

THE GENERA OF ARACEAE PROJECT

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Abstract A new treatment of the genera of the Araceae is currently being prepared and will be published by the Royal Botanic Gardens, Kew in 1995/96. The main emphases of the book are keys to the genera, a complete set of up-to-date generic and tribal descriptions and a complete set of full-sized black and white line analytical drawings, one for each genus; the artist is Eleanor Catherine. A general part will give condensed treatments of the major character fields, taxonomic history, economic botany, ethnobotany and cultivation. Other botanists are contributing in various ways, including provision of material for drawing and critical review. Chapters on anatomy and chemistry have been contributed by Prof. J. C. French and Prof. R. Hegnauer, respectively. "The Genera of the Araceae" will be organized according to a new systematic arrangement that has been worked out with the help of cladistic methods. It is hoped that through an active exchange of views with other aroid specialists a classification can be agreed which will serve the practical needs for the future. The authors nevertheless consider that current rapid advances in phylogenetic and molecular studies and generic revisions within the family are likely to mean that the family classification will be unstable for some time to come.

Key words Araceae, treatment of genera, classification, systematics.

INTRODUCTION

The idea for this book germinated in 1980 when the first international workshop on the systematics of Araceae was held at the Marie Selby Botanical Garden, Sarasota, Florida, organized by Dr. Michael Madison. Madison and Simon Mayo began a manuscript but the project never came to fruition. In 1987, with the encouragement of Prof. Grenville Lucas, Keeper of the Kew Herbarium, Mayo and Josef Bogner of the Munich Botanic Garden resolved to tackle the task anew. Peter Boyce joined soon afterwards. Eleanor Catherine, the artist, completed the team at a later stage.

The format of this book (Table 1) is modeled on that of the Genera *Palmarum* by Dr. Natalie Uhl and Dr. John Dransfield (Uhl & Dransfield 1987). The delimitation and circumscription of all the genera have been critically re-examined considering modern studies. Since A. Engler's last monograph in the Das Pflanzenreich series (Engler 1905, 1911, 1912, 1915, 1920a, 1920b; Engler & Krause 1908, 1920; Krause 1908, 1913), new genera have been described and old ones reduced to synonymy. F. Gagnepain described *Pycnospatha* from Laos, H. Jumelle Arophyton and Carlephyton from Madagascar and S. Buchet Colletogyne, also from Madagascar. M. Hotta contributed four new genera, *Heteroaridarum*, *Pedicellarum* and *Phymatarum* from Sarawak, and *Furtadoa* from Sumatra and the Malay Peninsula. D. H. Nicolson and his colleagues contributed *Bognera* and *Filarum* from tropical America and *Hottarum* from Borneo. G. S. Bunting described the extraordinary aquatic *Jasarum* and *Lasimorpha*, a synonym of *Cyrtosperma* according to Engler, has been re-established by A. Hay. Hay also recently described *Anaphylloopsis* from tropical America and *Lazarum* from Australia. Despite these changes, the total number of genera treated here (105 without *Acorus*) is much the same as that presented by Engler (108 without *Acorus*). However, cladistic analyses of morphological and molecular data in recent years have meant that the classification has changed considerably since Engler's time.

Table 1. Format of The Genera of the Araceae

Foreword	15. Geography
Preface	16. Uses
Acknowledgments	17. Cultivation
A. GENERAL PART	18. Conservation
1. History	19. Fossil Record
2. Vegetative Morphology	20. Phylogenetic relationships within the Monocotyledons
3. Vegetative Anatomy (by J. C. French)	21. Phylogenetic relationships within the family
4. Floral Morphology	22. Previous classifications
5. Flora Anatomy	B. TAXONOMIC PART
6. Fruit and Seed	23. Synopsis of the Classification
7. Seedling Morphology	24. Family Description
8. Embryology	25. Keys to Genera
9. Cytology	26. Tribal and Generic Descriptions
10. Palynology	27. References and selected taxonomic literature
11. Phytochemistry and Chemotaxonomy (by R. Hegnauer)	28. Glossary
12. Ecology	29. Appendix: Pollinators, Fungal Parasites, Previous Classifications (tables)
13. Pollination Biology	30. Index
14. Dispersal	

We have deliberately laid the primary emphasis on the preparation of completely revised and detailed descriptions of the genera, together with analytical illustrations for each. The plates are all original drawings by Eleanor Catherine based on a combination of herbarium, spirit (from the Kew spirit collection) and living specimens, supplemented when necessary by photographs. The chapters of the General Part are intended to be summaries, in some cases quite brief, of various aspects of Araceae that are of taxonomic and general interest. In two instances the treatments are much more detailed, namely chapter 3 on vegetative anatomy and chapter 11 on phytochemistry and chemotaxonomy. These we were very fortunate to receive from Prof. J. C. French and Prof. R. Hegnauer, respectively. Their contributions are the first modern reviews in English of these subjects for the Araceae and are therefore of value for all plant taxonomists.

We have omitted any general treatment of the molecular systematics of the family, which is being studied, in particular, by Prof. French and his colleagues at Rutgers University, New Jersey. They have generously allowed us access to their most important phylogenetic conclusions, thus greatly improving our discussion of the family's phylogeny.

We have included material on *Acorus*, including a generic treatment, although we accept that this genus does not belong to the Araceae. However, it was felt that it would be convenient to the non-specialist reader, who might expect to find something on the genus in a general treatment of aroids.

In contrast we have not included any systematic account of the *Lemnaceae* which, according to the molecular work of French and colleagues (French, Chung & Hur in press), seem clearly to be embedded within the Araceae. Our reasons are again pragmatic. The taxonomy of the *Lemnaceae* has been comprehensively revised in recent years by Prof. E. Landolt (Landolt 1986; Landolt & Kandeler 1987). Furthermore, French's results (French Chung & Hur in press) became available only in the final stages of preparation of this book. Throughout the text we have employed the terms "aroid" and "araceous" as synonymous adjectives referring to any member of the family, and the noun "aroid" likewise. The reader should not therefore interpret "aroid" as referring only to members of the subfamily *Aroideae*. Previous work on the classification of the Araceae has reached a reasonable consensus on the circumscription of the tribes and subtribes. The major difficulties re-

volve around the subfamily concepts. These were introduced by Engler and have been found to be very useful by subsequent authors. It is much easier to think taxonomically of 8 subfamilies rather than about 30 tribes. The reluctance of modern authors to abandon the subfamily concept, despite the obviously superior taxonomic quality of the tribal groups, is shown by their constant use in aroid literature. A stage has now been reached in which confusion abounds. Current classifications differ radically in the composition of several subfamilies and it is no longer possible to speak, for example, of the *Aroideae*, *Lasioideae* or *Philodendroideae* without citing the author of the system being used. We therefore carried out a series of cladistic analyses using all genera as terminal taxa, and without assuming any higher groupings at the outset. Our classification (Table 2) is based on the results.

CLASSIFICATION

1. Major Group Protoaroids.

This clade consists of subfamilies *Gymnostachydoideae* and *Orontioideae* and is defined by the following characters: medium sized pollen, condensed, non corn-like thickened stem, subterranean stem, usually unilocular ovaries and locules with 1 – 2 ovules.

These are rather weak and highly homoplasious synapomorphies, which suggests that the group may be paraphyletic rather than monophyletic. It is noteworthy, however, that French et al. (French, Chung & Hur in press) independently and consistently found the same group using cpDNA data.

1). Subfamily *Gymnostachydoideae*.

Among other peculiar characters, *Gymnostachys* has linear leaves with parallel venation and a flowering shoot of unique structure. We therefore prefer to keep it in its own monotypic subfamily.

2). Subfamily *Orontioideae*.

This group corresponds to tribe *Orontieae* of previous classifications. The synapomorphies are: leaf blade expanded not linear, anatropous or hemianatropous ovules, endosperm sparse to absent, base chromosome number $x = 13$.

Table 2. Synopsis of the Classification

Family Aracéae Jussieu	MAJOR GROUP TRUE ARACEAE
A. FLOWERS BISEXUAL	III. Subfamily <i>Pothoideae</i> Engler
MAJOR GROUP PROTO – ARACEAE	Tribe <i>Pothoeae</i> Engler
I. Subfamily <i>Gymnostachydoideae</i>	5. <i>Pothos</i> L.
Bogner et Nicolson	6. <i>Pedicellarum</i> M. Hotta
1. <i>Gymnostachys</i> R. Brown	7. <i>Pothidium</i> Schott
II. Subfamily <i>Orontioideae</i> Mayo, Bogner et Boyce	Tribe <i>Anthurieae</i> Engler
2. <i>Orontium</i> L.	8. <i>Anthurium</i> Schott
3. <i>Lysichiton</i> Schott	IV. Subfamily <i>Monsteroideae</i> Engler
4. <i>Symplocarpus</i> Nuttall	Tribe <i>Spathiphyllae</i> Engler
	9. <i>Spathiphyllum</i> Schott
	10. <i>Holochlamys</i> Engler

Tribe Anadendreae Bogner et French11. *Anadendrum* Schott**Tribe Heteropsidae** Engler12. *Heteropsis* Kunth**Tribe Monstereae** Engler13. *Amydrium* Schott14. *Rhaphidophora* Hasskarl15. *Epipremnum* Schott16. *Scindapsus* Schott17. *Monstera* Adanson18. *Alloschemone* Schott19. *Rhodospatha* Poeppig20. *Stenospermation* Schott**V. Subfamily Lasioideae** Engler21. *Dracontium* L.22. *Dracontioides* Engler23. *Anaphyllopsis* A. Hay24. *Pycnospatha* Gagnepain25. *Anaphyllum* Schott26. *Cyrtosperma* Griffith27. *Lasimorpha* Schott28. *Podolasia* N. E. Brown29. *Lasia* Loureiro30. *Urospatha* Schott**VI. Subfamily Calloideae** Endlicher31. *Calla* L.**B. FLOWERS UNISEXUAL****VII. Subfamily Aroideae**

PARAPHYLETIC GROUP:

PERIGONATE AROIDEAE (perigone present)

Tribe Zamioculcaeeae Engler32. *Zamioculcas* Schott33. *Gonatopus* Engler**Tribe Stylochaetoneae** Schott34. *Stylochaeton* Leprieur

MONOPHYLETIC GROUP:

APERIGONATE AROIDEAE (perigone absent)

Dieffenbachia Alliance**Tribe Dieffenbachieae** Engler35. *Dieffenbachia* Schott36. *Bognera* Mayo et Nicolson**Tribe Spathicarpeae** Schott37. *Mangonia* Schott38. *Taccarum* Schott39. *Asterostigma* F. E. L. Fischer et C. A. Meyer40. *Gorgonidium* Schott41. *Synandropadix* Engler42. *Gearum* N. E. Brown43. *Spathantheum* Schott44. *Spathicarpa* W. J. Hooker**Philodendron Alliance****Tribe Philodendreae** Schott45. *Philodendron* Schott**Tribe Homalomeneae** (Schott) M. Hotta46. *Furtadoa* M. Hotta47. *Homalomena* Schott**Tribe Anubiadeae** Engler48. *Anubias* Schott**Schismatoglottis Alliance****Tribe Schismatoglottideae** Nakai49. *Schismatoglottis* Zollinger et Moritzi50. *Piptospatha* N. E. Brown51. *Hottarum* Bogner et Nicolson52. *Bucephalandra* Schott53. *Phymatarum* M. Hotta54. *Aridarum* Ridey55. *Heteroaridarum* M. Hotta**Tribe Cryptocoryneae** Blume56. *Lagenandra* Dalzell57. *Cryptocoryne* Wydler**Caladium Alliance****Tribe Zomicarpeae** Schott58. *Zomicarpa* Schott59. *Zomicarpella* N. E. Brown60. *Ulearum* Engler61. *Filarum* Nicolson**Tribe Caladieae** Schott62. *Scaphispatha* Brongniart ex Schott63. *Caladium* Ventenat64. *Jasarum* Bunting65. *Xanthosoma* Schott66. *Chlorospatha* Engler67. *Syngonium* Schott68. *Hapaline* Schott**No Alliance****Tribe Nephthytideae** Engler

69. <i>Nepthytis</i> Schott	86. <i>Arisarum</i> P. Miller
70. <i>Anchomanes</i> Schott	Tribe Ambrosineae Schott
71. <i>Pseudohydrosme</i> Engler	87. <i>Ambrosina</i> Bassi
Tribe Aglaonemateae Engler	Tribe Areae L.
72. <i>Aglaonema</i> Schott	88. <i>Arum</i> L.
73. <i>Aglaodorum</i> Schott	89. <i>Eminium</i> (Blume) Schott
Tribe Culcasieae Engler	90. <i>Dracunculus</i> P. Miller
74. <i>Culcasia</i> Palisot de Beauvois	91. <i>Helicodiceros</i> K. Koch
75. <i>Cercestis</i> Schott	92. <i>Therophonum</i> Blume
Tribe Montrichardiæ Engler	93. <i>Typonium</i> Schott
76. <i>Montrichardia</i> H. Cruger	94. <i>Sauromatum</i> Schott
Tribe Zantedeschieae Engler	95. <i>Lazarum</i> A. Hay
77. <i>Zantedeschia</i> K. Sprengel	96. <i>Biarum</i> Schott
Tribe Callopsideae Engler	Tribe Arisaemateae Nakai
78. <i>Calloopsis</i> Engler	97. <i>Pinellia</i> Tenore
Tribe Thomsonieae Blume	98. <i>Arisaema</i> Martius
79. <i>Amorphophallus</i> Decaisne	Tribe Colocasieae Engler
80. <i>Pseudodracontium</i> N.E. Brown	99. <i>Ariopsis</i> Nimmo
Tribe Arophyteae Bogner	100. <i>Protarum</i> Engler
81. <i>Arophyton</i> Jumelle	101. <i>Stuednera</i> K. Koch
82. <i>Carlephyton</i> Jumelle	102. <i>Remusatia</i> Schott
83. <i>Colletogyne</i> Buchet	103. <i>Colocasia</i> Schott
Tribe Peltandreæ Engler	104. <i>Alocasia</i> (Schott) G. Don
84. <i>Peltandra</i> Rafinesque	Tribe Pistieae Blume
85. <i>Typhonodorum</i> Schott	105. <i>Pistia</i> L.
Tribe Arisareae Dumortier	

2. Major Group True Araceae.

This is a previously unrecognized group and is supported by the following synapomorphies: – conspicuous or flag – like spathe; major internode of inflorescence between spathe and next leaf below, continuation shoot in axil of penultimate leaf before spathe, leaf blade expanded not linear, basal or near – basal placentation. These characters are strong and less homoplasious which suggests that the group is indeed very probably monophyletic.

3). Subfamily Pothoideae.

Tribe *Pothoeae* is a consistent group defined by the following synapomorphies: – monopodial shoot architecture, lack of endosperm, chromosome base number $x = 12$. The genus *Anthurium* failed to group consistently either with the *Pothoeae* or any other group in our analysis. French et al. (French, Chung & Hur in press), however, found that *Anthurium* consistently grouped with *Pothoeae* and we have adopted this to form the subfamily *Pothoideae*. Fig. 2 is an example of one family of cladograms which show the two taxa as sister groups, and in this case they share a single synapomorphy: – fine leaf venation with secondary and tertiary veins forming mostly cross veins to primaries; the plesiomorphic condition in *Anthurium* was assumed to be that shown in *Anthurium* sect. *Digitinervium*.

4). Subfamily Monsteroideae.

In our analysis the genera of the tribes *Monstereae*, *Heteropsidaeae* and *Anadendreae* form a single consis-

tent clade. The synapomorphies are: spathe undifferentiated into tube and lamina and soon deciduous or marcescent with distinct basal abscission, perigone connate. The latter character occurs only in *Anadendrum*, the perigone being lost further up the clade. The tribe *Spathiphyllae* failed to group consistently with these three tribes but does so in the cpNDA analysis of French *et al.* (French, Chung & Hur in press). Our *Monsteroideae* thus differs from Engler's only by the addition of *Anadendrum* and *Heteropsis*.

5). Subfamily *Lasioideae*

Our *Lasioideae* corresponds to tribe *Lasieae* of earlier systems and is a very stable and consistent clade.

The synapomorphies are: monosulcate pollen (derived by reversal from the inaperturate state), absence of pollen starch, basal ribs of primary veins very well developed, dracontoid leaf margin development, spadix with basipetal flowering sequence, anthers dehiscing by oblique pore – like slits and very often unilocular ovaries.

Monosulcate pollen is normally regarded as primitive in the family and it is possible that its occurrence as a reversal here may be an artefact contingent on the topology of this particular cladogram (see discussion under subfamily *Aroideae*).

6). Subfamily *Calloideae*

The genus *Calla* consistently emerges as a single clade and was usually among the basal branches in our analysis (Figs. 1 and 2). French *et al.* (French, Chung & Hur in press) also found that *Calla* emerged consistently as an independent clade, but in their analysis it occurred further up the tree. The autapomorphies are: perigone absent, pollen diaperturate, pollen globose, simple laticifers, petiole sheath long – ligulate, ovary unilocular, chromosome base number $x = 18$. *Calla* seems to be highly autapomorphic and its sister relationships remain obscure.

7). Subfamily *Aroideae*

The most striking feature of the analysis is the large clade which contains all the monoecious genera. This group corresponds to Schott's "Dielines" (Schott 1860) and is not recognized in the classifications of Engler (1876, 1920), Grayum (1990), Bogner & Nicolson (1991), Hay & Mabberley (1992) and Mayo, Bogner & Boyce (in press 2), which all embody the idea that monoecy and associated advanced spathe and spadix characters must have evolved several times from bisexual – flowered ancestors.

Strong support for our concept comes from the DNA work of French *et al.* (French, Chung & Hur in press) which also produces a single clade for all monoecious taxa. On the basis of both studies, we therefore feel confident in advocating the taxonomic recognition of this group as subfamily *Aroideae* since it represents a major advance and simplification in our understanding of aroid phylogeny.

There is a question as to precisely where to draw the boundary of the subfamily. our cladogram offers two possibilities which are supported by strong characters. A subfamily *Aroideae* which excluded the tribes *Zamioculcadeae* and *Stylochaetoneae* would be defined by absence of perigone, presence of simple laticifers, thick stamen connectives and porose anther dehiscence. By contrast, subfamily *Aroideae* including these tribes is defined by unisexual flowers, clear differentiation of the spathe into a tube and blade, and spadix differentiated into male and female zones. The later, more inclusive concept is a better fit with the DNA cladogram of French *et al.* (French, Chung & Hur in press). A further consideration is that these characters are of more practical use for distinguishing the *Aroideae*, since unisexuality and gross morphology of the inflorescence is a much more obvious combination of features than absence of a perigone, presence of laticifers or small floral characters. This is therefore the concept we have opted for. Despite our strong advocacy of this taxon, it should be pointed out that the distribution of certain characters on the cladogram, especially inaperturate pollen, is unsatisfactory. Inaperturate pollen arises between the *Spathiphyllae* and the other monsterooid clade

low down on the stem of the cladogram, requiring the re-evolution of monosulcate pollen from inaperturate in the Lasioideae. This also seems highly implausible. A much more likely arrangement would have inaperturate pollen evolving between *Stylochaeton* and the *Spathicarpeae*, in association with loss of perigone, further strengthening this important clade. Inaperturate pollen in the *Spathiphyllae* and *Anadendrum* would then be homoplastic. A further point here is that V. Tarasevich (pers. comm.) has suggested on the basis of TEM studies that *Spathiphyllum* pollen is in fact multi-aperturate.

The internal topology of our subfamily *Aroideae* concept remains largely unresolved above the tribal level and is a problem to which future phylogenetic studies should be devoted. We have, for convenience, recognized an informal paraphyletic "Perigoniatae *Aroideae*" and a monophyletic "Aperigoniatae *Aroideae*", the latter being a strong clade as noted earlier. Our analysis has thus not made very much further progress in clarifying the relationships of the tribes of the Englerian subfamilies *Aroideae*, *Philodendroideae* and *Colocasioideae*. Under the influence of the molecular studies of French et al. (French, Chung & Hur in press), we have adopted Grayum's (1984, 1990) device of grouping certain tribes into informal alliances.

The *Dieffenbachia* alliance is taken directly from their results. Our analysis never associated *Spathicarpeae* and *Dieffenbachieae*, but we think this is a very interesting possibility and the molecular results give strong support to this clade.

Recognition of the Philodendron Alliance reflects the fact that both morphological and molecular analyses gave a similar result. The *Schismatoglottis* alliance is a strong clade in the molecular analysis and although not present in our analysis with *Tofieldia* as outgroup, it was commonly found in analyses with other outgroups.

The *Caladium* alliance is a novel group which emerged strongly in the molecular analysis of French et al. (French, Chung & Hur in press). In our morphological analysis the *Zomicarpeae* were problematic, failing to emerge as a monophyletic group and on the whole being associated with the clade including the *Areae*. The results of French et al. reconcile the known presence of anastomosing laticifers in *Zomicarpeae* with their occurrence in *Caladieae*, the neotropical distribution of both tribes and the possibly intermediate status of *Scaphispatha* between them. On this basis we have adopted their result for our classification. One of the consequences of this is that the old Englerian *Colocasioideae* is no longer recognized in the classification, despite the fact that it emerges consistently in our morphological analysis. This clade is associated in our analysis with the tribes *Peltandreae* and *Ariopsidae* and this larger clade is defined by the following synapomorphies: short distinct leaf basal ribs, presence of a sympodial leaf submarginal vein, thickened stamen connectives, connate stamens, presence of staminodes in the female spadix zone, and base chromosome number of $x = 14$.

The other tribes are not arranged into remain non-committal. In our analysis a consistent group is formed by *Arisarum*, *Ambrosina* and *Pistia*. With *Tofieldia* as outgroup, the *Arophyteae* also associated consistently with these three genera, although with other outgroups it emerged in a different position. French et al. (French, Chung & Hur in press) found a somewhat similar result, except that *Pistieae* grouped with the *Areae* and *Colocasieae*. We have followed their results in keeping *Pistieae* separate.

Clearly there are many possibilities for alternative topologies within the subfamily *Aroideae*. The tribes of the *Aroideae* are likely to remain, more or less as circumscribed here, as reliable taxonomic units, but it may be expected that in the future they will undergo much rearrangement. The cost of our approach is measured in redundancy in the classification since there are still many monotypic tribes. A desirable future objective would be to find partners for these solitary genera since in our opinion a classification is more useful if it emphasizes sister group relationships rather than degree of anagenesis. Monotypic tribes are a way of roughly indicating that a genus has no obvious sister group relationships. These should therefore be priority targets for improving the classification in the future.

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