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THE ARACEAE OF INDOMALAYA & TROPICAL AUSTRALASIA

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2 by Peter C. Boyce & Wong Sin Yeng

Peter C. Boyce

3 Pusat Pengajian Sains Kajihayat [School of Biological Sciences]
Universiti Sains Malaysia 11800 USM
Pulau Pinang, Malaysia
4 phymatarum@gmail.com

Wong Sin Yeng

Department of Plant Science & Environmental Ecology
Faculty of Resource Science & Technology
Universiti Malaysia Sarawak
94300 Kota Samarahan
Sarawak, Malaysia
sywong@frst.unimas.my

ABSTRACT

A key to the higher taxa of aroids of Indomalaya and tropical Australasia is offered. Example images are provided for most taxa.

INTRODUCTION

Work on the revising the aroids of Indomalaya and Australasia has progressed considerably in the last 15 years. Nonetheless, much remains to be done before there is a comprehensive body of published data for all genera to species level. Indeed, in recent years increased fieldwork activities in some parts of these ecozones (notably on Borneo and more recently in NE Peninsular Malaysia) have revealed a wealth of novel species such that for even recently revised genera (e.g., *Alocasia* and *Schismatoglottis*, etc.), it is apparent that a great deal more awaits discovery, and that the aroid biota (at least those of Indomalaya) is considerably richer and more diverse than hitherto suspected.

Additional to the discovery in the wild of much that is taxonomically new, molecular analyses continue to provide insights into pre-existing taxa, in many instances forcing re-examination of long-held generic

concepts.

Against this background of much new data published in numerous different journals, changing higher taxon concepts, and the high probability that 'complete' monographs for most genera are still many years away, we thought it useful to provide a key to the higher taxa of aroids in Indomalaya and Australasia that reflects current taxonomic conditions.

The key presented here is unorthodox in that it not only keys out all the currently accepted genera but also keys out separately major generic subordinal units, and those species that no longer fit comfortably in their former generic placement.

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Editor : Carla Kostelac

Layout : Albert Huntington

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Figure 1. *Lemna minor* L. Although radically different in appearance to the rest of the Araceae, molecular analyses and study of the inflorescences of the duckweeds (which are bisexual) have established their position embedded in the family and sister to the Pothoideae.



Figure 2. *Anaphyllum wightii* Schott. A genus of two species restricted to SW India. Relationships of *Anaphyllum* to the other extant lasioids imply that they are vestiges of an ancient lineage of aroids. Image © René Stalder, used with permission.



Figure 3. *Pycnospatha arietina* Gagnep. *Pycnospatha* may be seen as the Asian 'equivalent' of Neotropical *Dracontium*. Although superficially very similar in flora and vegetative appearance, *Pycnospatha* is immediately distinguished by the flowers lacking tepals. The dracontoid leaf of *Pycnospatha* is shared with *Dracontium* and also occurs, certainly independently, in the Afrotropics genus *Anchomanes*. Image © René Stalder, used with permission.



Figure 4. *Lasia spinosa* (L.) Thwaites. One of the most wide-spread species of lasioid, often persisting in cleared land owing to the use of the emerging leaves and inflorescences as a vegetable. Here the distinctive spinulose fruits are shown.



Figure 5. *Cyrtosperma ferox* N.E.Br. Another striking species of the Lasiodeae. Here shown in fruit. Unlike *Lasia* the infructescence is declinate and the fruits smooth.



Figure 6. *Podolasia stipitata* N.E.Br. While rather similar in appearance to *Cyrtosperma*, the peastswamp-dwelling genus *Podolasia* produces erect spikes of red berries.



Figure 7. *Pedicellarum paiei* M.Hotta. *Pedicellarum* is very close in appearance to several *Pothos* species, notably those of the Goniurus complex with scattered flowers. Molecular work is underway to resolve the relationships between the various species groups.



Figure 8. *Pothoidium lobbianum* Schott. *Pothoidium* closely resembles some species of *Pothos*, notably *P. repens* (Lour.) Druce and *P. longipes* Schott, but differs in the unique architecture of the inflorescences, and in being functionally dioecious. Pictured is a pistillate plant in young fruit.



Figure 9. *Pothos ovalifolius* Merr. Ripe infructescence. Note that the individual fruits are pointed (compare with the truncate-topped fruits of *Anadendrum* in Fig. 11).



Figure 10. *Spathiphyllum commutatum* Schott. *Spathiphyllum* is currently the only aroid genus that is definitely represented in the Asian and Neotropics. Formerly *Schismatoglottis* and *Homalomena* were both considered to be distributed in the manner, but recent and on-going research has established that the Neotropical genera are different. *Spathiphyllum commutatum* is one of three species in the Asian tropics.



Figure 11. *Anadendrum*. Is perhaps the least-well understood genus of climbing aroids in Indomalaya. Most of the species are yet to be described, including the one figured here. Note that truncate-topped fruits.



Figure 12. *Amydrium medium* (Zoll. & Moritz) Nicolson. *Amydrium* fruits are berries (here shown ripe) and do not shed the stylar plate to reveal the seeds in the manner of other Monstereae (see Fig. 12).



Figure 13. *Scindapsus geniculatus* Engl. Unlike the Neotropics, epiphytic aroids are rare in the Asian tropics. Exceptions occur in *Remusatia* (most), a few *Arisaema*, and in the genus *Scindapsus*, where the ca 20 species (most yet to be described) related to *S. geniculatus* are obligate trash-basket epiphytes. The plant here is growing on *Tristaniopsis beccarii* (Myrtaceae).



Figure 14. *Rhaphidophora lobbii* Schott. Here shown with a ripe infructescence (monstercarp) shedding stylar plates to reveal seeds embedded in pulp. The stylar plates are full of raphides and cause intense irritation if bitten or handled incautiously. However, the pulp cavity is free of these structures and, indeed, the pulp is sweet-tasting.



Figure 15. *Epipremnum pinnatum* (L.) Engl. This is a large growing species that is frequently limestone-associated in habitat. The species is widespread in tropical Asia, with numerous localized and often distinctive populations, notably on the Philippine Islands. The plant featured here originates from eastern Sabah, the only place on Borneo that this species occurs.



Figure 16. *Pistia stratiotes* L. The ubiquitous water lettuce, *Pistia* can become pestilential on slow-moving waterbodies.



Figure 17. *Amorphophallus ranchanensis* Ipor, A.Simon & Meekiong. *Amorphophallus* continues to surprise with new species. *Amorphophallus ranchanensis*, described from basalt close to Serian in western Sarawak seems to be closest in appearance to species from Sabah. Borneo's *Amorphophallus* flora now stands at 19 described species, an increase of 15 since 2000. In Thailand half of all aroids are either *Amorphophallus* or *Typhonium*.



Figure 18. *Arisaema filiforme* Blume. *Arisaema* is richest in warm-temperate and subtropical Asia. However, there are several species in the Asian wet tropics. Image © Eric Hunt, used with permission.



Figure 19. 'Lazarum', is a group of species restricted to Australia formerly included in *Typhonium*. Here an as yet undescribed species is shown, with the spathe artificially opened to show the thickened 'ring' separating the lower spathe and spathe limb. Although well-supported by molecular data, the morphological separation of *Lazarum* from *Typhonium* remains problematic.



Figure 20. *Typhonium trilobatum* (L.) Schott. *Typhonium* is richest and most diverse in strongly seasonal tropical habitats, notably Thailand and Indochina. Image © John Mood, used with permission.



Figure 21. *Sauromatum horsfieldii* Miq. *Sauromatum* has recently been once-again removed from *Typhonium* and expanded to include several additional species. *Sauromatum horsfieldii* is a widespread species, occurring from SW China, though Jawa, to Bali.



Figure 22. *Cryptocoryne longicauda* Becc. ex Engl. Photographed in deep saturated peat layers overlaying limestone in Mulu N.P. *Cryptocoryne* species are important environmental indicators as they are highly dependent on unpolluted water and good forest cover.



Figure 23. *Aglaodorum griffithii* (Schott) Schott. Superficially similar to (and closely related to) *Aglaonema* (Fig.24 & 25), *Aglaodorum* is a helophyte with large green spongy fruits. When mature they fall and float away.



Figure 24. *Aglaonema simplex* (Blume) Blume. One of several widespread species in the genus. Here photographed at the Niah Caves in N Sarawak.



Figure 25. *Aglaonema nitidum* (Jack) Kunth. Here fruiting in forest not far from Kuching. The red fruits are eaten by birds such as spiderhunters (*Arachnothera*).



Figure 26. *Nephthytis bintuluensis* A.Hay, Bogner & P.C.Boyce. Plants in the type locality. Note that the inflorescences are some distance from the accompanying (preceding) foliage leaf. The locality, photographed here in the dry season, is inundated to 1 metre (ca 3 ft) or more for days at a time during the wet season.



Figure 27. *Nephthytis bintuluensis* A.Hay, Bogner & P.C.Boyce. Although vegetatively quite dissimilar to the related *Aglaonema*, the similarity of the inflorescence of *Nephthytis* to that of *Aglaonema* is striking.



Figure 28. *Furtadoa mixta* (Ridl.) M.Hotta. Although the plants look very similar to *Homalomena* belonging to the Chamaecladon Supergroup, the arrangement of flowers is quite different (see Fig. 31). Image © Zulhazman bin Hamzah, used with permission.



Figure 29. *Furtadoa mixta* (Ridl.) M.Hotta. Note that each staminate flower accompanied by and is overtopped by a flask-shaped pistillode. Image © Zulhazman bin Hamzah, used with permission.

KEY TO HIGHER TAXA OF INDOMALAYAN AND TROPICAL AUSTRALASIAN ARACEAE

1. Plants comprising small to minute few-rooted or rootless free-floating thallus-like leafless bodies . . . **Lemnoideae (>2)**
 2. Roots 1 per plant body; plant bodies with 1–3 veins, without a scale at the base . . . *Lemna*
 3. Roots absent; plant body without veins; the daughter plant bodies originating from a single terminal pouch or cavity at the base of the plant body; inflorescence originating in a cavity on the plant body upper surface . . . *Wolffia*
 2. Roots 1–21 per plant body; plant body with 1–21 veins; the daughter plant bodies and inflorescences originating from 2 lateral pouches at the base of the plant body
 3. Roots (1–)2–21 per plant body; plant bodies with (3–)5–21 veins, surrounded at its base by a small scale (prophyll) covering the point of attachment of the roots
 4. Plant bodies 1–1.5 times as long as wide, with 7–12 roots of which 1(–)2 perforate the scale . . . *Spirodela*
 4. Plant bodies 1.5–2 times as long as wide, with (3–)5–7 veins and (1–)2–7(–)12 roots all of which perforate the scale . . . *Landoltia*
1. Plants not as above. If free-floating then leaves forming a conspicuous rosette with copious roots hanging beneath
 5. Flowers bisexual, mostly with a perigone of conspicuous tepals
 6. Plants terrestrial, mostly armed with prickles; leaf development acroscopic **Lasioideae (>7)**
 7. Geophytes with 'dracontoid' leaf blades; petioles somewhat asperate but never prickly; flowers without tepals . . . *Pycnospatha*
 7. Armoured or unarmoured helophytes (rarely peatswamp mesophytes, or rheophytes) with hastate to 4×pinnatifid leaves; flowers with a perigone of conspicuous tepals
 8. Unarmoured helophytes; spathe open, often twisted; seed testa membranous *Anaphyllum*
 8. Armoured helophytes, rarely peatswamp mesophytes, or rheophytes
 9. Stems suffruticose, erect to decumbent, usually with prickly conspicuous internodes; leaves hastate to (4×)pinnatifid; spathe caducous or marcescent; placentation apical; fruit usually spinulose . . . *Lasia*
 9. Stem a condensed rhizome, rarely with distinct internodes, and these then unarmed; leaves entire, sagittate to hastate; spathe persistent to marcescent; placentation not apical; fruit smooth
 10. Infructescence nodding, fruits barely emerging from between the tepals, ripening dull purple; seeds crested or warty; plant with spines mixed straight and up-turned . . . *Cyrtosperma*
 10. Infructescence erect, fruits emerging fully from between the tepals, ripening bright red; seeds smooth; plant with spines mixed straight and downturned . . . *Podolasia*
 6. Plants mostly climbing hemiepiphytes; flowers naked or perigoniate; if terrestrial helophytes then tepals fused into a thickened ring-like structure; leaf development basicopic
 11. Climbing hemiepiphytes; tepals free or, if fused, then not forming a thickened ring; ripe fruits red, well-extruded from spadix . . . **Pothoideae: Potheae (>12)**
 12. Flowers pedicellate, with a distinct receptacle; tepals of perigone connate forming a conspicuous 'cup' . . . *Pedicellarum*
 12. Flowers sessile, without a receptacle; tepals of perigone free, very rarely united and then not forming a 'cup'
 13. Flowering shoot terminating in a (leafless) branching system of spadices; flowers functionally unisexual . . . *Pothoidium*
 13. Flowering shoot with inflorescences mostly axillary or infra-axillary, if terminal then inflorescence system not branching, and leafy; flowers bisexual . . . *Pothos*
 11. Terrestrial helophytes; tepals fused into a thickened ring-like structure; ripe fruits green, encased in persistent green tepals . . . **Monsteroideae: Spathiphyllae (>14)**
 14. Inflorescences held down among the leaf bases; spathe limb enclosing the spadix throughout anthesis, not expanding;

- marcescent into fruiting . . . *Holochlamys*
14. Inflorescences held above the leaves; spathe limb spreading expanding; persistent and turning green during fruiting, later falling . . . *Spathiphyllum*
5. Flowers bisexual, mostly without a perigone of tepals; if tepals present then membranous *and* very inconspicuous; or flowers unisexual
15. Flowers bisexual, perigone (if present) membranous and inconspicuous; mostly climbing hemiepiphytes, rarely rheophytic
- Monsteroideae: Monstereae (>16)**
16. Flowers with a perigon of fused membranous tepals; inflorescences long-slender-pedunculate, numerous in a distichous fan; spathe in bud conspicuously long-beaked (beak to $\frac{1}{3}$ length of entire spathe); infructescence with discrete, truncate berries; trichosclereids absent *Anadendrum*
16. Flowers naked; inflorescences very short to long-stout-pedunculate, solitary or few, not carried in a fan; spathe is not conspicuously long-beaked (beak if present less than $\frac{1}{6}$ length of entire spathe); infructescence mostly a monstercarp, if with discrete berries, then these not truncate; trichosclereids present (very sparse in *Amydrium*)
17. Venation reticulate; infructescence with discrete berries; trichosclereids very sparse . . . *Amydrium*
17. Primary venation striate; higher order venation reticulate; infructescence a monstercarp; trichosclereids abundant
18. Ovules solitary, placentation basal; fruits each with a solitary large seed . . . *Scindapsus*
18. Ovules 2–6 or more, placentation parietal; fruits with more than one seed
19. Ovules 8 or more, superposed on 2 (rarely 3) parietal placentas; seeds many, ellipsoid, straight, 1.3–3.2 mm long, 0.6–1 mm wide; testa brittle, smooth . . . *Rhaphidophora*
19. Ovules 2–4(–6) at base of a single intrusive placenta; seeds few, curved, 3–7 mm long, 1.5–4 mm wide; testa bony and ornamented . . . *Epipremnum*
15. Flowers unisexual . . . **Aroideae (>20)**
20. Free-floating plants with leaves forming a conspicuous rosette with copious roots hanging beneath . . . **Pistieae (*Pistia*)**
20. Not free-floating and otherwise not as above
21. Tuberous-stemmed geophytes; leaf blades mostly variously divided
22. Leaf blade decomposed; inflorescences usually appearing before leaf emergence, with flowers of both sexes (i.e., monoecious) . . . **Thomsonieae (*Amorphophallus*)**
22. Leaf blade often trifoliolate to pentafoliolate, rarely hastate or simple; inflorescences produced with leaves
23. Inflorescences usually single-sexed, paradioecious; ripe fruits red . . . **Arisaemateae (*Arisaema*)**
23. Inflorescences monoecious; ripe fruits never red . . . **Areae (>24)**
24. Spathe internally septate into two chambers or at least the constriction between the lower spathe and spathe limb internally thickened. Australia *Lazarum*
24. Spathe not internally septate
25. Sterile zone between pistillate and staminate zones with smooth naked distal part, base with various numbers of staminodes, or whole zone covered with staminodes but then leaves always entire and proximal staminodes spatulate (in *T. flagelliforme*) . . . **Typhonium**
25. Sterile zone between pistillate and staminate zones fully covered with staminodes, or grooved and with staminodes only at base; leaves usually pedate, rarely entire; staminodes never spatulate . . . **Sauromatum**
21. Not geophytes; leaf blade simple, ranging from linear-lanceolate to hastate
26. Aquatic plants; infructescences composed of carpels connate into a syncarp . . . **Cryptocoryneae (>27)**
27. Carpels opening from base; leaf ptyxis involute *Lagenandra*
27. Carpels opening from the apex; leaf ptyxis convolute. . . *Cryptocoryne*
26. Plants not aquatic; infructescences comprised of berries
28. Plants suffruticose, or with a creeping rhizome-like stem; fruits conspicuous red or pink or green berries not surrounded by a persistent spathe . . . **Aglaonemateineae (>29)**
29. Colonial helophytes with creeping spongy rhizomes and erect, spongy petioles; fruits large, ripening green and functioning as floating dispersal units . . . *Aglaodorum*
29. Terrestrial forest herbs with erect (rarely creeping) firm stems, and erect solid petioles; fruits medium-sized, ripening red or rarely pink, not water-dispersed . . . *Aglaonema*
28. Plants not suffruticose; fruits various, mostly green, if red or orange-red then berries surrounded by a persistent spathe
30. Entire spathe closing after anthesis and then persisting until fruit maturity
31. Rhizomatous geophytes; leaves solitary or rarely 2 together, distant from each other; inflorescences arising directly from the ground; spathe forced open by developing fruits but not actively splitting; fruits a large conspicuous red berry containing a large solitary green seed . . . **Nepththydineae (*Nepthtytis*)**
31. Clumping mesophytes, rarely colonial helophytes; leaves many together; inflorescences arising from leafy shoots; spathe actively splitting from the base and peeling upwards to reveal fruits; fruits many, whitish to very pale pink, each containing many tiny brown or black seeds . . . **Philodendrinae (>32)**
32. Staminate flower consisting of solitary stamen overtopped by flask-shaped pistillode; ovary 1-locular, placenta basal . . . *Furtadoa*
32. Staminate flower consisting of 2–6 stamens, pistillodes absent; ovary incompletely

- 2–5 locular, placentas parietal and axile . . . *Homalomena*
30. Upper spathe mostly shedding during or soon after anthesis, and lower spathe persisting until fruit maturity; if upper spathe persisting then attached portion of petiolar sheath very short and the remainder free-ligular *or* absent and the protective role taken on by prophyll/cataphyll
33. Staminate flowers forming synandria . . . (**Colocasieae [& Caladieae] >34**)
34. Spathe differentiated into an upper limb and a tubular or convolute lower part separated by one or sometimes two pronounced constrictions
35. Plant with conspicuous erect aerial stolons bearing along their distal portion numerous barbed bulbils . . . *Remusatia* (incl. *Gonatanthus*)
35. Plant without conspicuous erect aerial stolons with barbed bulbils; if stolons present then these decumbent and bearing tubercles at the tips
36. Leaf blades abaxially with waxy glands in the axils of the primary veins; mature infructescences erect; fruit red when ripe, odourless; seeds large, few per fruit *Alocasia*
36. Leaf blade glands absent
37. Seasonally deciduous lithophytes of Karst limestone; stolons simple, decumbent, bearing tubercles at the tips; mature infructescences erect; fruit red when ripe, odourless; seeds large, few per fruit . . . *Alocasia hypnosa*
37. Evergreen plants of a variety of substrates; stolons if present branching, spreading, viviparous but without tubercles; mature infructescences declinate to pendent or erect; fruit pale yellow to brown and fruit-smelling when ripe; seeds small, very numerous per fruit
38. Plants small to medium; leaf blades and petioles at most only weakly grey-glaucous; spathe usually yellow; mature infructescences declinate or pendent; stolons mostly present . . . *Colocasia*
38. Plants usually gigantic; leaf blades and petioles pruinose; spathe pure white; mature infructescences erect; stolons absent . . . *Colocasia gigantea*
34. Spathe not differentiated into an upper limb and lower part by one or more constrictions
39. Synandria connate; thecae of adjacent synandria encircling pits in the spadix, each pit with a somewhat prominent upper margin; leaf blade peltate . . . *Ariopsis*
39. Synandria not so; leaf blade peltate or hastate
40. Spathes brightly coloured (internally commonly yellow or purple-red); pistillate flowers with staminodes; stem a repent or suberect epigeal rhizome *Stuednera*
40. Spathe white; pistillate flowers without staminodes; stem a hypogeal tuber or stolon . . . **Caladieae (Hapaline)**
33. Staminate flowers not forming synandria . . . **Schismatoglottideae (>41)**
41. Modules monophyllous, congested in a distichous arrangement; petiolar sheath with a long-persistent, long ligular free portion . . . *Pichinia*
41. Modules mostly polyphyllous, if monophyllous then never distichous; petiolar sheath fully attached, persistent or marcescent; if free ligular then soon-marcescent
42. Wings of petiolar sheath fully or almost fully attached to the petiole; seeds never with a micropylar appendage
43. Inflorescences on very slender peduncles, nodding at anthesis, peduncle at spathe insertion flexing 180° from vertical axis; infructescences narrowly campanulate, nodding; plants of podzols . . . *Hestia*
43. Inflorescences erect to nodding at anthesis, if nodding, then plants massive pachycauls, and peduncle very stout; infructescences fusiform with a constricted orifice, if campanulate, then thick-walled and erect, never nodding; plants of various substrates but never on podzols
44. Shoot modules hapaxanthic . . . *Schismatoglottis* [Calyprata Group]
44. Shoot modules pleioanthic
45. Petiole sheathing only at extreme base; each foliage leaf alternating with a cataphyll . . . *Schismatoglottis* [Tectura Group]
45. Petiole usually sheathing for at least a third of its length (rarely less); individual foliage leaves not alternating with cataphylls
46. Pistillate and staminate flower zones separated by a conspicuous partly naked somewhat swollen interstice; inflorescences erect; spathe limb semi-persistent and barely opening during anthesis and then clasping the spadix, falling

- with spent parts of the spadix; petiolar sheath wings usually (but not always) deciduous . . . *Apoballis*
46. Pistillate and staminate flower zones not separated by a naked interstice; spathe not persistent or, if so, the inflorescence nodding; petiolar sheath wings persistent
47. Small to medium plants, often with asperate petioles and sometime the whole plant coarsely hairy; inflorescence erect; spathe limb irregularly crumbling and breaking away at or after staminate anthesis . . . *Schismatoglottis* [*Asperata* Group]
47. Massive glabrous pachycauls; inflorescence nodding; spathe limb clasping the spadix and more-or-less marcescent after anthesis, finally falling with spent parts of spadix . . . *Schismatoglottis* [*Corneri* Group]
42. Wings of petiolar sheath always extended into a free ligular portion; seeds often with a micropylar appendage
48. Spathe not constricted; plants glabrous or at most minutely puberulent
49. Thecae of anther never with horn- or needle-like projections
50. Spadix free; spathe limb caducous during anthesis; infructescence on erect peduncle; lower spathe forming a splash-cup . . . *Piptospatha* (>51)
51. Anther connective extended into a pronounced elongated beak . . . *Piptospatha insignis*
51. Anther connective not so, or if elevated then shortly so and obtuse
52. Spathe white; leaf blade with conspicuously tessellate tertiary venation on both surfaces . . . *Piptospatha perakensis*
52. Spathe pink; leaf blade without tessellate venation, or if present then on very faint and only abaxially . . . *Piptospatha*
50. Spadix partially to almost completely adnate to spathe; spathe limb not caducous during anthesis; infructescence on declinate peduncle; lower spathe not forming a splash-cup
53. Staminate flowers mostly sterile with a narrow zone of fertile flowers exposed by the spathe opening; spathe persistent into fruiting, at fruit maturity swiftly drying, reflexing and opening basally by tearing at peduncle insertion to expose fruits but remaining distally convolute and while in this situation clasping the spadix; ovules basal; seeds with a blunt micropyle . . . *Bakoa*
53. Staminate flowers all fertile; spathe persistent throughout the fruit dispersal; ovules parietal; seeds with a pronounced, hooked, micropylar appendage . . . *Ooia*
49. Thecae of anther each with a horn- or needle-like projection, although sometimes visible only after pistillate anthesis
54. Thecae with needle-like projection extending only after pistillate anthesis; projection tipped with a weakly peltate ovate-triangular flap; appendix composed of pistillodes . . . *Schottariella*
54. Thecae with a horn- or needle-like projection present prior to pistillate anthesis; with the projection pointed and never associated with a terminal flap; appendix, where present, composed of staminodes
55. Sterile interstice of spadix with flattened scale-like staminodes; anthers not excavated . . . *Bucephalandra*
55. Sterile interstice absent, or with truncate staminodes; anthers mostly with the top excavated
56. Anthers clearly excavated . . . *Aridarum*
56. Anthers not excavated
57. Thecae horns short, robust, their bases occupying the whole upper surface of the anther; stamens and staminodes smooth .

. *Aridarum incavatum*

57. Thecae horns very slender; stamens and staminodes coarsely verrucate . . . *Aridarum rostratum*

48. Spathe mostly constricted

58. Thecae of anther each with horn- or needle-like projections; ovules on basal placenta; seeds with a long, hooked micropylar appendage . . .

. *Phymatarum*

58. Thecae of anther without horn- or needle-like projections; ovules on parietal or basal placenta; seeds without a micropylar appendage

59. Placentation basal *Schottarum*

59. Placentation parietal *Schismatoglottis* [Multiflora Group]



Figure 30. *Homalomena symplocarpifolia* P.C.Boyce, S.Y.Wong & Fasih. A recently described species from central Sarawak. *Homalomena* is by far the largest Indomalayan genus of Araceae, with probably in excess of 350 species, the majority yet to be formally described.



Figure 31. *Homalomena symplocarpifolia* P.C.Boyce, S.Y.Wong & Fasih. Many *Homalomena* are pollinated by large beetles of the Scarabidae, however, *H. symplocarpifolia* and its relative appear to have evolved pollination utilizing much smaller beetles belonging to the Nitidulidae, seen here on the spathe limb. Just visible behind the spadix is a Chrysomelidae beetle; chrysomelids are frequently pollen-robbers in Araceae, often chewing through the unopened spathe to reach the spadix.



Figure 32. *Remusatia pumila* (D.Don) H.Li & A.Hay. Detail of the bulbil-bearing stolon. Each scale is a minute leaf, the lower portion equivalent to the petiolar sheath, while the 'hook' is a petiole and leaf blade analogue. Image © John Mood, used with permission.



Figure 33. *Alocasia* sp. Portion of the abaxial surface of the leaf blade showing the generically diagnostic waxy glands.



Figure 34. *Alocasia hypnosa* J.T.Yin, Y.H.Wang & Z.F.Xu. Growing in habitat on Karst limestone in Thailand. The colony has formed primarily through the extensive production of stolons. Image © David Prehler, used with permission.



Figure 35. *Alocasia hypnosa* J.T.Yin, Y.H.Wang & Z.F.Xu. Although currently placed in *Alocasia*, this species differs on a number of key characters, including lacking waxy glands on the abaxial surface of the leaf blade. The inflation of the spathe limb is also not matched in *Alocasia*.



Figure 36. *Colocasia oresbia* A.Hay. The only unequivocally indigenous *Colocasia* in Malesia. Here photographed in the hills above Nanga Gaat, central Sarawak.



Figure 37. *Colocasia gigantea* Blume. An ultimately enormous plant with glistening white spathes carried in a fan. The peduncles remain erect into fruiting, in contrast to other *Colocasia* species in which the peduncle is declinate. Note the pruinose petiole and peduncles.



Figure 38. *Ariopsis protanthera* N.E.Br. A genus of two species. One restricted to the Western Ghats of SW India and one (depicted here) occurring from NE India to NE Thailand. Image © Rachun Pooma, used with permission.



Figure 39. *Steudnera discolor* W.Bull. One of perhaps nine species occurring from NE India to SW China and south into Indochina. Image © Wilbert L.A.Hetterscheid, used with permission.



Figure 40. *Hapaline benthamiana* Schott. Another small genus, with most species locally restricted and seemingly also rare. One exception is *H. benthamiana*, which occurs through much of Thailand on exposed limestone.



Figure 41. *Apoballis mutata* (Hook.f.) S.Y.Wong & P.C.Boyce. Long included in *Schismatoglottis* despite some striking morphological differences, recent molecular and palynological research has shown it to be highly distinct. The spadix is shown here (with the spathe artificially removed) to reveal the inflated, almost naked interstice separating the pistillate (below, pale green) and staminate (above, salmon-orange) flower zones.



Figure 42. *Pichinia disticha* S.Y.Wong & P.C.Boyce. Endemic to an isolated limestone massif in SW Sarawak, *Pichinia* has a unique vegetative morphology in the tribe Schismatoglottideae: with each leaf in the fan representing a single branch (similar morphology occurs in some *Anthurium* and *Philodendron*). Although reminiscent of *Schismatoglottis* Multiflora Group (see Fig. 46) *Pichinia* falls outside *Schismatoglottis* in molecular analyses, although its exact position is yet to be established.



Figure 43. *Hestia longifolia* (Ridl.) S.Y.Wong & P.C.Boyce. A recently recognized segregate from *Schismatoglottis*, *Hestia* is readily distinguished by the fascicles of very slender-pedunculate inflorescences with a sharply nodding spathe.



Figure 44. *Schismatoglottis viridissima* A.Hay. A member of the *Schismatoglottis* Calyprata Group, and typically for this group forming colonies by the production of numerous stolons.



Figure 45. An undescribed species in the *Schismatoglottis* Tecturata Group. This photo shows the very short petiolar sheath. The protective role of the petiolar sheath is taken over by the large prophyll, remains of which are marked by the dark brown, papery tissue at the base of the petiole.



Figure 46. *Schismatoglottis nicolsonii* A.Hay, a typical member of the *Schismatoglottis* Multiflora Group. The free-ligular portion of the petiole sheaths are clearly visible.



Figure 47. *Schismatoglottis asperata* Engl., photographed in habitat on Matang, Sarawak, exemplifies some of the critical morphologies of the *Schismatoglottis* Asperata Group. The fruiting spathe is held erect, with the thick-walled persistent lower part half constricted at the mouth. Note, too, the asperate petioles and (just visible) the short, open, petiolar sheath.



Figure 48. *Schismatoglottis corneri* A.Hay, the sole member of the *Schismatoglottis* Corneri Group, showing the diagnostic inflorescences. Plants can attain over 2 m in height. Image © Kohei (Takenaka) Takano, used with permission.



Figure 49. *Piptospatha viridistigma* P.C.Boyce, S.Y.Wong & Bogner. The nodding pink inflorescences and erect splash-cup are diagnostic for the genus.



Figure 50. *Piptospatha perakensis* (Engl.) Ridl. A highly distinctive species, the only *Piptospatha* with a white spathe, and a powerfully fragrant inflorescence. Molecular analysis clearly separates *P. perakensis* from the 'core' *Piptospatha* as represented by *P. viridistigma* (Fig. 49).



Figure 51. *Bakoa brevipedunculata* (H.Okada & Y.Mori) S.Y.Wong. The second described species of this Bornean-endemic genus demonstrates well the difficulties that sometimes best botanists. Originally described in 2000 in the genus *Hottarum*, it was moved in the same year to *Piptospatha*, although fitting neither genus convincingly. Later combined molecular and morphological analyses revealed it to fall outside of both and, together with *Hottarum* (later *Piptospatha*) *lucens*, supported the recognition of a new genus: *Bakoa*.



Figure 52. *Ooia kinabaluensis* (Bogner) S.Y.Wong & P.C.Boyce. Another species that has been bounced from genus to genus before, with the help of combined molecular and morphological analyses, being found a taxonomically convincing 'home'. Image © Kohei (Takenaka) Takano, used with permission.



Figure 53. *Schottariella mirifica* P.C.Boyce & S.Y.Wong. One of several newly recognized genera of the Schismatoglottideae occurring almost exclusively on Borneo. The damage to the spathe limb interior is caused by the pollinator, a chrysomelid beetle (just visible behind the spadix).



Figure 54. *Bucephalandra motleyana* Schott. Inflorescence at pistillate anthesis (spathe limb and the nearside part of the lower spathe artificially removed). The shield-like staminodes above the pistillate flowers are erect.



Figure 55. *Bucephalandra motleyana* Schott. Inflorescence at staminate anthesis (also with the spathe limb and the nearside part of the lower spathe artificially removed). Note that the shield-like staminodes above the pistillate flowers are now lowered, closing off the lower spathe (which is persistent throughout fruiting) and protecting the developing infructescence.



Figure 56. *Phymatarum borneense* M.Hotta. Inflorescence at pistillate anthesis. The numerous small flies (*Drosophilidae*) are attracted by a powerful esteric (model airplane glue) smell.



Figure 57. *Phymatarum borneense* M.Hotta. Detail of the spadix showing the tuberculate staminate flowers with their need-like thecae horns, and the appendix comprised of similarly tuberculate staminodes.



Figure 58. *Aridarum montanum* Ridl. This plant well matches the only known specimen of the type species, collected once, in 1905, and never since refound; confirmation of its identity through flowering is eagerly awaited. Image © Mike Lo, used with permission.



Figure 59. *Aridarum rostratum* Bogner & A.Hay. One of several relatively recently described *Aridarum* species recognition of which has considerably stretched the boundaries of the genus. It seems probable that as with *Piptospatha* molecular analysis will result in changes to the generic boundaries of *Aridarum*.



Figure 60. *Schottarum sarikeense* (Bogner & M.Hotta) P.C.Boyce & S.Y.Wong. Although very similar in overall appearance to *Schismatoglottis* of the Multiflora Group (see Fig. 46), *Schottarum* is in fact much more closely related to *Aridarum*.

Scouting the Jama-Coaque

by Jason P. Hernandez

In August and September 2011, I traveled to the west coast of Ecuador to do a permaculture internship with Third Millennium Alliance. Third Millennium is a relatively new nonprofit organization which owns a forest reserve in the Jama-Coaque Mountains of Manabí Province. The Reserve lies within the southern end of the Chocó-Manabí Biodiversity Hotspot, which extends from the Chocó region of Colombia, south through the provinces of Esmeraldas and Manabí in Ecuador. This corridor is the most floristically diverse part of the Neotropics, with 25% of its plant species endemic to the region. However, it is also one of the most imperiled, with the forest cover of Manabí reduced to but a tiny fraction of its aboriginal extent (Third Millennium Alliance 2010). The Araceae of the Chocó have been partially documented by Mora *et al.* (2006), which was used in the identifications on this expedition.

The Jama-Coaque Mountains form the southern end of an extensive cordillera encompassing the Mache-Chindul Mountains of Esmeraldas, the Cojimies Mountains of northernmost Manabí, and the Jama-Coaque. This cordillera spans a climatic transition zone from the wet climate of the Chocó to the arid climate of the Peruvian coast. Traveling from the coastline to the ridge of the cordillera, one encounters four distinct forest types: tropical dry forest at the coast; semideciduous tropical forest at the community of Camarones; tropical moist forest encompassing most of the Reserve; and premontane cloud forest on the highest peaks.

As is the case with most of the Neotropics, the area outside the Reserve is largely deforested, with extensive scrubby pastures and small forest remnants. Even here, however, there are Araceae, albeit not very interesting ones botanically, and all confined to the stream bed. The only conspicuous species was *Alocasia plumbea* or something similar, so long naturalized along the gravel bars that the local inhabitants think of it as indigenous. Where the stream widens into sluggish swamps, *Lemna* sp. and *Spirodela* sp. occur, though seldom together; the *Lemna* mainly near the village, *Spirodela* extending downstream to the lowlands.

Of the remaining forest, I found Araceae entirely absent from the dry and semideciduous forest types, with the exception of one species of birdsnest *Anthurium* (sect. *Pachyneurium*) growing in forest remnants at the upper limit of the semideciduous zone. I therefore concentrated my search in the moist forest and cloud forest zones. There is an extensive network of maintained trails within the Reserve, and over the course of my two months, I walked several of them, as well as the course of the Río Camarones and its tributaries. Rather than describe a specific route, therefore, I will give a general account of which Araceae occur where. Unfortunately, the theft of the camera containing the memory card has made it impossible to include photos of any of the plants.

Beginning in the river itself, there are large specimens of *Xanthosoma undipes* (C. Koch & Bouché) C. Koch. This species is widespread in Ecuador, occurring in the coastal, Andean, and Amazonian regions, and commonly appears in gardens, croplands, trails, and riverbanks (Quitigüña *et al.* 2008). It has various local common names, of which one is *inda caleña*. Small, weedy seedlings, hardly resembling the impressive streambank specimens, are present in the vegetable gardens at the Reserve.

Another aroid associated with the river, commonly seen on the rock faces of waterfalls, is a scandent *Anthurium* (sect. *Belonchium*) somewhat resembling *A. giganteum* Matuda but smaller. *Anthurium giganteum* grows at rather higher elevations than are found in the Reserve (Quitigüña *et al.* 2008), so this one is most likely a different species, possibly *A. concinatum* Schott or something similar. At the time of my survey, a few inflorescences were still present, but most had begun to develop infructescences. Occasional *Deffenbachia* sp. 1 grew tangled among other vegetation on river rocks and banks.

Ascending away from the river, the same *Anthurium* is still seen, along with a birdsnest type which is likely the same as that lower down in the semideciduous zone, two more scandent *Anthurium* as well as three scandent species of *Philodendron*, including *P. hederaceum* (Jacq.) Schott. By far the most abundant aroid of the moist forest, though, was *Monstera dubia* (Kunth) Engl. & K. Krause, which persisted also in relict trees in pastures. A few *Monstera pinnatifidita* Schott were also seen. The second most common was *Syngonium macrophyllum* Engl. The terrestrial *Homalomena peltata* Mast. was rare, but occurred in banana groves as well as the forest.

By far the most interesting zone for Araceae, though, was the cloud forest, confined to the highest peaks: Cerro Sagrado and Gavilán. At 648 m, Cerro Sagrado is the fourth-highest peak in western Ecuador (Third Millennium Alliance 2010). In this zone were at least three species of *Anthurium* different from those of the moist forest, including one resembling *A. paludosum* Engl.; three of *Philodendron* – one of which had purple under surfaces of the leaves – also different from those of the moist forest; one of *Monstera* with entire leaves; and one of an unknown terrestrial genus bearing a resemblance to *Rhodospatha*. At this season, most species had developing infructescences, so it was not possible to determine the appearance of the spathes.

In addition to Araceae, there are also a number of species of a sister family, the Cyclanthaceae. Along the river grows a strictly-rheophytic species, which was the most abundant riparian vegetation along the Río Camarones, Río Ronquillo, and lowest section of the Río Chila, but entirely absent from the shallower Río Matapalo and Río Pomarosa. This species grew mainly on emersed rocks, its roots extending along the rock surface into the flowing water. The streams from which it was absent had generally muddy bottoms, as opposed to the rocky and sandy bottoms of streams where it was present.

Throughout most of the moist forest zone was an abundance of the famous "Panama-hat plant," *Carludovica palmata* Ruiz & Pav., often forming thickets in disturbed areas or secondary growth, but also abundant in primary forest. However, once again, it is the cloud forest that proves most interesting for Cyclanthaceae. *Cyclanthus bipartitus* Poit. has different juvenile and adult forms: in the juvenile stage, the leaves are entire, but with two midribs, whereas the adult stage has two leaflets each with one midrib. It also has unusual, ridged inflorescences. There is also a scandent species (possibly *Thoracocarpus bissectus* (Vell.) Harling), climbing up tree trunks.

Jerry Toth, Director of Jama-Coaque Reserve, is very interested in documenting the biodiversity in this largely scientifically-unexplored area. He would definitely be interested in hosting a proper botanical expedition, i.e. one with the proper collecting permits and equipment, which I unfortunately did not have. In 2009, herpetologist Paul Hamilton came to Jama-Coaque Reserve and discovered two species of frogs new to science (Third Millennium Alliance 2010). Given the high rate of plant endemism in the Chocó-Manabí corridor, I consider it highly likely that Araceae as yet unknown to science are present here.

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Figure 1. *Hapaline appendiculata* Ridl. Plants in habitat on basalt at Nanga Perom, Betong Division, Sarawak.

94300 Kota Samarahan
Sarawak, Malaysia
sywong@frst.unimas.my

ABSTRACT

Mature infructescences of *Hapaline appendiculata* Ridl., are described and illustrated for the first time.

INTRODUCTION

Hapaline Schott is a genus of eight species of terrestrial, usually deciduous geophytes occurring from Myanmar through SW China to Borneo. With the exception of the rather widespread *H. benthaminana* Schott, *Hapaline* species are all locally restricted; most species are associated with forested Karst limestone, although one, *H. celatrix* P.C.Boyce, occurs only on shales while another, *H. appendiculata* occurs on both limestone and basalt.

Hapaline species are seldom collected, possibly owing to their small stature and periodic dormancy (plants usually deciduous). Another factor maybe their often highly localized occurrence; paradoxically, however, where they do occur plants are often locally abundant [as noted by Burkill (1912)].

When the first author revised the genus (Boyce, 1996) he was fortunate to have access to living collections of three of the seven then-recognized species. This enabled accurate observation of the tiny but complex flowers. However, despite several attempts at pollination mature fruit were never produced; fruit descriptions given in Boyce (1996) are without exception based on preserved (pressed) material.

Two *Hapaline* species occur on Borneo: *H. appendiculata* Ridl. (Ridley, 1908), described from Kampung Puak, Bau, Kuching Division, Sarawak, where it is associated with Karst limestone, but extending as far east as the Belaga drainages (Kapit Division), where it occurs on basalt, and shale-obligated *H. celatrix* P.C.Boyce, described from Brunei, but also occurring in adjacent Miri and Limbang Divisions, Sarawak (Boyce & Wong, 2008). Since 2002 fieldwork by the authors has located a significant population of *H. appendiculata* at Tringgus, Bau (Boyce, et al., 2005), and further smaller populations close to the Kuching – Kalimantan border; all on karst limestone. Most recently a population on basalt was located in Nanga Perom, Betong Division and proved of particular interest since many plants were carrying ripe infructescences (Figure 1).



Figure 3. *Hapaline appendiculata* Ridl. Submature infructescence with the fruit forcing open the lower spathe. Note the green, opaque pericarp.

The Infructescences of *Hapaline appendiculata* Ridl.

by Peter C. Boyce and Wong Sin Yeng

Peter C. Boyce

Pusat Pengajian Sains Kajihayat [School of Biological Sciences]
Universiti Sains Malaysia 11800 USM
Pulau Pinang, Malaysia
phymatarum@gmail.com

Wong Sin Yeng

Department of Plant Science & Environmental Ecology
Faculty of Resource Science & Technology
Universiti Malaysia Sarawak



Figure 2. *Hapaline appendiculata* Ridl. Young infructescences. Note the spathe limb, and all spent portions of the spadix are already shed (brown scar), and that the persistent lower spathe partially envelops the developing fruits. Note that the stigma is uppermost on the berry.

Developing (submature) infructescences consist of the persistent lower spathe and associated fruit. The spathe limb, and all spent portions of the spadix are already shed, and the lower spathe partially envelops the developing fruits, which are turned to present the stigma uppermost (Figure 2). As the fruits continue to grow their increase in size forces open the lower spathe (Figure 3). It was observed that while younger infructescences often have two, rarely even three berries, none of the later stage infructescences have more than one. Once the fruit has reached full maturity the spathe quite suddenly reflexes, in a matter of a few minutes, to 'display' the ripe berry. At this point the pericarp also rapidly turns from opaque green to semi-transparent white, allowing the large bright green seed to be visible (Figures 4 & 5). It was noticed that once the spathe reflexed the berry became only loosely attached to the spadix, dislodging at a touch. The pericarp of fallen fruits is readily damaged, and sticky once so. It is speculated that the fruits/seeds are dispersed by foraging ants but observations are required to confirm this.

One further observation possible from this newly found site is that the plants appear to retain their

leaves for some time, as witnessed by the abundance of epicuticular cryptogams on the leaf blades (Figure 6). This is in contrast to the plants in west Sarawak (Kuching Division), which become dormant (deciduous) during extended periods of low rainfall.

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Figure 4. *Hapaline appendiculata* Ridl. Fruit at full maturity – lateral view. Note that the spathe has reflexed to 'display' the ripe berry. Note that the pericarp is now semi-transparent white, allowing the large bright green seed to be visible.



Figure 5. *Hapaline appendiculata* Ridl. Fruit at full maturity – ventral view. Note that the spathe has reflexed to 'display' the ripe berry. Note that the pericarp is now semi-transparent white, allowing the large bright green seed to be visible.



Figure 6. *Hapaline appendiculata* Ridl. The presence epicuticular cryptogams on the leaf blades suggest that the leaves are long-lived.

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Bernard Jadin, Husband of Aroider Frieda Billiet Dies in Belgium

by Thomas B. Croat, Missouri Botanical Garden



Figure 1. Frieda Billiet & Bernard Jadin.

Bernard Jadin was born on Sept. 30 September, 1948 at Namur, Belgium and died January 3rd, 2012 at Ottignies, Belgium. He worked more than 30 years at the commune (administrative division) of Rixensart. Bernard was in charge of the service Plantations (trees, shrubs and flowers of the public areas of Rixensart). Later he was transferred to the service Urbanism and Environment. Bernard retired in October 2008. He was passionately fond of zoology (especially birds) and botany. Autodidact, he became scientific collaborator of the Institut Royal des Sciences Naturelles de Belgique and also of the Fonds Leopold III pour l'Exploration et la Conservation de la Nature. This enabled Bernard to travel with his wife, Frieda Billiet, around the world, especially in America (Paraguay, Colombia, Venezuela, Ecuador, Peru, Bolivia, Chile, Argentina and mainly in French Guiana). He was clever with photography and enjoyed taking pictures of plants and scenery.

Bernard's wife Frieda was in charge of the living collections of the National Botanical Garden of Belgium at Meise and she is particularly fond of Araceae. She worked at Meise for more than 30 years and retired in October, 2005. Frieda still goes to the Garden once a week to make identifications of the numerous herbarium collections that she and Bernard made in Latin America. She also helps her colleagues maintain proper names on the living collections of plants, especially for the Bromeliads and aroids.

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