

Taxonomic Status of Neotropical Araceae

Thomas B. Croat
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299
USA

INTRODUCTION

The Araceae, with 106 genera and roughly 3,200 species is nearly world wide in distribution. There are two major centers of species diversity, in tropical Asia and tropical America, with nearly an equal number of indigenous genera, 43 for Asia and 36 for America (Croat, 1979). Of these totals 33 are endemic to the American tropics while 32 are endemic to Asia. Africa, a less important center of species diversity, has only 19 indigenous genera with only 12 of them endemic. While the Paleotropics has more genera than the Neotropics (60 versus 36) the latter area contains roughly two-thirds the species of the world's Araceae. Our level of knowledge of the systematics of the neotropical Araceae varies greatly from area to area, owing largely to recent revisionary work or to the interest and area concentrated on by particular workers, e.g. G. S. Bunting in Mexico (Bunting, 1965) and Venezuela, Croat in Panama and Central America (Croat, 1978, 1983, 1986a, 1986b, 1988a, 1991) and Croat & Grayum in Costa Rica. Central America is much more well known than South America, largely owing to the more prolonged effort by aroid taxonomists in the region, but also owing to the fact that some parts of the area are much less rich in species per unit area than many parts of South America, especially the species-rich northwestern part of that continent (Croat, 1992). Most of the earlier work in Central America was undertaken by P. C. Standley in a series of floristic works (Standley, 1927, 1928, 1930, 1933, 1937, 1944).

Species diversity generally increases in Central America as one approaches South America (Croat, 1986a, 1986b). Knowledge

of Araceae in South America is spotty, with some areas being relatively well known and others, especially Andean areas of the continent, being very poorly known. Some areas for which floristic surveys have been conducted in the past thirty years or so are relatively well known. This is especially true of Venezuela where extensive work has been done, especially by G. S. Bunting (Bunting, 1975, 1979, 1986, 1988, 1989) but also by Croat & Lambert (1986). The Venezuelan flora contains 266 species with an additional 25 subspecies or varieties.

The Guiana region is relatively well known at least in part because it is relatively species-poor rather than because of the extent of the collecting effort. Suriname was, until recent years, the only part of the Guianas that received much attention in regard to Araceae, this largely owing to the work of Jonker-Verhoef & Jonker (1953) in Suriname. More recently, the whole region is receiving more attention owing to work on the "Flora of the Guianas" project and to the Araceae treatment being carried out by Croat and collaborators. In addition, Bunting (in press) has completed the Araceae treatment for the Flora of the Venezuelan Guyana, the Venezuelan counterpart of this flora.

Another example of a relatively well known area is the state of Bahía in Brazil where Simon Mayo and other members of the Kew Garden staff, especially R. Harley, have made a number of expeditions. Mayo has also prepared a checklist for Brazil and any reference to the number of species in Brazil for any genus discussed in this paper relies heavily on his unpublished work. Mayo has also worked closely with many Brazilian botanists to encourage their par-

ticipation in work with Araceae of Brazil (see *Aroideana* for a discussion of these efforts).

Parts of southern South America are by now also well known, where floristic treatments for Argentina (Crisci, 1971) and Paraguay (Croat & Mount, 1988) have been completed. In addition, a floristic treatment has been completed for the state of Santa Catarina (Reitz, 1957).

The published Flora of Peru (Macbride, 1936), though falling short of giving an accurate picture of the species count for Peru, does come close to indicating the number of species actually described for Peru, since, except for *Anthurium* sect. *Pachyneurium* (Croat, 1991), few groups have had many species described from Peru since that publication. A more accurate accounting for the number of species of Araceae in Peru is published in the "Catalogue of the Flowering Plants and Gymnosperms of Peru" (Croat, 1993). Though not a thorough revision of the species occurring in Peru, this list takes into account all species of plants described for Peru as well as all species represented only by identified herbarium specimens which were able to be verified by experts for each family. The checklist contains 210 species of Araceae for Peru but it does not include any unpublished names and many species remain to be described.

While there is no completed Araceae treatment for the flora for Ecuador, a recently published checklist for the Amazonian lowlands (Renner et al., 1990), which lists 92 species of Araceae (a few of them undescribed), gives some indication of the species diversity of that part of Ecuador. Unfortunately the Amazonian lowlands represent one of the most species-poor portions of the country if its area is taken into account, owing to the widespread nature of the species in that zone.

The above-mentioned treatments, though regional in nature, help to give an indication of species diversity on the continent of South America, and any reference to species counts for any genus is based on them.

The lowland Amazon basin is also relatively well known, principally owing to the

fact that the species inhabiting the Amazon lowlands are in general wide-ranging, often common species. Despite the presence of a few endemic species near the mouth of the Amazon, e.g. *Philodendron ecordatum* Schott, the vast Amazonian region lying between the Atlantic coast and the foothills of the Andes has moderately few, mostly wide-ranging species. Species diversity increases dramatically as one approaches the foothills of the Andes in the west. Species occurring on the lowermost slopes of the Andes tend to range widely in a north-south direction, often from Colombia to Bolivia and thus tend not to be endemic. However, some of the species of this region are currently believed to be endemic. The degree of endemism increases as elevation increases on the slopes of the Andes and as the terrain becomes more dissected with river valleys (Croat, 1994).

To the east of the Amazon basin, especially in the Guiana Highlands and in eastern Brazil, from the state of Bahiá south almost to Uruguay, the rate of endemism is much higher. Nearly all the species occurring in this region are endemic to eastern Brazil, and few range into the Amazon basin. For example, five of the eight *Anthurium* species from Santa Catarina are endemic to eastern Brazil, including *A. acutatum* N. E. Br., *A. gaudicbaudianum* Kunth, *A. harrisii* (Grah.) Endl., *A. lacerdae* Reitz, and *A. pilonense* Reitz.

Though many species have been described from eastern Brazil, by early aroid specialists, including Schott, K. Koch, and Engler, based on the early collecting efforts by botanists such as Glaziou, Regel, Riedl, and others, these areas remain poorly known, principally because of the taxonomic complexity in such groups as *Anthurium* section *Urospadix*, which dominates the area. Perhaps the only group of aroids well known in the region are members of the recently revised *Philodendron* subgenus *Meconostigma* (Mayo, 1991).

The truly temperate parts of the continent are devoid of aroids, and the subtropical portions of the continent, while containing a number of small, frequently en-

demic genera in the tribe Spathocarpeae, are also relatively species-poor.

Species diversity is high throughout the extent of the South American Andes but especially along the northwestern slope extending from Chocó Province in Ecuador, as well as on both the eastern and western slopes in the Andes in the region of the equator and on the eastern slopes of the Andes in Peru. Species diversity is also relatively high in the Cordillera de Merida of western Venezuela, but remarkably less so in the northern part of the Eastern Cordillera of Colombia and on the entire western flank of the Eastern Cordillera in Colombia (Croat, 1992). Species diversity is also relatively low in the Central Cordillera of Colombia. In all cases high species diversity is correlated with high precipitation and with the absence of prolonged dry seasons.

Species richness is greatest between sea level and middle elevations up to about 1,500 meters. While some species may range up to about 3,750 m (*Anthurium caucanum* Engl.; Colombia: Antioquia: Villa Artega, *Hodge 7045*), diversity drops off dramatically above 2,000 m elevation. Seasonally dry areas, such as the central plateau of eastern Brazil and the lower Amazon basin, are relatively species-poor, as are the generally treeless llanos of Venezuela.

Endemism is also especially high in the Andes of western South America, including the eastern range of the Andes which extends into Venezuela. Endemism is also high in the Guiana Highlands and in parts of North America, especially in Mexico and in lower Central America, in Costa Rica, and Panama. For example, Mexico, with 41 taxa of *Anthurium* has 26 endemic taxa. Guatemala has only three endemic species. Both Honduras and Nicaragua have a single endemic species each. Costa Rica has 68 taxa with 22 species endemic, and Panama has 150 with 82 species, 55 percent of the total, considered to be endemic.

Because of the high rate of endemism and the very high speciation in many parts of the Andes, our taxonomic knowledge of all but a few areas of the Andes is very poor. Although selected areas of the Colombian Andes, such as the region of Popayán in

Cauca Department, the department of Antioquia, and the department of Cundinamarca, especially around Bogota, were well collected in the late Nineteenth Century by collectors such as Lehmann, in time to have their material included in the revisions of both Schott (1860) and Engler (1905), many areas have not been collected until recent times.

Pichincha Province and a few other areas of Pacific coastal Ecuador were well collected by L. Sodiro (1901a, 1901b, 1903a, 1903b, 1905a, 1905b, 1905c, 1906, 1907, 1908) and 257 species (including 281 taxa) were described. Despite this, the region remains poorly known, largely because of the inability to locate and study the widely scattered and poorly documented collections of Sodiro. Some Sodiro specimens are deposited in European herbaria (Croat, 1989), but most collections are deposited in the poorly curated herbarium (QPLS) of the monastery in Quito where Sodiro originally worked. The collections may not be borrowed and the conditions in the herbarium make their study there very difficult (Croat, 1989). Nevertheless, some recent attempts at revisionary work have taken place in Ecuador in Pichincha Province. Floristic surveys of the Araceae have been made of the Reserva ENDESA on the western slopes of Volcán Pichincha. This work, begun by Jimena Rodríguez de Salvador while a student at the Universidad Católica in Quito, was subsequently augmented by investigations of my own, and is nearing completion and is expected to be published in 1995. The paper will be entitled *Anthurium* of Reserva ENDESA (Pichincha Province, Ecuador).

Other Andean regions are being studied on a local basis. With the assistance of Jeff Lake of Grinnell College I have completed a revision of the Araceae for the Flora of La Planada, a natural history reserve in Nariño. This revision is also expected to be published soon.

With the assistance of another student, Dorothy Bay, I am also working on a revision of the Araceae of Bajo Calima. This flora is an exceptionally rich one with many new species, and despite about six separate

collecting trips made to this region over the past ten years it remains still poorly known. Bay will work on the flora as a part of a Ph.D. dissertation at St. Louis University. The project is expected to take three additional years to complete.

This has been a general overview of the distribution of the neotropical Araceae. The remainder of this paper will deal individually with different genera to discuss the general level of knowledge of each genus, the predicted number of species in each genus, and what is currently known of their phytogeography. A review of the ecology and life forms of the genera is summarized in Croat (1988a).

Discussions of the suprageneric placement of the genera to follow are based on the latest system of classification, an as yet unpublished work by S. Mayo, J. Bogner, and P. Boyce (in prep.). This work reflects many of the ideas expressed by M. Grayum (1984, 1990) and by Bogner & Nicolson (1991). It also takes into account unpublished molecular work by French et al. (in press) on chloroplast DNA and an extensive cladistic analysis of the family by Mayo et al. (in prep.). Thus, though perhaps not the final word on the suprageneric classification of the family, it constitutes a consensus of modern thinking on the classification of the Araceae. For a discussion of all but the most recent revision, including that of Hotta (1970) see Croat, 1990.

In order to avoid confusion with names used in earlier works brief mention should be made of the major conclusions reached in the work being prepared by Mayo, Bogner & Boyce. These are as follows: the family has been divided into two major groups, the Protoaroids consisting of subfamilies Gymnostachyoideae and Orontioideae and the True Araceae, consisting of subfamilies Calloideae, Pothoideae, Monsteroideae, Lasioideae, and Aroideae. The most significant change with earlier systems as outlined in Croat (1990) is that all genera with unisexual flowers (previously incorporated variously in Colocasioideae, Philodendroideae, and Aroideae) are now included in Aroideae. For further details, one must await

the publication of the book, currently scheduled at Kew during fiscal year 1994.

ALLOSCHEMONE

This genus with two species in tribe Monstereae is a hemiepiphytic appressed climber endemic to the western Amazon basin in Brazil and Bolivia. Its placement has been somewhat controversial. Madison (1976) considered it to be a member of the genus *Scindapsus*, otherwise known only from the Old World tropics but later reestablished it as a distinct genus (Madison, 1977). It was also treated as a distinct genus by Grayum (1990) and Bogner & Nicolson (1991). *Alloschemone occidentalis* (Poeppig) Engl. & K. Krause is still poorly collected and is known only from a few localities (Croat, 1985b). It has been collected on the Rio Solimoes at Tefe, on the Rio Madeira at Humayta, along the Rio Marie, a tributary of the Rio Negro, on the Rio Japura near Maraá the Department of Pando, province of Frederico Roman along the Rio Negro.

The genus is still poorly known in many respects and living material should be acquired for additional study.

ANAPHYLLOPSIS

This lasioid genus (tribe Lasieae; subtribe Dracontiinae) of three terrestrial, rhizomatous species is endemic to northern Brazil (Pará) and the Guianas. One of the three species, *A. americana* (Engl.) A. Hay from French Guiana and Surinam, had long been considered a *Cyrtosperma*, but Hay (1988) found that it differs from Asian members of *Cyrtosperma* by having fenestrate leaf blades, as well as both prophylls and cataphylls on the rhizome. In addition to placing this species into the new genus *Anaphyllopsis*, he described two new species, *A. pinnata* A. Hay, from the upper Rio Negro in Amazonas State of Brazil, and *A. cururuana* A. Hay, from the upper Rio Tapajos along the Rio Cururu in Pará State of Brazil.

None of the species are particularly well known and the two most recently described are known only from a single collection

each. Certainly more collections should be made to determine the true nature of morphological variability and geographical range.

Two other species previously thought to belong to *Cyrtosperma*, *C. wurdackii* Bunting and *C. spruceanum* (Schott) Engl., were placed by Hay (1988) in *Urospatha* and *Dracontium*, respectively. Thus, *Cyrtosperma* is eliminated as a neotropical genus and is restricted to the Asian tropics.

ANTHURIUM

There is now agreement as to the placement of *Anthurium* in tribe Anthurieae in subfamily Pothoideae.

The genus *Anthurium* is the largest genus in the family with an estimated 1,000 species. Admittedly, the margin of error in counting the number of species in this genus is great. Indeed, the margin of error in estimating the number of species existing for *Anthurium* and *Philodendron*, the two largest genera in the family, is greater than the total number of all other species in all other neotropical genera combined. While the number of species of *Anthurium* in Central America (221 spp.) and some parts of South America, e.g. Venezuela (68 species including seven varieties or subspecies), the Guianas, the Amazon basin, and Paraguay, is well known, other areas, especially eastern Brazil and the Andean region of western South America are doubtful. Mayo has produced a checklist for Brazil containing a total of about 100 species, eight of which are new to science. Still, owing to the taxonomic uncertainty of many species of section *Urospadix*, a complex group of species which are difficult to separate, the total is likely to be higher than that projected by Mayo.

It is in the Andean region of the continent where specific counts of species are most difficult to obtain. While a few areas, notably, the departments of Antioquia and Cundinamarca as well as the region of Popayán in the department of Cauca, have had many species described and probably even have a number of species (especially at the higher elevations) which must be placed

in synonymy, many regions were poorly collected prior to Schott's or Engler's revisions, and thus have few species described. Interestingly, these same areas, notably those along the Pacific slope of western Colombia, probably are the most species-rich. For this reason, substantial numbers of new species exist. In some areas which have now been well collected, such as the region of the lower Calima River basin, a region commonly referred to as "Bajo Calima," the majority of species appear to be new to science. The region is largely a transition zone between *Tropical wet forest* and *Tropical forest* and has yielded, so far, 133 species including 63 species of *Anthurium* and 40 species of *Philodendron*, with only a few species yet to be determined and most appearing to be new to science. The Pacific slope also appears to have a high rate of endemism, especially between different life zones and at different elevations. For example, in the department of Nariño, three study sites, all located relatively near one another and all located within a *Premontane forest* life zone (according to the Colombian life zone map), contained relatively few species which were shared between sites (Croat, 1992).

Probably regions of *Tropical forest*, which are restricted to northwestern South America, will prove to be the most species-rich of all. Some parts of this life zone, especially the area south of Quibdó, have been relatively well collected, but the material has not yet been analyzed for a determination of its species diversity.

The situation in Ecuador is even more complex regarding exact numbers of species, especially in Carchí and Esmeraldas Provinces in northwestern Ecuador. Much of Ecuador is probably as rich per unit area as the Pacific slope of Colombia. Both slopes of the Andes in Central Ecuador in Imbabura, Pichincha, Los Rios and Cotopaxi, Bolívar, Tungurahua, Chimborazo and Cañar, especially at middle elevations on the Pacific slope and at all but the higher elevations on the Amazonian slope, are rich in species. The same is true of the Amazonian slopes of Loja and in the principally lowland provinces of the so called "Oriente,"

Sucumbios, Napo, Pastaza, Morona-Santiago, and Zamora-Chinchipec. Renner et al. (1990) report 32 species for this region but the actual number is certainly much higher. Much of the middle elevations of the north-eastern slopes of the Andes as well as the southeastern slopes remain unexplored. Recent surveys of the Cordillera del Condor, along the Peruvian border, indicates a high rate of endemism. The same is true of the Serrania de Cutucú further to the north.

The Amazonian lowlands, though containing some new species, have mostly rather wide-ranging species in common with other areas of the Amazon basin. An example of the area, now reasonably well collected is that of Jatun Sacha which has a flora of at least 50 species, including 25 species of *Anthurium*. Of this total only three species are believed to be endemic to Ecuador.

In contrast to the remainder of Ecuador, the Pacific lowlands of western Ecuador south of Esmeraldas are either mostly deforested or seasonally dry and contain relatively few aroid species. This is particularly true of the southwestern part of the country in El Oro and Loja.

The region of northwestern Peru, like that of southeastern Ecuador is relatively dry with a depauperate aroid flora. Species diversity is substantially greater in the mountains of northern Peru in the state of Amazonas, but the region has yet to be well collected. Most collections existing are the result of University of California anthropologist Brent Berlin and his workers who collected in the region of the Río Cenepa and the Río Santiago. This area is home to the rare and poorly collected genus *Filarum*. The drier highland regions of Peru are relatively poor in species. One particularly variable species ranging throughout the highlands from southern Peru to Central Ecuador is *A. dombeyanum* Brongn. ex Schott. The middle elevations are particularly rich in members of *Anthurium* sect. *Pachyneurium* (see discussion of this section below).

The entire Pacific coastal region of Peru, much like the southwestern part of Ecuador is arid, indeed too arid for many aroid spe-

cies to occur. The same is essentially true for the intermountain valleys in Central Peru. Only in the foothills of the Andes on the eastern slopes do any significant number of species occur but species diversity here does not come close to matching that in Ecuador. The species occurring there, including *A. breviscapum* Schott, also tend to be much more widespread but there are also significant centers of species richness and endemism such as the areas around Tingo Maria in Huanuco Department and at Tarapoto in San Martín Department.

The species distribution in the Amazon lowlands of Peru mirrors that in the lowlands of Ecuador, tending to be wide-ranging species, many of which also enter Brazil. Examples include *Anthurium atropurpureum* R. Schultes & Maguire, *A. oxycarpum* Poeppig, *A. lorentense* Croat, and *A. rubrinervium* (Link) G. Don.

The Flora of Peru (Macbride, 1936) is of relatively little value. The treatment contains 55 species of *Anthurium*, with eleven names being synonyms of other species treated and an additional two names of plants which do not occur in Peru. The remaining names are probably correct, but may represent as few as one-third of the species in the country. The up to date checklist for Peru (Croat, 1993) has 76 taxa but many remain to be described.

Bolivia is relatively poor in *Anthurium* species but has a significant number of endemic species. No aroids occur in the dry eastern portion of the country, but a number of species of *Anthurium* occur in the relatively humid intermountain valleys beginning in Nor Yungas east of La Paz and extending to the lowlands of Beni and to a lesser extent to the east in Cochabamba.

Paraguay has a depauperate aroid flora with only 16 species, including two species of *Anthurium*. Argentina has 17 species, including only one *Anthurium*, *A. paraguayense* Engl. That species ranges north to Bolivia and southern Brazil. Uruguay and Chile have no *Anthurium* (indeed Chile has only the pantropical genus *Pistia*) and Uruguay has only four species in three genera). In contrast to the northern hemisphere where several genera, including *Ar-*

isaema, *Calla*, and *Lysichiton*, range well north of 45 degrees latitude, few Araceae range very far into temperate South America. The southernmost is *Pistia*, found at 35 degrees latitude in the basin of the Río de la Plata near Buenos Aires.

Sections of genus *Anthurium* are not equally distributed. The sectional classification discussed here, somewhat modified from that of either Schott (1860) or Engler (1906) is outlined by Croat & Sheffer (1983).

Some sections, such as section *Pachyneurium*, are widespread, ranging throughout most of the range of the genus, with the exception of the wettest part of the range, such as in northwestern Colombia. Most members of the section, especially series *Pachyneurium*, are most common in areas of seasonally dry forest. The center of diversity for sect. *Pachyneurium* is in Ecuador, where 36 species occur, and in Peru with 28 species. These countries are also the centers of endemism with 23 and 13 species respectively. Central America is a second center of diversity for sect. *Pachyneurium*, especially Costa Rica and Panama, with 23 and 22 species (seven and five species endemic) respectively (Croat, 1991). A portion of this section, including all the cordate species, is restricted to Costa Rica and Panama. Another group, series *Multinervia*, is nearly restricted to Ecuador with only a few outlying species occurring in Colombia (*A. carchiense* Croat, *A. napaeum* Engl., and *A. narinoense* Croat) or Peru (*A. soukupii* Croat and *A. ottonis* K. Krause).

Section *Calomystrium* is also widespread, but with the vast majority of its species occurring between Costa Rica, Venezuela, and Peru, especially at middle elevations on both slopes of the Andes. A significant percentage of the species, perhaps as much as 50 percent is new to science. The percentages of new species are particularly high in Panama, with 15 of 18 species in the section new to science (Croat, 1986b). The percentages in South America, especially in Colombia where the diversity is greatest, could be as high or higher.

Section *Porphyrochitonium* has a range similar to that of sect. *Calomystrium* and is

well represented in Panama with 50 species but has an even greater concentration in northwestern South America, especially in the wettest forest types at lower elevations. It is particularly well represented in *Tropical forest* and *Tropical Premontane forest* in Chocó Department of Colombia. For example, 27 species are already known from one small area at Bajo Calima near Buenaventura in the Department of Valle, in transitional zone between *Tropical wet* and *Pluvial forest*.

Relatively few species in the section occur in the Amazon basin. Most of the species in the group are new to science. Because of their generally similar appearance, the species are easily overlooked or even mixed up by collectors. Probably no section has such a high percentage of species new to science, perhaps owing to their inconspicuous nature (by aroid standards). For example, in Panama, 39 taxa (of a total of 80 new taxa described) are members of sect. *Porphyrochitonium*. The greatest concentration of section *Porphyrochitonium* is on the Pacific coast of Colombia, most appear to be endemic and undescribed. Schott (1860) described only one member of the section, *A. scherzerianum*, and Engler (1906) described only 17 additional species while Sodiro (1901a, 1901b, 1902, 1903a, 1903b, 1904, 1905a, 1905b, 1906, 1907, 1908) described only 12 species. Though most of the species of section *Porphyrochitonium* described by Engler were included in his section *Urospadix*, a few were included in other sections, including *Tetraspermium* (*A. margaricarpum* Sodiro) and in *Xialophyllum* (*A. angosturense* Engl., *A. filiforme* Engl., and *A. tenuinerve* Sodiro). A few species placed in sect. *Porphyrochitonium* in the Central American revision of *Anthurium* are now believed to be aberrant members of sect. *Calomystrium*. This group of species occur in or along streams and has mostly slender leaves which are not noticeably punctate on the lower surfaces. The group consists of *A. amnicola* Dressler, *A. antioquiense* Engl., *A. antrophyoides* Killip, *A. rupicola* Croat, *A. sytsmae* Croat, and *A. werffii* ined. Croat sp. nov. Because of their short internodes

and slender leaves they were confused with sect. *Porphyrochitonium* but breeding studies have shown that they do not interbreed with other members of that section but instead breed readily with sect. *Calomystrum* and are believed to be specially adapted members of that group. Perhaps they independently evolved slender leaves which survive much easier in rapidly moving water.

Section *Digitinervium* is a small group with leathery, plicately-veined, glandular-punctate leaf blades and scalariform venation. It ranges from Costa Rica to Venezuela and Peru, particularly at middle to high elevations. The section is centered in the mountains of Ecuador, and most species were described by Sodiro (loc. cit.). Only a few species exist in this section and relatively few of them are believed to be new to science.

Section *Cardiolonchium* is also heavily concentrated in the Andean region at low to middle elevations, especially on the western slopes of the Andes. A few species occur in the lower part of Central America and one species, *A. costatum* K. Koch & Bouché occurs in the coastal range of northern Venezuela. One species, *A. rubrinervium* (Link) Don (probably to include both *A. polyrrhizum* K. Koch & Augustin and *A. alienatum* Schott) is widespread in the Amazon basin, ranging from lowland Ecuador and Peru to the Guianas. Section *Cardiolonchium*, with frequently velvety, often discolored leaf blades, was represented among the earliest introductions into European glasshouses. Many species are narrowly restricted and now rare. Most have probably already been described but a few new species remain.

Despite having velvety leaves, a few Mexican species appear to be unrelated to Section *Cardiolonchium*. They include *A. clarinervium* Matuda, *A. lezamae* Matuda, and *A. leuconeurum* Lem. These species will hybridize with other Mexican species including species in unrelated groups such as *A. pedatoradiatum* Schott but not with *Cardiolonchium* species in other areas. This again points out the isolated nature of the Mexican species of *Anthurium*. Indeed,

Central American species of *Anthurium* in general are not closely related to those of South America. For example, of the 221 Central American species, only two, *A. scandens* (Aublet) Engl. and *A. gracile* (Rudge) Schott, are truly wide-ranging, i.e. from Mexico to Brazil. While quite a large number enter northern Colombia, or barely enter Panama from South America, only ten additional species from Middle America enter into non-Colombian portions of South America (Croat, 1986a).

Another example pointing out the isolated nature of Central America is the breeding behavior of *Anthurium* sect. *Pachyneurium*. While Central and South American species respectively will readily interbreed within their own group, few Central American species will cross with South American species (Croat, 1991).

In contrast to those groups mentioned above, which have the majority of their species in the Andean regions, section *Urospadix* is almost exclusively known from eastern South America and is most heavily concentrated on slopes of the eroded plateau of central and southern Brazil. Here it clearly represents the most dominant group of Araceae. Mayo reports approximately 60 species of sect. *Urospadix*, and there are numerous new species in the region. Some members of the section range as far north as the Guiana Highlands, and at least one member believed to be in the group, *A. lilacinum* Bunting, even occurs in the Cordillera de la Costa in northern Venezuela.

Another unique section, *Chamaerapium*, represented only by *A. radicans* K. Koch & Haage, is restricted to eastern Brazil. Though now represented in cultivated collections in many places, it is apparently rare in the wild.

Few groups of *Anthurium* are restricted to Central America, but one as yet unnamed group possibly deserving sectional status, represented by plants with cordate, glandular-punctate blades, is restricted to Mesoamerica and centered in Mexico. Examples include *A. lucidum* Standley ex Yuncker, *A. chiapasense* Standley, and *A. verapazense* Engl. This group, as well as many other endemic Mexican species, ap-

pears to share little in common with other species from other parts of Central America. The *Anthurium* flora of Costa Rica and Panama, though also highly endemic, at least shows signs of relationships with species from South America. Most of these species occur in groups which are much better represented in the Andes of South America.

The section *Polyphyllum*, consisting of two scandent species, *A. flexile* Schott and *A. clidemioides* Standley, is also restricted to Central America. The group is distinguished by having several internodes between successive flowering internodes and in having roots produced along the internodes (Croat & Baker, 1978).

Another largely Central American group is section *Schizoplacium*. This small group, with deeply palmately lobed leaves, is known primarily from Mexico, the West Indies (represented there by *A. palmatum* [L.] Don) and northern Venezuela (represented by *A. longissimum* Pittier).

The section *Semaeophyllum* (deeply trilobed blades) is concentrated in southern Central America and in the Andean portion of northern South America. Despite previous work by Madison (1978), the group has a number of new species, especially in South America. A new revision of the section is currently being carried out.

Section *Xialophyllum* is an unnatural group (Croat & Sheffer, 1983) with at least two elements. One group, with thin, bulate leaves or at least prominently raised tertiary veins, is represented by such species as *A. microspadix* Schott, *A. columbianum* Engl., and *A. myosuroides* (Kunth) Endl. Another group, with more coriaceous, smooth leaves is represented by such species as *A. mindense* Sodiro, *A. sarmen-tosa* Engl., and *A. popayanense* Engl. Section *Xialophyllum* is primarily Andean but ranges from Mexico to Bolivia with the greatest concentration at middle to high elevations in the Andes of Colombia, Ecuador, and Peru. This group probably contains a number of new species.

Other primarily Andean groups are sections *Polyneurium* and *Belolonchium*. Section *Polyneurium* ranges from Nicaragua to the mountains of western Venezuela and

Peru, with greatest concentrations of species in the Andes of Colombia and Ecuador. This group probably includes many new species. It almost certainly includes two disparate groups which will have to be recognized, one represented by *A. cuspidatum* Master and its allies and the other *A. panduriforme* Schott and *A. corrugatum* Sodiro.

Section *Belolonchium sensu* Schott is almost exclusively Andean, occurring primarily in cloud forests at higher elevations and characterized by the widespread *A. pulchrum* Engl. which usually is the dominant species at elevations above 1,000 m in many parts of Ecuador and Colombia. The section also ranges into western Venezuela (e.g. *A. berryi* Bunting, *A. betanianum* Croat, *A. ginesii* Croat, *A. nubicola* Bunting, and *A. signatum* K. Koch & Mathieu). Engler's circumscription of section *Belolonchium* was much broader and included many species which occur at lower elevations, even at sea level.

Section *Tetraspermium* is widespread, owing to two species, namely *A. scandens* (Aublet) Engl. and *A. trinerve* Miq., but a number of mostly Andean species remain undescribed. Most species range from very dry areas, such as *Tropical dry forest* (*A. poblii* Engl.) to *Tropical moist forest*, but a few species, such as *A. scandens* ssp. *pusillum* Sheffer and *A. lacinosum* Sodiro, range into *Premontane wet forest* and *Premontane rain forest*.

Another small but widespread section is *Dactylophyllum*, a group with palmately compound blades. It ranges throughout most of the range of the genus (except in Paraguay and Argentina) and is most abundant in regions of *Tropical moist forest*. The section is most diverse in eastern South America and in the Amazon basin. It is represented by such species as *A. eminens* Schott, *A. pentaphyllum* (Aublet) Don and *A. clavigerum* Poeppig. A few species from eastern South America may be new to science.

A well known but insignificant group is *Leptanthurium*. It is represented by *A. gracile* (Rudge) Schott, one of the most widespread species in the genus. This is

the only *Anthurium* species with a chromosome base number of 10 and is believed to be unrelated to any described and the section is not closely related to any other section. A few additional undescribed Andean species probably also belong here, but their chromosomes have not yet been studied.

Two monotypic sections are very geographically isolated. Section *Chamaerapium* with a single species, *A. radicans* Koch & Haage occurs in eastern Brazil while *A. gymnopus* Griseb. in section *Gymnopodium* is endemic to Cuba. Neither group appears to have any close relatives.

A large number of *Anthurium* species remain unclassified as to section. Species involved mostly consist of larger cordate-leaved species which clearly do not belong in any of the other described cordate groups, e. g. *Cardiolonchium*, *Calomystrium*, *Polyneurium*, or *Belolonchium*. Probably several small sections will have to be created to accommodate them. Engler placed most of such species known to him in section *Belolonchium*. Another somewhat smaller group which does not fit into any recognized section includes more or less oblong to lanceolate-leaved plants lacking glandular punctations, e.g. *A. michelii* Guilloumin. Both groups contain new species.

Future work on *Anthurium* must concentrate in two areas: the Andean countries, especially Colombia, Ecuador, and Peru as well as in eastern Brazil. The problems in these two areas are very different. In eastern Brazil the majority of the species have been described but are still poorly defined and little understood. They are very similar to one another, and the type localities are very much degraded. Some species may be lost altogether.

In the Andes of western South America species diversity is much higher, and there are many undescribed or poorly known species. A great deal of time and space will be needed just to sort out the specimens to determine how many species there are.

ASTEROSTIGMA

This is a genus of terrestrial, tuberous herbs in tribe Spathicarpeae of subfamily

Aroideae, occurring usually as understory plants, from near sea level to 2,300 meters.

The genus *Asterostigma* consists of only six species, all but a few of them rather poorly known. Those in the Andes, such as *A. integrifolium* Madison and *A. pavonii* Schott, occur in cool mountain valleys, often on steep slopes. Only the latter occurs in Peru. *Asterostigma riedelianum* (Schott) Kuntze is endemic to the state of Bahiá in eastern Brazil, while *A. tweedianum* Schott is endemic to Santa Catarina in southeastern Brazil. *Asterostigma luschnathianum* Schott is known from Minas Gerais and Rio de Janeiro states, and *A. lividum* (Lodd.) Engl. is the most widespread species, ranging from Minas Gerais to Rio Grande do Sul.

Collecting *Asterostigma* poses no particular problem, although they are not common, and few species have been well collected. Recollections are necessary, especially of the Brazilian species to confirm Engler's treatment.

Another problem with *Asterostigma* concerns the name *A. cubense* (A. Rich.) K. Krause ex Bogner, purportedly from Cuba (Bogner, 1969). The species is related to *A. riedelianum* (J. Bogner, pers. comm.). This name is based on a mixed collection with *Xanthosoma cubense* (Schott) Engl. Although *Asterostigma* has never been collected in Cuba and is probably restricted to southern South America, the true nature of *A. cubense* has, in my opinion, never been determined.

BOGNERA

This monotypic genus (tribe Dieffenbachieae), represented by *B. recondita* (Madison) Mayo & Nicolson, is known only from the western part of the state of Amazonas on the Rio Javari. Madison (1980) initially described it as a species of *Ulearum*. Since it is in cultivation at the Munich Botanical Garden and elsewhere, it is now quite well known. It is very similar to Dieffenbachieae, according to J. Bogner (pers. comm.). The tribe Dieffenbachieae is placed in the *Dieffenbachia* Alliance in subfamily Aroideae. Little remains to be

done with *Bognera* except to determine the exact extent of its range.

CALADIUM

A modest-sized genus of 17 species (tribe Caladieae in the *Caladium* Alliance of subfamily Aroideae) ranging from sea level to at least 1,000 m, this principally South American group is often confused with *Xanthosoma*. While chiefly tuberous, and preferring semideciduous, seasonally dry forest, the plants are sometimes rhizomatous and caulescent as in *Caladium lindenii* (André) Madison. This species inhabits wet forest areas in Colombia and Panama. Species in semideciduous forest often lose their leaves and go dormant during the dry season.

The genus ranges from southwestern Costa Rica to the West Indies and Trinidad, Venezuela, northern Brazil (Amazonas and Pará, except for the widespread *C. bicolor* [Ait.] Vent.), and Peru. Mayo reports only four species for Brazil, including *C. bicolor*, *C. humboldtii* Schott, *C. macrotites* Schott, and *C. picturatum* K. Koch. Only *C. bicolor* and *C. picturatum* are reported for Peru (Croat, 1993).

A major center of diversity appears to be Venezuela and the Guianas. Only two species, *C. bicolor* and *C. lindenii* (André) Madison, occur naturally in Central America and the latter is restricted to Panama. *Caladium bicolor* has been introduced widely throughout Central America. Venezuela has eight species, several of them recently described (Bunting, 1975) and still poorly known. At least five species, including *C. aturense* Bunting, *C. bicolor*, *C. humboldtii*, *C. macrotites*, and *C. picturatum*, occur in southeastern Venezuela on the margin of the Amazon basin, and an additional species, *C. schomburgkii* Schott, occurs in the adjacent Guianas. The Cordillera de Merida also has several species, including *C. coerulescens* Bunting, *C. smaragdinum* K. Koch & Bouché, and *C. steyermarkii* Bunting.

Several species treated as *Caladium* by Bunting (1979) have proven to belong to *Xanthosoma*. These include *C. akkerman-*

sii Bunting, *C. aristeguietae* Bunting, and *C. striatipes* K. Koch & Bouché. All have been transferred to *Xanthosoma* (Madison, 1981) or by Croat & Lambert (1986). This is an indication of the close proximity of these two genera taxonomically. While most species of *Xanthosoma* and *Caladium* are distinctive by a suite of characters, many appear quite intermediate. Madison (1981) determined that the only definitive character for separation of the two genera is in the nature of pollen presentation, with *Caladium* having pollen borne in monads and *Xanthosoma* having tetrads. While work by Madison was important in defining the two genera, it is believed that his treatment of *Caladium*, wherein 39 taxa were synonymized under *C. bicolor*, was unrealistic. Bunting (1979), for example, has recognized as distinct two species synonymized by Madison, e.g. *C. picturatum* K. Koch and *C. smaragdinum* K. Koch & Bouché.

Caladium appears to be less richly developed in the Andes of western South America than in northeastern South America, but numerous collections in the *Caladium bicolor* complex remain unidentified.

CHLOROSPATHA

This is a genus of fifteen species of understory herbs in middle elevation wet forest at elevations of 275 to 1,800 (2,500) meters. The genus is placed in tribe Caladieae (Aroideae).

Madison (1981) provided a revision of *Chlorospatha* including ten species. Subsequently an additional four taxa were described by M. H. Grayum (1986, 1991). Three species occur in Panama including *C. croatii* Grayum, *C. croatii* var. *enneaphyllum* Grayum, and *C. hammelianum* Croat & Grayum. Four species occur in Colombia including *C. gentryi* Grayum, *C. kolbii* Engl., *C. lehmannii* (Engl.) Madison, and *C. mirabilis* (Masters) Madison. Ecuador is the center of species diversity with six species, *C. atropurpureum* Madison, *C. besseae* Madison, *C. castula* (Madison) Madison, *C. cutucuense* Madison, *C. dod-*

sonii (Bunting) Madison, *C. ilensis* Madison, and *C. longipoda* (K. Krause) Madison.

DIEFFENBACHIA

The genus comprises the monotypic tribe Dieffenbachieae (Aroideae) and has an estimated 85 species, consisting of mostly caulescent, understory, terrestrial herbs, occasionally occurring along clearings or rarely in swampy areas. It ranges from Mexico (Veracruz) to the West Indies, Trinidad, the Guianas, Paraguay, and northeast Argentina, and is certainly the most overall poorly known aroid genus in the neotropics. In Central America, where it is dramatically more well known than in South America, there are 26 species; 20 believed new to science. *Dieffenbachia* is believed to be just as diverse in South America as in Central America, and it may have an equally large percentage of species new to science. However, more species have already been described from South America than from Central America.

There are seven species in Venezuela, six species in the Guianas, and at least six species in Brazil. Macbride (1936) treated 11 species of *Dieffenbachia* for Peru, but a modern checklist (Croat, 1993) treats only 9 species. In all, 21 species (recognized by Engler in his 1915 revision) have been described from South America, but little is known about the majority of them.

The tribe Dieffenbachieae is a member of the *Dieffenbachia* Alliance in subfamily Aroideae.

One species name used throughout much of the Neotropics and certainly representing a variety of species (perhaps a different species in Central and South America) is *Dieffenbachia seguine* (Jacq.) Schott (Standley, 1944); (Standley & Steyermark, 1958); (Engler, 1915); (Matuda, 1954); (Jonker-Verhoef & Jonker, 1953); and (Bunting, 1979). Since Jacquin's original material came from the West Indies, probably from Martinique, it is necessary to study there to determine the true nature of *D. seguine*. Only a single species of *Dieffenbachia* was found in the Dominican Republic, and it appears to be a different species than the

Dieffenbachia going by that name in Venezuela, the Guianas, and in Central America. Living material from Martinique must be studied to see if it is the same as that from the Dominican Republic.

Dieffenbachia is, in general, well collected since plants provide no particular obstacle, being terrestrial and readily accessible. However, some are very large, and all are fleshy. Many are rich in oxalic acid so the sap may burn the skin, and they may be very foul during the drying process. Some collectors avoid them for these reasons. The chief problem with their taxonomy, however, is species circumscription. Species are either highly variable or there are many species. In Panama and Costa Rica where they have been studied most closely, each population is in some way different from the next, yet with distinct patterns of variation that lead one to believe they might all be closely related. Helen Young, during her studies at La Selva (Organization for Tropical Studies) in Costa Rica, found that the beetles pollinating *Dieffenbachia* sometimes cross-pollinated different species of *Dieffenbachia* and plants pollinated in such manner did produce viable fruit (Young, 1986, 1988a, 1988b). It is not yet known if the offspring are capable of reproducing, but the possibility exists that much of the variation seen in the field is the result of hybridization. The genus warrants a thorough biosystematic study. Plants are readily brought into cultivation, and many species are now growing at the Missouri Botanical Garden and elsewhere.

Dieffenbachia species are rarely found in great numbers at any locality. It is rare to find more than one or two species at any particular neotropical site. La Selva, an area of *Tropical wet forest*, is unusually rich in having seven species. Barro Colorado Island in central Panama, is typical for the genus in having two species, both extremely common. Four species have been collected at Cerro Neblina in southern Venezuela, and four species are also known from *Tropical wet forest* at the Jatun Sacha Reserve at 450 m along the Río Napo in Ecuador. At study sites in Colombia, four species have been collected at Bajo Calima in

Premontane pluvial forest at near sea level, but no species were collected in *Premon-tane forest* at 1,800 m elevation at La Plan-ada in Nariño. Typically, *Dieffenbachia* is much more abundant at lower elevations than at higher elevations, especially above 1,000 m elevation.

DRACONTIOIDES

This is a monotypic genus in tribe Lasieae, subtribe Dracontiinae, with a spongy rhizome. It is represented by *D. desciscens* (Schott) Engl., occurring in swampy areas of eastern Brazil in Baía and Espiritu Santo. Relatively few collections exist but the genus poses no particular problem taxonomically. It is in cultivation in several botanical gardens, including the Missouri Botanical Garden, and it will be studied as an outgroup in a cladistic analysis of *Dracontium* by Guanghua Zhu.

DRACONTIUM

This small, tuberous lasioid genus (tribe Lasieae, subtribe Dracontiinae) of about 18 species ranges from southern Mexico to Panama, Colombia, Ecuador, and Peru on the Pacific coast as well as to Venezuela, the Guianas, Brazil, Bolivia, and Paraguay. It also occurs in Puerto Rico. It has long been among the most troublesome neotropical aroid genera from the taxonomic standpoint owing to both morphological and ecological characteristics. Firstly, populations are frequently rare. Only 29 collections have been personally collected by me in my 25 years of collecting Araceae. Secondly, type collections are often incomplete, since plants often are sterile or have inflorescences with no leaves. Thirdly, plants are often huge, often to 2 m or more in height and usually consist of a single leaf. Collections rarely contain the whole leaf, or they are folded and difficult to study. Thus, specimens are not only rare but also, in many cases, inadequate. *Dracontium* is represented in the West Indies by probably a single species, purportedly *D. polyphyllum* L.; Central America has four species of *Dracontium* including *D. costaricense* Engl., from Costa Rica and Panama; *D. gigas*

(Seemann) Engl. from Costa Rica and Nicaragua; *D. pittieri* Engl. from Costa Rica; and *D. soconuscum* Matuda ranging from Mexico to Panama.

Venezuela has four species, *D. asperum* K. Koch, *D. changuango* Bunting, *D. margaretae* Bogner and *D. polyphyllum* L. *Dracontium margaretae* Bogner has been collected only from Apure, Venezuela and Paraguay. This species differs from all other *Dracontium* by having linear leaves and it may belong to a different genus. Three species are known from the Guianas, *D. asperum* K. Koch, *D. foecundum* Hook, f., and *D. polyphyllum* L. Brazil has at least four species, including *D. asperum*, *D. longipes* Engl., *D. margaretae* Bogner, and *D. ulei* K. Krause. The latter, as well as *D. loretense* K. Krause were reported from Peru (Macbride, 1936). *Dracontium loretense* ranges to Ecuador and is the most common species in the upper Amazon region. The genus is apparently rare in Colombia but is known from only a few sites in Chocó Department at 240–260 m in *Premontane wet forest*. Elsewhere on the Pacific slope *Dracontium* is known from Ecuador at El Centinela. It is possibly the same species as those collected in Colombia.

The genus *Echidnium* Schott with two species, recognized by Engler (1911) has been synonymized with *Dracontium* (Bogner, 1985).

The genus is currently being revised by Mr. Guanghua Zhu, a graduate student at the University of Missouri, St. Louis, working with me at the Missouri Botanical Garden. About half of the species are currently in cultivation at the Missouri Botanical Garden.

FILARUM

This rare, monotypic genus is in tribe Zomicarpeae in the *Caladium* Alliance of subfamily Aroideae. It is in much need of further investigation, including anatomical, cytological, and molecular studies. The genus is represented by *F. manserichense* Nicolson, a tuberous understory herb in primary forest, known from Loreto Department as well as the type locality at Pongo

de Manseriche in the department of Amazonas, along the Río Marañón. More collections are needed to determine the extent of its range and morphological variability.

GEARUM

This is a monotypic tuberous genus (tribe Spathicarpeae in *Dieffenbachia* Alliance of Aroideae) growing in seasonally inundated areas. It is endemic to southern Brazil in Goiás and was very poorly known until recollected by A. de Araujo Dias in 1978. More collections are needed to determine the true extent of its range and morphological variability.

GORGONIDIUM

The genus (tribe Spathicarpeae as above) consists of three species in the southern Andes of Bolivia, Peru, and northeastern Argentina. None of the species have been particularly well collected, but a modern revision exists (Bogner & Nicolson, 1988). *Gorgonidium vermicidum* (Speg.) Bogner & Nicolson occurs in Argentina. *G. mirabile* Schott occurs in Bolivia (Depts. La Paz and Cochabamba), and *G. vargasii* Bogner occurs in Peru (Departments Cuzco and Apurimac at 2,800–3,000 m but collected recently at a lower elevation in Lima Province, Lima Department). The plants have rhizomatous tubers and occur in seasonally dry areas at up to 3,000 meters. More collections need to be made to determine the true nature of morphological variation in all of the species.

HETEROPSIS

Heteropsis in tribe Heteropsidae of subfamily Monsteroideae is a genus of loosely climbing hemiepiphytes ranging from Nicaragua to the Guianas, Brazil, and Bolivia. It is absent from the West Indies, including Trinidad, despite the fact that it is particularly abundant in Venezuela. Species are heavily concentrated in eastern South America, especially in forests north of the Amazon River. Southeastern Venezuela and the adjacent Guianas represent a center of

diversity. Seven taxa, including five species, occur in the region. These include *H. flexuosa* (Kunth) Bunting, *H. melinonii* (Engl.) Jonker-Verhoef & Jonker, *H. spruceana* Schott (two varieties), *H. steyermarkii* Bunting, and *H. tenuispadix* Bunting. Even single localities, such as the Río Mawrinuma, near the base of Cerro Neblina in southern Venezuela, may have as many as four species. As many as six species, many of them remaining unidentified, occur in the department of Caquetá in eastern Colombia at Araracura on the Río Caquetá. Elsewhere in the Neotropics, *Heteropsis* appears to be relatively rare, though individuals of a species may be locally abundant. Central America has but a single species, currently deemed to be *H. oblongata* Kunth, and only a single species, *H. ecuadorensis* Sodiro, occurs along the Pacific slope in Ecuador. Four species are reported for Peru, including *H. linearis* A. C. Smith, *H. oblongifolia* Kunth, *H. peruviana* K. Krause, and *H. spruceana* Schott var. *robusta* Bunting. Most of the same species are also known for Ecuador.

Five species occur in Amazonian Brazil, the majority of which probably enter the lowlands of either Ecuador or Peru (or both). These include *H. linearis* A.C. Smith, *H. longispathacea* Engl., *H. macrophylla* A. C. Smith, *H. oblongifolia* Kunth, and *H. spruceana* Schott. At least two species occur in eastern Brazil: *H. rigidifolia* Engl. ranges from São Paulo State to the state of Santa Catarina of Brazil (Reitz, 1957), and *H. salicifolia* Kunth ranges from São Paulo State to perhaps as far north as Bahía. Neither occurs in the Amazon basin.

Heteropsis is not a particularly troublesome genus taxonomically. Species seem to be distinct and not markedly variable, but the genus is difficult to collect since plants often flower high up in the canopy. In addition, they are exceedingly difficult to bring into cultivation because of their slender, somewhat woody stems with long internodes. Some success in recent years has been made in growing them from seeds, and one chromosome count has been made for *Heteropsis oblongifolia* Kunth from Costa Rica. In several areas of Latin America

some species are being exploited commercially for weaving into baskets or used in making furniture. This may create a problem with local extinction in these sometimes rare plants and would justify prompt revisionary attention.

HOMALOMENA

The neotropical species of this chiefly paleotropical genus are as yet poorly known. The genus consists of between 10 and 17 taxa comprising terrestrial, rhizomatous herbs, with frequently aromatic sap (anise-scented), and frequently armed petioles and/or pubescent parts. In these features they are nearly unique among neotropical aroids. Still, they may be easily confused with *Philodendron*. A definitive means of separation is the presence of staminodia among the female flowers.

Homalomena is placed in tribe Homalomenae in the subfamily Aroideae. The neotropical species of the genus were revised during the mid 1980s by Mark Moffler as a part of a Ph.D. thesis at the University of South Florida in Tampa, under the direction of Dr. Fred Essig. Though Moffler died in 1986 the thesis is being reworked extensively by Dr. Richard Wunderlin, who seems inclined to reduce the number of recognized species to only seven. Certainly this does not reflect an accurately true number of species in the genus. An example of this reduction is the placement of *H. peltata* Masters under *H. wendlandii* Schott. I have studied both of these species in the field and there is no doubt as to their distinctness. The study is not yet complete, so the final word is still out on *Homalomena*. Many species are still poorly known and collecting, especially in the Andean region of Colombia and Ecuador, is much needed. A few species, such as *H. wendlandii*, are well known and well collected. Central America has four species, including *H. peltata*, *H. roezlii* (Masters) Regel, *H. wallisii* Regel, and *H. wendlandii*. Three additional species occur in northern Colombia, including *H. moffleri* Croat & Grayum sp. nov., *H. speariae* Bogner & Moffler, and *H. picturata* (Linden & André) Regel, the latter

also widespread in the northern Amazon basin. At least three additional species occur in the northern Amazon basin, including *H. erythropus* (Schott) Engl., from southeastern Colombia and northwestern Brazil, *H. crinipes* Engl., from southwestern Colombia to northern Peru, *H. peltata* from the slopes of the Andes in Peru, and *H. solimoensis* G. Barroso in the upper Amazon basin in western Brazil and eastern Peru.

The thorniest problem in the genus is the taxonomy of the peltate-leaved plants which have gone by the name *H. peltata*. Plants in this group are wide-ranging and the distribution of the *H. peltata* complex is particularly curious. In Central America peltate plants are rare, having been collected only in the Isthmus of Panama at only a few localities, including the Pipeline Road north of Gamboa, Matachui in Colón Province and at Puerto Obaldia in the Comarca of San Blas. In South America, similar plants have been collected at a few sites in the department of Chocó, Colombia, in the region of the Río Palenque Biological Reserve south of Santo Domingo de los Colorados, and at La Centinela (both in the province of Los Rios, Ecuador). The only other place where similar plants have been collected in South America is on the other side of the Andes in Huanuco Department of Peru. This is a curious distribution, and I believe, not likely to have resulted from the vagaries of collecting. It is possible that at least some of these populations actually represent different taxa. It is necessary to cultivate representatives of these species together to determine if there are differences not apparent in the dried herbarium material.

JASARUM

This monotypic, submerged aquatic genus in tribe Caladieae in the *Caladium* Alliance of Aroideae represents perhaps the most unusual aroid. Plants are persistently submergent except for the inflorescence at flowering time. *Jasarum steyermarkii* Bunting (Bunting, 1975) occurs only in a few rapidly flowing streams off the Gran Sabana

in the Guiana Highlands of Venezuela in the state of Bolívar and in Guayana in the Mazaruni River basin. Though rare, it is now reasonably well known owing to the work of J. Bogner, who collected it and has it in cultivation at the Munich Botanical Garden (Bogner, 1977, 1984, 1985).

MANGONIA

This tuberous genus of two species, a member of the tribe Spathicarpeae (*Diefenbachia* Alliance of Aroideae) is endemic to southeastern temperate South America. *Mangonia tweediana* Schott occurs in southern Brazil and adjacent Uruguay. *Mangonia uruguayana* (Hicken) Bogner is endemic to Uruguay. Plants occur in seasonally dry areas. Though still poorly known, it has been studied in recent years by Bogner (1973).

MONSTERA

The genus *Monstera*, one of four neotropical genera in the tribe Monstereae (Aroideae), was last revised by Mike Madison (1977) in his Ph.D. thesis at Harvard University. The revision treated 22 species, including three varieties, but perhaps a more realistic estimate of the number of species in the genus, as it is known today, is closer to 60 (Croat, 1988a). For example, Madison recognized 20 taxa for Central America, but studies there by Croat and Grayum, who are working on a revision of the Araceae of Costa Rica, have found that there are at least 39 species of *Monstera* for Central America. There are 22 species in Costa Rica alone, equalling the total number of species included in Madison's 1977 revision. Although *Monstera* is particularly rich in Central America, the South American continent is expected to have a proportionately larger increase owing to the fact that it is not only a vastly larger area, but also because it remains poorly collected. Indeed, since many of the Central American species are endemic, the number of species for the genus will probably exceed sixty.

Venezuela currently is known to have seven taxa (Croat & Lambert, 1986); about

four species occur in the Guianas, five are reported for Brazil by Mayo and seven taxa are reported for Peru (Croat, 1993). *Monstera* is primarily centered in the northern Andes and lower Central America (Costa Rica and Panama) (Madison, 1977). The most widespread "species" in the genus is *M. adansonii* (Schott) Madison which, under three varieties, ranges throughout the neotropics from Nicaragua to the West Indies, the Guianas, and eastern Brazil to Santa Catarina, and in the Amazon basin to Peru and Bolivia in South America. Madison (1977) reported that species diversity in South America was greatest in an arc ranging from Peru north to the Guianas. *Monstera* was divided by Madison into four sections, *Monstera*, *Marcgraviopsis*, *Tornelia*, and *Echinospadix*. In Madison's revision section *Monstera* is the largest section (13 species) with sect. *Marcgraviopsis* having six species and *Echinospadix* and *Tornelia* with a single species each (*M. tuberculata* Lundell and *M. deliciosa* Liebm. respectively). Based on the modern day distribution of the sections (all in Mexico versus two in South America), Madison (1977) believes that *Monstera* is a remnant of the Paleogene tropical flora of North America and that it spread into South America during the Neogene times. Nevertheless, it is clear that considerable evolution of the genus has taken place in South America. Numerous species in South America, especially in the Amazon lowlands, do not fit species he circumscribed.

Monstera is not highly diverse at any of the wetter forest sites on the Pacific slope. For example, only two species have been found at La Planada in Nariño and at Bajo Calima in Valle Department of Colombia, two well studied areas involved in a comparative study sponsored by the National Geographic Society.

Monstera represents a difficult group to study because of the difficulty of collecting them. They are usually firmly appressed-climbing hemiepiphytes or sometimes loosely scandent canopy vines, growing higher in the canopy (e.g. *M. pittieri* Engl. and *M. tuberculata* Lundell) than most aroids, and on average they are very large,

contributing to the lack of many well-prepared, and well-documented collections. Another feature making the genus difficult to understand is the well developed heteroblastic leaf development (Madison, 1977) which they exhibit. Juvenile, preadult, and adult plants often exhibit marked differences. Seedlings exhibit scototropic growth until they become established on trees when they change their growth patterns and begin growing toward light (Strong & Ray, 1975).

MONTRICHARDIA

This genus (tribe Montrichardieae) of two species is widespread, occurring at low elevations and ranging from Guatemala and Belíze to Panama, Colombia, the Guianas, Brazil, and Peru. Plants are shrub-like with erect, sometimes armed stems and somewhat hastate simple blades, and occur principally in standing water along the margins of streams or lakes and in swampy areas and estuaries but may also occur in the understory near watercourses. *Montrichardia arborescens* (L.) Schott, which makes up the northern range of the genus, occurs in the south of Venezuela in the states of Bolívar, Amazonas, and Apure, but it is mostly replaced with *M. linitifera* (Arruda) Schott in the Amazon basin. An unusual population, believed to be *M. arborescens*, located in the lower Rio Negro north of Manaus has blades which may sometimes be completely three-parted. This population deserves more investigation since this feature is not known elsewhere in the genus. Otherwise the genus warrants very little work even though no modern revision exists.

PHILODENDRON

The genus is a member of tribe Philodendreae of the *Philodendron* Alliance of subfamily Aroideae. It is the second largest in the family and is as widespread as *Anthurium*, ranging from Central Mexico to the West Indies, the Guianas, and Argentina. Like *Anthurium* it is difficult to know exactly how many species there are, but it can be reliably estimated that there are as many as 700 species. In some respects the

genus is even more poorly known than *Anthurium*. This is especially true of the larger species, which are poorly collected and represented by poorly made, poorly described collections. Much of what was said about the areas of high species diversity for *Anthurium* is true of *Philodendron* as well, but *Philodendron* is much more abundant at lower elevations than is *Anthurium*. Owing to the much more degraded nature of lowland forest throughout much of the Neotropics, plants are often more difficult to find. This coupled with the fact that *Philodendron* species are often much larger in size and frequently high in trees means that they are often neglected by the average collector.

There are 107 taxa including 96 species of *Philodendron* in Central America with the majority (87 species) occurring in Costa Rica and Panama. There are 121 taxa including 108 species in Venezuela (versus 77 taxa, including 71 species of *Anthurium*), ten species in Trinidad, 43 species in the Guianas, 100 taxa including 97 species in Brazil, 62 in Peru, four in Paraguay, and five in Argentina. Ten species range as far south as Santa Catarina State in Brazil (Reitz, 1957), three of them being members of subgenus *Pteromischum*, i.e. *P. obliquifolium* Engl., *P. ochrostemon* Schott, and *P. sonderianum* Schott. All species in Santa Catarina are endemic to eastern Brazil except *P. bipinnatifidum* Schott ex Endlicher. That latter ranges to Argentina, Paraguay, and Bolivia.

Any counts for the Andean countries would have a margin of error of more than 30 percent, but the richness of the *Philodendron* floras more or less mirrors that of *Anthurium* since all of these countries have a range of lowland, middle elevation, and higher elevation forest. Perhaps only in Bolivia would the *Philodendron* species outnumber the *Anthurium* species, this owing to the fact that there is a broad stretch of lowland forest in Beni contiguous with the Amazon basin and the forests of higher elevations are often very cold, often quite arid, and have relatively few species of Araceae compared to forests of similar elevations at higher latitudes.

Nevertheless, *Philodendron* definitely becomes more dominant in areas with large expanses of lowland forest (especially seasonally dry forest), such as in the Amazon basin or in Venezuela. For example, while *Anthurium* species outnumber *Philodendron* species in the Andean countries, *Philodendron* is much the larger genus in Venezuela, with 118 versus 77 species of *Anthurium*. In contrast, Costa Rica and Panama which reflects the distribution of Araceae in the Andes of South America have proportionately more species of *Anthurium*. Costa Rica has 75 species of *Anthurium* and 51 species of *Philodendron* while Panama has about 160 species of *Anthurium* and only 77 species of *Philodendron*.

Sectional groupings of *Philodendron* are much more poorly understood than those of *Anthurium*, but the three subgenera are distinct and their distributions are now reasonably well known. The subgenus *Meconostigma* (Mayo, 1991) with 15 species is largely distributed in southern Brazil but ranges north into the Amazon basin. The subgenus *Pteromischum*, with an estimated 75 species occurs throughout most of the range of the genus from Mexico (San Luis Potosí) to the West Indies (three species), the Guianas, and Argentina, but has a major center of distribution in lower Central America and northwestern South America. Relatively few species occur in the south of the continent, but considerable numbers (each 10 species) occur in the Guianas and in the Amazon basin (at least 12 species). Venezuela has a total of about 15 species. A few species, especially *P. inaequilaterum* Liebm. are wide-ranging and extend from Mexico to Venezuela and Ecuador, but none of the species in the Amazon basin range into Central America or to the western coast of South America, according to M. Grayum (pers. comm.). A common distribution pattern is from the Atlantic slope of lower Central America to the Pacific coast of Colombia to Ecuador. This same pattern is evident for species of subgenus *Philodendron* but the largest share of the Central American species of this group is endemic to Central America.

The subgenus *Philodendron* comprises

the vast majority of species in the genus, and there are numerous taxonomic problems in the group. Not only are many species poorly known or new to science but the sectional classification of Engler must be carefully reinvestigated. Many sections, especially but not exclusively *Philodendron* and *Calostigma*, appear to be artificial with unrelated elements. It is probable that the reliance principally upon ovular structure alone, which appears to characterize Engler's revision, is artificial. Still, no better system of grouping species has been devised, so until a more thorough investigation is made it seems best to discuss the genus in terms of the existing classification. Some sections, especially *Macrolonchium*, with *P. fragrantissimum* (Hook.) Kunth, *P. simsii* Kunth, *P. melinonii* Brongn. ex Regel, and *P. roraimae* K. Krause (all admittedly similar species), include what appear to be aberrant elements in them. For example, this group also contains *P. pinnatifidum* (Jacq.) Schott with its few-ovulate locules and pinnately lobed blades, which would appear to be more well placed in section *Polytomium*, along with *P. angustisectum* Engl. and *P. distantilobum* K. Krause. Considering the immense variation in some sections, especially in sections of *Philodendron* and *Calostigma*, the section may prove to be unworthy of recognition.

The majority of species in the subgenus *Philodendron* are in sections *Philodendron* or *Calostigma* (recently reclassified from sections *Polyspermium* and *Oligospermium* (Schott) Pfeiffer, respectively (Mayo, 1990)). Both sections occur nearly throughout the range of the genus. Subsection *Belocardium* of section *Calostigma*, with often elongate leaves with frequently tumid petioles and a dark, purplish ring demarcating the petiole and blade, is particularly distinctive and is well distributed in lower Central America and on the lower slopes of the eastern slopes of the Andes.

Section *Macrolonchium* (mentioned above) occurs in Central America, northern Venezuela, the Guianas, and the Amazon basin. It has only about six species.

Section *Boursia* has only a few species in Central America, in northern Venezuela

or on the Pacific slope of Colombia and Ecuador. The majority of the species in the section occur in eastern Brazil, the Amazon basin, or the lower eastern slopes of the Andes. Section *Tritomophyllum*, with its trilobed blades and single ovule per locule is primarily Central American but ranges down the western coast of South America to Ecuador. It is a small group with probably fewer than ten highly variable taxa, several of which are new. The section, as defined by Engler, certainly appears to be an unnatural one.

Section *Schizophyllum* ranges from northeastern Venezuela and the lowland Guianas to southern Brazil, and throughout the Amazon basin to Bolivia in the southwest. Only *P. pedatum* (Hook.) Kunth is very widespread, and most of the approximately six species are restricted to the lower Amazon basin and to eastern South America. A new species exists in French Guiana.

Section *Polytomium*, a small group with mostly large, pinnately lobed leaves and few-ovulate locules, ranges from Mexico to the Greater Antilles, northern Venezuela, northern Colombia, and the Amazon basin. Only *P. lacerum* (Jacq.) Schott occurs in the West Indies (Cuba, Hispaniola, and Jamaica), while three species occur in Central America: *P. radiatum* Schott, *P. warscewiczii* K. Koch, and *P. dressleri* Bunting. *Philodendron fendleri* K. Krause occurs in northern Venezuela and Trinidad while *P. elegans* K. Krause occurs in northern Colombia. Two species, *P. distantilobum* K. Krause and *P. angustisectum* Engl., are restricted to the Amazon basin.

A newly described section, *Philopsamos* Bunting, with probably fewer than 15 species, is known only from the Amazon basin and especially the region of the Guiana Highlands. The group is distinguished primarily by the elongate, many-veined leaf blades. The most widespread species in the group, *P. pulchrum* G. Barroso, ranges from southern Venezuela to Brazil (Roraima and Amazonas) to Colombia (Vaupes and Putumayo) and Peru (Amazonas, Loreto and San Martín).

Two small sections, both unique in the

structure of their ovules, differ remarkably in distribution. Section *Macrogynium*, represented only by *P. bederaceum* (Jacq.) Schott, ranges from Mexico (both slopes) to Panama, northern Colombia, Venezuela, and the Guianas, primarily in areas of seasonally dry forest. In contrast, section *Camptogynium*, represented by only *P. longistilum* K. Krause is known only from the upper Amazon basin in Brazil. While most of the species in subgenus *Philodendron* from the lowland Amazon basin are reasonably well known, as are those from Central America, Venezuela, the Guianas, and eastern Brazil, the species from the Andean countries of western South America are even more poorly known than those of *Anthurium* from the same region. Much of the material collected in the Andean countries by earlier collectors, especially Lehmann in Colombia, Fendler and Pittier in Venezuela, and Poeppig in Peru, was studied by either Schott or Engler, and many species were described as new. The same is true to a lesser extent with *Philodendron* collected by Luis Sodiro in Ecuador, but whereas Sodiro was keenly interested in *Anthurium* and described 281 taxa of *Anthurium* (including 257 species) chiefly from Central Ecuador, he described no *Philodendron*. Thus many of the species from Ecuador remain undescribed. Perhaps more importantly, the areas which are probably richest for Araceae, namely the lowland Pacific coastal regions, were not opened up to easy access until relatively recent times. More specimens have been made from these regions in the past 25 years than in all the preceding centuries. These regions of very wet forest contain an exceedingly rich, mostly endemic flora remaining very poorly known. The majority of species appear to be new to science. An example is the site known as "Bajo Calima," a region of lowland *Premontane wet pluvial transition forest* in Valle Department near Buenaventura, Colombia, which has yielded 40 species of *Philodendron*. Relatively few of these species have yet been identified, and a large percentage of the species is clearly new to science. The region to the north, in *Pluvial forest* in the

department of Chocó, is likely to be even richer. Colombia and Ecuador together probably have more than all the rest of South America. The Pacific slope of Colombia is much dissected with rivers, and considerable endemism is apparent from investigations there. For example, studies in Nariño in three sites of *Premontane wet forest* (Croat, 1992) have shown that even sites relatively near one another, e.g. Río Nembí and Río Nambí, separated by only about 15 km and at the same elevation, shared few species in common. Investigation of wetter life zones in Nariño are expected to provide even more startling differences. In short, much work remains to be done with *Philodendron* in South America.

PISTIA

This monotypic floating aquatic genus in tribe Pistieae (Aroideae), represented by *Pistia stratiotes* L., is both well collected and moderately well studied, but no recent study has been made, the last by Engler in Das Pflanzenreich (Engler, 1920). It ranges from southern Florida to the West Indies and throughout Central and South America to as far as 35 degrees south in the region of Buenos Aires in Argentina (Crisci, 1971).

RHODOSPATHA

This genus of hemiepiphytic appressed climbers or caulescent terrestrial herbs in tribe Monstereae ranges from Mexico to Panama, Venezuela, Trinidad, the Guianas, eastern Brazil, and the Amazon basin to Peru and Bolivia. The last revision of *Rhodospatha* by Engler in Das Pflanzenreich included eleven names. Three of the species proved to be members of other genera: *Monstera* (*M. costaricensis* [Engl. & K. Krause] Croat & Grayum), *Stenospermatium* (*S. tuerckheimii* [Engl.] Croat), and *Heteropsis* (*H. melinonii* [Engl.] Jonker-Verhoef & Jonker). Three additional names have been synonymized: *R. longipes* Engl. and *R. blanda* Schott under *R. oblongata* Poeppig and *R. picta* Nicolson under *R. moritziana* Schott. This left only five species: *R. densinervia* Engl., *R. heliconiifolia* Schott, *R. latifolia* Poeppig, *R. oblongata*

Poeppig, and *R. wendlandii* Schott. In the current revision being carried out by Croat, 78 taxa and 75 species of *Rhodospatha* are recognized. Species diversity is highest in Venezuela and in the western Andes of South America as well as in Central America. Central America has 14 species and 15 taxa, most of them in Costa Rica and Panama. Venezuela has 13 species, the Guianas has four species, and eastern Brazil has four species, including *R. oblongata*, *R. latifolia*, and two new species. *Rhodospatha latifolia* and *R. oblongata* are widespread in the upper Amazon basin and range to eastern Ecuador and Peru. Macbride reported these two species in his treatment for the Flora of Peru but included seven additional names which are now placed in *Stenospermatium*. Only one additional species, *R. moritziana* was cited in the recent checklist for the Flora of Peru (Croat, 1993), but there are believed to be as many as 16 additional species in Peru, most of them new to science. Species diversity is especially high in Ecuador with approximately 27 species, most of them new to science.

Rhodospatha is a difficult genus because of the lack of definitive key characters. The inflorescences are less valuable than in most genera and the spathe, which usually falls off just after anthesis, is often lacking. Spathe and spadix color is not greatly variable and fruits are almost always lacking, and in cases where they are present, are not particularly variable in any important respect. Plants are difficult to collect, generally being high up on tree trunks where they usually require a clipper pole to bring them down. Characters separating species often involve coloration of dried plants, which, though consistent for a species, is difficult to quantify.

SCAPHISPATHA

This monotypic tuberous genus of herbs in tribe Caladieae (*Caladium* Alliance, Aroideae) ranges from eastern Bolivia to eastern Brazil. It was very poorly known until recollected by J. Bogner in 1976 (Bogner, 1980) in the state of Ceara. The plants flower before the leaves are produced. The peltate leaf blades look much like those of

the common *Caladium bicolor*. The only species, *S. gracilis* Brongn. ex Schott, poses no special taxonomic problem, but more collections are needed to determine geographic distribution.

SCHISMATOGLOTTIS

The genus is primarily Old World, but two species occur in the Venezuelan Guianas, the lowlands of southern Venezuela, and in adjacent Suriname and the Amazon basin. *Schismatoglottis bolivarana* Bunting & Steyermark is endemic to Venezuela, known from both Bolivar and Amazonas, whereas *S. spruceana* (Schott) Bunting, which includes two varieties, occurs in the same states but also in Brazil and Peru. Relatively few collections exist for *S. bolivarana*. *Schismatoglottis americana* Jonk. & Jonk. occurs only in Suriname on Tafelberg.

Schismatoglottis is a member of tribe Schismatoglottideae of the *Schismatoglottis* Alliance in subfamily Aroideae.

SPATHANTHEUM

This tuberous-stemmed genus of two species is still poorly known. One of the species, *S. orbignyanum* Schott, is known only from northern Argentina, Bolivia, and Peru, ranging up to 2,400 m elevation. This species, once poorly collected, is now known from a number of well documented collections. *Spathanthium heterandrum* (Baker) N. E. Br., is now considered to be a synonym of the former. The second species, *S. intermedium* Bogner is a distinct undescribed species from Peru. *Spathanthium* is a member of tribe Spathicarpeae in the Aroideae.

SPATHICARPA

This small group in tribe Spathicarpeae (with the same subfamilial placement as *Spathanthium*) consists of small herbs with tubers, rhizomes, or rhizomatous tubers occurring as understory herbs in humid or marshy forests, but also in dry forest (caatinga), where the vegetative parts may die back during the dry season (Croat, 1988a).

This genus of five to seven species has had no serious revision since Engler's time, though two species were treated in the Flora of Paraguay (Croat, 1988b) and in the Flora de Argentina (Crisci, 1971).

Spathicarpa occurs in eastern Brazil (from Bahia south to Rio Grande do Sul) as well as Uruguay, Paraguay, Bolivia, and northeast Argentina. Along with *Mangonia* and *Pistia*, it is one of the few aroid genera in Uruguay. One species, *S. bastifolia* Hook., occurs in Bolivia, Argentina, and Uruguay as well as in Paraguay and eastern Brazil, where it ranges from Minas Gerais to Rio Grande do Sul. *Spathicarpa lanceolata* Engl. occurs in Paraguay and southern Brazil (Santa Catarina and Rio Grande do Sul). The remaining species are all Brazilian and are more poorly known. *Spathicarpa burchelliana* Engl. occurs in Goiás and Ceará and *S. gardneri* Schott in Ceará, Pernambuco, Piauí, and Goiás in the northeast of Brazil, while *S. tweediana* Schott occurs in São Paulo State.

Engler (1920) treated *S. gardneri* as a variety of *S. sagittifolia*, whereas Mayo includes it as a distinct species. This genus is a highly variable one, especially in leaf size and shape. More collections need to be made of the last three species mentioned, and other species need to be brought into cultivation to determine the validity of the last taxonomic treatment.

SPATHIPHYLLUM

This genus of about 60 terrestrial or rupicolous species in the tribe Spathiphyllae (Monsteroideae) ranges from central Mexico to Trinidad, the Guianas, Brazil, and Peru primarily at lower elevations. Bunting's revision (1960) included 36 species, but many species have been subsequently collected during the past three decades. Baker & Burger (1976) revised the Costa Rican species and described two new taxa. Twenty-four species and two varieties occur in Central America (including several new species); eleven species and one subspecies occur in Venezuela; five in the Guianas; four in Brazil; and at least seven in Peru. There are relatively few species in

the Amazon basin, but one widespread species, *S. cannifolium* (Dryander) Schott is the most common and widespread species in the genus ranging from Trinidad and the lowland Guianas to just south of the Amazon River in Brazil and west to Colombia and Peru as far south as Pasco Department. Curiously, it has not been found in Bolivia. While most *Spathiphyllum* species are understory herbs, some species, such as *S. friedrichsthali* Schott, often occur in open marshy areas or along the banks of streams or lakes. Others, including *S. quindiuense* Engl., are rheophytes, occurring along or in streams. Costa Rica and Panama probably constitute a center of diversity with 17 species, but Mexico is also diverse with six species. In South America, the Guiana region (including the Venezuelan Guyana) is a center of diversity with eight species occurring there (Bunting, 1960).

STENOSPERMATION

A primarily epiphytic genus in tribe Monstereae (Monsteroideae) with approximately 60 species, the majority of which are new to science. The genus ranges from Guatemala to the Guianas, Brazil, and Peru, but it is known primarily from the Andes, especially in Colombia and Ecuador. Only ten species occur in Central America, nine of these in Panama (Gomez, 1983). Costa Rica has seven species, but few occur in Middle America. For example, there are only two species each in Guatemala and Nicaragua. Seven species occur in Venezuela, four species occur in the Guianas, and Mayo reports only two species for Brazil. Araceae listed in The Catalogue of the Flowering Plants and Gymnosperms of Peru (Croat, 1993) report nine species for Peru.

Stenospermation occurs primarily at middle elevations in areas of very *wet forest*. Relatively few species occur at lower elevations except in the wettest life zones. For example, in Colombia, the La Planada reserve in Nariño at 1,800 m has seven species, and Bajo Calima in Valle Department, located near sea level, has eight species, whereas in *Tropical moist forest* on Barro Colorado Island in Panama (Croat, 1978)

there is only one species, the widespread *S. angustifolium* Hemsley. Even in *Tropical wet forest* at the Jatun Sacha reserve on the Río Napo there is only one species known. There are relatively few, mostly widespread, species in the lowland Amazon basin (surely fewer than five species). Next to *Dieffenbachia*, *Stenospermation* is probably the most difficult genus taxonomically and certainly one of the most poorly known of all aroid genera in the neotropics. The taxonomic difficulty is owing largely to the absence of pronounced differences between species. Whereas most genera of Araceae have valuable taxonomic characters in leaf venation, *Stenospermation* leaf blades offer little in the way of taxonomic value, mostly lacking differences in the midrib on either surface and usually lacking pronounced primary lateral veins altogether. Yet conventional sorting of specimens by texture, color, thickness, size, elevation, and lifezone clearly show that there are many species, judged by standards of speciation in other genera. However, because pronounced differences are lacking between the species, the construction of dichotomous keys is extremely difficult.

SYNANDROSPADIX

The genus is a member of tribe Spathicarpeae in the *Dieffenbachia* Alliance of subfamily Aroideae. It is a monotypic, tuberous genus from northern Argentina, Bolivia, and Peru. *Synandrospadix vermitoxicus* (Griseb.) Engl. is well known and poses no taxonomic problems. It has been well described and illustrated by Crisci (1971) in the Flora Argentina. It is in cultivation in the Miami area as well as at the Munich Botanical Garden, the Missouri Botanical Garden, and elsewhere.

SYNGONIUM

Syngonium, of tribe Caladieae in the *Caladium* Alliance of Aroideae, is a genus of hemiepiphytic, appressed climbers and vines. The genus, recently revised (Croat, 1981), has an estimated 36 species. The center of diversity for *Syngonium* is in Cos-

ta Rica and Panama which together have a total of 17 species. Costa Rica has 14 species, including four undescribed species, while Panama has 11 species. Mexico is a secondary center of diversity with eight species. Only three species from Central America, *S. angustatum* Schott, *S. macrophyllum* Engl., and *S. podophyllum* Schott, are very wide-ranging, with all others endemic to either Mexico or to Costa Rica and Panama. *Syngonium podophyllum* is particularly wide-ranging, from Mexico to Brazil.

The West Indies have but a single species, *S. auritum* L. Relatively few species of *Syngonium* occur in South America, though several collections made in recent years probably represent additional new species. Eleven species are endemic to South America with four of them occurring in Peru; *S. gentryanum* Croat, *S. bastifolium* Engl., *S. podophyllum* Schott, and *S. yurimaguense* Engl.

Syngonium is divided into four sections, all of which occur in Central America. The sections include section *Syngonium*, with pedate leaves, the largest and most widespread section occurring throughout the range of the genus; section *Cordatum*, with simple cordate blades, ranging from Mexico to Brazil; section *Oblongatum*, with simple, oblong blades, from Costa Rica and Panama; and section *Pinnatilobum*, with pinnately lobed blades, known only from Mexico and Guatemala (Croat & Bogner, 1987). *Syngonium* exhibits pronounced heterophily (Ray, 1981, 1986, 1987) and each growth phase from juvenile to preadult to adult plants must be collected for proper study.

TACCARUM

Taccarum is a tuberous-stemmed genus of five species in tribe Spathicarpeae (*Diefenbachia* Alliance of Aroideae) restricted to temperate South America in Southern Brazil, Bolivia, Paraguay, and Argentina. It grows in damp soil in the understory or along roadsides in humid to seasonally dry areas. The genus is recognized by its tuberous stem, highly divided leaf and stip-

itate male flowers. Two species, *T. peregrinum* (Schott) Engl. and *T. weddellianum* Brongn. ex. Schott, occur in Paraguay (Croat, 1988a). The former also occurs in southern Brazil and in northern Argentina. *Taccarum weddellianum* is the most widespread species in the genus, ranging to Bolivia, Peru, and Brazil (Acre and Matto Grosso). Several other species occur in Bolivia, including *T. cardenasianum* Bogner and *T. caudatum* Rusby. *Taccarum warmingii* Engl. occurs in southern Brazil in São Paulo State.

Only *Taccarum weddellianum* is very well known (Croat, 1985c). It is in cultivation at the Missouri Botanical Garden and elsewhere.

ULEARUM

The genus, in tribe Zomicarpeae of the *Caladium* Alliance in Aroideae, is a genus of understory rhizomatous herbs from "terra firme" forest in the upper Amazon basin of western Brazil and Peru. Engler described *Ulearum sagittatum* from an Ule collection (6323) from Pongo de Cainarcho (now called Shanusi) in San Martín department of Peru. Josef Bogner recently acquired material of the genus from Brazil. It had been collected by Jacques Jangoux along the Rio Jurua Miry in the state of Acre. This was another collecting locality of Ule and it is not distant from the Peruvian border. Bogner has recognized a new variety, *U. sagittatum* var. *viridispadix*, from this material in Acre. Both varieties are in cultivation at the Munich Botanical Garden.

A collection described by Madison (1980) as *Ulearum recondita* Madison has proven to represent a new genus, *Bognera*.

UROSPATHA

The genus (of tribe Lasieae subfamily Lasioideae) consists of fewer than ten species of rhizomatous herbs occurring in swampy areas or along streams or lakes at low elevations, mostly in open habitats including wet places in savannas. In Central America there is but a single species, *U. grandis* Schott, occurring in swamps very near the Caribbean coast. Another species, *U. sag-*

ittifolia (Rudge) Schott, is widespread in the Amazon basin. Engler treated 12 species, based mostly on leaf shape, but blade shape is immensely variable in the well known species, and a reevaluation of the remaining species must be made. Jonker-Verhoef & Jonker (1953) have already reduced three species, namely *U. decipiens* Schott, *U. dubia* Schott, and *U. hostmanii* Schott under *U. sagittifolia* (Rudge) Schott, and in Central America *U. tonduzii* Engl. is a synonym of *U. grandis* Schott (previously *U. friedrichsthalii* Schott). The type of the latter name has proven to be a member of the genus *Sagittaria* in the Alismataceae (Hay, 1992). In addition, considering the high degree of variability in the genus, it is possible that the Central American species is synonymous with the widespread *U. sagittifolia*. Perhaps the total number of species will be even further reduced.

According to Hay (1992) the recently described genus *Urospathella* Bunting (Bunting, 1988a), based on a plant originally described as *Cyrtosperma wurdackii* Bunting, is a synonym of *Urospatha*. Hay (1988) transferred the species to *Urospatha* as *U. wurdackii* (Bunting) Hay.

XANTHOSOMA

This genus (tribe Caladieae of subfamily Aroideae) of approximately 45 species ranges from Mexico to the West Indies, Trinidad, the Guianas, and Argentina. As many as 12 species occur in Central America, and four in the West Indies. Twenty species are known from Venezuela, perhaps owing as much to the more than twenty years of activity by G. S. Bunting in Venezuela than to real differences in the distribution of *Xanthosoma*. Two native species occur in Trinidad; nine species in the Guianas; ten in Brazil; two in Paraguay; and ten in Peru (Croat, 1993). Only a few species usually occur at a typical site, and lowland and upland sites tend to have about the same number of species. For example, at study sites in Colombia, three species occur at La Planada in Nariño in *Premon-*

tane wet forest at 1,800 m and two species occur at Bajo Calima in Valle Department in *Premontane pluvial forest* at near sea level. Three species occur at Jatun Sacha along the upper Río Napo in a *Tropical wet forest* life zone, four species occur in *Tropical wet forest* at La Selva in Heredia Province of Costa Rica (Croat & Grayum, ined.), and two native species occur in *Tropical moist forest* on Barro Colorado Island in Panama (Croat, 1978).

Xanthosoma ranges through a wide variety of life zones from *Tropical moist forest* to *Tropical forest* and from sea level to at least 2,200 meters. It may occur in the forest understory, along the edges of roads and streams, or in open swampy areas. In seasonally dry areas the stems are tuberous, usually depressed-globose with roots around the upper periphery, or in wetter areas it may be caulescent or even arborescent with trunks to 4 m tall. Like many other genera, the leaf blades range from simple to compound. *Xanthosoma* remains one of the more poorly understood genera in the neotropics. This is not so much owing to real differences in distinguishing species as it is to the poor preservation of most specimens and the fact that such a large percentage of the species described were derived from cultivated collections of unknown origin. The plants are sometimes very large with very fleshy and juicy parts, especially the petioles, though the leaves are usually membranaceous. This makes drying the plants difficult. Blades, when folded, often stick together and cannot be unfolded. It is imperative that collections be properly cut into sections or folded in such a manner that they can be studied after they are dried.

Xanthosoma is being revised by Sue Thompson at the Carnegie Museum of Natural History (CM). While no specimens have been available for study, a review of the type photo collection at the Missouri Botanical Garden indicates that there are perhaps names that should be synonymized. However, it is difficult to predict any specific numbers. Certainly the genus needs to be extensively collected with detailed notes and photographs throughout its range, ex-

cept for some of the widespread weedier species.

ZOMICARPA

Zomicarpa is a member of tribe Zomicarpeae in the *Caladium* Alliance of tribe Aroideae. It is a genus of terrestrial, tuberous herbs comprised of three species from eastern Brazil (Ceará to Pernambuco and Bahia). Engler (1920) reported all three from a single locality, near Ilheos in Bahia with *Z. pythonium* (Bl.) Schott also occurring elsewhere in Bahia at Almada. Until recently two of the three species, *Z. steigeriana* Schott and *Z. riedeliana* Schott, were known only from Ilheos until J. Bogner collected *Z. riedeliana* in the state of Ceará. The characteristics separating the species do not appear to be strong ones, and the populations should be recollected to determine the validity of the species, since it is curious that three species of a rare genus should be so narrowly circumscribed geographically. *Zomicarpa steigeriana* keys out as having trisect leaves, whereas the other two have pedatisect leaves with either five or seven lobes. Considering the variation in leaf morphology of other genera, the characteristics separating these three species may not hold up. Bogner (pers. comm.) reports that in Ceará, the plants are only evident during the rainy season and are dormant during the dry season.

ZOMICARPELLA

This genus is a member of tribe Zomicarpeae in the *Caladium* Alliance of Aroideae. It consists of two species with creeping rhizomatous stems and is endemic to the upper Amazon region in western Brazil (and no doubt adjacent Peru). The genus was considered to be monotypic until recently, when J. Bogner collected a new species, *Z. amazonica*, in loamy soil in "terra firme" forest along the Rio Javari in western Brazil. It is in cultivation at the Munich Botanical Garden. The same species was collected by Murça Pires at Benjamin Constant in 1943, but remained unidentified until recently. *Zomicarpella maculata* N.

E. Br. was described from Colombia based on a Linden collection without exact locality. The latter should be recollected.

LITERATURE CITED

- Baker, R. A. & W. C. Burger. 1976. Key and commentary on the species of *Spathiphyllum* (Araceae) in Costa Rica, including *S. silvicola*, sp. nov. *Phytologia* 33(7):447-453.
- Bogner, J. 1969. A propos du jenera *Andromycia* A. Rich. (Aracees). *Adansonia* Ser. 2, 9(1):125-130.
- . 1973. Otra especie de *Mangonia* (Araceae) del Uruguay. *Darwiniana* 18(1/2):70-79.
- . 1977. *Jasarum steyermarkii* Bunting (Araceae). *Aqua Planta* 2/3:4-7.
- . 1980. The genus *Scaphispatha* Brongn. ex Schott. *Aroideana* 3:4-12.
- . 1984. Das Pflanzenportrait: *Jasarum steyermarkii* Bunting. *Aqua Planta* 4-84:15-16.
- . 1985. *Jasarum steyermarkii* Bunting, an aquatic aroid from Guyana highland. *Aroideana* 8:55-63.
- Bogner, J., S. J. Mayo & P. Boyce. 1994. *The Genera of the Araceae*. Royal Botanic Garden, Kew (in prep.)
- Bogner, J. & D. H. Nicolson. 1988. Revision of the South American genus *Gorgonidium* Schott (Araceae) *Spathicarpeae*. *Bot. Jahrb. Syst.* 109(4):529-554.
- . 1991. A revised classification of Araceae with dichotomous keys. *Willdenowia* 21:35-50.
- Bunting, G. S. 1960. A revision of *Spathiphyllum* (Araceae). *Mem. N. Y. Bot. Gard.* 10:1-53.
- . 1965. Commentary on Mexican Araceae. *Gentes Herb.* 9:289-382.
- . 1975. Nuevas especies para la revision de las Araceas Venezolanas. *Acta Bot. Ven.* 10:263-335.
- . 1979. Sinopsis de las Araceae de Venezuela. *Rev. Fac. Agron. (Maracay)*. 10(1-4):139-290.
- . 1986. New taxa of Venezuelan Araceae. *Phytologia* 60:293-344.
- . 1988. New taxa of Venezuelan Araceae II. *Phytologia* 64:459-486.

- . 1988a. *Urospathella*, a new genus of Venezuelan Araceae. *Phytologia* 65: 139–141.
- . 1989. Notes on Araceae. *Ann. Missouri Bot. Gard.* 76:917–919.
- . (In press). Araceae. In J. Steyermark, P. Berry & B. Holst (eds.), *Flora of Venezuelan Guyana*. Timber Press, Portland, OR.
- Crisci, J. V. 1971. Flora Argentina: Araceae. *Revista del Museo de la Plata (Nueva Serie)* 11:193–284.
- Croat, T. B. 1978. *Flora of Barro Colorado Island (Panama Canal Zone)*. Stanford University Press, Stanford, CA.
- . 1979. The distribution of Araceae. In K. Larsen & L. B. Holm-Nielsen (eds.), *Tropical Botany*, 291–308. Academic Press, London.
- . 1981 (1982). A revision of *Syngonium* (Araceae). *Ann. Missouri Bot. Gard.* 68:565–651.
- . 1983. A Revision of *Anthurium* (Araceae) for Mexico and Central America. Part 1. Mexico and Middle America. *Ann. Missouri Bot. Gard.* 70: 211–240.
- . 1985a. The large monocots of Panama. In W. G. D'Arcy & M. D. Correa (eds.), *Natural History of Panama*. Missouri Botanical Garden, St. Louis, MO.
- . 1985b. A new collection of the rare *Alloschemone* (Poepp.) Engl. & K. Krause. *Aroideana* 8:80–82.
- . 1985c. Aroid Profile No. 10. *Taccarum weddellianum*. *Aroideana* 8: 94–95.
- . 1986a. A revision of *Anthurium* (Araceae) of Mexico and Central America. Part 2. Panama. *Monogr. Syst. Bot. Missouri Bot. Gard.* 14:1–205.
- . 1986b. The distribution of *Anthurium* (Araceae) in Mexico, Middle America and Panama. *Selbyana* 9:94–99.
- . 1988. Ecology and lifeforms of Araceae. *Aroideana* 11(3-4):4–55.
- . 1989. Important collections of New World Araceae. *Taxon* 37:43–55.
- . 1990. A comparison of aroid classification systems. *Aroideana* 13:44–63.
- . 1991. A revision of *Anthurium* sect. *Pachyneurium* (Araceae). *Ann. Missouri Bot. Gard.* 78:539–855.
- . 1992. Species diversity of Araceae in Colombia: a preliminary survey. *Ann. Missouri Bot. Gard.* 79:17–28.
- . 1993. Araceae. In L. Brako & J. Zarucchi (eds.), Catalogue of the flowering plants and Gymnosperms of Peru, 71–82. *Monogr. Syst. Missouri Bot. Gard.* 45.
- . 1994. Floristic comparison of six Ecuadorian Florulas. In S. P. Churchill, H. Balslev, & J. Luteyn (eds.), *Neotropical Montane Forests: Biodiversity and Conservation*. New York Botanical Garden.
- Croat, T. B. & R. A. Baker. 1978. Studies in Araceae II, *Anthurium* sect. *Polyphyllum*. *Selbyana* 2:230–238.
- Croat, T. B. & J. Bogner. 1987. Aroid profile 11: *Syngonium steyermarkii* Croat. *Aroideana* 10:20–22.
- Croat, T. B. & N. Lambert. 1986. The Araceae of Venezuela. *Aroideana* 9(1-4): 3–213.
- Croat, T. B. & D. Mount. 1988a. Araceae. In R. Spichiger & J. M. Mascherpa (eds.), *Flora of Paraguay*, 7–46. Conservatoire et Jardin Botanique, Geneva and Missouri Botanical Garden. Imprimeries Populaires, Geneve.
- . 1988b. Araceae. In R. Spichiger & J. M. Mascherpa (eds.), *Flora del Paraguay*. Conservatoire et Jardin Botanique. Geneva & Missouri Bot. Gard. Pp. 7–46.
- Croat, T. B. & R. S. Sheffer. 1983. The sectional groupings of *Anthurium* (Araceae). *Aroideana* 6:85–123.
- Engler, A. 1905. Pothoideae. In A. Engler (ed.), *Das Pflanzenreich* IV. 23B(Heft 21), 1–330.
- . 1911. Lasioideae. In A. Engler (ed.), *Das Pflanzenreich* IV. 23B(Heft 21), 1–130.
- . 1915. Anubiadae, Aglaonemateae, Dieffenbachieae, Zantedeschieae, Typhonodorea, Peltandreae. In A. Engler (ed.), *Das Pflanzenreich* IV. 23Dc(Heft 64), 1–78.
- . 1920. Aroideae-Pistioideae. In A.

- Engler (ed.), *Das Pflanzenreich* IV. 23F(Heft 73), 1–274.
- French, J. C., M. Chung & Y. Hur. cpDNA phylogeny of Ariflorae. In P. Rudall et al. (eds.), *Monocotyledons: Classification and Evolution*. Royal Botanic Gardens, Kew. (In press).
- Gomez, A. 1983. A revision of *Stenospermatum* (Araceae) in Central America. Masters Thesis, St. Louis University, St. Louis, MO.
- Grayum, M. H. 1984. Palynology and phenology of the Araceae. Ph.D. Dissertation, University of Massachusetts, Amherst.
- . 1986. New taxa of *Caladium*, *Chlorospatha*, and *Xanthosoma* (Araceae: Colocasioideae) from southern Central America and northwestern Colombia. *Ann. Missouri Bot. Gard.* 73: 462–474.
- . 1990. Evolution and phylogeny of Araceae. *Ann. Missouri Bot. Gard.* 77: 628–677.
- . 1991. *Chlorospatha kressii* (Araceae), a new compound-leaved species from Chocó Department, Colombia. *Novon* 1:12–14.
- Hay, A. 1988. *Cyrtosperma* (Araceae) and its Old World allies. *Blumea* 33:427–469.
- . 1992. Tribal and subtribal delimitation and circumscription of the genera of Araceae tribe Lasieae. *Ann. Missouri Bot. Gard.* 79:184–205.
- Hotta, M. 1970. A system of the family Araceae in Japan and adjacent areas. *I. Mem. Fac. Sci. Kyoto Imp. Univ. Ser. Biol.* 4:72–96.
- Jonker-Verhoef, A. M. E. & F. P. Jonker. 1953. Araceae. In A. A. Pulle & J. Lanjouw (eds.), *Flora of Suriname, Vol. I, Part 2*, 1–80, 380–412. Royal Tropical Institute, Amsterdam.
- Macbride, J. F. 1936. Araceae in The Flora of Peru. *Field Mus. Nat. Hist., Bot. Ser.* 15:431–434.
- Madison, M. 1976. *Alloschemone* and *Scindapsus* (Araceae). *Selbyana* 1:325–327.
- . 1977. A revision of *Monstera* (Araceae). *Contr. Gray Herb. Harvard Univ.* 207:3–100.
- . 1978. The species of the *Anthurium* with palmately divided leaves. *Selbyana* 2:239–282.
- . 1980. A new species of *Ulearum* from Brazil. *Aroideana* 3:101–102.
- . 1981. Notes of *Caladium* (Araceae) and its allies. *Selbyana* 5:342–377.
- Matuda, E. 1954. Las Araceas Mexicanas. *Inst. Biol. Mexico* 25:176.
- Mayo, S. J. 1990. History and infrageneric nomenclature of *Philodendron* (Araceae). *Kew Bull.* 45(1):37–71.
- . 1991. A revision of *Philodendron* subgenus *Meconostigma* (Araceae). *Kew Bull.* 46(4):601–681.
- Mayo, S. J., J. Bogner, & P. C. Boyce. 1994. A new cladistic classification of the Araceae. *Kew Bull.* (In press).
- . (In prep.) *The Genera of Araceae*, with contributions from J. C. French and R. Hegnauer: illustrations by Elenor Catherine, Royal Botanic Garden, Kew.
- Nicolson, D. 1983. Sodiro's publications on Araceae. *Huntia* 5(1):3–15.
- Ray, T. S. 1981. Growth and heterophylly in an herbaceous vine, *Syngonium* (Araceae). Ph.D. Dissertation, Harvard University, Boston, MA.
- . 1986. Growth correlations with the segment in the Araceae. *Amer. J. Bot.* 73:993–1001.
- . 1987. Cyclic heterophylly in *Syngonium* (Araceae). *Amer. J. Bot.* 74:16–26.
- Reitz, D. R. 1957. *Araceas catarinenses*. *Sellowia* 8:20–70.
- Renner, S. S., H. Balslev & L. B. Holm-Nielsen. 1990. Flowering plants of Amazonian Ecuador, a checklist. *AAU Reports* 24:54–58.
- Schott, H. C. 1860. *Prodromus Systematis Aroidearum*. Vindobonae.
- Sodiro, L. 1900. *Anturia Ecuadorensia* Nova. *Rev. Chilena Hist. Nat.* 4(6):77–82.
- . 1901a. Anturios Ecuatorianos: diagnoses previas. *Anales Univ. Centr. Ecuador* 15(108):1–18.

- . 1901b. Anturios Ecuatorianos: diagnoses previas. Pp. 1–17. Quito.
- . 1902–1903. Anturios Ecuatorianos. *Anales Univ. Centr. Ecuador* 15–17: 1903a. [Periodical edition covering period from Jan. 1902 through March 1930], see Nicolson (1983).
- . 1903b. Anturios Ecuatorianos. *Monografía II. Contribuciones al conocimiento de la flora Ecuatoriana*. Pp. i–xxxii 1–231, 1–7 (Adiciones). Quito.
- . 1905a. Suplemento I. Anturios Ecuatorianos. *Anales Univ. Centr. Ecuador* 19–20.
- . 1905b. Suplemento I. Anturios Ecuatorianos. *Monografía II. Contribuciones al conocimiento de la flora Ecuatoriana*. Pp. I–III, (1–3), 4–100, (101–112), pls. A, I–X. Quito.
- . 1905c. Anturios Ecuatorianos. *Rev. Chilena Hist. Nat.* 9(4–6):191–211, 242–263, 274–281.
- . 1906. Suplemento II. Anturios Ecuatorianos. *Anales Univ. Centr. Ecuador* 22(156):20–39.
- . 1907. Suplemento II. Anturios Ecuatorianos. Pp. 1–23. Quito.
- . 1908. Aroideae. In *Sertula Florae Ecuadorensis*. *Anales Univ. Centr. Ecuador* 22(162):257–278.
- Standley, P. C. 1927. The flora of Barro Colorado Island. *Smithsonian Misc. Collect.* 78(8):1–32.
- . 1928. Flora of Panama Canal Zone. *Contr. U. S. Nat. Herb.* 27:1–416.
- . 1930. A second supplement to the Flora of Barro Colorado Island, Panama. *J. Arnold Arb.* 11:119–129.
- . 1933. The flora of Barro Colorado Island. *Contr. Arnold Arb.* 5:1–178.
- . 1937. Flora of Costa Rica. *Field Mus. Nat. Hist.* 18:131–146.
- . 1944. Araceae. Part II. Fascicle 3. In R. E. Woodson Jr. & R. E. Schery, *Flora of Panama*. *Ann. Missouri Bot. Gard.* 31:1–60.
- Standley, P. C. & J. A. Steyermark. 1958. Araceae, Flora of Guatemala. *Field Mus. Nat. Hist., Bot. Ser.*, pp. 304–363.
- Strong, D. R. & T. S. Ray, Jr. 1975. Host tree location behavior of a tropical vine (*Monstera gigantea*) by skototropism. *Science* 190:804–806.
- Young, H. J. 1986. Beetle pollination biology of *Dieffenbachia longispatha* (Araceae). *Amer. J. Bot.* 73:931–944.
- . 1988a. Differential importance of beetle species pollinating *Dieffenbachia longispatha* (Araceae). *Ecology* 69: 832–844.
- . 1988b. Neighborhood size in a beetle pollinated tropical aroid: effects of low density and asynchronous flowering. *Oecologia* 76:461–466.