three well-developed locules; upper valve is missing and now is filled with sediment; arrow shows detail from H. H, Acetate peel from G; notice elongate and twisted fibers forming a messy network. I, Acetate peel from G; notice isodiametric cells of the seed coat (arrow). J–L, UF 603-56356. J, Lateral view of endocarp; arrow shows bipartition of germination valve. K, Transverse section from J, showing five radially arranged locules, germination valves, and central vascular bundle. L, Close-up from K; arrow shows a seed coat membrane that has partially shrunk away from the locule. M–Q, UF 19356-059033. M, Basal view of endocarp; arrow shows germination valve. N, Apical view of endocarp; arrow shows germination valve. O, Lateral view of endocarp; arrow shows bipartition of germination valve. P, Equatorial transverse section from O; arrow shows valve. Q, Close-up from P; left arrow shows vascular bundle, right arrow remnants of seed. R, UF 19355-058713. Arrow shows edge of germination valve; notice conspicuous lacunae. Scale bars = 5 mm in A–C, E–G, J, K, M–P; 2 mm in D, L; 200  $\mu$ m in H; 100  $\mu$ m in I; 1 mm in Q; and 1 cm in R.





~34–50 Ma (Cuatrecasas 1961; Romero 1986; Burnham and Johnson 2004; Herrera et al. 2010), but are now considered latest early Oligocene age (~30–28.5 Ma) instead (Manchester et al. 2012).

Charcoalified endocarps (UF 19356-059033; fig. 2M–2Q) found recently in the late Miocene Gatun Formation are indistinguishable from those of *V. cipaconensis*. They range from ~14 to ~14.6 mm in length and from ~10 to ~11.4 mm in width. The shape of the endocarps is ellipsoidal, with six radially arranged conspicuous valves (fig. 2M, 2N, 2O). These valves have a median furrow on the surface, are lingulate in shape, and never reach the top or the base of the endocarp (fig. 2O). Septa enlarging outward, as seen in cross section (fig. 2P). Seeds one per locule, thin and lacking endosperm tissue, as observed in modern *Vantanea* endocarps (Herrera et al. 2010). One seminal cavity per fruit, approximately pentagonal in shape as viewed in cross section (fig. 2Q). Cavities and foramina absent. Vascular strand present along the central axis of the endocarp.

We also found a new record of *S. tertiaria* (Berry) Herrera from the early Oligocene of Puerto Rico (fig. 2R). The single specimen (UF 19355-058713) is a coalified endocarp with evidence of taphonomic lateral compression. The specimen is about 30 mm long and 29 mm wide, with five broad valves that appear to have split along the thin septa as a result of compression (fig. 2R). A central vascular strand is visible at one end of the endocarp. Abundant cavities ranging from 1 to 2 mm in diameter occur in the endocarp wall, most of which are filled with sediment.

### Overview of Extant and Fossil Wood of Humiriaceae

Our overview of wood sections and literature on the anatomy of seven extant genera of Humiriaceae draws on previous descriptions of the general morphology of the family (e.g., Metcalfe and Chalk 1950; Détienne and Jacquet 1983; Araujo and Mattos-Filho 1985; Miller and Détienne 2001; table 1). Wood of Humiriaceae is characterized by the lack of distinct growth ring boundaries; diffuse porosity; vessels exclusively solitary (rarely arranged in a radial to diagonal pattern; e.g., *Humiria*, *Sacoglottis*, *Vantanea*); scalariform perforation plates, usually with less than 20 bars in mature samples (immature wood frequently with up to 40 bars per perforation plate); alternate intervessel pits (rarely opposite, e.g., *Humiria*, *Humiriastrum*), usually 4 to >10  $\mu\text{m}$  in size; vessel-ray pitting with reduced borders of large and various shapes (predominantly in *Duckesia*, *Endopleura*, and *Vantanea*) to distinct (predominantly in *Humiriastrum* and *Hylocarpa*). *Humiria*

and *Sacoglottis* show a combination of reduced borders and distinct vessel-ray pits, fibers very thick walled, nonseptate, with distinctly bordered pits on both radial and tangential walls, apotracheal parenchyma absent/diffuse to diffuse-in-aggregates, paratracheal parenchyma from scanty to short winged, rays 1–2 (rarely 3) seriate, heterocellular with procumbent cells in the body of the ray with two to usually more than four rows of upright/square marginal cells, and abundant prismatic crystals present in chambered axial parenchyma in both upright and procumbent rays cells (fig. 3).

The combination of these characters facilitates recognition of humiriaceous wood within angiosperms (Metcalfe and Chalk 1950; Détienne and Jacquet 1983; Araujo and Mattos-Filho 1985; Miller and Détienne 2001; table 1). However, at the generic level, wood characters appear to be highly similar across all genera of the family. This suggests that reasonably well-preserved wood of Humiriaceae can be identified in the fossil record, but assignment of a fossil wood to a particular extant genus should be avoided, as current information does not indicate that any one genus has a unique combination of characters. Differences in type of vessel-ray parenchyma pitting (fig. 3G–3K; table 1) have potential for distinguishing between some genera (i.e., reduced borders: *Duckesia*, *Endopleura*, and *Vantanea*; distinct borders: *Humiriastrum* and *Hylocarpa*). However, additional samples need to be examined to determine whether these characters are exclusive to these genera or whether they appear as a combination of both vessel-ray pit types, as in *Humiria* and *Sacoglottis*.

Stern and Eyde (1963) reported a humiriaceous fossil wood from Ocu, Panama, now considered to be late Eocene, which they attributed to extant *Vantanea*. Based on the examination of the original thin sections prepared by those authors and additional sections made from recently collected specimens, we confirm the humiriaceous affinity. However, Stern and Eyde (1963) did not describe the wood anatomy and provided only an image of a cross section without tangential and radial views, and they did not provide detailed justification for the generic identification as *Vantanea*. Below we present a taxonomic description.

### *Humiriaceae* Juss

Humiriaceoxylon Herrera, Manchester,  
Vélez-Juarbe et Jaramillo gen. n.

*Generic diagnosis.* Growth ring boundaries indistinct; wood diffuse-porous; vessels solitary; perforation plates exclusively scalariform; intervessel pitting alternate; rays 1–2 se-

**Fig. 3** Wood of extant Humiriaceae. A–G, *Hylocarpa heterocarpa* (Ducke) Cuatrec. (12034, M. Wood Collection, Brazil). A, Vessels exclusively solitary. B, Fibers very thick walled, apotracheal parenchyma diffuse, scanty paratracheal parenchyma. C, Scalariform perforation plate. D, Heterocellular ray, procumbent body cells with >4 rows of upright/square marginal cells. E, Same as D. F, Narrow rays, mostly 1–(2) seriate; nonseptate fibers. G, Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape. H, *Endopleura uchi* (Huber) Cuatrec. (MO9994, immature sample). Vessel-ray pits with much reduced borders, pits horizontal (scalariform, gash-like). I, *Humiria balsamifera* Aubl (MO1164329, Coll. AC Smith, 2423, Guyana, immature sample). Vessel-ray pits with much reduced borders, pits horizontal (scalariform, gash-like) to rounded. J, *Sacoglottis amazonica* Mart. (MO1264039, Coll. A. Ducke, 1174, Brazil, immature sample). Vessel-ray pits with much reduced borders, pits horizontal (scalariform, gash-like) to rounded. K, *Vantanea barbourii* Standl. (MO9995). Vessel-ray pits with much reduced borders, pits horizontal (scalariform, gash-like) to rounded. A, B, Cross section; C–E, G–K, radial section; F, tangential section. Scale bars = 400  $\mu\text{m}$  in A, D–F; 200  $\mu\text{m}$  in B, C; 50  $\mu\text{m}$  in G–K.



riate, heterocellular, and consisting mainly of procumbent body cells; fibers nonseptate.

*Derivation of generic name.* From the Humiriaceae family and the Greek root “xyl” for “wood.”

*Type.* *Humiriaceoxylon ocuensis* Herrera, Manchester, Vélez-Juarbe et Jaramillo sp. n.

*Diagnosis.* Vessel-ray pits with distinct borders; axial parenchyma apotracheal absent to diffuse, paratracheal scanty.

*Holotype.* USNM 312574. Figure 4.

*Paratype.* UF 604-54280.

*Occurrence and age of paratype.* Ocu, Azuero Peninsula. Locality UF 606 (lat. 7°55.476'N, long. 80°47.959'W). Late Eocene (ca. 37.2–33.9 Ma).

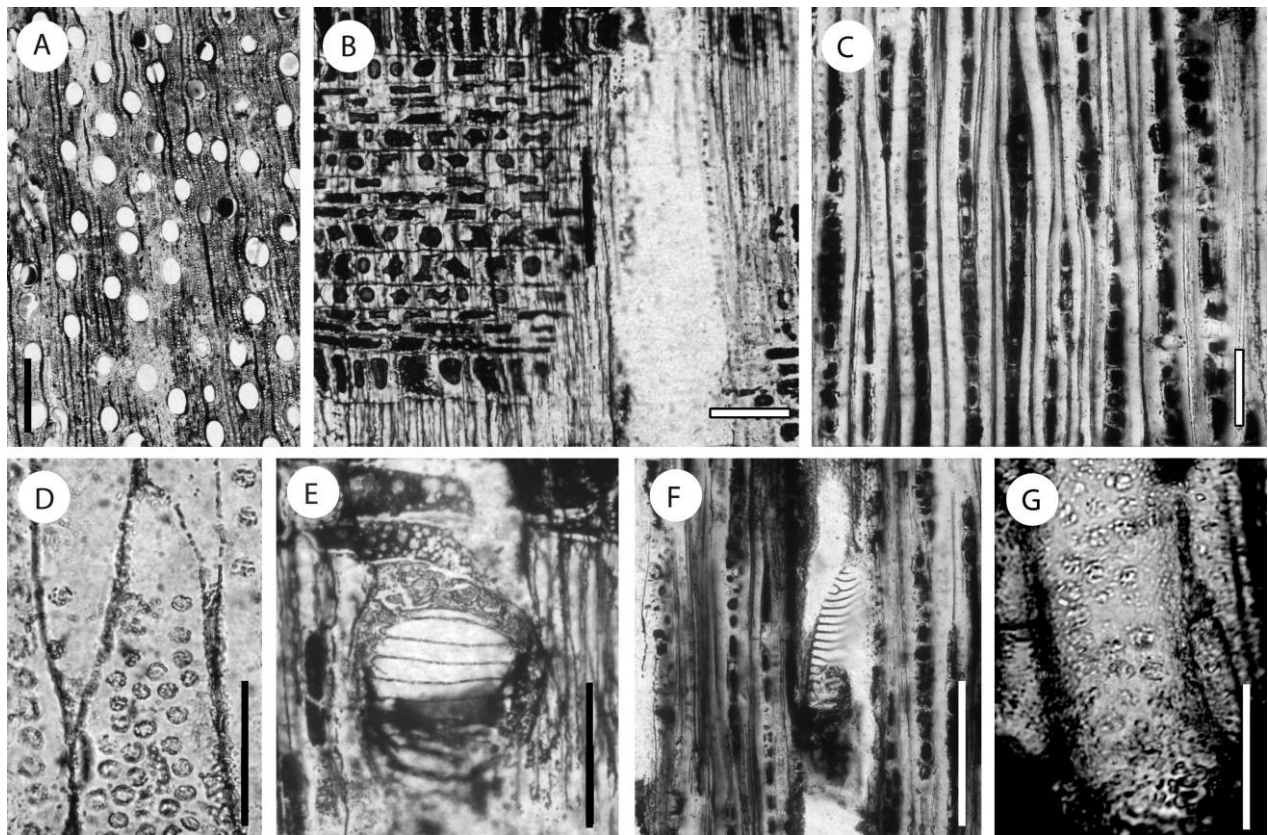
*Description.* Growth ring boundaries indistinct. Wood diffuse-porous. Vessels exclusively solitary (>90%; fig. 4A), predominantly elliptic to circular in outline, vessel diameter range of 102–145  $\mu\text{m}$ , vessels 4–12/mm<sup>2</sup>, perforation plates exclusively scalariform with 5–13 bars (fig. 4E, 4F). Intervessel pitting alternate (8–15  $\mu\text{m}$  in size; fig. 4D). Vessel-ray parenchyma pits with distinct borders, similar to intervessel pits in size and shape (fig. 4G). Axial parenchyma apotracheal absent to diffuse, paratracheal scanty. Rays commonly 1(–2) seriate

(fig. 4C, 4F), 4–12/mm, heterocellular, not storied, and consisting of procumbent body cells and more than four rows of upright/square marginal cells (fig. 4B). Fibers nonseptate, very thick walled, with distinctly bordered pits (fig. 4C), common in radial and tangential walls.

*Derivation of specific epithet.* From Ocu, Panama.

*Comments.* Based on our overview of the extant wood in the family, we place the Ocu material in a new fossil genus for wood with anatomy corresponding to Humiriaceae including vessel-ray pits with distinct borders.

Other humiriaceous fossil woods have been reported only from the Amazonian basin (Jupiassú 1970; Pons and De Franceschi 2007; Kloster et al. 2012). Jupiassú (1970) reported fragments of silicified wood from the Pará State (Irituia locality) from Brazil of Cenozoic age. This locality could be assigned to the early Miocene Pirabas Formation based on its geographic position and abundant marine fossils reported from the same region (de Araújo-Távora et al. 2010). The Pará specimens were placed as a species of the genus *Sacoglottis* (i.e., *Sacoglottis paraensis*); however, a more detailed description of the fossil material will be required to support its generic placement. The additional records from the middle Miocene



**Fig. 4** *Humiriaceoxylon ocuensis* Herrera, Manchester, Vélez-Juarbe et Jaramillo sp. n. Holotype USNM 312574. A, Growth rings absent, wood diffuse-porous, vessels exclusively solitary, apotracheal parenchyma diffuse. B, Heterocellular ray, procumbent body cells with >4 rows of upright/square marginal cells. C, Narrow rays, mostly 1 seriate; nonseptate fibers with distinctly bordered pits on their tangential walls. D, Alternate intervessel pits located toward the ends of the vessel elements. E, Scalariform perforation plate. F, Scalariform perforation plate. G, Vessel-ray pits with distinct borders. A, Cross section; B, E, G, radial section; C, D, F, tangential section. Scale bars = 400  $\mu\text{m}$  in A, B; 200  $\mu\text{m}$  in C, F; 100  $\mu\text{m}$  in D, E; 50  $\mu\text{m}$  in G.



Pebas/Solimoes Formation of Peru (Pons and De Franceschi 2007) and Brazil (Kloster et al. 2012) also coincide with Humiriaceae (although no photos were published). From these two records, the vessel-ray pitting was described only from Kloster et al. (2012; alternate with distinct borders and similar to intervessel pits in size and shape), and it is comparable to that of *Humiriaceoxylon*.

### Discussion

The sedimentology of the Oligocene Belén locality of Peru indicates that the fossils of *Duckesia berryi* and *Vantanea cipaconensis* were deposited in a coastal plain–lagoon environment (Olsson 1931; Manchester et al. 2012). The occurrence of these two fossil taxa in the Pacific coast of Peru indicates a wider distribution for Humiriaceae during the Oligocene; now the family is absent from the western part of the central Andes. Today, the Belén area has very low rainfall (<50 mm/yr), and the vegetation is typical of arid coastal environments. The genera *Vantanea* and *Duckesia* are mainly confined to moist tropical forests (rainfall >2300 mm/yr; Cuatrecasas 1961), and the latter genus is now restricted to the central-western lowland rainforests of Amazonia. The humiriaceous fossils and other families identified from the Belén flora (e.g., Annonaceae, Arecaceae, Cucurbitaceae, Fabaceae, Euphorbiaceae, Icacinaceae, Rutaceae, Sapindaceae, and Vitaceae) suggest the presence of a humid and stratified forest canopy during the Oligocene in western Peru. It is likely that the rise of the Andes produced a strong rain shadow on the western Central Andes, together with the aridifying effect of the Humboldt Current and changes in the position and width of the Intertropical Convergence Zone, caused the extinction of the Pacific humid forests in western Peru at some point during the late Neogene (Berry 1929a, 1929b; Manchester et al. 2012).

*Sacoglottis tertiaria* from the early Oligocene of Puerto Rico is the earliest record for this fossil species and the first record of Humiriaceae in the Caribbean Islands. The coalified fossil was collected from deltaic sediments of the San Sebastian Formation. Lignitic-coal layers and abundant plant macrofossils (fruits, seeds, and leaves) and microfossils have been previously reported from the Oligocene San Sebastian Formation (Hollick 1928; Graham and Jarzen 1969; Graham 1996). Some of the macrofossils and microfossils identified at the family/order level include Cycadaceae, Arecaceae, Fabaceae, Juglandaceae, Malvaceae, Melastomataceae, and Zingiberales, among many others. Graham and Jarzen (1969) identified 44 genera based on pollen grains, and only 31 presently grow in Puerto Rico. The remaining genera grow today in South America, other islands of the Antilles, and temperate latitudes (Graham and Jarzen 1969).

The newly discovered Panamanian endocarps of *V. cipaconensis* from the late Miocene of Gatun were found together with fruits of Arecaceae and abundant shallow marine invertebrate and shark tooth fossils (Gillette 1984; Pimiento et al. 2010). These fossils were accumulated in a shallow-water embayment (Hendy 2013). Therefore, it is possible that the Panamanian endocarps might represent local elements of the coastal flora of central Panama or elements transported by sea currents from nearby floras of northern South America. A hy-

pothetical late Miocene dispersal of *Vantanea* from South America into central Panama is also supported by the lack of fossil endocarps of this genus in both the late Eocene and early Miocene floras from Panama where endocarps of extinct Humiriaceae and *Sacoglottis* have been found (Herrera et al. 2010, 2012).

The new fossil wood taxon *Humiriaceoxylon* from the late Eocene of Ocu in Panama provides additional support for the presence of the Humiriaceae in ancestral Central America. *Lacunofructus cuatrecasana* Herrera, an extinct humiriaceous fossil genus based on permineralized endocarps, was recently reported from nearby localities of similar age (Herrera et al. 2012). Although they are not known in physical attachment, we hypothesize that *L. cuatrecasana* and *Humiriaceoxylon* were produced by the same plant due to their co-occurrence and shared familial affinity. The early to middle Miocene Amazonian fossil woods reported from Amazonia (Jupiassú 1970; Pons and De Franceschi 2007; Kloster et al. 2012) are confirmed based on the descriptions presented by the authors. Central Amazonia has the highest diversity for the family today, and these fossil woods, together with the fossil pollen record of *Psilabrevitricolporites devriesii* (related to *Humiria*; Herrera et al. 2010), indicate that Humiriaceae were present in central Amazonia at least since the early-middle Miocene.

A recent phylogeny of angiosperms placed Humiriaceae as sister to all other families within Malpighiales, although with weak bootstrap support (Soltis et al. 2011). Xi et al. (2012) in a more inclusive phylogeny of Malpighiales placed Humiriaceae within a major subclade of the order and as sister to the parietal clade (including families such as Achariaceae, Violaceae, Passifloraceae, and Salicaceae). Molecular time divergence estimates suggested that Humiriaceae might have originated during the middle Cretaceous (Davis et al. 2005; Wurdack and Davis 2009). These divergence estimates are much older than the fossil evidence currently available. The Humiriaceae have an abundant fossil record that preserves well and are easily recognized (based on fruits, wood, and pollen). Fossils indicate a late Eocene age for the oldest record of the family, leaving a ~60-Ma gap between the molecular estimates and the empirical fossil evidence. We see three alternative explanations for this disparity: (1) crown Humiriaceae evolved in the late Paleogene, and all Humiriaceae stem lineages went extinct; (2) we have failed to recognize fossil Humiriaceae in the 60-Ma gap (middle Cretaceous to middle Eocene), although we find an abundant and geographically extensive record since the Late Eocene; and (3) there is bias in the assumptions used to analyze the molecular data of Humiriaceae and relatives that produce much older origination estimates.

Based on this review of the fossils of Humiriaceae, we reemphasize our initial hypothesis about the Neotropical origin for this family (Herrera et al. 2010). Although there is one species of *Sacoglottis* in Africa today, prior reports of humiriaceous fossils in Europe and Australia have been refuted (Dettmann and Clifford 2002; Manchester and Hottenrott 2009; Herrera et al. 2010). The new fossils presented here provide evidence for a reduction of the geographic range for Humiriaceae, suggesting that orogenic and climatic events during the Neogene may have been, to some extent, responsible for the modern-day distribution of the family.

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