



**FLORISTIC AND PHYTOGEOGRAPHIC ASPECTS OF ARACEAE IN CERRO
PIRRE (DARIÉN, PANAMA)**

**ORLANDO O. ORTIZ ¹, MARÍA S. DE STAPF ^{1,2}, RICCARDO M. BALDINI ³ AND
THOMAS B. CROAT ⁴**

¹Herbario PMA, Universidad de Panamá, Estafeta Universitaria, Ciudad de Panamá, Panamá.

²Departamento de Botánica, Universidad de Panamá, Estafeta Universitaria, Ciudad de Panamá, Panamá.

³Centro Studi Erbario Tropicale (FT herbarium) and Dipartimento di Biologia, Università di Firenze, Via

La Pira 4, 50121, Firenze, Italy

⁴Missouri Botanical Garden, 4344 Shaw Blvd., St. Louis, MO 63110, USA.

Correspondence author: Orlando O. Ortiz, ortizopma@gmail.com

SUMMARY

The aroid flora in Panama includes 436 described species in 26 genera, representing the richest country of Araceae in Central America. Much of the existing knowledge of the Panamanian aroids has been generated in the last 50 years, mainly due to extensive taxonomic studies and, to a lesser extent, by floristic studies. Floristic studies generated valuable information to better understand biodiversity, especially in the poorly-explored areas. For this reason, the main objective of this work is to study the floristic composition of the aroids of a botanically important region: Cerro Pirre (Darién Province). As a result, 430 specimens were

studied, comprising 94 species in 12 genera. The Aroid flora of Cerro Pirre is formed by species of wide geographic distribution (53%) and, to a lesser extent, endemic species (27%). Of the total species, approximately 43% are nomadic vines, 33% epiphytes, 23% terrestrial and a single species epilithic (1%). Ten new records for the flora of Cerro Pirre were recorded and one new record for Panama. Nine species new to science were discovered. The surprisingly high number of new records and new species emphasizes the need for complementary inventories, through field work in unexplored areas and herbarium work through the comprehensive review of botanical material.

KEYWORDS

Biodiversity, flora of Panama, Central America, aroids, endemism.

INTRODUCTION

In general terms, the Araceae family is notable for comprising a great diversity of species, as well as for its impressive morphological variation (Grayum, 1990), variation in life forms (geophytes, climbers, epiphytes, helophytes and free-floating aquatic) (Croat, 1988; Mayo *et al.*, 1997). This family represents one of the groups with greater economic importance (Duke, 1968; Croat, 1994a; Mayo *et al.*, 1997), owing to edible tubers and especially to its great ornamental value.

According to Boyce and Croat (2018), the Araceae consist of about 3645 species in 144 genera. In Central America, there are 778 species in 26 native aroid genera (Croat, 2017). In this region, the diversity of species is mainly concentrated in Panama and Costa Rica. In the case of Panama, the aroid flora currently comprises 436 described species in 26

genera, but it is estimated that there are more than 600 species in total, representing the richest country for Araceae in Central America (Ortiz *et al.*, 2018).

Most of the existing knowledge of the aroid flora of Panama has been generated in the last fifty years and has been mainly due to the development of taxonomic studies (Ortiz *et al.*, 2018). Currently, there are very few published floristic studies of the Panamanian Araceae. Among them, those of Standley (1928, 1933, 1944) and Croat (1978), were conducted mainly in the former Canal Zone. So far, there are no published intensive inventories or detailed studies on the Araceae in other areas of the country. Floristic studies generate valuable biodiversity information, especially in poorly explored areas and is a fundamental prerequisite for research in ecology, agronomy, forestry, conservation biology and biogeography (Barkley, 2000; Phillips *et al.*, 2003). For this reason, the main objective of this work is to analyze the floristic composition of the aroids of a botanically important region, such as Cerro Pirre, due to its high degree of endemism (Bermúdez *et al.*, 2000; ANAM, 2010). The taxonomic and ecological aspects of the aroid flora of Cerro Pirre was published in a second and third part (Ortiz *et al.*, 2019a, 2019b). The information generated in this work can be used to better understand this important group of plants and, in turn, the information that could be used to design useful conservation measures within the Darién National Park.

MATERIALS AND METHODS

The study was carried out in the vicinity of Cerro Pirre (near the biological station of Rancho Frío), a mountain located to the north of the Serranía de Pirre (Figure 1), within

the geographic coordinates of 8°1'8.80"N, 77°44'5.30"W. The name "Rancho Frío" was originally applied to a camp on the Rancho Frío-Cerro Pirre trail; at present, it refers only to the station of the Ministry of the Environment (formerly ANAM) (Siegel *et al.*, 2008). Cerro Pirre has an elevation gradient from 90 to 1550 m (Robbins *et al.*, 1985). The climate of the area is humid tropical, with the average annual temperature is 20–25°C, and the average annual rainfall is 3000 to 3500 mm. There is a pronounced dry season beginning January and ending in April (Gradstein and Salazar, 1992).

To collect material, photograph and study the species, three field trips were made (April, July-August and December of 2016), with each field work session lasting 8 to 12 days. The collections were made using the methodology proposed by Croat (1985). All the material collected was processed and deposited in the University of Panama herbarium (PMA) and duplicates in the Missouri Botanical Garden (MO) and University of Florence (FT) herbaria. The determination of life forms was made using the classifications proposed by Croat (1988) and Mayo *et al.* (1997). We use the term “nomadic vine”, which includes all climbing plants that germinate on the ground and may lose the older parts of their stem in the process of ascending (see Zotz, 2013). This term includes many aroid species that were previously described as secondary hemiepiphytes (Croat, 1988).



Figure 1. Location map of the study site (blue colored) and the Cerro Pirre summit (red dot) in Darién National Park (gray colored).

In order to complement the list of species for the floristic inventory, databases and collections deposited in PMA, MO and Smithsonian Tropical Research Institute (SCZ) herbaria were consulted. The abbreviations (Alpha-2 code) used for the countries are according to ISO 3166 (ISO, 2018). The geographical distribution of the species was obtained from Balick *et al.* (2000), Brako and Zarucchi (1993), Croat (1983, 1986, 1991, 1999, 2004), Croat and Acebey (2014), Croat and Carlsen (2013), Croat and Hannon (2015), Croat and Ortiz (2016), Croat and Stiebel (2001), Correa *et al.* (2004), Idárraga-Piedrahita *et al.* (2011), Funk *et al.* (2007), Dorr and Stergios (2014), Grayum (1996, 2003), Madison (1977), TROPICOS (2018), Nelson (2008) and Wong *et al.* (2016).

RESULTS AND DISCUSSION

Floristic composition

A total of 430 herbarium specimens were reviewed. The oldest collections of Araceae from Cerro Pirre dated from 1962 by the botanists James Duke and Narciso Bristán. The majority of the specimens were collected by the botanist Thomas Croat during the years 1976, 1988 and 1994 (104 specimens), followed by the botanists Ronald Hartman in 1977–1979 (44 specimens) and James Folsom during 1977 and 1980 (40 specimens). Through this study, 134 specimens were collected, representing 31% of the total of the reviewed specimens.

Through intensive sampling and the revision of herbarium specimens, 10 new records were made for the flora of Cerro Pirre (cf. TROPICOS, 2018): *Adelonema panamense* Croat & Mansell, *A. wendlandii* (Schott) S.Y. Wong & Croat, *Anthurium brownii* Mast., *A. pentaphyllum* var. *bombacifolium* (Schott) Madison, *A. salvinii* Hemsl., *A. talamancae* Engl., *A. clavigerum* Poepp. & Endl., *Heteropsis oblongifolia* Kunth, *Monstera dubia* (Kunth) Engl. & K. Krause and *M. spruceana* (Schott) Engl. Also, *Stenospermation ellipticum* Croat & D.C. Bay was registered for the first time for the flora of Panama (for more details see Ortiz *et al.*, 2018). Additionally, nine new species to science were identified, two of which having been recently published (Croat *et al.*, 2017a; 2017b)—all currently only known from Panama.

The Araceae of Cerro Pirre consists of 94 species, distributed in 12 genera (Appendix 1). Comparing the results obtained with other works carried out in Panama and other parts of the Neotropics, the Cerro Pirre area represents one of the sites with the greatest diversity

of Araceae species (Table 1). But when comparing the results of this study (Cerro Pirre: 94 spp., 100–1550 m) to others conducted in Neotropical areas with similar elevations such as El Cerrado (64 spp., 300–1300 m), Las Quinchas (52 spp., 380–1500 m), Quincemil (47 spp., 650–1200 m) and Reserva de la Biosfera Los Tuxtlas (34 spp., 100–1700 m), it is observed that the diversity of Araceae in Cerro Pirre is greatest.

The diversity of species of Araceae varies considerably within the tropical areas, with temperature, humidity, precipitation and elevation being some of the most determining factors. The high species richness has been correlated with high levels of precipitation coupled with the absence of prolonged dry seasons (Croat, 1998). Croat (1994b) mentions that the diversity is greater between the sea level and elevations up to about 1500 m; after 2000 m, the diversity decreases dramatically. Leimbeck *et al.* (2004) analyzed the diversity patterns of Araceae in Ecuador and concluded a strong correlation with elevation and, to a greater extent, by humidity. This, in part, agrees with that proposed by Gentry (1988), who mentions that the richness of neotropical plant species generally increases with absolute annual precipitation. For example, Bajo Calima and Cabo Corrientes (both sites located in the Colombian Chocó), are characterized by lowland areas (<150 m), high levels of precipitation (6000–8000 mm annual in Bajo Calima and 5000 mm annual in Cabo Corrientes) and extremely high diversity compared to other sites (see Table 1). But, Fortuna Forest Reserve, an area that includes mid-elevation areas (700–2200 m), seems to be one of the most diverse sites in the Neotropics (Table 1). Although Fortuna has lower levels of precipitation (5470 mm annual) than Bajo Calima (6000–8000 mm annual),

Fortuna is characterized as the most cloudy place in Central America, where the coverage with clouds is about 70% during the rainy season (STRI, 2014).

In poorly diverse lowland sites (< 145 m), such as Barro Colorado Island and Usina São José (see Table 1), there are relatively low levels of precipitation (2750 mm annual in Barro Colorado Island and 1687 mm annual in Usina São José). In the case of Cerro Pirre, although it include sites from lowlands (100 m) to mid-elevation areas (1550 m) and have moderate precipitation records (3000–3500 mm annual), it has a relatively high aroid diversity. Probably, this is due to the high heterogeneity in the vegetation of Cerro Pirre (see Myers, 1969), which comprises three types of vegetation and four life zones (*sensu* Holdridge *et al.*, 1971), and the changes in temperature and humidity along the elevation gradient (ANAM, 2010).

Table 1. Comparison of aroid diversity in different Neotropical locations.

No.	Site	Country	Taxa	Genera	Elevation (m)	Size (km ²)
1	R.F. Fortuna	Panama	142	11	700–2200	195
2	Bajo Calima	Colombia	137	13	0–150	800
3	R.N. El Amargal	Colombia	114	14	0–120	c. 40
4	La Selva	Costa Rica	106	16	35–137	16
5	Cerro Pirre	Panama	94	12	100–1550	c. 83
6	La Planada	Colombia	71	7	1300–2100	32
7	Cerrado Province	Brazil	64	18	300–1300	c. 1.2 M
8	Veracruz	Mexico	53	10	0–2500	241
9	Macagual	Colombia	53	16	300	-

No.	Site	Country	Taxa	Genera	Elevation (m)	Size (km ²)
10	Serranía de Las Quinchas	Colombia	52	10	380–1500	-
11	Barro Colorado Island	Panama	51	14	0–145	15.6
12	Rio Palenque	Ecuador	49	13	150–220	-
13	Nourages N.R.	French Guiana	49	13	40–400	c. 770
14	Quincemil	Peru	47	16	650–1200	-
15	Parque Amacayacu	Colombia	46	13	80–200	2930
16	Tabasco	Mexico	44	9	40–1000	24,731
17	Balcanes	Colombia	35	11	250	-
18	R.B. Los Tuxtlas	Mexico	34	9	100–1700	6.4
19	E.B. Los Amigos	Peru	30	10	268	c. 1.5
20	Pantiacolla	Peru	27	10	400–1500	-
21	Quindío	Colombia	25	8	1000–1160	-
22	Tipacoque	Colombia	21	11	1850	73
23	Usina São José	Brazil	18	9	20	247
24	P.N. Tatamá	Colombia	18	2	2400–3000	519
25	E.B. Wayqecha	Peru	13	6	2200–3200	7

Note. References per site (number): (1) McPherson *et al.* (2010), Ortiz *et al.* (2015b); (2) Croat *et al.* (2006); (3) Mora *et al.* (2006); (4) Grayum (2007); (5) this study; (6) Croat *et al.* (2009); (7) Gonçalves (2004); (8) Acebey *et al.* (2008); (9) Trujillo *et al.* (2014); (10) Balcázar-Vargas *et al.* (2000); (11) Croat (1978); (12) Croat (1995); (13) Belbenoit *et al.* (2001); (14) Lingán-Chávez (2008); (15) Rudas and Prieto (1998); (16) Díaz *et al.* (2015); (17) Trujillo *et al.* (2014); (18) Acebey and Krömer (2008); (19) Lingán-Chávez (2008); (20) Lingán-Chávez (2008); (21) Trujillo *et al.* (2014); (22) Hernández (2011); (23) Arruda *et al.* (2010); (24) Sierra *et al.* (2013); (25) Lingán-Chávez (2008).

Chorological affinities

Almost half of the taxa present in Cerro Pirre has a wide distribution (Figure 2). These species are also distributed in other countries of Central and South America. There are only two strictly Central American species, both of the genus *Syngonium* (*S. schottianum*

H. Wendl. ex Schott and *S. hoffmannii* Schott). According to Croat (1981), the center of diversity for this genus is Costa Rica and Panama.

Four species are distributed exclusively from Costa Rica to Colombia (*Anthurium cucullispathum* Croat, *A. talamancae* Engl., *Monstera pittieri* Engl. and *Philodendron rayanum* Croat & Grayum); two species are distributed only in Panama, Colombia and Ecuador [*Chlorospatha mirabilis* (Mast.) Madison and *Philodendron ichthyoderma* Croat & Grayum]. *Chlorospatha mirabilis* was recently recorded for the flora of Panama and is only known from a few collections made in the Province of Darién (Cerro Tacarcuna and Cerro Pirre) (Croat and Hannon, 2015).

In the case of binational species, there are two distributed in Costa Rica and Panama: *Monstera oreophila* Madison and *Philodendron wilburii* Croat & Grayum. Another 11 taxa are exclusive to Panama and Colombia: *Anthurium crystallinum* Linden & André, *A. pendens* Croat, *A. rotundistigmatum* Croat, *Dieffenbachia isthmia* Croat, *Philodendron albisuccus* Croat, *P. lazorii* Croat, *P. immixtum* Croat, *P. ligulatum* var. *heraclioanum* Croat, *P. panamense* K. Krause, *P. pseudauriculatum* Croat and *Stenospermation ellipticum* Croat & D.C. Bay. The Panamanian populations currently known of *Anthurium crystallinum*, *A. rotundistigmatum*, *Philodendron albisuccus* and *Stenospermation ellipticum* are found only in Darién Province (TROPICOS, 2018).

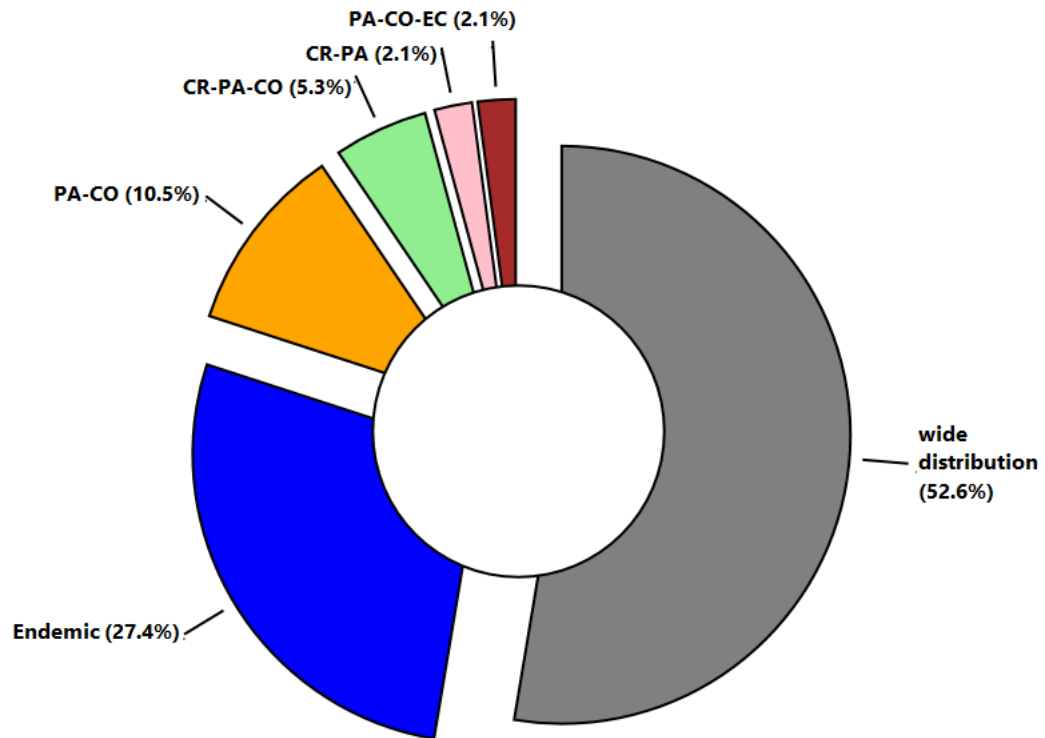


Figure 2. Geographic distribution of the Araceae of Cerro Pirre. Note: PA (Panama), CO (Colombia), CR (Costa Rica), EC (Ecuador).

It is important to note that the Cerro Pirre area contains a significant level of endemism of Araceae (see Figure 2). Twenty-three species (24% of the total aroid flora of Cerro Pirre) are also endemic to Serranía de Pirre (Appendix 1). The Cerro Pirre area is included in the *Eastern Panamanian montane forests* (Bermúdez *et al.*, 2000; ANAM, 2010), which includes several isolated mountains. Due to the complex heterogeneity of habitats present along the mountainous regions of Darién and the isolation between the mountain ranges, these sites are characterized by high endemism and great biological diversity (WWF, 2018).

Life-forms

The species of Araceae on Cerro Pirre are categorized into four life forms: epiphytes, nomadic vines, terrestrials and epilithics. Of the total species, about 43% are nomadic vines, 33% epiphytes, 23% terrestrials and a single species was epilithic (1%) (Figure 3). These results are similar to those obtained by Mora *et al.* (2006), Acebey and Krömer (2008), Trujillo *et al.* (2014) and Díaz *et al.* (2015), where the hemiepiphytic lifeform is predominant in the aroid flora (referred here as nomadic vines).

Some of the species recorded in this study exhibited two different life forms (Appendix 1). Previous studies have reported that aroid species can develop more than one lifeform, depending on the habitats where they grow (see Croat, 1988; Zotz, 2004; Benavides *et al.*, 2005). For example, in the study area, *Anthurium cuspidatum* Mast. (*sensu* Croat and Ortiz, 2016), is commonly terrestrial, but at higher elevations (above 1100 m), epiphytic individuals can be observed. Croat (1988) mentions that in the cloud forests the conditions of soils and trunks of the host trees are very similar, due to the continuous drainage of water and the excessive accumulation of organic matter. On the other hand, terrestrial, epiphytic and epilithic individuals were observed in *A. salvinii* Hemsl. Given its conglomerate roots and the arrangement of leaves (in rosettes), this species can accumulate detritus and moisture, as litter-trapping plants (see Zona and Christenhusz, 2015). Probably, this mechanism allows the plant to establish itself successfully and grow in dry soils with few nutrients, as well as, provides a wide degree of adaptation to various habitats. Other case was identified in which the life form observed contrast with the

original descriptions of the species. Croat (1986) described *Anthurium rubrifructum* Croat and *A. niqueanum* Croat as "climbing epiphytes". However, in Cerro Pirre they were observed as nomadic vines. Individuals of both species usually can climb trees from five to 10 meters without disconnecting from the ground.

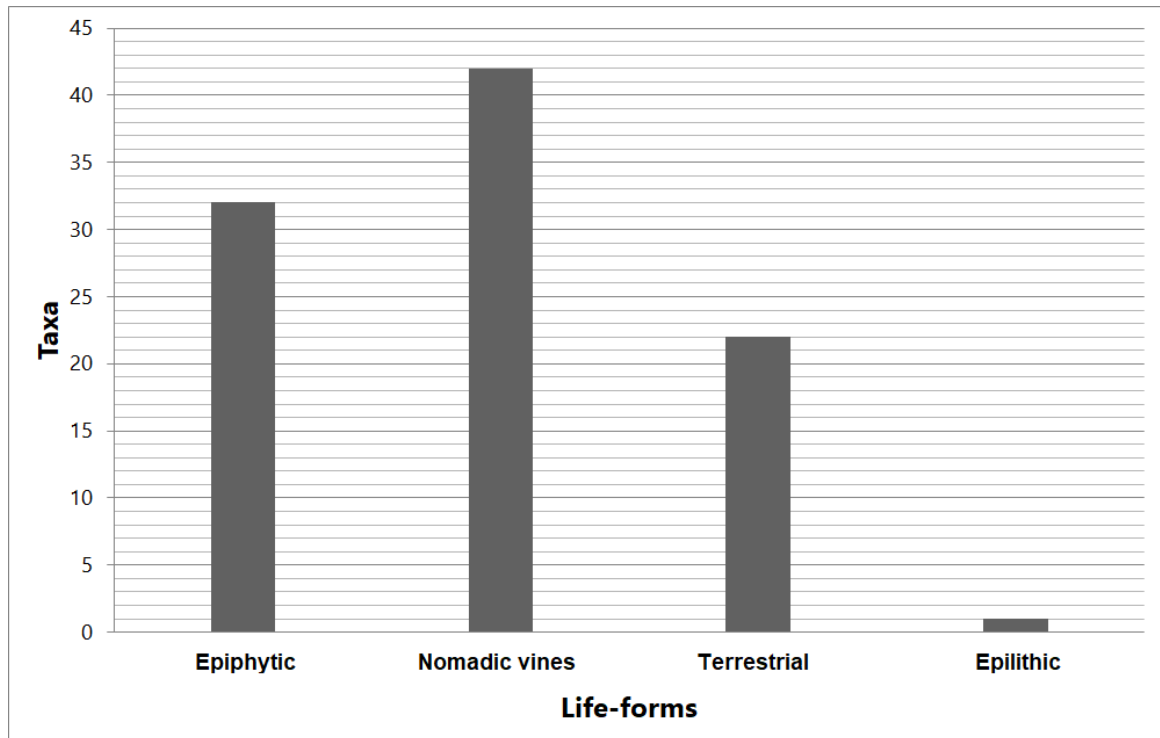


Figure 3. Life-forms of aroid species in the Cerro Pirre area.

CONCLUSIONS

The Cerro Pirre area represents one of the sites with the greatest aroid diversity compared to other areas of the Neotropics. This site has 94 species, which mostly have wide distribution (53%), although relatively high percentages of endemic species were also

reported (27%). Most of the recorded species were nomadic vines (43%), followed by epiphytes (33%), terrestrials (23%) and epilithic (1%).

Through the review of herbarium specimens and the field work carried out, 10 new records for the flora of Cerro Pirre, one new record for the flora of Panama and nine new species to science, were identified. The surprisingly high number of new records and new species emphasizes the need to carry out future field work in unexplored areas, as well as the importance of herbarium work through the thorough review of botanical material.

ASPECTOS FLORÍSTICOS Y FITOGEOGRÁFICOS DE ARACEAE EN CERRO PIRRE (DARIÉN, PANAMÁ)

RESUMEN

La flora de Araceae en Panamá comprende 436 especies descritas en 26 géneros, representando el país con mayor riqueza de Araceae de la región centroamericana. Gran parte del conocimiento existente de las aráceas de Panamá se ha generado en los últimos 50 años, debido principalmente por la realización de estudios taxonómicos, y en menor medida, por estudios florísticos. Los estudios florísticos generan información valiosa para conocer la biodiversidad, especialmente en áreas poco exploradas. Por este motivo, el objetivo principal de este trabajo es estudiar la composición florística de las aráceas de una región botánicamente importante como lo es Cerro Pirre (Provincia de Darién). Como resultado, se revisaron 430 especímenes de Araceae, distribuidos en 94 especies y 12 géneros. La flora de Araceae de Cerro Pirre está conformada por especies de amplia distribución geográfica (53%) y en menor medida por especies endémicas (27%). Del total de especies, aproximadamente el 43% son bejucos nómadas, 33% son epífitas, 23% son terrestres y 1 especie resultó ser epilítica (1%). Se identificaron 10 nuevos registros para la flora de Cerro Pirre, 1 nuevo registro para la flora de Panamá y 9 especies nuevas para la ciencia. El número

sorprendentemente alto de nuevos registros y nuevas especies enfatizan la necesidad de realizar inventarios complementarios, por medio de trabajo de campo en áreas inexploradas y trabajo de herbario a través de la revisión exhaustiva del material botánico.

PALABRAS CLAVES

Biodiversidad, Flora de Panamá, Centroamérica, aráceas, endemismo.

ACKNOWLEDGMENTS

We are very grateful to the curators of PMA, MO, SCZ, UCH herbaria and Juvenal Batista and Jorge Aranda for allowing access to their collections. We would also like to thank Tilson Contreras, Crispulo, Yoyi, Mario Arosemena, Alina Ortega, Alexis Moreno, Dilma Castillo, Rodolfo Flores, Ernesto Campos, Yessenia Guadalupe and Roberto Vergara for assisting in the field trips; Carla Kostelac and all volunteers of the Araceae Lab of the Missouri Botanical Garden for the support provided in the MO herbarium. Special thanks go to Oris Rodríguez and Jerry Harrison for their revisions and suggestions. Last, but not least, we offer our gratitude to SENACYT and Fondo Darién (Fundación NATURA-GEMAS) for financing the field work.

BIBLIOGRAPHICAL REFERENCES

- ACEBEY, A. and KRÖMER, T. 2008. Diversidad y distribución de Araceae de la Reserva de la Biósfera Los Tuxtlas, Veracruz, México. *Revista Mexicana de Biodiversidad*, 79: 465-471.
- ACEBEY, A., CROAT, T.B. and KRÖMER, T. 2009. Diversidad de Araceae en Veracruz. In: **Monocotiledóneas sin fronteras**. Xalapa, Veracruz, México.

- ANAM (Autoridad Nacional del Ambiente). 2010. **Atlas Ambiental de la República de Panamá**. Panamá: Editora Novo Art, S.A. 187 pp.
- ARRUDA, T., DE ANDRADE, I.M. and ALVES, M. 2010. Flora da Usina sao José, Igarassu, Pernambuco: Araceae. *Rodriguésia* 61: 689-704.
- BALCÁZAR-VARGAS, M.P., ORLANDO RANGEL, J.C. and LINARES-C., E.L. 2000. Diversidad Florística de la Serranía de las Quinchas, Magdalena medio (Colombia). *Caldasia*, 22: 191-224.
- BALICK, M.J., NEE, M.H. and ATHA, D.E. 2000. Checklist of the Vascular Plants of Belize. *Memoirs of the New York Botanical Garden*, 85: 1-246.
- BARKLEY, T.M. 2000. Floristic studies in contemporary Botany. *Madroño*, 47: 253-258.
- BELBENOIT, P., PONCY, O., SABATIE, R D., PREVOST, M.-F., RIERA, B., BLANC, P. *et al.* 2001. Floristic checklist of the Nourages area. In: **Nourages. Dynamics and Plant-Animal Interactions in a Neotropical Forest**. Eds: F. Bongers, P. Charles-Dominique, P. Forget-M. and M. Thery. p. 301–341. Dordrecht: Kluwer Academic Publishers.
- BENAVIDES, A.M., DUQUE, A.J., DUIVENVOORDEN, J.F., VASCO, G.A. and CALLEJAS, R. (2005). A first quantitative census of vascular epiphytes in rain forests of Colombian Amazonia. *Biodiversity and Conservation*, 14: 739-758.
- BERMÚDEZ, M.M. and SÁNCHEZ, J.S. (Eds). 2000. **Identificación de vacíos de información botánica en Centroamérica**. Turrialba: WWF, Museo Nacional de Costa Rica. 99 pp.

- BOYCE, P. C. and CROAT, T.B. 2018. **The Überlist of Araceae: Totals for Published and Estimated Number of Species in Aroid Genera.** Available from: <http://www.aroid.org/genera/180211uberlist.pdf> (accessed 15 march 2018).
- BRAKO, L. and ZARUCCHI, J.L. 1993. Catalogue of the flowering plants and gymnosperms of Peru. **Monographs in Systematic Botany from the Missouri Botanical Garden**, 45: 1-1286.
- CORREA, A.M.D., GALDAMES, C. and DE STAPF, M.S. 2004. **Catálogo de las Plantas Vasculares de Panamá.** Bogotá: Quebecor World. 599 pp.
- CROAT, T.B. 1978. **Flora of Barro Colorado Island.** Palo Alto: Stanford University Press. 943 pp.
- CROAT, T.B. 1981. A revision of *Syngonium* (Araceae). *Annals of the Missouri Botanical Garden*, 68: 565-651.
- CROAT, T.B. 1983. A revision of the genus *Anthurium* (Araceae) of Mexico and Central America. Part I: Mexico and Middle America. *Annals of the Missouri Botanical Garden*, 70: 211-416.
- CROAT, T.B. 1986. A revision of genus *Anthurium* (Araceae) of Mexico and Central America. Part II: Panama. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 14: 1-204.
- CROAT, T.B. 1988. Ecology and life forms of Araceae. *Aroideana*, 11: 4-55.
- CROAT, T.B. 1991. A revision of *Anthurium* Section *Pachyneurium* (Araceae). *Annals of the Missouri Botanical Garden*, 78: 539-855.
- CROAT, T.B. 1994a. The use of the New World as Drug Plants. *Journal of Japanese Botany*, 69: 185-203.

- CROAT, T.B. 1994b. Taxonomic Status of Neotropical Araceae. *Aroideana*, 17: 33-60.
- CROAT, T.B. 1995. Floristic comparisons of Araceae in six Ecuadorian florulas. In: **Biodiversity and conservation of Neotropical montane forest**. Eds: S.P. Churchill, H. Balslev, E. Forero y J.L. Luteyn. p. 489-499. Bronx: The New York Botanical Garden.
- CROAT, T.B. 1998. Tropical aroids: taxonomy, diversity and ecology. In: **Diversity and Taxonomy of Tropical Flowering Plants**. Eds: P. Mathew y M. Sivadasan. p. 235-286. Calicut: Mentor Books.
- CROAT, T.B. 1999. Araceae. In: Catalogue of the vascular plants of Ecuador. Eds: P.M Jørgensen y S. León-Yáñez. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 75: 227-246.
- CROAT, T.B. 2004. Revision of *Dieffenbachia* (Araceae) of Mexico, Central America, and the West Indies. *Annals of the Missouri Botanical Garden*, 91: 668-772.
- CROAT, T.B. 2017. A revision of the Araceae of Central America. XII International Aroid Conference, 6-10 july. Cali, Colombia.
- CROAT, T.B. and ACEBEY, A. 2014. Araceae. In: Catálogo de las plantas vasculares de Bolivia. Eds: P.M. Jørgensen, M.H. Nee y S.G. Beck. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 127: 257-268.
- CROAT, T.B. and CARLSEN, M. 2013. A reassessment of *Anthurium* species with palmately divided leaves, and a reinterpretation of *Anthurium* section *Dactylophyllum* (Araceae). *PhytoKeys*, 23: 41-54.
- CROAT, T.B. and HANNON, L.P. 2015. A revision of the genus *Chlorospatha* (Araceae). *Annals of the Missouri Botanical Garden*, 101: 1-259.

- CROAT, T.B. and ORTIZ, O.O. 2016. A Reappraisal of the *Anthurium cuspidatum* Masters Complex, section *Polyneurium* (Araceae). *Aroideana*, 39: 134-186.
- CROAT, T.B. and STIEBEL, T. 2001. Araceae. In: Flora de Nicaragua. Eds: W.D. Stevens, C. Ulloa-Ulloa, A. Pool y O.M. Montiel. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 85: 136-188.
- CROAT, T.B., BAY, D. and YATES, E.D. 2006. New Taxa of *Anthurium* (Araceae) from the Bajo Calima Region (Valle, Chocó), Colombia and Ecuador. *Novon*, 16: 25-50.
- CROAT, T.B., BELT, D. and DEAL, J. 2017a. New species of *Anthurium* sect. *Calomystrium* (Araceae) from Mexico and Panama. *Aroideana*, 40: 97-116.
- CROAT, T.B., DELANNAY, X. and ORTIZ, O.O. 2017b. Revision of *Xanthosoma* (Araceae). Part 2: Central America. *Aroideana*, 40: 504-581.
- CROAT, T. B., HUANG, P., LAKE, J.K. and KOSTELAC, C.V. 2009. Araceae of the flora of reserva La Planada, Nariño Department, Colombia (Part 1). *Aroideana*, 32: 30-122.
- DÍAZ, J.P., GUADARRAMA-OLIVERA, M.A. and CROAT, T.B. 2015. Diversidad Florística de Araceae en el Estado de Tabasco, México. *Botanical Sciences*, 93: 131-142.
- DORR, L.J. and STERGIOS, B. 2014. Araceae. In: Flora of Guaramacal (Venezuela): Monocotyledons. Ed: Dorr, L.J. *Smithsonian Contributions to Botany*, 100: 1-289.
- DUKE, J.A. 1968. **Darien Ethnobotanical Dictionary**. Ohio: Batelle Memorial Institute. Columbus.
- FUNK, V.A., BERRY, P.E., ALEXANDER, S., HOLLOWELL, T.H. and KELLOFF, C.L. 2007. Checklist of the plants of the Guiana Shield (Venezuela: Amazonas, Bolivar,

Delta Amacuro; Guyana, Surinam, French Guiana). *Contributions from the United States National Herbarium*, 55: 1-584.

GENTRY A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, 75: 1-34.

GÓMEZ-DIAZ, J.A. 2010. **Comparación florística de epífitas vasculares entre un Bosque Mesófilo de Montaña y un Acahual en el Municipio de Tlalnahuayocán, Veracruz.** Master thesis, Universidad Veracruzana, México. 117 pp.

GONÇALVES, E.G. 2004. Araceae from Central Brazil: comments on their diversity and biogeography. *Annals of the Missouri Botanical Garden*, 91: 457-463.

GRADSTEIN, S.R. and SALAZAR, A.N. 1992. Bryophyte diversity along an altitudinal gradient in Darién National Park, Panama. *Tropical Bryology*, 5: 61-71.

GRAYUM, M.H. 1990. Evolution and Phylogeny of the Araceae. *Annals of the Missouri Botanical Garden*, 77: 628-697.

GRAYUM, M.H. 1996. Revision of *Philodendron* Subgenus *Pteromischum* (Araceae) for Pacific and Caribbean Tropical America. *Systematic Botany Monographs*, 47: 1-233.

GRAYUM, M.H. 2003. Araceae. In: Manual de plantas de Costa Rica Vol. 2 Gimnospermas y Monocotiledóneas (Agavaceae-Musaceae). Eds: B.E. Hammel, M.H. Grayum, C. Herrera and N. Zamora. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 92: 59-200.

GRAYUM, M.H. 2007. Araceae. Flora Digital de la Selva. Available from: <http://sura.ots.ac.cr/florula4/families/ARACEAE.pdf> (accessed 17 march 2017).

- HERNÁNDEZ, L.A. 2011. **Las Aráceas del municipio de Tipacoque, Boyacá-Colombia**. Universidad Pedagógica y Tecnológica de Colombia. Bachelor thesis, Universidad Pedagógica y Tecnológica de Colombia. 104 pp.
- HOLDRIDGE, L.R., GRENKE, W.C., HATHEWAY, W.H., LIANG, T. and TOSI, J.A. 1971. **Forest Environments in Tropical Life Zones: a pilot study**. New York: Pergamon Press. 747 pp.
- IDÁRRAGA-PIEDRAHITA, A., ORTIZ, R., CALLEJAS POSADA, R. and MERELLO, M. 2011. **Flora de Antioquia: Catálogo de las Plantas Vasculares del Departamento de Antioquia (Colombia), Vol. 2**. Medellín: Universidad de Antioquia. 943 pp.
- ISO (International Organization for Standardization). 2018. Country Codes-ISO 3166. Available from: <https://www.iso.org/obp/ui/#search/code/> (accessed 20 march 2018).
- LEIMBECK, R.M. and BALSLEV, H. 2001. Species richness and abundance of epiphytic Araceae on adjacent floodplain and upland forest in Amazonian Ecuador. *Biodiversity and Conservation*, 10: 1579-1593.
- LINGÁN-CHÁVEZ, J.C. 2008. **A Comparative Analysis of the Diversity, Distribution, and Biogeography of Araceae in Southeastern Peru (Cusco and Madre de Dios, Perú)**. Master thesis, Texas Christian University. 100 pp.
- MADISON, M.T. 1977. A revision of *Monstera* (Araceae). *Contributions from the Gray Herbarium of Harvard University*, 207: 1-100.
- MAYO, S.J., BOGNER, J. and BOYCE, P.C. 1997. **The genera of Araceae**. Kew: The Trustees, Royal Botanic Gardens. 370 pp.

- MCPHERSON, G., MERELLO, M. and FICA, M. 2010. A Checklist of the Fortuna Dam Region, Chiriqui/Bocas del Toro, Panama. Available from: <http://www.mobot.org/mobot/research/fortuna.shtml> (accessed 17 march 2017).
- MORA, M., BERNAL, R., CROAT, T.B. and JÁCOME, J. 2006. A phylogeographic analysis of Araceae of Cabo Corrientes (Chocó, Colombia) and comparable lowland tropical American floras. *Annals of the Missouri Botanical Garden*, 93: 359-366.
- MYERS, C.W. 1969. The ecological geography of cloud forest in Panama. *American Museum Novitates*, 2396: 1-51.
- NELSON, C.H. 2008. Catálogo de plantas vasculares de Honduras, espermatofitas. Tegucigalpa: Editorial Guaymuras. 1576 pp.
- ORTIZ, O.O., CROAT, T.B. and BALDINI, R.M. 2015. Diversidad del Género *Anthurium* (Araceae) en la Reserva Forestal Fortuna, República de Panamá. XXVII Congreso Científico Nacional, 19-23 octubre. Universidad de Panamá.
- ORTIZ, O.O., CROAT, T.B. and BALDINI, R.M. 2018. Current status of aroid species diversity in Panama, including new records for the Country. *Webbia*, 73: 141-153.
- ORTIZ, O.O., DE STAPF, M.S., BALDINI, R.M. and CROAT, T.B. 2019a. Synopsis of Aroids (Alismatales, Araceae) from Cerro Pirre (Darién Province, Panama). *Check List*, 15: 651-689.
- ORTIZ, O.O., DE STAPF, M.S and CROAT, T.B. 2019b. Diversity and distributional patterns of aroids (Alismatales: Araceae) along an elevational gradient in Darién, Panama. *Webbia*, 75: 339-352.

- PHILLIPS, O.L., MARTINEZ, R.V., VARGAS, P.N., *et al.* 2003. Efficient plot-based floristic assessment of tropical forests. *Journal of Tropical Ecology*, 19: 629-645
- ROBBINS, M.B., PARKER, T.A. and ALLEN, S.E. 1985. The avifauna of Cerro Pirre, Darién, eastern Panama. *Ornithological Monographs*, 78:198-232.
- RUDAS, L. and PRIETO, C. 1998. Floristic analysis of the Amacayacu National Park in the Mocagua Island, Amazon (Colombia). *Caldasia*, 20:142-172.
- SIEGEL, D.C., OLSON, S.L. and WETMORE, A. 2008. **The birds of the Republic of Panama: ornithological gazetteer and bibliography**. Shipman: Buteo Books. 516 pp.
- SIERRA, J.A., SANÍN, D., COCA, L.F. and POSADA, J.M. 2013. Araceae in a high Andean forest of the Colombian occidental cordillera (Natural National Park Tatamá). *Aroideana*, 36E: 76-91.
- STANDLEY, P.C. 1928. Flora of Panama Canal Zone. *Contributions from the U.S. National Herbarium*, 27: 1-416.
- STANDLEY, P.C. 1933. The flora of Barro Colorado Island, Panama. *Contributions from the Arnold Arboretum of Harvard University*, 5: 5-159.
- STANDLEY, P.C. 1944. Araceae. In: Flora of Panama. Eds: R.E. Woodson y R.W. Schery. *Annals of the Missouri Botanical Garden*, 31: 1-60.
- STRI (Smithsonian Tropical Research Institute). 2014. Reporte Técnico sobre la Importancia de la Reserva Forestal Fortuna para Investigación Científica, Educación Ambiental, y Conservación de la Biodiversidad. Available from: <http://www.life.illinois.edu/dalling/Fortunareportecientifico.pdf> (accessed 19 march 2017).

TROPICOS. 2018. Tropicos online database. Missouri Botanical Garden, St. Louis. MO, USA. Available from: <http://www.tropicos.org> (accessed 16 march 2018).

TRUJILLO, E.T., CASTRO-ROJAS, D.E. and MORALES-BARRETO, J.A. 2014. Inventario de la familia Araceae en la Granja Experimental Agroecológica Balcanes de la Universidad de la Amazonia. *Momentos de Ciencia*, 11: 17-22.

WONG, S.Y, MEEROW, A.W. and CROAT, T.B. 2016. Resurrection and new species of the Neotropical genus *Adelonema* (Araceae: *Philodendron* clade). *Systematic Botany*, 41: 32-48.

WWF (World Wildlife Fund). 2018. Ecoregions: Central America: Panama and Colombia. Available from: <https://www.worldwildlife.org/ecoregions/nt0122> (accessed 15 May 2018).

ZONA, S. and CHRISTENHUSZ, M.J.M. 2015. Litter-trapping plants: filter-feeders of the plant kingdom. *Botanical Journal of the Linnean Society*, 179: 554–586.

ZOTZ, G. 2004. How prevalent is crassulacean acid metabolism among vascular epiphytes? *Oecologia*, 138: 184-192.

ZOTZ, G. 2013. ‘Hemiepiphyte’: a confusing term and its history. *Annals of Botany*, 111: 1015-1020.

Appendix 1. List of aroids from Cerro Pirre, with life-forms and geographical distribution. Note: TE (terrestrial), EP (epiphytic), NV (nomadic vine), EL (epilithic).

Taxon	Life-form	Distribution
<i>Adelonema panamense</i> Croat & Mansell	TE	PA (endemic)
<i>Adelonema wendlandii</i> (Schott) S.Y. Wong & Croat	TE	Central America and CO
<i>Anthurium brownii</i> Mast.	EP	CO, CR, EC, PA, VE

Taxon	Life-form	Distribution
<i>Anthurium cerropirrense</i> Croat	EP	PA (Serranía de Pirre)
<i>Anthurium clavigerum</i> Poepp. & Endl.	NV	BZ, BO, BR, CO, CR, EC, GY GF, GY, HN, NI, PA, PE, VE
<i>Anthurium crassitepalum</i> Croat	EP	PA (Serranía de Pirre)
<i>Anthurium crystallinum</i> Linden & André	TE	CO, PA
<i>Anthurium cucullispathum</i> Croat	EP	CO, CR, PA
<i>Anthurium curvispadix</i> Croat	EP	PA (endemic)
<i>Anthurium cuspidatum</i> Mast.	EP, TE	CO, CR, EC, PA
<i>Anthurium dukei</i> Croat	EP	PA (Serranía de Pirre)
<i>Anthurium friedrichsthalii</i> Schott	EP	CO, CR, EC, NI, PA
<i>Anthurium hartmanii</i> Croat & O.Ortiz	TE	PA (Serranía de Pirre)
<i>Anthurium interruptum</i> Sodiro	EP	BZ, BO, CO, CR, EC, GT, NI, PA
<i>Anthurium kunthii</i> Poepp.	NV	BO, BR, CO, CR, EC, PA, PE, VE
<i>Anthurium lancifolium</i> Schott	TE	CO, CR, NI, PA
<i>Anthurium michelii</i> Guillaumin	EP	CO, CR, EC, PA, PE.
<i>Anthurium niqueanum</i> Croat	NV	PA (Serranía de Pirre)
<i>Anthurium obtusum</i> (Engl.) Grayum	EP	BZ, BO, BR, CO, CR, EC, SV, GY, GY GF, HN, MX, PA, PE, SR, VE.
<i>Anthurium ochranthum</i> K. Koch	TE	CO, CR, HN, NI, PA.
<i>Anthurium panduriforme</i> Schott	EP	CO, CR, EC, PA
<i>Anthurium pendens</i> Croat	EP	CO, PA
<i>Anthurium pentaphyllum</i> var. <i>bombacifolium</i> (Schott) Madison	NV	BZ, CR, GT, HN, MX, NI, PA
<i>Anthurium pirrense</i> Croat	EP	PA (Serranía de Pirre)
<i>Anthurium ramonense</i> Engl. ex K. Krause	EP	CO, CR, NI, PA
<i>Anthurium ravenii</i> Croat & R.A. Baker	EP	CO, CR, EC, HN, NI, PA.
<i>Anthurium rotundistigmatum</i> Croat	EP	CO, PA
<i>Anthurium rubrifractum</i> Croat	NV	PA (Serranía de Pirre)

Taxon	Life-form	Distribution
<i>Anthurium salvinii</i> Hemsl.	EP, TE, EL	CO, CR, GT, HN, MX, NI, PA
<i>Anthurium scandens</i> subsp. <i>pusillum</i> R. Sheffer	EP	CO, CR, EC, HN, NI, PA, VE
<i>Anthurium talamancae</i> Engl.	EP	CR, CO, PA
<i>Anthurium terryaе</i> Standl. & L.O. Williams	EP	PA (Serranía de Pirre)
<i>Anthurium tonduzii</i> Engl.	EP	CO, CR, EC, PA
<i>Anthurium trilobum</i> hort. ex André	EP	CO, CR, EC, PA
<i>Anthurium</i> sp. 1	EP	PA (Serranía de Pirre)
<i>Anthurium</i> sp. 2, sp. nov.	EP	PA (Serranía de Pirre)
<i>Anthurium</i> sp. 3, sp. nov	EP	PA (Serranía de Pirre)
<i>Anthurium</i> sp. 4, sp. nov	TE	PA (Serranía de Pirre)
<i>Anthurium</i> sp. 5, sp. nov	EP	PA (Serranía de Pirre)
<i>Anthurium</i> sp. 6, sp. nov	EP	PA (Serranía de Pirre)
<i>Anthurium</i> sp. 7	EP	PA (Serranía de Pirre)
<i>Chlorospatha mirabilis</i> (Mast.) Madison	TE	CO, EC, PA
<i>Chlorospatha</i> sp. nov. 1	TE	PA (Serranía de Pirre)
<i>Dieffenbachia isthmia</i> Croat	TE	CO, PA
<i>Dieffenbachia killipii</i> Croat	TE	CO, CR, EC, PA, PE.
<i>Dieffenbachia longispatha</i> Engl. & K. Krause	TE	CO, CR, NI, PA
<i>Heteropsis oblongifolia</i> Kunth	NV	BO, BR, CO, CR, EC, NI, PA, VE
<i>Monstera dubia</i> (Kunth) Engl. & K. Krause	NV	BZ, BO, BR, CO, CR, EC, GT, GY, GY GF, HN, MX, NI, PA, PE, VE.
<i>Monstera pinnatipartita</i> Schott	NV	BO, CO, CR, EC, SV, PA, VE.
<i>Monstera adansonii</i> Schott subsp. <i>laniata</i> (Schott) Mayo & I.M. Andrade	NV	Lesser Antilles, BR, CO, CR, AN (Curaçao), EC, SV, GT, GY, GY GF, HN, NI, PA, PE, SR, VE.
<i>Monstera oreophila</i> Madison	NV	CR, PA.
<i>Monstera spruceana</i> (Schott) Engl.	NV	BO, BR, CO, CR, EC, GY GF, PA, PE, SR, VE.
<i>Monstera pittieri</i> Engl.	NV	CO, CR, PA.

Taxon	Life-form	Distribution
<i>Philodendron albisuccus</i> Croat	NV	CO, PA
<i>Philodendron alliodorum</i> Croat & Grayum	NV	CO, CR, EC, NI, PA
<i>Philodendron clewellii</i> Croat	NV	PA (Serranía de Pirre)
<i>Philodendron edenuatum</i> Croat	NV	PA (endemic)
<i>Philodendron ensifolium</i> Croat & Grayum subsp. <i>ensifolium</i>	NV	CO, CR, EC, PA.
<i>Philodendron fragrantissimum</i> (Hook.) G. Don	NV	BZ, BR, CU, CO, CR, EC, GT, GY, GY GF, HN, NI, PA, PE, SR, VE.
<i>Philodendron grandipes</i> K. Krause	TE	CO, CR, EC, NI, PA.
<i>Philodendron ichthyoderma</i> Croat & Grayum	NV, TE	CO, EC, PA
<i>Philodendron lazorii</i> Croat	NV	CO, PA
<i>Philodendron immixtum</i> Croat	NV	CO, PA
<i>Philodendron inaequilaterum</i> Liebm.	NV	BZ, BO, BR, CO, CR, EC, SV, GT, HN, MX, NI, PA, PE, VE.
<i>Philodendron ligulatum</i> var. <i>heraclioanum</i> Croat	NV	CO, PA
<i>Philodendron niqueanum</i> Croat	NV	PA (Serranía de Pirre)
<i>Philodendron opacum</i> Croat & Grayum	NV	CO, CR, EC, NI, PA
<i>Philodendron panamense</i> K. Krause	NV	CO, PA
<i>Philodendron pirrense</i> Croat	NV	PA (Serranía de Pirre)
<i>Philodendron platypetiolatum</i> Madison	NV	CO, CR, EC, NI, PA
<i>Philodendron pseudauriculatum</i> Croat	NV	CO, PA
<i>Philodendron purpureoviride</i> Engl.	NV	CO, CR, EC, PA
<i>Philodendron rayanum</i> Croat & Grayum	NV	CO, CR, PA
<i>Philodendron sagittifolium</i> Liebm.	NV	BZ, CO, CR, GT, HN, MX, NI, PA, VE.
<i>Philodendron sulcatum</i> K. Krause	NV	CO, CR, EC, NI, PA
<i>Philodendron tenue</i> K. Koch & Augustin	TE	CO, CR, EC, HN, NI, PA, VE.
<i>Philodendron tripartitum</i> (Jacq.) Schott	NV	BR, CO, CR, SV, GT, HN, JM, MX, NI, PA, PE, VE.
<i>Philodendron tuerckheimii</i> Grayum	NV	CO, CR, EC, SV, GT, HN, MX, NI, PA, VE.

Taxon	Life-form	Distribution
<i>Philodendron verrucosum</i> L. Mathieu ex Schott	NV	CO, CR, EC, NI, PA, PE.
<i>Philodendron wilburii</i> var. <i>longipedunculatum</i> Croat & Grayum	NV	CR, PA.
<i>Philodendron</i> sp. nov. 1	NV	PA (Serranía de Pirre)
<i>Rhodospatha moritziana</i> Schott	TE	CO, CR, EC, PA, PE, VE.
<i>Rhodospatha wendlandii</i> Schott	NV	BZ, CO, CR, GT, HN, MX, NI, PA
<i>Spathiphyllum laeve</i> Engl.	TE	CO, CR, EC, SV, NI, PA
<i>Spathiphyllum phryniifolium</i> Schott	TE	BZ, CO, CR, SV, GT, HN, MX, PA.
<i>Stenospermation angustifolium</i> Hemsl.	EP	CO, CR, EC, HN, NI, PA, PE
<i>Stenospermation ellipticum</i> Croat & D.C. Bay	EP	CO, PA.
<i>Stenospermation</i> sp. nov. 1	EP	PA (Serranía de Pirre)
<i>Syngonium schottianum</i> H. Wendl. ex Schott	NV	CR, HN, NI, PA.
<i>Syngonium hoffmannii</i> Schott	NV	CR, HN, NI, PA.
<i>Syngonium podophyllum</i> Schott	NV	Lesser Antilles, BS, BZ, BO, BR, CO, CR, CU, EC, SV, GT, GY, GY GF, HT, HN, MX, NI, PA, PE, SR, TT, US, VE.
<i>Syngonium</i> sp. 1	NV	PA (Serranía de Pirre)
<i>Xanthosoma mexicanum</i> Liebm.	TE	BR, CO, CR, SV, GT, MX, NI, PA, VE.
<i>Xanthosoma hammelii</i> Croat, Delannay & O.Ortiz	TE	PA (Serranía de Pirre)