

# A Comparison of Aroid Classification Systems

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## Abstract

The paper compares four systems of classification of the Araceae: Engler's original (1905-1920), M. Hotta's (1970), J. Bogner and D. Nicolson's (in press) and M. Grayum's (1990). All are compared against the backdrop of the traditional system of classification by Adolf Engler and against each other.

## Introduction

A review of the systems of classification in the Araceae between the time of Linnaeus and the modern era was presented by Nicolson (1960, 1987). The last thorough systematic treatment of the Araceae was published by Adolf Engler in *Das Pflanzenreich* (Engler, 1905, 1911, 1912, 1915, 1920a, 1920b; Engler & Krause, 1908, 1920; Krause 1908, 1913). This subfamilial classification has served as the basis for virtually all non-taxonomic studies of aroid morphology to this date. Although major subfamilial revisions of the Araceae have been published (Hotta, 1970 and Hutchinson, 1973), they have not gained wide acceptance. The system by Hotta, based primarily on the Englerian model, is probably the more natural of the two. A synopsis of the Hotta system will be presented and discussed later. The only other important treatment of the Araceae in this century was that of Lemée (1941) in his *Dictionnaire....phanerogams*. This work, published in French, is merely a version of Engler's treatment which included four genera published since Engler's treatment was published. In contrast, Hutchinson's system is an extension of the one devised by J. D.

Hooker (1883) which in turn was based on the first monograph of the family by H. Schott (1860).

Like the Schott system, Hutchinson based his classification primarily on floral morphology. However, he divided the genera not into subfamilies but into 18 tribes. Although Hutchinson's system has been used by some workers in general review papers (e.g., Marchant, 1970, 1971a, 1971b, 1972, 1974; Raven and Axelrod, 1974; Li, 1979, 1980), it has been deemed quite unnatural by modern workers of the Araceae and it will not be dealt with further.

Since no other work has been so widely accepted, it is important that a synopsis of Engler's original classification be presented here. The modified Englerian system which follows differs from the original version only by the inclusion of 14 accepted new genera published since the appearance of Engler's revision. Originally, Engler had included 107 genera arranged in eight subfamilies. These retain their original numbers in the modification presented while those added later into the system are assigned lower case letters, as in 54a, *Amauriella*. Genera added since Engler are assigned upper case letters and also bear an asterisk. With minor exceptions (see placement of *Heteroaridarum*, *Hotatarum* and *Jasarum*, more recently switched by Bogner [pers. comm.]), placement of new taxa within Engler's system is based on their assignment in "A Critical List of Aroid Genera" (Bogner, 1978). Three published genera have been added subsequent to the appearance of Bogner's list: *Furtadoa* (Hotta, 1981) and *Bognera* (Nicolson, 1984),

both in the subfamily Philodendroideae (Calloideae in Grayum, 1990) and *Anaphyllopsis* Hay in the Lasioideae.

*Lasiomorpha* was resurrected to the generic level by Hay. These have been included, using the same lettering system as for genera previously added.

Genera accepted by Engler but subsequently placed into synonymy are also indicated. The author who placed it into synonymy is added in brackets. Some of the authors of Engler's generic names have been changed to reflect proper nomenclature.

### The Subfamilial Classification of the Araceae by Engler (1905-1920)

#### Subfamily I. POTHOIDEAE Engl.

(Properly ACOROIDEAE, according to the rules of nomenclature when *Acorus* is included.)

- Tribe 1. POTHEAE Engl. (1. *Pothos* L., 2. *Pothoidium* Schott, \*2A. *Pedicellarum* M. Hotta, 3. *Anadendrum* Schott (as *Anadendron*), 3a. *Epipremnopsis* Engl. = *Amydrium* [Nicolson])
- Tribe 2. HETEROPSIDEAE Engl. (4. *Heteropsis* Kunth)
- Tribe 3. ANTHURIEAE Engl. (5. *Anthurium* Schott)
- Tribe 4. CULCASIEAE Engl. (6. *Culcasia* P. Beauv.)
- Tribe 5. ZAMIOCULCADEAE Engl. (7. *Zamioculcas* Schott, 8. *Gonatopus* Hook. f.)
- Tribe 6. ACOREAE Engl. (9. *Acorus* L. = *Acoraceae*, 10. *Gymnostachys* R. Br.)

#### Subfamily II. MONSTEROIDEAE Engl.

- Tribe 1. MONSTEREAE Engl. (11. *Rhaphidophora* Hassk. (as *Rhaphidophora*) Engl. 12. *Afrorhaphidophora* Engl. = *Rhaphidophora* [Hepper], 13. *Epipremnum* Schott, 14. *Scindapsus* Schott, 15. *Stenospermation* Schott (as *Stenospermationium*), 16. *Rhodospatha* Poepp., 17. *Anepsias* Schott = *Rbo-*

*dospatha* [Croat], 18. *Monstera* Adans., 19. *Alloschemone* Schott, 20. *Amydrium* Schott)

- Tribe 2. SPATHIPHYLLEAE Engl. (21. *Spathiphyllum* Schott, 22. *Holochlamys* Engl.)

#### Subfamily III. CALLOIDEAE Schott

- Tribe 1. SYMPLOCARPEAE Engl. (Appropriately now ORONTIEAE) (23. *Lysichiton* Schott (as *Lyschitum*) 24. *Symplocarpus* Salisb., 25. *Orontium* L.)

- Tribe 2. CALLEAE Schott (26. *Calla* L.)

#### Subfamily IV. LASIOIDEAE Engl.

- Tribe 1. LASIEAE Engl. (27. *Cyrtosperma* Griff., \*27A. *Lasiomorpha* Schott [Hay] (1989), 28. *Lasia* Lour. 29. *Anaphyllum* Schott, 29A. *Anaphyllopsis* Hay, 30. *Podolasia* N. E. Brown, 31. *Urospatha* Schott [Bogner], (1988, 1989) 32. *Dracontioides* Engl., 33. *Echidnium* Schott = *Dracontium* [Bogner], 34. *Dracontium* L., \*34A. *Pycnospatha* Thorel ex Gagnep.)

- Tribe 2. AMORPHOPHALLEAE Engl. (Now correctly THOMSONIEAE) (35. *Pseudohydrosme* Engl., 36. *Plesmonium* Schott = *Amorphophallus* [Bogner], 37. *Anchomanes* Schott, 38. *Thomsonia* Wall. = *Amorphophallus* [Bogner, Mayo & Sivadasan], 39. *Pseudodracontium* N. E. Brown, 40. *Amorphophallus* Blume)

- Tribe 3. NEPHTHYTIDEAE Engl. (41. *Nephtytis* Schott, 42. *Cercestis* Schott, 43. *Rhaptophyllum* N. E. Brown = *Cercestis* [Bogner])

- Tribe 4. MONTRICHARDIEAE Engl. (44. *Montrichardia* Crüger)

#### Subfamily V. PHILODENDROIDEAE Engl.

- Tribe 1. PHILODENDREAE Schott

SubTribe 1. HOMALOMENINAE Schott, (\*45A. *Furta-doa* M. Hotta 45. *Homalomena* Schott, 46. *Diandriella* Engl. = *Homalomena* [Bogner])



Fig. 1. *Cercestis kamerunianus* N.E. Br. in Dyer, Croat 53498. Nigeria. Photo by T. B. Croat.

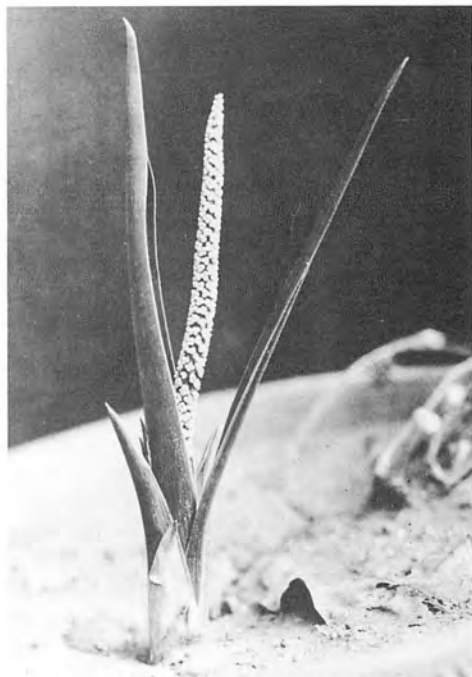


Fig. 2. *Mangonia uruguayana* (Hicken) Bogner, F. Felippone s.n. (type), Uruguay. Photo by F. Felippone.



Fig. 3. *Calla palustris* L., de Graaf 508. Photo by A. de Graaf.



Fig. 4. *Chlorospatha croatiama* Grayum, Croat 67109, Panama. Photo by T. B. Croat.

Subtribe 2. SCHISMATOG-  
LOTTIDINAE Schott (47. *Schis-  
matoglottis* Zoll. & Mor., 48.  
*Bucephalandra* Schott, \*48A.  
*Phymatarum* M. Hotta, 49. *Ari-  
darum* Ridley, \*49A. *Heteroari-  
darum* M. Hotta, \*49B. *Hotta-  
rum* Bogner & Nicolson, 50.  
*Piptospatha* N. E. Brown, 51.  
*Microcasia* Beccari = *Buceph-  
alandra* [Bogner])

Subtribe 3. PHILODEN-  
DRINAE Schott (52. *Philoden-  
dron* Schott [Krause (1913) rec-  
ognized *Thaumatophyllum*  
Schott, now = *Philodendron*  
[Bunting], without numbering it  
or putting it in a key], 53.  
*Philonotion* Schott = *Schisma-  
toglottis* [Bunting])

Tribe 2. ANUBIADEAE Engl. (54A.  
*Amauriella* Rendle = *Anubias*  
[Bogner], 54B. *Anubias* Schott)

Tribe 2A. BOGNEREAE Mayo & Ni-  
colson (\*54A. *Bognera* Mayo  
& Nicolson)

Tribe 3. AGLAONEMATEAE Engl. (55.  
*Aglanonema* Schott, 56.  
*Agladodorum* Schott)

Tribe 4. DIEFFENBACHIEAE Engl. (57.  
*Dieffenbachia* Schott)

Tribe 5. ZANTEDESCHIEAE Engl. (58.  
*Zantedeschia* Spreng.)

Tribe 6. TYPHONODOREAE Engl. (59.  
*Typhonodorum* Lindl.)

Tribe 7. PELTANDREAE Engl. (60. *Pel-  
tandra* Raf.)

### Subfamily VI. COLOCASIOIDEAE Engl.

Tribe 1. COLOCASIEAE Engl.

Subtribe 1. STEUDNERINAE  
Engl. & K. Kr. (61. *Stuednera*  
K. Koch, 62. *Remusatia* Schott,  
63. *Gonatanthus* Klotzsch

Subtribe 2. HAPALININAE  
Engl. & K. Kr. (64. *Hapaline*  
Schott)

Subtribe 3. CALADIINAE  
Engl. & K. Kr. (65. *Caladiopsis*  
Engl. = *Chlorospatha* [Madi-  
son], 66. *Caladium* Vent., \*66A.

*Jasarum* Bunting, 67. *Aphyl-  
larum* S. Moore, = *Caladium*  
[Bogner & Mayo] 68. *Chlorospa-  
tha* Engl., 69. *Xanthosoma*  
Schott)

Subtribe 4. COLOCASII-  
NAE Schott (70. *Colocasia*  
Schott)

Subtribe 5. ALOCASIINAE  
Schott (71. *Alocasia* (Schott) G.  
Don, 72. *Schizocasia* Engler =  
*Xenophya* [Nicolson] = *Alocasia*  
[A. Hay])

Tribe 2. SYNGONIEAE Engl. (73. *Por-  
phyrospatha* Engl. = *Syngo-  
nium* [Croat], 74. *Syngonium*  
Schott)

Tribe 3. ARIOPSIDEAE Engl. (75. *Ariop-  
sis* Nimmo ex J. Graham)

### Subfamily VII. AROIDEAE Engl.

Tribe 1. STYLOCHAETONIEAE Schott  
(76. *Stylochaeton* Lepr. as *Sty-  
lochiton*)

Tribe 1A. AROPHYTEAE Bogner (\*76A.  
*Carlephyton* Jum., \*76B. *Colle-  
togyne* S. Buchet \*76C. *Aro-  
phyton* Jum.)

Tribe 2. ASTEROSTIGMATEAE Schott  
(77. *Mangonia* Schott, 78. *And-  
romyca* A. Rich. = *Aster-  
ostigma* [Bogner], 79. *Tac-  
carum* Brongn. ex Schott, 80.  
*Asterostigma* Fisch. & Mey., 81.  
*Synandrospadix* Engl., 82 .  
*Spathantheum* Schott, 83.  
*Gorgonidium* Schott, 84.  
*Gearum* N. E. Brown, 85. *Spath-  
icarpa* Hook.)

Tribe 3. PROTAREAE Engl. (86. *Prota-  
rum* Engl.)

Tribe 4. CALLOPSIDEAE Engl. (87. *Cal-  
lopsis* Engl.)

Tribe 5. ZOMICARPEAE Engl. (88.  
*Scaphispatha* Brongn. ex  
Schott, 89. *Xenophya* Schott =  
*Alocasia* [Hay], 90. *Zomicarpa*  
Schott, 91. *Zomicarpella* N. E.  
Brown, \*91A. *Filarum* Nicolson,  
92. *Ulearum* Engl.)

Tribe 6. AREAE Engl.

Subtribe 1. ARINAE Schott (93. *Arum* L., 94. *Dracunculus* Schott, 95. *Helicodicerus* Schott, 96. *Therriophonum* Blume, 97. *Typhonium* Schott, 98. *Sauromatum* Schott, 99. *Eminium* (Blume) Schott, 100. *Biarum* Schott)

Subtribe 2. ARISARINAE Schott (101. *Arisarum* Targ.-Tozz.)

Subtribe 3. ARISAEMATINAE Engl. (102. *Arisaema* Mart.)

Subtribe 4. PINELLIINAE Schott (103. *Pinellia* Ten.)

Subtribe 5. AMBROSININAE Schott (104. *Ambrosina* Bassi)

Subtribe 6. CRYPTOCORYNINAE Schott (105. *Lagenandra* Dalzell, 106. *Cryptocoryne* Fisch. ex Wydl.)

#### **Subfamily VIII. PISTIOIDEAE Engl.** (107. *Pistia* L.)

#### **Recent Revisions of the Subfamilial Classification of the Araceae**

It is important to give recognition to the work of a small group of active researchers working in different parts of the world. These include J. Bogner (Munich), J. C. French & P. B. Tomlinson (Rutgers and Harvard Forest, respectively), M. H. Grayum (formerly of Univ. of Massachusetts, now Missouri Botanical Garden), A. Hay, (Royal Botanic Gardens, Sydney), W. Hettterscheid (Holland), M. Madison (formerly of Selby Gardens), S. J. Mayo & P. Boyce (Kew), D. H. Nicolson (Smithsonian) and M. Serebryanyi (Moscow). Bogner, Mayo & Boyce are currently completing the Araceae treatment for K. Kubitzki's *Families and Genera of Flowering Plants*. Recently two major subfamilial classifications were completed (Grayum, 1990; Bogner & Nicolson, in press). With the permission of the authors, both of these

systems will be presented here in synoptic form. These, as well as the system of Hotta, will be compared with Engler's classification. All of these systems have benefited from a substantial amount of information not available to Engler. This included extensive surveys of the anatomy (Solereeder & Meyer, 1928; Cheadle, 1942; Metcalfe, 1967), including the extensive surveys of vascular stem patterns by French and Tomlinson (1980, 1981a, 1981b, 1981c, 1981d, 1983), and floral anatomy (Eyde et al., 1967) as well as leaf blade nervature (Ertl, 1932), embryology (Jüssen, 1928), and of seedling morphology (Tillich, 1985).

Recent investigations by J. C. French and his associates have provided surveys on patterns of anther endothelial wall thickenings (French, 1986a), ovular vasculature (French, 1986b), stamen vasculature (French, 1986c), structure of ovular and placental trichomes (French, 1987a), the occurrence of sclerotic hypodermis in roots (French, 1987b), the occurrence of resin canals in roots (French, 1987c), the presence of anastomosing laticifers (French, 1988), and the presence of latex particles (Fox & French, in prep.). A single survey or the study of a single character rarely provides conclusive evidence for the correctness of the placement of any member in the suprageneric system of classification; however, the accumulation of evidence from these broad surveys often suggests certain evolutionary trends which swing the evidence toward adding or removing elements of any group of plants.

Plant chemistry, poorly known in Engler's time, has been surveyed by a number of workers including Hegnauer (1963), Gibbs (1974), Fairbrothers et al. (1975), Harris & Hartley (1980), Williams et al. (1981), Dahlgren & Clifford (1982), Harborne (1982) and Fox & French (1988), as well as others. A great deal has been learned about the cytology of the family including extensive surveys by Jones (1957), Marchant (1970, 1971a,

1971b, 1972, 1974), and especially Petersen (1989). In addition, the important subject of continental drift (Raven & Axelrod, 1974; Schuster, 1976) has been helpful in dealing with the intricate phytogeographical problems posed by this wide-ranging family.

Other important work includes surveys of palynology by Thanikaimoni (1969) and by Grayum (1984). Important surveys of molecular systematics in the Araceae concentrating on restriction site variation in chloroplast DNA are currently being carried out by J. C. French. There is already preliminary evidence that these surveys will be rich in information concerning the evolution of the Araceae. All of these listed above, coupled with many modern revisions of aroid taxa have combined to yield an important body of useful knowledge to modern-day revisionists of the Araceae.

All three of the modern systems demonstrate significant differences from that of Engler. The system by Hotta will be presented first, followed by the system of Bogner & Nicolson, and finally by that of Grayum.

### The Subfamilial Classification of the Araceae by Hotta (1970)

The following system by Hotta is based solely on genera in Eastern Asia and Malesia. It deals with members of all of Engler's subfamilies of Araceae but includes only 39 genera (fewer if one accepts the synonymization of those genera indicated). It cannot thus be considered a thorough revision of the family because there are many tribes which are restricted to Africa or the Americas which were not considered (though some were included in synonymy). The system contains six subfamilies, but only 14 tribes, because he was not dealing with the entire family.

### A Synopsis of Hotta's System

#### Subfamily I. ACOROIDEAE

Tribe 1. ACOREAE (*Acorus* [also *Gymnostachys* in this subfamily,

though out of his study area])

#### Subfamily II. POTHOIDEAE

Tribe 1. POTHEAE (*Pothos*, *Pothodium*)

Tribe 2. MONSTEREAE (*Rhabdophora*, *Anadendrum*, *Amydrium*, *Scindapsus*)

Tribe 3. SPATHIPHYLLEAE (*Spathiphyllum*, *Holochlamys*)

#### Subfamily III. LASIOIDEAE

Tribe 1. SYMPLOCARPEAE (*Lysichiton*, *Symplocarpus*)

Tribe 2. LASIEAE (*Cyrtosperma*, *Lasia*, *Pycnospatha*)

Tribe 3. AMORPHOPHALLEAE [Thomsonieae] (*Thomsonia* = *Amorphophallus*, *Pseudodracontium*, *Amorphophallus*)

#### Subfamily IV. PHILODENDROIDEAE

Tribe 1. CALLEAE (*Calla*)

Tribe 2. AGLAONEMATEAE (*Aglaonema*, *Aglaodorum*)

Tribe 3. HOMALOMENEAE (*Homalomena*, *Diandriella* = *Homalomena* [fide Bogner & Nicolson])

Tribe 4. SCHISMATOGLOTTIDEAE (*Schismatoglottis*, *Phymatarum*, *Bucephalandra*, *Microcasia* = *Bucephalandra*, *Aridarum*, *Piptospatha*)

Tribe 5. COLOCASIEAE (*Remusatia*, *Gonatanthus*, *Hapaline*, *Colocasia*, *Alocasia*, *Schizocasia* = *Xenophya* = *Alocasia*)

#### Subfamily V. AROIDEAE

Tribe 1. AREAE (*Typhonium*, *Arisaema*, *Pinellia*)

Tribe 2. CRYPTOCORYNEAE (*Cryptocoryne*)

#### Subfamily VI. PISTIOIDEAE

(*Pistia*)

### Discussion

Although Hotta's arrangement of subfamilies is in some ways more radical than that of Bogner & Nicolson, he does not separate *Acorus* from the family, but places it in its own subfamily with *Gymnostachys*. However, the latter is out of the range of Hotta's study. Hotta departs radically from Bogner & Ni-

colson in merging the subfamily Monsteroideae into the Pothoideae. Six characteristics are included as justification for this, including: 1) a tendency toward a climbing habit; 2) the presence of vessels in the stems; 3) reticulated leaf blade venation; 4) the common occurrence of geniculate petioles; 5) the presence of bisexual flowers; and 6) the unreliability of the character involving the presence or absence of trichosclereids which has been used by Engler to separate the two subfamilies. He also specifically states that the tribe Zamioculcadeae is not closely related to the *Pothos* and *Rhaphidophora* group and places it with the subfamily Lasioideae (not actually treating it, but including it in synonymy).

In addition, Hotta also departs further from the typical Englerian system in: 1) eliminating the subfamily Calloideae; 2) submerging *Lysichiton*, *Symplocarpus* and *Orontium* (though out of the range of his study), in his tribe Symplocarpeae in the subfamily Lasioideae; and 3) by placing *Calla* in the tribe Calleae at the head of the subfamily Philodendroideae. He also placed *Dracontium* from the Lasioideae into synonymy under his tribe Amorphophalleae (now Thomsonieae).

The Philodendroideae in Hotta's treatment remains substantially intact with respect to the Asian genera. He does not deal with many of the American and African tribes of the subfamily. Nevertheless, the subfamily is radically altered by the inclusion of *Calla* as tribe Calleae, the tribe Asterostigmatae (from Engler's subfamily Aroideae) and the entire subfamily Colocasioideae as tribe Colocasieae. Though Hotta treats only the tribe Colocasieae, he synonymizes the entire subfamily Colocasioideae under the subfamily Philodendroideae. He also synonymizes Engler's tribe Philodendreae.

Hotta's subfamily Aroideae deals with only a few genera. Aside from removing the Asterostigmatae (as mentioned above), he basically follows Engler's classification for the included genera he treats but raises the subtribe Cryptoco-

ryninae to tribal level. He makes no change in the subfamily Pistioideae.

Hotta was well ahead of most aroid taxonomists in proposing major changes in Engler's system. Some of these proposed changes have been adopted by Grayum.

### **The Subfamilial Classification of the Araceae by Bogner & Nicolson (*in press*)**

This system was first presented at the Aroid Workshop at Harvard Forest in May 1984 and was submitted as a chapter (as was the present paper) of "The Biology of the Araceae," a much-cited, but now defunct work to have been published by Cornell University Press. After the collapse of this proposed book, the paper was accepted for publication in *Willdenowia*, where it will soon appear. The classification system is based on more than two decades of critical observations by both authors, but especially on the long-standing and intense interest of the first author. Bogner has cultivated and observed most aroid genera at the Botanical Garden in Munich. His persevering interest in obtaining live material to study has carried him to most parts of the world (at his own expense) and has given him not only the world's best generic collection of Araceae, but also an insight into the taxonomy of the family not afforded many of his predecessors or contemporaries. Nicolson, owing to his long career with Araceae (beginning 25 years ago in Asia), his intense bibliographic interest coupled with language translation skills and a keen interest in nomenclatural problems, makes him a unique addition to the team. The system contains nine subfamilies, 35 tribes and 13 subtribes.

### **A Synopsis of Bogner & Nicolson's System**

#### **Subfamily 1. GYMNSTACHYDOIDEAE**

Tribe 1. Gymnostachydeae (1. *Gymnostachys*)

**Subfamily II. POTHOIDEAE**

Tribe 1. Potheae (2. *Pothos*, 3. *Pedicellarum*, 4. *Pothoidium*)

**Subfamily III. MONSTEROIDEAE**

Tribe 1. ANADENDREAE (5. *Anaden-drum*)

Tribe 2. MONSTEREAE (6. *Amydrium*, 7. *Rhaphidophora*, 8. *Epi-premnum*, 9. *Scindapsus*, 10. *Alloschemone*, 11. *Steno-spermatum*, 12. *Rhodospatha*, 13. *Monstera*)

Tribe 3. HETEROPSIDEAE (14. *Heter-opsis*)

Tribe 4. SPATHIPHYLLEAE (15. *Spathiphyllum*, 16. *Holochlamys*)

**Subfamily IV. CALLOIDEAE**

Tribe 1. Calleae (17. *Calla*)

**Subfamily V. LASIOIDEAE**

Tribe 1. ORONTIEAE (18. *Lysichiton*, 19. *Symplocarpus*, 20. *Orontium*)

Tribe 2. ANTHURIEAE (21. *Anthurium*)

Tribe 3. LASIEAE

Subtribe 1. DRACONTIINAE (22. *Cyrtosperma*, 23. *Lasiomorpha*, 24. *Lasia*, 25. *Anaphyllum*, 26. *Anaphyllopsis*, 27. *Podolasia*, 28. *Urospatha*, 29. *Dracontioides*, 30. *Dracontium*)

Subtribe 2. PYCNOSPATHTHINAE (31. *Pycnospatha*)

Tribe 4. ZAMIOCULCADEAE (32. *Zamioculcas*, 33. *Gonatopus*)

Tribe 5. CALLOPSIDEAE (34. *Callopsis*)

Tribe 6. NEPHTHYTIDEAE (35. *Pseudohydrosme*, 36. *Anchomanes*, 37. *Nephtythis*, 38. *Cercestis*)

Tribe 7. CULCASIEAE (39. *Culcasia*)

Tribe 8. MONTRICHARDIEAE (40. *Mon-trichardia*)

**Subfamily VI. PHILODENDROIDEAE**

Tribe 1. PHILODENDREAE

Subtribe 1. HOMALOMENINAE (41. *Furtadoa*, 42. *Homalomena*)

Subtribe 2. SCHISMATOGLOTTIDINAE (43. *Schisma-toglottis*, 44. *Piptospatha*, 45.

*Hottarum*, 46. *Bucephalandra*, 47. *Phymatarum*, 48. *Ari-darum*, 49. *Heteroaridarum*)

Subtribe 3. PHILODENDRINAE (50. *Philodendron*)

Tribe 2. ANUBIADEAE (51. *Anubias*)

Tribe 3. BOGNEREAE (52. *Bognera*)

Tribe 4. AGLAONEMATEAE (53. *Aglaonema*, 54. *Aglaodorum*)

Tribe 5. DIEFFENBACHIEAE (55. *Dieff-fenbachia*)

Tribe 6. ZANTEDESCHIEAE (56. *Zantedeschia*)

Tribe 7. TYPHONODOREAE (57. *Typh-nodorum*)

Tribe 8. PELTANDREAE (58. *Peltandra*)

**Subfamily VII. COLOCASIOIDEAE**

Tribe 1. CALADIEAE (59. *Xanthosoma*, 60. *Chlorospatha*, 61. *Caladium*, 62. *Scaphispatha*, 63. *Jasarum*)

Tribe 2. STEUDNERAE

SubTribe 1. STEUDNERI-NAE (64. *Steudnera*, 65. *Remusatia*, 66. *Gonatantbus*)

SubTribe 2. HAPALIN-INA (67. *Hapaline*)

Tribe 3. PROTAREAE (68. *Protarum*)

Tribe 4. COLOCASIEAE (69. *Colocasia*, 70. *Alocasia*)

Tribe 5. SYNGONIEAE (71. *Syngon-nium*)

Tribe 6. ARIOPSIDEAE (72. *Ariopsis*)

**Subfamily VIII. AROIDEAE**

Tribe 1. STYLOCHAETONIEAE (73. *Sty-lochaeton*)

Tribe 2. AROPHYTEAE (74. *Carle-phyton*, 75. *Colletogyne*, 76. *Arophyton*)

Tribe 3. SPATHICARPEAE (77. *Mangonia*, 78. *Taccarum*, 79. *Aster-ostigma*, 80. *Gorgonidium*, 81. *Synandrospadix*, 82. *Gearum*, 83. *Spathantbeum*, 84. *Spathi-carpa*)

Tribe 4. ZOMICARPEAE (85. *Zomi-carpa*, 86. *Filarum*, 87. *Zomi-carpella*, 88. *Ulearum*)

Tribe 5. THOMSONIEAE (89. *Amor-phoballus*, 90. *Pseudodra-contium*)



## Tribe 6. AREAE

Subtribe 1. ARINAE (91. *Arum*, 92. *Dracunculus*, 93. *Helicodiceros*, 94. *Theriophonum*, 95. *Typhonium*, 96. *Sauromatum*, 97. *Eminium*, 98. *Biarum*)

Subtribe 2. ARISARINAE (99. *Arisarum*)

Subtribe 3. ARISAEMATINAE (100. *Arisaema*)

Subtribe 4. ATHERURINAE (101. *Pinellia*)

Subtribe 5. AMBROSININAE (102. *Ambrosina*)

Subtribe 6. CRYPTO-CORYNINAE (103. *Lagenandra*, 104. *Cryptocoryne*)

**Subfamily IX. PISTIOIDEAE**

(105. *Pistia*)

**Discussion**

Bogner & Nicolson's system, with 105 genera, reduces the number of genera from the 110 recognized by Bogner (1978). Those genera reduced to synonymy since the 1978 paper are: *Thomsonia* and *Plesmonium* = *Amorphophallus*, *Echidnium* = *Dracontium*, *Rhekto-phyllum* = *Cercestis*, *Diandriella* = *Homalomena*. Two other genera reduced to synonymy in recent years are: *Caladiopsis* = *Chlorospatha* (Madison, 1981), and *Porphyrospatha* = *Syngonium* (Croat, 1981).

Five genera have been added since Bogner's 1978 list was published in *Aroideana*. These include the reinstatement of *Alloschemone* next to *Scindapsus* in the Monstereae, the incorporation of *Bognera* following the tribe Anubiadeae in the subfamily Philodendroideae, *Furtadoa* in the subtribe Homalomeninae of tribe Philodendreae, and *Lasiomorpha* and *Anaphyllopsis* in the subtribe Dracontiinae of the tribe Lasieae.

The most significant changes in the revised system by Bogner & Nicolson, as outlined above, include the following: 1) the removal of *Acorus* from the family; 2)

the separation of *Gymnostachys* from the Pothoideae into the subfamily Gymnostachydoideae; 3) the transfer of the Anthurieae from the Pothoideae to the Lasioideae; 4) the Heteropsidae from Pothoideae to Monsteroideae; 5) the Orontieae from the Calloideae to Lasioideae; 6) the Thomsonieae from the Lasioideae to Aroideae; and 7) the Callopsideae from Aroideae to Lasioideae.

The suggestion that *Acorus* was not a good member of the Pothoideae was already accepted by several other authors (Eyde et al., 1967; Hotta, 1970; Thorne, 1976, 1983), but its exclusion from the Araceae was first suggested by Deyl (1955) and later by Grayum (1984, 1987) and Tillich (1985). Other significant changes involved major realignments in the Pothoideae and Lasioideae.

Many alterations involved changes in rank within the subfamilies or the movement of a few genera from one established subfamily to another. *Anaden-drum* was moved from tribe Potheae in the subfamily Pothoideae to its own tribe, the Anadendreae in the Monsteroideae. Also transferred from the Pothoideae were the tribes Zamioculcadeae and Culcasieae, which were placed in the subfamily Lasioideae. Other genera transferred were *Protarum* (tribe Protar-eae) to the Colocasioideae, and *Scaphispatha* (tribe Zomicarpeae) from the subfamily Aroideae to the tribe Caladieae in the subfamily Colocasioideae (Bogner, 1980). Earlier (Bogner 1980a), *Jasarum* was moved from the subtribe Alocasiinae to the tribe Caladieae.

Some subtribes were merged, such as the Alocasiinae into Colocasiinae. In other cases, new subtribes were created, such as in the Lasioideae, with the subtribe Dracontiinae of the Lasieae accomodating all genera in the tribe Lasieae except *Pycnospatha*. The new subtribe Pycnospathinae contains only the latter genus (Bogner, 1973).

The subtribe Steudnerinae in the Colocasioideae was elevated to tribal status

(Stuednereae) and split into two subtribes which are the Steudnerinae with *Stuednera*, *Remusatia* and *Gonatanthus* and the Hapalininae with *Hapaline*. Also elevated was the subtribe Caladiinae in the subfamily Colocasioideae, which became the tribe Caladieae. It was also shifted to the first tribe of the subfamily.

The remainder of the changes incorporated by Bogner & Nicolson involved changing positions of genera within existing tribes or subtribes. These include movement of 1) *Amydrium* closer to *Rhaphidophora* in the tribe Monstereae; 2) *Piptospatha* from the last position in the subtribe Schismatoglottidinae (subfamily Philodendroideae) to the second position following *Schismatoglottis*; and 3) moving *Hottarum* from the next to the last position in subtribe Schismatoglottidinae to the third position following *Piptospatha*.

Overall the proposed changes in the Englerian system were generally conservative ones which have definitely resulted in an improvement in the subfamilial classification.

### The Subfamilial Classification of the Araceae by Grayum (1990)

Working concurrently with Bogner & Nicolson yet independently from them, M. H. Grayum, under the direction of J. Walker at the University of Massachusetts (Amherst), prepared his own subfamilial classification of the family. His research, though concentrating on the first rigorous survey of pollen using scanning-electron microscopy, also involved the most thorough analysis of all morphological character states since the time of Engler and of the three systems analyzed, his is the only one which is accompanied by a complete explanation of the rationale behind the placement of the taxa involved.

Grayum has proposed the most radical alterations in the subfamilial classification of the Araceae to date. The system contains five subfamilies, 40 tribes and 13 subtribes.

## A Synopsis of Grayum's System

### I. Subfamily POTHOIDEAE

1. Tribe GYMNOSTACHYDEAE (*Gymnostachys*)
2. Tribe SPATHIPHYLLEAE (*Spathiphyllum*, *Holochlamys*)
3. Tribe ANTHURIEAE (*Anthurium*)
4. Tribe POTHEAE (*Pothos*, *Pedicularum*, *Pothoidium*)
5. Tribe ANADENDREAE (*Anadendrum*)
6. Tribe MONSTEREAE
  - a. Subtribe HETEROPSIDINAE (*Heteropsis*)
  - b. Subtribe MONSTERINAE (*Rhaphidophora*, *Monstera*, *Amydrium*, *Epipremnum*, *Scindapsus*, *Alloschemone*, *Stenospermatum*, *Rhodospatha*)
7. Tribe ZAMIOCULCADEAE (*Zamioculcas*, *Gonatopus*)

### II. Subfamily CALLOIDEAE (Referred to later in this paper for comparative purposes only as "Philodendroideae")

- A. *Calla* Alliance
  8. Tribe CALLEAE (*Calla*)
- B. *Nephtytis* Alliance
  9. Tribe NEPHTHYTIDEAE (*Nephtytis*, *Anchomanes*, *Pseudohydrosme*)
  10. Tribe CALLOPSIDEAE (*Calloopsis*, *Ulearum*, *Filarum*, *Zomicarpella*)
  11. Tribe MONTRICHARDIEAE (*Montrichardia*)
- C. *Aglaonema* Alliance
  12. Tribe ANUBIADEAE (*Anubias*)
  13. Tribe ZANTEDESCHIEAE (*Zantedeschia*)
  14. Tribe AGLAONEMATEAE (*Aglaonema*, *Aglaodorum*)
  15. Tribe SPATHICARPEAE (*Mangonia*, *Asterostigma*, *Synandrospadix*, *Taccarum*, *Gorgonidium*, *Gearum*, *Spathanthbeum*, *Spathicarpa*)
  16. Tribe DIEFFENBACHIEAE (*Dieffenbachia*)
  17. Tribe BOGNEREAE (*Bognera*)
- D. *Peltandra* Alliance

18. Tribe PELTANDREAE (*Peltandra*, *Typhonodorum*)
19. Tribe AROPHYTEAE (*Arophyton*, *Carlephyton*, *Colletogyne*)
20. Tribe SCHISMATOGLOTTIDEAE (*Schismatoglottis*, *Piptospatha*, *Bucephalandra*, *Phymatarum*, *Aridarum*, *Heteroaridarum*, *Hotatarum*)

E. *Philodendron* Alliance

21. Tribe CULCASIEAE (*Culcasia*)
22. Tribe CERCESTIDEAE (*Cercestis*)
23. Tribe HOMALOMENEAE (*Furtadoa*, *Homalomena*)
24. Tribe PHILODENDREAE (*Philodendron*)

III. Subfamily COLOCASIOIDEAE

25. Tribe ZOMICARPEAE (*Zomicarpa*)
26. Tribe COLOCASIEAE
  - a. Subtribe PROTARINAE (*Protarum*)
  - b. Subtribe STEUDNERINAE (*Steudnera*)
  - c. Subtribe REMUSATIINAE (*Remusatia*, *Gonatanthus*)
  - d. Subtribe COLOCASIINAE (*Colocasia*, *Alocasia*)
27. Tribe CALADIEAE Schott
  - a. Subtribe JASARINAE (*Jasarum*)
  - b. Subtribe SCAPHISPATHINAE (*Scaphispatha*)
  - c. Subtribe CALADIINAE (*Caladium*, *Xanthosoma*, *Chlorospatha*, *Aphyllarum*)
  - d. Subtribe SYNGONIINAE (*Syngonium*)
  - e. Subtribe HAPALININAE (*Hapaline*)

IV. Subfamily LASIOIDEAE

28. Tribe SYMPLOCARPEAE (*Symplocarpus*, *Lysichiton*)
29. Tribe ORONTIEAE (*Orontium*)
30. Tribe LASIEAE
  - a. Subtribe DRACONTIINAE (*Anaphyllopsis*\*, *Cyrtosperma*, *Lasia*, *Lasiomorpha*\*, *Anaphyllum*, *Podolasia*, *Urospatha*, *Dracontiodes*, *Dracontium*)
  - b. Subtribe PYCNOSPATHINAE (*Pycnospatha*)

31. Tribe STYLOCHAETONIEAE (*Stylochaeton*)

V. Subfamily AROIDEAE

32. Tribe THOMSONIEAE (*Pseudodracontium*, *Amorphoballus*)
33. Tribe ARISAREAE (*Arisarum*)
34. Tribe PINELLIEAE (*Pinellia*)
35. Tribe PISTIEAE (*Pistia*)
36. Tribe CRYPTO-CORYNEAE (*Cryptocoryne*, *Lagenandra*)
37. Tribe AMBROSINEAE (*Ambrosina*)
38. Tribe ARIOPSIDEAE (*Ariopsis*)
39. Tribe ARISAEMATEAE (*Arisaema*)
40. Tribe AREAE (*Arum*, *Dracunculus*, *Helicodiceros*, *Theriophonum*, *Typhonium*, *Sauromatum*, *Eminium*, *Biarum*)

\* These genera added since 1990 paper (Grayum, pers. comm.).

Discussion

In agreement with Hotta (1970), Grayum also merges the Pothoideae and Monsteroideae and places the tribes Calleeae, Spathicarpeae and Zantedeschieae in the Calloideae (previously named Philodendroideae). Unlike Hotta, he leaves the tribe Zamioculcadeae in the Pothoideae. Similarities with the system of Hotta end here, but Grayum makes other radical departures from the Englerian system. Because the changes made by Grayum in Engler's system are many, the discussion will proceed section by section.

POTHOIDEAE

Grayum's system appeared originally in his Ph.D. thesis (Grayum, 1984) and was subsequently published with some modifications (Grayum, 1990). This paper will deal primarily with the latest revision. Grayum considers the linear sequencing of his taxa of no significance. Although Grayum (1984) removed *Gymnostachys* from Engler's Acoreae to its own subfamily, the *Gymnostachydoideae*, his 1990 revision retains it in the

subfamily Pothoideae and the tribe Gymnostachydeae. With the subfamily Monsteroideae merged with the Pothoideae, *Anadendrum* is retained in the tribe Potheae and placed in its own tribe (Anadendreae). The tribe Heteropsidae is reduced to a subtribe of the Monstereae.

### **CALLOIDEAE sensu Engler**

The subfamily Calloideae of Schott is disbanded, with *Symplocarpus*, *Lysichiton* and *Orontium* comprising two subtribes in the tribe Orontieae. Philodendroideae, for reasons of priority, is renamed as subfamily Calloideae.

### **PHILODENDROIDEAE sensu Engler CALLOIDEAE**

As redefined, the subfamily Calloideae is arranged in five major "alliances": *Calla*, *Nephtytis*, *Aglaonema*, *Peltandra*, and *Philodendron*.

The main changes within the Calloideae include a number of taxa that are added to the subfamily from other subfamilies. These include:

1. The addition of the tribe Culcasieae to the *Nephtytis* Alliance from the Pothoideae.
2. The movement of the tribe Nephtytideae from Lasioideae to the *Nephtytis* Alliance.
3. The placement of the genera *Anchomanes* and *Pseudohydrosme* of the tribe Thomsonieae (Amorphophalleae) of the Lasioideae into the tribe Nephtytideae in the *Nephtytis* Alliance. Grayum placed *Zomicarpella* in the tribe Callopsideae, but now believes (pers. comm.), as a result of Jim French's recent discovery of laticifers in *Zomicarpella*, that it really belongs in Zomicarpeae of the Colocasioideae.
4. The transfer of tribe Callopsideae from the Aroideae to the *Nephtytis* Alliance.

5. The movement of the tribe Monstreichardieae from the Lasioideae to the *Nephtytis* Alliance.
6. The movement of the tribe Spathicarpeae (Engler's Asterostigmateae) to Calloideae in the *Aglaonema* Alliance.

The *Aglaonema* Alliance is otherwise made up completely of Englerian philodendroid members with the tribes Anubiadeae, Zantedeschieae and Aglaonemateae clustered there.

The *Peltandra* Alliance finds tribes Peltandreae and Typhonodoreae merged into the former. A major change in the *Peltandra* Alliance is the transfer of tribe Arophyteae from the Aroideae.

Finally the *Aglaonema* Alliance differs radically from the Englerian system in that the entire tribe Asterostigmateae from the subfamily Aroideae is transferred to subfamily Calloideae. Grayum's *Aglaonema* Alliance underwent changes from his 1984 treatment. These include:

1. The removal of the Homalomeneae to the *Philodendron* Alliance.
2. The inclusion of tribe Dieffenbachieae, with *Dieffenbachia* only, and Bognereae, with *Bognera* only. Grayum (pers. comm.), based on unpublished investigations by Bogner, now believes that *Bognera* should be included in tribe Dieffenbachieae.

### **COLOCASIOIDEAE**

Substantial changes were also made in the subfamily Colocasioideae, the principal change being the transfer of Zomicarpeae (now to include both *Zomicarpella* and *Zomicarpa* according to Grayum, pers. comm.) from Engler's Aroideae and the recognition of two coordinate tribes, Colocasieae and Caladieae, the first in the Old World, the second in the New World (except Hapalininae). Grayum accepts two of Engler's three tribes, e.g., Colocasieae (much altered) and Syngonieae (as a subtribe), but he creates more subtribes in the Colocasioideae. The

following alterations occur in his treatment of the subfamily.

1. The tribe Ariopsidae is moved to the subfamily Aroideae.
2. The tribe Protareae is moved from the subfamily Aroideae and placed in the tribe Colocasieae as subtribe Protarinae. (Bogner & Nicolson agree with its placement in the Colocasioideae.)
3. The subtribe Steudnerinae is not moved, but the subtribe Remusatinae is segregated out with *Remusatia* and *Gonatanthus* (considered probably synonymous).
4. The subtribe Colocasiinae absorbs the subtribe Alocasiinae, while the Hapalininae is moved to tribe Caladieae.
5. *Jasarum*, added to the system since Engler's revision, is placed in its own subtribe Jasarinae at the head of the tribe Caladieae.
6. *Scaphispatha* is transferred (following Bogner) into the Colocasioideae from the tribe Zomicarpeae (subfamily Aroideae) and is placed in the Caladieae in its own subtribe.

## LASIOIDEAE

Major changes within the Lasioideae include:

1. The movement of the tribe Thomsonieae (Amorphophalleae) to the subfamily Aroideae.
2. The placement of tribes Nephthytideae and Montrichardieae in the Philodendroideae, substantially reducing the size of the subfamily Lasioideae. As already mentioned, however, three temperate genera from the tribe Orontieae are added to the Lasioideae.
3. The division of Engler's tribe Lasieae (following Bogner) into the two subtribes Dracontiinae and Pycnospathinae, with the latter containing only *Pycnospatha*.
4. The transfer of the tribe Stylochaetoniae (*Stylochaeton*) from the Aroideae to the Lasioideae.

## AROIDEAE

Perhaps the most important change in the subfamily Aroideae is the inclusion of the genus *Pistia*, which previously was generally included in its own subfamily.

Other important changes in the subfamily Aroideae include:

1. The transfer of tribe Thomsonieae (Amorphophalleae) from Lasioideae.
2. The transfer of tribe Ariopsidae from the Colocasioideae to the Aroideae.
3. The movement of tribe Stylochaetoniae to Lasioideae.
4. A shift of Zomicarpeae, Spathicarpeae, and Callopsideae to the "Philodendroideae."
5. Transfer of Protareae, which becomes subtribe Protarinae, to the Colocasioideae and breaking up of the Zomicarpeae with *Ulearum*, *Filarum* or *Zomicarpella* being incorporated in the tribe Callopsidae of subfamily Calloideae and *Zomicarpa* being placed in the Colocasioideae (as tribe Zomicarpeae). *Grayum* now (pers. comm.) would also place *Zomicarpella* here.

These changes radically alter the make-up of the subfamily Aroideae. The remainder of this subfamily, including all of the tribe Areae, survives intact. However, the subtribe Arineae is elevated to tribal status.

It is evident that Grayum has made major alterations in Engler's system of classification. Though it is not the purpose of this discourse to explain the rationale behind the many changes proposed, Grayum has made a convincing argument in most cases for the changes made. His system will no doubt be carefully considered within the next few years. Now that there are two newly proposed suprageneric classification systems, research efforts have been directed at a resolution of the differences between these two systems in an attempt to come up with a system that can be agreed upon by most aroid workers.

### General Comparisons of Three Recent Systems of Classification of the Araceae

One of the most difficult things about making the comparison of the three systems involved the subfamilies Philodendroideae and Calloideae. Because Grayum included *Calla* in the Philodendroideae and because the name Calloideae has priority, the subfamily name had to be changed. In order to avoid confusion between the Calloideae of Bogner & Nicolson (containing only *Calla*) and the Calloideae of Grayum, I will refer to Calloideae of Grayum for the purposes of this final comparison as "Philodendroideae."

All three systems outlined here indicate that at least the genus *Acorus* does not fit well into the main body of the Pothoideae. Hotta removes it, along with *Gymnostachys*, to the subfamily Acoroideae. Bogner & Nicolson, as well as Grayum, go further in rejecting it from the family all together.

Following Deyl (1955), Grayum (1984, 1987) proposed to remove *Acorus* from the Araceae into its own family. He cites 15 major characters in which *Acorus* differs from all other Araceae (including *Gymnostachys*). Tillich (1985) independently arrived at the same conclusion based on his study of aroid seedling morphology.

All three systems reflect a close relationship between Pothoideae and the Monsteroideae. Both Hotta and Grayum treat the two subfamilies as one, the Pothoideae. Bogner & Nicolson include *Anadendrum* and *Heteropsis* in the Monsteroideae and further suggest that *Amydrium* is a transitional genus (partly in that it lacks trichosclereids) which could be placed in either subfamily "depending on what characters one emphasizes in delimiting the two subfamilies." Grayum states (pers. comm.) that *Pothos* and *Pothidium* are also transitional in the same sense in that they possess trichosclereids and that *Anaden-*

*drum* and *Heteropsis* are transitional genera as well.

While Grayum sees little relationship between the Pothoideae and the subfamily Lasioideae, Bogner & Nicolson place two of Engler's original pothoid tribes in the Lasioideae, namely the Anthurieae and Zamioculcadeae. Grayum leaves both in the subfamily Pothoideae. This would appear to be one of the several more marked differences between the system of Bogner & Nicolson and that of Grayum. Both Hotta and Grayum disband the Calloideae altogether and place the Orontieae in the Lasioideae while placing the tribe Calleae in the "Philodendroideae." Bogner & Nicolson retain *Calla* in the monotypic subfamily Calloideae. They agree with the other two authors in placing *Lysichiton*, *Symplocarpus*, and *Orontium* in the Lasioideae. While Bogner & Nicolson include all three of these temperate genera in the same tribe, Grayum separates *Orontium* into its own tribe.

Aside from the placement of the Symplocarpeae in the Lasioideae, Hotta leaves the Lasioideae intact. Bogner & Nicolson agree with the transfer of Symplocarpeae, but also add to the Lasioideae the Anthurieae, Culcasieae, and the Zamioculcadeae from the Pothoideae. In addition, they transfer the Callopsideae from the Aroideae to the Lasioideae. Hotta places *Culcasia* here as well. Grayum, on the other hand, places the Culcasieae in the "Philodendroideae," moving *Anchomanes* and *Pseudohydrosme* from the Lasioideae to "Philodendroideae" as tribe Nephthyideae. He also moves the Montrichardieae and Nephthyideae to "Philodendroideae."

Despite what appears to be a lot of disagreement with the placement of many of the above-mentioned genera, Grayum, as well as Bogner & Nicolson, agree that the Culcasieae, Nephthyideae, Callopsidae, *Montrichardia* and *Anchomanes* are all related. They

just do not agree to which subfamily they belong.

In the subfamily "Philodendroideae," Hotta and Grayum agree on the inclusion of *Calla*, but Hotta broadens the subfamily substantially by including all of the Colocasioideae (i.e., at least the Asian genera he studied). The "Philodendroideae" of Grayum is substantially larger than that of Bogner & Nicolson, with 40 genera arranged in 17 tribes and five alliances. This contrasts with the 18 genera in eight tribes according to Bogner & Nicolson. The size of Grayum's "Philodendroideae" has resulted largely from the inclusion of Spathicarpeae from the subfamily Aroideae as well as the other tribes from Pothoideae and Lasioideae already mentioned. The latter include Calleae, Culcasieae, Nephthytideae, Callopsiidae, and Montricharideae.

Other major departures of Grayum from Bogner & Nicolson include the incorporation of Arophyteae and Schismatoglottideae into the "Philodendroideae." The latter is placed in the *Peltandra* Alliance. Bogner & Nicolson, on the other hand, retain Arophyteae in the Aroideae (Bogner, 1978) along with the Cryptocoryninae. Hotta also leaves Cryptocoryninae in the Aroideae, but does not deal with Arophyteae.

Hotta incorporates the Colocasioideae into the Philodendroideae while Bogner & Nicolson leave it essentially intact, except for the inclusion of Protareae from the Aroideae. Grayum's Colocasioideae differs from Bogner & Nicolson's largely in the arrangement of the tribes within the subfamily. Both treatments include the same genera with the exception of *Ariopsis* which Grayum places in the Aroideae. Grayum also moves *Jasarum* and *Scaphispatha* to their own subtribes and reduces the tribe Protareae to a subtribe of his tribe Colocasieae. Bogner & Nicolson include *Xanthosoma*, *Aphyllarum*, *Chlorospatha*, *Caladium*, *Scaphispatha*, and *Jasarum* in their tribe Caladieae while including *Colocasia* and

*Alocasia* in their tribe Colocasieae. Grayum includes the Old World genera *Colocasia* and *Alocasia* in the subtribe Colocasiinae of tribe Colocasieae and places the other four New World genera (*Caladium*, *Xanthosoma*, *Chlorospatha* and *Aphyllarum*) in his subtribe Caladiinae of tribe Caladieae along with Hapalininae.

Except for moving the tribe Asterostigmateae to the subfamily Philodendroideae, Hotta appears to have left the subfamily Aroideae intact, although he did not deal with it in great detail. The other two systems agree on the movement of Protareae to Colocasioideae as well as on the removal of the Callopsiidae. Grayum places the latter in his "Philodendroideae" while Bogner & Nicolson placed it in the Lasioideae. In addition Grayum transfers the tribe Thomsonieae (Amorphophalleae) from the Lasioideae to the Aroideae, and also the Zomicarpeae (which Bogner & Nicolson maintain) from the Aroideae partly to the Colocasioideae and partly to the *Nephthytis* Alliance. More importantly, he adds *Pistia*, thus eliminating the subfamily Pistioideae. The two systems otherwise agree except for the order of the taxa within the subfamily, which Grayum regards as of no significance.

## Conclusion

It is clear from the comparisons above that despite recent studies (or perhaps even because of them), disagreement still exists concerning the placement of taxa at all levels within the family but especially on the composition of the subfamilies. It is for this reason that no attempt will be made here to construct a description of the respective subfamilial groupings. Further work in a variety of disciplines will be needed on the more poorly known genera. It is expected that the new molecular systematics studies being carried out by James French and his colleagues from Rutgers will provide the next important source of information for a realignment of the Araceae. I hope

that a consensus will emerge regarding the classification of the Araceae.

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### LITERATURE CITED

- Bogner, J. 1973. Die gattung *Pycnospatha* Thorel ex Gagnep. (Araceae) *Oesterr. Bot. Z.* 122:199-216.
- \_\_\_\_\_. 1978 [1979]. A critical list of the aroid genera. *Aroideana* 1:63-73.
- \_\_\_\_\_. 1980. The genus *Scaphispatha* Brongn. ex Schott. *Aroideana* 3:4-12.
- \_\_\_\_\_. 1980a. Berichtigungen und Ergänzungen zu *Jasarum steyermarkii* Bunt. und *Lagenandra insignis* Trim. *Aqua-Planta* 3-80:2.
- \_\_\_\_\_. & D. H. Nicolson. A revised classification of Araceae with dichotomous keys. *Willdenowia*. (in press).
- Cheadle, V. I. 1942. The occurrence and types of vessels in the various organs of the plant in the Monocotyledonae. *Amer. J. Bot.* 29:441-450.
- Croat, T. B. 1981. A revision of *Syngonium* (Araceae). *Ann. Missouri Bot. Gard.* 68:565-651.
- Dahlgren, R. M. T. & H. T. Clifford. 1982. *The Monocotyledons: A Comparative Study*. Academic Press, London.
- \_\_\_\_\_. & P. F. Yeo. 1985. *The Families of the Monocotyledons. Structure, Evolution and Taxonomy*. Springer, Berlin, New York, Tokyo.
- Deyl, M. 1955. The evolution of the plants and the taxonomy of the monocotyledons. *Sborn. Nár. Mus. v. Praze, Rada B, Prír Vedy* 11(6), *Botanica* 3:1-143.
- 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*. 23C (Heft 48):1-130.
- \_\_\_\_\_. 1912. Homalomeninae und Schismatoglottidinae. In A. Engler (ed.), *Das Pflanzenreich IV*. 23Da (Heft 55):1-134.
- \_\_\_\_\_. 1915. Anubiadeae, Aglaonemateae, Dieffenbachieae, Zantedeschieae, Typhonodoreae, Peltandreae. In A. Engler (ed.), *Das Pflanzenreich IV*. 23Dc (Heft 64):1-78.
- \_\_\_\_\_. 1920a. Aroideae und Pistioideae. In A. Engler (ed.), *Das Pflanzenreich IV*. 23F (Heft 73):1-274.
- \_\_\_\_\_. 1920b. Araceae pars generalis et index familiae generalis. In A. Engler (ed.), *Das Pflanzenreich IV*. 23A (Heft 74):1-71.
- \_\_\_\_\_. & K. Krause. 1908. Monsteroideae. In A. Engler (ed.), *Das Pflanzenreich IV*. 23B (Heft 37):4-138.
- \_\_\_\_\_. & \_\_\_\_\_. 1920. Colocasioideae. In A. Engler (ed.), *Das Pflanzenreich IV*. 23E (Heft 71):1-139.
- Ertl, P. O. 1932. Vergleichende Untersuchungen über die Entwicklung der Blattnervatur der Araceen. *Flora* 126:115-248.
- Eyde, R. H., D. H. Nicolson & P. Sherwin. 1967. A survey of floral anatomy in Araceae. *Amer. J. Bot.* 54:475-497.
- Fairbrothers, D. E., J. J. Mabry, R. L. Scogin & B. L. Turner. 1975. The bases of angiosperm phylogeny: chemotaxonomy. *Ann. Missouri Bot. Gard.* 62:765-800.



- Fox, M. G. & J. C. French. 1988. Systematic occurrence of sterols in Araceae: subfamily Colocasioideae. *Amer. J. Bot.* 75: 132-137.
- \_\_\_\_\_. & \_\_\_\_\_. Systematic survey of four types of latex particles in Araceae: subfamily Colocasioideae. (in prep.).
- French, J. C. 1986a. Patterns of endothelial wall thickenings in Araceae: subfamilies Colocasioideae, Aroideae, and Pistioideae. *Bot. Gaz.* 147: 166-179.
- \_\_\_\_\_. 1986b. Ovular vasculature in Araceae. *Bot. Gaz.* 147: 478-495.
- \_\_\_\_\_. 1986c. Patterns of stamen vasculature in Araceae. *Amer. J. Bot.* 73: 434-449.
- \_\_\_\_\_. 1987a. Structure of ovular and placental trichomes in Araceae. *Bot. Gaz.* 148: 198-208.
- \_\_\_\_\_. 1987b. Systematic occurrence of a sclerotic hypodermis in roots of Araceae. *Amer. J. Bot.* 74: 891-903.
- \_\_\_\_\_. 1987c. Systematic occurrence of resin canals in roots of Araceae. *Bot. Gaz.* 148: 360-371.
- \_\_\_\_\_. 1988. Systematic occurrence of anastomosing laticifers in Araceae. *Bot. Gaz.* 149: 71-81.
- \_\_\_\_\_. & P. B. Tomlinson. 1980. Preliminary observations on the vascular systems in stems of certain Araceae. In C. D. Brickell, D. F. Cutler & M. Gregory (eds.), *Petaloid Monocotyledons*. Academic Press, London, pp. 105-116.
- \_\_\_\_\_. & \_\_\_\_\_. 1981a. Vascular patterns in stems of Araceae: subfamilies Calloideae and Lasioideae. *Bot. Gaz.* (Crawfordsville) 142:366-381.
- \_\_\_\_\_. & \_\_\_\_\_. 1981b. Vascular patterns in stems of Araceae: subfamily Pothoideae. *Amer. J. Bot.* 68:713-729.
- \_\_\_\_\_. & \_\_\_\_\_. 1981c. Vascular patterns in stems of Araceae: subfamily Monsteroideae. *Amer. J. Bot.* 68:1115-1129.
- \_\_\_\_\_. & \_\_\_\_\_. 1981d. Vascular patterns in stems of Araceae: subfamily Philodendroideae. *Bot. Gaz.* (Crawfordsville) 142:550-563.
- \_\_\_\_\_. & \_\_\_\_\_. 1983. Vascular patterns in stems of Araceae: subfamilies Colocasioideae, Aroideae and Pistioideae. *Amer. J. Bot.* 70:756-771.
- \_\_\_\_\_. & \_\_\_\_\_. 1984. Patterns of Stem Vasculature in Philodendron. *Amer. J. Bot.* 71:1432-1443.
- Gibbs, R. D. 1974. *Chemotaxonomy of flowering plants*, Vol. III. McGill-Queen's Univ. Press, Montreal.
- Grayum, M. H. 1984. Palynology and phylogeny of the Araceae. Ph.D. Thesis, University of Massachusetts, Amherst.
- \_\_\_\_\_. 1987. A summary of evidence and arguments supporting the removal of *Acorus* from the Araceae. *Taxon* 36:723-729.
- \_\_\_\_\_. 1990. Evolution and phylogeny of the Araceae. *Ann. Missouri Bot. Gard.* 77:628-697.
- Harborne, J. B. 1982. Flavonoid compounds. In R. M. T. Dahlgren & H. T. Clifford, *The Monocotyledons: A Comparative Study*. Academic Press, London, pp. 264-274.
- Harris, P. J. & R. D. Hartley. 1980. Phenolic constituents of the cell walls of monocotyledons. *Biochem. Syst. Ecol.* 8:153-160.
- Hegnauer, R. 1963. *Chemotaxonomie der Pflanzen*. 2. *Monocotyledoneae*. Birkhauser, Basel.
- Hooker, J. D. 1883. Aroideae. In G. Bentham & J. D. Hooker, *Genera Plantarum*, Vol. 3. London, pp. 955-1000.
- Hotta, M. 1970. A system of the family Araceae in Japan and adjacent areas. *Mem. Fac. Sci. Kyoto Imp. Univ., Ser. Biol.* 4: 72-96.
- \_\_\_\_\_. 1981. A new genus of the family Araceae from West Sumatra. *Acta Phytotax. Geobot.* 32: 142-145.

- Hutchinson, J. 1973. *The families of flowering plants*. Clarendon Press, London.
- Jones, G. E. 1957. Chromosome numbers and phylogenetic relationships in the Araceae. Ph. D. Thesis, University of Virginia, Charlottesville.
- Jüssen, F. J. 1928. Die Haploidgeneration der Araceen und ihre Verwertung für die System. *Bot. Jahrb. Syst.* 62: 155-283.
- Krause, K. 1908. Calloideae. In A. Engler (ed.), *Das Pflanzenreich IV*. 23B (Heft 37): 140-155.
- \_\_\_\_\_. 1913. Philodendrinae. In A. Engler (ed.), *Das Pflanzenreich IV*. 23Db (Heft 60): 1-143.
- Li, H. 1979. Angiospermae, Monocotyledoneae, Araceae, Lemnaceae. In C. Y. Wu & H. Li (editors), *Flora Reipublicae Popularis Sinicae*, Vol. 13(2).
- \_\_\_\_\_. 1980. Himalayas-Hengduan Mountains—the centre of distribution and differentiation of the genus *Arisaema*; to discuss the problems about the origin and migration of this genus. *Acta Bot. Yunnanica* 2: 402-416.
- Lemée, A. 1941. Aracées. In Dictionaire Descriptif et Synonymique des Genres de Plantes Phanerogames 8: 88-101. Brest.
- Madison, M. T. 1981. Notes on *Caladium* (Araceae) and its allies. *Selbyana* 5: 342-377.
- Marchant, C. J. 1970. Chromosome variation in Araceae: I. Pothoeae to Stylochitonaeae. *Kew Bull.* 24: 315-322.
- \_\_\_\_\_. 1971a. Chromosome variation in Araceae: II. Richardieae to Colocasiaeae. *Kew Bull.* 25: 47-56.
- \_\_\_\_\_. 1971b. Chromosome variation in Araceae: III. Philodendreae to Pythonieae. *Kew Bull.* 25: 323-329.
- \_\_\_\_\_. 1972. Chromosome variation in Araceae: IV. Areae. *Kew Bull.* 26: 395-404.
- \_\_\_\_\_. 1974. Chromosome variation in Araceae: V. Acoreae to Lasieae. *Kew Bull.* 28: 199-210.
- Metcalf, C. R. 1967. Distribution of latex in the plant kingdom. *Econ. Bot.* 21: 115-127.
- Nicolson, D. H. 1960. A brief review of classifications in the Araceae. *Baileya* 8: 62-67.
- \_\_\_\_\_. 1984. Suprageneric names attributable to Araceae. *Taxon* 33: 680-690.
- \_\_\_\_\_. 1987. Derivation of aroid generic names. *Aroideana* 10: 15-25.
- Petersen, G. 1989. Cytology and systematics of Araceae. *Nordic J. Bot.* 119-166.
- Raven, P. H. & D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539-673.
- Schott, H. 1860. *Prodromus Systematis Aroidearum*. Congregationis Mechitharisticae, Vindobonae.
- Schuster, R. M. 1976. Plate tectonics and its bearing on the geographical origin and dispersal of angiosperms. In C. B. Beck (ed.), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York, pp. 48-138.
- Solereder, H. & F. J. Meyer. 1928. Systematische Anatomie der Monokotyledonen. Heft 3. Principes—Synanthae—Spathiflorae. Gebrüder Borntraeger, Berlin.
- Thanikaimoni, G. 1969. Esquisse palynologique des Aracées. Inst. Franç. Pondichéry, *Trav. Sect. Sci. Tech.* 5(5): 1-31.
- Thorne, R. F. 1976. A phylogenetic classification of the Angiospermae. *Evol. Biol.* 9: 35-106.
- \_\_\_\_\_. 1983. Proposed new realignments in the angiosperms. *Nordic J. Bot.* 3: 85-117.
- Tillich, H. J. 1985. Keimlingsbau und verwandtschaftliche Beziehungen der Araceae. *Gleditschia* 13: 63-73.
- Williams, C. A., J. B. Harborne & S. J. Mayo. 1981. Anthocyanin pigments and leaf flavonoids in the family Araceae. *Phytochemistry* 20: 217-234.



Fig. 5. *Typhonium pedatisectum* Gage, Philippines. Photo by unknown.



Fig. 6. *Hapaline brownii* Hook. f., Hay 2036, Malaysia, cultivated at Kew. Photo by T. B. Croat.

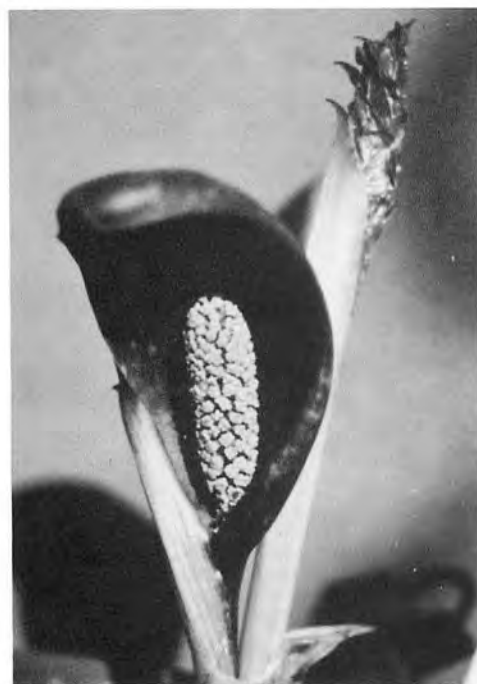


Fig. 7. *Gorgonidium vermicidum* (Speg.) Bogner & Nicolson, Croat 68462, Argentina. Photo by T. B. Croat.

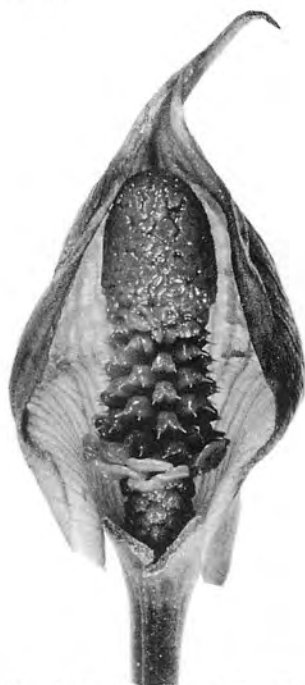


Fig. 8. *Bucephalandra motleyana*, Bogner 1366, Sarawak (spathe artificially opened). Photo by J. Bogner.



Fig. 9. *Theriophonum fischeri* Sivadasan, Tamilnadu, India. Photo by G. J. Thiyagaraj.



Fig. 10. *Phymatarum borneense* M. Hotta, *Bogner 1506*, Sarawak. Photo by A. Tangerini.



Fig. 11. *Culcasia striolata* Engl. Croat 53499, Nigeria. Photo by T. B. Croat.



Fig. 12. *Gonatanthus pumilus* Engl. & K. Krause, Thailand. Photo by L. Birk.