Acta Societatis Botanicorum Poloniae

Authors' Contributions
The principle author (TBC) wrote the initial manuscript but sought the help of the junior author (OOO) who greatly modified and improved the article owing to his mastery of the newer literature.

Competing Interests
No competing interests have been declared.

Distribution of Araceae and the Diversity of Life Forms

Thomas B. Croat [1*], Orlando O. Ortiz [2,3]
[1] Missouri Botanical Garden, St. Louis, Missouri, United States
[2] Universidad de Panamá, Panama City, Panama
[3] Coiba Scientific Station (COIBA AIP), Panama City, Panama

*To whom correspondence should be addressed. Email: thomas.croat@mobot.org

Abstract

This paper discusses the family Araceae, emphasizing its worldwide distribution and the diversity of morphological and ecological characteristics of the family that have enabled it to reach such a prominent position with diverse habitats. Few families of its size have come to inhabit such a diverse spectrum of habits and biomes. The family has important habit forms and growth structures that have enabled such distributional patterns. The very broad spectrum of life forms it demonstrates is one of the main characteristics of the family, namely broad habitat diversity. This coupled with high species diversity; high rates of endemism and the presence of large numbers of unknown species (probably the highest of any family percentage-wise) constitute principal characteristics of the family.

Keywords

aroids; distributional patterns; growth structures; habit forms; endemism

1. Introduction

The Araceae is a family of 144 genera and 3,645 published species, worldwide in distribution (Boyce & Croat, 2011; Croat, 1979). It is the third largest family of monocots and is divided into eight subfamilies, all of which had evolved before the K/T boundary (Cretaceous/Tertiary) and is one of the oldest members of the angiosperms (Croat, 2019; Hesse & Zetter, 2007; Nauheimer et al., 2012; Stevens, 2020) with fossil pollen assignable to the clade Pothoideae–Monsteroideae from the Late Barremian–Aptian (Early Cretaceous) period, about 120–110 million years ago (Friis et al., 2004), and macrofossils apparently related to Aroideae, found in other deposits with a similar age (Friis et al., 2010). This paper will discuss the worldwide distribution of the family and will enumerate the diversity of morphological modifications in life form, systems of pollination and fruit dispersal that may have led to the extraordinary rates of endemism that characterize the Araceae.

2. Life Form Diversity

Members of the eight subfamilies often have unique distributions at least partly dictated by their morphology (Croat, 1988). Several of the subfamilies, particularly the more basal members (those referred to as Proto-Araceae by Mayo et al., 1997) are (excepting the Gymnostachydoideae) exclusively aquatic or are from cold marshy habitats (*Symplocarpus*). These constitute the subfamily Orontioideae with two genera *Orontium* (golden club) in Eastern North America and *Lysichiton* with two disjunct species (Western North America and temperate East Asia) as well as *Symplocarpus* (with two disjunct species, boreal North America and boreal northeastern Russia and on the Kamchatka Peninsula). Thus, the major group Proto-Araceae consists of only four small genera. The sole exception to the aquatic habitat is the monotypic *Gymnostachys*, which might have evolved out of wet habitat with the drying up of the Australian continent (Nauheimer et al., 2012; Stevens, 2020).

The other subfamilies (except Lemnoideae) are included in the megadiverse True Araceae clade (Cusimano et al., 2011; Mayo et al., 1997). In this clade, the habit diversity is variable, ranging from species occurring in seasonally dry habitats (ranging from only a few weeks of arid condition to periods of several months). For subfamily Pothoideae this is notably true for tribe Anthureae, the massive group containing Neotropical *Anthurium*, a genus comprising an estimated 3,000 species which inhabits nearly every corner of the neotropics as well as its smaller Asian component, the tribe Potheae with what is increasingly considered to consist of a single genus, *Pothos* (Boyce & Croat, 2011; Wong et al., 2020).

The subfamily Monsteroideae comprises 12 genera in four tribes: Spathiphylleae, Anadendreae, Heteropsideae, and Monstereae (Mayo et al., 1997). Molecular work by Tam et al. (2004) showed strong support for the subfamily but not much support for clades within the subfamily. The classification of Monsteroideae by Cusimano et al. (2011) recognizes 12 genera grouped into three clades: (*i*) tropical American clade (*Heteropsis* clade): *Alloschemone, Heteropsis, Rhodospatha, Stenospermation*; (*ii*) the tribe Spathiphylleae: *Holochlamys* and *Spathiphyllum*; (*iii*) mostly Old World clade (*Rhaphidophora* clade): *Amydrium, Anadendrum, Epipremnum, Monstera, Scindapsus*, and *Rhaphidophora*. Recent molecular studies by Zuluaga et al. (2019) found high support for the monophyly of the three major clades (Spathiphylleae sister to *Heteropsis* and *Rhaphidophora* clades), and for six of the genera within Monsteroideae, the Old World genera *Anadendrum* (Boyce, 2009), *Scindapsus*, as well as the New World *Monstera* (Madison, 1977a) in one clade, along with *Rhodospatha, Stenospermation*, and *Heteropsis* in another clade. The subfamily Monsteroideae inhabits largely seasonally moist forests. Being mainly a group of epiphytic appressed-climbing plants, they are susceptible to periods of drought but manage to survive owing to their thick leaves and numerous adventitious roots, which are very adept at clinging to surfaces of any kind.

The Spathiphylleae are certainly frequently excluded from seasonal habitats since *Spathiphyllum* commonly occurs on wet roadside banks, swamps, and on rapids in full sun. *Holochlamys*, closely related to Asian *Spathiphyllum*, are likewise usually a facultative rheophyte. The genus *Heteropsis* is particularly vulnerable to changes in rainfall but survives high in trees by sending long feeder roots to the ground (Balcázar-Vargas, 2013). Native people to make baskets and other useful products harvest these feeder roots. Naturally, the plant populations suffer from this harvesting. Attempts to cultivate the plant lower to the ground have not been successful (Soares et al., 2013). The Asian genus *Anadendrum* is similar in growth pattern to tribe Monstereae, growing as hemiephytic climbers or nomadic vines in seasonal forests (Nguyen et al., 2019). The *Rhaphidophora* clade with six genera, *Amydrium, Anadendrum, Rhaphidophora, Epipremnum*, and *Scindapsus* all from the Old World tropics cluster with *Monstera*, while *Stenospermation, Rhodospatha, Heterospis*, and *Aloschemone* from the New World tropics form another clade (*Heteropsis* clade) (Zuluaga et al., 2019). In both cases, the genera are mostly hemiepiphytic climbers inhabiting seasonally moist forests. Possible exceptions to a marked seasonal habit include the genus *Stenospermation* (Castaño-Rubiano, 2011; Gómez de Pérez, 1983), which sometimes inhabits ever-wet cloud forest life zones (Croat, 1988).

Genera of subfamily Lasioideae have leaves that are thin and often much subdivided (Hay, 1981). Most species occur either in directly aquatic habitats or in seasonal habitats where they lose their leaves and survive underground during the drier months with usually large storage tubers. In the former swampy category are *Anaphyllopsis* (Hay, 1988a), *Dracontioides*, and *Urospatha* from the neotropics and some *Cyrtosperma* (Hay, 1986, 1988b), *Lasimorpha, Podolasia*, and *Lasia* from the paleotropics plus Indian *Anaphyllum*. Alternatively, *Dracontium* typically occurs in seasonally dry habitats and have large starchy tubers also Indochinese *Pycnospatha*. Since these tubers are mostly consumed in the process of rebuilding the leaf, it is important that the leaves survive until the tuber can regenerate (Zhu, 1995). The reptilian pattern on most petioles of such genera (including in the unrelated

Amorphophallus) may deflect animals from approaching the plant (since in reality the petioles are soft and easily broken), thus preventing the now reduced tuber from being endangered.

The position of *Calla palustris* represented as subfamily Calloideae (sensu Bogner & Nicolson, 1991; Mayo et al., 1997) lacks a defined phylogenetic status at present. This is because the subfamily has bisexual flowers but otherwise has many features found in the more highly evolved group of genera in subfamily Aroideae. These features include the possession of unisexual flowers, which lack a perianth and have inaperturate pollen as well as laticifers and biforine raphides but lack sproropollenin. According to Barabé et al. (2004), *Calla* was embedded in Aroideae (without strong support). In another molecular work (Cabrera et al., 2008), *Calla* came out in a clade of Aroideae along with other rooted marsh plants, but its position was unclear in both morphological and restriction site analyses. Recently, the phylogenomics study of Henriquez et al. (2014) supports the inclusion of *Calla* in the Aroideae subfamily as well as suggests that *Calla* and *Schismatoglottis* formed a clade (with weak support), that was sister to one of the two major clades within Aroideae. With *Calla* and the more basal Araceae with bisexual flowers set aside, the prediction of habit diversity in the remainder of the family Araceae (here constituting only the massive subfamily Aroideae) is more complex. Tribe Pistieae (with a single pantropical genus apparently consisting of one species) is a free-floating aquatic. It was long thought to be closely related to the subfamily Lemnoideae, but is now been shown to be entirely subsumed into the Aroideae (*Pistia* clade) (Renner & Zhang, 2004; Rothwell et al., 2004). The Lemnoideae is a pantropical group of five genera and 47 species are minute floating aquatics (Boyce & Croat, 2011). The members of this subfamily can occur in permanent or seasonal lentic habitats, lotic habitats, and, rarely, can grow on mud, wet rock walls, or in the drip of waterfalls (Landolt, 1986, 1998, 2000); in some cases, large colonies comprising up to three Lemnoideae species can grow on waterfall's vertical rocks at the same time (Blanco & Jiménez, 2019). The most outstanding characteristic of this group is its small size, the reduction of its organs and the small morphological differentiation. The most extreme condition occurs in *Wolffia*, in which the plants comprise a spherical and taloid body of only 0.5 mm in diameter (Landolt & Schmidt-Mumm, 2009), and they are among the smallest flowering plants in the world.

Before discussing the balance of the family, now primarily subfamily Aroideae, three unusual African genera, *Stylochaeton*, *Zamioculcas*, and *Gonatopus* need to be discussed. All have unisexual perigonate flowers, unlike any other group of aroids, so they belong not with basal groups of Araceae with bisexual perigonate flowered genera nor with the subfamily Aroideae with unisexual naked flowers. Mayo et al. (1997) placed *Zamioculcas* and *Gonatopus* in subfamily Aroideae, tribe Zamioculcadeae, while placing *Stylochaeton* in tribe Stylochaetoneae, also in subfamily Aroideae. Subsequently, Bogner and Hesse (2005) described the subfamily Zamioculcadoideae that includes *Gonatopus* and *Zamioculcas*, based on anatomical, morphological, and molecular data. Later molecular studies of Cuasimano et al. (2011) proposed the *Stylochaeton* clade that includes *Stylochaeton* as a sister group to Zamioculcadoideae (*Zamioculcas* + *Gonatopus*). Henriquez et al. (2014) suggested that subfamily Zamioculcadoideae should be expanded to include *Stylochaeton*. The genus *Stylochaeton* with 25 species, has subterranean rhizomes and they range across sub-Saharan Africa. *Zamioculcas*, with two species ranges up the tropical east and subtropical southeast coast of Africa. *Gonatopus* with five species has a range similar to *Zamioculcas*. Both have short thick rhizomes and compound leaves. It has been documented that *Z. zamiifolia* has the ability to tolerate water stress and low light, as it can also grow in various types of dry or semidry habitats (humid to seasonally dry forests, open bushland, and savannas) (Mayo et al., 1997; Newton, 1997). So far, *Z. zamiifolia* is the only nonaquatic CAM species of the order Alismatales; this survival characteristic allows it to grow effectively in habitats with seasonal droughts, due to the reduction of water loss and the constant carbon gain (Holtum et al., 2007).

The subfamily Aroideae is an enormous group consisting of 24 tribes (sensu Mayo et al., 1997). Recent studies show that this subfamily, which consists of more than 1,500 species in 75 genera (Nauheimer et al., 2012), is supported by both

molecular data and morphological characters (except for the particular case of *Calla*), characterized by the loss of the perigone, presence of laticifers, and loss of sporopollenin in the ektexine (Cusimano et al., 2011). According to Cusimano et al. (2011), the Aroideae clade (No. 39) is composed of Clades 32 (*Zantedeschia* clade) and 38 (*Philonotion* clade) together with the genera *Callopsis*, *Montrichardia*, and *Anubias*. Tribe Callopsideae (sensu Mayo et al., 1997) with the single genus *Callopsis* with one species is native to tropical West Africa (Benin) occurring in the understory of lowland evergreen forest at elevations up to 800 m (Bogner, 1969). The tribe Anubiadeae with a single genus *Anubias* is an aquatic group in tropical West Africa. In turn, the Neotropical tribe Montrichardieae has only one genus, *Montrichardia*, with two wide-ranging species, one in Central America and northern South America, the other in the Amazon basin (Croat et al., 2005). *Anubias* and *Montrichardia* both share an inferred ancestral haploid chromosome number of *n* = 12 and the only feature shared is a helophytic habit (Henriquez et al., 2014). These are large rooted freshwater aquatics that inhabit the banks of watercourses and have water dispersed berries (Lins, 1994).

Recently, Henriquez et al. (2014) demonstrated that *Anubias* and *Montrichardia* (excluding *Calla*) form a clade that is sister to the *Zantedeschia* clade, and in addition, the South African genus *Zantedeschia* is sister to the Old World *Anchomanes* clade, which comprises the tribes Nephthytideae and Aglaonemateae. The monotypic African tribe Zantedeschieae inhabits Southern Africa (Letty, 1973; Sing, 1996) but at least one species, *Zantedeschia aethiopica*, has escaped from cultivation and inhabits cold wet highland regions of both Central and South America. The tribe Nephthytideae are almost exclusively African but with one species of *Nephthytis* from central Borneo in Sarawak. *Anchomanes* have thick rhizomes and occur in seasonally dry areas in forest understory across Central Africa (Tchiakpè, 1979). They are often leafless during the dry period. The very rare *Pseudohydrosme* with a tuberous stem occurs in seasonally dry forests in Gabon in tropical West Africa (Bogner, 1981). In turn, the tribe Aglaonemateae, traditionally with two Asian genera, is divided in habitat with *Aglaodorum* occurring exclusively as rhizomatous herbs in tidal swamps and *Aglaonema* occurring in the understory of mostly moist forests (Nicolson, 1969). Recently, Boyce and Croat (2011) have mentioned that *Aglaodorum* will be merged into *Aglaonema*.

The Neotropical tribe Spathicarpeae includes the genera *Dieffenbachia*, *Bognera*, *Mangonia*, *Taccarum*, *Asterostigma*, *Gorgonidium*, *Synandrospadix*, *Gearum* (Bogner & Gonçalves, 1999), *Spathantheum*, *Spathicarpa*, *Croatiella*, *Incarum*, and *Lorenzia* (Gonçalves, 2012; Gonçalves et al., 2007). *Dieffenbachia* and *Bognera* (formerly included in a separate tribe, Dieffenbachieae) are essentially understory herbs, but *Dieffenbachia* is often capable of surviving for long periods of time under water in várzea (annually flooded) forest along the rivers of the upper Amazon where the river banks remain under water for months at a time. The remaining genera of the tribe are all endemic to South America. They mostly occur in open habitats or as understory herbs (Gonçalves, 2002).

According to Mayo et al. (1997), the Philodendreae tribe, certainly the largest of all tribes in subfamily Aroideae, is diverse in its growth habits but most species are hemiepiphytic and occur in seasonally moist to very wet forest, as you would expect from species which have to survive without a lot of its root system affixed to the soil. Tribe Homalomeneae (with amendments by Wong et al., 2013, 2016) has three genera, *Furtadoa*, *Homalomena*, and *Adelonema*, but *Furtadoa* is polyphyletic and is nested within *Homalomena* (Wong et al., 2016). The two former genera are Asian, terrestrial, and largely occur in the forest understory and as riparian herbs along streams. *Homalomena* has evolved extensively in Borneo with many species adapted to different edaphic conditions (Boyce & Wong, 2019). *Adelonema*, in the neotropics consists of understory herbs largely in moist to wet forest (Wong et al., 2013). It should be noted that Cusimano et al. (2011) resolved *Philodendron*, *Homalomena*, and *Furtadoa* in a specific clade, the *Philodendron* clade, equivalent to the combined tribes Homalomeneae and Philodendreae sensu Mayo et al. (1997), and sister to African tribe Culcasieae (for more information of the *Philodendron* clade, see Wong et al., 2016). Tribe Culcasieae has two African genera, *Cercestis* and *Culcasia*

(Hepper, 1967), both of which are primarily hemiepiphytic climbers [*Culcasia* may have purely terrestrial species like *C. mannii* (Hook. f.) Engl.] occurring in the understory of seasonally wet primary forest or sometimes in secondary forest.

The rheophytes clade (sensu Cusimano et al., 2011), which includes a high representation of rheophytes (Boyce & Wong, 2019) and aquatics, comprises two main subclades: Cryptocoryneae and Schismatoglottideae. The Asian tribe Schismatoglottideae has a growth habit similar to *Homalomena* with many species evolving in edaphically unique habitats, mostly aquatic or riparian habitats, but also as understory herbs that are not directly associated with streams. Wong et al. (2010), proposed that the Neotropical *Schismatoglottis* is sister to the Paleotropical Schismatoglottideae + Cryptocoryneae, therefore, they resurrected the genus *Philonotion* for the Neotropical species (these inhabiting open swampy areas) and include them in a new tribe, Philonotieae S. Y. Wong & P. C. Boyce. Combined molecular and morphological analyses in Schismatoglottideae concluded that this tribe comprises 29 genera: *Apoballis*, *Aridarum*, *Bakoa*, *Bakoaella*, *Bidayuha*, *Bucephalandra*, *Burttianthus*, *Colobogynium*, *Fenestratarum*, *Galantharum*, *Gamogyne*, *Gosong*, *Hera*, *Heteroaridarum*, *Hottarum*, *Kiewia*, *Nabalu*, *Naiadia*, *Ooia*, *Phymatarum*, *Pichinia*, *Piptospatha*, *Pursegloveia*, *Rhynchopyle*, *Schismatoglottis*, *Schottariella*, *Schottarum*, *Tawaia*, and *Toga* (Boyce & Wong, 2018; Low et al., 2018). The tribe Cryptocoryneae has two Asian genera, *Lagenandra* (Wit, 1978) and *Cryptocoryne*, both of which are obligate aquatic groups (Graf & Arends, 1986; Hay, 1986; Jacobsen, 1979; Rataj, 1975).

The molecular work of Cuasimano et al. (2011) placed two subgroups, the tribes Thompsonieae and Caladieae, in the *Amorphophallus* clade. The mostly American tribe Caladieae is very diverse in habit, ranging from *Jasarum*, a rooted but totally submerged aquatic plant (Bogner, 1977), to *Scaphispatha*, which occurs in dry open grassy areas or in temporary wet spots in Bolivia or southern Brazil (Gonçalves, 2013; Madison, 1981). *Caladium* and *Xanthosoma* share similar habits, usually in seasonally wet forests. The former is nearly always seasonally dormant as are those *Xanthosoma* with underground tubers. *Xanthosoma* frequently has erect stems, and these species occur in wet forest habitats. *Chlorospatha* occurs principally in areas of moist or wet forest but those occurring in seasonally dry habitats in the Amazon basin have short rhizomatous stems that can lose their leaves and remain dormant in the dry season. *Syngonium* is a hemiephytic climber and inhabits moist to wet forest, never really going dormant (Croat, 1981). Molecular and anatomic evidence (Cuasimano et al., 2011; Keating, 2004) indicates that the members of South American tribe Zomicarpeae (sensu Mayo et al., 1997) are part of Caladieae. The genera *Zomicarpa*, *Zomicarpella*, *Ulearum*, and *Filarum* are mostly from western Amazonia (Nicolson, 1966) and consist of species with rhizomatous tubers occurring in seasonally wet forest on "tierra firme" (forest not seasonally flooded and subject to low periods of inundation) (Bogner, 2007). Recently, Gonçalves (2018) described an additional monotypic genus *Idimanthus* Gonçalves, which is represented by the species, *I. amorphophalloides*, from northern Rio de Janeiro State. With these additions, Caladieae now comprises 12 genera. *Hapaline* is the only Asian representative of the tribe. *Hapaline* is a tuberous understory herb from Southeastern Asia, which grows among deposits of humus in rocky moist seasonally wet habitats (Madison, 1981). Its geophytic life form and typically large tuberous stems (Boyce, 1996) characterize tribe Thompsonieae with the single genus, *Amorphophallus*. It occurs in seasonally dry areas across sub-Saharan tropical and subtropical Africa east to tropical and subtropical Asia to as far east as New Guinea and eastern Australia. Most species grow in secondary forests (Grob et al., 2002; Ham et al., 1998; Hetterscheid & Ittenbach, 1996).

The *Colletogyne* clade (sensu Cusimano et al., 2011) includes tribe Arisareae and the *Typhonodorum* clade (*Peltandra*, *Typhonodorum*, and the tribe Arophyteae). Tribe Arisareae with the genus *Arisarum* is a Mediterranean group consisting of three species (Boyce, 1990), all tuberous or rhizomatous species inhabiting seasonally dry, more or less open habitats. The tribe is very similar to the tribe Ambrosineae, a monospecific group with tuberous stems from the Mediterranean region. The endemic Madagascan tribe Arophyteae (Bogner, 1972, 1975) with three small

genera, *Arophyton*, *Carlephyton*, and *Collectogyne*, is represented by plants with tuberous stems and inhabit seasonally dry understory forest mostly in the more mesic portions of the Island of Madagascar (Bogner & Nusbaumer, 2012). Tribe Peltandreae (sensu Mayo et al., 1997) with a strange disjunct distribution has two aquatic genera. *Typhonodorum* with a single species is a massive thick-stemmed aquatic native to Madagascar and South Africa, whereas *Peltandra* is a much smaller aquatic plant with two species occurring in the Southern United States.

The *Pistia* clade has two main subgroups: the *Colocasia* clade and the *Alocasia* clade. The most distinctive subgroup of the *Alocasia* clade is the Areae (Cusimano et al., 2011). The tribe Areae, while heavily centered in the Mediterranean region and the Near East, is one of the most widespread of all groups in the Aroideae with some genera from India, East Asia, and Australia. The group has largely tuberous stems and occurs in seasonally dry habitats. Some species of *Arum* occur in Northern European woodlands, while others are better suited to the hot dry summer and cold wet winters of the Mediterranean region. The genera *Dracunculus* and *Helicodiceros* (Boyce, 1994) as well as *Biarum* occur in the latter life zone (Talvera, 1976). *Eminium*, heavily concentrated in the Near East and ranging east to Tajikistan relies on a Mediterranean climate (Boyce, 1989, 1993; Riedl, 1979) or regions of monsoon forests with decided dry periods (Riedl, 1969). *Theriophonum*, with six species, is largely endemic to the Indian subcontinent (Nicholson & Sivadasan, 1982). It is a group with tuberous stems inhabiting seasonally wet forests. The genus *Sauromatum*, the only member of tribe Areae to occur in Africa other than *Arum*, occurs in Central Africa, the Arabian Peninsula, and in tropical and subtropical Southern Asia. They are tuberous and seasonally dormant. The genus *Typhonium*, an Asian genus with tuberous stems (Sriboonma et al., 1994), occurs in a wide range of habitats from seasonal to evergreen forests over a wide range of elevations. *Lazarum*, formerly a part of *Typhonium* (Cusimano et al., 2010), is an Australian genus of 18 species occurring in seasonally dry habitats (Hay, 1993). Tribe Arisamateae with *Pinella* and *Arisaema* (with 125 and eight species, respectively) is the most widespread group in subfamily Aroideae with species ranging from Eastern North America and Mexico to Eastern Africa, southern Arabian Peninsula to most of southern continental Asia, Japan, the Malayan Archipelago and Philippines, occurring mostly in the understory of upland tropical forests and in temperate areas (Gusman & Gusman, 2006; Murata, 1984).

Finally, the tribe Colocasieae with four genera (Ly et al., 2017): *Ariopsis* with two species occurs in South West India and the Himalayas and grows as geophytes in evergreen forest; *Remusatia*, centered principally in the Himalaya/Indochina/South China, like the rest of tribe Colocasieae is more widespread owing to the common *R. vivipara*. It has four species occurring across Central Africa, the southern Arabian Peninsula, Southern Asia, and northern Australia and have tuberous stems and special epizoochorous vegetative propagules (Li, 1992); *Steudnera*, another genus with tuberous stems, occurs in Southeastern Asia in South China and Indochina (Krause, 1920); *Colocasia*, now with 14 accepted species which are terrestrial or epilythic herbs mostly in Southeastern Asia. Published studies (Ly et al., 2017) have shown that the rank Colocasieae must be redefined since it constitutes a polyphyletic assemblage with *Leucocasia* and *Alocasia*. Thus, the authors suggest that it be referred to as the *Alocasia-Colocasia* clade. The formal tribe Alocasieae now also contains four genera: *Engleranum*, newly described (Nauheimer & Boyce, 2013), *Vietnamocasia*, another new species from Vietnam (Ly et al., 2017) along with the resurrected genus *Leucocasia* (Ly et al., 2017) and the widespread genus *Alocasia*, which ranges from India to Southeastern Asia, Japan, Melanesia, New Guinea, and eastern Australia (Hay & Wise, 1991). *Colocasia*, a much smaller genus than *Alocasia* (eight species vs. 78) but occupies much of the same range albeit ranging further to the west on the Indian subcontinent and only as far east as Java and Lesser Sunda in Indonesia. Most of the members of the *Alocasia-Colocasia* clade occur in ever-wet to seasonal forest mostly as understory herbs or as weedy plants in open areas. *Colocasia* and *Alocasia*, which have tuberous or rhizomatous stems, are both moderately species-rich and widespread in Southeastern Asia. After a serious rearrangement of tribes Colocasieae and Alocasieae (Ly et al., 2017), the genus

Protarum is left alone in its own tribe (presumably tribe Protareae) with a single species with a tuberous stem from the Seychelles Island in the Indian Ocean where it occurs in seasonally wet forest (Bogner, 1973). *Protarum* is sister to everything else in the *Alocasia-Colocasia* clade and should therefore be maintained as a tribe with the remainder of the former Alocasioideae and Colocasoideae constituting another tribe and probably three subtribes (Peter Boyce, personal communication, 2020). A review of the above listed tribes of Araceae in subfamily Aroideae shows five tribes (Anubiadeae, Cryptocoryneae, Montrichardieae, Peltandreae, and Pistieae) have species, which consistently occur in wet habitats. Four additional tribes (Homalomenaeae, Schismatoglottideae, Caladieae, and Aglaonemateae) have significant percentages of their species occurring in dry habitats but also in wet habitats. The remaining 14 tribes have species that are predominantly occurring in seasonal forests and rely on mostly tuberous or well-protected rhizomatous stems to withstand periods of drought and a generally leafless condition.

3. Modifications in Life Form

What is it that has enabled the Araceae to inhabit such a wide spectrum of habitats? Obviously, morphological changes have evolved in every part of the plant throughout the family to accomplish the changes needed to allow aroids to adapt to so many different habits throughout the world.

3.1. Roots

Tremendous variations have taken place in root systems along with corollary changes in the stem. Plants developed different types of roots, some for clasping to hold the climbing stem to the tree, others for descending to the ground (feeder roots). To accommodate an epiphytic life form so important in the Neotropical aroids, stems have undergone many changes. Since epiphytes often get only moments of time to capture water during brief rains, roots have developed root hairs that are more compact or developed many more roots per node, e.g., *Anthurium* sect. *Pachyneurium* (Croat, 1991). In special cases where water and nutrients are particularly rare some aroids such as *Anthurium gracile* (Rudge) Schott in sect. *Leptanthurium* developed roots with velamen capable of extracting water directly from the air. In most cases epiphytes have developed thicker leaves to prevent the loss of water, more compacted root systems for capturing more water, and have evolved an active geniculum and thickened sheathed portion at the base of the petioles to better orient the leaf blades to get more or less light to better suit demands for survival.

For trap forming epiphytes such as *Anthurium* sect. *Pachyneurium* and sect. *Porphyrochitonium*, the roots at the upper internodes are usually narrowly tapered and held stiffly erect, forming an ideal debris-collecting basket which creates a good environment for trapping water and nutrients (Dressler, 1985; Zona & Christenhusz, 2015).

Many tuberous aroids have small propagules on the upper surface that can be loosened by peccaries and rodents such as agoutis (Altrichter et al., 2000). These will produce new plants vegetatively, but their growth is very close to the surface of the soil and must in due course be further buried. Older and larger tubers must be more deeply buried. Some species of *Dracontium* and *Amorphophallus* have evolved contractile roots which cause the tubers to be pulled deeper into the ground with each successive growing season when the tuber shrinks as the new leaf is produced, leaving a temporary void in the ground. Contractile roots pull the tuber into a void.

3.2. Stems

Climbing stems of hemiepiphytic plants have developed differential growth, long and slender internodes for early stages of climbing, thick short internodes for slow climbing once a plant has reached its optimal height in the trees. Despite that, variations in length and diameter of the article (nodes structure) ended up with the same volume (Ray, 1986) but without this modification in relative length versus width a plant would quickly go from an ideal spot in the canopy to one perilous for its existence, too sunny and exposed.

The secondary hemiepiphytic life form can provide the ability to mobilize in response to favorable growth conditions, such as higher luminosity and availability of host trees, allowing individuals to move and find suitable sites with adequate conditions for their development (Croat, 1997; Lee & Richards, 1991; Madison, 1977b). Once a plant reaches its most favorable position, it may produce slender flagellate growth (e.g., *Philodendron linnaei* Kunth) with long internodes to spread quickly to other parts of the same tree or even different trees to take advantage of a new site. Aroids are very adept at repositioning themselves in relation to their environment and repeatedly returning to the ground, seeking another source of support and climbing, all the while changing their stems, petioles and leaves to adapt to their constantly changing needs (Ray, 1981, 1987a, 1989). In the case of juvenile plants of hemiepiphytic climbing genera, the skototropic growth probably evolved to enable find proper sources of host plant (or rocks) upon which to climb (Strong & Ray, 1975). Under these circumstances, the juvenile plants grow toward the darkest area on the horizon until they come in contact with a tree, a large stone, or a cliff and the growing stem tip is forced to turns upward. At that point, auxin control causes growth to shift to phototropic growth and the stem elongates upward toward light.

Most hemiepiphytic species are considered secondary hemiepiphytes, starting their life as a terrestrial plant, finding a tree, then climbing it, and later sometimes losing connection with ground. Zotz (2020) prefers to call these secondary hemiepiphytes nomadic vines and has found that most such plants still have feeder roots extending to the ground. Nevertheless, aroids differ from ordinary vines in that the stem often retains a certain fixed length. As it climbs and elongates at the apex it also rots off on the trailing end. Regular vines on the other hand do not have adventitious roots and usually do not survive after being severed above the soil line. Primary hemiepiphytes (Zotz, 2013, 2016) on the other hand start their life from seeds deposited high in the canopy and grow there for years until they are strong enough to produce long pendent roots that grow to the ground to enable the plant to gain easier access to water and nutrients.

Vegetative growth of stems of Araceae is usually extremely well developed so that even without reproduction plants may form large stands in the understory even before breeding populations are established. In the case of introduced or escaped species, e.g., *Colocasia esculenta*, *Epipremnum aureum*, *Rhaphophora aurea*, or *Alocasia macorrhizos*, flowering is rare even when the species is widespread and common. Even native species fully capable of flowering and fruiting sometimes appear to rely extensively on vegetative reproduction. *Syngonium erythrophyllum* on Barro Colorado Island (Croat, 1978) produces thousands of juvenile plants in many parts of the island but adult flowering plants are rare. In *Philodendron*, it has been documented that some species are abundant in the lowland forests of central Panama, but with irregular distribution throughout the forest (Croat, 1978; Royo & Carson, 2005). The vegetative reproduction in *Philodendron* probably allows a rapid colonization, which leads to the formation of large conglomerate colonies throughout the tree hosts, and the displacement of other hemiepiphytic and epiphytic species. In a study conducted in Panama by Ortiz et al. (2019), the authors reported that members of *Philodendron* subgenus *Pteromischum* (*P. alliodorum*, *P. inaequilaterum*, *P. ichthyoderma*, and *P. opacum*) are the more abundant aroid taxa in a seasonal lowland tropical forest (758 individuals in 3,200 m^2). They argue that the ability to reproduce vegetatively through flagelliform shoots, which are common structures in *Pteromischum* (Grayum, 1996), could drive high colonization and dominance throughout the forest.

Dieffenbachia and *Xanthosoma* may produce vast stands of plants all looking alike and probably all genetically identical, yet in other parts of the forest yet another form can be found in large stands. These different large populations often represent the same species, but each stand is in itself unique in all looking the same. This is no doubt the result of vegetative growth. Animals, especially peccaries, often root around such populations, no doubt breaking up the stems. This can result in the production of new branches.

Aroids are almost unique in having a caudex instead of a regular stem like most

dicotyledonous plants. The caudex differs in that it has the regular stem growth interspersed with roots. Each node of the stem is capable of producing a leaf (and perhaps an inflorescence). The presence of roots at all the nodes makes an epiphytic habit possible since the stem continues its growth up the side of a tree and always has its roots present, even when the older portion of the stem dies. It also allows for easy separation of the stem with each portion continuing to grow since each node also has that ability to produce new branches. It is the nature of this special caudex that explains the overwhelming popularity of Araceae as ornamental plants because even small pieces of the stem can potentially produce new growth. This is true not only for *Monstera* and other climbers but also for traditionally terrestrial species with erect stems like *Dieffenbachia* or creeping stems like *Spathiphyllum*. Most aroid stems can be cut into pieces repeatedly to create new plants. This makes them popular and easy to share with others, a feature many plant families do not have. It is perhaps for this reason that aroids are among the most popular of all ornamental plants. Few plant families can be so easily reproduced and few can so easily be brought into cultivation from cuttings as the aroid family. Studies show that year after year aroids make up to half or more of the top dozen ornamental plants sold each year in North America (United States Department Agriculture, 2001).

Stems and leaves have made many corollary changes owing to their epiphytic lifestyle. Young plants near the ground get little light so their leaves are usually velvety, allowing for more light penetration. Later the opposite is true. So smooth and glossy leaves allow better water shedding and light reflection to prevent being sunburned. Heteroblastic leaf development is more common in Araceae than any other family (Ray, 1987a, 1987b), and these changes in leaf morphology have much to do with the differences in the requirements of juvenile and preadult plants and those of the adult plants.

The number of stem modifications is enormous and could be the subject of an entire book. Suffice it to say here that these modifications have enabled Araceae to fill so many niches worldwide and are responsible for much of their success at adapting to new and different habitats.

The relative positioning of leaves on a stem can make a big difference in the survival of a plant. Some species, those with short internodes, often have leaf blades supported by short petioles and arranged in a tight rosette. This enables the leaves to form a basket that directs water and nutrients into the center and base of the basket where the roots can absorb them (Zona & Christenhusz, 2015). Even the disposition of the primary lateral veins and the sulcate petioles act to direct even small amounts of accumulated water directly to the roots. This is especially important in areas of low rainfall but where afternoon cloud forests with saturated air cause precipitation in the form of dew that accumulates on leaves. The afternoon cloud forests along the Pacific Coast in Ecuador for example are rich in epiphytes despite low annual rainfall.

Whether the vast changes in leaf morphology is dictated by the growth of the plant, there is little doubt that no other family has such a wide spectrum of leaf shape, blade size, blade texture, and blade coloration.

4. Systems of Pollination

The manner in which plants are pollinated has a strong influence on speciation, therefore, much of existing floral evolution must be driven by pollinators mediated natural selection (Fenster et al., 2004; van der Niet & Johnson, 2012). There are many factors that can directly influence the sexual reproduction processes of angiosperms. Among the most relevant are the flowering time, flower morphology, color, and floral scent (Kudo, 2006). But it is not only enough to know the factors involved, it is also important to determine the connection between the macroevolutionary patterns of this floral diversity and the microevolutionary processes of the populations (Harder & Johnson, 2009).

Since aroid species, at least in some groups (*Anthurium* and *Philodendron* for example) have evolved into many species, it is important to ask how the systems of pollination with Araceae might have affected the number of species. Although

much has been published about pollination biology of aroids, especially regarding its ability for thermogenesis (self-production of heat in the inflorescence which in turn volatilize floral scent for attracting pollinators) in some genera (Seymour & Gibernau, 2008, Seymour et al., 2009), little is still known overall about pollination of aroids. The subject of thermogenesis in temperate plants and observations of pollination on temperate aroids such as *Arum* is so extensive that it will be ignored here but the situation with tropical aroids is quite different. Currently this is changing and many new researchers are actively engaged in creating a better understanding of the systems of pollination (Gibernau, 2016), especially with *Amorphophallus* (Kite & Hetterscheid, 2017), *Anthurium* (Bleiweiss, Sornoza-Molina, et al., 2019; Bleiweiss, Trujillo, et al., 2019; Díaz-Jiménez, Hentrich, Aguilar-Rodríguez, et al., 2019; Etl et al., 2017; Franz, 2007; Gómez-Murillo & Cuartas-Hernández, 2016; Hartley & Gibernau, 2018; Hartley et al., 2017; Hentrich et al., 2010; Schwerdtfeger et al., 2002), *Dieffenbachia* (Beath, 1999; Etl et al., 2016; Gibernau, 2015a, 2015b; Gibernau et al., 2001; Young, 1986, 1988a, 1988b, 1990), *Monstera* (Cedeño, 2019; Chouteau et al., 2007; Díaz-Jiménez et al., 2020; Díaz-Jiménez, Hentrich, Aguilar-Rodríguez, et al., 2019; Prieto & Cascante-Marín, 2017; Vilela & Prieto, 2018), *Montrichardia* (Gibernau, 2003; Gibernau & Barabé, 2003; Gibernau et al., 2003), *Spathiphyllum* (Díaz-Jiménez, Hentrich, Ruiz-Idarraga, et al., 2019; Hentrich et al., 2010; Montalvo & Ackerman, 1986), *Taccarum* (Maia, Gibernau, et al., 2012; Maia et al., 2013), *Caladium* (Maia, Dötterl, et al., 2012), *Xanthosoma* (García-Robledo et al., 2004, 2005; Gómez-Murillo & Cuartas-Hernández, 2016; Milet-Pinheiro et al., 2017), and *Philodendron* sensu lato including *Thaumatophyllum* (Barbosa et al., 2019; Dötterl et al., 2012; Gibernau & Barabé, 2000a, 2000b, 2002; Gibernau et al., 1999; Gonçalves-Souza et al., 2018; Gottsberger & Amaral, 1984; Gottsberger et al., 2013; Maia et al., 2010; Pereira et al., 2014; Young, 1987).

In many angiosperm groups, flower morphology may be crucial for pollination effectiveness, due to the fit between the body of the pollinators and the floral organs (Nilsson, 1988), but in the case of Araceae, the inflorescence morphology and floral scents seem to also represent very determining factors in the transfer of pollen. A lot of this research is much advanced owing to the now readily available means of capturing scents produced by the plant during anthesis in situ without damaging the sampled plant and the easy manner of identifying behaviorally the active compound with gas chromatography as well as by electroantennographic screening experiments and computerized databases of scents. Small syringes coated with adsorbent polymers (SPME fibers) can be exposed to the floral scent to collect the volatile compounds. Also, small portable battery powered devices can suck the floral scent produced by the inflorescences through tiny charcoal cylinders which trap the volatile compounds. These, in turn, can be sent off for analysis by gas chromatography coupled to mass spectrometry (GC-MS). This has been a major pursuit of some researchers, particularly Artur Maia at the Federal University of Paraiba in Brazil, who has used this technique on a variety of different plants, including palms, water lilies and aroids (Maia & Schlindwein, 2006; Maia et al., 2010, 2013). Florian Etl at the University of Vienna in Austria has shown for example that not only is there a difference in the scent produced, but has shown that bees can be induced to visit inflorescences only at specific times, so that it is a combination of the scent produced and the exact timing of that scent production that enable species to be in flower at seemingly the same time without being cross-pollinated. Furthermore, Pedro Díaz-Jiménez from Mexico and Heiko Hentrich from Germany have found that in addition to the aroma, the type of habitat, the way the plants grow (grouped or scattered), and the type of flowering (synchronous or asynchronous) are important factors to determine the group of attracted pollinators. Insect pollination systems are not only separated temporally but also altitudinally (Gómez-Murillo & Cuartas-Hernández, 2016). In the forest, some beetles are visiting species near the ground, especially *Dieffenbachia*, *Caladium*, and *Xanthosoma*, for example, with other beetles visiting species higher in the trees pollinating high-climbing plants like *Philodendron*. Since aroids, unlike orchids, have rather open pollination systems with their flowers easily capable of being pollinated by any nearby insects, aroids have evolved elaborate methods of timing

and especially the production of scents. These different scents have coevolved with their pollinators (mostly beetles for species with unisexual flowers and mostly bees for genera like *Anthurium* with bisexual flower).

Euglossine bees have coevolved with *Anthurium* for example with many bee species visiting only specific *Anthurium* species and at specific times of the day (Díaz-Jiménez, Hentrich, Aguilar-Rodríguez, et al., 2019). This is also true of beetle-pollinated plants like *Dieffenbachia*, *Monstera*, *Philodendron*, and *Xanthosoma*. Increasingly, we are finding strange scents for which no known pollination syndrome is known, particularly in the megagenus *Anthurium*, where an undescribed species from Ecuador (Morona-Santiago near El Pangui) in sect. *Belolonchium* has an inflorescence that smells like burning steel when in flower (Simon Wellinga, personal communication, 2020). Another species, *Anthurium clidemiodes* Standl., has been shown by Jay Vannini (personal communication, 2020) to produce a foul scent quite unlike one you would expect to be bee pollinated. The same is true of *A. decipiens* A. Hay and M. Cedeño (sect. *Belolonchium*) that has a foul-smell, which attracts *Sarcophaga* flies (these are usually associated with dung or carrion) (Hay & Cedeño-Fonseca, 2019). Some species like a Jamaican endemic species (yet unnamed) seem to produce no scent at all, day or night. Others, like *Anthurium fragrantissimum* Croat (sect. *Porphyrochitonium*), have highly predictable times of flowering (in this case from 11:30 a.m. to 1:00 p.m.) (Thomas B. Croat, personal observation, 2020). The montane endemic species from Panama, *Anthurium sapense* Croat (sect. *Calomystrium*), have a strong chewing gum scent in the afternoon (4:00 to 5:00 p.m.) (Orlando O. Ortiz, personal observation, 2014). Danny Beath (personal communication, 1999) found that some euglossine pollinated plants produced scent for only short periods of time in the early morning hours (perhaps when bees consumed less energy than hotter times of the day). However, floral scents in *Anthurium* might be as variable as the high diversity of visiting insects (Hartley & Gibernau, 2018). For example, species visited by Cecidomyiidae midges are scentless to the human nose, while those visited by Drosophilidae emit alcoholic or rotten fruit smells, but most studied species emitted strong, agreeable perfumes in the morning hours in accordance with euglossine bee syndrome (Schwerdtfeger et al., 2002).

Despite these observations, it can be reported that we have investigated only a few (less than 300 species) of the thousands of aroid species (Gibernau, 2016) and many species of aroids, especially species of *Anthurium* do not seem to have scents that are associated with the presently known systems of pollination. Although Drosophilidae flies have been observed in inflorescences in several *Anthurium* species, particularly in those with fermented fruit aroma, so far there is no detailed study confirming these insects as their main pollinators (Schwerdtfeger et al., 2002). Chemistry of floral scents, in the particular case of *Anthurium*, could be of great importance to clarify its infrageneric classification. The problem is that many diagnostic morphological characters used in the sectional classification are highly homoplasious within *Anthurium*, hindering a morphological interpretation of the lineages identified in the recent constructed phylogenies (Carlsen & Croat, 2019). In this case, perhaps studies on the chemical composition of floral scent volatile emissions could yield relevant information that could be used to support *Anthurium* clades by means of a chemophenetic characterization. Certainly, pollination systems have evolved which reflect the differences in habitat. In cloud forests, for example where *Anthurium* sect. *Belolonchium* are prominent, the spathes are typically designed to form a roof over the typically long and pendent spadix, no doubt to prevent the pollen from being washed away by the constantly dripping conditions found there. In addition, bees flying around in the rain find the dry spadix more inviting and probably spend more time visiting the flowers during rain. *Anthurium gualeanum* Engl., also occurring in high cloud forest where temperatures are often quite low, produces a shape that essentially completely encloses the spadix with only a small entry window at anthesis. Thus, it not only provides shelter from the rain but the wind and cold as well.

In the same manner, *Stenospermation*, also occurring in cloud forests, is designed to turn its entire inflorescence upside down because otherwise the spathe would form

a perfect funnel and fill with water, which would destroy the pollen and drown the visiting beetles. *Anthurium* sect. *Calomystrium*, while usually not occurring so high and flowering under better climatic conditions, also often have the spathe cucullate at the apex to provide a roof to protect the usually suberect spadix.

While by no means a tropical plant, the temperate aroid *Symplocarpus foetidus* (L.) Salisb. ex W. Barton when flowering in the early spring in North America may emerge from the snow. Here, thermogenesis (the rapid oxidation of stored starch triggered by acetocylic acid) creates a warm and welcoming pollination area for its foul-scented stone fly-pollinated flowers (Thorington, 2000).

Philodendron species are known to be pollinated by large Dynastine scarab beetles (Moore & Jameson, 2013), especially species of *Cyclocephala* and *Erioscelis*, which visit the flowers to find mating sites at dusk following scents being wafted out of the inflorescences owing to thermogenic activity. Beetles fly in zigzag patterns following scents until near the inflorescence where the usually paler interior spathe surface provides a landing target. Beetles aggregate, sometimes in large numbers where they breed, eat the sterile male flower, and affect pollination of then receptive protogynous female flowers (Gottsberger & Amaral, 1984; Gottsberger et al., 2013; Maia et al., 2010). They spend the night and all of the following day in the spathe tube (no doubt to avoid being eaten by ever-vigilant birds). Near or at dusk of the following day when thermogenic heat causes the male flowers to burst their pollen deposits and cause oozing fibers of pollen to emerge, the beetles are forced to leave the inflorescence by the now closing spathe, forcing them to climb the spadix and be covered with pollen. Almost invariably, the spathe also provides a resinous substance produced on the spathe or spadix to cover much of the otherwise shiny slick carapace of the beetle with stickiness to hold the adhering dry pollen (Gibernau et al., 1999; Maia et al., 2010).

It is not the purpose here to review all the possibilities in the field of pollination of aroids (see reviews by Gibernau, 2003, 2011, 2016) but only to point out that pollination is clearly driving speciation, in association with comparable speciation in the associated insect groups, notably Euglossine bees in *Anthurium* and Dynastine scarab beetle in genera with unisexual flowers. These complex systems already studied show great potential for many more insect pollination systems to be discovered.

5. Endemism

Aroids are well known for their high rates of endemism (Croat, 1983, 1986, 1991, 1992, 1997, 2004; Croat & Delannay, 2017a, 2017b; Croat, Delannay, & Hannon, 2017; Croat, Delannay, & Ortiz, 2017; Croat & Hannon, 2015; Croat & Lambert, 1987; Zhu & Croat, 2004), and this endemism is particularly evident in the Andes of South America. Aroid species in the Amazon basin are very often wide-ranging; some extending from the Guianas to the Beni River basin in Bolivia, but aroids growing in the Andes are much more likely to be endemic. This is probably owing to the difference in topography. While elevational change and even life zone ecology (Holdridge, 1967) are more uniform in the Amazon basin, much of which consists of tropical moist forest (Holdridge, 1967). The Andes Mountains provide a veritable kaleidoscope of colors when viewing a Holdridge life zone map of Colombia, Ecuador, or Peru (where maps exist). Bolivia, where maps do not exist, has even more life zones (48) based on Holdridge publication of the life zone of that country (Tosi et al., 1975). The life zone may change repeatedly as one ascends or descends the slopes of the Andes, going from one river system to another. All the while, a careful observer will notice that the species visible along the road are constantly changing. Many species do not leave the river system in which they evolve.

Why is it that so many aroids remain endemic in such areas? I contend that much of this endemism is owing to a lack of fruit dispersal. Most aroids, and certainly *Anthurium*, are largely bird dispersed. They grow primarily in the understory of forests where birds tend to be secluded and territorial. Purportedly such birds are even reluctant to cross broad rivers. Under such circumstances, it is not

surprising that many species, which arise through mutations or hybridization, tend to remain localized. Aroid species are also severely restricted within sometimes narrow elevational ranges (Ortiz et al., 2019). At the La Planada Reserve in Nariño Department of Colombia, where the senior author studied Araceae (Croat et al., 2009, 2010), the species were found to be severely restricted. The Río Imbi, well within view of the La Planada field station but lying at 1,100 m, shares not a single species with the higher site. Even more surprising was that a trip to the Río Ñambí located only 37 km away at the same elevation and same life zone (Premontane wet forest) showed few species in common with the Río Imbi. To show that even adjacent river valleys can have their own unique flora, the senior author can cite studies in the Lita-San Lorenzo region in the valley of the Río Mira where few species are found in common with the Valley of the Río San Juan not very far to the north (Croat et al., 2018, 2019).

5.1. Species Diversity

Knowledge of the Araceae has undergone unprecedented growth in just the past 40 years. This growth is expected to continue. For example, the Araceae of the flora of Panama (Standley, 1944) comprised 82 names but the present number of species of Araceae known in Panama is 610 species (Ortiz et al., 2018). Similar increases would be found in all tropical American floristic studies. In just the past 40 years, the increase in the size of Neotropical genera (i.e., species known per genus) ranged from 13% to 78% with the average more than 50% for all genera (Croat, 2019). During this same period, nearly 1,000 Araceae species were published as new. Moreover, this appears to be an unceasing situation with more species being discovered even in well-known areas of Central America. *Xanthosoma*, once considered by the senior author to be the most poorly know genus, yielded over 100 new species on a recently completed revision of most of its natural range (Croat & Delannay, 2017a, 2017b; Croat, Delannay, & Hannon, 2017; Croat, Delannay, & Ortiz, 2017). The genus *Anthurium* in Central America last revised in the mid-1980s (Croat, 1983, 1986) went from 121 species to 222 species with many sterile specimens seemingly distinct but remaining uncounted. Moreover, studies have shown that species diversity increases dramatically with increases in rainfall. In Central America, the large but moderately dry Mexican component, while moderately rich in endemics (65% of the total flora) contributes proportionally about the same number of species per unit area (one species per 14,089 km^2) in Mexico as the more mesic areas in Middle America (here defined as constituting Belize, Guatemala, El Salvador, Honduras, Nicaragua, and Costa Rica), which has an average of one species per 1,569 km^2. Middle America, in contrast to Mexico, has low rates of endemism and, excepting Costa Rica, has rates that range from zero in El Salvador to 18% in Guatemala with Honduras and Nicaragua having 6% and 4% endemism, respectively. Therefore, both areas share roughly equivalent levels of species diversity despite radical differences in the rate of endemism.

What changes radically to the east of the San Juan depression (valley of Río San Juan on border of Costa Rica) is rainfall and with it a dramatic increase in both the number of species and the rates of endemism. Costa Rica shows a dramatic increase in the number of species (329 versus 108 in adjacent Nicaragua; most of these found near the border of Costa Rica) and vast increase in the number of endemic species (46% versus 2% for Nicaragua). Still richer by far is Panama with 615 species and a rate of endemism of 90%. In the following segment of this paper, we will demonstrate that we have by no means come to the end of discovery and are probably woefully underestimating the number of tropical species.

5.2. High Capacity to Increase

Many parts of the tropics have barely been explored and are expected to be the most species-rich with very high percentages of their flora largely unknown. This includes the wettest parts of the Neotropical biome, including parts of Darién Province of Panama, the Colombian departments of Chocó, Valle del Cauca, Cauca, and Nariño as well as the Ecuadorian provinces of Carchi and Esmeraldas. This region is the overall wettest in the world on average and easily constitutes the richest biome in

the world (Croat, 2019). Very little of its overall surface has been explored and a thorough study of the region could potentially produce numbers of species that would dwarf existing number of known species. Similar studies in some parts of Asia may be equally rewarding, particularly in Southeastern Asia, in Borneo, where evolution has taken a path dictated by edaphic differences in soil type among a largely riparian group of Aroids, mainly in Homalomeneae and Colocasioideae and possibly also in Schismatoglottideae (Boyce & Wong, 2019). The high potential for novel species is reflected in a list published online (Boyce & Croat, 2011) which attempts to reflect the present status of all aroid genera in the world, listing the number of published species and the number of anticipated unpublished species. The list shows that some genera such as *Alocasia*, *Anthurium*, *Buchephalandra*, *Chlorospatha*, *Cryptocoryne*, *Dieffenbachia*, *Homalomena*, *Monstera*, *Philodendron*, *Pothos*, *Rhaphidophora*, *Rhodospatha*, *Schismatoglottis*, *Scindapsus*, *Spathiphyllum*, *Stenospermation*, and *Typhonium* (genera from both the neotropics and the paleotropics) show considerable potential for increase. That the projected increase for the single Neotropical genus *Anthurium* exceeds the potential growth for all other genera is particularly noteworthy. Nearly 2,000 species have already been confirmed as not having been described, and another 1,000 specimens, partly specimens on loan to MO, have failed to key out to any known species but have not yet been further processed. Moreover, on an OPUS-funded herbarium study of 51 herbaria with Neotropical specimens, a total of 8,000 photographs were taken of specimens that could not be determined, i.e., likely to represent undescribed specimens. Therefore, the world's herbaria collectively still hold many specimens not yet determined, which are likely to represent unpublished species.

6. Conclusions

This paper has shown that the Araceae is a family with a broad array of ecological aptitude, widely ranging and highly adaptive to a wide array of ecological niches but one that is still poorly known taxonomically with a great potential for growth in numbers of species. With molecular studies, we are establishing the broader relationships and the ages of major groups, coming to understand the distribution patterns of major groups (Canal et al., 2019) and producing good revisions of the smaller genera. Pollination biology of aroids, while still in its infancy, is beginning to show great promise to help elucidate differences between species. Much remains to be known about the infrageneric status of the larger genera, particularly *Anthurium* and *Philodendron*, and more refined molecular and genetic techniques are needed to resolve internal disputes in the taxonomy. Above all, more fieldwork is needed in the vast expanses of unexplored areas of Central and South America as well as many parts of Southeastern Asia where species diversity is highest. Certainly for some genera, notably *Anthurium*, *Philodendron*, and *Stenospermation*, probably not even half of the potential species have been discovered. At the same time, fewer resources and trained personnel are available to do this work while legal matters, conservation laws, permission procedures, political difficulties, and simple lack of interest will insure that many of these unknown species will go extinct before they are discovered, collected, and studied.

Acknowledgments

References

Altrichter, M., Saenz, J., Carillo, E., & Fuller, T. (2000). Dieta estacional del *Tayassu pecari* (Artiodactyla; Tayassuidae) en el Parque Nacional Corcovado, Costa Rica [Seasonal diet of the *Tayassu pecari* (Artiodactyla: Tayassuidae) in Corcovado National Park, Costa Rica]. *Revista de Biologia Tropical*, *48*(2–3), 689–702.

Balcázar-Vargas, M. P. (2013). *From forest floor to the canopy: Life history of secondary Hemiepiphytes (Heteropsis species) in the Colombian Amazon* [Unpublished doctoral dissertation]. University of Utrecht.

Barabé, D., Lacroix, C., Bruneau, A., Archambault, A., & Giberneau, M. (2004). Floral development and phylogenetic position of *Schismatoglottis* (Araceae). *International Journal of Plant Sciences*, *165*(1), 173–189. https://doi.org/10.1086/380980

Barbosa, J. F., Sakuragui, C. M., & Rodrigues, D. (2019). Pollination of *Philodendron propinquum* Schott (Araceae): A new pattern in the lineage *Philodendron*. *International Journal of Plant Sciences*, *180*(2), 153–159. https://doi.org/10.1086/700970

Beath, D. (1999). Dynastine scarab beetle pollination in *Dieffenbachia longispatha* (Araceae) on Barro Colorado Island (Panama) compared with La Selva Biological Station (Costa Rica). *Aroideana – Journal of the International Aroid Society*, *22*, 63–71.

Blanco, M. A., & Jiménez, J. E. (2019). Duckweeds (Araceae: Lemnoideae) growing on wet, vertical rocks behind a waterfall in Costa Rica, with a new country record of *Wolffiella oblonga* (Phil.) Hegelm. *Adansonia*, *41*(1), 193–200. https://doi.org/10.5252/adansonia2019v41a15

Bleiweiss, R., Sornoza-Molina, F., Freire, E., & Croat, T. B. (2019). Bird visitation to a high Andean *Anthurium* (Araceae) in eastern Ecuador. *Flora*, *255*, 80–85. https://doi.org/10.1016/j.flora.2019.02.010

Bleiweiss, R., Trujillo, A. S. N., Croat, T. B., & Santomaro, C. G. (2019). First observations of butterfly (Pedaliodes: Satyrinae: Nymphalidae) visits to a wild *Anthurium* (Araceae). *Aroideana – Journal of the International Aroid Society*, *42*(2–3), 139–151. https://doi.org/10.1016/j.flora.2019.02.010

Bogner, J. (1969). Une nouvelle espèce du genre *Callopsis* Engl. (Aracées) et considerations taxonomiques sur se genre [A new species of the genus *Callopsis* Engl. (Araceae) and taxonomic considerations on this genus]. *Adansonia*, *9*, 285–291.

Bogner, J. (1972). Revision der Arophyteae (Araceae) [Revision of Arophyteae (Araceae)]. *Botanische Jahrbücher für Systematik*, *92*, 1–63.

Bogner, J. (1973). *Protarum sechellarum* Engl. *Palmengarten*, *37*(2), 40.

Bogner, J. (1975). Aracées [Araceae]. In H. Humbert (Ed.), *Flore de Madagascar et des Comores* [Flora of Madagascar and the Comoros] (pp. 3–75). Muséum National d'Histoire Naturelle.

Bogner, J. (1977). *Jasarum steyermarkii* Bunting (Araceae). *Aqua-Planta*, *2–3*, 4–7.

Bogner, J. (1981). *Pseudohydrosme gabunensis* Engl. *Aroideana – Journal of the International Aroid Society*, *4*, 31–37.

Bogner, J. (2007). *Zomicarpella maculata* (Araceae) rediscovered, with notes on the tribe Zomicarpeae. *Willdenowia*, *37*, 523–534. https://doi.org/10.3372/wi.37.37210

Bogner, J., & Gonçalves, E. G. (1999). The genus *Gearum* N. E. Br. (Araceae: tribe Spathicarpeae). *Aroideana – Journal of the International Aroid Society*, *22*, 20–29.

Bogner, J., & Hesse, M. (2005). Zamioculcadoideae, a new subfamily of Araceae. *Aroideana – Journal of the International Aroid Society*, *28*, 3–20.

Bogner, J., & Nicolson, D. H. (1991). A revised classification of Araceae with dichotomous keys. *Willdenowia*, *21*, 35–50.

Bogner, J., & Nusbaumer, L. (2012). A new species of *Carlephyton* (Araceae) from northern Madagascar with notes on the species of this genus. *Willdenowia*, *42*, 209–217. https://doi.org/10.3372/wi.42.42206

Boyce, P. C. (1989). A new classification of *Arum* with keys to the infrageneric taxa. *Kew Bulletin*, *44*(3), 383–395. https://doi.org/10.2307/4110359

Boyce, P. C. (1990). Friar's cowls and mouse plants: The genus *Arisarum*. *The Kew Magazine*, *7*, 14–21. https://doi.org/10.1111/j.1467-8748.1990.tb00142.x

Boyce, P. C. (1993). *The genus Arum*. HMSO.

Boyce, P. C. (1994). A synopsis of *Dracunculus* and *Helicodiceros* (Araceae: Aroideae). *Thaiszia*, *4*, 175–182.

Boyce, P. C. (1996). The genus *Hapaline* (Araceae: Aroideae: Caladieae). *Kew Bulletin*, *51*(1), 63–82. https://doi.org/10.2307/4118745

Boyce, P. C. (2009). *Anadendrum* (Araceae: Monsteroideae: Anadendreae) in Thailand. *Thai Forest Bulletin (Botany)*, *37*, 1–8.

Boyce, P. C., & Croat, T. B. (2011). *The Überlist of Araceae, totals for published and estimated number of species in aroid genera*. https://doi.org/10.13140/RG.2.2.24820.09605

Boyce, P. C., & Wong, S. Y. (2018). Recent changes to generic delimitations in the Schismatoglottideae. *Aroideana – Journal of the International Aroid Society*, *41*(1), 149–234.

Boyce, P. C., & Wong, S. Y. (2019). Borneo and its disproportionately large rheophytic aroid flora. *Gardens' Bulletin Singapore*, *71*(Suppl. 2), 497–524. https://doi.org/10.26492/gbs71(suppl.2).2019-24

Cabrera, L. I., Salazar, G. A., Chase, M. W., Mayo, S. J., Bogner, J., & Davila, P. (2008). Phylogenetics of aroids and duckweeds (Araceae) inferred from coding and noncoding plastid DNA. *American Journal of Botany*, *95*(9), 1153–1165. https://doi.org/10.3732/ajb.0800073

Canal, D., Koster, N., Celis, M., Croat, T. B., Borsch, T., & Jones, K. E. (2019). Out of Amazonia and back again: Historical biogeography of the species-rich Neotropical genus *Philodendron* (Araceae). *Annals of the Missouri Botanical Garden*, *104*(1), 49–68. https://doi.org/10.3417/2018266

Carlsen, M., & Croat, T. B. (2019). An analysis of the sectional classification of *Anthurium* (Araceae): Comparing infrageneric groupings and their diagnostic morphology with a molecular phylogeny of the genus. *Annals of the Missouri Botanical Garden*, *104*(1), 69–82. https://doi.org/10.3417/2018215

Castaño-Rubiano, N. (2011). *Revisíon taxonómica de Stenospermation (Araceae) para Colombia* [Taxonomic revision of *Stenospermation* (Araceae) in Colombia] [Unpublished master's thesis]. Universidad Nacional de Colombia.

Cedeño, M. V. (2019). *Revisión taxonómica del género Monstera (Araceae) en Costa Rica* [Taxonomic revision of the genus *Monstera* (Araceae) in Costa Rica] [Master's thesis, Universidad de Costa Rica]. http://hdl.handle.net/10669/80147

Chouteau, M., McClure, M., & Gibernau, M. (2007). Pollination ecology of *Monstera obliqua* (Araceae) in French Guiana. *Journal of Tropical Ecology*, *23*, 607–610. https://doi.org/10.1017/S0266467407004427

Croat, T. B. (1978). *Flora of Barro Colorado Island*. Stanford University Press.

Croat, T. B. (1979). The distribution of Araceae. In K. Larsen & L. B. Holm-Nielsen (Eds.), *Tropical botany* (pp. 291–308). Academic Press.

Croat, T. B. (1981). A revision of *Syngonium* (Araceae). *Annals of the Missouri Botanical Garden*, *68*(4), 565–651. https://doi.org/10.2307/2398892

Croat, T. B. (1983). A revision of the genus *Anthurium* (Araceae) of Mexico and Central America. Part 1: Mexico and Middle America. *Annals of the Missouri Botanical Garden*, *70*(2), 211–417. https://doi.org/10.2307/2399049

Croat, T. B. (1986). *A revision of the genus Anthurium (Araceae) of Mexico and Central America. Part 2: Panama*. Missouri Botanical Garden. https://doi.org/10.5962/bhl.title.102860

Croat, T. B. (1988). The ecology and life forms of Araceae. *Aroideana – Journal of the International Aroid Society*, *11*(3–4), 4–56.

Croat, T. B. (1991). A revision of *Anthurium* section *Pachyneurium* (Araceae). *Annals of the Missouri Botanical Garden*, *78*(3), 539–855. https://doi.org/10.2307/2399801

Croat, T. B. (1992). Species diversity of Araceae in Colombia: A preliminary survey. *Annals of the Missouri Botanical Garden*, *79*(1), 17–28. https://doi.org/10.2307/2399806

Croat, T. B. (1997). A revision of *Philodendron* subgenus *Philodendron* (Araceae) for Mexico and Central America. *Annals of the Missouri Botanical Garden*, *84*(3), 311–704. https://doi.org/10.2307/2992022

Croat, T. B. (2004). A revision of the genus *Dieffenbachia* (Araceae) of Mexico and Central America. *Annals of the Missouri Botanical Garden*, *91*(4), 668–772.

Croat, T. B. (2019). Araceae, a family with great potential. *Annals of the Missouri Botanical Garden*, *104*(1), 3–9. https://doi.org/10.3417/2018213

Croat, T. B., & Delannay, X. (2017a). A revision of *Xanthosoma* (Araceae). Part 3. Guianas. *Aroideana – Journal of the International Aroid Society*, *40*(2), 582–648.

Croat, T. B., & Delannay, X. (2017b). A revision of *Xanthosoma* (Araceae). Part 4: New species from Venezuela and other Caribbean countries. *Aroideana – Journal of the International Aroid Society*, *40*(2), 649–690.

Croat, T. B., Delannay, X., & Hannon, L. P. (2017). A revision of *Xanthosoma* (Araceae). Part 1. Western South America. *Aroideana – Journal of the International Aroid Society*, *40*(2), 4–503.

Croat, T. B., Delannay, X., & Ortiz, O. (2017). A revision of *Xanthosoma* (Araceae). Part 2. Central America. *Aroideana – Journal of the International Aroid Society*, *40*(2), 504–581.

Croat, T. B., Delannay, X., & Wood, R. (2018). A revision of *Anthurium* (Araceae) section *Polyneurium* for Carchi Province, Ecuador. *Aroideana – Journal of the International Aroid Society*, *41*(1), 4–126.

Croat, T. B., Fernández-Concha, G. C., & González, L. I. (2005). *Montrichardia arborescens* (L.) Schott (Araceae) newly reported for Mexico. *Aroideana – Journal of the International Aroid Society*, *28*, 86–87.

Croat, T. B., & Hannon, L. P. (2015). Revision of *Chlorspatha* (Araceae). *Annals of the Missouri Botanical Garden*, *101*(1), 1–229. https://doi.org/10.3417/2005079

Croat, T. B., Huang, P., Lake, J., & Kostelac, C. V. (2009). Araceae of the flora of Reserva La Planada, Nariño Department, Colombia (part 1). *Aroideana – Journal of the International Aroid Society*, *32*, 30–122.

Croat, T. B., Huang, P., Lake, J., & Kostelac, C. V. (2010). Araceae of the flora of Reserva La Planada, Nariño Department, Colombia (part 2). *Aroideana – Journal of the International Aroid Society*, *33*, 75–142.

Croat, T. B., & Lambert, N. (1987). The Araceae of Venezuela. *Aroideana – Journal of the International Aroid Society*, *9*, 3–214.

Croat, T. B., Teisher, J., Hannon, L. P., & Kostelac, C. V. (2019). Araceae of the Lita-San Lorenzo Region (Esmeraldas Province, Ecuador). Part 1: *Anthurium* sect. *Polyneurium*. *Annals of the Missouri Botanical Garden*, *104*(1), 105–168. https://doi.org/10.3417/2018071

Cusimano, N., Barrett, M. D., Hetterscheid, W. L. A., & Renner, S. S. (2010). A phylogeny of the Areae (Araceae) implies that *Typhonium, Sauromatum*, and the Australian species of *Typhonium* are distinct clades. *Taxon*, *59*(2), 439–447. https://doi.org/10.1002/tax.592009

Cusimano, N., Bogner, J., Mayo, S. J., Boyce, P. C., Wong, S. Y., Hesse, M., Hettersheid, W. L. A., Keating, R. C., & French, J. C. (2011). Relationships within the Araceae: Comparison of morphological patterns with molecular phylogenies. *American Journal of Botany*, *98*(4), 654–668. https://doi.org/10.3732/ajb.1000158

Díaz-Jiménez, P., Aguilar-Rodríguez, P. A., Cedeño-Fonseca, M., Zuluaga, A., Croat, T. B., Alarcón-Montano, M., Jiménez-Segura, M., López-Mora, M., MacSwiney, M. C., & Yovel, Y. (2020). *Monstera guzmanjacobiae* (Araceae), a new species from Mexico with notes on its reproductive biology. *Phytotaxa*, *437*(1), 39–46. https://doi.org/10.11646/phytotaxa.437.1.5

Díaz-Jiménez, P., Hentrich, H., Aguilar-Rodríguez, P. A., Krömer, A., Chartier, M., MacSwiney, M. C., & Gibernau, M. (2019). A review of the pollination of aroids with bisexual flowers. *Annals of the Missouri Botanical Garden*, *104*(1), 83–104. https://doi.org/10.3417/2018219

Díaz-Jiménez, P., Hentrich, H., Ruiz-Idarraga, J. M., Gibernau, M., & Zuluaga, A. (2019). The exceptional flowering behaviour of *Spathiphyllum grandifolium* Engl. (Araceae) – An indicator for self-pollination? *Ecotropica*, *21*, Article 201910.

Dötterl, S., David, A., Boland, W., Silberbauer-Gottsberger, I., & Gottsberger, G. (2012). Evidence for behavioral attractiveness of methoxylated aromatics in a dynastid scarab beetle-pollinated Araceae. *Journal of Chemical Ecology*, *38*, 1539–1543. https://doi.org/10.1007/s10886-012-0210-y

Dressler, R. L. (1985). Humus collecting shrubs in wet tropical forests. In K. C. Misra, H. N. Pandey, & S. R. Govie (Eds.), *Ecology and resource management in the tropics* (Vol. 1, pp. 289–294). International Society for Tropical Ecology.

Etl, F., Berger, A., Weber, A., Schönenberger, J., & Dötterl, S. (2016). Nocturnal plant bugs use *cis*-jasmone to locate inflorescences of an Araceae as feeding and mating site. *Journal of Chemical Ecology*, *42*, 300–304. https://doi.org/10.1007/s10886-016-0688-9

Etl, F., Franschitz, A., Aguiar, A., & Schönenberger, J. (2017). A perfume-collecting male oil bee? Evidences of a novel pollination system involving *Anthurium actuifolium* (Araceae) and *Paratetrapedia chocoensis* (Apidae, Tapinotaspidini). *Flora*, *232*, 7–15. https://doi.org/10.1016/j.flora.2017.02.020

Fenster, C. B., Armbruster, W. S., Wilson, P., Dudash, M. R., & Thomson, J. D. (2004). Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 375–403. https://doi.org/10.1146/annurev.ecolsys.34.011802.132347

Franz, N. M. (2007). Pollination of *Anthurium* (Araceae) by derelomine flower weevils (Coleoptera: Curculionidae). *Revista de Biológica Tropical*, *55*(1), 269–277.

Friis, E. M., Pedersen, K. R., & Crane, P. R. (2004). Araceae from the Early Cretaceous of Portugal: Evidence on the emergence of monocotyledons. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 16565–16570. https://doi.org/10.1073/pnas.0407174101

Friis, E. M., Raunsgard-Pedersen, K., & Crane, P. R. (2010). Diversity in obscurity: Fossil flowers and the early history of angiosperms. *Philosophical Transactions of the Royal Society London, Biological Series*, *365*, 369–382. https://doi.org/10.1098/rstb.2009.0227

García-Robledo, C., Kattan, G., Murcia, C., & Quintero-Marín, P. (2004). Beetle pollination and fruit predation of *Xanthosoma daguense* (Araceae) in an Andean cloud forest in Colombia. *Journal of Tropical Ecology*, *20*(4), 459–469. https://doi.org/10.1017/S0266467404001610

García-Robledo, C., Quintero-Marín, P., & Mora-Kepfer, F. (2005). Geographic variation and succession of arthropod communities in inflorescences and infructescences of *Xanthosoma* (Araceae). *Biotropica*, *37*(4), 650–656. https://doi.org/10.1111/j.1744-7429.2005.00082.x

Gibernau, M. (2003). Pollinators and visitors of aroid inflorescences. *Aroideana – Journal of the International Aroid Society*, *26*, 66–83.

Gibernau, M. (2011). Pollinators and visitors of aroid inflorescences: An addendum. *Aroideana – Journal of the International Aroid Society*, *34*, 70–83.

Gibernau, M. (2015a). Floral biology, pollination ecology and genetics of *Dieffenbachia* (Araceae) – A review. *Aroideana – Journal of the International Aroid Society*, *38*(2), 19–28.

Gibernau, M. (2015b). Pollination ecology of two *Dieffenbachia* in French Guiana. *Aroideana – Journal of International Aroid Society*, *38E*, 38–66.

Gibernau, M. (2016). Pollinators and visitors of aroid inflorescences III – Phylogenetic and chemical insights. *Aroideana – Journal of the International Aroid Society*, *39*(3), 4–22.

Gibernau, M., Albrie, J., Dejean, A., & Barabé, D. (2001). Seed predation in *Philodendron solimoesense* (Araceae) by chalcid wasps (Hymenoptera). *International Journal of Plant Sciences*, *163*(6), 1017–1023. https://doi.org/10.1086/342628

Gibernau, M., & Barabé, D. (2000a). Flowering and pollination of *Philodendron melinonii* (Araceae) in French Guiana. *Plant Biology*, *2*, 331–334. https://doi.org/10.1055/s-2000-3712

Gibernau, M., & Barabé, D. (2000b). Thermogenesis in three *Philodendron* species (Araceae) of French Guiana. *Canadian Journal of Botany*, *78*, 685–689. https://doi.org/10.1139/b00-038

Gibernau, M., & Barabé, D. (2002). Flowering and pollination of *Philodendron squamiferum* (Araceae). *Canadian Journal of Botany*, *80*, 316–320. https://doi.org/10.1139/b02-006

Gibernau, M., & Barabé, D. (2003). Beetle pollination of *Monrichardia arborescens*. *Journal of Tropical Ecology*, *19*, 103–107. https://doi.org/10.1017/S0266467403003134

Gibernau, M., Barabé, D., Cerdan, P., & Dejean, A. (1999). Beetle pollination of *Philodendron solimoesense* (Araceae) in French Guiana. *International Journal of Plant Sciences*, *160*(3), 1135–1143. https://doi.org/10.1086/314195

Gibernau, M., Barabé, D., Labat, D., Cerdan, P., & Dejean, A. (2003). Reproductive biology of *Montrichardia arborescens* (Araceae) in French Guiana. *Journal of Tropical Ecology*, *19*, 103–107. https://doi.org/10.1017/S0266467403003134

Gonçalves, E. G. (2002). *Sistemática e evolução da tribo Spathicarpeae (Araceae)* [Systematics and evolution of the Spathicarpeae tribe (Araceae)] [Unpublished doctoral dissertation]. Universidade de São Paulo.

Gonçalves, E. G. (2012). *Lorenzia* (Araceae – Spathicarpeae): A new genus supported by matk sequence data. *Systematic Botany*, *37*(1), 48–52. https://doi.org/10.1600/036364412X616620

Gonçalves, E. G. (2013). Five new Brazilian species for the tribe Caladieae (Araceae). *Aroideana – Journal of the International Aroid Society*, *36*, 73–86.

Gonçalves, E. G. (2018). *Idimanthus:* A new aroid genus (Araceae – Caladieae) from Rio de Janeiro State, Brasil. *Phytotaxa*, *351*, 88–92. https://doi.org/10.11646/hytotaxa.351.1.8

Gonçalves, E. G., Mayo, S. J., Sluy, M. A., & Salatino, A. (2007). Combined genotypic-phenotypic phylogeny of the tribe Spathicarpeae (Araceae) with reference to independent events of invasion to Andean regions. *Molecular Phylogenetics and Evolution*, *43*, 1023–1039. https://doi.org/10.1016/j.ympev.2007.01.008

Gonçalves-Souza, P., Schlindwein, C., & Paiva, E. A. S. (2018). Floral resins of *Philodendron adamantinum* (Araceae): Secretion, release and synchrony with pollinators. *Acta Botanica Brasilica*, *32*(3), 392–401. https://doi.org/10.1590/0102-33062018abb0115

Gottsberger, G., & Amaral, A., Jr. (1984). Pollination strategies in Brazilian *Philodendron* species. *Berichte der Deutschen Botanischen Gesellschaft*, *97*, 391–410.

Gottsberger, G., Silberbauer-Gottsberger, I., & Dötterl, S. (2013). Pollination and floral scent differentiation in species of the *Philodendron bipinnatifidum* complex (Araceae). *Plant Systematics and Evolution*, *299*, 793–809. https://doi.org/10.1007/s00606-013-0763-4

Gómez de Pérez, A. (1983). *A revision of Stenospermation (Araceae) in Central America* [Unpublished master's thesis]. Saint Louis University.

Gómez-Murillo, L., & Cuartas-Hernández, S. E. (2016). Patterns of diversity of flower-visitor assemblages to the understory Araceae in a tropical mountain forest in Colombia. *Journal of Insect Conservation*, *20*(6), 1069–1085. https://doi.org/10.1007/s10841-016-9945-z

Graf, A., & Arends, J. C. (1986). The occurrence of *Cryptocoryne* and *Lagenandra* (Araceae) in Sri Lanka. *Nordic Journal of Botany*, *6*(6), 757–764. https://doi.org/10.1111/j.1756-1051.1986.tb00476.x

Grayum, M. H. (1996). Revision of *Philodendron* subgenus *Pteromischum* (Araceae) for Pacific and Caribbean Tropical America. *Systematic Botany Monographs*, *47*, 1–233. https://doi.org/10.2307/25027858

Grob, G. B. J., Gravendeel, B., Eurlings, M. C. M., & Hetterscheid, W. L. A. (2002). Phylogeny of the tribe Thomsonieae (Araceae) based on chloroplast *mat*K and *trn*L intron sequences. *Systematic Botany*, *27*(3), 453–467. https://doi.org/10.1043/0363-6445-27.3.453

Gusman, G., & Gusman, L. (2006). *The genus Arisaema: A monograph of botanists and nature lovers*. A. R. G. Gantner Verlag.

Ham, R. W. J. M., Hetterscheid, W. L. A., & Heuvena, B. J. (1998). Notes on the genus *Amorphophallus* (Araceae) 1998: Pollen morphology of *Amorphophallus* and *Pseudodracontium*. *Review of Palaeobotany & Palynology*, *103*(3–4), 95–147. https://doi.org/10.1016/S0034-6667(98)00042-6

Harder, L. D., & Johnson, S. D. (2009). Darwin's beautiful contrivances: Evolutionary and functional evidence for floral adaptation. *New Phytologist*, *183*(3), 530–545. https://doi.org/10.1111/j.1469-8137.2009.02914.x

Hartley, N., & Gibernau, M. (2018). High diversity of biotic interactions in the megagenus *Anthurium* Schott (Araceae). *Aroideana – Journal of the International Aroid Society*, *41*(2–3), 237–342.

Hartley, N., Krömer, T., & Gibernau, M. (2017). Lepidopteran visitors of *Anthurium* inflorescences. *Aroideana – Journal of the International Aroid Society*, *40*(1), 84–96.

Hay, A. (1981). Araceae. In R. J. Johns & A. Hay (Eds.), *A students' guide to the monocotyledons of Papua New Guinea. Part 1* (pp. 31–84). Office of Forests.

Hay, A. (1986). *Cyrtosperma Griff. and the origin of aroids* [Unpublished doctoral dissertation]. Oxford University.

Hay, A. (1988a). *Anaphyllopsis:* A new Neotropical genus of Araceae–Lasieae. *Aroideana – Journal of the International Aroid Society*, *11*, 25–31.

Hay, A. (1988b). *Cyrtosperma* (Araceae) and its Old World allies. *Blumea*, *33*, 427–469.

Hay, A. (1993). The genus *Typhonium* (Araceae – Areae) in Australasia. *Blumea*, *37*, 345–376.

Hay, A., & Cedeño-Fonseca, M. (2019). *Anthurium decipiens*, a gigantic new and apparently sapromyophilous species from western Colombia, with notes on the related and often confused *Anthurium salgarense*. *Aroideana – Journal of the International Aroid Society*, *42*(1), 4–23.

Hay, A., & Wise, R. (1991). The genus *Alocasia* (Araceae) in Australia. *Blumea*, *35*, 499–545.

Henriquez, C. L., Arias, T., Pires, J. C., Croat, T. B., & Schaal, B. A. (2014). Phylogenomics of the plant family Araceae. *Molecular Phylogenetics and Evolution*, *75*, 91–102. https://doi.org/10.1016/j.ympev.2014.02.017

Hentrich, H., Kaiser, R., & Gottsberger, G. (2010). Floral biology and reproductive isolation by floral scent in three sympatric aroid species in French Guiana. *Plant Biology*, *12*(4), 587–596. https://doi.org/10.1111/j.1438-8677.2009.00256.x

Hepper, F. N. (1967). *Culcasia scandens* P. Beauv. (Araceae) and allied species in West Africa. *Kew Bulletin*, *21*(2), 315–326. https://doi.org/10.2307/4108528

Hesse, M., & Zetter, R. (2007). The fossil pollen record of Araceae. *Plant Systematics and Evolution*, *263*, 93–115. https://doi.org/10.1007/s00606-006-0468-z

Hetterscheid, W. L. A., & Ittenbach, S. (1996). Everything you always wanted to know about *Amorphophallus* but were afraid to stick your nose into! *Aroideana – Journal of the International Aroid Society*, *19*, 7–131.

Holdridge, L. R. (1967). *Life zone ecology*. Tropical Science Center.

Holtum, J. A. M., Winter, K., Weeks, M. A., & Sexton, T. R. (2007). Crassulacean acid metabolism in the ZZ plant, *Zamioculcas zamiifolia* (Araceae). *American Journal of Botany*, *94*(10), 1670–1676. https://doi.org/10.3732/ajb.94.10.1670

Jacobsen, N. (1979). *Cryptocoyne*. Clausen.

Keating, R. C. (2004). Vegetative anatomical data and its relationship to a revised classification of the genera of Araceae. *Annals of the Missouri Botanical Garden*, *91*(3), 485–494.

Kite, G. C., & Hetterscheid, W. L. A. (2017). Phylogenetic trends in the evolution of inflorescence odours in *Amorphophallus*. *Phytochemistry*, *142*, 126–142. https://doi.org/10.1016/j.phytochem.2017.06.006

Krause, K. (1920). *Steudnera*. In H. G. A. Engler (Ed.), *Das Pflanzenreich (IV.23E), Araceae–Colocasioideae* [The plant kingdom (IV.23E), Araceae–Colocasioideae] (pp. 10–16). Verlag von Wilhelm Engelmann.

Kudo, G. (2006). Flowering phenologies of animal-pollinated plants: Reproductive strategies and agents of selection. In L. D. Harder & S. C. H. Barrett (Eds.), *Ecology and evolution of flowers* (pp. 139–158). Oxford University Press.

Landolt, E. (1986). *The family of Lemnaceae – A monographic study* (Vol. 1). Geobotanisches Institut der ETH.

Landolt, E. (1998). *Lemna yungensis*, a new duckweed species from rocks of the Andean Yungas in Bolivia. *Bulletin of the Geobotanical Institute ETH*, *64*, 15–21.

Landolt, E. (2000). Contribution on the Lemnaceae of Ecuador. *Fragmenta Floristica et Geobotanica*, *45*, 221–237.

Landolt, E., & Schmidt-Mumm, U. (2009). Lemnaceae. *Flora de Colombia*, *24*, 1–54.

Lee, D. W., & Richards, J. H. (1991). Heteroblastic development in vines. In F. E. Putz & H. A. Mooney (Eds.), *The biology of vines* (pp. 205–244). Cambridge University Press. https://doi.org/10.1017/CBO9780511897658.010

Letty, C. (1973). The genus *Zantedeschia*. *Bothalia*, *11*(1–2), 5–26. https://doi.org/10.4102/abc.v11i1/2.1963

Li, H. (1992). Dormation of distribution area of *Remusatia* (Araceae) and its disjunction. *Acta Botanica Yunnanica*, *5*, 71–76.

Lins, A. L. (1994). *Aspectos morfológicos e anatômicos de raízes do gênero Montrichardia Crüger (Araceae)* [Morphology and anatomy of roots of the genus *Montrichardia* Crüger (Araceae)] [Unpublished master's thesis]. Universidade Federal do Rio Grande do Sul.

Low, S. L., Wong, S. Y., & Boyce, P. C. (2018). Naming the chaos – Generic redelimitation in Schismatoglottideae. *Webbia*, *73*(1), 1–100. https://doi.org/10.1080/00837792.2017.1409940

Ly, N., Wong, S. Y., Haevermans, T., Nyuyen, D. V., & Boyce, P. C. (2017). *Vietnamocasia*, a new genus from Central Vietnam belonging to the *Alocasia-Colocasia* clade (Araceae). *Phytotaxa*, *303*(3), 253–263. https://doi.org/10.11646/phytotaxa.303.3.5

Madison, M. T. (1977a). *A revision of Monstera (Araceae)*. Harvard University Herbaria.

Madison, M. T. (1977b). Vascular epiphytes: Their systematic occurrence and salient features. *Selbyana*, *2*, 1–13.

Madison, M. T. (1981). Notes on *Caladium* (Araceae) and its allies. *Selbyana*, *5*(3–4), 342–377.

Maia, A. C. D., Dötterl, S., Kaiser, R., Silberbauer-Gottsberger, I., Teichert, H., Gibernau, M., Navarro, D. M. A. F., Schlindwein, C., & Gottsberger, G. (2012). The key role of 4-methyl-5-vinylthiazole in the attraction of scarab beetle pollinators: A unique olfactory floral signal shared by Annonaceae and Araceae. *Journal of Chemical Ecology*, *38*, 1072–1080. https://doi.org/10.1007/s10886-012-0173-z

Maia, A. C. D., Gibernau, M., Carvalho, A. T., Gonçalves, E. G., & Schlindwein, C. (2012). The cowl does not make the monk: Scarab beetle pollination f the Neotropical aroid *Taccarum ulei* (Araceae, Spathicarpeae). *Biological Journal of the Linnean Society*, *108*(1), 22–34. https://doi.org/10.1111/j.1095-8312.2012.01985.x

Maia, A. C. D., Gibernau, M., Dötterl, S., Navarro, D. M. A. F., Seifert, K., Müller, T., & Schlindwein, C. (2013). The floral scent of *Taccarum ulei* (Araceae): Attraction of scarab beetle pollinators to an unusual aliphatic acyloin. *Phytochemistry*, *93*, 71–78. https://doi.org/10.1016/j.phytochem.2013.03.005

Maia, A. C. D., & Schlindwein, C. (2006). *Caladium bicolor* (Araceae) and *Cyclocephala celata* (Coleoptera, Dynastinae): A well-established pollination system in the Northern Atlantic rainforest of Pernambuco, Brazil. *Plant Biology*, *8*, 529–534. https://doi.org/10.1055/s-2006-924045

Maia, A. C. D., Schlindwein, C., Navarro, D. M. A. F., & Gibernau, M. (2010). Pollination of *Philodendron acutatum* (Araceae) in the Atlantic forest of Northeastern Brazil: A single scarab beetle species guarantees high fruit set. *International Journal of Plant Sciences*, *171*(7), 740–748. https://doi.org/10.1086/654846

Mayo, S. J., Bogner, J., & Boyce, P. C. (1997). *The genera of Araceae*. Royal Botanic Gardens.

Milet-Pinheiro, P., Gonçalves, E. G., Navarro, D. M. A. F., Nuñez-Avellaneda, L. A., & Maia, A. C. D. (2017). Floral scent chemistry and pollination in the Neotropical aroid genus *Xanthosoma* (Araceae). *Flora*, *231*, 1–10. https://doi.org/10.1016/j.flora.2017.03.006

Montalvo, A. M., & Ackerman, J. D. (1986). Relative pollinator effectiveness and evolution of floral traits in *Spathiphyllum friedrichsthalii* (Araceae). *American Journal of Botany*, *73*(12), 1665–1676. https://doi.org/10.1002/j.1537-2197.1986.tb09697.x

Moore, M. R., & Jameson, M. L. (2013). Floral associations of cyclocephaline scarab beetles. *Journal of Insect Sciences*, *13*, Article 100. https://doi.org/10.1673/031.013.10001

Murata, J. (1984). An attempt at an infrageneric classification of the genus *Arisaema* (Araceae). *Journal of the Faculty of Science, University of Tokyo, Section 3, Botany*, *13*, 431–482.

Nauheimer, L., & Boyce, P. C. (2013). *Englerarum* (Araceae, Aroideae): A new genus supported by plastid and nuclear phylogenies. *Plant Systematics and Evolution*, *300*, 709–715. https://doi.org/10.1007/s00606-013-0914-7

Nauheimer, L., Metzler, D., & Renner, S. (2012). Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist*, *195*(4), 938–950. https://doi.org/10.1111/j.1469-8137.2012.04220.x

Newton, L. (1997). *Zamioculcas zamiifolia. Ballya*, *4*(3), 68–69.

Nguyen, V. D., Dinh, Q. D., Ha, M. T., Quang, B. H., & Boyce, P. C. (2019). A new species of *Anadendrum* (Araceae – Anadendreae) from Vietnam. *Blumea*, *64*(2), 190–193. https://doi.org/10.3767/blumea.2019.64.02.11

Nicolson, D. H. (1966). *Filarum*, a new genus of Peruvian Araceae. *Brittonia*, *18*, 347–349. https://doi.org/10.2307/2805151

Nicolson, D. H. (1969). *A revision of the genus Aglaonema (Araceae)*. Smithsonian Institution Press. https://doi.org/10.5479/si.0081024X.1

Nicolson, D. H., & Sivadasan, M. (1982). A revision of *Theriophonum* (Araceae). *Kew Bulletin*, *37*(2), 277–290. https://doi.org/10.2307/4109970

Nilsson, A. L. (1988). The evolution of flowers with deep corolla tubes. *Nature*, *334*, 147–149. https://doi.org/10.1038/334147a0

Ortiz, O. O., Croat, T. B., & Baldini, R. M. (2018). Current status of aroid species diversity in Panama, including new records for the country. *Webbia*, *73*(1), 141–153. https://doi.org/10.1080/00837792.2018.1452451

Ortiz, O. O., Stapf, M. S., & Croat, T. B. (2019). Diversity and distributional patterns of aroids (Alismatales: Araceae) along an elevational gradient in Darién, Panama. *Webbia*, *75*(2), 339–352. https://doi.org/10.1080/00837792.2019.1646465

Pereira, J., Schlindwein, C., Antonini, Y., Maia, A. C. D., Dötterl, S., Martins, C., Navarro, D. M. A. F., & Oliveira, R. (2014). *Philodendron adamantinum* (Araceae) lures its single cyclocephaline scarab pollinator with specific dominant floral scent volatiles. *Biological Journal of the Linnean Society*, *111*(3), 679–691. https://doi.org/10.1111/bij.12232

Prieto, D., & Cascante-Marín, A. (2017). Pollination by nitidulid beetles in the hemi-epiphytic aroid *Monstera lentii* (Araceae: Monsteroideae). *Flora*, *231*, 57–64. https://doi.org/10.1016/j.flora.2017.04.010

Rataj, K. (1975). *Revision of the genus Cryptocoryne Fischer*. Academia nakladatelstvi Československé akademie věd.

Ray, T. S. (1981). *Growth and heterophylly in an herbaceous vine, Syngonium (Araceae)* [Unpublished doctoral dissertation]. Harvard University.

Ray, T. S. (1986). Growth correlations within the segment in the Araceae. *American Journal of Botany*, *73*(7), 993–1001. https://doi.org/10.1002/j.1537-2197.1986.tb08543.x

Ray, T. S. (1987a). Cyclic heterophylly in *Syngonium* (Araceae). *American Journal of Botany*, *74*(1), 16–26. https://doi.org/10.1002/j.1537-2197.1987.tb08575.x

Ray, T. S. (1987b). Leaf types in the Araceae. *American Journal of Botany*, *74*(9), 1359–1372. https://doi.org/10.1002/j.1537-2197.1987.tb08751.x

Ray, T. S. (1989). Diversification of growth habits in the Araceae. *American Journal of Botany*, *76*(Suppl.), 267.

Renner, S. S., & Zhang, L. B. (2004). Biogeography of the *Pistia* clade (Araceae): Based on chloroplast and mitochondrial DNA sequences and Bayesian divergence time inference. *Systematic Biology*, *53*(3), 422–432. https://doi.org/10.1080/10635150490445904

Riedl, H. (1969). Kritische Untersuchungen über die Gattung *Eminium* (Blume) Schott nebst Bemerkungen zu einigen anderen Aroidean der südwest-asiatischen Flora [Critical investigations on the genus *Eminium* (flower) Schott along with remarks on some other aroids of the Southwest Asian flora]. *Annalen des Naturhistorischen Museums in Wien*, *73*, 103–121.

Riedl, H. (1979). Araceae. In G. Hegi (Ed.), *Illustrierte Flora von Mitteleuropa* [Illustrated flora of Central Europe] (3rd ed., Vol. II, pp. 318–334). Verlag Paul Parey.

Rothwell, G. W., Van Atta, M. R., Ballard, H. E., Jr., & Stockey, R. A. (2004). Molecular phylogenetic relationships among Lemnaceae and Araceae using chloroplast *trn*L-*trn*F intergenic spacer. *Molecular Phylogenetics and Evolution*, *30*(2), 378–385. https://doi.org/10.1016/S1055-7903(03)00205-7

Royo, A. A., & Carson, W. P. (2005). The herb community of a tropical forest in central Panamá: Dynamics and impact of mammalian herbivores. *Oecologia*, *145*, 66–75. https://doi.org/10.1007/s00442-005-0079-3

Schwerdtfeger, M., Gerlach, G., & Kaiser, R. (2002). Anthecology in the Neotropical genus *Anthurium* (Araceae): A preliminary report. *Selbyana*, *23*, 258–267.

Seymour, R. S., & Gibernau, M. (2008). Respiration of thermogenic inflorescences of *Philodendron melinonii:* Natural pattern and responses to experimental temperatures. *Journal of Experimental Botany*, *59*(6), 1353–1362. https://doi.org/10.1093/jxb/ern042

Seymour, R. S., White, C. R., & Gibernau, M. (2009). Endothermy of dynastine scarab beetles (*Cyclocephala colasi*) associated with pollination biology of a thermogenic arum lily (*Philodendron solimoesense*). *Journal of Experimental Biology*, *212*, 2960–2968. https://doi.org/10.1242/jeb.032763

Singh, Y. (1996). *Contributions to the systematics of the genus Zantedeschia Spreng. (Araceae)* [Unpublished master's thesis]. University of Pretoria.

Soares, L. M., Mayo, S. J., & Gribel, R. (2013). A preliminary taxonomic revision of *Heteropsis* (Araceae). *Systematic Botany*, *38*(4), 925–974. https://doi.org/10.1600/036364413X674715

Sriboonma, D., Murata, J., & Iwatsuki, K. (1994). A revision of *Typhonium* (Araceae). *Journal of the Faculty of Science, University of Tokyo, Section 3, Botany*, *15*, 255–313.

Standley, P. C. (1944). Araceae. In R. E. Woodson & R. W. Schery (Eds.), *Flora of Panama* (pp. 405–464). Missouri Botanical Garden Press.

Stevens, P. F. (2020). *Angiosperm Phylogeny Website. Version 14, July 2017.* Retrieved March 26, 2020, from http://www.mobot.org/MOBOT/research/APweb/

Strong, D. R., Jr., & Ray, T. S. (1975). Host tree location behavior of a tropical vine (*Monstera gigantea*) by skototropism. *Science*, *190*(4216), 804–806. https://doi.org/10.1126/science.190.4216.804

Talvera, S. (1976). Revisión de las especies españolas del genero *Biarum* Schott (Araceae) [Revision of the Spanish species of the genus *Biarum* Schott (Araceae)]. *Lagascalia*, *6*(2), 275–296.

Tam, S. M., Boyce, P. C., Upson, T. M., Barabé, D., Bruneau, A., Forest, F., & Parker, J. S. (2004). Intergeneric and infrafamilial phylogeny of subfamily Monsteroideae (Araceae) revealed by chloroplast *trn*L-F sequences. *American Journal of Botany*, *91*(3), 490–498. https://doi.org/10.3732/ajb.91.3.490

Tchiakpè, L. (1979). *Contribution à l'étude d'une Aracée Africaine: Anchomanes difformis Engl.* [Contribution to the study of an African Araceae: *Anchomanes difformis* Engl.] [Unpublished doctoral dissertation]. Aix-Marseille Université.

Thorington, K. K. (2000). *Pollination and fruiting success in the eastern skunk cabbage Symplocarpus foetidus (L.) Salisb. ex Nutt*. Mount Holyoke College.

Tosi, J., Jr., Unzueta, O., Holdridge, L. R., & Gonzales, E. A. (1975). *Mapa ecológica de Bolivia* [Ecological map of Bolivia] [Map]. MACA.

United States Department Agriculture. (2001). *Floriculture crops: 2000 summary*. Diane Publishing.

van der Niet, T., & Johnson, S. D. (2012). Phylogenetic evidence for pollinator driven diversification of angiosperms. *Trends in Ecology & Evolution*, *27*(6), 353–361. https://doi.org/10.1016/j.tree.2012.02.002

Vilela, C. R., & Prieto, D. (2018). A new Costa Rican species of *Drosophila* visiting inflorescences of the hemi-epiphytic climber *Monstera lentii* (Araceae). *Revista Brasileira de Entomologia*, *62*(3), 225–231. https://doi.org/10.1016/j.rbe.2018.06.002

Wit, H. C. D. (1978). *Revisie van het genus Lagenandra Dalzell (Araceae)* [Revision of the genus Lagenandra Dalzell (Araceae)]. Veenman.

Wong, S. Y., Boyce, P. C., Othman, A. S., & Leaw, C. P. (2010). Molecular phylogeny of tribe Schismatoglottideae (Araceae) based on two plastid markers and recognition of a new tribe, Philonotieae, from the neotropics. *Taxon*, *59*(1), 117–124. https://doi.org/10.1002/tax.591012

Wong, S. Y., Joling, J., Pereira, J. T., Damit, A., Boyce, P. C., & Hay, A. (2020). Studies on Potheae (Araceae) of Borneo II: *Pedicellarum* M. Hotta subsumed into *Pothos* L., and recognition of three new species. *Webbia*, *75*, 89–103. https://doi.org/10.36253/jopt-7944

Wong, S. Y., Meerow, A. W., & Croat, T. B. (2016). Resurrection and new species of the Neotropical genus *Adelonema* (Araceae: *Philodendron* clade). *Systematic Botany*, *41*(1), 32–48. https://doi.org/10.1600/036364416X690732

Wong, S. Y., Tan, P. Z., Ng, K. K., Othman, A. S., Lee, H. B., Fasihuddin, B. A., & Boyce, P. C. (2013). Phylogeny of Asian *Homalomena* (Araceae) based on the ITS region combined with morphological and chemical data. *Systematic Botany*, *38*(3), 589–599. https://doi.org/10.1600/036364413X670430

Young, H. J. (1986). Beetle pollination of *Dieffenbachia longispatha* (Araceae). *American Journal of Botany*, *73*(6), 931–944. https://doi.org/10.1002/j.1537-2197.1986.tb12133.x

Young, H. J. (1987). Aroid observations: *Philodendron rothschuhianum*. *Aroideana – Journal of the International Aroid Society*, *10*(4), 27.

Young, H. J. (1988a). Differential importance of beetle species pollinating *Dieffenbachia longispatha* (Araceae). *Ecology*, *69*(3), 832–844. https://doi.org/10.2307/1941033

Young, H. J. (1988b). Neighborhood size in a beetle pollinated tropical aroid: Effects of low density and asynchronous flowering. *Oecologia*, *76*, 461–466. https://doi.org/10.1007/BF00377043

Young, H. J. (1990). Pollination and reproductive biology of an understory Neotropical aroid. In K. S. Bawa & M. Hadley (Eds.), *Reproductive ecology of tropical forest plants* (pp. 151–164). Parthenon Press.

Zhu, G. H. (1995). *Systematics of Dracontium L. (Araceae)* [Unpublished doctoral dissertation]. University of Missouri.

Zhu, G. H., & Croat, T. B. (2004). Revision of *Dracontium* (Araceae). *Annals of the Missouri Botanical Garden*, *91*(4), 593–667.

Zona, S., & Christenhusz, M. J. M. (2015). Litter-trapping plants: Filter-feeders of the plant kingdom. *Botanical Journal of the Linnean Society*, *179*(4), 554–586. https://doi.org/10.1111/boj.12346

Zotz, G. (2013). "Hemiepiphyte": A confusing term and its history. *Annals of Botany*, *111*(6), 1015–1020. https://doi.org/10.1093/aob/mct085

Zotz, G. (2016). *Plants on plants. The biology of vascular epiphytes*. Springer. https://doi.org/10.1007/978-3-319-39237-0

Zotz, G. (2020). Life forms in aroids – Natural variability vs. terminological confusion. *Aroideana – Journal of the International Aroid Society*, *43*, 315–333.

Zuluaga, A., Llano, M., & Cameron, K. (2019). Systematics, biogeography and morphological character evolution of the hemiepiphytic subfamily Monsteroideae (Araceae). *Annals of the Missouri Botanical Garden*, *104*(1), 33–48. https://doi.org/10.3417/2018269