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Research

The emergent macrophyte *Montrichardia linifera* (Arruda) Schott (Alismatales: Araceae), a rekindled old friend from the Pacific Slope of lower Central America and western Colombia

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The genus *Montrichardia* are among the most remarkable emergent macrophytes in tropical wetlands. It occurs exclusively in the Neotropics and contains two living species, *M. linifera* (Arruda) Schott and *M. arborescens* (L.) Schott. *Montrichardia linifera* has been reported mainly in the Amazon basin (southern Venezuela to Guyana, Brazil, Ecuador and Peru), whereas *M. arborescens* occurs in Central America (Mexico to Panama), the Lesser Antilles and northern South America. Based on our review of herbarium specimens from Central America and Colombia, as well as field documentation in Panama, we hereby provide the first report of the occurrence of *M. linifera* in Panama, Central America and western Colombia. Furthermore, this finding represents the first record on the Pacific Slope for this species in the Neotropics. The habitat, ecology, life-form, taxonomic remarks and morphological characteristics of the species are presented, discussed and illustrated. Additionally, a key for the species of the genus *Montrichardia* is included; we also provide a discussion about the helophyte concept for the genus *Montrichardia*.

Keywords: Arracacho, biogeography, Castaño, Chocó region, helophytes, new records

Introduction

Araceae is the most species-rich family within the order Alismatales (Chase 2004, Stevens 2020). The family comprises eight subfamilies with worldwide distribution, consisting of 3667 described species in 143 genera, occurring on all continents except Antarctica, in ecosystems that range from open freshwater to deserts (Mayo et al. 1997, Boyce and Croat 2020). Among the most outstanding features of Araceae is the very broad spectrum of life forms (broad habitat diversity), which comprise hemiepiphytes, lithophytes, geophytes, epiphytes, terrestrial, rheophytes, aquatics (submerged or periodically submerged), free-floating aquatics and helophytes (Croat 1988, Mayo et al. 1997).

The helophyte life-form, in both temperate and tropical aroid genera, is widespread throughout the family and is considered a relatively unspecialized life form in the



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majority of the genera (Mayo et al. 1997). Nevertheless, *Montrichardia*, a strictly helophytic genus, has adapted to colonize the silt that accumulates along rivers and wetlands (Lins and Oliveira 1995, Mayo et al. 1997). This genus usually occurs in standing water along the margins of streams or lakes and in swampy areas and estuaries but may also occur in the understory near watercourses, offering resistance to the movement of water and as a pioneer plant, it colonizes bare soil from the banks of the rivers (Huber 1943, Croat 1994, Richards 1996).

Montrichardia occurs exclusively in the Neotropics and contains one fossil species from the Palaeocene, *M. aquatica* Herrera, Jaramillo, Dilcher, Wing & Gomez-N, from Colombia (Herrera et al. 2008), and two living species, *M. linifera* (Arruda) Schott and *M. arborescens* (L.) Schott. *Montrichardia arborescens* occurs in Central America, the Lesser Antilles and the Amazon basin (Brazil, Colombia, Ecuador, French Guyana, Guyana, Peru, Suriname and Venezuela) (Bunting 1979, Croat et al. 2005, Lopes et al. 2016b). In Central America, this species is the only representative of the genus (Croat 1994). It ranges throughout the Caribbean slope from southern Mexico to Panama (Croat et al. 2005), but in the latter, it can also occur along the Pacific slopes of the Azuero Peninsula, Panama and Darién Provinces (Croat 1978, D'Arcy 1987, Correa et al. 2004, ANCON 2011). In the case of *M. linifera*, it occurs in the Orinoco and Amazon basins ranging from Venezuela (Apure, Bolívar, Guárico, Monagas and Sucre) to Guyana, Brazil, Colombia, Ecuador and Peru (Croat et al. 2005, Trujillo-Trujillo et al. 2006). It also occurs in the Atlantic regions of Brazil (Fig. 2A). The distributions of both *Montrichardia* species overlap in the Amazon Basin, where they often form monospecific stands along floodplain lakes and rivers (Lopes et al. 2016b).

The geographical distribution of *M. linifera* has historically mainly been restricted to the Amazon basin. In the past, Croat et al. (2005) suggested that a population from Darién (Panama) could represent individuals of *M. linifera*, but this assumption was based on a single observation without any collection. Nevertheless, through the exhaustive review of herbarium specimens from Panama and Colombia, we re-examined some older specimens collected in Darién Province and Chocó Department that were identified as *M. arborescens* but matched the morphological characteristics of *M. linifera*. Recently, during a floristic study carried out in the Matusagaratí wetland complex in Darién Province, the researchers (OO and AI) found, collected and documented specimens from this species in detail, and, thanks to this, it was possible to make an adequate identification and confirmation of *M. linifera*.

In this paper, we record the species *M. linifera* for the first time for Panama, Central America and western Colombia, based on new collected material and reexamination of previously collected misidentified herbarium specimens. Furthermore, this finding represents the first Pacific Slope record of the species in the Neotropics. The habitat, life-form, taxonomic remarks and morphological characteristics of the

species are presented, discussed and illustrated. Additionally, a key for the *Montrichardia* species is included; we also provide a discussion about the helophyte concept for the genus *Montrichardia*.

Material and methods

Specimens were collected in 2019, during a floristic study carried out in the Darién Province, Panama, throughout the Matusagaratí wetland complex (Fig. 2B). The collections were made using the methodology proposed by Croat (1985). Photographs of the species were taken, and fertile material was preserved in 70% alcohol. Vouchers were deposited at PMA and MO herbaria (acronyms according to Thiers 2020). In order to identify botanical specimens, we consulted taxonomic treatments by Croat and Lambert (1986) and Croat et al. (2005). Plant identifications were confirmed by comparing collected voucher specimens with those identified earlier and housed at COL, HUAZ, MO and PMA herbaria.

Herbarium specimens of *Montrichardia* from Panama and Colombia housed at COL, CUVU, HUAZ, MO, PMA, SCZ and UCH, were studied. Geographical distribution data were obtained from Croat et al. (2005) and Lopes et al. (2016b). In order to complement the distribution data, we consulted databases such as GBIF (2020), and other collections deposited in COL, HUA, PMA and MO herbaria. The descriptive terminology of vegetative morphology follows Croat and Bunting (1979). Inflorescence and floral morphology terminology follows Mayo et al. (1997).

Results

Montrichardia linifera (Arruda) Schott, Araceen Betreff.: 5. 1854. (Fig. 1).

Description

Robust aquatic emergent macrophyte herb, up to 7 m tall. Roots typically under water. Stem rhizomatous-arborescent (bamboo-like), 2–6 m tall, erect, mostly deeply sunken into muddy soil; internodes 8–25 cm diam., 25–27 cm long near base, smooth or tuberculate basally (never aculeate), drying brownish. Sap clear or clear-orange. Leaves spirally arranged; petioles 16–46 cm long, lacking geniculum, sheathed to the middle or to above middle, free portion D-shaped; petiole-sheath marcescent or persistent, 9–26 cm long; blades 15–45 × 15–40 cm, simple, broadly cordate to ovate-sagittate, basifixed, 0.9–1.0 longer than petiole, 1.0–1.1 longer than broad, subcoriaceous, weakly bicolorous, semiglossy adaxially, matte abaxially, drying brownish; anterior lobe 17.5–21.6 × 25.7–27.4 cm, generally about as broad as long, acute at apex; primary lateral veins 4–6 pairs, more or less paler than surface adaxially, markedly paler than surface abaxially, drying usually paler than surface below; posterior lobes 15.0–16.7 × 11.2–14.7 cm, generally as broad as long, obtuse; basal

veins 6–8 pairs, 1st pair free to the base, the remainder joined into a posterior rib, 4–5 basiscopic, 3 acroscopic, more or less paler than surface adaxially, markedly paler than surface abaxially; posterior rib well developed, naked usually for less than 1 cm, more or less paler than surface adaxially, markedly paler than surface abaxially; sinus closed (rhombic). Inflorescence 1 per axil; peduncle 5.0–11.0 cm long; spathe 17–28 cm long, erect, reflexed from the medial part toward apex, markedly differentiated into a basal tube and an apical blade, entirely deciduous after anthesis; spathe-tube 5.0–7.5 cm long, broadly ellipsoid, markedly auriculate at apex, greenish white internally, green externally; spathe-blade 15–23 cm long, creamy white internally, yellowish externally, cuspidate at apex, curved and reflexed at apex; spadix 17–23 cm long,

lacking sterile zones; staminate portion white, more or less fusiform, 19 cm long, sometimes with a yellowish resin at apex; pistillate portion yellowish, 3.5 cm long. Infructescence 9–10 cm long, 5–6 cm diam., subcylindric to subglobose; berries 2.5 cm long, 1.8 cm diam., obturbinate to obovoid, \pm spongy, green; seed 1, brownish.

Distribution

The specimens included in this study represent the first records of *M. linifera* in Central America and western Colombia (Fig. 2A). The Central American population occurs only in eastern Panama, specifically on the Pacific slope within the Matusagaratí wetland complex of Darién Province (Fig. 2B). On the other hand, the Colombian population occurs in



Figure 1. Vegetative and reproductive morphological characteristics of *M. linifera*. (A) habit, (B) stems, (C) leaf blade (abaxial surface), (D) leaf blade (adaxial surface), (E) infructescence, (F) inflorescence, (G) inflorescence (dissected), (H) spathe. Photo credits: Orlando O. Ortiz (A, C, D, F–H); Alicia Ibáñez (B and E).

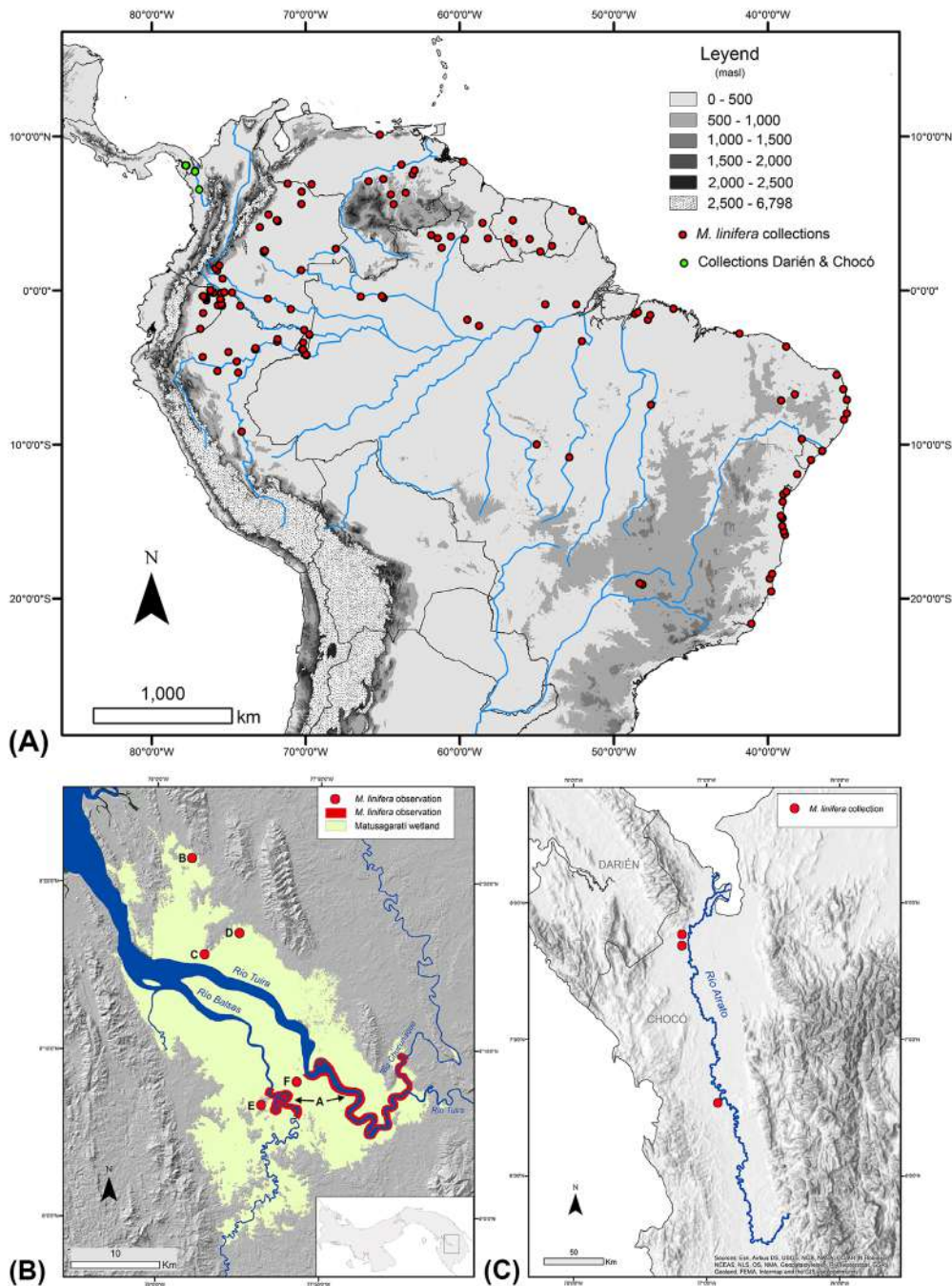


Figure 2. Distribution map of *M. linifera*. (A) New records (green circles) and previous records (red circles), (B) location map of *M. linifera* in Panama (capital letters represent the documented habitats that are presented in the Fig. 3), (C) location map of *M. linifera* in western Colombia.

western Colombia (Chocó), along the Atrato and Cacarcica rivers (Atrato basin) (Fig. 2C).

Habitat and ecology

In Panama, *Montrichardia linifera* has been found growing on the banks of the largest rivers of Darién: Tuira, Balsas and Chucunaque (Fig. 2B). It usually grows in large monospecific thickets on the margins of the rivers, mainly on the inner

bends, where there is active sedimentation. It is a successful pioneer plant species that colonizes bare soil on river margins under stressful conditions (Fig. 3A). Mayo-Menéndez (1965) counted 728 stems in a 100 m² plot with a medium height of ca 6 m. At his study site in the Tuira river, the *Montrichardia* band was 65 m wide. Usually the forests at the back of *Montrichardia* fields are composed of *Mora oleifera* (Triana ex Hemsl.) Ducke and/or *Prioria copaifera* Griseb. Besides this

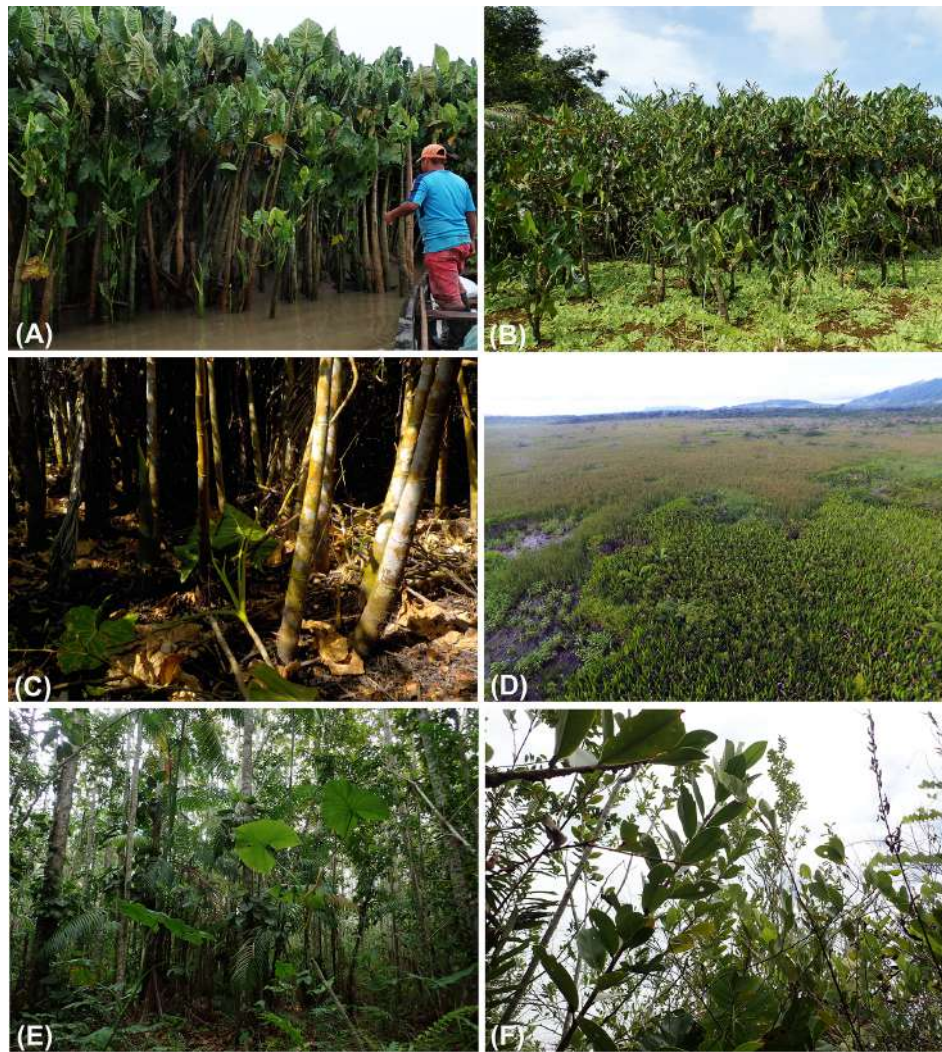


Figure 3. Documented *M. linifera* habitats in Panama (Darién). (A) along river banks, (B) in inland wetlands, (C) ecotone between *Mora oleifera* forest and inland wetland, (D) *M. linifera* mixed with *Heliconia marginata* in *Typha dominguensis* dominated wetland, (E) *Campnosperma panamense* – *Euterpe oleracea* swamp forests, (F) *Ilex guianensis* – *Chrysobalanus icaco* formations. Photo credits: Alicia Ibáñez.

main habitat, *M. linifera* also appears on wetland areas away from the river banks, where it grows on patches either monospecific or mixed with other wetland species (Fig. 2B).

Daily tidal amplitude in the Gulf of San Miguel, including the Tuira and Balsas rivers can vary from 2.25 to 6.37 m, with high tides up to 5.73 m at spring tides in a monthly cycle (Redwood 2020). These are very tough conditions for plants that have to stand strong currents and varying waterlogged conditions on a daily basis. Although *Montrichardia* can stand some salty water, in Darién rivers it thrives in those areas where sea influence is negligible (Mayo-Menéndez 1965, Carol unpubl., Fig. 3A).

Besides this main habitat, *M. linifera* has been found as mainly monospecific thickets in shrublands at the NW margin of the wetland (Fig. 3B), in the intergrade of the *Mora oleifera* forest and herbaceous wetland (Fig. 3C), as patches in the *Typha dominguensis* Pers. dominated wetland, here

mixed with *Heliconia marginata* (Griggs) Pittier (Fig. 3D), as scattered individuals in *Campnosperma panamense* Standl. – *Euterpe oleracea* Mart. swamp forests (Fig. 3E) and in *Ilex guianensis* (Aubl.) Kuntze – *Chrysobalanus icaco* L. formations (Fig. 3F).

Vernacular names and uses

This species is known vernacularly as ‘castaño’ (Panama, Darién), ‘arracacho’ (Colombian Chocó), ‘aninga’ (Colombian Amazon and Brazil), ‘aningaçú’ or ‘aningaíba’ (Brazil) (dos Santos et al. 2014). It has been reported that afro Darién people clear *Montrichardia* thickets along the rivers to grow rice. Lengths of the poles are used to line the bottoms of dugout canoes (Duke 1986, Méndez 2004). In some parts of South America, it has been documented that this species is used as antidote, antimalarial, antidiuretic or animal feed, as well as, to treat various health conditions,

such as nosebleeds, abscesses, tumors, respiratory conditions, rheumatism and ulcers (Plowman 1969, Amorozo and Gély 1998, Amarante et al. 2010, dos Santos et al. 2014, Frausin et al. 2015).

Additional specimens examined (new records)

Colombia, Chocó Department: hydrographic basin of the Atrato river, Bojayacito swamp near Bellavista; 06°32'40"N, 76°54'11"W; 40 m; 13 Apr 1982 (fr.); E. Forero 9189 (COL!, HUA!, MO!); Municipality of Riosucio, Los Katios National Natural Park, pangamal area on the left bank of the Atrato river; 07°44'45"N, 77°10'24"W; 50 m; 6–7 Jul 1976 (fr.); H. León 276 (COL!); Cacarica river, on its banks; 07°41'54"N, 77°10'1"W; 1 Jul 1957 (fl.); R. Romero-Castañeda 6328 (COL!). **Panamá**, Darién: Pinogana, 1/4 mile E of airport at El Real, along small brackish water stream; 8°08'N, 77°43'W; 20 May 1969 (fl.); R.L. Lazor & M.D. Correa 3365 (PMA!); banks of the Tuira river, near the 'sunken ship'; 8°7'22.98"N, 77°47'40.28"W; 10 m; 7 Feb 2019 (fl.); O. Ortiz, A. Ibáñez & N. Gálvez 3223 OO (MO!, PMA!); Matusagaratí wetland, floodplain area near the Tuira river, cativo forest (*Prioria copaiifera*) with abundance of 'barrigón' (*Pseudobombax septenatum*) and 'corocita' (*Elaeis oleifera*); 8°7'24.93"N, 77°47'25.67"W; 12 m; 9 Feb 2019 (sterile); A. Ibáñez, O. Ortiz & N. Gálvez 9620 AI (PMA!); 13 m; 8°5'50.66"N, 77°45'46.12"W; 13 m; 9 Nov 2019 (fr.); A. Ibáñez & R. Flores 9913 AI (PMA!)

Discussion

Morphological comparison between *Montrichardia* species

The individuals of *M. linifera* studied from Central America and western Colombia match with the morphological characteristics previously described by Croat and Lambert (1986) and Croat et al. (2005). To date, this is the only reported species of *Montrichardia* from western Colombia. Nonetheless in Central America and northern Chocó, *M. linifera* is easily confused with the other congener, *M. arborescens*, which also occurs in the Pacific slope of Central Panama (Correa et al. 2004) as well as in the Caribbean slope of Colombia.

Historically, there has been a debate about the taxonomic status the species of *Montrichardia* (Silva et al. 2012). Many authors have recognized the two species as different entities (Engler 1911, Croat and Lambert 1986, Croat 1994, Mayo et al. 1997, Croat et al. 2005), but other authors considered the existence of only one recognizable taxon at the species level (Bunting 1979, Howard 1979). At least in Central America, the differences between the two species are markedly evident, mainly in the stems, venations, leaf shape, color of spadices and both spathe shape and color (cf. Fig. 1 versus Fig. 4).

Recent studies have showed that morphological traits are important discriminating characters between species, among the most important are the internode size (length and

diameter), the number of primary lateral veins and the midrib length (Mirouze et al. 2012, Silva et al. 2012, Lopes et al. 2016a). This last character is extremely useful to separate the species, because the length of the midrib is linked to the length of the anterior lobe, therefore, we could use the proportions between the length of the anterior and posterior lobes. According to our field observations, other important discriminating characters (at least in Central America) are the color and shape of the spathe (cf. Fig. 1F–H versus Fig. 4F–H). As in many aroids, inflorescence-related characters are particularly important in *Montrichardia* because they are linked to its pollination strategy and pollinator size (beetles) (Gibernau et al. 2003).

The following key defines the differences between the *Montrichardia* species, based on the information mentioned above, as well as on field observations and herbarium work.

- 1a. Stems bamboo-like, smooth or tuberculate (never aculeate); internodes up to 25 cm diam. at the base; blades cordate to broadly ovate-sagittate, 1.0–1.1 times longer than broad, their anterior lobe 1.16–1.29 times longer than the posterior lobes; primary lateral veins generally 4 or more pairs; spathe-tube margins usually auriculate at apex; spathe-tube greenish-white internally; spathe-blade yellowish externally.....*M. linifera*
- Stems moderately slender, prominently aculeate; internodes up to 10 cm diam. at the base; blades markedly sagittate, 1.3–1.5 times longer than broad, their anterior lobe typically shorter than posterior lobes; primary lateral veins usually up to 3 pairs; spathe-tube margins not auriculate at apex (continuous margins); spathe-tube reddish internally; spathe-blade green externally.....*M. arborescens*

***Montrichardia* life-form and the helophyte concept**

Throughout the existing literature, many works have applied the term helophyte when referring the *Montrichardia* life-form (Mayo et al. 1997, Herrera et al. 2008, Mirouze et al. 2012, Silva et al. 2012, de Andrade et al. 2013); other studies consider that *Montrichardia* is an emerging macrophyte (Croat 1988, Lopes et al. 2016a, b). According to Mayo et al. (1997), aroid helophytes are plants which grow in swampy habitats or along river and stream margins. This definition could be a bit confusing, because it only considers the habitat type and there are some species with other non-helophyte life forms that can grow in swampy habitats, rivers or stream margins; e.g. some aquatic aroid species of *Lemnoideae* (floating aquatics) (Landolt 1986), or *Jasarum steyermarkii* (fully submerged aquatics) can grows in swamps (Croat 1988). Another example is that of some rheophytes such as *Spathiphyllum quindiuense*, that occurs on rocks or along muddy riverine margins but essentially does not fall into the typical helophyte species.

In the past, Clements (1902), in his classification of 'formations', used the term helophyta referring to the fresh marsh plants. According to the Raunkiaer's system (Raunkiaer 1905,



Figure 4. Vegetative and reproductive morphological characteristics of *M. arborescens*. (A) habit, (B) stems, (C) leaf blade (abaxial surface), (D) leaf blade (adaxial surface), (E) infructescence, (F) inflorescence, (G) inflorescence (dissected), (H) spathe. Photo credits: Orlando O. Ortiz (A–D, F–H); Olga M. Montiel (E).

1934), which was based on seasonal adaptation of plants, cryptophytes (plants with dormant parts below ground) are subdivided into two main types: hydrophytes and helophytes. The first ones are plants with perennial rhizomes or winter buds. In turn, helophytes are plants with buds at the bottom of the water or in the underlying soil (Smith 1913). In other words, the helophyte concept by Raunkiaer involves plants with a growing point that survives adverse seasons as resting bud in marshy ground, therefore, this definition does not fit very well with the usual *Montrichardia* life-form.

Other systems, such as the one proposed by Warming (1909), employed the term helophytes to arrange a specific plant community type according to soil properties (degree of soil wetness). According to this system, helophytes are a vegetation formation that grows in marsh (very wet soils). Following Warming's classification, Clements (1920) defined helophytes as 'amphibious' plants rooted in water or mud, possessing high rates of foliar transpiration and stomata on both surfaces and a stem often functioning as a leaf. Pound and Clements (1900) stated that amphibian plants are those

typical of marshes which may be either aquatic or terrestrial, that are rooted in the mud or sometimes growing through a stratum of water, always having their foliage aerial. Later, Weaver and Clements (1929) divided hydrophytes into three groups: submerged, floating (including floating-leaved rooted species) and amphibious plants. According to the authors, vascular amphibious plant species are closely related to mesophytes but are the least specialized of water plants, because many amphibious plants have a wide range of adjustment and may grow for a time as mesophytes or partially submerged. Also, the authors mentioned that transition events can occur between xerophytes, hydrophytes and mesophytes, where groups can change in a certain way between their closest life forms. Based on the latter statement, Tiner (2017) concluded that classifying a plant species as a hydrophyte or a mesophyte is not necessarily an easy task.

In conclusion, the term helophyte historically has been used in different contexts (Tiner 2017), has been widely diversified and has several connotations, and in most cases, the definition was used to define a survival plant strategy (Raunkiaer, 1905, 1934, Smith 1913, Cook 1990) or to describe different groups of plants in a particular aquatic habitat (plant community) (Warming 1909, Clements 1920). Because of this, perhaps a clearer system of classification would be based on the form of attachment to the substrate, which has also proven useful in morphological, physiological and ecological works (Arber 1920, Daubenmire 1947, Sculthorpe 1967, Schuyler 1984, Cronk and Fennessy 2001, Vymazal and Kröpfelová 2008, Bai et al. 2012, Lopes et al. 2016a, b, Tiner 2017, Schneider et al. 2018). For the genus *Montrichardia* and other rhizomatous aquatic aroid genera, we strongly recommend using the aquatic macrophyte classification system introduced by Schuyler (1984), which is based on relationships to water level, substrate and structural characteristics of plants. According to this system, *Montrichardia* would be classified within the benthophyte group as an emergent macrophyte, which is characterized by having the basal portion of plant in or on a substrate (benthic) and its vegetative plant body protruding above the surface of the water. This last life-form concept was accepted in part by Croat (1988) for some aquatic aroid genera.

Habitat characteristics and biogeographic remarks

The habitat and ecological characteristics of the *Montrichardia* population from Darién are consistent with documented specimens from South America (Jonker-Verhoef and Jonker 1968, van Roosmalen 1985, Bunting 1995). In general terms, *Montrichardia* usually occurs in areas with warm and humid climates, high annual precipitation (usually > 1800 mm year⁻¹) and total absence of a pronounced dry season (Lopes et al. 2016b). In the case of *M. linifera*, its occurrence seems to be tightly-linked to the nutritional characteristics of the environment, such as the high availability of nutrients that characterize white-water wetlands (Lopes et al. 2016a). Previous distribution models based on climatic

determinants for *M. linifera* (Lopes et al. 2016b), predicted values between 51 and 100% probability occurrence of the species in the northern part of the Chocó biogeographical region, which is consistent with the results obtained in this investigation. The Chocó biogeographical region comprises the pacific coast of eastern Panama, western Colombia and northwestern Ecuador and contains high levels of biodiversity and endemism throughout lowland wet forests, montane cloud forests, grasslands, coastal mangroves and forest swamps (Gentry 1986, Myers et al. 2000).

The Central American (Darién) and western Colombian (Chocó) populations of *M. linifera* are relatively close (ca 70 km), but are isolated by several mountain ranges (Serranías de 'Pirre', 'Sapo' and 'Darién') around the Darién Gap (Fig. 2). Both localities represent disjunctive populations, totally isolated from the rest of the *M. linifera* populations by geographic barriers such as the Isthmus of Panama and the northern Andes mountain ranges (Fig. 2). The geological and paleo-geographical history of the Isthmus of Panama and northern Andes is mainly related to the motion of continental and oceanic plates (Hooghiemstra et al. 2006). The geological history of the three Cordilleras in Colombia stretches across the Neogene, but in many places, vertical elevation or uplift took place between the Oligocene and the Pliocene, with the highest uplift rate during the Pliocene (van der Hammen 1961, Harrington 1962, Kroonenberg et al. 1990, Hoorn et al. 1995). Uplift occurred during the Miocene in some parts of the Western Cordillera, whereas parts of the Eastern Cordillera were uplifted between 10 and 4 Mya (Hooghiemstra et al. 2006). Similarly, the Colombian Central Cordillera rose between 22 and 18 million years ago (Mya). On the other hand, there is a common geological origin of the Chocó (western Colombia) and Darién (eastern Panama) regions, as both are part of the Panama microplate, more specifically, the Chucunaque–Atrato geological blocks (Borrero et al. 2012, Montes et al. 2015, Cardona et al. 2018, León et al. 2018). The collision of the Chucunaque – Atrato basin and its associated magmatic arc with South America began during the late Miocene circa 10 Mya, resulting in the collision that fused the Panamanian magmatic arc with the western Andes of Colombia along the Uramita suture (Montes et al. 2015, León et al. 2018). The geological history of the Chocó suggests that the modern landscape was established during the early Pleistocene (-2.7 Mya) (Pérez-Escobar et al. 2019).

One hypothesis about the origin of the disjunctive global distribution of *M. linifera* would be linked to vicariant events associated with the geological origin of Chocó and major uplifts of the northern Andes. Possibly in the past, *M. linifera* comprised a more widespread geographical distribution throughout South America (including the western part). The emergence of the northern Andes mountain ranges probably isolated the populations located in what is now the Amazon basin and in turn, resulting in population relics that became established in the Chucunaque – Atrato geological blocks (Chucunaque and Atrato basins) after the geological

formation of the Chocó. This last argument is speculative and its sole purpose is to attempt to explain the possible origin of the populations of *M. linifera* in the Pacific slope. Perhaps the current geographic distribution of *M. linifera* is related to these geological events, but to confirm this, additional phylogeographic and molecular population structure studies must be done, which should include individuals from other populations throughout their range of geographical distribution to possibly date the separation between the two geographically-separated populations.

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