

# UNEXPLORED AMAZONIAN DIVERSITY: RARE AND PHYLOGENETICALLY ENIGMATIC TREE SPECIES ARE NEWLY COLLECTED

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## ABSTRACT

The Amazon is renowned to hold an unprecedented, yet poorly-known or unexplored plant diversity. This study aimed to report new collections on five rare or little-known and phylogenetically enigmatic trees, *Aguiaria excelsa* (Malvaceae, Bombacoideae), *Hylocarpa heterocarpa* (Humiriaceae), and the papilionoid legumes *Monopteryx uauçu*, *Petaladenium urceoliferum*, and *Uleanthus erythrinoides*, that became available after recent fieldwork in the western and central Brazilian Amazon region. All five genera, except for *Monopteryx*, are monospecific and represented in herbaria by only the type or at most few collections made more than 30 years ago. Comments on morphological affinities, never-seen-before photographs, and a distribution map of all species are given. A lectotype for *U. erythrinoides* is here designated. We also provide a complete taxonomic description for *P. urceoliferum*, whose pods until presently were unknown. Since these genera are missing branches in the molecular phylogenetic trees of Leguminosae, Humiriaceae, and Malvaceae, the opportunity to include them in future phylogenetic studies will certainly clarify the evolutionary history and taxonomy of their respective families.

The Amazon rainforest is botanically poorly known, yet is renowned for its species diversity unprecedented to any terrestrial ecosystem in the world. Its incredible plant diversity is concentrated in Western Amazonia, where diversification was particularly rapid on pre-Quaternary new landscapes largely shaped by the Andean orogeny (Antonelli et al. 2009; Hoorn et al. 2010). The idiosyncratic ecology of Amazonian trees related to fast demographic traits (e.g. rapid resource acquisition, high dispersal ability, fast growth in size, and short generation times) might have boosted the spectacular rate of diversification in this biome (Baker et al. 2014). Estimates of species numbers for

Amazonia are ever increasing (Hubbell et al. 2008; ter Steege et al. 2010, 2013) and current extrapolations suggest it harbors roughly 16,000 tree species, of which only 227 species greatly dominate all over the region, whereas 11,000 species are rare or apparently characterized by geographically restricted distributions (ter Steege et al. 2013).

During extensive fieldwork in the western and central Brazilian Amazon (upper Rio Negro, upper Rio Solimões, and Manaus), we have collected five poorly-known and phylogenetically enigmatic trees: *Aguiaria excelsa* Ducke (Malvaceae, Bombacoideae), *Hylocarpa heterocarpa*

(Ducke) Cuatrec. (Humiriaceae), and the papilionoid legumes *Monopteryx uauçu* Spruce ex Benth., *Petaladenium urceoliferum* Ducke, and *Uleanthus erythrinoides* Harms (Figure 1). The relationships of these species remain enigmatic because they were never sampled in molecular phylogenetic analyses. Except for *Monopteryx* Spruce ex Benth., the other genera are monospecific and represented in herbaria by only the type or at most few collections made more than 30 years ago. Although *Hylocarpa* Cuatrec. and *Monopteryx* were recently reported in a tree inventory on white-sand and *terra firme* forests in the upper Rio Negro, no fertile specimens accompanied these reports (Stropp et al. 2011). The fact that most Amazonian trees have remained woefully undercollected may be due to a combination of their general rarity (ter Steege et al. 2013) and the sheer vastness of the botanically unexplored area in Amazonia (Hopkins 2007).

Interestingly, most species presented here (*Aguiaria excelsa*, *Hylocarpa heterocarpa*, and *Petaladenium urceoliferum*) were first discovered and taxonomically described by Adolpho Ducke (1876–1959), who, along with the British naturalist Richard Spruce (1817–1893), are the most outstanding Amazonian botanists and plant explorers of all times (Archer 1962; Seaward & Fitzgerald 1996). Ducke first collected *Aguiaria* in October 1932. His subsequent botanical explorations in the upper Rio Negro in February and November 1936 yielded the incredible discovery of two other genera (*Hylocarpa* and *Petaladenium*). Ducke also gathered complete collections of *Monopteryx uauçu* and *Uleanthus erythrinoides*. It was after following Ducke's notes handwritten in herbarium labels that we achieved success in finding all of these tree species.

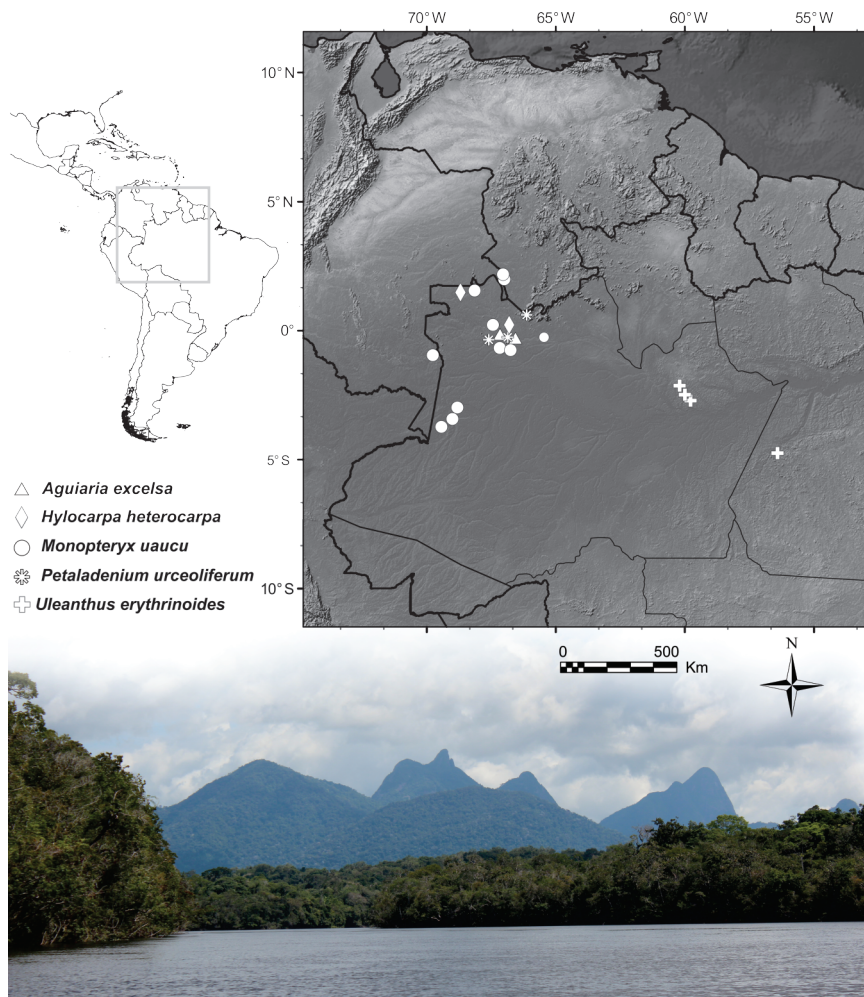
In this paper, we discuss the taxonomy and morphological affinities of the enigmatic tree species aforementioned. After discovering complete flowering and fruiting materials in

the field and among unidentified herbarium collections at INPA and K, it is now possible to provide a detailed taxonomic description for *Petaladenium urceoliferum*. Because the species presented here are missing branches in the molecular phylogenetic trees of Leguminosae (Cardoso et al. 2012a, 2013; LPWG 2013), Humiriaceae (Herrera et al. 2010), and Malvaceae (Baum et al. 2004; Duarte et al. 2011), it is expected that a forthcoming opportunity to evaluate them for the first time in a phylogenetic framework will elucidate their classification and evolutionary history.

## MATERIAL AND METHODS

We carried out three expeditions in the Brazilian Amazon in order to collect the targeted tree species. We mostly followed in Adolfo Ducke's footsteps as he made complete collections with detailed descriptions of the localities of all focal species in the early twentieth century. As such, a review of Ducke's historical collections currently available in national and international herbaria (F, G, IAN, INPA, K, MG, MO, NY, P, R, RB, US) was undertaken prior to the field expeditions. In August 2012, we went to the upper Rio Solimões to collect between São Paulo de Olivença and Tabatinga and also explored some localities near Manaus. The second expedition was carried out in March–April 2013, when we collected extensively around São Gabriel da Cachoeira in the upper Rio Negro mainly on the slopes of the Serra Curicuriari (also known as Serra Bela Adormecida). In the last expedition, in June 2013, we explored the igapó forest along Rio Urubu near Manaus. In addition to herbarium samples with at least ten duplicates, we also obtained silica-gel dried leaf samples for DNA analyses and preserved flowers in ethanol 70% for ontogenetic studies. All the specimens collected have been deposited in the HUEFS and INPA herbaria.

In addition to the examination of the type



**Figure 1.** Geographical distribution of the phylogenetically enigmatic trees *Aguiaria excelsa* (Malvaceae, Bombacoideae), *Hylocarpa heterocarpa* (Humiriaceae), *Monopteryx uauçu*, *Petaladenium urceoliferum*, and *Uleanthus erythrinoides* (Leguminosae, Papilionoideae) in the Amazonian rainforest. Below the Curicuriari river and Serra de Curicuriari (also known as Serra Bela Adormecida) in the upper Rio Negro, São Gabriel da Cachoeira, Amazonas, Brazil, where most trees were collected. Photograph by Dirce Komura.

specimens of all species reported here, a careful revision of unidentified legumes in the INPA, K, and RB collections was carried out in an attempt at discovering long misidentified specimens. All examined specimens were used to prepare distribution maps using ArcMap

software (ESRI: ArcGIS v. 9.3), and to record flower and fruit phenology. We did not attempt here to accommodate the species in any IUCN conservation status (IUCN 2001) because the Amazonian tree flora is understudied and rarity seems to be an

inherent ecological feature of the bulk of the species in the Amazon (ter Steege et al. 2013).

## RESULTS

Our field trips achieved success in finding the targeted enigmatic Amazonian trees *Aguiaria excelsa*, *Hylocarpa heterocarpa*, *Monopteryx uauacu*, *Petaladenium urceoliferum*, and *Uleanthus erythrinoides*, most of them occurring in the upper Rio Negro, around the municipality of São Gabriel da Cachoeira, state of Amazonas, Brazil (Figure 1). We obtained complete flowering and fruiting collections for *Petaladenium* and *Uleanthus*, but for *Aguiaria*, *Hylocarpa*, and *Monopteryx* we collected only fruiting and sterile specimens (Figures 2–7). In addition to duplicate specimens that have been shared with other herbaria, our new collections rendered to HUEFS and INPA the addition of four new specimens of *Aguiaria excelsa* (known previously in herbaria from only two specimens), three of *Hylocarpa heterocarpa* (known previously from only four specimens), four of *Monopteryx uauacu* (known before from several specimens), six of *Petaladenium urceoliferum* (known previously from only six specimens), and four of *Uleanthus erythrinoides* (known before from only six specimens).

The revision of unidentified herbarium legume collections revealed new specimens of *Petaladenium* and *Uleanthus*, which had remained unknown or misidentified for a long time. For example, the specimen *Lima et al. 3301* (collected in 1987) is the first known fruiting collection of *Petaladenium* since the genus was described in 1938.

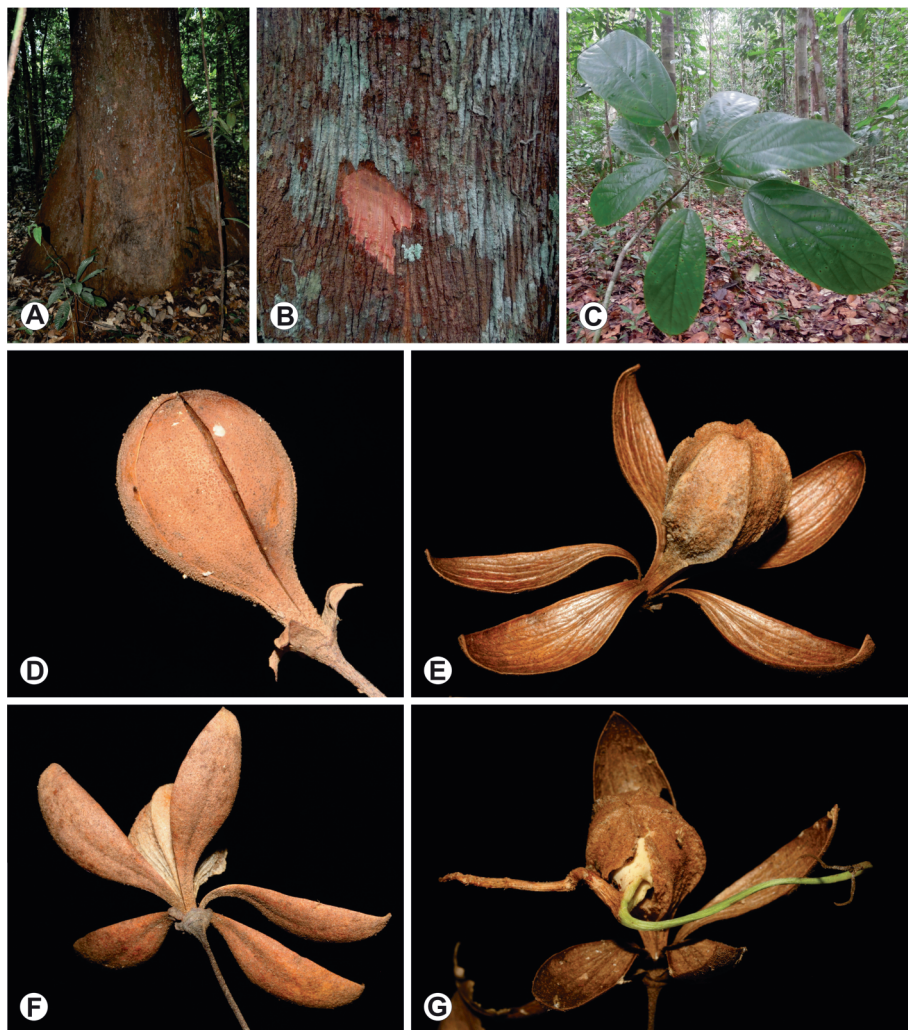
## TAXONOMIC SYNOPSIS

*Aguiaria excelsa* Ducke, Ann. Acad. Brasil. Sci. 7: 329. 1935. Type: BRAZIL, Amazonas: “Alto Rio Negro, Rio Negro acima da foz do Curicuriary, mata de terra

firme”, 24 Oct 1932 (fr), *A. Ducke s.n.* (Holotype: RB 25188!; Isotypes: K!, US!).

**TAXONOMIC REMARKS.** The genus *Aguiaria* was described by Ducke (1935) to accommodate a single giant tree species of Bombacoideae (Malvaceae), *A. excelsa*, so far only known from *terra firme* forests in the upper Rio Negro, around São Gabriel da Cachoeira (Figure 1). At the type locality along the Curicuriari river, it is relatively common and widely known by indigenous people as “duraque” or “duraca”, probably in reference to the heavy wood that is presently used locally for general construction and historically used in naval construction of wooden steamboats near Manaus (Ducke 1935). Since Ducke’s type collection, *Aguiaria excelsa* had yet to be collected in the last 75 years. The specimen *Ducke 144* deposited at R herbarium is erroneously designated as an isotype collection of *A. excelsa*. This specimen indeed represents the first collection of the flowers and was gathered later after Ducke had already described the genus (Ducke 1935). The only flowering collection of *A. excelsa* was obtained in November 1936, whereas its fruits are known in October and from February to April.

The species can reach as high as 50 m tall and possesses small, up to 50 cm tall buttresses. Not only had the huge size of *A. excelsa* impressed Ducke as well as us, but also the remarkable morphology of its anemochoric fruits that are unique among Bombacoideae and angiosperms as a whole. The small, less than 4 cm long fruits of *Aguiaria* have dehiscent exocarp that splits off into five valves, but these remain attached to the indehiscent endocarp (Figure 2), superficially resembling the fruits in the genus *Cedrela* P.Browne (Meliaceae). The very unusual fruit morphology of *Aguiaria* had perplexed Ducke as we can see in his original description of the genus: “Não tenho conhecimento de aparelhamento igual da semente, em qualquer outra espécie vegetal!” [I am not aware of



**Figure 2.** General morphology of *Aguiaria excelsa* (Malvaceae, Bombacoideae): **A.** mature buttressed individual; **B.** scratched bark; **C.** the simple leaves clustered at branch apex; **D.** fruit before dehiscence; **E, F.** different views of the fruit with dehiscent exocarp showing the spongy-fibrous endocarp (**E**); **G.** germinating seed from inside endocarp. Photographs by Domingos Cardoso.

similar seed chamber in any other plant species] (Ducke 1935: 331).

The lack of phylogenetic information for *Aguiaria* precludes inferences bearing on its evolutionary relationships. Previous phylogenetic studies with focus on the Bombacoideae (Baum

et al. 2004; Duarte et al. 2011) did not sample *Aguiaria*. The genus has morphological ties to the Amazonian *Catostemma* Benth. and *Scleronema* Benth., based on wood anatomy (Metcalfe & Chalk 1950; Detienne et al. 1983) and the shared relatively small

flowers and simple leaves borne on long petioles and clustered at branches apices (Figure 2).

**SPECIMENS EXAMINED.** BRAZIL, Amazonas: “São Gabriel, Rio Negro”, 16 Feb 1936 (fr), 16 Nov 1936 (fl), *A. Ducke s.n.* (INPA [two sheets], P [two sheets], R [labeled as *Ducke 144*], RB 29024, US [two sheets]); São Gabriel da Cachoeira, Alto Rio Negro, comunidade de Itacoatiara-Mirim, 00°09'43"S, 67°00'30"W, 28 Mar 2013 (st), *D. Cardoso et al. 3304* (HUEFS, INPA); São Gabriel da Cachoeira, Alto Rio Negro, trilha em mata de terra firme para a Serra Bela Adormecida ao longo do Rio Curicuriari, 00°14'07"S, 66°51'05"W, 31 Mar 2013 (fr), *D. Cardoso et al. 3343* (HUEFS, INPA); São Gabriel da Cachoeira, Alto Rio Negro, trilha para o segundo acampamento na Serra Bela Adormecida ao longo do Rio Curicuriari, 00°16'14"S, 66°50'15"W, 2 Apr 2013 (fr), *D. Cardoso et al. 3384* (HUEFS, INPA); São Gabriel da Cachoeira, Alto Rio Negro, trilha Serra Bela Adormecida, 00°14'07"S, 66°51'05"W, 31 Mar 2013 (fr), *C.E. Zartman et al. 9515* (HUEFS, INPA).

***Hylocarpa heterocarpa*** (Ducke) Cuatrec., *Contr. U.S. Natl. Herb.* 35(2): 85. 1961. *Sacoglottis heterocarpa* Ducke, *Arq. Inst. Biol. Veg.* 4(1): 27. 1938. Type: BRAZIL, Amazonas: “Rio Curicuriary affl. R. Negro (Amazonas), catinga perto da cachoeira Cajú”, 21 Feb 1936 (fr), 18 Nov 1936 (fl), *A. Ducke s.n.* (Holotype: RB 30137!; Isotypes: G, K!).

**TAXONOMIC REMARKS.** A complete taxonomic description and illustrations of *Hylocarpa heterocarpa* are found in Cuatrecasas' (1961) monograph of the Humiriaceae. This species, locally known in the upper Rio Negro as “fruta-de-xiri”, “cumatê-da-catinga” or “cumaterana”, was originally described in *Sacoglottis* Mart. (Ducke 1938), but later transferred by Cuatrecasas (1961)

to the monospecific genus *Hylocarpa*. The species grows as a medium-sized tree but can reach as high as 30 m tall. It has an ecological predilection for white-sand forests (*campinarana*) along the upper Rio Negro (Figure 1), where it has been collected in flower between October and November, and in fruit in November, February, and March. *Hylocarpa heterocarpa* is represented in herbaria by only a few collections, and seems to be a very rare species. After two weeks of fieldwork around São Gabriel da Cachoeira we came across only two individuals in fruit. Stropp et al. (2011) performed a tree inventory of eight one-hectare plots on white-sand forests and *terra firme* forests in the upper Rio Negro and registered merely 16 trees of *H. heterocarpa* (specimens identified by one of us, CEZ) out of the surveyed total of 4,703 trees  $\geq$  10 cm of diameter at breast height.

There is no published molecular phylogenetic analysis that has comprehensively sampled across the taxonomic diversity of Humiriaceae, thus a robust hypothesis on the position of *Hylocarpa* among the seven accepted genera within the family is still lacking. In a recent cladistic study of morphological data, Herrera et al. (2010) found *Hylocarpa* as sister to *Duckesia* Cuatrec., another monospecific genus endemic to lowland Amazonian forests. Apart from the shared number of stamens (Cuatrecasas 1961) and ovules per locule (one), these genera share little in common. Furthermore, *Duckesia* has drupes with a resinous-lacunose, evenly costate and spongy-lignose endocarp, whereas the compact-woody drupe of *Hylocarpa* is not resinous-lacunose and has sharply 5-ribbed and corrugated endocarp surface (Figure 3). The drupe of *Hylocarpa* is in fact more similar to those of the Amazonian endemic monospecific genus *Endopleura* Cuatrec., which also has a drupe with a densely woody endocarp but has sharp, bifurcate ribs, giving it a 10-radiate shape in transverse section. In addition,



**Figure 3.** General morphology of *Hylocarpa heterocarpa* (Humiriaceae): **A.** branches with fruits; **B.** mature buttressed individual with the bark scratched; **C.** the characteristic slightly crenate, coriaceous leaf; **D.** immature drupes and a floor-collected drupe showing the densely-woody endocarp; **E.** drupes collected on the floor (note the ribbed endocarp with sharp long apex); **F, G.** branches holding immature and mature drupes. Photographs by Charles Zartman.

*Hylocarpa* differs from both *Duckesia* and *Endopleura* in having anthers with two unilocular thecae (vs. anthers with four unilocular thecae) (Cuatrecasas 1961).

**SPECIMENS EXAMINED.** BRAZIL, Amazonas: São Gabriel da Cachoeira, Rio Içana, Tunuí, 23 Oct 1947 (fl), *J. Murça Pires 708* (IAN); São Gabriel da Cachoeira, Área da Força Aérea, próximo ao Igarapé Mindú, July 2007 (st), *J. Stropp & P.*

*Assunção 629* (EAFM); São Gabriel da Cachoeira, comunidade de Itacoatiara-Mirim, July 2007 (st), *J. Stropp & P. Assunção s.n.* (EAFM 1798); São Gabriel da Cachoeira, Alto Rio Negro, comunidade de Itacoatiara-Mirim, 00°09'59"S, 67°00'42"W, 28 Mar 2013 (fr), *D. Cardoso et al. 3311* (HUEFS, INPA); São Gabriel da Cachoeira, Alto Rio Negro, Itacoatiara-Mirim, entroncamento do aeroporto, na estrada para Camanaus, 00°09'38"S, 67°00'01"W, 29 Mar 2013 (fr),

*D. Cardoso et al.* 3321 (HUEFS, INPA); São Gabriel da Cachoeira, 00°09'59"S, 70°02'40"W, 28 Mar 2013 (fr), *C.E. Zartman et al.* 9508 (HUEFS, INPA).

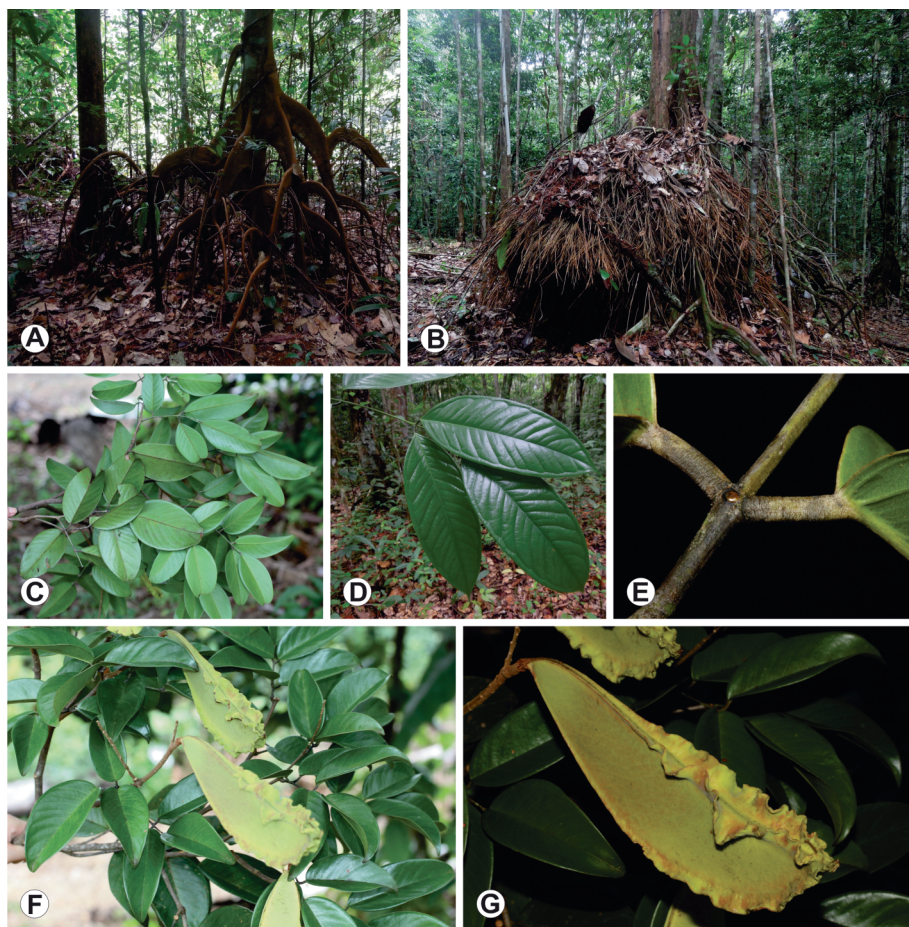
*Monopteryx uauçu* Spruce ex Benth., Fl. Bras. (Martius) 15(1): 307, t. 308. 1862. Type: BRAZIL, Amazonas: "In sylvis fl. Uaupés", Nov 1852 (fl), *R. Spruce 2850* (Holotype: K!; Isotype: P!).

**TAXONOMIC REMARKS.** This species occurs in Brazil, Colombia, and Venezuela, along the upper Rio Negro (Figure 1), where it is locally common in seasonally inundated blackwater forests (*igapó* and *chavascal*) or non-flooded white-sand or sand-loam *terra firme* forests. A tree inventory in the upper Rio Negro recorded *M. uauçu* (74 trees, ca. 3%) along with the legumes *Clathrotropis macrocarpa* Ducke (138 trees, ca. 6%) and *Pterocarpus* sp. (126 trees, ca. 6%) as the three most abundant species in *terra firme* plots (Stropp et al. 2011). *Monopteryx uauçu* was also relatively well represented in white-sand forests, with 60 trees. There are only two collections (*Ducke s.n.* RB 23927 and *Krukoff 8505*) known from the upper Rio Solimões. Unfortunately, we failed in our attempt to locate the species there. In the Brazilian upper Rio Negro region, the species is widely known by the indigenous people as "uacú" or "uauçu". In Venezuela, it is known as "guaco" or "huaco". Ducke (1939, 1949) reports that the seeds are eaten baked or roasted and produce an edible oil that can also serve for lighting. Uauçu trees grow up to 30 m tall and are easily recognized in the field by the extrafloral nectary on the leaf rachis, a rare feature in papilionoids, in addition to the glabrous brochidodromous leaflets with a conspicuous intramarginal vein and the characteristic profusely branched, large aerial roots (Figure 4; Ducke 1939, 1949). Flowers were collected from September to May, and fruits in February, March, and July.

The genus *Monopteryx* still remains phylogenetically unresolved. It has been traditionally classified in Sophoreae (Polhill 1981; Pennington et al. 2005), because of the nonpapilionate corolla in which the wing petals are much reduced and the keel petals are connate and open out exposing the free stamens. However, the distinctive floral morphology of *Monopteryx* probably bears close homology with the truly papilionate flowers with fused stamens of the Dipterygeae genera *Pterodon* Vogel, *Dipteryx* Schreb., and *Taralea* Aubl. (only the last two have Amazonian representatives). In a chloroplast molecular phylogeny of the early-diverging clades of Papilionoideae, Cardoso et al. (2012a, 2013) resolved *Monopteryx inpae* W.A.Rodrigues as sister to the Dipterygeae. They suggested that the typical two-lipped calyx of the Dipterygeae might be a morphological synapomorphy for an expanded concept of the tribe to include *Monopteryx*. As such, the apparently divergent calyx of Dipterygeae and *Monopteryx* is because the two upper, wing-like lobes in the Dipterygeae genera are completely separate to their base, whereas in *Monopteryx* the upper enlarged lobes are connate and assume a standard-like position. Notwithstanding, the systematics of *Monopteryx* is not yet fully resolved as Cardoso et al. (2012a, 2013) sampled only *M. inpae*, the most florally and vegetatively divergent species in the genus (Rodrigues 1975; Barneby & Grimes 1984). Both *M. uauçu* and its morphologically similar *M. angustifolia* Spruce ex Benth. were originally used to base the description of *Monopteryx* in *Flora Brasiliensis* (Benth 1862), yet they have not been sampled in phylogenetic analyses. We believe that our newly collected accessions of *M. uauçu* will be helpful to confirm the current phylogenetic classification of *Monopteryx* and thus to understand the remarkable floral and fruit evolution in the Dipterygeae.

If *Monopteryx* is confirmed close to the Dipterygeae, then it will be easily distinguished not only on the basis of floral features but also on





**Figure 4.** General morphology of *Monopteryx uauçu* (Leguminosae, Papilionoideae): **A, B**, the species is readily recognized by its profusely branched tabular and aerial roots; **C, D**, the broadly ovate glabrous leaflets and characteristic brochidodromous venation; **E**, extrafloral nectary on the leaf rachis, a rare feature in the papilionoids; **F, G**, legumes (note the crimped marginal wings, another unusual feature in the papilionoids). Photographs by Domingos Cardoso.

the fruits. *Pterodon* has flattened samaras with a wing around the raised central seed-chamber, whereas *Dipteryx* has drupaceous fruits. *Monopteryx* and *Taralea* have elastically dehiscent flattened pods with woody valves. However, *Taralea* pods are mostly ovate to suborbicular. The fruits of *M. angustifolia* are yet unknown. Those of *M. inpaë* and *M.*

*uauçu* are elongate to long-obovate and falcate. *Monopteryx uauçu* additionally produces much larger (> 20 cm long) pods, in which the margins bear crimped wings (Figure 4). In addition, we are not aware of extrafloral nectaries on the leaf rachis (Figure 4) of any other Dipterygeae species other than in *M. uauçu* and *M. angustifolia*.

SPECIMENS EXAMINED. BRAZIL, Amazonas: Rio Jacurupá affl. do baixo Içá, 15 Oct 1931 (fl), *A. Ducke s.n.* (F, P, RB 23926); Rio Negro, acima da boca do Curicuriary, 26 Dec 1931 (fl), *A. Ducke s.n.* (P, RB 23352); São Gabriel, Rio Negro, 2 Jan 1932 (fl), *A. Ducke s.n.* (F, NY, P, RB 23928); Rio Solimões, São Jeronymo infra Tabatinga, 4 Feb 1932 (fr), *A. Ducke s.n.* (NY, P, RB 23927); Rio Negro, Enuixy, lago Dondena, 19 May 1947 (fl), *R.L. Fróes* 22339 (RB); São Gabriel da Cachoeira, Alto Rio Negro, Foz do Rio Içana, acima da comunidade de Boa Vista, lugar Grilo, 12 Nov 1987 (st), *H.C. de Lima et al.* 3161 (INPA, RB); São Gabriel da Cachoeira, Alto Rio Negro, estrada para Camanaus, logo após o entroncamento da estrada para o aeroporto, 24 Nov 1987 (st), *H.C. de Lima et al.* 3299 (INPA, RB); São Gabriel da Cachoeira, Itacoatiara Mirim, na estrada de Camanaus, 00°09'31"S, 67°00'35"W, 5 July 2007 (fr), *L.A.G. de Souza & A. Cortes* 34 (INPA); São Gabriel da Cachoeira, Alto Rio Negro, comunidade de Itacoatiara-Mirim, 00°09'43"S, 67°00'30"W, 28 Mar 2013 (st), *D. Cardoso et al.* 3301 (HUEFS, INPA); *ibidem*, 00°09'43"S, 67°00'30"W, 28 Mar 2013 (st), *D. Cardoso et al.* 3302 (HUEFS, INPA); *ibidem*, 00°09'17"S, 67°00'18"W, 28 Mar 2013 (fr), *D. Cardoso et al.* 3306 (HUEFS, INPA); São Gabriel da Cachoeira, Alto Rio Negro, trilha em mata de terra firme para a Serra Bela Adormecida ao longo do Rio Curicuriari, 00°14'07"S, 66°51'05"W, 31 Mar 2013 (fr), *D. Cardoso et al.* 3347 (HUEFS, INPA); São Paulo de Olivença, near Palmares, 11 Sep – 26 Oct 1936 (fl), *B.A. Krukoff* 8505 (MO, P). COLOMBIA, Vaupés: Estación Biológica Caparú, within 3 km of the north bank of Lago Taraira, 14 May 1990 (st), *S. Defler* 743 (MO). VENEZUELA, Amazonas: San Carlos, Rio Negro, 1942 (fr), *L. Williams* 14511 (F, MO); San Carlos de Rio Negro, ca 20 km S of confluence of Rio Negro and Brazo Casiquiare, 01°56'N, 67°03'W, 12 Mar 1983 (fl), *J. Saldariaga s.n.* (MO); *ibidem*,

01°56'N, 67°03'W, Mar 1983 (fl), *C.F. Uhl* 467 (MO); 8 km NE of San Carlos de Rio Negro, 7 Apr 1984 (st), *A. Gentry et al.* 46430 (MO); Bosque de tierra firme a 0.5-1 km al sur del cruce de Caño Marimajari (asentamiento de conuco), a unos 3 km al sureste en vuelo de pájaro de San Carlos de Rio Negro, por la pica que va de San Carlos a Marimajari, 01°54'43"N, 67°02'21"W, 27 Mar 2000 (st), *P.E. Berry & G. Aymard* 7224 (MO).

*Petaladenium urceoliferum* Ducke, Arq. Inst. Biol. Veg. 4(1): 20. 1938. Type: BRAZIL, Amazonas: "Rio Curicuriary (affl. R. Negro) loco Mirapara silva terris altis loco humido", 15 Feb 1936 (fl), *A. Ducke s.n.* (Holotype: RB 35183 [three sheets!]; Isotypes: IAN!, K [two sheets!], NY [two sheets!], P!, US!).

**Tree** 8–30 m tall; bark grey brown to pale brown, smooth or flaking slightly, deeply vertically fissured and often with lenticels; slash pale red-brown, producing small quantities of thick, red exudate; twigs pubescent, lenticellate. Stipules not seen. **Leaves** 5–9(–11)-foliolate, imparipinnate; petiole 3–10 cm long, including a distinct, swollen pulvinus; rachis 12–30 cm long, ridged or finely so, occasionally lenticellate, puberulous; stipels absent; pulvinules 5–11 mm long, dull green; leaflets 9–21 × 3.5–8 (–10.5) cm, opposite, sub-opposite, or clearly alternate, the terminal one usually broadest, lower pairs often smaller, elliptic-oblong to lanceolate, sometimes ovate, base often slightly asymmetric, round or obtuse, apex acute to long acuminate, acumen up to 3 cm long, chartaceous, finely pubescent, dark green and nitid above, pale green below, venation eucamptodromous, secondary veins in 7–11 pairs, 1–2 cm apart, raised below, the tertiary veins more or less parallel and at right angles to the secondary veins. **Inflorescence** 9–22 cm long, ramiflorous or axillary in simple lateral 1–4-branched racemes or panicles,

densely reddish-brown tomentose; bracts 6–8 mm long, lanceolate, cucullate, apex acute, persistent; bracteoles 5–8 mm long, linear-lanceolate, oppositely attached in the middle of a 8–10 mm long pedicel. **Flowers** 14–17 mm long; calyx 8–11 mm long, including a 3–4 mm long hypanthium, campanulate, densely reddish-brown pubescent outside, glabrous inside, lobes unequal, acute, triangular, fused for one-third of their length; petals white-pinkish to pale lilac; standard 16–20 × 16–20 mm, suborbicular, apex emarginate, base 2-auriculate, reddish brown tomentose near the apex of inner face and on the outer surface, with a large triangular white nectar-guide, occasionally very darkly veined, claw broad, 2.5–3.5 mm long; wing petals 14–17 × 6–7 mm, 2-auriculate, petal sculpturing absent, glabrous, fimbriate, each margin with 3–5 short-stipitate, urceolate, whitish gland-like structures, claw 4.5–5.5 mm long; keel petals 14–17 × 6–7 mm, free, but firmly attached by interlocking folds, bi-auriculate, glabrous, claw 4.5–5.5 mm long; stamens 10, united unevenly from 1–5 mm, unequal, the longest stamens 13–15 mm long, the shortest stamens 7–8 mm long, anthers ca. 3 mm long, oblong, brownish, dehiscing by a longitudinal slit; gynoeceum up to 12 mm long, stipitate, ovary narrowly obovate, ovules 3–4, style tapering to an incurved tip, stigma minute, truncate. **Pods** 18–22 × 3–4 cm long, including a stipe up to 2.5 cm long, elastically dehiscent, linear-oblong to linear-obovate, very flattened, valves woody, greenish when immature, turning brownish during maturity, glabrous. **Seeds** 2–3, ca. 15 × 12 × 2 mm, flattened and obovate in outline; testa dark reddish-brown, slightly wrinkled; hilum ca. 1.5 mm long, oblong. (Figure 5).

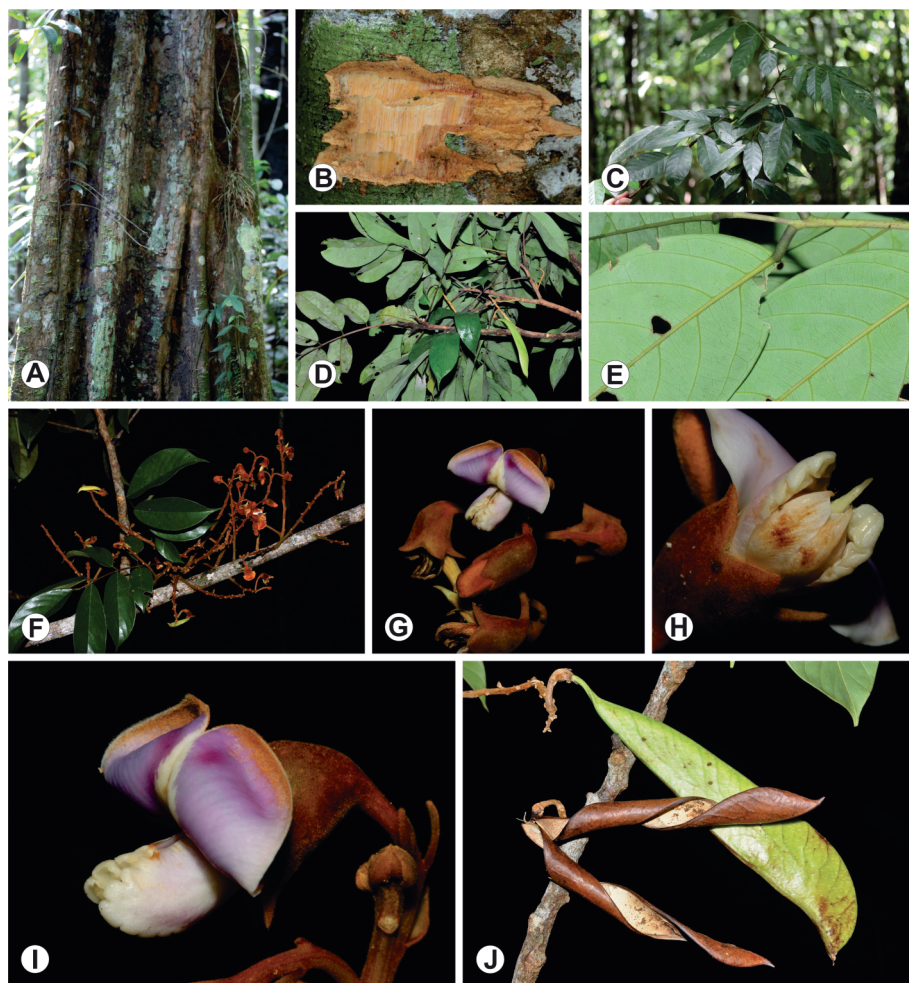
**TAXONOMIC REMARKS.** This is another striking example of a poorly collected, rare, and geographically restricted tree in *terra firme* forests in a single drainage (Rio Curicuriari) of the upper Rio Negro (Figure 1). It was described by Ducke (1938) after having

collected a single flowering specimen. Four additional flowering specimens were collected in the 1960s and 1970s and the first fruit collection (*Lima et al. 3301*) gathered in the 1980s was unidentified until recently among the legume collections at INPA, K, and RB herbaria. During our field expedition to the Serra de Curicuriari, we recollected complete flowering and fruiting materials of *Petaladenium*. It is now reported in flower from February to April and in fruit in November, March, and April.

*Petaladenium* is among the few early-branching papilionoid genera that remain with uncertain phylogenetic relationships (Cardoso et al. 2012a, 2013; LPWG 2013). The nearly free stamens of *Petaladenium* were crucial to include the genus in the morphologically diverse Sophoreae (Ducke 1939; Polhill 1981; Pennington et al. 2005). The broad polyphyly of Sophoreae as showed by phylogenetic analyses of multiple chloroplast DNA sequences (Pennington et al. 2001; Wojciechowski et al. 2004; Cardoso et al. 2012a; LPWG 2013) elucidated many generic relationships in the basal Papilionoideae, yet left unanswered the placement of unsampled genera, such as *Petaladenium*. As Ducke (1938) and others (Pennington et al. 2005; Cardoso et al. 2012a, 2013) have pointed out, the overall vegetative and inflorescence morphology, and the papilionate flowers with white-pinkish to light lilac petals and basally fused stamens of *Petaladenium* (Figure 6) are somewhat similar to those of *Clathrotropis* Harms and *Ormosia* Jacks., whereas the linear-oblong elastically dehiscent pods are similar to those of *Panurea* Spruce ex Benth. & Hook.f. and *Spirotropis* Tul. (Cardoso et al. 2012a, 2013). However, the fimbriate-glandular wing petals of *Petaladenium* are markedly distinctive and unknown to occur in any other Papilionoideae. The generic name and specific epithet indeed derive from this unique feature and refer to the concave, urceolate, gland-like structures along the margins of the wing petals (Figure 6).



**Figure 5.** Detailed morphology of *Petaladenium urceoliferum* (Leguminosae, Papilionoideae): **A.** flowering branch showing the ramiflorous inflorescence,  $\times\frac{1}{2}$ ; **B.** leaflet in abaxial view,  $\times 1$ ; **C.** detail of abaxial surface of a leaflet showing the parallel tertiary veins,  $\times 1$ ; **D.** flower bud,  $\times 2$ ; **E.** very immature flower bud showing the bracteole attachment,  $\times 2$ ; **F.** bracteole,  $\times 2$ ; **G.** detail of an inflorescence axis to show the bract attachment,  $\times 2$ ; **H.** bract,  $\times 3$ ; **I.** flower,  $\times 2$ ; **J.** calyx opened out,  $\times 3$ ; **K.** standard petal,  $\times 3$ ; **L.** keel petal,  $\times 3$ ; **M.** wing petal,  $\times 3$ ; **N.** detail of the apex of the wing petal showing the urceolate-glandular margins,  $\times 10$ ; **O.** androecium,  $\times 3$ ; **P.** Detail of the apex of a stamen to show the anther,  $\times 6$ ; **Q.** gynoecium and exposed ovules,  $\times 4$ ; **R.** detail of the style to show the stigma,  $\times 12$ . Drawn by Angela J. Beaumont from an isotype at K (*Ducke s.n.* RB 35183).



**Figure 6.** General morphology of *Petaladenium urceoliferum* (Leguminosae, Papilionoideae): **A.** the common trunk in this species is vertically deeply fissured; **B.** the bark generally produces small quantities of thick, red exudate; **C, D.** leafy branches; **E.** close-up of leaflets, showing the eucamptodromous venation; **F.** inflorescences are more commonly ramiflorous or develop from the leafy axils of terminal branches; **G.** flower; **H.** close-up of the inferior side of the flower, showing the glandular wing petals; **I.** close-up of the flower (note again the glands on the margin of the wing petals and the ferruginous tomentose indumentum in the apex of inner face of the standard); **J.** immature and elastically dehiscent legumes. Photographs by Domingos Cardoso.

**SPECIMENS EXAMINED.** BRAZIL, Amazonas: São Gabriel da Cachoeira, along margin of Rio Cauaburi, between Rio Maturacá and Rio Yá, 2 Feb 1966 (fl), *N.T. Silva & U. Brazão* 60953 (K, NY, RB); Rio

Negro, Uaupés, margem da Estrada Perimetral Norte, 4 Mar 1975 (fl), *B.G.S. Ribeiro* 838 (IAN, RB); Rio Negro, Estrada Perimetral Norte, Km 24, 6 Mar 1975 (fl), *J.M. Pires & L.R. Marinho* 15677 (IAN, RB [two sheets]);

Rio Negro, Uaupés, Estrada Perimetral Norte, 11 Mar 1975 (fl), *J.M. Pires & L.R. Marinho 15775* (IAN); São Gabriel da Cachoeira, Alto Rio Negro, estrada para Camanaus, logo após o entroncamento da estrada para o aeroporto, 24 Nov 1987 (fr), *H.C. de Lima et al. 3301* (INPA, K, NY, RB); São Gabriel da Cachoeira, Alto Rio Negro, trilha em mata de terra firme para a Serra Bela Adormecida ao longo do Rio Curicuriari, 00°14'07"S, 66°51'05"W, 31 Mar 2013 (fl, fr), *D. Cardoso et al. 3341* (HUEFS, INPA); ibidem, 00°14'07"S, 66°51'05"W, 31 Mar 2013 (fl, fr), *D. Cardoso et al. 3345* (HUEFS, INPA); São Gabriel da Cachoeira, Alto Rio Negro, trilha para a Serra Bela Adormecida ao longo do Rio Curicuriari, arredores do primeiro acampamento ao lado de um iacá-iacá (*Cedrelinga catenaeformis*) e da cachoeira Mamanga, 00°15'41"S, 66°50'23"W, 31 Mar 2013 (fl), *D. Cardoso et al. 3352* (HUEFS, INPA); São Gabriel da Cachoeira, Alto Rio Negro, Serra Bela Adormecida ao longo do Rio Curicuriari, mata de terra firme no entorno do terceiro acampamento, 00°18'36"S, 66°49'58"W, 2 Apr 2013 (fr), *D. Cardoso et al. 3377* (HUEFS, INPA); São Gabriel da Cachoeira, Estrada Perimetral Norte, sentido marco da linha imaginária do Equador, Km 27, 00°02'57"S, 66°57'45"W, 6 Apr 2013 (st), *D. Cardoso et al. 3399* (HUEFS, INPA); São Gabriel da Cachoeira, Alto Rio Negro, terra-firme forest at base of Serra Bela Adormecida along Rio Curicuriari, 00°14'07"S, 66°51'05"W, 31 Mar 2013 (fl, fr), *C.E. Zartman et al. 9521* (HUEFS, INPA).

*Uleanthus erythrinoides* Harms, Verh. Bot. Vereins Prov. Brandenburg 47: 151. 1905. Type: BRAZIL, Amazonas: "Rio Madeira, Marmellos", Mar 1902 (fl), *E. Ule 6093* (Holotype: B, destroyed [F negative 1894!]; Lectotype designated here: K!; Isolectotypes: CORD!, G!, MG!).

**TAXONOMIC REMARKS.** Despite being relatively widespread in the Brazilian

Amazon (Figure 1), this species is rare, only known in herbaria from sporadic old collections. It is a small tree up to 15 m tall frequently associated with periodically flooded forests (*mata de várzea*), seldom occurring in the *terra firme* forests. Flowers were collected in March and from June to August, and fruits in June and August.

Because the holotype originally deposited at B was destroyed, we designated here a lectotype based on an isotype collection at K. Povydysh et al. (2011) had mistakenly designated a F negative image for lectotype, but Art. 9.12 of the ICBN (McNeill et al. 2012) is clear with respect to lectotype designation in that an isotype must be chosen if such exists.

The floral variation in the specimen *Ducke s.n.* MG 16407 from the Tapajós river (lateral petals lanceolate and standard obovate vs. filamentous and suborbicular in the type specimen) was suggested by Povydysh et al. (2011) as indicative of a probably new species of *Uleanthus*. We share Ducke's (1939, 1949) opinion that such variation observed in only a single specimen is taxonomically insignificant and thus his collection should remain as *U. erythrinoides*.

Vegetatively, *Uleanthus* can be easily confounded with the swartzoid *Bocoa viridiflora* (Ducke) R.S.Cowan and *Swartzia aptera* DC., but the bark of *Uleanthus* does not produce red resin. The 4.5–5.5 cm long flowers of *U. erythrinoides* are made up of showy red calyces and red-pinkish or blue-lilac standard petal oddly occurring in the same individual (Figure 7). Ducke (1939, 1949) observed that the standard maintains one color from pre-anthesis until flower senescence. Such petal color polymorphism may be driven by specific pollinators with certain color preference or as a response for selective herbivore pressures (Jones & Reithel 2001; Irwin et al. 2003). Additional studies on the floral biology and pollination ecology of *U. erythrinoides* would be important to address these hypotheses.

The phylogenetic placement of *Uleanthus* remains unassessed (Cardoso et al. 2012a; LPWG 2013). Traditionally, it has been placed in Sophoreae mainly because of the free stamens (Ducke 1939; Polhill 1981; Pennington et al. 2005). The floral morphology and elastically dehiscent elongate pods suggest that *Uleanthus* might belong to the newly reestablished tribe Angylocalyceae (Cardoso et al. 2013), an earliest-diverging papilionoid clade comprised of the Amazonian *Alexa* Moq., Australian *Castanospermum* A.Cunn. ex Hook., and African *Angylocalyx* Taub. and *Xanthocercis* Baill. This clade is strongly marked by an ornithophilous floral syndrome in which the calyx and hypanthium are enlarged and showy, the petals often red or orange, the standard mostly distinctly large, the lower petals undifferentiated or sometimes highly reduced, and the stamens and gynoeceum exerted. A cladistic analysis of morphological data confirmed the close affinity of *Uleanthus* with Angylocalyceae (Povydysh et al. 2011).

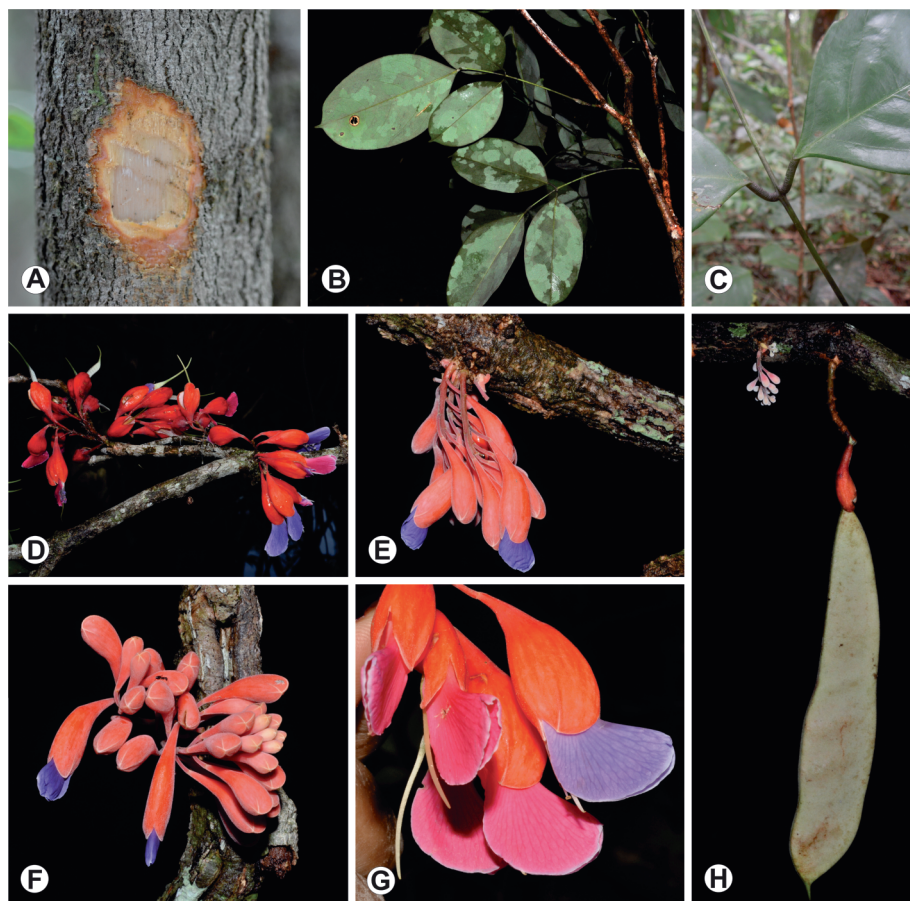
**SPECIMENS EXAMINED.** BRAZIL, Amazonas: Manaus, estrada Z.F.1 Km 9, 12 June 1978 (fl, fr), *L. Coelho et al.* 785 (INPA); Presidente Figueiredo, Rio Urubu abaixo da Cachoeira Iracema, praia alta na boca do Igarapé Água Fria, 7 June 1941 (fl), *A. Ducke* 769 (IAN, MG, NY); Presidente Figueiredo, Rio Urubu, between intersection with Manaus-Caracará Road and Serra da Lua, 31 July 1979 (fl), *C.E. Calderon et al.* 2884 (NY); Presidente Figueiredo, Rio Urubu, beira do rio após a ponte da AM-174, 02°29' 17"S, 59°54'50"W, 29 June 2013 (fl), *D.L. Komura et al.* 1707 (INPA); ibidem, 02°08' 47"S, 60°02'60"W, 29 June 2013 (fl), *D.L. Komura et al.* 1708 (INPA); Rio Preto da Eva, ZF1, ca. 10.5 km do Instituto Novo Mundo, entrando no Km 53 da AM-010, 02°39'38"S, 59°53'40"W, 7 Aug 2012 (st), *L.P. de Queiroz et al.* 15725 (HUEFS, INPA); Rio Preto da Eva, ZF1, ca. 10 km da entrada para a comunidade Mundo Novo no Km 53 da AM-010, 02°39'37"S, 59°53'40"W, 7 Aug

2012 (st), *J.G. de Carvalho-Sobrinho et al.* 3273 (HUEFS, INPA). Pará: "Rio Tapajoz", 28 Aug 1916 (fl, fr), *A. Ducke s.n.* (MG 16407, P); Rio Tapajós, Cachoeira do Acará, 30 Jul 1973 (fl), *B.G.S. Ribeiro* 281 (IAN).

## DISCUSSION

Except for the relatively well-collected *Monopteryx uauçu*, the other species (*Aguaiaria excelsa*, *Hylocarpa heterocarpa*, *Petaladenium urceoliferum*, and *Uleanthus erythrinoides*) represent excellent examples of the assemblage of ~11,000 rare trees that make up the hyperdiverse Amazonian tropical rainforest (ter Steege et al. 2013). Our study highlights how extensive fieldwork in remote areas of Amazonia provides a new and exciting opportunity to retrieve long-undercollected and phylogenetically poorly-known species. Our new specimens of *M. uauçu*, *A. excelsa*, *H. heterocarpa*, *P. urceoliferum*, and *U. erythrinoides* represent an important addition to herbarium collections, revisionary taxonomic monographs, and to effectively design future conservation initiatives for these striking tree species. Since they were never evaluated in molecular phylogenies of Leguminosae, Humiriaceae, and Malvaceae, now we are hoping to clarify their enigmatic evolutionary history and deep level classification.

Our next to step is to contribute with DNA sequence data for a robust estimate of the relationships within Humiriaceae, bombacoid Malvaceae, and papilionoid legumes. To improve taxon sampling in such plant clades is critical, especially with respect to phylogenetically unplaced genera. For example, a recent review of the legume systematics flagged 57 Papilionoideae genera without molecular phylogenetic hypothesis (LPWG 2013). Among these, five genera, including the Amazonian species-poor *Guianodendron* Sch.Rodr. & A.M.G.Azevedo, *Panurea*, and *Spirotropis*, were recently well covered in our studies (Cardoso et al. 2012a, 2012b), but not yet *Monopteryx*, *Petaladenium*, and



**Figure 7.** General morphology of *Uleanthus erythrinoides* (Leguminosae, Papilionoideae): **A.** scratched bark; **B.** leaf branch; **C.** close-up of a leaf rachis, showing the long pulvinules; **D.** the characteristic ramiflorous inflorescences (note the showy red calyces); **E, F.** close-up of an inflorescence in different views, showing floral-buds and flowers; **G.** close-up of flowers (note strange double color of the standard petal); **H.** immature pod (note the persistent showy red calyx). Photographs by Dirce Komura.

*Uleanthus*. After the newly available collections reported herein, we expect that soon the generic-level sampling gaps within Amazonian legumes will be left to only the monospecific caesalpinoid *Androcalymma* Dwyer (LPWG 2013). This very rare or little-known genus is only reported from Boris Krukoff's type collection made in 1936 of a single tree in the upper Rio Solimões (Koeppen 1963). Unfortunately, we did not have success in

our attempt to locate *Androcalymma glabrifolium* Dwyer in the field, but at least we are almost sure about the very locality where Krukoff collected many of his yet poorly known plant species. We believe that spending more time with considerable fieldwork seems to be the most effective strategy to fill in the gaps of phylogenetic knowledge about the Amazonian rare tree flora.



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