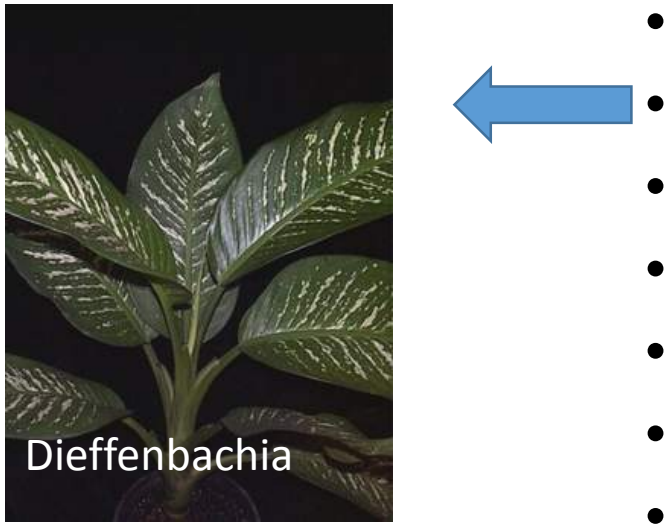

John J. Dwyer Lecture
The Philodendron Family (Araceae): Diverse, Interesting and Still Growing"
Thomas B. Croat, P. A. Schulze Curator of Botany
Missouri Botanical Garden

What is an AROID (Araceae)?

- Unifying Characteristics: Flowers arranged in dense spikes (spadix); spadix subtended by a leaf-like spathe.
- Plants typically associated with aroids.
  - Anthurium
  - Dieffenbachia
  - Monstera (M. deliciosa) [split leaf Philodendron]
  - Philodendron (P. hederaceum)
  - Peace Lily (Spathiphyllum)
  - Golden Pothos (Rhaphidophora aurea)
  - Syngonium (S. podophyllum)


Dieffenbachia


Anthurium

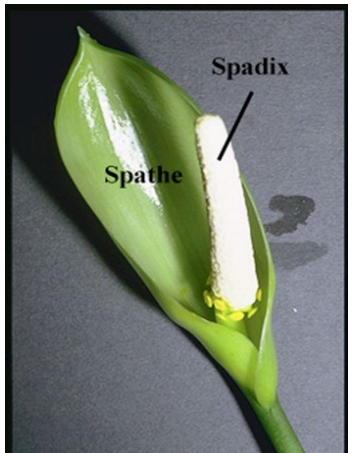

Philodendron


Spathiphyllum


Monstera deliciosa

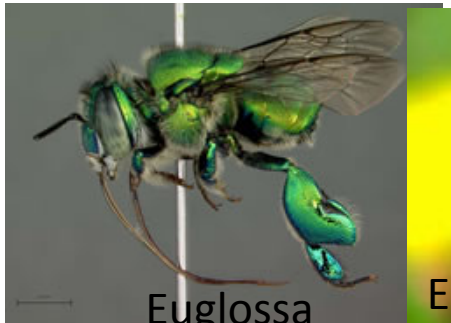

Rhaphidophora


Syngonium



Important characteristics of aroids

- High species diversity
- High habit diversity
- High rates of endemism- Mexico, 69%; Guatemala 22, Costa Rica, 50%; Panama, 95%
- High levels of undescribed species
  - Most new species seem to be narrow endemics
  - Causes of high speciation?
    - Co-evolution with species-diverse insects, beetles & bees
    - Fruit dispersal by territorial birds


Euglossa


Eulema

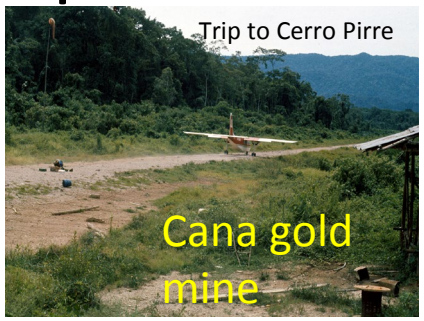

Trigona

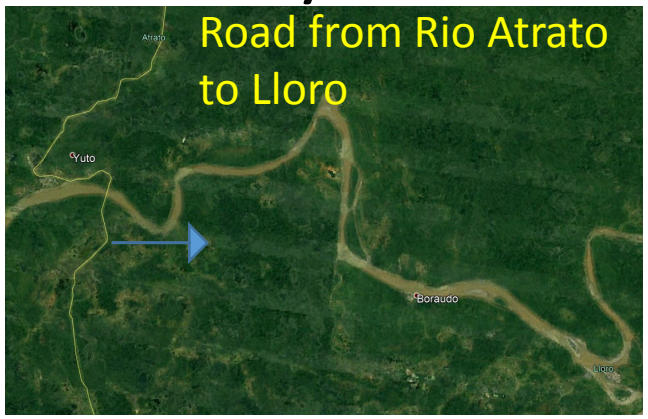

Cyclocephala


Cyclocephala beetles feeding on pollen
Photo courtesy Marc Gibernau

High Species Diversity

267 collections in a single day, 70 Araceae,, 20 new species

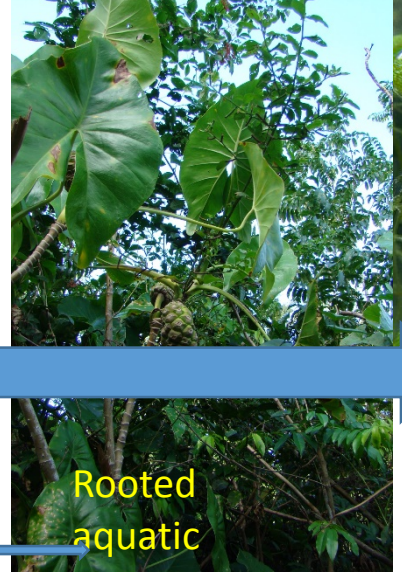




- Cerro Pirre
- Chocó diversity
- Bajo Calima
- Alto Tambo
- El Chical
- Río Medellín
- Dry forest in Sucre Department, Colombia

High Habit diversity

- Free-floating aquatics
- Tree-like rooted aquatics
- Tuberous, rhizomatous, cauline
- Understory terrestrial herbs
- Epiphytes
  - True epiphytes
  - Primary hemiepiphytes
  - Secondary hemiepiphytes
  - Vines vs. appressed climbers



http://forums.gardenweb.com/discussions/2147182/saving-voodoo-lily-seeds

https://www.flickr.com/photos/grandma-shirley/5874835780/

http://junglemikey.blogspot.com/2011/10/schismatoglottis-jipomii-from-pakan.html

http://www.fmueller.com/home/aquaristic/125g/plants/anubias/

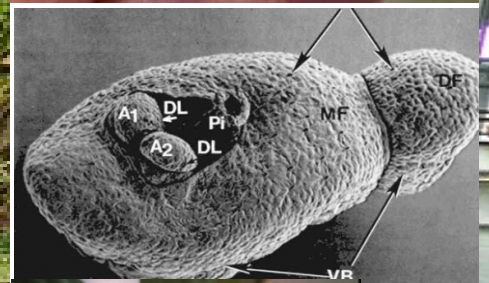
https://commons.wikimedia.org/wiki/File:Eastern_Skunk_Cabbage_Takemori_Koshu-City_B.JPG

http://www.plantsrescue.com/tag/pistia-minor/

Diversity of size

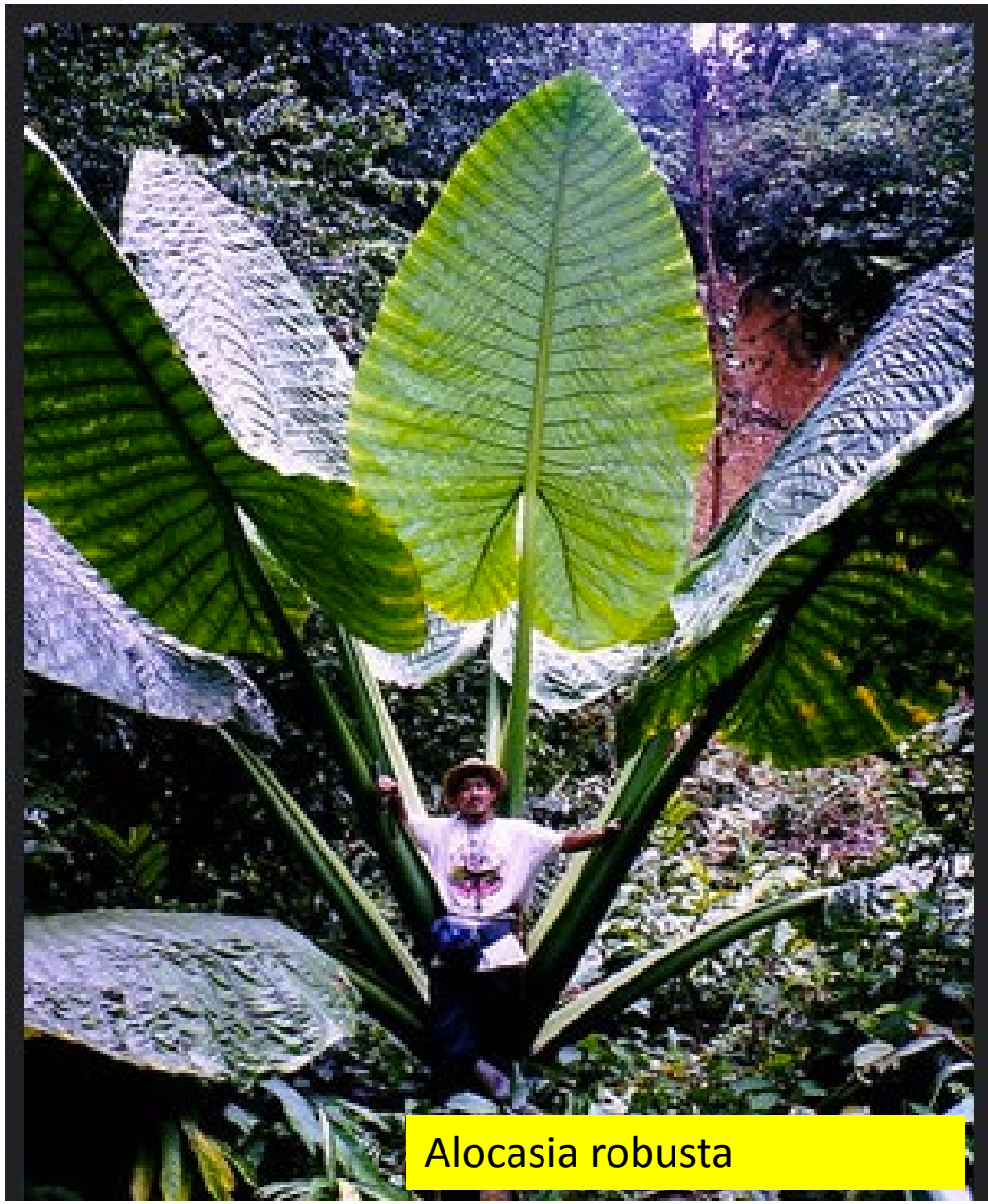
Amophophallus titianum

Lemna



Pistia

Amorphophallus titanum



Alocasia robusta

https://www.flickr.com/photos/21117187@N06/2100002484

High leaf shape diversity

http://www.rareplants.co.uk/product/arisaema-heterophyllum/

http://www.exoticrainforest.com/Alocasia%20micholitziana%20%20pc.html/

Diverse Systems of Reproductive biology

Pollinators

Fungus gnats, beetles, flies

Foul odors like feces and rotting flesh attract flies, beetles or fungus gnats

Aroid Crops

http://www.growingontheedge.net/viewtopic.php?p=85243

http://www.nunatsiaqonline.ca/stories/article/international_effort_promotes_traditional_diet_for_health/

Cyrtosperma merkusii – Giant Swamp Taro

Xanthosoma sagittifoilum - Cocoyam

3rd root and tuber crop in Nigeria

3rd starch food in Nicaragua

Nutritionally superior to yam and cassava

http://www.rtb.cgiar.org/cocoyams-potential-for-nutrition-and-income-still-untapped/

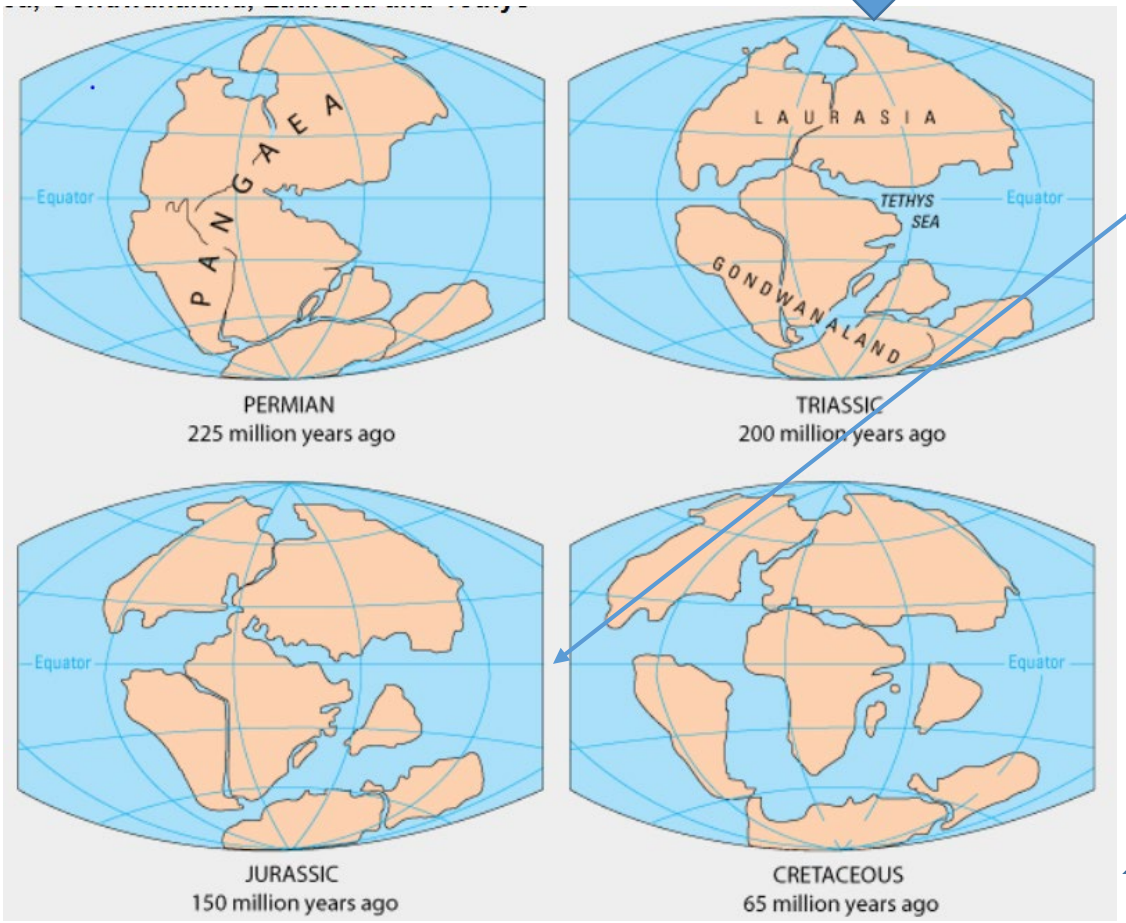
http://anpez.org/nagenda.php

Colocasia esculenta - 'Taro'

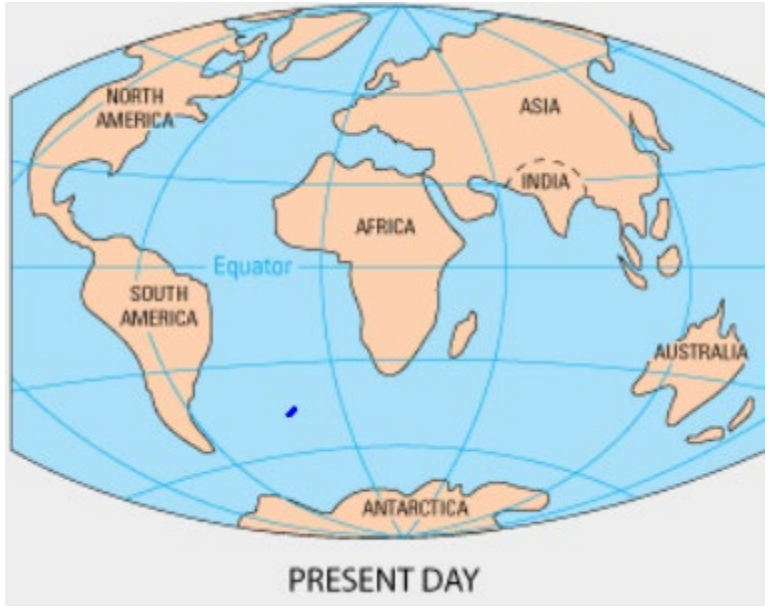
14th most consumed vegetable worldwide

Florida, Cuba, Egypt, Hawaii, PNG, Thailand, S China

Araceae, one of the oldest plant families first evolved in Laurasia



Araceae evolved 128 million years ago at beginning of Cretacecous (oldest known flowering plant is 130 my old)



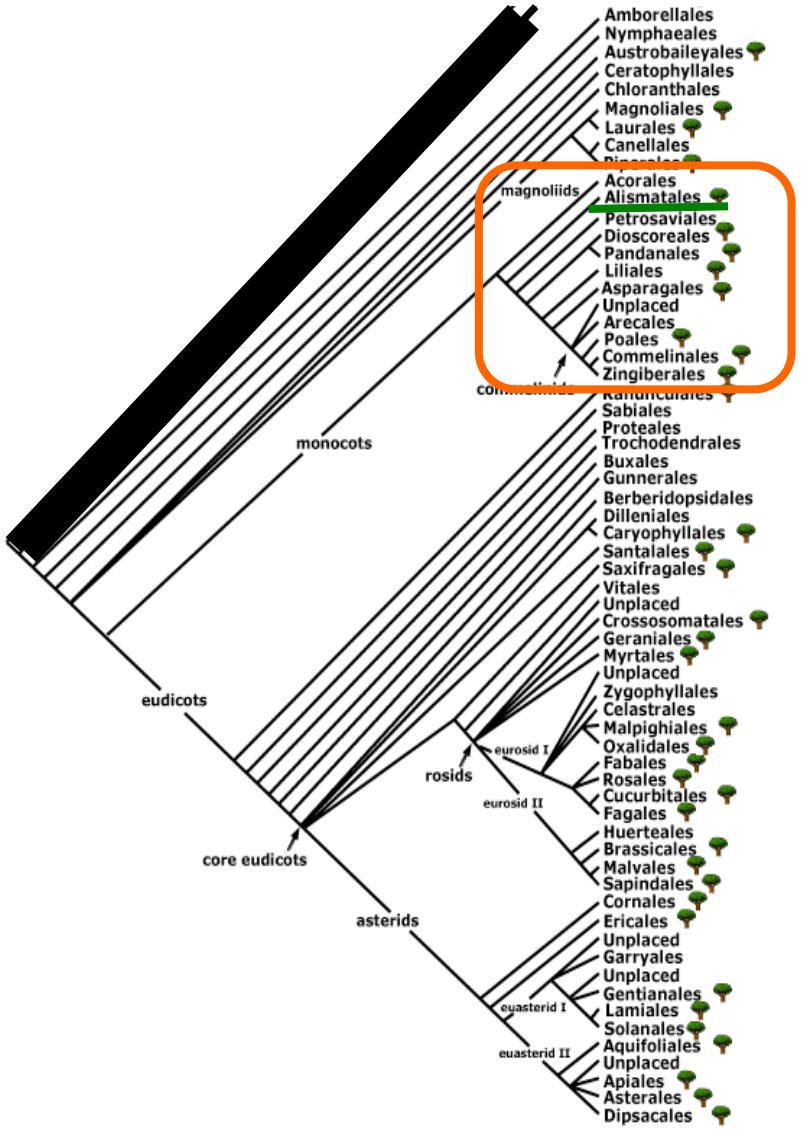
TERTIARY PERIOD

CENAZOIC ERA

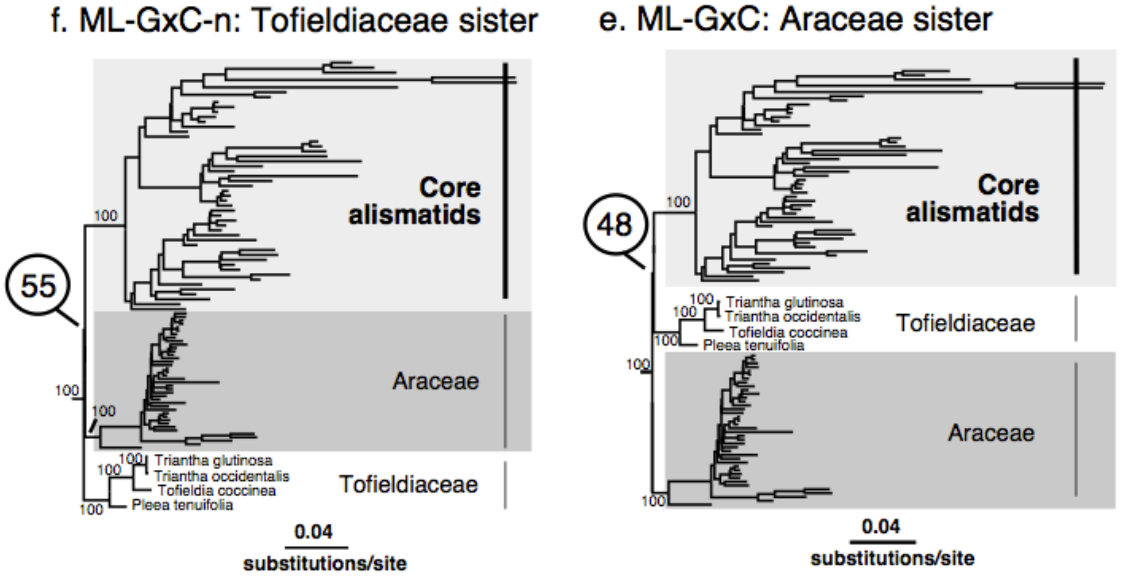
KT Boundary 65 million years ago, All subfamilies already present

144 genera
3645 species (Predicted estimates 6500)

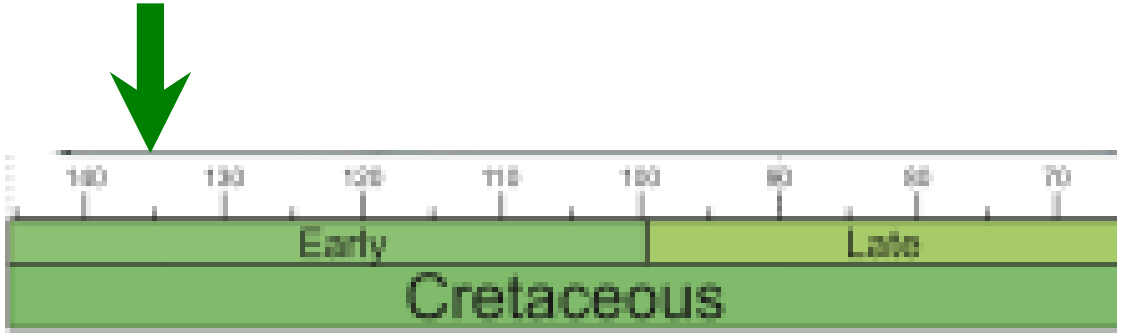
- 3rd Largest Family of Moncots after Orchidaceae and Arecaceae (palms)
- Seven Subfamilies



Stevens, 2001 onwards

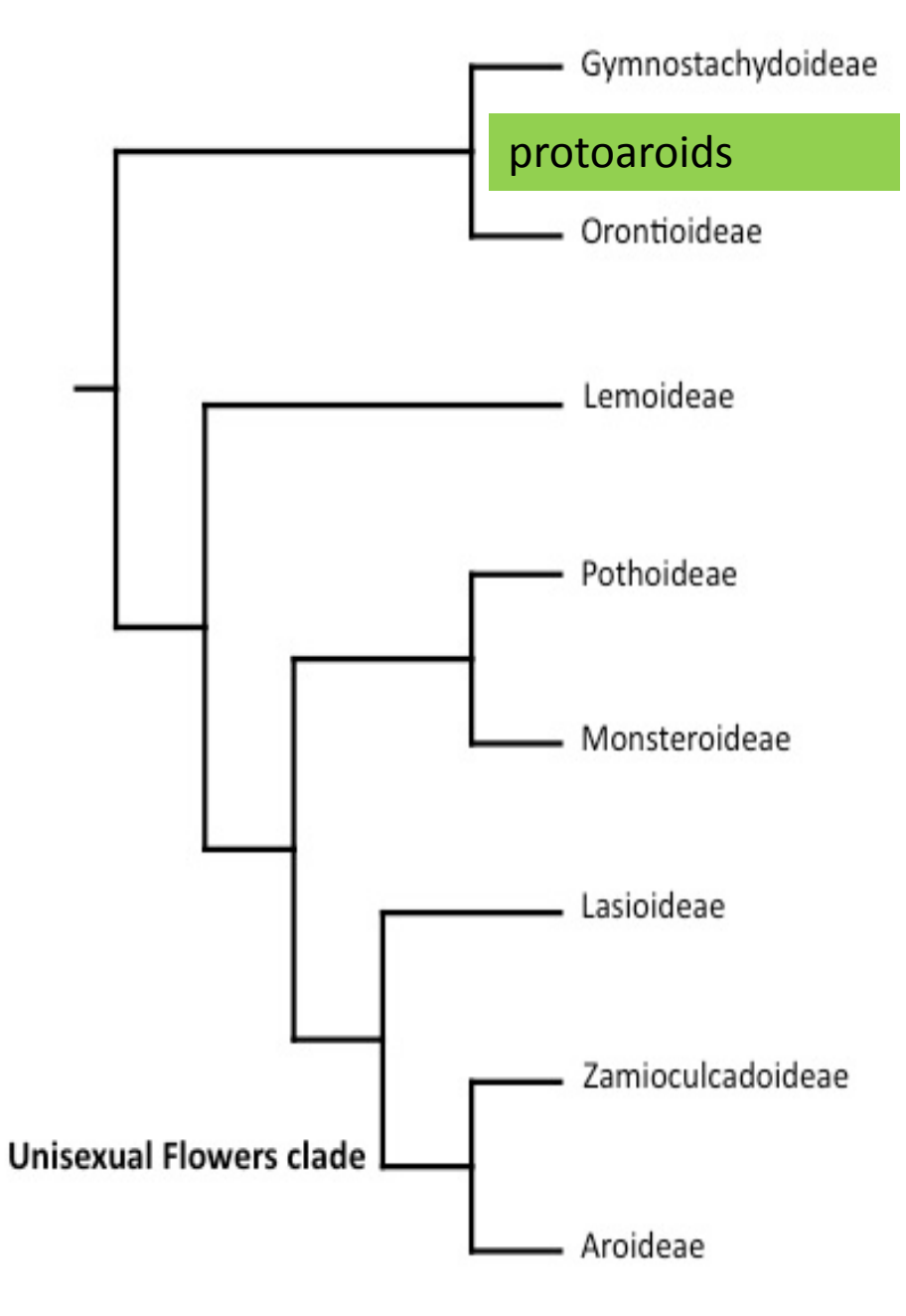


Ross et al. (2015)



Nauheimer et al. (2012)

8 subfamilies, 44 clades



Bisexual flowers

No laticifers

Sporopollenin +

Pollen aperturate

Perigoniate [tepals]

Unisexual flowers

Laticifers

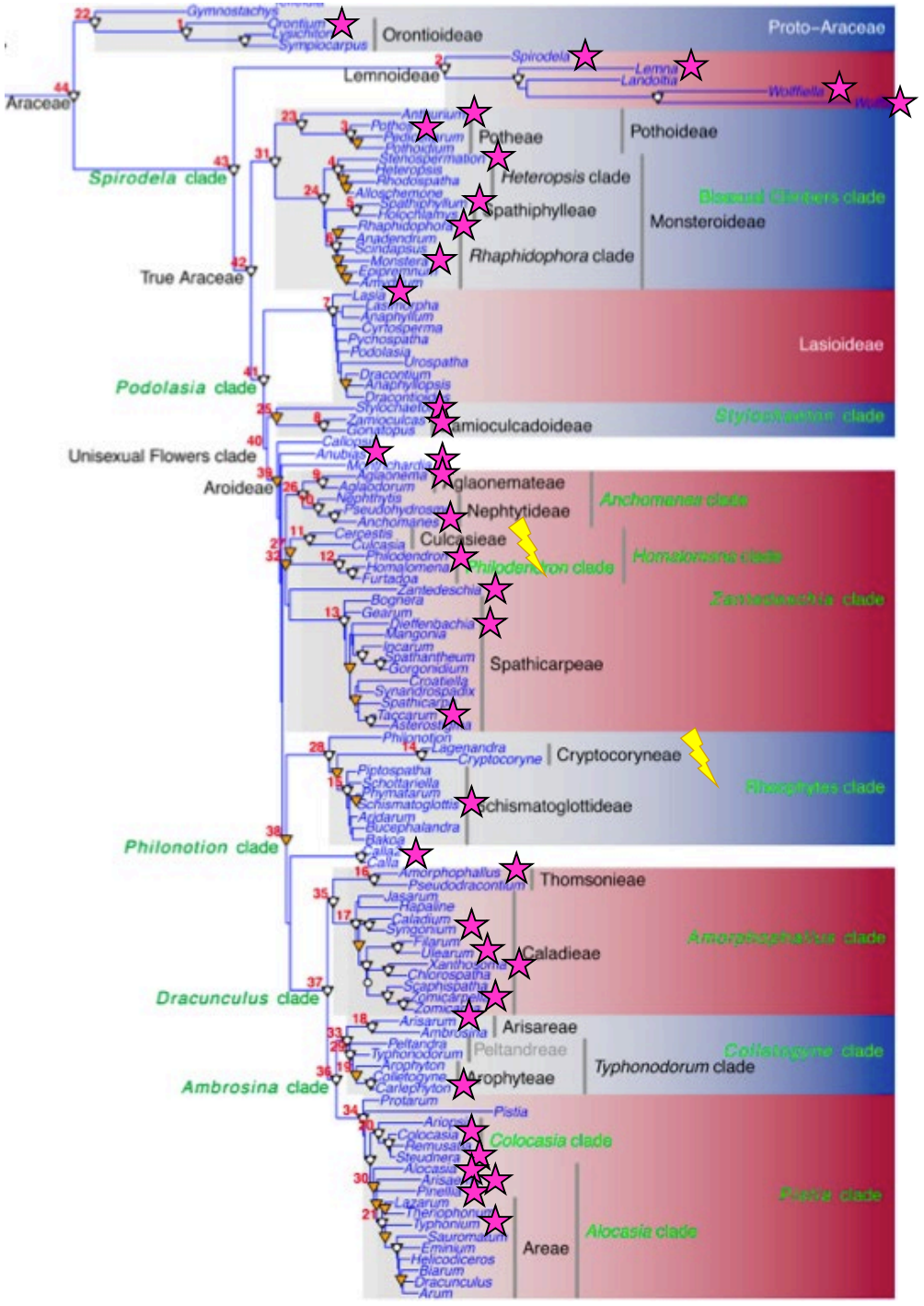
No sporopollenin

Pollen inaperturate

Biforine raphides

Aperigoniate [no tepals]

Cabrera et al. (2008), Cusimano et al. (2011)



Next Generation Sequencing

37 genera, 42 of 44 clades

Illumina data

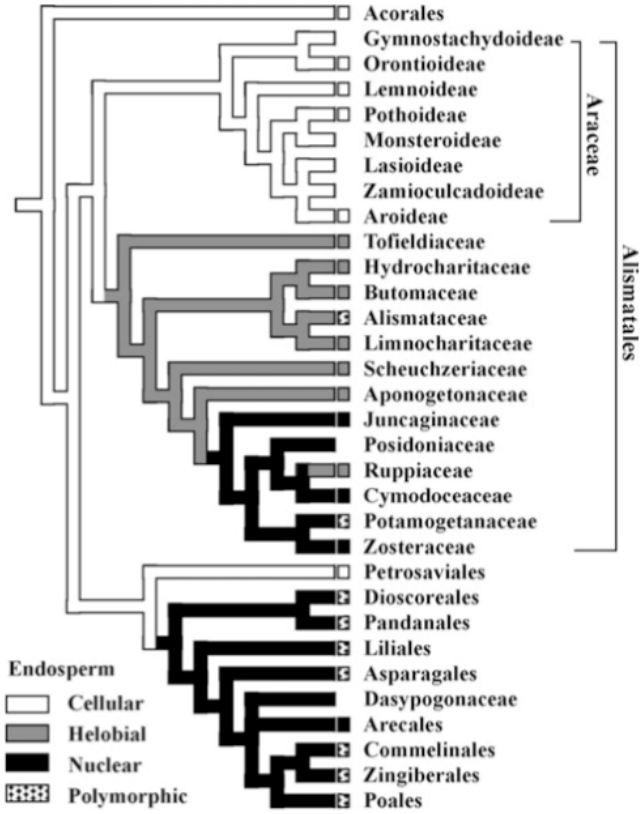
Reference based – *Lemna*

Phylogenetic Context

APG

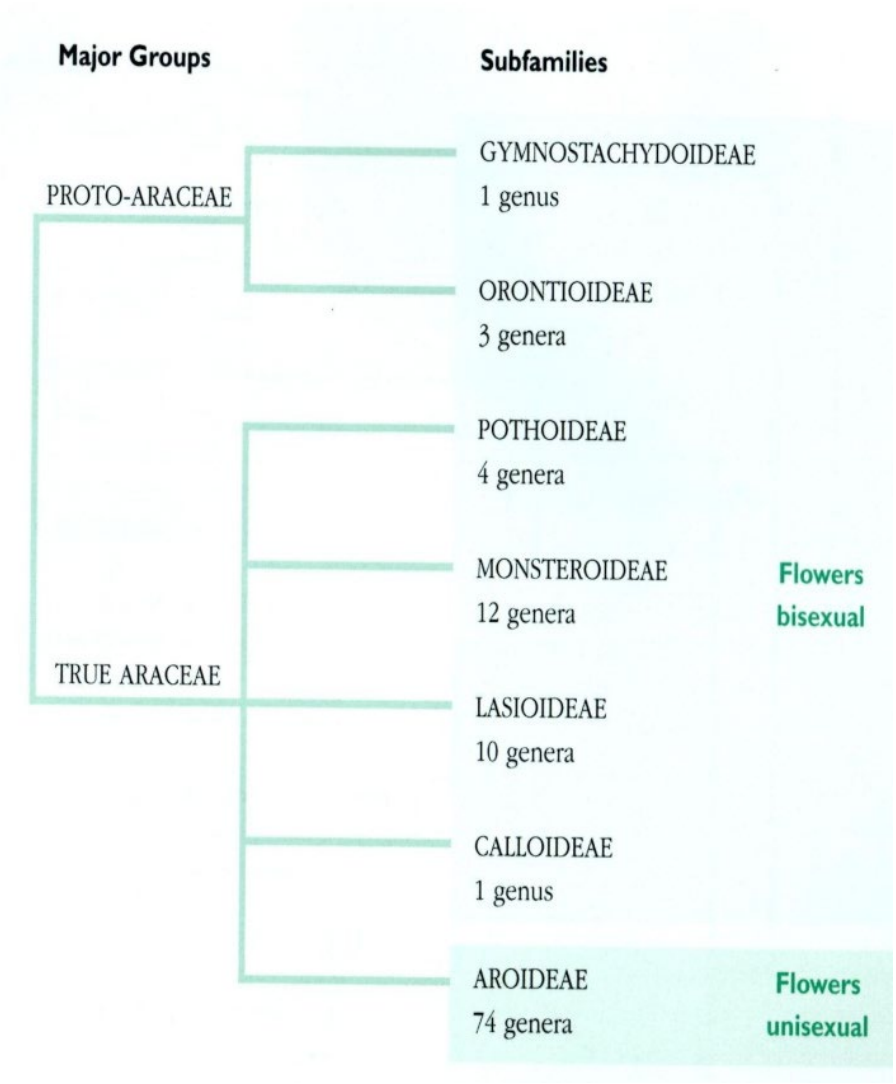
Basal monocot

Acorus calamus (long included in Araceae)



Tobe & Kadokawa, 2010

Phylogenetic Context

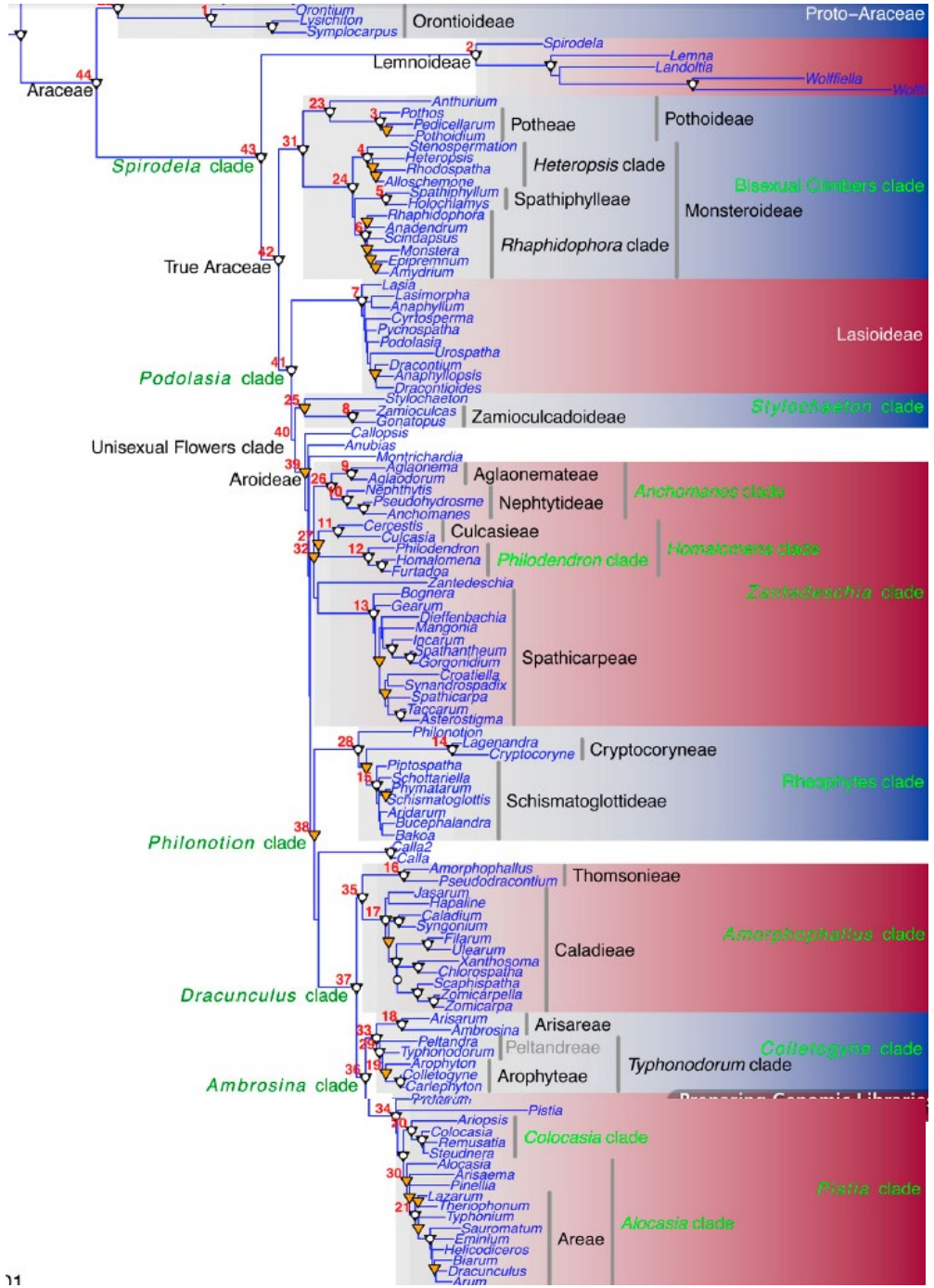


Mayo et al 1997-French et al 1995

Morpho-anatomical & restriction site

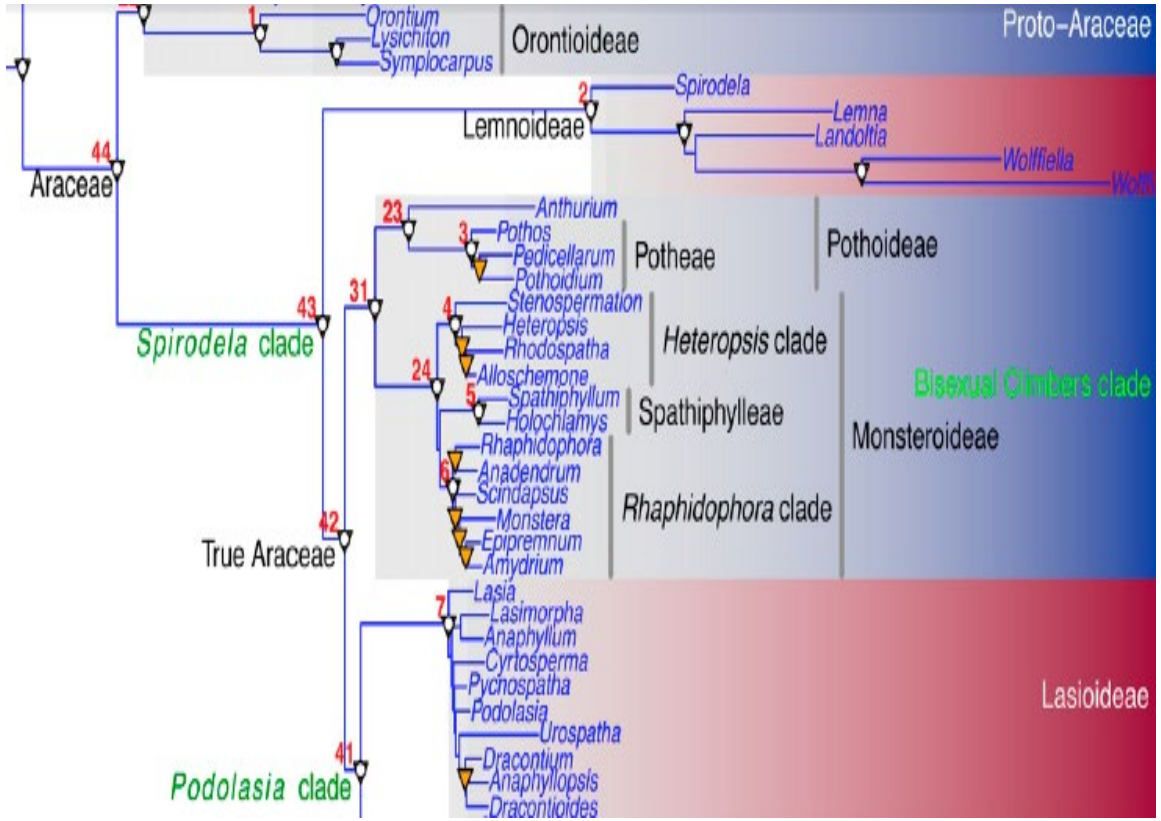
7 subfamilies

Lemnaceae not included



7 subfamilies

44 major clades



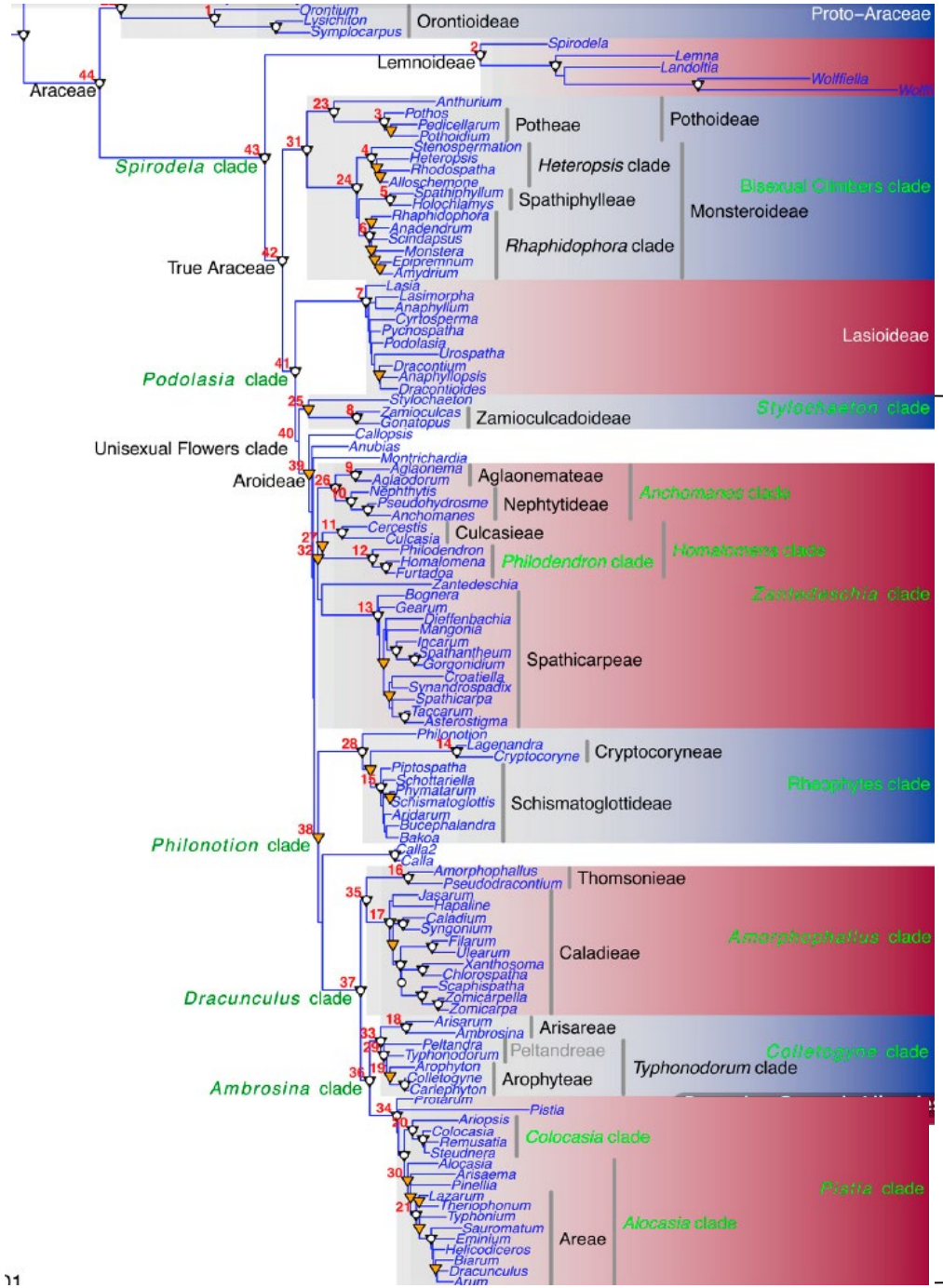
Bisexual, perigoniate flowers

Absence of laticifers

Presence of sporopollenin

Pollen aperturate

No spadix zonation



Unisexual flowers

Laticifers

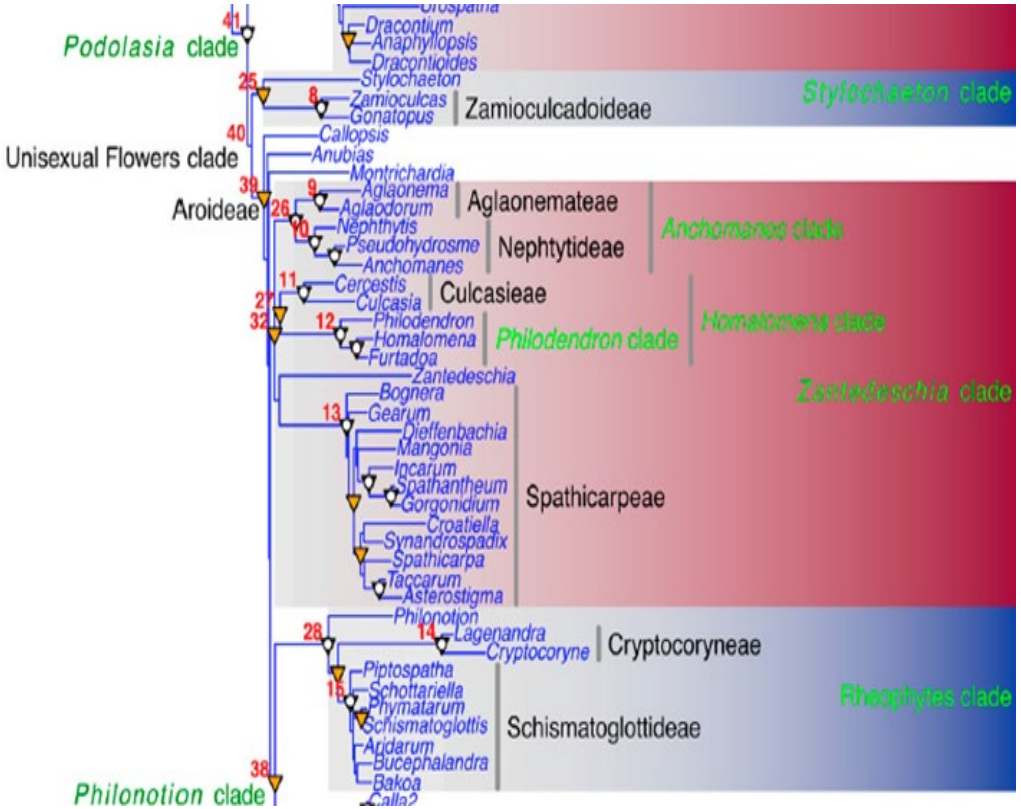
No sporopollenin

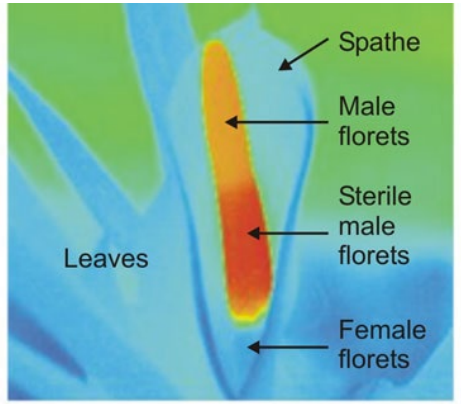
Spadix /spathe zonation

Pollen inaperturate

Aperigoniate flowers

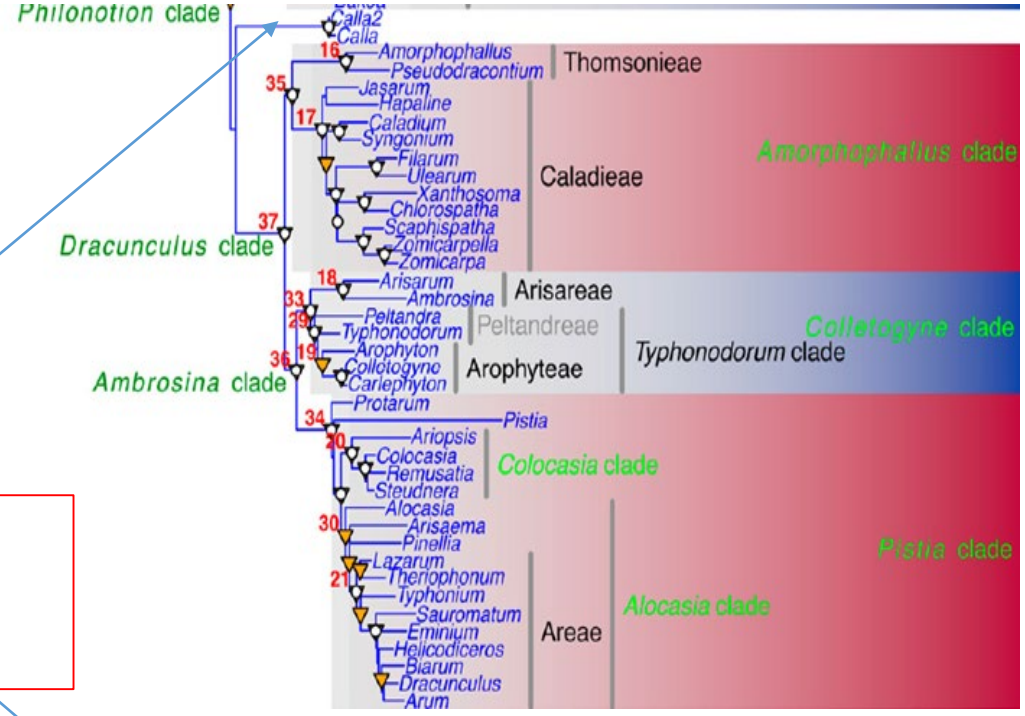
Biforine raphides



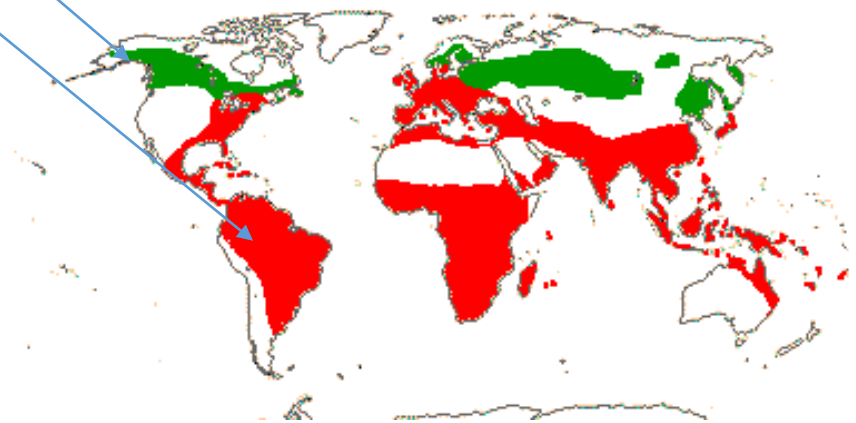


Thermogenesis is often present with genera with unisexual flowers

Seymour, R , 2010

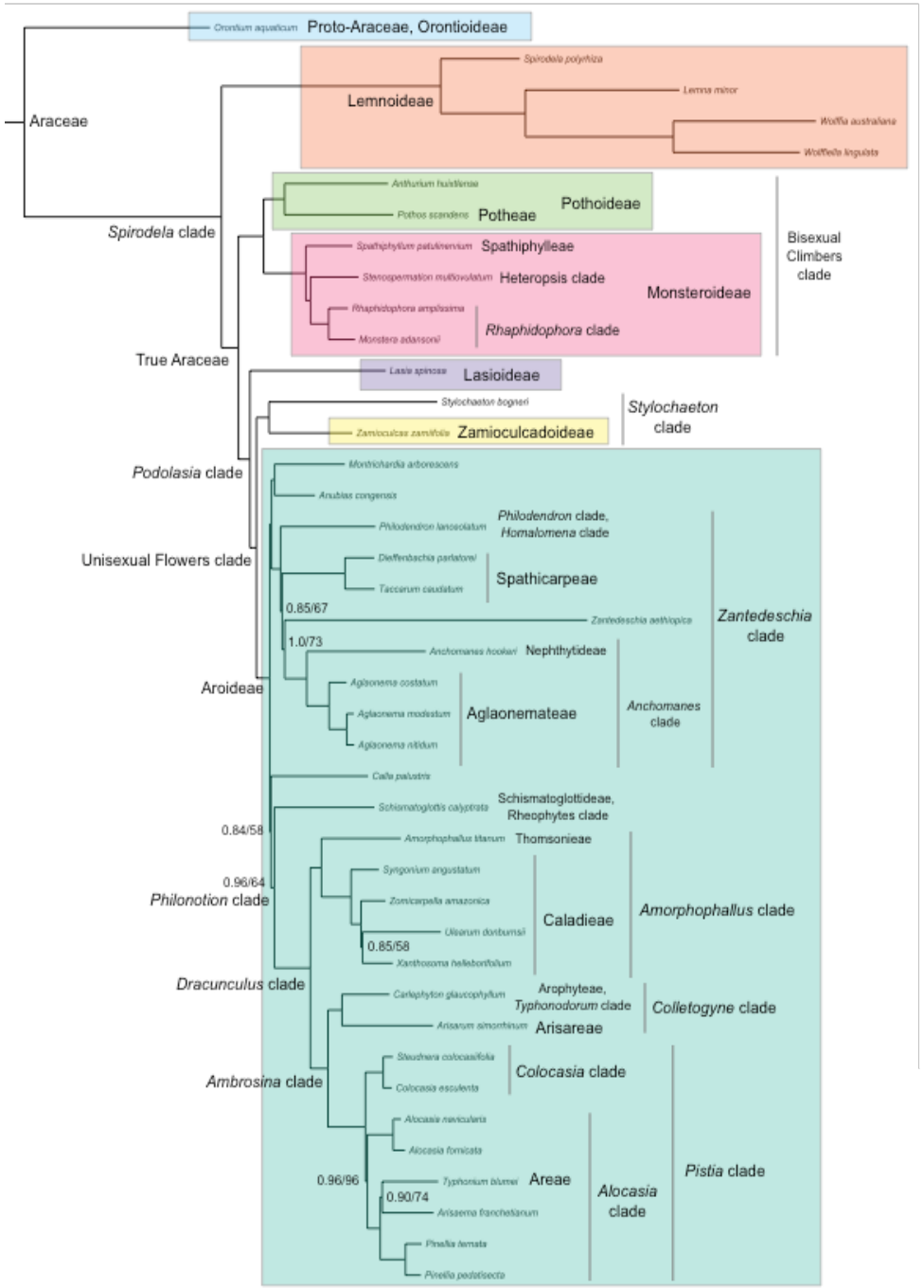


Distribution of
Caloideae and
Aroideae



Bisexual flowers
Aperturate pollen
Massive sporopollenin
But…
Laticifers

Tribe Calloieae does not fit well in any other subfamily



Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Phylogenomics of the plant family Araceae

Claudia L. Henriquez [a,b,*], Tatiana Arias [d], J. Chris Pires [c], Thomas B. Croat [b], Barbara A. Schaal [a]

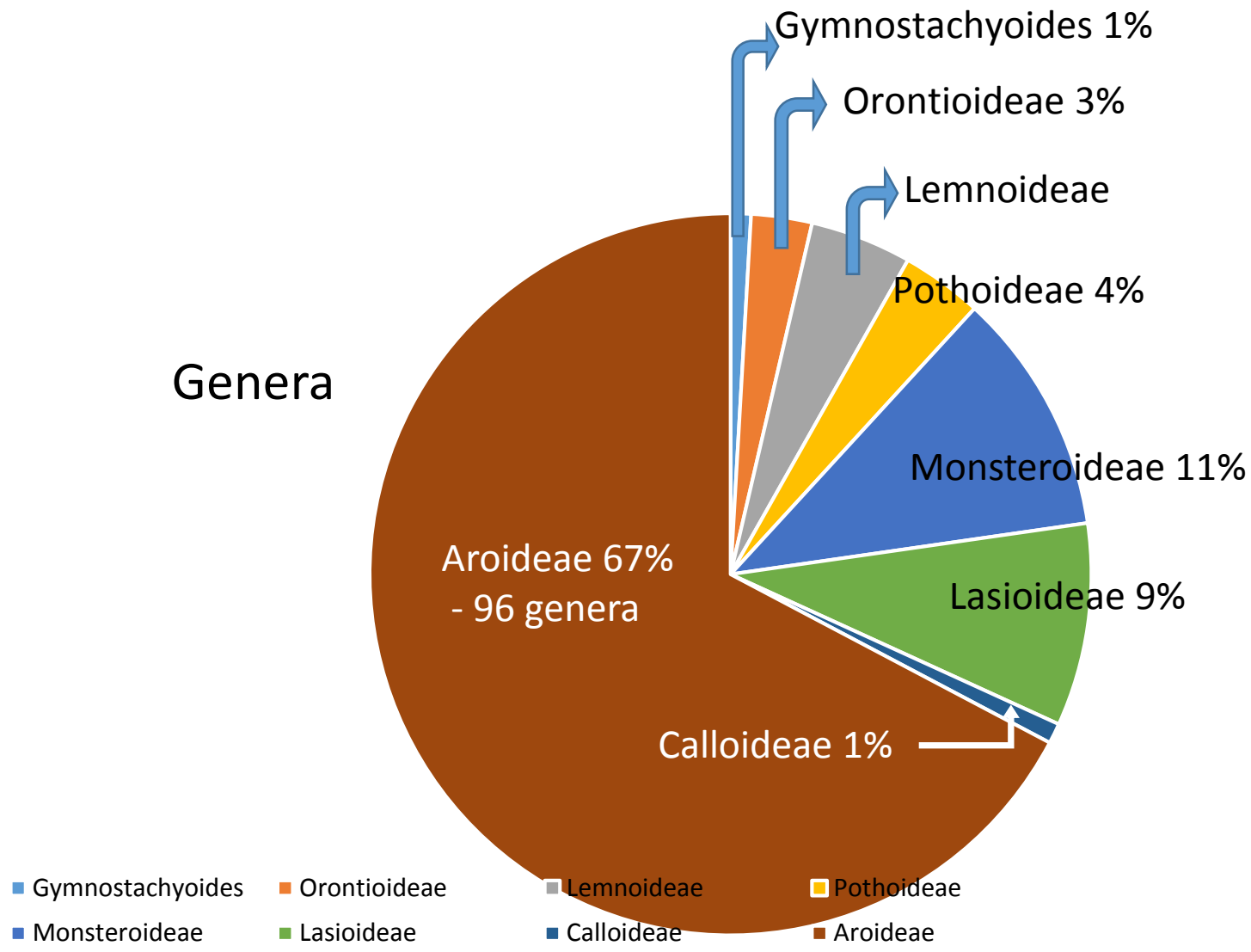
70 protein-coding genes

>9,000 Parsimony informative

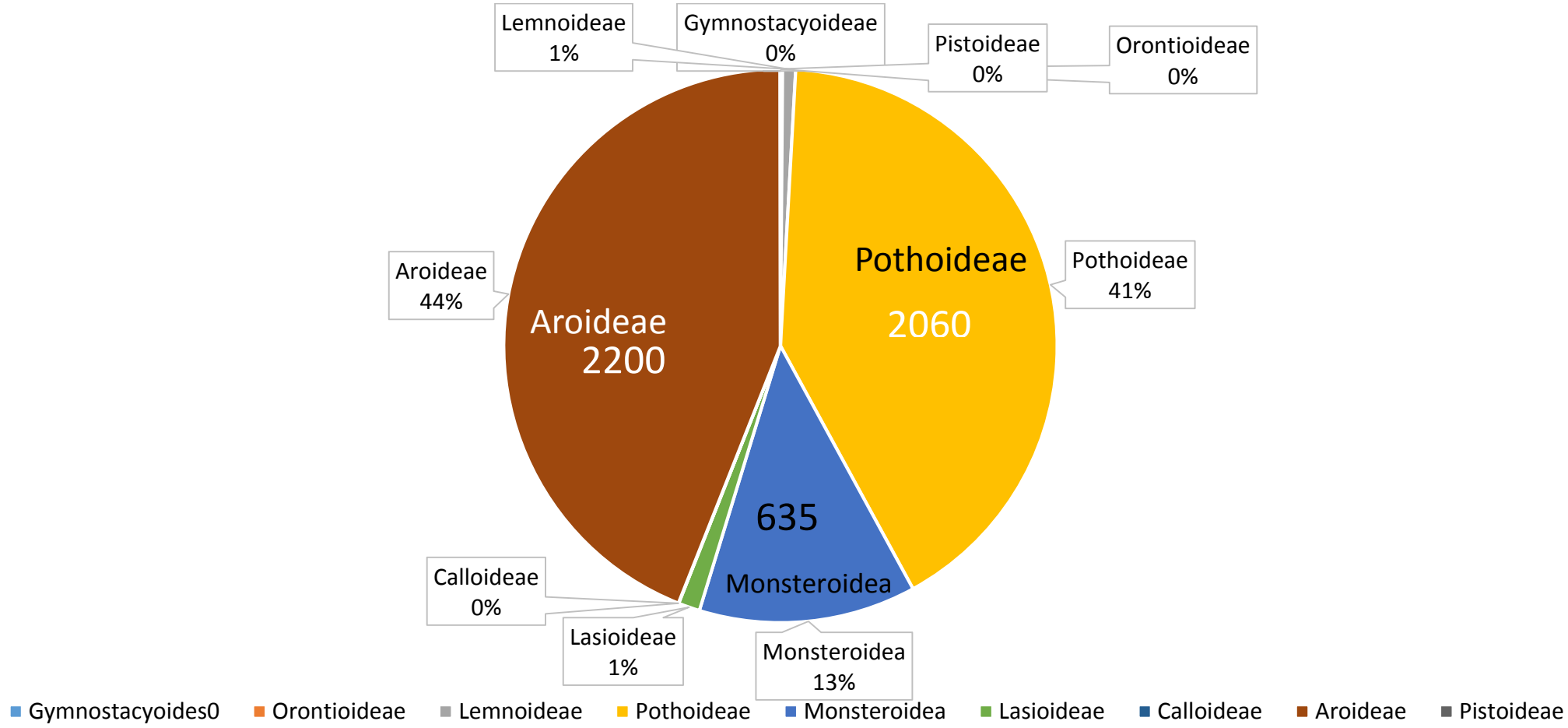
Araceae distribution

- World wide in distribution
- Most genera in Asia- 68 genera (27 in Borneo alone)
- Tropical Africa (9 genera); N. Africa (Meditterranean 7 species); S. Africa 3 genera
- Most species in Americas (2/3 of all species) (41 genera- 3 times larger than in Asia)
- Most Aroids in Tropical Areas (9 genera and 19 species in N. America)
- Europe has 9 genera but fewer total species owing to having fewer species of Lemna.

Respective Sizes of Subfamilies in Genera



Respective Size of Subfamilies in Species



Araceae 7 subfamilies

Gymnostachys anceps

Subfamily Gymnostachyoides

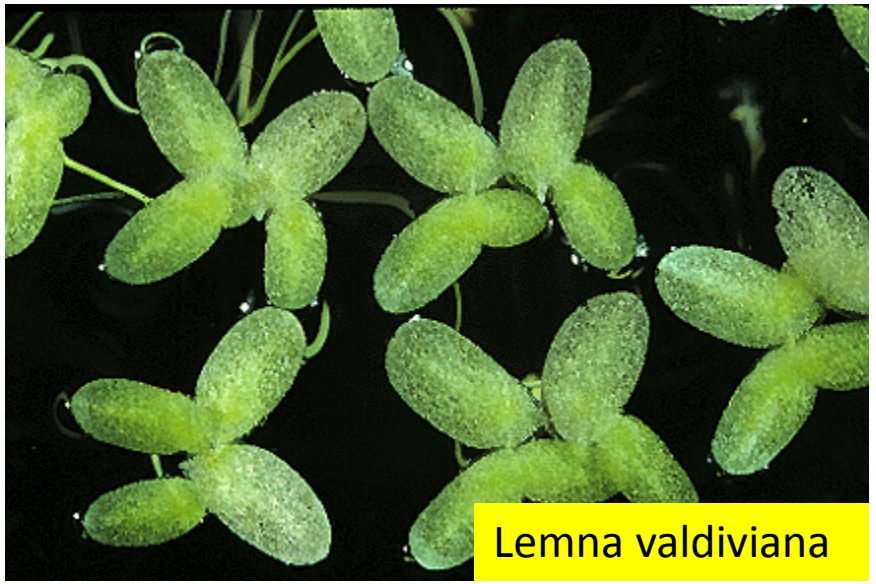
Orontium aquaticum

Subfamily Orontioideae

Symplocarpus foetidus

Subfamily Lemnoideae

Duck weeds



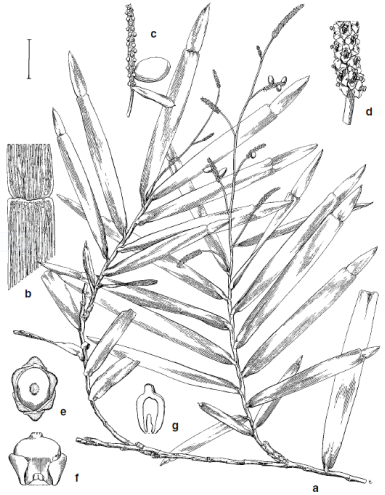
Earliest aroids were probably aquatics

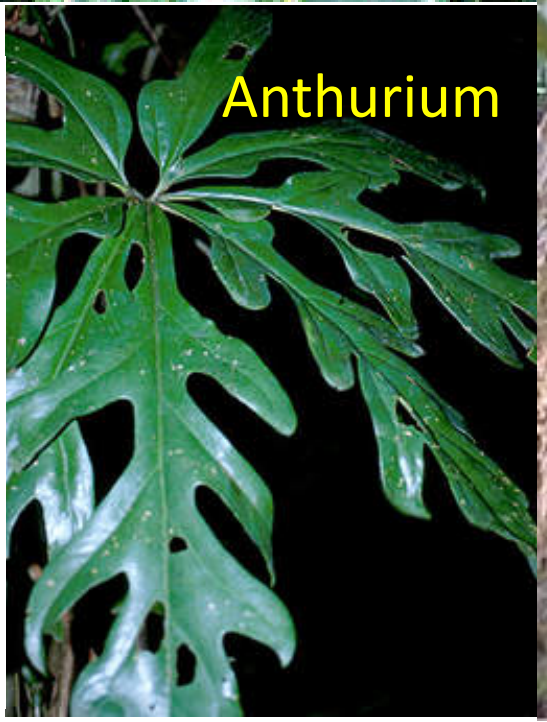
- Many modern day genera (or tribes) have reverted to aquatic habitat. (Red = New World Black = Old World)
  - Anaphyllopsis
  - Anubias
  - Calla
  - Cyrtosperma
  - Dieffenbachia
  - Dracontioides
  - Lasia
  - Lasiomorpha
  - Montrichardia
  - Philodendron
  - Philonotion
  - Spathiphyllum & Holochlamys
  - Urospatha
  - Shismatoglottidae – 6 genera
  - Cryptocoryneae (2 genera)

Subfamily Pothoideae

Pothos

Pothoideum

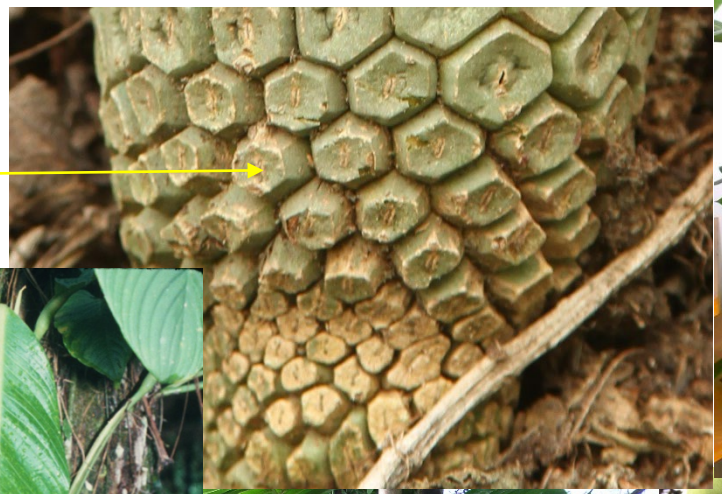




Subfamily Monsteroideae

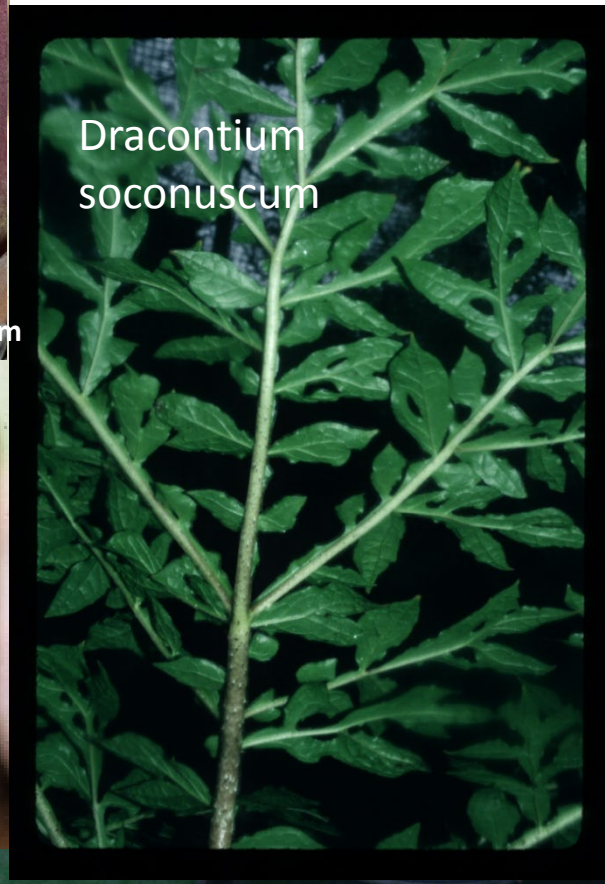
Spathiphyllum has tepals

Naked flowers



Subfamily Lasioideae

Cormlet production



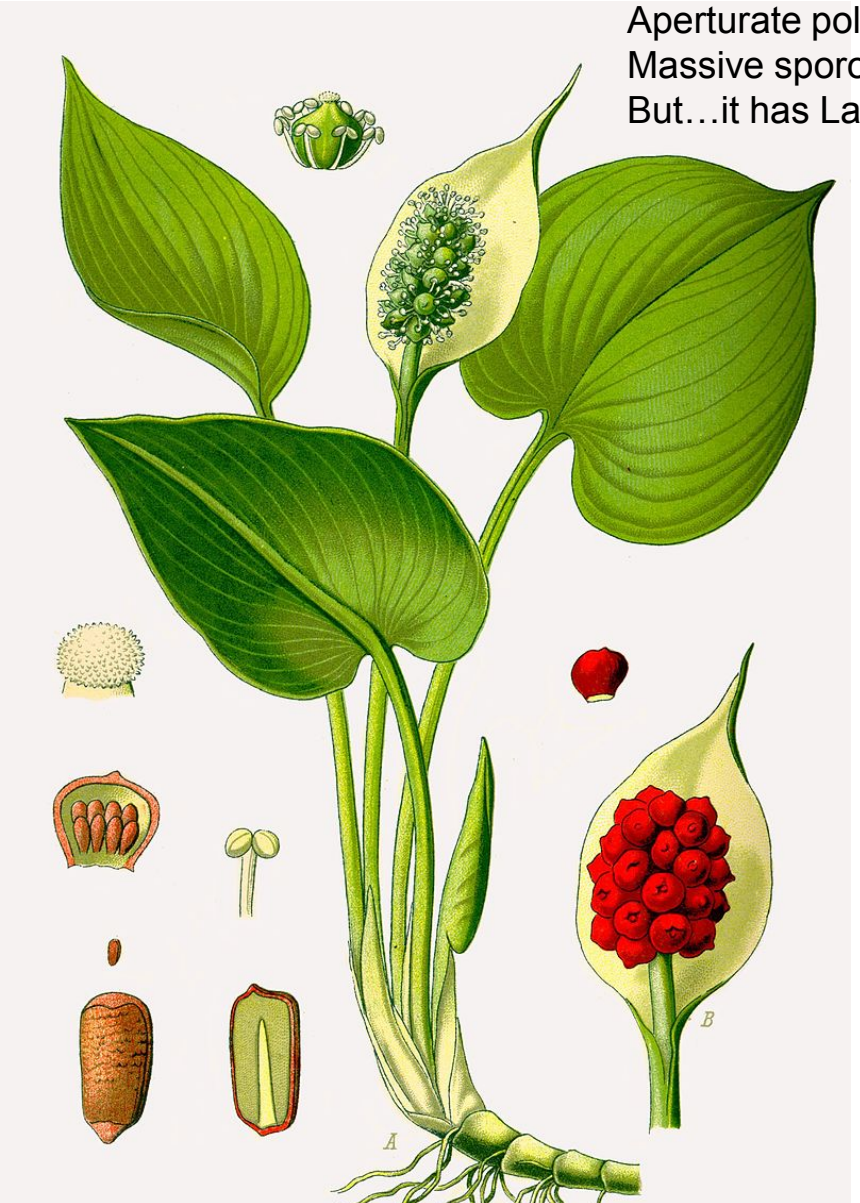
Lasiomorpha senegalense

Dracontium croatii

Subfamily Calloiodeae

1 widespread circum-boreal species, 0-1270 m

Bisexual flowers
Aperturate pollen
Massive sporopollenin
But…it has Laticifers

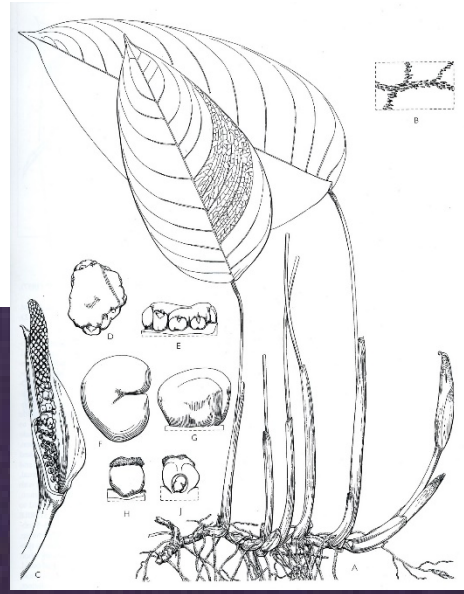


Subfamily Zamioculadeae

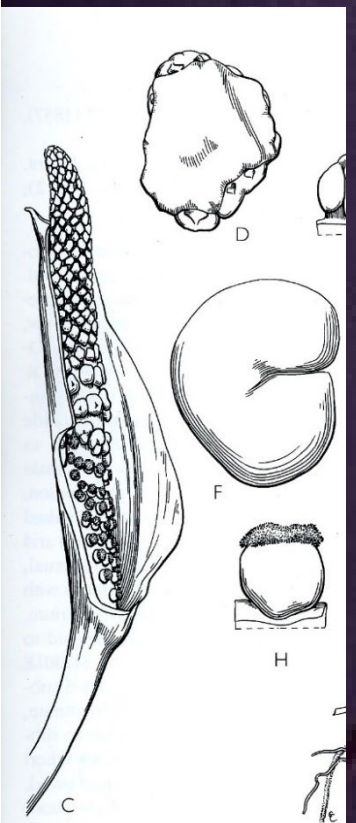
The subfamily is unusual in that it unisexual flowers but also the flowers have tepals

Subfamily Aroideae- Tribe *Dieffenbacheae*

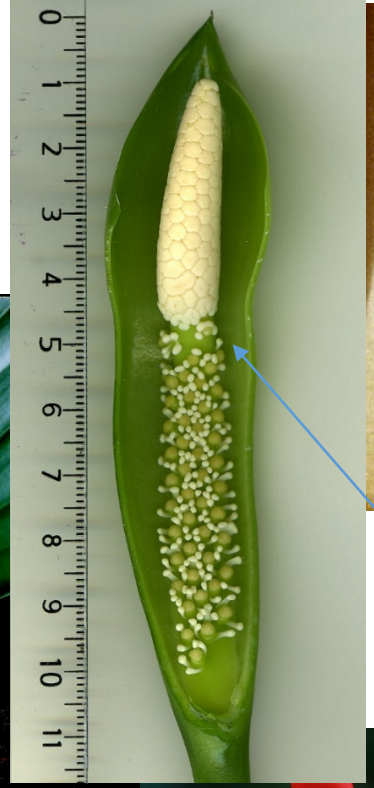
Subfamily Aroideae has overwhelmingly the most genera with 67% of the total.



Bognera recondita



Dieffenbachia oerstedii



Sterile segment, lacking staminodia

Dieffenbachia oerstedii

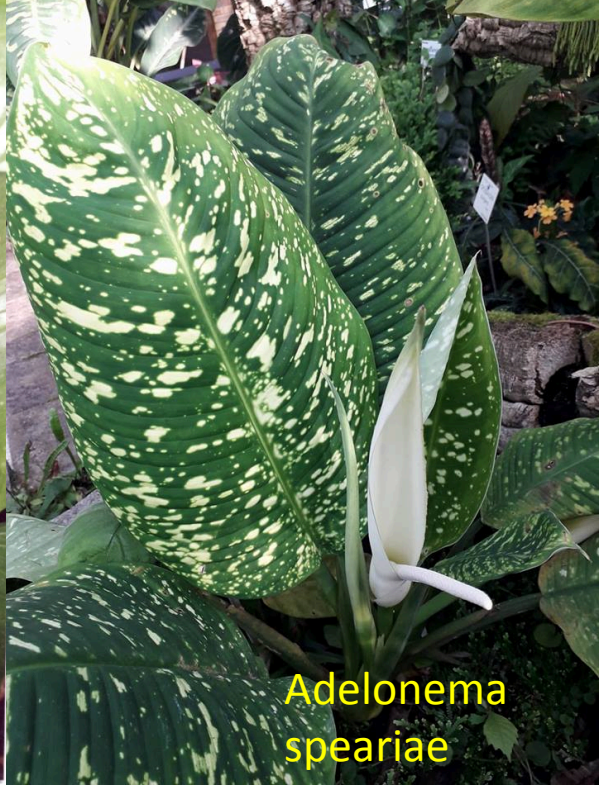
Tribe Spathicarpeae, 9 genera

Synandrospadix vermitoxicum

Asterostigma, 7 species

Croatiella integrifolia, 1 sp.

Tribe Philodendreae

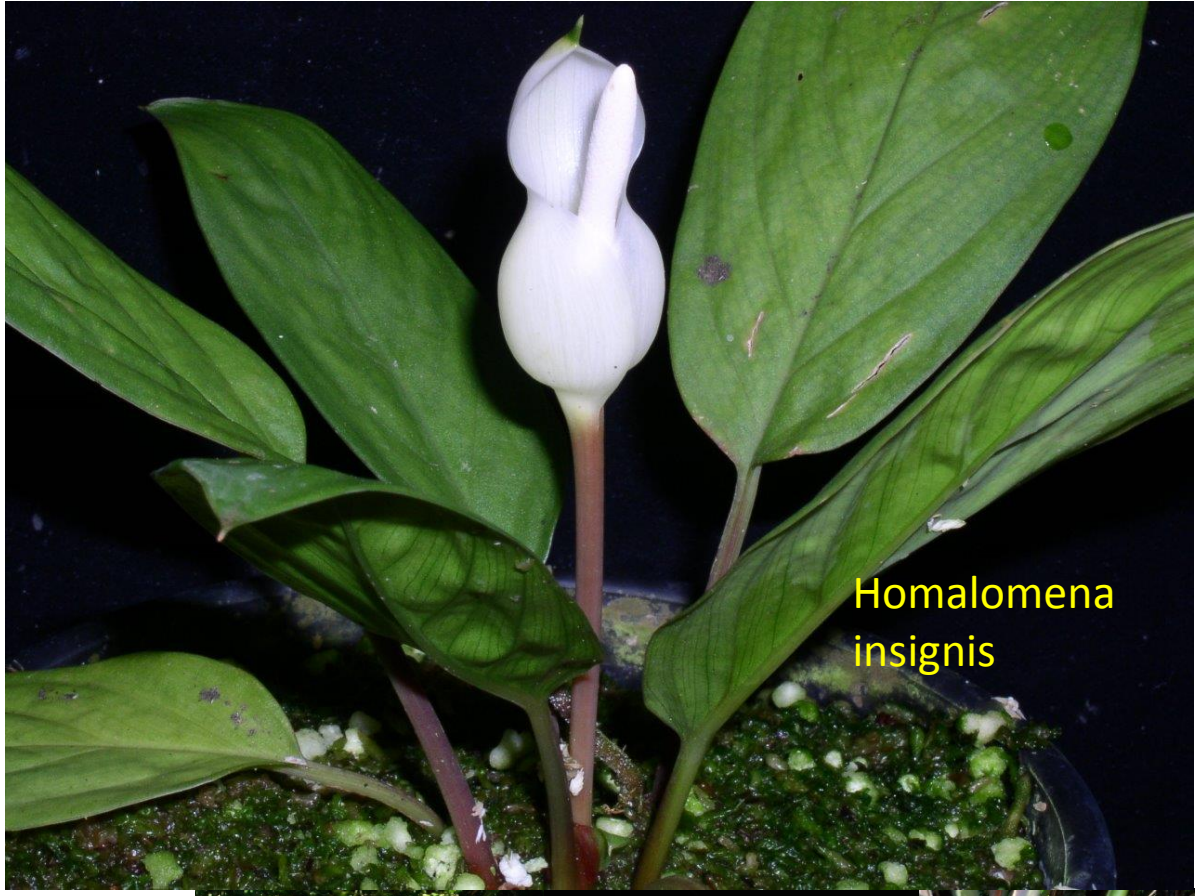


Tribe Homalomeniae

Homalomena imitator

Homalomena scutata

Differs from Philodendron by its consistently terrestrial habit, non-resinous inflorescence, mostly 1-locular ovary; Asia.



Homalomena insignis

Only 98 species described but up to 500 are expected

Homalomena vellutipedunculum

Tribe Anubiae

Anubias- Africa, mostly aquatic

Terrestrial, creeping rhizomes, unisexual flowers; berries sublobular, many seeded

8 species, Toropical West Afriaca.

Tribe Schismatoglottideae

Shismatoglottis 29 species.
Philonoton 3 species

Schismatoglottis petradoxa

Circumscissally deciduous

Inflorescences 1-3 per axil; flower unsexual; Asian

Schismatoglottis calyptrata

Philonotion americanum

Philonotion spruceanum

Schismatoglottideae - Rupicolous group

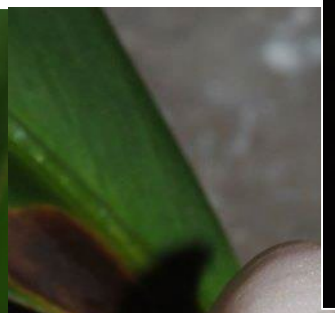
All photos P. Boyce

Borneo endemics

Splash cup seed dispersal

Burttianthus hansenii

Bucephalandra goliath



Galantharum kishii, 1 sp. Borneo

Bucephalandra goliath

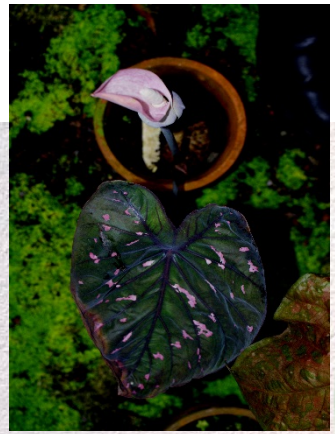
Tribe Cryptocoryneae

2 genera, SE Asia

Tribe Zomicarpeae

Zomicarpela americanum

Tribe Caladieae



Caladium humboldtii

Caladium palaciosii

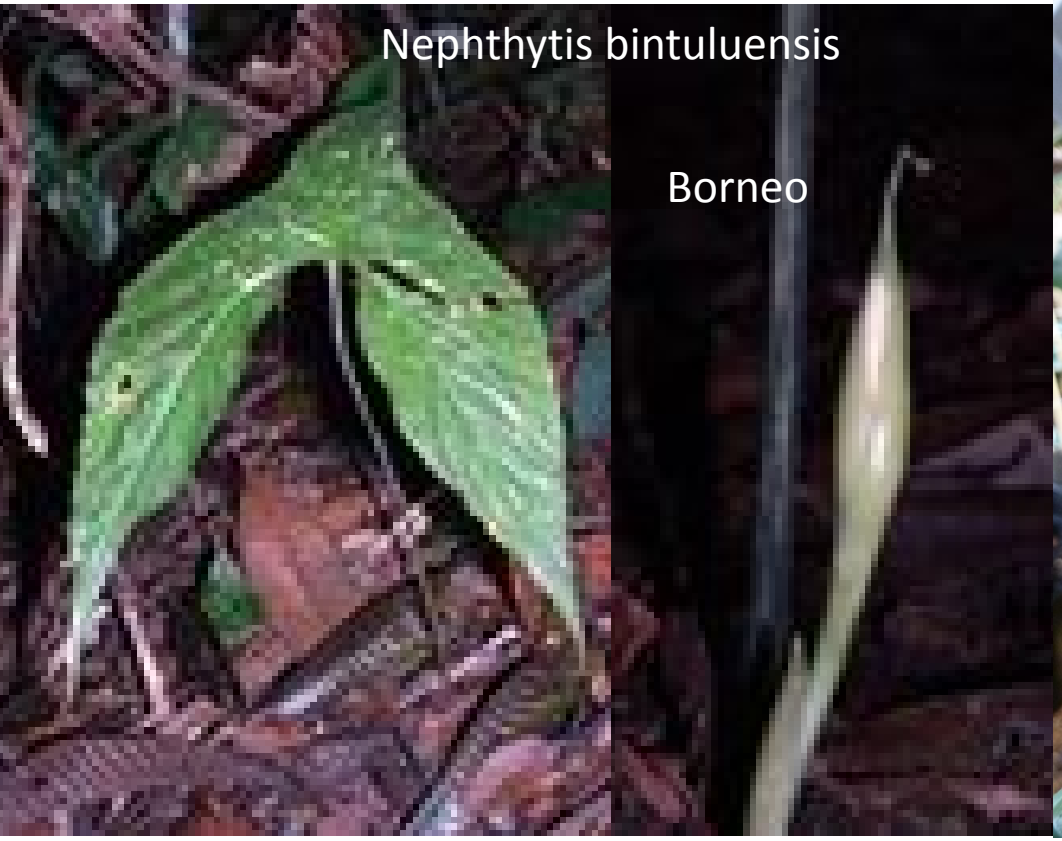
C. bicolor

C. rubricundum

Caladium lindenii

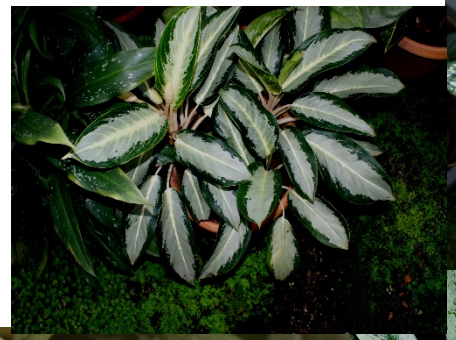
Tribe Nephthytideae

Nephthytis 5 ssp. 1 Asia, 4 Africa



Tribe Aglaonemateae

25 spp. Asia



Aglaonema brevispathum

Aglaonema costatum

Tribe Aglaonemateae-

Tribe Culcasieae

Culcasia 28 spp. Africa

Culcasia scandens

Culcasia mannii

Zambia

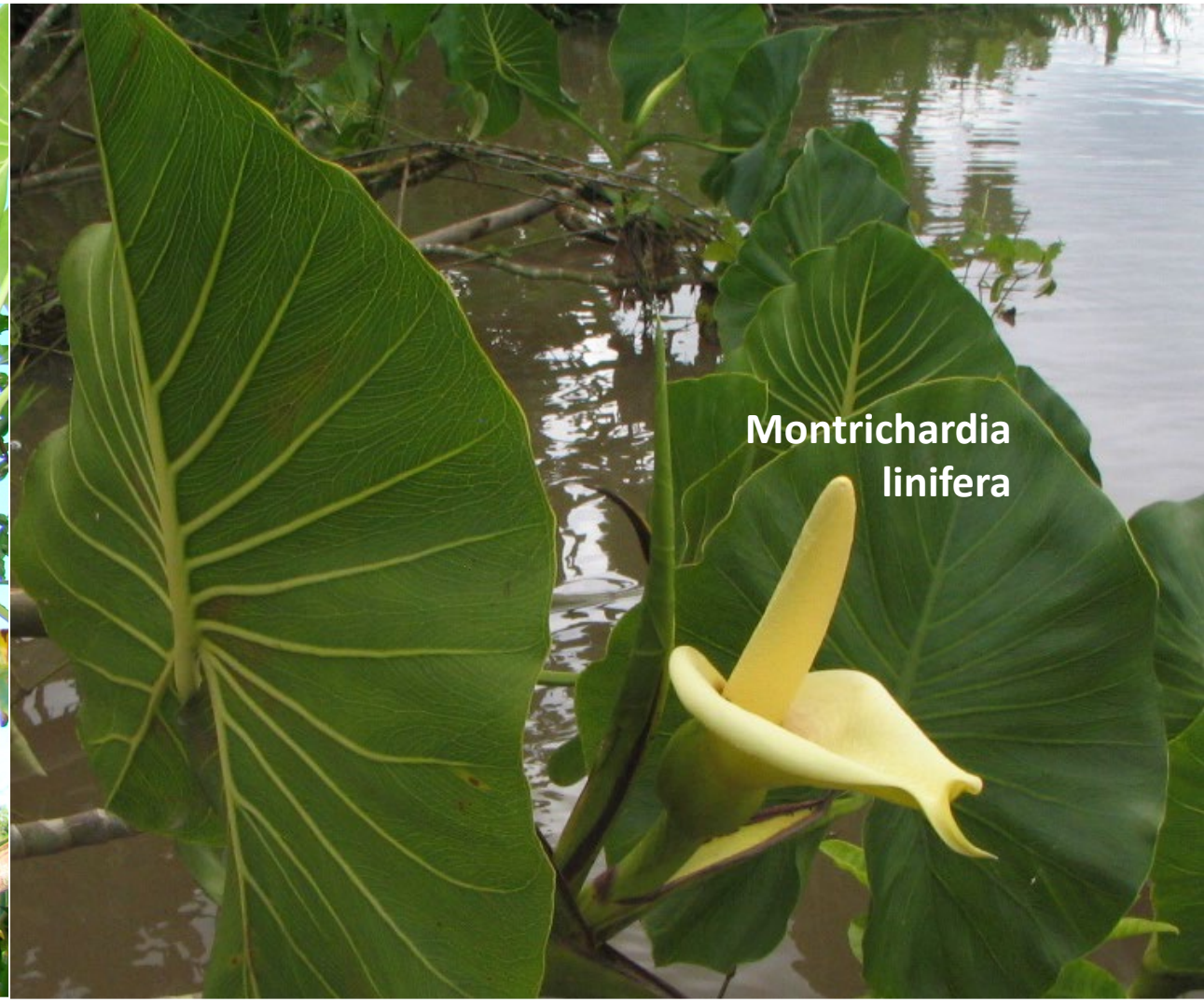
Mozambique

Tribe Montrichardieae

2 spp.

American Tropics

Montrichardia arborescens



Montrichardia linifera

Tribe Zantedeschieae

8 species
South Africa

Tribe Callopsideae

Callopsis - Kenya, Tanzania

Flowers unisexual, ovary 1-locular with 1 ovule

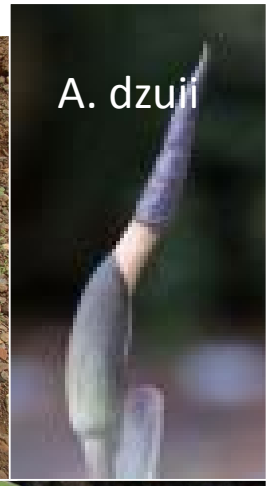
Tribe Thompsonieae

Amorphophallus

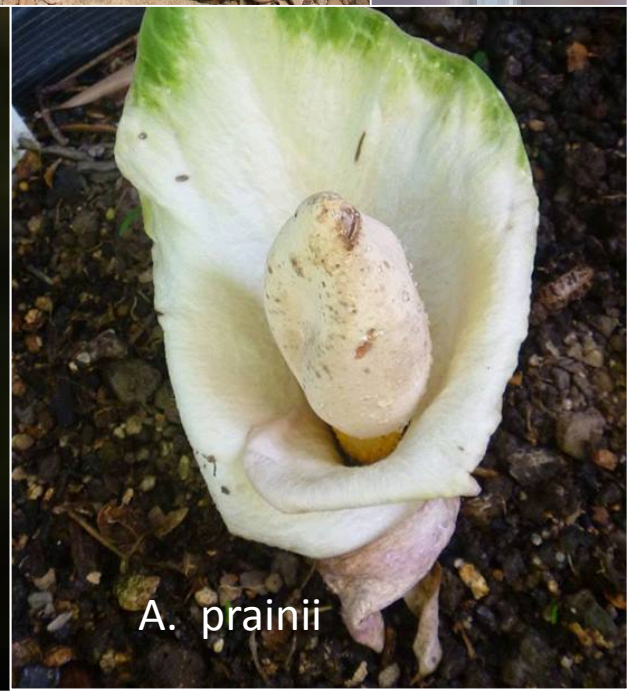
197 species; Africa and Asia


A. croatii


A. dracontioides


A. dzuii


A. sylvaticus


A. prainii


Emily Colletti with Amorphophallus titanum

Pseudodracontium

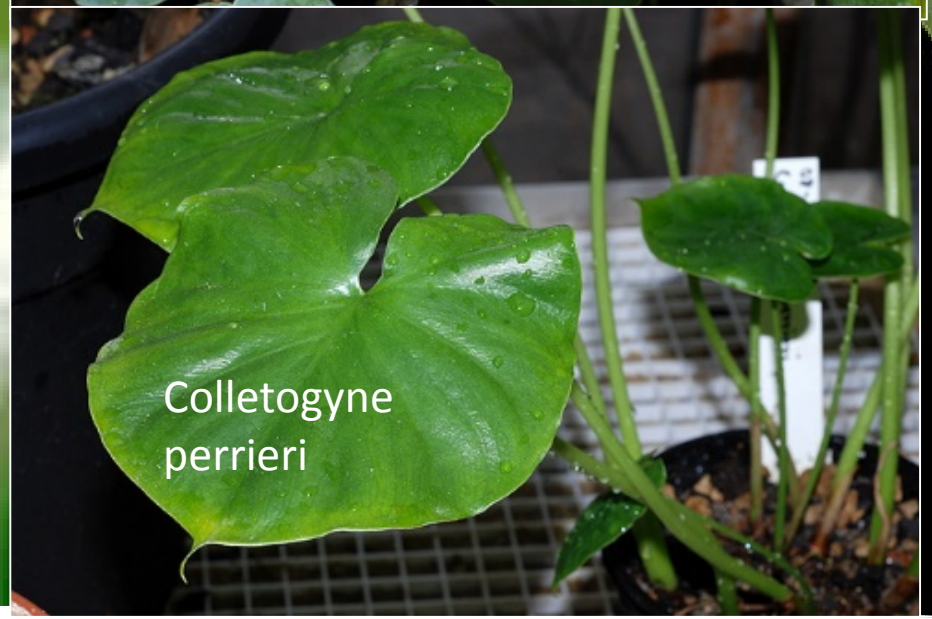
Cambodia, Laos, Thailand, Vietnam


Recently merged with Amorphophalllus

Tribe - Arophyteae

Endemic to Madagascar

- Arophyton - 7 species
- Carlephyton - 3 species
- Colletogyne - 1 species



Tribe Peltandreae

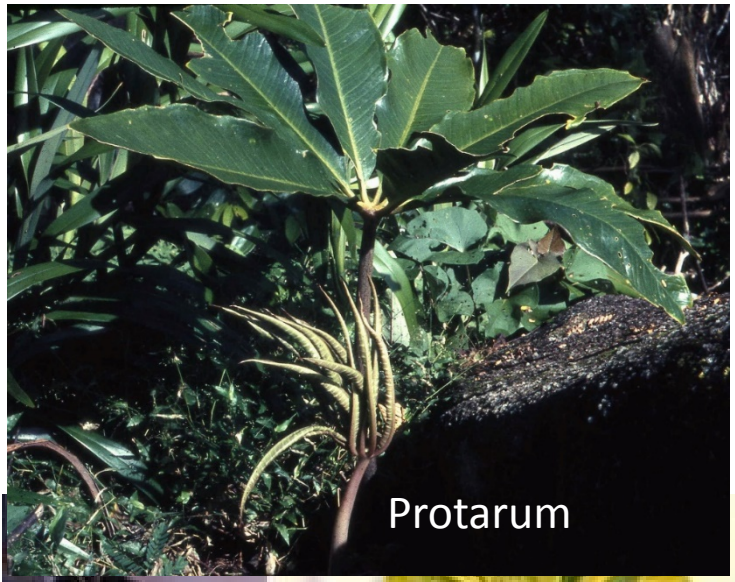
Peltandra virginica

Peltandra – 2 spp
Eastern North America

Typhonodorum 1 sp.
Africa – Madagascar

Typhonodorum - Madagascar

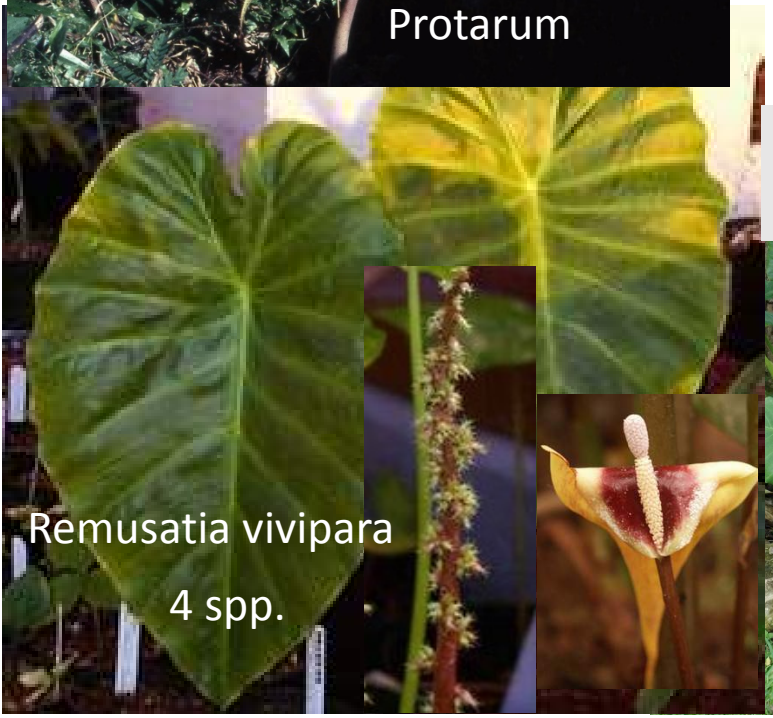
Tribe Colocasieae



Appendix
Male spadix
Female spadix

Monotypic
- Seychelles

Colocasia gigantea



Alocasia
- 78 spp.

Tribe Arisareae

Arisarum- Circum-Mediterranean- 3 spp

Arisarum porboscideum

Arisarum vulgare

Arisarum simorrhinum

Tribe Ambrosineae

Ambrosina- N. Africa, Sicily, S. Italy, 1 sp.

Pollination by flies with
deciept trapping mechanism

Tribe Areae

7 genera, mostly Meditteranean

Arum- Europe, Middle East, India- 7 spp.

Eminium- Middle East to Afghanistan- 9 spp.

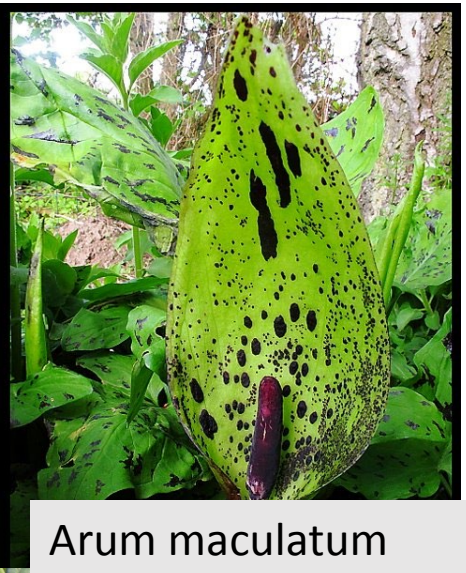
Dracunculus- N. edge of Mediterranean- 2 spp.

Helicodisceros- Sardinia, Baleric Is., Corsica- 1 sp.

Typhonium- Asia, Melanesia, Australia- 65 spp.

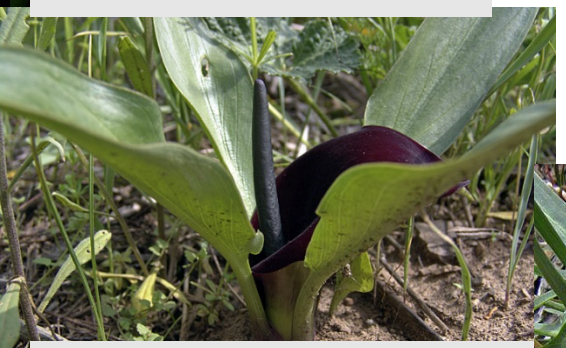
Sauromatum- Central Africa, India to China- 9 spp.

Biarum- Circum Meditteranean, Middle East- 23 spp



Arum maculatum

Biarum carduchorum



Eminium lehmanii - Iraq

Helicodiceros muscivorus

Typhonium croatii

Sauromatum venosum

Dracunculus vulgarus

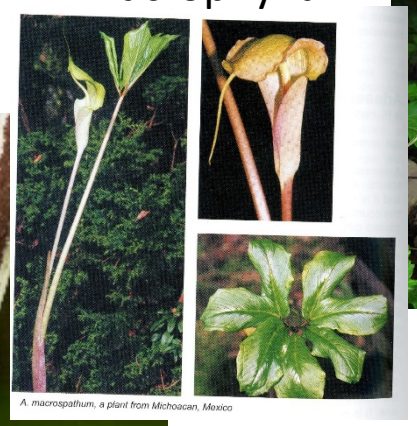
Arisaemateae

A. ringens

Arisaema - E. N. America, Mexico, E. Africa, India to Japan, Eastern Melanesia

Ovary several ovulate; female spadix free from spathe; septum lacking

A. macrophyllum



A. dilatum

A. heterophyllum

A. triphyllum

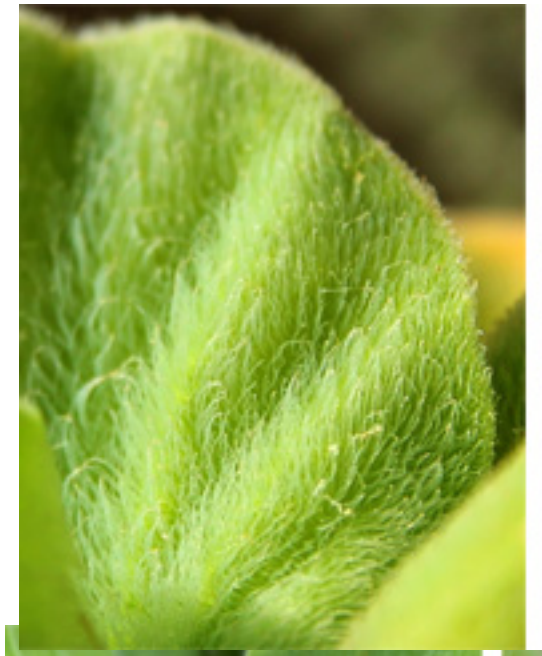
Arisaema dracontium

Pinellia - N. Asia

Ovary 1 - ovulate; female spadix fused to spathe; septum separating male and female flowers

Pinellia cordata

Pinellia ternata



Notable facts about Aroids

- Perhaps the diversity of habit, leaf form and floral complexity is not the most interesting thing about Araceae.
  - More than perhaps any other family the group is species-rich beyond comparison.
  - No other family of comparable size is producing so many novelties.
  - A recent floristic survey in Carchi Province, Ecuador had 130 species in just one section of Anthurium sect. Porphyrochitonium from a single Province (Esmeraldas). More than 95% of these proved to be new to science. Moreover it is estimated that probably fewer than half of the total species in that group have been collected.

Most growth in the size of Araceae has occurred in the past 40 years during my career

- *Adelonema* (42%)
- *Anthurium* (71%)
- *Chlorospatha* (66%)
- *Dieffenbachia* (77%)
- *Dracontium* (16%)
- *Monstera* (65%)
- *Philodendron* (70%)
- *Rhodospatha* (71%)
- *Spathiphyllum* (13%)
- *Stenospermation* (71%)
- *Syngonium* (43%)
- *Xanthosoma* (78%)

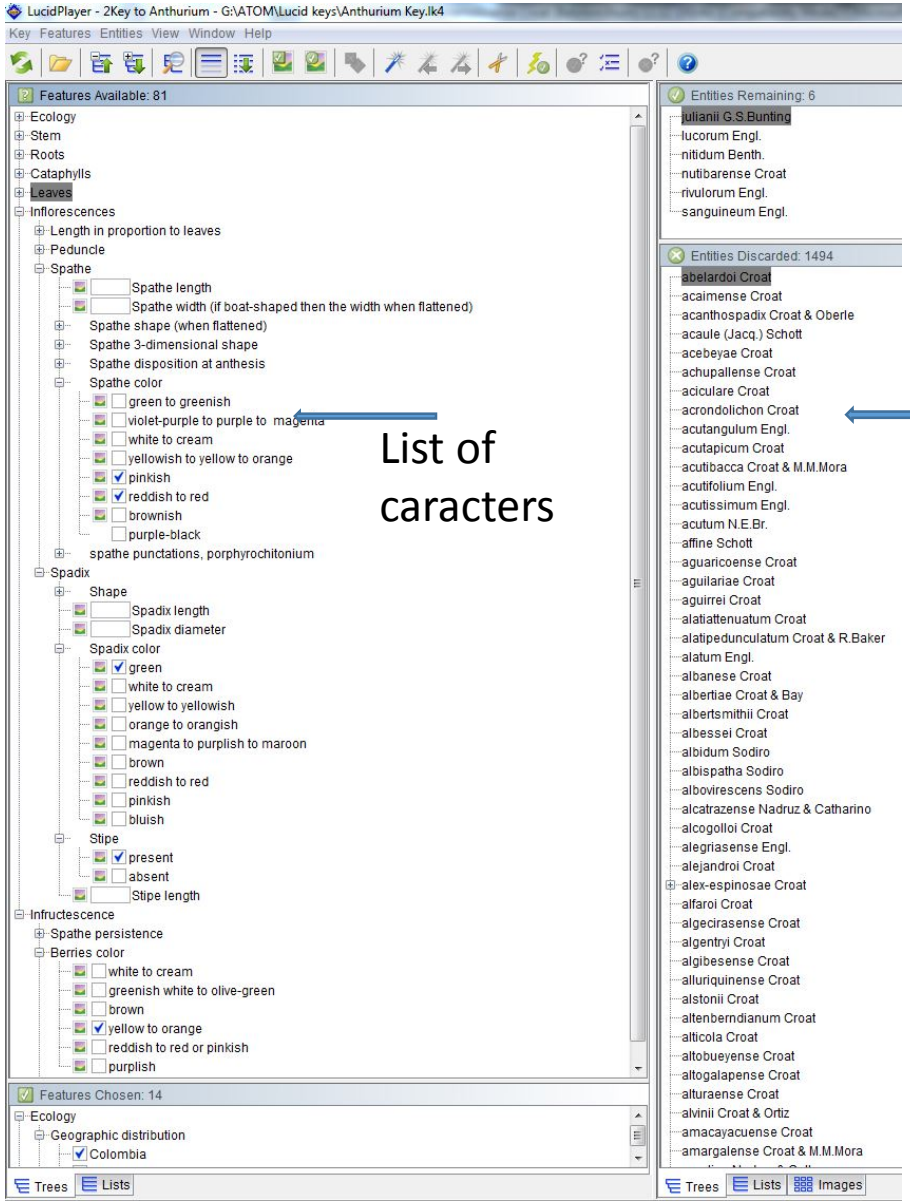
Evidence of great increases in the number of species in these genera

The case for an even much larger Araceae

- Development of electronic keys (Lucid) enables greater confidence in determination.
- In Anthurium has 1635 species present with each species compared on many characters.
- Hundreds of specimens fail to key out (determined) in Lucid.
- Perhaps as many as 500 seemingly distinct and new species have not yet been entered into Lucid owing to incomplete descriptions. Most of these undescribed species are from South America.
- Lucid Keys have been produced for Adelonema, Dracontium, Philodendron, Spathiphyllum, Stenospermation and Xanthosoma.

Lucid Menu of Characters

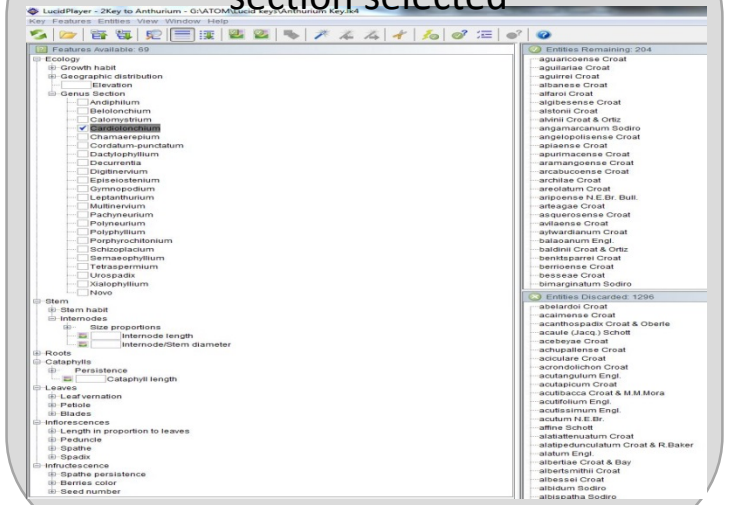
The Lucid Key operated by the elimination of species which do not share the chosen character. The computer finds and rejects those. . As the balance diminishes one reaches a point where the most likely related species are left. These can be then compared with images and descriptions.



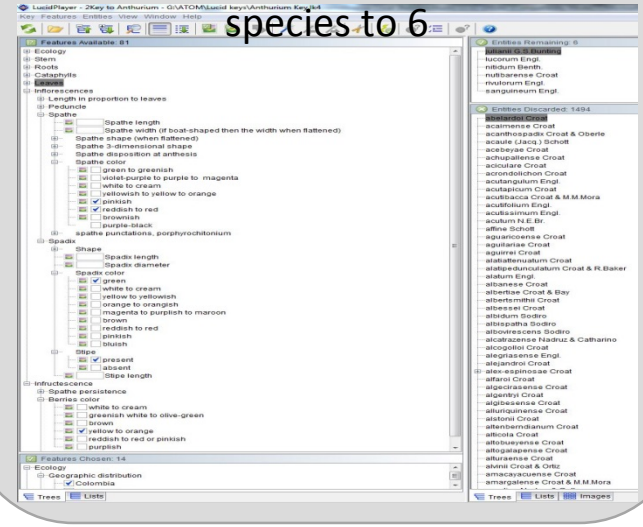
Determination Tool For Anthurium & Philodendron

Step 1: Specimen to determine

Step 2: Lucid Player, section selected



Step 3: Lucid Player, certain characters used to reduce species to 6



Step 4: Look up species selected in Determination Tool

Anthurium julianii

Anthurium lucorum

Anthurium nitidum

Anthurium nutibarense

Anthurium sanguineum

Anthurium rivulorum

Result: Species confirmed as *Anthurium sanguineum*

Missouri Botanical Garden

Thomas B. Croat, Ph.D., P.A. Schulze Curator of Botany

Steve Aylward, Volunteer Research Associate

Araceae Checklist for Central America

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V
1	CHECKLIST OF ARACEAE OF CENTRAL AME				Mexic	Guat.	Bel.	El Sal	Hond.	Nic.	CR	Pan	Middle	Mexic	Guat.	Belize	El Sal	Hond	Nic	CR	Pan	COL
23	X. robustum Schott	1			1	1	1	1	1	1	1											
24	X. sagittifolium (L) Schott Introduced	1			1	1	1	1	1	1	1	1										1
25	X. cerrosapense Croat & O. Ortiz	1										1									1	
26	X. undipes C. Koch	1									1	1										
27	X. violaceum Schott	1																				
28	X. wendlandii (Schott) Standley	1			1	1		1	1	1	1											
29	X. yucatanense Engler	1			1									1								
30	Total Xanthosoma	18	0	0	6	4	3	4	3	4	8	10		2	0	0	0	0	0	2	6	
31																						
32	ZANTEDESHIA																					
33	Z. aethiopica										1	1										
34	TOTAL ZANTEDESHIA	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	
35	Grand Total Species	781	35		135	90	53	30	67	103	311	622		94	14	2	0	4	2	154	591	85
36			816		17%	12%	7%	4%	9%	13%	40%	80%		70%	16%	4%	0%	6%	2%	50%	95%	90%
37	Total Genera	25																				

Floristic Comparisons of Central and South America

- A complete aroid flora exists for Central America (781 species).
- Most explored parts of Central America are reasonably well known.[Probably 10% of the flora is still not yet collected]
- Endemism and Species Diversity increases dramatically as one approaches South America.
- Panama (with 80% of all the species in Central America) has 622 species, 95% of them presently believed to be endemic.
- Colombia, **15 times larger** in area and many times more diverse has only 820 Species (Panama currently has 4/5 as many as Colombia)

Conservative extrapolation assures great increases

- Colombia alone must have between 8,000 and 12,000 undiscovered species.
- Collecting has essentially stopped or is progressing too slowly to prevent mass extinction before these species are collected, studied and described.
- Experts must be encouraged to collect for greatest efficiency.
  - Jatun Sacha- great increases with less than 6 hours collecting

Study in England found that most new species were discovered by less than 3% of all collectors. Megacollectors had 3 characteristics.

- Collected throughout most of their professional lifetime (58 yrs).
- Collected in many different areas (> 5000 localities; 142 countries - collected in 42 of these).
- Have a special taxonomic group that keeps them searching. Keeps them going to the field (Araceae).

Important Need for Inventory Studies

- Collecting is no longer considered important.
- Too few students are doing floristic studies where they learn large and complex groups of plants.
- Floristic studies are considered unimportant-can’t even be published.
- Floristic studies are often the basis for in-depth collecting and understanding.
- Without initial collecting activity experts don’t even know where to go.

Legal and Logistical Impediments

- Most countries have serious impediments to collecting
- Some countries allow only experts permission and disallow general collecting despite the inefficiencies.
- Requirements for permits discourage all but most persistent from getting permits.
- In country movement of plants is prohibited creating even more obstacles.

Conservation measures don’t prevent forest destruction

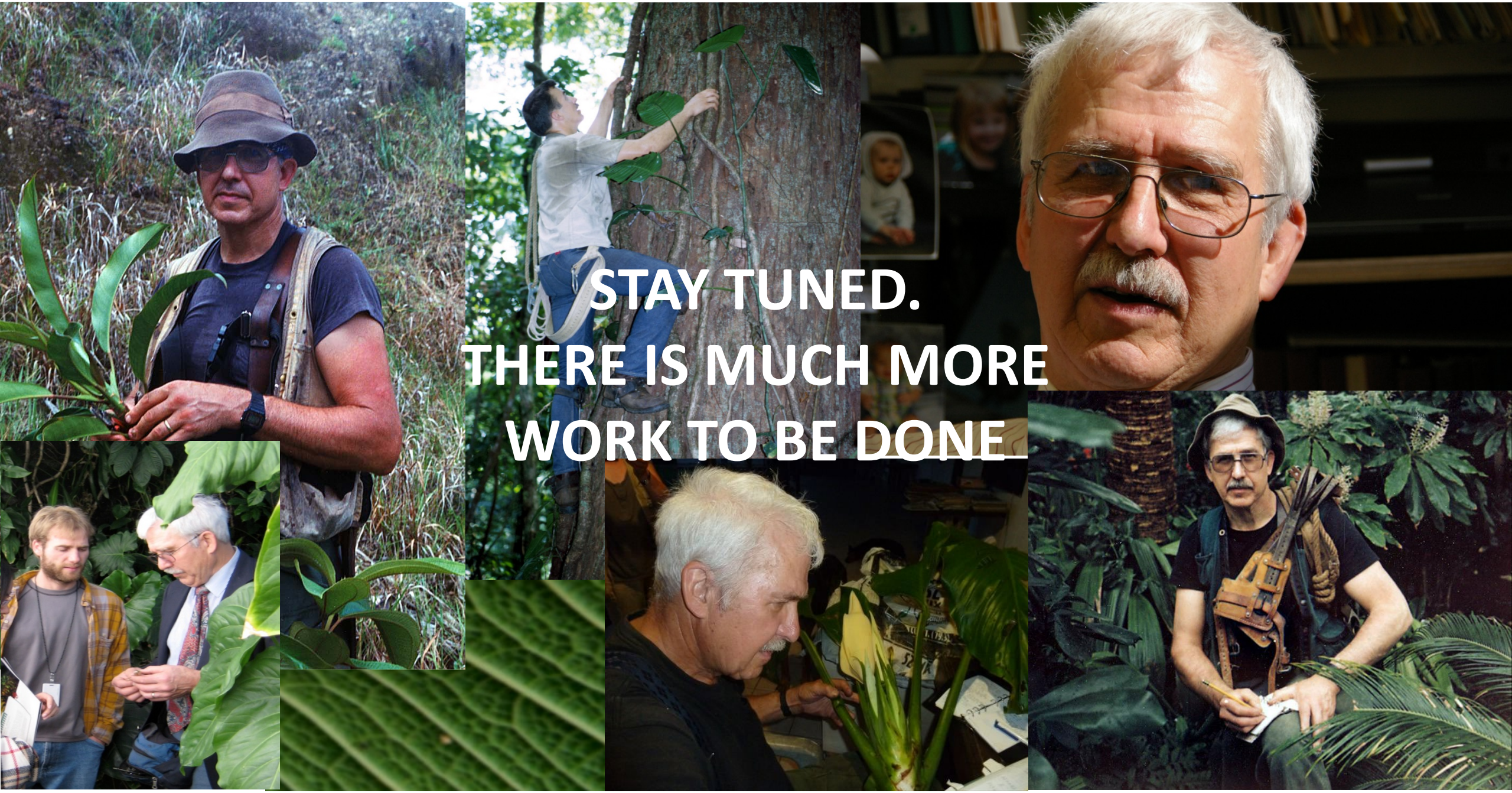
- Most forested area are NOT in parks or preserves.
- Roads lead to destruction and roads are leading EVERYWHERE.
- In my 50 year career of collecting virtually all of my collecting localities have disappeared.
- Rates of forest destruction is increasing, not slowing, despite laws. Owing to high endemism this means extinction everywhere.

Role of the Missouri Botanical Garden in the Process of Discovery

- Newly Described Species
- The Importance of Field Work
- The Importance of Exploring New Areas when they first become accessible

Conclusions

- Araceae have **vast potential for new species**, especially in NW South America, Panama, Andean countries of South America but even in mesic and dry habitats not previously studied.
- Efforts should be made to **increase collecting activities**.
- Local **floristic studies should be encouraged** in the tropics and such studies should be published to encourage such studies.
- Tropical **florulas develop expertise**, interest and eventual specialists. These are ideal studies for Latin American students.


STAY TUNED.
THERE IS MUCH MORE
WORK TO BE DONE

- Closing Remarks
- As you can see we know a lot about the Araceae. I believe I have advanced our scientific knowledge of this family in a major way. God has blessed me with abundant energy, strength and good health. I have the support of a very capable and loving wife who has allowed me to traipse around the jungles of the world for more than 52 years. Family vacations were taken without me so my children had to manage on their own. They did very well. The Missouri Botanical Garden is a marvelous place to work. **The horticultural staff** supports the study of thousands of living plants. **The research division** provides tremendous help in processing, cataloging and studying the collections. I have also had support from the **National Science Foundation** and the **National Geographic Society**. I have **collaborators** here and throughout the world who work together on this family. The **International Aroid Society** is a very active and enthusiastic group and I have served on their Board for 40 years. I also have many (presently 40) dedicated and talented volunteers who aid in the identification, describing and publication of new species as well as with filing, labeling of digital images, in designing web sites and constructing Lucid keys. In the past two years I have travelled throughout South and Central America and Europe, engaging with young botanists to inform them about the wonders of aroids and to interest them in joining in the research that needs to be done. As you can see there is much more work to do and we will continue this work immediately.