A Review of Studies of Neotropical Araceae

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ABSTRACT

The last decade has seen many changes in research with neotropical Araceae. There have been a lot of revisionary efforts especially with smaller genera but relatively few changes in the largest and most complex genera. Several key floristic studies have been completed and several more are underway. Increasingly phylogenetic studies are being carried out among genera of all sizes. This review will provide a history of past monographic and floristic efforts and will summarize by suggesting the areas most in need of further work.

REVISIONARY STUDIES

The largest genus, Anthurium, remains still poorly known overall with only three sections, namely Pachyneurium (Croat, 1991), Polyphyllum (Croat, 1978) and Semaephylllum (Croat & Carlsen, 2004) that have been revised. With the discovery of many new species, especially in the Andes of Western South America, the number of named and described (albeit not yet published) species exceeds 1690 and the upper limit will certainly exceed 2000 when more sections, especially section Porphyrochitonium, are studied. A Lucid multichotomous key for Anthurium was created by staff at Kew Gardens and has been used to key out potential new species. The diagnosis of the putative species can then be written to show differences from species already published. It has been continuously upgraded during the last five years by adding new species and by making modifications in the key to make it more useful. The Lucid Anthurium key now contains about twice as many species as were present when initially made available.

A recent paper by Croat & Carlsen (2013) realigns the palmately lobed Anthurium species, merging Schott’s section Schizoplaclium to section Dactylophyllum and excluding three Mexican species and a single Colombian species.

Marcus Nadruz Coelho published a revision of Anthurium section Urospadix subsection Flavescentiaviridia (Coelho et al., 2009) and Livia Temponi (Temponi, 2006) did a molecular analysis on section Urospadix resulting in considerable
realignment of the section and the sinking of section *Chamaepipum*, a previously endemic section to Brazil.

*Philodendron* is perhaps more fully known, with subgenus *Meconostigma* (Mayo, 1991; Gonçalves & Salviani, 2002), the subgenus *Pteromischum* from Central America, West Indies and Pacific Tropical South America and Central America having being fully revised (Grayum, 1992; 1996). Some published work also has occurred in the Guianas (Croat & Grayum, 1994). In addition *Philodendron* subgenus *Philodendron* section *Macrobelium* of Brazil has been revised (Sakuragui, 1998; Sakuragui & D. C. Zappi, 2005). A Lucid multichotomous key for *Philodendron* prepared by Marcela Mora contains most of the species with the exception of some new species from Brazil. The initial key with 465 species resides on the CATE website and Thomas Croat and his staff of volunteers are continuing to populate it with new species. It now contains 529 species for an increase of 12% during the past 6 years.

The genus *Dracontium* with 23 species has been revised (Zhu & Croat, 2004) and a Lucid key for *Dracontium* is being prepared by Croat. The *Chlorospatha* with 68 species (Croat & L. P. Hannon, 2015; in press) have now been revised and a Lucid key is contemplated as well.

*Adelonema* with 16 species has recently been revised (Croat et al., in prep) and is expected to be submitted for publication sometime in 2015.

Revisionary work is being carried out on *Monstera* for the Flora of Mesoamerica (Croat, in prep.) and Alejandro Zuluaga, now a Ph.D. student at the University of Wisconsin, Madison, is concentrating on a molecular phylogeny of the genus. The very useful revision by Madison (Madison, 1977) is now somewhat out of date, especially with many new species in Central America (Grayum, 1997).

The genus *Spathiphyllum* with an estimated 63 species was last revised by Bunting (Bunting, 1960) where 36 species were covered. *Spathiphyllum* is now being studied by Felipe Cardona at the Universidad de Antioquia (Cardona, 2000; 2001; 2004). In Central America there are about 25 species of *Spathiphyllum*.

*Stenospermation*, with an estimated 250 mostly undescribed species is one of the most poorly know of all aroid genera. No complete revision has been made since that of Engler in Das Pflanzenreich (Engler, 1908) which covered only 20 species. A revision of *Stenospermation* for Central America (A. P. Gómez, 1983) comprised only 9 species but since that time many species have been found, especially in Panama and Costa Rica with as many as 30 species now reported (Croat, in prep.). Numbers of new species are even larger in South America. A recent survey of *Stenospermation* in Carchi Province in
Ecuador yielded 26 new species. Natalia Castaño Rubiano from Colombia is working on a revision of Colombian species of *Stenospermatum* (Castaño Rubiano, 2013) and is also working on the creation of a Lucid key for the genus.

*Dieffenbachia* with an estimated 140 species has been revised for Central America (Croat, 2004) with 26 species represented but most of the species in South America are still poorly known. An unpublished key to South America with 104 species has been prepared (Croat, in prep.) and a Lucid key to *Dieffenbachia* is being planned.

*Xanthosoma* with an estimated 90 species remains poorly known, certainly one of the most poorly known genera in the neotropics. Central America has about 13 species but there are many new species in the western Andes (Croat et al., in prep.) and even in the Guianas (Croat et al., in press). Eduardo Gonçalves is working on *Xanthosoma* and has described 10 new species (Gonçalves, 1999; 2000; 2011).

Most of the smaller neotropical genera are by now relatively well known, especially the recently revised *Spathicarpeae* inhabiting eastern South America and the western Andes (Gonçalves, 2002a). That revision covered initially 8 genera in subtribe Spathicarpeae, namely *Incarum*, *Asterostigma*, *Spathicarpa*, *Synandrospadix*, *Mangonia Gorgonidium*, *Spathantheum* and *Gearum*. Later the new genera *Croatiella* (Gonçalves, 2005) and *Lorenzia* (Gonçalves, 2012) were added.

The study compared subtribe *Spathicarpeae* with the related subtribe *Bognerineae* and subtribe *Dieffenbachineae*.

*Rhodospatha* with about 79 species has been at least partially revised and a Lucid key to the genus is anticipated.

### FLORISTIC STUDIES

Much of the neotropics is undergoing a floristic review of the Araceae. In Central America completed floristic studies have been made for Costa Rica (Grayum, 1982; Grayum et al. 1983; 2003, 2003a), Guatemala (Croat & Vannini, in prep.) and Nicaragua (Croat & Stiebel, 2001), Veracruz (Croat & Acebey, 2015). The Flora of Mesoamerica treatment of the Araceae is expected to be completed by 2016. Although the largest genera *Anthurium* (Croat, 1983; 1986) and *Philodendron* (Croat, 1997) and well as several smaller genera, *Chlorospatha* (Croat & L. P. Hannon; in press), *Dieffenbachia* (Croat, 2004), *Dracontium* (Zhu & Croat, 2004) have been completed for Central America this Flora of Mesoamerica treatment will result in the first revision of most of the smaller genera. Floristic studies in South America are a more daunting task owing to its much greater complexity. The Andean countries have been partly reviewed with modern Araceae Checklists having been created for Peru (Croat, 1993), Ecuador (Croat, 1999) and Bolivia (Kessler & Croat, 1999; Croat & Acebey, 2015). Colombia, clearly the largest floristic region in all of South America does not have a published flora but an effort is
underway by a group of Colombian aroiders to produce such a checklist. Venezuela is reasonably well known floristically owing to work by Bunting (1979) as well as a later study by Croat & Lambert (1986). The Guianas are now reasonably well known floristically after a National Geographic Sponsored expedition of four months made to the region. The flora of the Guianas comprises about 160 species and treatment is expected to be completed in four years. Brazilian aroiders are also generating a Checklist of the Araceae and the current total is 477 species; Argentina has only 17 species (Crisci, 1971). Paraguay, the only other country with a significant aroid flora has a completed flora with 9 genera and 16 species of Araceae (Croat & Mount, 1988).

Floristic studies are more all encompassing with published or in press floristic studies having been carried out in Paraguay and checklist treatments of Ecuador, Peru and Bolivia have been completed in the past ten years. Floristic accounts of Venezuela have been completed and a checklist for the Flora of Colombia and for is nearing completion. The Araceae for the Flora of Mesoamerica and for the Guianas is expected to be completed in the next five years.

MOLECULAR STUDIES

Molecular studies of neotropical Araceae are still in their infancy but significant studies have been made on Tribe Spathicarpeae by E. G. Gonçalves (Gonçalves, 2002b). His studies showed a close relationship between the Spathicarpeae to both Bognera and Dieffenbachia.

Alejandro Zuluaga is carrying out molecular studies with Monstera and these studies will be published as a part of his Ph.D. thesis. Molecular studies carried out by Peter Boyce and Sin Yeng Wong principally on Old World Homalomena have shown the American element, namely Homalomena section Curmeria Linden & Andrè to be distinct from Asian species so that group will adopt the generic name, Adelonema (Wong & Croat, in press). Adelonema has 12 species and ranges from Costa Rica to most of northern South America as well as the Amazon basin. As yet unpublished molecular studies with 8 species by Merrow & Croat showed Adelonema to cluster in three well-supported clades. Two molecular studies (Gauthier et al., 2008; Tam et al., 2004) found Adelonema to fall within Philodendron but this conflicts with studies by Wong & Croat (in press) that show it to be distinct from Philodendron, though most closely related to Philodendron subgenus Pteromischum and completely distinct from the Asian Homalomena.

Currently two separate molecular studies are being carried out on Philodendron, one by Nils Köster and Dubán Canal working at the Berlin Botanical Garden and one by Santelmo Vasconcellosas from Brazil. Both involve collaboration with Croat.

Molecular studies of Anthurium (Carlsen, pers. com.) have successfully separated 18
clades and have major advances in our understanding of the sectional classification of *Anthurium*. Among the findings are a validation of a West Indian clade corresponding to Engler’s section *Episeiostenium*, the isolation of two new distinct Mexican clades, one of which corresponds to Schott’s section *Andiphlium* and one which represents species with cordate-sagittate blades with dark glandular punctations on the lower blade surfaces. *Anthurium* section *Pachyneurium* series *Multinervium* is recognized at the sectional level as section *Multinervium* Croat and *Anthurium* at the sectional level are either completed or ongoing.

Molecular studies are also being carried out on *Philodendron* and *Monstera*.

**POLLINATION STUDIES**

Pollination biology of Araceae is still much understudied and most serious studies of pollination are still in their infancy in the neotropics with only a few total species having been studied for their pollinators but several important studies are ongoing.

Nevertheless we have strong initiatives, especially through the efforts of Marc Gibernau working in French Guiana and sometimes working with Denis Barabé at the Montreal Botanical Garden, Quebec, Canada, Gerhard Gottsberger working in Brazil and Heiko Hentrich from Germany, working in Mexico with Pedro Diaz.

Danny Beath, employing techniques learned in Central West Africa made significant observations on pollination of *Anthurium* and *Dieffenbachia* while working in Costa Rica (Beath, 1999). Julio Sierra-Giraldo has made observations on pollinators in the Andes of western South America in Risaralda Department and reported what appears to be a likely pollination system involving frogs pollinating Araceae (Sierra-Giraldo, 2014).

Considering the vast array of syndromes and the incredible richness of the Neotropical aroid flora pollination, the biology of Araceae is likely to be a very lucrative field of study for many years to come.

**DISCOVERY OF NEW SPECIES**

Perhaps the most significant effect of research with Araceae in recent years is the realization that more than any other tropical plant family so far studied the Araceae represents a group that is proving to be exceedingly rich in species. Most genera have grown in size (numbers of species) but percentage-wise the growth has been greatest in the two largest genera of Araceae, namely *Anthurium* and *Philodendron*. *Anthurium* has grown from about 600 species to 1392 species in less than 5 years with most of the growth in species coming from Panama, Colombia, Ecuador and Peru. *Philodendron*, though not heavily studied is also growing dramatically from 469 species to 529 species at present. Moreover it looks
like this rate of increase will not soon diminish with the addition of hundreds of new collections from areas not previously explored. This single attribute of Araceae, namely the ability to produce many new species, makes it seemingly unique though I do not know what is happening to other families. Single site visits often yield an array of unknown species, most of which are apparently new and the same thing could be found true in clearly related sites. Despite repeated visits to the El Queremal-Anchicaya region on the western slopes of the Andes between Cali and Buenaventura, each visit presents a surely unique set of discoveries of new species for each stop.

Interestingly, though perhaps less dramatic, the situation in Asia also shows that many new species still exist there. Since 1980 Amorphophallus has grown by about 90 species and now totals 210 species. About 80% of this growth is due to the efforts of Wilbert Hetterschied. Both Homalomena and Schismatoglottis have grown dramatically owing to the efforts of Hay & Yuzammi (2000) and Bogner & Hay (2000) but especially by Peter Boyce and Sin Yeng Wong in Sarawak. In the tribe Schismatoglottideae the genus Apobalis was resurrected; Aridarum has increased from 9 to 24 species; Bakoa was described as a new genus with 4 new species; Bucephalandra increased from 2 to 28 species; Hestia was described as a new genus; Hottarum with 2 species was resurrected from Piptospatha; Ooia was described as a new genus with 3 species; Pichinia is described as a new monotypic genus; Piptospatha with 15 species increased by 9 species; Schismatoglottis with 110 species has increased by 35 species; Schottariella a new monotypic genus is described and Schottarum with 2 species is described. In Homalomena with 93 species about 40 species have been described by Boyce and or Sin Yeng alone.

At least in the neotropics and Asia where vast expanses of forest in poorly explored areas still exist and especially in light of the high rate of narrow endemism in the family, this process of discovery of new species is likely to continue for a long time.

**USE OF LUCID MULTICHOTOMOUS KEY**

What have made determinations of new species possible are the Lucid keys which have been developed for both Anthurium and Philodendron. The Lucid database stores all of the important qualitative and quantitative information on all published species for all species in a specific genus. The key enables one to select a series of conservative features which in turn causes the key to reject any species not possessing that feature. After passing through a series of characters the remnant list of species is then compared with the plant being determined to see if there is a match.

Lucid keys are powerful tools when fully developed and they should be developed for other genera. Mention has already been made about the development of Lucid keys for Monstera and Stenopermation which have
already been developed but others will be developed for *Aglaonema, Chlorospatha, Dieffenbachia, Dracontium* and *Rhodospatha*.

**CONCLUSIONS**

The results of our collective investigations with Neotropical Araceae have been fruitful in recent years with significant monographic, floristic and molecular studies produced especially in smaller taxonomic groups. Floristic, studies though by now widespread, are needed for more areas and they must be continuously reviewed with the ability to make updates as new species or new country or regional record are added since they otherwise quickly become outdated. Larger groups, especially *Anthurium* and *Philodendron* have proven to be so species-rich that any end product remains somewhat elusive though attempts are under way to at least describe species and add them to Lucid keys. Molecular studies are beginning to produce reliable end products that were previously dubious. Nevertheless broader and more species-rich surveys are required to better understand the sectional classification of the larger genera. Studies of pollination must be encouraged at all levels since we have scarcely begun this study and the results are so promising at both the biological and taxonomic level.

**LITERATURE CITED**


Croat, 2015


Grayum, M. H. 1992. New species of *Philodendron* subgenus *Pteromischum* (Araceae) from Mesoamerica and


**IN PREPARATION**

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