

The Araceae of Malesia I: Introduction

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A summary of the aroids of Malesia at the rank of genus and above is offered, covering 44 indigenous genera. Four additional genera (*Caladium* Vent., *Dieffenbachia* Schott, *Syngonium* Schott, and *Xanthosoma* Schott) are recorded as adventives. The aroid flora of Malesia currently encompasses 1105 indigenous species, with this figure based significantly on understanding of the flora of a few well-studied areas such as Peninsular Malaysia, Jawa, and parts of Malaysian Borneo. Large areas that remain very poorly known include Kalimantan (comprising more than 70% of the land surface area of Borneo), Sumatera, and much of the island of New Guinea. It is estimated that the total will readily exceed 1900 species. General notes on life-forms and taxonomically important morphologies are provided, together with a glossary. A key to Malesian aroid taxa at the rank of genus and above is presented.

Keywords. Araceae, Malesia, Indonesia, Malaysia, Philippines, Borneo, Sumatera, Jawa.

INTRODUCTION

The Araceae is a robustly monophyletic family comprising about 118 genera and approximately 3500 published species (Boyce and Croat, 2011) of herbaceous monocotyledons basal to the rest of the Alismatales (Stevens 2001). The current generic framework is essentially that of Mayo et al., 1997, although since publication there have been significant changes, including the recognition of several new genera in Indomalaya. The most recent molecular phylogenetic analyses of the entire Araceae are Cabrera et al. (2008) and Cusimano et al. (2011). A recent paper also analyses chromosome number evolution (Cusimano *et al.*, 2012). All recent molecular analyses provide good support of much of the internal topography proposed by French et al., (1995) and Mayo et al. (1997). Both also support former Lemnaceae (the duckweeds) to be nested in Araceae and sister to Pothoideae. *Acorus*, long treated as part of the Araceae, is now unequivocally a separate family

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in its own order, and basal to all extant monocots (Grayum 1987, Stevens, 2001).

The family is predominantly tropical in distribution, with 90% of genera and about 95% of species restricted to the tropics.

The family Araceae is most readily defined by characters of the inflorescence: small flowers borne on a fleshy axis (the spadix) subtended by a modified leaf (the spathe).

The sex of the individual flowers and their arrangement on the spadix are among the characters used to define taxonomic groups. The spadix may bear either unisexual or bisexual flowers. If bearing bisexual flowers these are mostly uniformly and densely arranged over the spadix.

Bisexual flowers are often subtended by reduced tepals termed a perigon. Unisexual flowers are usually arranged with the pistillate flowers at the base of the spadix and the staminate flowers above, with the zones occasionally separated by a further zone of sterile flowers. In the genus *Arisaema* individual inflorescences are usually either staminate or pistillate and the sex of the inflorescence is governed by the age of the plant, its health and the type of conditions in which it is growing. Young plants, or mature plants in poor condition or growing in a less than ideal habitat, will produce male inflorescences, while mature plants in good condition growing in an optimum habitat will produce female inflorescences. The ability to alter the sex of the inflorescence in this way is termed paradioecy. Unisexual flowers of aroids are almost without exception naked, that is, lacking a perigon.

LIFE-FORMS

Aroids for the greater part are plants dependent on abundant available water and prevailing high atmospheric humidity. Since both structurally and physiologically aroids are not well adapted for growth in arid or cold conditions, none are known occur in the most extreme environments, while those that occur in seasonally cold or arid habitats are for the most part geophytes (see below). Araceae are most diverse and abundant in the humid tropics, and it is there that the richest variety of their life forms is found. Indeed, relatively few genera inhabit temperate regions of the world and as noted these are either geophytes (e.g., *Arum*, *Biarum*, *Dracunculus*, *Eminium*, etc.) or helophytes (e.g., *Calla*, *Lysichiton*, *Orontium*, *Symplocarpus*, etc.).

The Araceae has perhaps the greatest life-form diversity of any flowering plant family with numerous life-form niches having at least one representative species. The most detailed general reviews ecology and life forms are those of Croat (1990, 1992) and Govaerts and Frodin (2003). Using the system Raunkiær (1934) with modifications, primarily from of Schimper (1903) life-forms include climbing or suffruticose primary and secondary hemiepiphytes (e.g., *Pothos*, most *Rhaphidophora*, etc.), epiphytes (rare in Asia, but including *Remusatia* and some *Scindapsus*), nanophanerophytes (stems persisting for several years; renewal buds above soil level but normally below 3 m – e.g., most *Aglaonema*, most *Apoballis*), mesophytic herbaceous phanerophytes (stems herbaceous and persisting for several

years; renewal buds above soil level – e.g., most *Homalomena*, some *Apoballis*), mesophytic chamerophytes (stems herbaceous and persisting for several years; renewal buds on or just above soil level, and never above 50 cm – e.g., most *Schismatoglottis*), lithophytes, rheophytes, and chasmophytes (growing in crevices of vertical rock, with vegetative and often reproductive structures pendent) (e.g., many *Schismatoglottis*, all *Piptospatha*), hemicryptophytes (stems, herbaceous, often dying back after the growing season, with shoots at soil level surviving; renewal buds just on or below soil level – e.g., *Hapaline*), geophytes (*Amorphophallus*), inland (fresh-water – e.g., some *Homalomena*, *Lasia*) or estuary (brackish-water, e.g., *Aglaodorum*) helophytes (hemicryptophytes growing in soil saturated with water or in water with the leaf and flower bearing shoots rising above water), amphibious or true hydrophytes (e.g., most *Cryptocoryne*), hydrohemicryptophytes (as for hemicryptophytes, but aquatic – *Pistia*), and hydrotherophytes (an aquatic therophyte – that is a plant that survived unfavourable seasons as minute resting buds, or as seeds – Lemnoideae).

The least specialized life-form is probably that of mesophytic herbaceous phanerophyte. This is typical of terrestrial herbs from perhumid to everwet and rainforest. Mesophytes are intolerant of atmospheric dryness, dry roots, and direct sun-exposure. They are among the first species to die-out when forests are heavily disturbed. Although mesophytism has been judged primitive in the family by some previous authors (e.g., Grayum, 1990), it is found predominantly in the more ‘advanced’ genera. Typical Malesian mesophytes are *Aglaonema*, *Homalomena*, and *Schismatoglottis* (all subfamily Aroideae). Among so-called ‘primitive’ groups only tribe Spathiphyllae (*Spathiphyllum* and *Holochlamys*), and some terrestrial *Anthurium* species, have this lifeform.

Amphibious or true hydrophytes, hydrohemicryptophytes (e.g., *Pistia*), and hydrotherophytes (Lemnoideae), are scattered throughout the family from very primitive groups (e.g., subfamily Orontioideae) and the Lemnoideae, to very advanced ones such as tribe Cryptocoryneae and *Pistia* (Aroideae). Within subfamily Lasioideae, *Lasia*, *Podolasia*, and many species of *Cyrtosperma*, have life-forms that appear intermediate between helophytic/mesophytic and geophytic/mesophytic. Predominantly African (but with one species in N Borneo) *Nephtytis* Schott, in which the rhizomes normally grow superficially, has a considerably more mesophytic habit than the strongly tuberous stemmed *Anchomanes* Schott and *Pseudohydrosme* Engl., the other two genera of tribe Nephtytideae. African *Culcasia* has many terrestrial species, spanning the hemiepiphytic/mesophytic categories, and *Philodendron* is similar. *Anubias* is predominantly helophytic but *Dieffenbachia* and *Spathiphyllum*, while typical of wetter habitats, also occur on drier ground within a humid tropical habitat.

Hemiepiphytes are commonest in the more primitive tribes and subfamilies. Most genera of subfamilies Pothoideae and Monsteroideae are hemiepiphytes and among more advanced genera this life form occurs only in African tribe Culcasieae, *Philodendron*, and *Syngonium*, all belonging to subfamily Aroideae. These genera show marked structural adaptations in their habit and in these features must be considered derived.

In the predominantly geophytic tribes Caladieae and Colocasieae, *Alocasia*, *Colocasia* and *Xanthosoma* each contain mesophytic species with decumbent to erect, arborescent stems; *Stuednera* and *Chlorospatha* are exclusively of this type. The most primitive Araceae, subfamilies Gymnostachydoideae and Orontioideae, are geophytes, rhizomatous helophytes or aquatics, and largely extra-tropical. While their habits are doubtless a prerequisite for survival in a more demanding climate, and therefore could have evolved from a mesophytic common ancestor, it is nevertheless equally possible that the mesophytic habit has evolved various times within the more advanced subfamilies from geophytic or helophytic ancestors. The geophytic habit is strongly represented in the relatively primitive subfamily Lasioideae and particularly common in the most advanced subfamily Aroideae. The rheophytic habit is characteristic of tribe Schismatoglottideae, the genera being almost exclusively rheophytic except for *Schismatoglottis*, which consists mainly of terrestrial mesophytic herbs.

Hemiepiphytes

Humid tropical forests are the characteristic habitat of hemiepiphytic genera. The species vary considerably in size, from shortly climbing plants found on the major branches or trunks of trees to huge plants with attached stems growing high into the forest canopy and producing enormously long, pendent flowering stems (e.g., *Scindapsus pictus*).

Hemiepiphytes can be divided into primary and secondary hemiepiphytes. Primary hemiepiphytes begin growth above ground level but produce feeder roots which eventually grow down to the forest floor. Secondary hemiepiphytes germinate on the forest floor, grow up tree boles, become detached from the ground by rotting of the juvenile stem but then become reconnected later by feeder roots which grow down from the upper internodes. Hemiepiphytic aroids typically have anchor roots as well, and are thus often called 'root climbers'. Flagelliform shoots, heteroblastic leaf development and shingle plants are characteristic features of hemiepiphytic Araceae, though not present in all species of each genus.

Highly developed heteroblasty coupled with skototropism, a specific growth strategy for seeking host tree boles, has been described in *Monstera* (Madison 1977, Strong and Ray 1975) and occurs in all climbing aroids in Malesia. In certain species the seedling is a very slender, plant with long internodes and minute scale leaves. Having germinated on the forest floor it seeks the defined area of shadow represented by the nearest tree bole. Once the tree has been reached the plant transforms itself into the shingle form and later, higher up, into a mature flowering plant. Vegetative reproduction may then take place by the production of flagelliform shoots. Seed size is almost certainly an important element in the growth strategies adopted by hemiepiphytes. The mature flowering region of the stem is short with abbreviated internodes and more-or-less rosulate foliage leaves. The continuation shoot climbs upwards and is slender and flagelliform with cataphylls instead of foliage leaves. After an interval it produces another rosulate-leaved mature zone. The repetition of this pattern produces a series of connected rosulate plants

one above the other on a single tree trunk.

Epiphytes

True epiphytes, which never become connected to the ground by feeder roots, are found in *Anthurium*, *Arophyton*, *Philodendron*, *Remusatia*, *Scindapsus* and *Stenospermation*. The seeds presumably germinate directly on the host tree after dispersal by birds or other animals. Many species of *Anthurium* sect. *Pachyneurium*, some *Philodendron*, and some species of *Scindapsus* are litter-basket epiphytes. The large leaves form an inverted cone in which leaf litter and other debris accumulate and into which the roots grow and ramify in a dense mass. *Remusatia vivipara*, which has a tuberous stem, is a widespread epiphyte, owing to the dispersal of hooked bulbils which are probably transported by birds and primates high in the forest canopy.

Lithophytes

Many hemiepiphytes, epiphytes and geophytes are also found as lithophytes in suitable conditions. Lianescent hemiepiphytes frequently grow on rocks in forest regions wherever shade and humidity are sufficient, the rock surface providing much the same conditions for attachment as tree boles. A number of geophytes are characteristically found growing in the eroded, litter or humus-filled cavities of limestone outcrops; examples are numerous *Amorphophallus*, and *Typhonium* species in S.E. Asia. Rheophytes are also typically lithophytic.

Geophytes

This category includes all genera with tuberous, rhizomatous, subterranean or partly subterranean stems. Geophytic aroids characteristically have periodic dormant periods when no leaves are present and these normally correspond to the dry season (or winter) of their habitat. However, rainforest geophytes exhibit growth periodicity and dormancy even in non-seasonal climates, e.g., *Amorphophallus* and *Typhonium*. Several genera occur in more than one kind of climatic regime. The genera *Amorphophallus* and *Dracontium* are similarly diverse ecologically, with species in rainforest or in seasonal evergreen forest, deciduous forest, savannas or grasslands. Strongly seasonal grassland species flower without the leaves at the end of the dry season, mostly after the first rains fall. Leaf and fruit development take place during the rainy season.

Rheophytes

Rheophytes (*sensu* van Steenis 1981, 1987) are flood-resistant plants, usually of tropical rainforests, growing in or along swift-running streams or rivers up to the flood level. They are characterized by narrow, leathery leaves and a firmly attached, usually epilithic stem. In addition to tribe Schismatoglottideae, in which the majority of genera have this habit, rheophytes are also found in *Homalomena*, *Anubias* and *Holochlamys*, and rarely in *Anthurium* and *Spathiphyllum*.

Submerged or periodically submerged aquatics

Many *Cryptocoryne* species are permanently submerged plants, either aquatic (permanently in water) or amphibious (subjected to seasonal drying-out of the habitat, often accompanied by plant dormancy). Either the inflorescence as a whole or its upper portion is held above the water surface while all other parts are completely submerged. *Cryptocoryne* is the largest genus of aquatic aroids and merits more detailed consideration. There are a number of species which are usually submerged but which are emergent at times of exceptionally low water (e.g., *C. affinis*). The submerged leaves of such species are relatively large, whereas the emergent leaves are quite small, indicating that such conditions are unfavourable to their growth. The submerged and emergent leaves of the same species generally look very different in shape, size, colour and structure. Submerged leaves are softer and emergent ones more coriaceous. Many species occur in the freshwater tidal zone where there is a daily cycle of exposure and submersion. Some species are found only in freshwater, like *C. affinis*, and *C. cordata*, while others can grow both in fresh and brackish water (*C. ciliata*). A few species are helophytes, preferring swampy conditions and growing during the dry season completely emergent in normal soil, like *C. spiralis*, a weed of rice fields in India. Usually *Cryptocoryne* species flower at low water level when the plants become emergent.

Helophytes

Helophytes are widespread throughout the family in many different taxonomic groups in both temperate and tropical genera. There is little constancy in habit type. The stem may be tuberous (e.g., *Caladium*, *Typhonium*), rhizomatous (*Homalomena rostrata*), rhizomatous and arborescent (*Montrichardia*), semi-prostrate to aerial (*Lasia*), erect and arborescent (*Philodendron*) or merely shortly erect and aerial (*Homalomena*). The helophytic life form may be considered relatively unspecialized in the majority of genera which exhibit it. Tuberous or rhizomatous stems may be associated with seasonally flooded habitats and a marked dry season. Rhizomes may, on the other hand, be adaptations for colonizing muddy riverine margins as in the case of the strict helophytes *Typhonodorum* and *Montrichardia*. Genera such as *Dieffenbachia*, *Homalomena* and *Spathiphyllum* generally exhibit no special adaptations in their helophytic species, which appear to take advantage of wetter habitats for more vigorous growth rather than because of a strict requirement for a flooded substrate.

Free-floating aquatics

The only free-floating species of Araceae are the pantropical *Pistia stratiotes* and the five genera of the Lemnoideae (former Lemnaceae – the duckweeds), four of which are native to Malesia.

INFLORESCENCES

The inflorescence of Araceae is composed of an unbranched spike bearing flowers, the spadix, subtended by a bract termed the spathe. Flowers are usually numerous, mostly small, sessile in most genera (exceptions include *Arisaema*, *Arisarum*, and *Pedicellarum*), and always lack floral bracts. Flowers are generally spirally arranged and usually tightly packed, although in some species of *Pothos*, *Pedicellarum*, *Amorphophallus* (staminate and pistillate flowers), tribe Spathicarpeae (pistillate flowers), and many species of *Arisaema* and *Arisarum* (staminate flowers), they may be somewhat distant from one another. The spathe is, strictly speaking, the last leaf of a flowering article [module]. It is often a specialized attractive organ, although in some genera (e.g., *Gymnostachys*, *Orontium*, *Pothos*, etc.) it is inconspicuous. The internode between spathe and spadix (the spadix stipe) is usually short or absent, while the peduncle – the internode between spathe and last foliage leaf or cataphyll – is usually much longer. However, in some basal taxa this arrangement is reversed (e.g., *Gymnostachys*, Orontioideae, some *Pothos* species, etc.).

The typical aroid inflorescence pattern has given rise to a wide range of morphological ‘forms’ in the different genera, which appear to represent an evolutionary trend of increasing integration towards a synflorescence.

Spathe and spadix modifications are often closely related so that the spathe may be seen evolutionarily as becoming increasingly integrated into the inflorescence itself, until in extreme cases, such as Cryptocoryneae, and the genera *Ambrosina*, *Pistia* and *Pinellia*, fusion and still more elaborate modifications have brought about division of the spathe into separate chambers. Other notable specializations of the inflorescence include the wide range of odours found in different genera, colour patterns, especially on the spathe, and the relative persistence of different regions of the spathe. In *Homalomena* and *Philodendron*, for example, the entire spathe persists until fruit, while in most genera of tribes Colocasieae, Caladieae, Peltandreae and Schismatoglottideae the spathe limb withers or falls during or very soon after anthesis while the lower spathe persists into fruiting. In many Monstereae the entire spathe withers or falls soon after flowering, a behaviour which is correlated in this tribe with the presence of numerous protective trichosclereids in the style tissue.

Terminal appendices of the spadix occur in tribes Areae, Arisaemateae, Colocasieae, Schismatoglottideae, Thomsonieae and Zomicarpeae, sporadically elsewhere in the family. The function of the appendix, where it has been investigated, is to produce odours to attract pollinators (osmophore, Vogel 1963, 1990). The appendix is either clearly composed of staminodes (e.g. some *Amorphophallus*) or partially to entirely smooth with no vestiges of floral organs (e.g., *Typhonium*).

Flowers in Araceae may be 2- or 3-merous. In perigyniate flowers the tepals, when free, are organized in two whorls. The tepals are usually more-or-less fleshy and fornicate apically. In some taxa (*Anadendrum*, *Holochlamys*, *Pedicellarum*, *Spathiphyllum* sect. *Massowia*, and *Stylochaeton*) the tepals are fused into a cup-like structure. Stamens in perigyniate flowers and in naked bisexual flowers of

most Monsteroideae have distinct (usually flattened) filaments, basifixed anthers and a slender, inconspicuous connective. In the unisexual flowers of many tribes of subfamily Aroideae, however, filaments are typically very short or effectively lacking, and there is a thick, fleshy connective which probably acts as an osmophore (Aglaonemateae, Culcasieae, Homalomeneae, Montrichardieae, Nephthytideae, Philodendreae, and Zantedeschieae). Stamens of tribes Anubiadeae, Caladieae, Colocasieae, Peltandreae, and Spathicarpeae are essentially similar but are always fused into synandria. In tribe Arophyteae the stamens may be fused or not and exhibit a diversity of structure. Large connectives also occur in tribe Spathicarpeae but their different morphology suggests that they are not homologous with those of the other tribes of subfamily Aroideae mentioned above.

Anthers are almost always extrorse (introrse in *Zamioculcas*, latrorse in *Pedicellarum*). Theca dehiscence may be by a longitudinal or rarely transverse slit (most genera with bisexual flowers and some unisexual-flowered genera: *Anubias*, some *Areae*, *Arisaema*, *Arisarum*, and *Stylochaeton*) or by apical or subapical pores, or short slits. In many genera of subfamily Aroideae dehiscence of each theca is by a subapical stomial pore and this morphology is frequently correlated with the extrusion of pollen in strands.

The gynoecium usually varies between 1- and 3locular, and when unilocular often shows traces of 2- or 3-merous origin through the presence of a several lobed stigma (e.g., *Typhonodorum*), or more than one placenta (e.g., *Schismatoglottis*). Gynoecia with more than 3 locules are less common, but occur in tribe Spathicarpeae (1–8 locular), and in *Philodendron* (2–47 locular). Placentation varies from axile to parietal, basal, apical or basal and apical (the latter in *Dracunculus*, *Helicodiceris*, some *Aridarum*, and *Theriophonum*), with many intermediates.

Ovules may be anatropous, campylotropous, orthotropous or intermediate between these types. Funicle trichomes are usually present (French 1987) and secrete a clear, mucilaginous substance which in many genera (e.g. tribe Monstereae, *Philodendron*) entirely fills the ovary locules; this secretion appears to play a role in pollen tube growth (Buzgó 1994). The style may be narrowed and elongated (e.g., *Dracontium* and some *Philodendron*) but in most genera is relatively inconspicuous externally. However, there is very often a thick stylar region between the ovary locules and stigma (e.g. *Philodendron*, Mayo 1989b). In tribe Monstereae this stylar region is especially well developed and densely filled with trichosclereids. Here the style seems to substitute functionally for a perianth in protecting the sexual organs of the flower. Stigmas are always wet in Araceae and in some genera (*Anthurium*, *Arum*, and several *Lasioideae*) produce conspicuous nectar droplets at anthesis. In *Amorphophallus*, *Dieffenbachia* and some Spathicarpeae, the lobing of the stigma can be very pronounced, or the stigma relatively massive. In subfamily Monsteroideae stigmas vary from subcapitate to conspicuously elongated, either transversely (e.g. *Anadendrum*) or longitudinally.

Infructescences

Fruits of Araceae are typically juicy berries, very rarely dry and/or leathery. The

berries are almost always free. Exceptions are *Syngonium*, in which the berries form an indehiscent syncarp, *Cryptocoryne* which has an apically-dehiscent syncarp, and *Lagenandra* in which the syncarpels open actively at the base to release the seeds. In the most Monstereae, the thick stylar region of the bisexual flower is shed to reveal the seeds. The stylar region is filled with trichosclereids which are thought to protect the developing seeds. In perigoniate genera such as most Lasioideae, and *Anthurium*, the perigone seems to play a protective role and keeps pace during growth of the developing berry, with the latter only becoming fully exposed at maturity by extrusion from the flower. In *Anthurium* the berries are held at the level of the tepals by slender filaments torn from the inner epidermis of the tepals. In *Lysichiton*, also perigoniate, the stylar region and tepal apices protect the young berry, eventually breaking off to reveal the ripe seeds (Hultén and St. John 1931).

In many unisexual-flowered genera a protective function is assumed by the persistent spathe or lower spathe. Spathe growth continues around the developing fruits until maturity when the spathe may split open (*Alocasia*, *Dieffenbachia*) or abscise at the base (*Philodendron*), exposing the infructescence of white or coloured berries. In other monoecious genera, however, the spathe is marcescent and plays no role in fruit protection. In such cases (e.g., *Arisaema*) protection may possibly be through the presence of toxic chemical compounds in the berries.

WEB RESOURCES

The following websites provide excellent and more importantly scientifically accurate information for the Araceae:

The International Aroid Society website: <http://www.aroid.org/>

Creating a Taxonomic e-Science – Araceae: <http://www.cate-araceae.org/>

Tropicos: <http://www.tropicos.org/>

International Plant Names Index: <http://www.ipni.org/>

World Checklist of Selected Plant Families (a constantly updated list of published plant names): <http://apps.kew.org/wcsp/>

The Crypts Pages (site dedicated to *Cryptocoryne* and *Lagenandra*): <http://crypts.home.xs4all.nl/Cryptocoryne/index.html>

Cryptocory.net (in Japanese but excellent images with scientific names: <http://cryptolove.jimdo.com/>

David Scherberich: <http://www.aroidpictures.fr/>

Bulletin of Russian *Anubias* forum: <http://anubias-engl.blogspot.com/>

Lemnoideae (duckweeds): <http://waynesword.palomar.edu/1wayindx.htm>

TAXONOMIC TREATMENT

Araceae Juss., Gen. Pl.: 23 (1789) ('Aroideae'), *nom. cons.*

Type genus: *Arum* L.

Lemnaceae Martynov, Tekhno-Bot. Slovar: 362. (1820) ('Lemnoides'), *nom. cons.*;

Lemnaceae Gray, Nat. Arr. Brit. Pl. 2: 729. (1822), *nom. cons.*

Type genus: *Lemna* L.

Pistiaceae Rich. ex C. Agardh, Aphor. Bot.: 130. (1822).

Type genus: *Pistia* L.

Callaceae Rchb. ex Bartl., Ord. Nat. Pl.: 25, 66. (1830).

Type genus: *Calla* L.

Orontiaceae Bartl., Ord. Nat. Pl.: 24, 68. (1830).

Type genus: *Orontium* L.

Arisaraceae Raf., Fl. Tellur. 4: 16. (1838).

Type genus: *Arisarum* Mill.

Pothaceae Raf., Fl. Tellur. 4: 16. (1838).

Type genus: *Pothos* L.

Cryptocorynaceae J. Agardh, Theoria Syst. Pl.: 32. (1858).

Type genus: *Cryptocoryne* Fischer ex Wydler

Dracontiaceae Salisb., Gen. Pl.: 7. (1866).

Type genus: *Dracontium* L.

Caladiaceae Salisb., Gen. Pl.: 5. (1866).

Type genus: *Caladium* Vent.

Philodendraceae Vines, Stud. Text-book Bot. 2: 540. (1895).

Type genus: *Philodendron* Schott

Monsteraceae Vines, Stud. Text-book Bot. 2: 540. (1895).

Type genus: *Monstera* Adans.

Colocasiaceae Vines, Stud. Text-book Bot. 2: 541. (1895).

Type genus: *Colocasia* Schott

Wolffiaceae Bubani, Fl. Pyren. 4: 22. (1902).

Type genus: *Wolffia* Horkel ex Schleid.

SCIENTIFIC DESCRIPTION OF ARACEAE

Perennial, evergreen or seasonally dormant bisexual, monoecious, rarely paradioecious, very rarely dioecious, sometimes gigantic, very rarely sub-microscopic, often laticiferous or sometimes resiniferous herbs; common life-forms (modified from Raunkiær, 1934 and Schimper, 1903) include climbing or suffruticose primary and secondary hemiepiphytes (e.g., *Pothos*, most *Rhaphidophora*, etc.), epiphytes (rare in Asia, but including *Remusatia* and some *Scindapsus*), nanophanerophytes (e.g., most *Aglaonema*, most *Apoballis*), mesophytic herbaceous phanerophytes (e.g., most *Homalomena*, some *Apoballis*), mesophytic chamaerophytes (e.g., most *Schismatoglottis*), lithophytes, rheophytes, and chasmophytes (many *Schismatoglottis*, all *Piptospatha*), hemicryptophytes (e.g., *Hapaline*), geophytes (*Amorphophallus*), inland (fresh-water – e.g., some *Homalomena*, *Lasia*) or estuary (brackish-water, e.g., *Aglaodorum*) helophytes, amphibious or true hydrophytes (e.g., most *Cryptocoryne*), hydrohemicryptophytes (*Pistia*), and hydrotherophytes (Lemnoideae). *Stems* aerial and erect to climbing or creeping with very short (plant rosulate) to very long (plant scandent) internodes, or subterranean and consisting of a subglobose to depressed-globose tuber (sometimes turnip- or carrot-like or irregular in shape) or horizontal to erect rhizome; shoot modules mono- to multi-phyllous, physiognomically monopodial with sympodia superposed, or very rarely true monopodial flowering terminally with the continuation shoot arising two nodes, rarely one node – Orontioideae) below the inflorescence, or apical portion of the shoot not renewing growth after flowering and the plant persisting by the release of lateral buds low on the shoot, the remainder of which subsequently dying; terrestrial plants and helophytes sometimes arborescent with massive stem and terminal rosette of leaves (*Alocasia*) or arborescent with a pseudostem of petiole sheaths (*Arisaema*, *Typhonodorum*); geophytes often with solitary leaf. *Leaves* usually spirally arranged, sometimes distichous; normally differentiated into petiole and expanded limb, usually glabrous, rarely pubescent, tomentose, villous, or with small to large and complex trichomes, or papillae, on the petiole or blade. *Prophylls* and *cataphylls* caducous, marcescent, deciduous or persistent, sometimes beautifully mottled and patterned (e.g., *Arisaema*, some *Alocasia*), sometimes prominently 1 or 2-ribbed, when persistent sometimes a conspicuous feature of plant and either membranous or forming fibrous mass (e.g., *Rhaphidophora korthalsii*). *Petiole* often as long as or longer than blade, usually smooth, sometimes hairy, papillose, warty, prickly or aculeate (e.g., Lasioideae, some *Amorphophallus*), often pulvinate apically (e.g., *Scindapsus*), basally or rarely centrally (e.g., most *Homalomena*); *petiolar sheath* normally well-developed, often at least half as long as entire petiole, frequently sheathed throughout in *Spathiphyllum*, *Rhodospatha* and *Philodendron* subgen. *Pteromischum*, sometimes ligulate apically (e.g., *Piptospatha*), less often much reduced (e.g., *Aglaonema brevispathum*). *Blade* simple to compound, extremely variable in shape – rarely filiform (e.g., some *Cryptocoryne*), linear (certain *Typhonium*), most commonly elliptic, ovate, oblong, sagittate, hastate, less commonly trifid to trisect, pedatifid to pedatisect, radiatisect, ‘dracontoid’ or ‘decompound’ (i.e., trisect with

each primary division further much divided), pinnatifid to pinnatisect, bipinnatifid, tripinnatifid to quadripinnatifid, fenestrate (*Rhaphidophora*) or laciniate (i.e., fenestrate with slit-like holes: *Amydrium medium*); heteroblasty frequent, especially in climbing hemiepiphytes, 'shingle leaves' sometimes formed (e.g., some Potheae, some Monstereae), sometimes markedly inequilateral (*Monstera*, *Philodendron* subgen *Pteromischum*); *venation*: midrib almost always differentiated, sometimes massive and succulent; primary veins usually arising pinnately from midrib (and then called primary lateral veins), either running into marginal vein (e.g., *Homalomena*) or joining distally to form a submarginal collective vein on each side (e.g., *Pothos*, *Anthurium*), sometimes primary veins all arising from petiole insertion and running arcuately into leaf apex (e.g., *Ariopsis*), rarely strictly parallel (not in Malesia) or subparallel (*Pistia*), sometimes not differentiated at all (e.g., *Epipremnum giganteum*); secondary and tertiary veins either reticulate (e.g., *Typhonium*), or parallel-pinnate, i.e., running parallel to primaries (e.g., *Piptospatha*), or arising from primaries at a wide angle and then arching strongly towards leaf margin (e.g., *Colocasia*), sometimes forming sinuous or zigzag interprimary collecting veins ('colocasioid' venation); higher order venation reticulated or forming cross connections between lower order veins (tessellate). *Inflorescence* terminal, solitary, or 2 to many in a synflorescence, consisting of a spadix (spike) of small flowers and subtended by a spathe (bract), usually erect, sometimes pendent (e.g., *Rhaphidophora hookeri*, *Piptospatha*), sometimes becoming pendent after anthesis (e.g., *Schismatoglottis*). *Peduncle* very short to very long, usually similar to petiole in appearance, coloration, pubescence or armature, normally longer than spadix stipe, sometimes \pm suppressed and spadix stipe elongated (e.g., some *Pothos*). *Spathe* nearly always conspicuous (except some *Pothos*), very variable in shape and colour, simpler forms often green, reflexed or spreading, more complex forms often showy and highly coloured, erect, usually either boat-shaped or constricted centrally to form a basal tube and an apical limb; tube may enclose the pistillate zone of the spadix or both fertile zones or rarely the entire spadix (e.g., *Cryptocoryne*), very occasionally much longer than limb (e.g., many *Cryptocoryne* spp.), tube margins usually convolute, sometimes connate (e.g., some *Sauromatum* and *Amorphophallus*); limb usually erect and gaping, sometimes widely spreading, twisted, reflexed or rarely margins \pm closed forming slit-like opening; spathe constriction may lie between or above staminate and pistillate zones or occur in two places (e.g., some *Remusatia* spp.); spathe entirely deciduous soon after anthesis (e.g., most Monstereae), or lower part persistent to fruiting and limb marcescent to deciduous after anthesis (most Schismatoglottideae), or spathe entirely persistent until fruiting (e.g., *Homalomena*) or whole spathe gradually withering and rotting (most Areae). *Spadix* usually erect but very variable, often fleshy and relatively thick, sessile or shortly stipitate, rarely very long-stipitate, usually free, sometimes adnate basally (e.g., *Hapaline*, *Schismatoglottis*) or entirely to spathe, either \pm uniform in appearance (flowers bisexual), or divided into distinct, usually horizontally demarcated, floral zones (flowers unisexual), fertile zones contiguous or separated by sterile zones, pistillate zone always basal and staminate zone either apical or intermediate in position; sterile zones basal, intermediate or

apical or any combination of these, apical sterile zone usually known as a terminal appendix and this often bereft of floral remains; rarely a single plant producing inflorescences bearing staminate flowers only, followed in later years by inflorescences bearing pistillate flowers only, and vice versa (paradioecious: *Arisaema*). *Flowers* 2- to 3-merous, bisexual or unisexual, often very small, protogynous, lacking floral bracteoles, usually numerous (except e.g., *Pistia*), almost always sessile, usually densely arranged, sometimes laxly so; bisexual flowers with or without a perigone (perianth), unisexual flowers usually without a perigone but sometimes including rudimentary organs representing modified sexual parts of the other sex (e.g., staminodes of pistillate flowers in *Steudnera*). *Perigone* composed of free or partially connate tepals, or consisting of a single cup-like structure; when free, tepals 4 to 6 (–8) and imbricate in 2 whorls, membranaceous or more commonly thickened at least apically, truncate to cucullate. *Pistillate flowers* (unisexual, aperigoniata flowers) with gynoecium sometimes surrounded by a whorl of variously shaped staminodes (e.g., *Steudnera*), or sometimes ± regularly associated with a single clavate staminode (e.g., *Homalomena*). *Gynoecium* (bisexual and unisexual flowers) with ovary usually 1–3 locular, rarely more, 1-locular ovaries probably always pseudomonomerous; ovules 1–many per locule, orthotropous, hemiorthotropous, campylotropous, amphitropous, hemianatropous or anatropous; placenta 1–several, axile, parietal, apical, basal, or basal and apical; stylar region (tissue lying between ovary and stigmatic epidermis) usually well developed, usually at least as broad as ovary, sometimes attenuate and elongate (e.g., some *Amorphophallus*, *Arisaema*) or massive and truncate (most *Monstereae spp.*); stigma hemispheric, capitate, discoid, umbonate, more-or-less strongly lobed (e.g., some *Amorphophallus*, *Alocasia*.), rarely stellately lobed (*Ariopsis*). *Appendix* present in some genera (e.g., Thomsonieae, Areae, most Schismatoglottideae), ranging from massively conic to filiform, mostly erect, rarely spreading or pendent, partly or completely covered with staminodes, variously rugose or corrugated or entirely smooth. *Sterile organs* (pistillodes, staminodes, synandrades) often forming zones between fertile zones, sometimes present below pistillate zone (Schismatoglottideae), or on base of terminal appendix, very variable in shape, most often ± truncate and prismatic less often filiform, subulate, bristle-like or elongate-clavate, spatulate, cylindrical (*Aridarum*) or enlarged and pearl-like, palmate to otherwise branched; the longer and more complex structures often motile. *Stamens* of bisexual perigoniata, bisexual non-perigoniata and unisexual perigoniata flowers usually free, equal in number and opposite to tepals (when present); filaments distinct, often ± oblong and flattened, rarely filiform, usually rapidly elongating to push anthers above perigone or gynoecium at anthesis; anthers usually terminal, basifixed, extrorse, composed of 2 thecae each with 2 microsporangia; connective usually slender, inconspicuous, often overtopped by thecae, thecae dehiscing by single longitudinal slit or apical stomial pore, with all intermediate degrees occurring. *Pistillate flowers* (unisexual aperigoniata flowers): 1–8-androus, floral grouping of stamens sometimes obvious in mature inflorescence (e.g., many *Philodendron* and *Homalomena spp.*, sometimes not, e.g., *Aglaonema*); stamens free or partially to completely connate to form a synandrium. *Stamens* (unisexual

aperigoniata flowers): usually sessile to subsessile, filament sometimes distinct (e.g., *Schismatoglottis*), connective sometimes \pm slender but often strongly thickened, apically broad, fleshy, thecae lying opposite or adjacent on one side of stamen, dehiscing by single longitudinal slit or apical pore, rarely theca prolonged apically into a horn dehiscing by single pore (tribe Cryptocoryneae). *Synandrium* (unisexual non-perigoniata flowers) usually \pm sessile, sometimes formed by fusion of filaments only (e.g., *Arisaema*), most commonly composed of completely connate stamens and then usually apically truncate and \pm prismatic (e.g., *Colocasia*, *Alocasia*), very rarely the synandria themselves connate (*Ariopsis*); common connective (synconnective) usually broad, fleshy (e.g., *Alocasia*); thecae either lateral, apical or marginal depending on the degree of elongation of the thecae and the extent to which they are overtopped by the synconnective. *Infructescence* usually densely packed, uncommonly few-fruited or fruits scattered, cylindrical to globose, exposed by withering, basal abscission (e.g., *Homalomena*) or apical splitting (e.g., *Alocasia*) of spathe, rarely fruits dehiscent, either basally (*Lagenandra* – absent from Malesia) or apically (*Cryptocoryne*) or with seeds exposed by \pm simultaneous sloughing of stylar regions of all fruits ('monsterocarps' in Monstereae). *Fruit* mostly a juicy berry, rarely mesocarp leathery, less commonly an apically (*Cryptocoryne*) or basally (*Lagenandra*) dehiscent carpel or with the stylar regions sloughing ('monsterocarp' in Monstereae); berries normally free, rarely connate (*Syngonium*), often usually red, orange or purplish red, but white (e.g., some *Amorphophallus*), yellow (some *Amorphophallus*), green (some *Typhonium*, *Pycnospatha*, *Lasia*), blue (some *Amorphophallus*), purple (some *Typhonium*) or brownish (some *Typhonium*) occurring. *Seed* 1–many per fruit; testa thick to thin, smooth, roughened, verrucose or striate-costate, papery in seeds with highly developed embryos, sometimes decaying at maturity, or lacking altogether, sometimes arillate with a conspicuous strophiole (e.g., many *Araceae*), rarely operculate (e.g., *Pistia*); embryo usually straight, sometimes curved, usually undifferentiated, rarely with highly developed plumule (e.g., *Cryptocoryne ciliata*) and then endosperm lacking and outer cell layers of embryo chlorophyllous; endosperm copious or absent, with all intermediate states occurring.

The *Araceae* is subcosmopolitan in distribution, but most abundant and diverse in the humid, perhumid and everwet tropics. *Araceae* is currently considered to comprise ca. 121 genera, and maybe ca 6000 species (Boyce and Croat, 2011). A high percentage of this species total is still awaiting formal description, and undoubtedly many more, including new genera, await discovery.

GLOSSARY

The *Araceae* present a series of morphologies, including several unique floral structures, and still others with their own terminology. There are here presented together with morphological terms that the authors feel are frequently misapplied in common usage.

adnate – the fusion of *two different structures*, e.g., spathe and spadix; *c.f.*, connate.

amphitropous (ovule) – an ovule with its axis strongly curved like a horse-shoe so that the micropyle and funicle are situated near to each other.

anastomosing laticifers – laticifers which branch and fuse with others forming a network.

anatropous (ovule) – ovule with a more-or-less straight axis.

anchor root – roots which anchor a hemiepiphyte or epiphyte to its substrate, generally a tree or rock.

anterior division [of leaf blade]– that part of the leaf blade which lies above a horizontal line drawn through the petiole insertion (i.e., perpendicular to the midrib); that part of the leaf blade which surrounds the midrib; *q.v.* posterior division.

apical placentation – placenta situated at the apex of the ovary locule.

article (or module) – a sympodial unit; a determinate unit of a sympodium derived from a single meristem.

axile placentation – placenta (or placentae) situated along the central angle formed by the septa of a multilocular ovary.

basal placentation – placenta situated at the base of the ovary locule.

bipinnatifid (leaf blade) – a leaf blade divided pinnately, with each primary pinna (or lobe) itself divided pinnately; *see also -fid*.

bisexual flower – hermaphrodite, i.e., a fertile gynoecium and androecium present in each flower.

caducous – cataphyll or spathe falling when tissues are still fresh and alive.

campylotropous (ovule) – ovule with its axis slightly curved; *q.v.* **amphitropous**.

cataphyll – a modified leaf which lacks a limb and in appearance corresponds to a petiole sheath; may be used to describe other leaf types whose technical names are defined by position rather than form, e.g., prophylls are usually of cataphyll shape in Araceae, *q.v.* **prophyll**.

chasmophyte – species adapted to growing on vertical surfaces with no running surface water.

colocasioid venation – a type of higher order leaf venation found primarily in tribes Colocasieae and Caladieae in which the finer veins branch almost at right angles from the primary lateral veins and then arch strongly towards the leaf margin, often fusing along the way to form a more-or-less sinuose interprimary collective vein between the primary lateral veins, and finally joining within the margin to form a submarginal collective vein.

connate – of two organs *of the same type* which are fused together, e.g., stamens; *q.v.* adnate.

connective – the tissue which connects the thecae of an anther; *see also* **synconnective**.

continuation shoot – the succeeding sympodial unit (= article or module) at any point in a sympodium.

contractile root – a type of root common in, e.g., tribes Areae and Arisareae that contracts following initial extension and serves to prevent the tuber from growing above the soil surface, or even pulls the tuber further into the soil.

convolute – *see* supervolute

decompound (leaf blade) – leaves with the blade trisect, the primary divisions usually pinnatisect, bipinnatisect or dichotomously further divided, rarely undivided, highest order divisions (leaflets) entire, never fenestrate or lobed and only ever with one tip and bases decurrent, rarely petiolulate; *see* *Amorphophallus* and *q.v.* ‘**dracontioïd**’.

‘**dracontioïd**’ (leaf blade) – elaborated forms of sagittate, hastate or trisect leaf blades in which the anterior and posterior divisions are highly dissected and subdivided, highest order divisions entire, often fenestrate, or lobed and with two tips or more tips; *see* *Pycnospatha* and *q.v.* **decompound leaf**..

epigeal — of an organ or process located above the ground, usually applied to stems, *q.v.* **hypogeal**.

epiphyte – a non-parasitic plant which grows on another plant, its host, and which is not connected to the ground during its life cycle.

female flower – a flower composed only of a gynoecium, sometimes associated with one or several staminodes, a perigone maybe present or absent; = **pistillate** flower.

fenestrate (leaf blade) – equivalent to perforate; a leaf blade with holes between the major veins that have arisen by necrosis at an early stage in ontogeny.

-fid – division of a leaf blade in which the sinus between each lobe extends only part way to the midrib; *q.v.* **-sect**.

flagelliform (branch/shoot) – fast-growing branches in which the internodes are more elongated and the leaves somewhat to highly reduced; a typical adaptation of hemiepiphytes for searching out and colonizing new host trees.

floral sympodium – that part of the sympodial flowering shoot composed of two or more successive inflorescences and their associated cataphyllary prophylls, e.g., the pseudoaxillary spadix clusters in *Homalomena*, many *Philodendron* species, etc.,

geniculum, geniculate – *see* **pulvinus, pulvinate**

geophyte – plants that have subterranean stems, implies a tuberous or rhizomatous habit

gynoeceium – equivalent to pistil; the female organ consisting of ovary, styler region or style and stigma.

hapaxanthic (shoot) – shoot which ceases growth after flowering and does not flower again, *q.v.* **pleioanthic**

helophyte – plants adapted to grow in swampy conditions but with the leaves and shoots in full sun.

hemiepiphyte – plants which grow on hosts and are detached from the ground at some stage of their life cycle, later becoming reconnected with the ground by sending down feeder roots.

hemiorthisotropous (ovule) – an ovule in which the micropyle points away from the funicle but in which the funicle is attached sublaterally near the chalazal end and not terminally; *see* **orthotropous**.

hypogean – of an organ or process located below ground, usually applied to stems, *q.v.* **epigeal**.

heteroblasty – the production of leaves of differing shape and size during the development from juvenile to mature form; typical of hemiepiphytes.

imbricate – overlapping.

infructescence – the inflorescence at fruiting stage, i.e., the mass of fruits considered as one composite structure.

interprimary vein – a vein, thicker than the fine veins but thinner than the primary lateral veins, lying approximately parallel to and between them.

intramarginal collective vein – leaf; a vein running parallel to and near the leaf margin into which the primary lateral veins run, diagnostic of brochidodromous leaf venation; *see Pothos*.

intrusive, intrusive-parietal (placenta) – a placenta borne on a septum that extends from the ovary wall almost to the centre of the locule.

involute – a form of folding of a single leaf in which the two leaf margins are each in-rolled without either clasping the other, as in *Lagenandra*. *Anthurium* sect. *Pachyneurium*

kettle – a basal tubular portion of the spathe in which the margins are connate, forming a chamber; characteristic of *Lagenandra* and *Cryptocoryne*.

laticifers – longitudinal rows of slender, tubular cells usually associated with vascular bundles and containing clear or milky fluid called ‘latex’.

ligule, ligulate – a free extension of the apex of the petiole sheath; very elongated in most genera of the Schismatoglottideae.

lithophytes – plants that grow on rocks.

male flower – a flower composed only of an androecium, sometimes associated with a pistillode, a perigone maybe present or absent; = staminate flower.

marcescent – cataphyll or spathe; remaining attached to the plant after death and partial decomposition of tissues.

microsporangium, microsporangia – the individual pollen sacs making up the thecae and anthers; in Araceae each theca is normally composed of 2 microsporangia, and each anther of 2 thecae, although there are exceptions in, e.g., *Homalomena* [*H. monandra* M.Hotta].

midrib – the large, central, axial vein of the anterior division of the leaf.

monopodium, monopodial – a shoot axis which is formed by the vegetative extension of a single apical meristem.

‘monsterocarp’ – infructescences with individual fruits with stylar regions greatly enlarged and at fruit maturity transversely dehiscent, the abscission developing at the base of the enlarged to massive stylar region and this falling, taking with it the raphides that serve protect the developing fruit, to expose the ovary cavity with

the many seeds embedded in variously coloured sticky pulp.

orthotropous (ovule) – ovule in which the body of the ovule is straight, the micropyle faces directly away from the funicle and the funicle is attached terminally (not laterally) to the chalazal end of the ovule.

paradioecy – the production, from the same stem, of entirely male or entirely female inflorescences in different seasons; in Araceae observed only in *Arisaema*.

parietal – borne on a wall, of ovules in which the placenta and hence the funicle attachment lie on the side walls of the ovary.

pedate (pedatifid, pedatisect) – literally, foot-shaped; of a leaf divided in such a way that the midribs of the lateral segments, lobes or pinnae are inserted successively on two basal ribs rather than all together at the petiole insertion; cf. **radiati-**; see e.g., *Sauromatum*.

peduncle – the internode between the spathe and the preceding leaf.

perianth – the floral envelope consisting of calyx and corolla; in Araceae referred to as a perigone.

perigone – the floral envelope of a flower in which there is no differentiation of calyx from corolla, it may be a single structure (connate tepals) or composed of individual, similar tepals; - see also **perigoniate**.

perigoniate – of a flower which possesses a perigone.

persistent – of a leaf or spathe which remains attached, with its tissues alive and functioning.

petiole sheath – the basal, sheathing part of the petiole which normally has an annular insertion at the node; the sheath may be conspicuous or not, and persistent or not.

pinnati- (pinnatifid, pinnatisect) – of a leaf blade divided pinnately; *q.v.* **-fid** and **-sect**.

pistil – equivalent to gynoecium.

pistillate – female flowers or the [pistillate] zone of the spadix bearing female flowers.

pistillode – sterile floral structures considered homologous (in position or form or both) to gynoecia (pistils), but which lack ovules.

placenta (plural: **placentae**) – specialized area of tissue within the ovary to which the ovules are attached by their funicles; in Araceae the placentae are almost always covered with a dense epithelium of glandular hairs which secrete a clear, mucilaginous substance.

placentation – the position of the placenta or placentae within the ovary; e.g., apical, axile, basal, parietal, etc.

pleioanthic (shoot) – one which resumes growth after flowering and may flower again, *q.v.* **hapaxanthic**

primary lateral veins – the veins which extend into the leaf blade from the stem via the petiole.

prophyll – the first leaf of a branch (or sympodial unit); in Araceae almost always a 2-keeled cataphyll, often confused with cataphyll:– cataphyll refers to a particular type of morphology (reduced leaf), prophyll refers to the position of the leaf along a branch.

protogynous – a plant or inflorescence or flower in which the stigmas become receptive before the anthers release their pollen.

pseudostem – an erect, stem-like structure formed by tightly imbricate leaf sheaths, as in bananas; *see Arisaema*.

ptyxis – the manner in which a single leaf is folded while still in bud; *see involute, supervolute*. Note: This term has been confused with “vernation”.

pulvinus, pulvinate – swelling or joint located usually at the apex of the petiole that permits independent movement of the leaf blade during leaf development but which movement ceases once leaf is mature; *q.v.*, **geniculum, geniculate**

raphides – microscopic to macroscopic (up to 1 cm) needle-like crystals of calcium oxalate.

resin canal – tubular structures within vegetative and floral tissues of certain genera which contain as yet inexactly determined substances, probably of terpenoid type; resin canals are often conspicuous as translucent lines or dots on leaf blades, and petioles e.g., *Homalomena*.

reticulate (leaf venation) – fine leaf venation of a net-like pattern.

rheophytes – plants which grow usually attached to rocks in the flood zone fast-flowing streams between the high and low seasonal water levels and usually submerged during the flood season and exposed to desiccation during the dry season.

sessile – lacking a stalk, pedicel, peduncle, style or stipe.

secondary and tertiary veins – leaf veins of successively higher order branching and (usually) finer than the primary lateral veins.

-sect – division of a leaf blade in which the sinus between each lobe extends completely to the midrib; *q.v.*, **-fid**.

shingle (climber, leaves, plant) – a type of juvenile morphology, found in some hemiepiphytic species, in which the petiole is very short and the leaf blade relatively broad and more-or-less overlapping with its neighbours to resemble the tiles (or shingles) of a roof; such plants are found climbing up larger tree trunks; e.g., *Pothos curtisii*, *Rhaphidophora korthalsii*, *Monstera* sect. *Marcgraviopsis*

simple (leaf blade) – a leaf blade which is neither lobed nor subdivided.

spadix – a spike (racemose inflorescence with sessile flowers) with a thickened axis; in Araceae the axis is almost always rather fleshy and the flowers are not subtended by floral bracts; *see* spathe.

spathe – a simple, bract-like foliar organ associated with the spadix; morphologically the last ‘leaf’ of the flowering shoot (sympodial unit) in Araceae; the spathe is usually coloured and may have a complex shape; the combined unit of spathe and spadix is widely regarded as the ‘inflorescence’ in Araceae, since there is such an intimate morphological and functional relationship between them; however, in strictly morphological terms it is the spadix which is the inflorescence, while the spathe is a modified leaf; *see* spadix.

spathe limb – the upper, expanded (sometimes only temporarily) part of the spathe.

spathe constriction – a constricted portion of the spathe occurring in many genera of Araceae; generally occurring at the point corresponding to the junction between the staminate and pistillate zones of the spadix (e.g., *Alocasia*).

spathe ‘tube’ – the lower part of the spathe formed by the supervolute (= convolute) or sometimes connate margins.

staminate – Male flowers or the [staminate] zone of the spadix bearing male flowers.

staminode, staminodes, staminodia – sterile floral structures considered homologous (in position or form or both) to stamens but which lack microsporangia. The term is often applied in the Araceae to structures which are substantially different in form to the fertile stamens; *see e.g.*, *Typhonium*.

sterile appendix – a terminal portion of a spadix which is covered with sterile

flowers, staminodia or may be merely rough to smooth; probably always omphophoric; e.g., *Amorphophallus*, *Typhonium*.

sterile flower – this term is often applied in Araceae literature to infertile floral structures occurring on the spadix that bear little or no resemblance to fertile flowers, but which are probably derived ontogenetically from primordia which are homologous to floral primordia.

sterile interstice – a portion of the spadix which bears sterile flowers or lacks fertile floral organs or tissues, or lacks any kind of floral organ or specialized tissues, and consists of a simple, smooth axis.

stipe – a stalk; in Araceae used especially to refer to the axial region commonly present between the spathe insertion and the base of the floral zone of the spadix proper; see e.g., *Pothos*.

stipitate – borne on a stipe or stalk.

stolon – a stem branch specialized for vegetative reproduction by long internodes and, usually, reduced leaves.

striate – marked with fine, longitudinal parallel lines.

strophiole – an aril-like (fleshy) outgrowth of the raphe of a seed, usually appearing as an appendage to the hilum ; thought to be a structure that plays a role in seed dispersal (?food attractant to vectors).

stylar region – tissue lying between ovary locules and stigmatic epidermis, distinguished from ‘style’ because it is often as thick as the ovary in Araceae.

style – a stylar region which is narrower than the ovary and somewhat elongated.

suffruticose – shrubby growth; in aroids such plants mainly branch basally.

supervolute – a type of ptyxis in which one side of the leaf blade is wrapped around the other; also called convolute; *q.v.* **involute**

sympodium, sympodial – a shoot axis built up by a linear series of units (sympodial units), each new distal unit developing from a single apical meristem arising from an axillary bud situated on the previous unit; the axis is thus constructed successively by the activity of several different apical meristems; *q.v.* **monopodium**.

synandrium, synandria – a male flower composed of connate stamens, often over-topped by greatly expanded common connective tissue termed a **synconnective**.

synandroidium, synandroides, synandrodia – a sterile synandrium, i.e., shaped like a synandrium but lacking microsporangia.

syncarp – an infructescence in which the component fruits are congenitally or post-genitally fused together.

synconnective – the common connective tissue derived from few to many stamens connate into a synandrium.

synflorescence – (in Araceae) complex inflorescence composed of several spadices; equivalent to floral sympodium.

tepals – the individual component parts of the floral envelope or perigone; distinguished from sepals and petals in that the tepals of a single flower are all similar in shape and colour.

terminal appendix – *see* sterile appendix.

terrestrial – of a plant which grows on the ground (in contrast to, e.g., an epiphyte) or on dry land (as distinct from an aquatic or helophyte).

theca, thecae – an adjoining pair of microsporangia; *see* **microsporangium**.

trichosclereid – a microscopic hair-like sclereid; fibre cells (cells with thick, lignified walls) which are very slender and elongated so as to be visible to the naked eye as hair-like structures (e.g., on tearing the leaf blade they can be seen emerging from the torn edge, as in e.g., *Rhaphidophora*); either T or H-shaped.

tri (trifid, trisect) – of a leaf blade which is subdivided, partially or completely, into three parts:– a central anterior division and two posterior divisions.

tuber – in Araceae used to describe the swollen, subterranean stems characteristic of many genera, e.g., *Arisaema*, *Amorphophallus*, *Typhonium*, etc.

tubercule – small tubers that develop from axillary buds or accessory buds on leaves, e.g., *Amorphophallus*, *Typhonium*.

KEY TO MALESIAN ARACEAE UP TO THE RANK OF GENUS

- 1a. Plants comprising small to minute few-rooted or rootless free-floating thallus-like leafless bodies Lemnoideae (>2)
- 2a. 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
- 3a. 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

- 4a. Plant bodies 1–1.5 times as long as wide, with 7–12 roots of which 1(–2) perforate the scale *Spirodela*
- 4b. 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*
- 2b. Roots 1 per plant body; plant bodies with 1–3 veins, without a scale at the base *Lemma*
- 3b. 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*
- 1b. Plants not as above. If free-floating then leaves forming a conspicuous rosette with copious roots hanging beneath
- 5a. Flowers bisexual, each with a perigone of conspicuous tepals
- 6a. Armoured helophytes (or rarely peat-swamp mesophytes) with hastate to 4×pinnatifid leaves Lasioideae (>7)
- 7a. Stems suffruticose, erect to decumbent, usually with prickly conspicuous internodes; leaves hastate to (4×)pinnatifid; spathe caducous, rarely marcescent; placentation apical; fruit usually spinulose *Lasia*
- 7b. 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
- 8a. Spathe interior white, 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*
- 8b. Spathe interior red-purple, infructescence erect, fruits emerging fully from between the tepals, ripening bright red; seeds smooth; plant with spines mixed straight and down-turned *Podolasia*
- 6b. Plants never armoured, mostly climbing hemiepiphytes, some mesophytes
- 9a. Climbing hemiepiphytes; spathe often inconspicuous, variously coloured but never white; fruits a free berry, ripening red or orange, very rarely white or purple Pothoideae: Potheae (>10)
- 10a. Flowers pedicellate, with a distinct receptacle; tepals of perigone connate forming a conspicuous ‘cup’ *Pedicellarum*
- 10b. Flowers sessile, without a receptacle; tepals of perigone free, very rarely united, if united then not forming a ‘cup’
- 11a. Flowering shoot terminating in a (leafless) branching system of spadices; flowers functionally unisexual *Pothodium*
- 11b. Flowering shoot with inflorescences mostly axillary or infra-axillary, if terminal then inflorescence system not branching, and leafy; flowers bisexual *Pothos*
- 9b. Mesophytes; spathe large, white; fruits green, encased in persistent green tepals Monsteroideae: Spathiphyllae (>12)
- 12a. Inflorescences held down among the leaf bases; spathe limb enclosing the spadix throughout anthesis, not expanding; marcescent into fruiting *Holochlamys*
- 12b. Inflorescences held above the leaves; spathe limb spreading expanding; persistent and turning green during fruiting, later falling *Spathiphyllum*
- 5b. Flowers bisexual, naked, or bisexual with a perigone of inconspicuous tepals, or unisexual
- 13a. Flowers bisexual, perigone (if present) membranous and inconspicuous; mostly climbing hemiepiphytes, rarely rheophytic Monsteroideae: Monstereae (>14)
- 14a. 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*
- 14b. Flowers naked; inflorescences very short to long-stout-pedunculate, solitary or few, not carried in a fan; spathe in 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*)
- 15a. Venation reticulate; infructescence with discrete berries; trichosclereids very sparse ... *Amydrium*
- 15b. Primary venation striate; higher order venation reticulate; infructescence a monstercarp; trichosclereids abundant
- 16a. Ovules solitary, placentation basal; fruits each with a solitary large seed *Scindapsus*
- 16b. Ovules 2–6 or more, placentation parietal; fruits with more than one seed
- 17a. 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*
- 17b. 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*
- 13b. Flowers unisexual Aroideae (>18)
- 18a. Free-floating plants with leaves forming a conspicuous rosette with copious roots hanging beneath Pistieae (*Pistia*)
- 18b. Not so, stems attached to substrate.
- 19a. Leaf blade variously divided
- 20a. Leaf blade decompose; inflorescences usually appearing before leaf emergence, with flowers of both sexes (i.e., monoecious) Thomsonieae (*Amorphophallus*)
- 20b. Leaf blade trifoliate to pentafoliate; inflorescences produced with leaves, usually single-sexed Arisaemateae (*Arisaema*)
- 19b. Leaf blade simple, ranging from linear-lanceolate to hastate
- 21a. Aquatic plants; infructescences composed of carpels connate into a syncarp, each carpel opening from the apex Cryptocoryneae (*Cryptocoryne*)
- 21b. Plants not aquatic; infructescences comprised of berries.
- 22a. Plants suffruticose, or with a creeping rhizome-like stem; fruits conspicuous red or pink or green berries not surrounded by a persistent spathe Aglaonematineae (>23)
- 23a. Colonial helophytes with creeping spongy rhizomes and erect, spongy petioles; fruits large, ripening green and functioning as floating dispersal units *Aglaodorum*
- 23b. 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*
- 22b. Plants not suffruticose; fruits various, mostly green, if red or orange red berries then surrounded by a persistent spathe
- 24a. Entire spathe closing after anthesis and then persisting until fruit maturity
- 25a. 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 Nephthytidineae – *Nephthytis*
- 25b. 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 (>26)
- 26a. Staminate flower consisting of solitary stamen overtopped by flask-shaped pistillode; ovary 1-locular, placenta basal *Furtadoa*

- 26b. Staminate flower consisting of 2–6 stamens, pistillodes absent; ovary incompletely 2–5 locular, placentas parietal and axile *Homalomena*
- 24b. 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
- 27a. Staminate flowers forming synandria (Colocasieae [and Caladieae] >28)
- 28a. Spathe not obviously with a lower tubular part separated from the spathe limb by a conspicuous constriction; spathe white; pistillate flowers few, arrange in two longitudinal rows; fruits ripening white, enclosed in the folded lower spathe, this reflexing to reveal the fruits but not actively splitting; pericarp very thin, seed large, bright green Caladieae (*Hapaline*)
- 28b. Spathe with a well-defined lower tubular part separated from the spathe limb by a pronounced constriction and forming a chamber enclosing all or most of the pistillate flower zone; pistillate flowers many, arranged in a dense spiral; fruits ripening red or yellow-brown, usually exposed by the lower spathe actively splitting; pericarp thick, seeds medium to very small, brown
- 29a. Plant with conspicuous erect aerial stolons bearing numerous barbed bulbils *Remusatia*
- 29b. Plant without conspicuous erect aerial stolons, if stolons present then these decumbent and bearing tubercles at tips
- 30a. Mature infructescences erect; placentation basal; fruit red when ripe, odourless; seeds large, few per fruit; leaf blades abaxially with waxy glands in the axils of at least the primary veins *Alocasia*
- 30b. Mature infructescences declined to pendent; placentation parietal; fruit pale yellow to brown and fruit-smelling when ripe; seeds small, very numerous per fruit; leaf blade glands absent *Colocasia*
- 27b. Staminate flowers not forming synandria
- 31a. Tuberos-stemmed geophytes; sterile flowers between the staminate and pistillate flower morphologically distinct from fertile flowers; spadix with a conspicuous naked appendix Areae (>32)
- 32a. 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*
- 32b. Sterile zone between pistillate and staminate zones fully covered with staminodes, or grooved and with staminodes only at base; leaves usually pedate, rarely entire (in *S. giganteum*); staminodes never spatulate *Sauromatum*
- 31b. Mesophytes, rheophytes, lithophytes and chasmophytes, stems never tuberos; sterile flowers between the staminate and pistillate flower zones) if present) morphologically similar to fertile flowers; spadix appendix (if present), never naked Schismatoglottideae (>33)
- 33a. Wings of petiolar sheath fully or almost fully attached to the petiole, if free ligular then foliage leaves arranged distichously; seeds never with a micropylar appendage
- 34a. Inflorescences on very slender peduncles, nodding at anthesis, peduncle at spathe insertion flexing 180° from vertical axis; infructescences narrowly campanulate, nodding; plants of podsols *Hestia*
- 34b. Inflorescences erect to nodding at anthesis, if nodding, then either peduncle massive, and peduncle at spathe insertion at most 45° from vertical axis. Infructescences fusiform with a constricted orifice, if campanulate, then thick-walled and erect, never nodding; plants of various substrates but never on podsols
- 35a. Modules monophyllous, congested in a distichous arrangement; petiolar sheath ligular free portion persistent *Pichinia*
- 33b. Wings of petiolar sheath always extended into a free ligular portion; seeds sometimes with micropylar appendage

- 36a. Spathe not constricted; plants glabrous
- 37a. Thecae of anther never with horn- or needle-like projections
- 38a. 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
- 39a. 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*
- 39b. Staminate flowers all fertile; spathe persistent throughout the fruit dispersal; ovules parietal; seeds with a pronounced, hooked, micropylar appendage *Ooia*
- 38b. Spadix free; spathe limb caducous during anthesis; infructescence on erect peduncle; lower spathe forming a splash-cup *Piptospatha*
- 37b. Thecae of anther each with a horn- or needle-like projection, although these sometimes visible only after pistillate anthesis
- 40a. Thecae with needle-like projection extending only after pistillate anthesis; projection tipped with a weakly peltate ovate-triangular flap; appendix composed of pistillodes *Schottariella*
- 40b. 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
- 41a. Sterile interstice of spadix with flattened scale-like staminodes; anthers not excavated *Bucephalandra*
- 41b. Sterile interstice absent or with truncate staminodes; anthers nearly always with the top excavated *Aridarum*
- 36b. Spathe mostly constricted, if not obviously constricted then plant with at least petioles asperate and more often entire plant coarsely hairy
- 42a. Thecae of anther, each with horn- or needle-like projections; ovules on basal placenta; seeds with a long, hooked micropylar appendage *Phymatarum*
- 42b. Thecae of anther without horn- or needle-like projections; ovules on parietal or basal placenta; seeds without a micropylar appendage
- 43a. Placentation basal *Schottarum*
- 43b. Placentation parietal *Schismatoglottis* [Multiflora Group]
- 35b. Modules mostly polyphyllous, never distichous; petiolar sheath fully attached, persistent or marcescent
- 44a. Shoot modules hapaxanthic *Schismatoglottis* [Calyptrata Group]
- 44b. Shoot modules pleioanthic
- 45a. Leaf sheath free-ligular *Schismatoglottis* Multiflora Group
- 45b. Leaf sheath fully attached to petiole or with at most a briefly auriculate tip
- 46a. Petiole sheathing only at extreme base; each foliage leaf alternating with a cataphyll *Schismatoglottis* [Tecturata Group]
- 46b. Petiole usually sheathing for at least a third of its length (rarely less); foliage leaves not individually alternating with cataphylls
- 47a. 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*

- 47a. Pistillate and staminate flower zones not separated by a naked interstice; spathe not persistent or, if so, the inflorescence nodding; petiolar sheath wings persistent
- 48a. Small to medium plants; inflorescence erect; spathe limb irregularly crumbling and breaking away at or after staminate anthesis *Schismatoglottis* [Asperata Group]
- 48b. Massive 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]

Subfamily Lemnoideae

Despite their strikingly different appearance from the remainder of all other aroids evidence now overwhelmingly supports the inclusion of the duckweeds (formerly the family Lemnaceae) in the Araceae, where they are basal to all bisexual-flowered aroids above Gymnostachyoideae+Orontioideae (Cabrera *et al.*, 2008; Cusimano, et al., 2011). The extremely reduced vegetative form and minute reproductive structures make studying the species a delicate and time-consuming activity, although fortunately the taxonomy of the duckweeds has been extensively and rigorously studied by Landolt (1986). A useful website with numerous excellent images may be found at www.waynesword.palomar.edu/1wayindx.htm.

Four genera and 10 species in Malesia.

1. *Spirodela* Schleid., *Linnaea* 13: 391 (1839).
2. *Landoltia* Les and D.J.Crawford, *Novon* 9:532 ('1999' 2000).
3. *Lemna* L., *Sp. Pl.*: 970 (1753).
4. *Wolffia* Horkel ex Schleid., *Beitr. Bot.* 1: 233 (1844).

Subfamily Pothoideae

Tribe Potheae

Potheae comprises three genera of forest-dwelling primary hemiepiphytes: *Pothos* L., *Pedicellarum* M.Hotta, and *Pothoidium* Schott. Species of tribe Potheae are readily distinguished by their bisexual flowers with a prominent leathery perigone, and infructescences of discrete ellipsoid berries ripening red or orange, very rarely white or purple.

Two genera and ca. 50 species in Malesia.

5. *Pothos* L., *Sp. Pl.*: 968 (1753).
6. *Pedicellarum* M.Hotta, *Acta Phytotax. Geobot.* 27:61 (1976).

Subfamily Monsteroideae

Tribe Spathiphyllae

Most of species of Spathiphyllae are neotropical; however, two species of *Spathiphyllum*, and the single species of *Holochlamys* occur in Malesia. A further

species, *Spathiphyllum solomonense* is endemic to Palau, New Britain, and the Solomon Islands.

Two genera and 3 species in Malesia.

7. *Spathiphyllum* Schott in H.W.Schott and S.L.Endlicher, *Melet. Bot.*: 22 (1832).

8. *Holochlamys* Engl. in O.Beccari, *Malesia* 1: 265 (1883).

Tribe Monstereae

All Indomalayan genera of Monstereae (except *Anadendrum* and *Amydrium*) are distinguished by a mature infructescence in which the surface is comprised of tough thickened stilar tissue that, when the fruits are ripe, fall as irregular plates to expose the ovary cavity with the seed embedded in copious, variously coloured pulp. *Anadendrum* and *Amydrium* produce infructescences of discrete berries. Those of *Anadendrum* are truncate and ripen red or orange. The berries of *Amydrium* are rounded and ripening white or orange. All genera except *Anadendrum* and *Amydrium* have trichoscleroids in all tissues (very sparse in *Amydrium*); these are observable by tearing a mature leaf blade and looking for 'hairs' protruding from the damaged edges.

Five genera and ca. 130 species in Malesia.

9. *Amydrium* Schott, *Ann. Mus. Bot. Lugduno-Batavum* 1:127. (1863).

10. *Anadendrum* Schott, *Bonplandia (Hannover)* 5:45. (1857).

11. *Epipremnum* Schott, *Bonplandia (Hannover)* 5:45. (1857).

12. *Rhaphidophora* Hassk. *Flora* 25(2 Beibl. 1):11. (1842).

13. *Scindapsus* Schott in H.W.Schott and S.L.Endlicher, *Melet. Bot.* 21 (1832).

Subfamily Lasioideae

The lasioids are slender to massive, usually solitary or clump-forming stoutly rhizomatous and sometimes stoloniferous herbs with large hastate to sagittate, rarely pinnately-divided leaves on prickly, often mottled petioles to 3 m long. Two of the three Malesian genera, *Cyrtosperma* Griff. and *Lasia* Lour. are commonly found in marshy open grassland close to habitation; the third, *Podolasia* N.E.Br., is restricted to deep peat deposits in seasonally inundated broadleaf forest.

Three genera and ca. 16 species in Malesia.

14. *Cyrtosperma* Griff., *Not. Pl. Asiat.* 3:149. (1851).

15. *Lasia* Lour. *Fl. Cochinch.* 1:64, 81. (1790).

16. *Podolasia* N.E.Br., *Gard. Chron.*, n.s., 1882(2):70. (1882).

Subfamily Aroideae

The Aroideae comprises all genera with naked unisexual flowers; thus all taxa are monoecious or very rarely paradioecious (*Arisaema*).

Tribe Nephthytideae

Subtribe Aglaonematinae

A subtribe of two genera, one (*Aglaonema*) a colonial helophyte in freshwater and brackish tidal zones, usually in full sun, the other (*Aglaonema*) mesophytic in secondary perhumid to everwet broadleaf evergreen forests with a few species are restricted to kerangas or monsoonal perhumid semi-deciduous forests. Both genera have conspicuous berries, ripening green in *Aglaodorum* and mostly red in *Aglaonema*.

Two genera and 23 species in Malesia.

17. *Aglaodorum* Schott, *Gen. Aroid.*:58. (1858).

18. *Aglaonema* Schott, *Wiener Z. Kunst* 1829: 892. (1829).

Subtribe Nephthytidinae

The discovery in Borneo of an undescribed species of *Nephthytis*, a genus hitherto restricted to wet tropical West Africa, was, to say the least, unexpected. While many angiosperm genera extend through tropical Africa and Indomalesia [including *Rhaphidophora*, *Remusatia*, *Sauromatum*, *Arisaema*, *Amorphophallus*, and *Pothos* (Madagascar) in the Araceae], Malesian-African tropical *disjunctions* were hitherto unknown in aroids, and do not seem to be common generally.

One genus and 1 species in Malesia.

19. *Nephthytis* Schott, *Oesterr. Bot. Wochenbl.* 7: 406. (1857).

Tribe Philodendreae

Subtribe Philodendrinae

Two very closely similar genera in Asia, *Homalomena* Schott and *Furtadoa* M.Hotta, mostly with strongly aromatic (terpenoids) tissues and spathes fully persistent to fruit maturity. *Homalomena* is widespread throughout tropical and subtropical Asia, with significant centres of endemism on Sumatera, Borneo, and New Guinea. *Furtadoa* is restricted to Sumatera and Peninsular Malaysia and differs from *Homalomena* primarily by each staminate flower with an associated pistillode, and basal placentation. Species of *Homalomena* are frequently confused with *Schismatoglottis*, although the infructescences of *Homalomena*, in which the spathes wholly persistent to fruit maturity, and then split basally and upwards to reveal the fruits, are very different from those of *Schismatoglottis* in which the spathe limb is shed, often while still fresh, during anthesis, while the lower spathe persists into fruiting as a barrel-shaped to ellipsoid covering, splitting from the top downwards to release the ripe fruits.

Two genera and at least 350 species in Malesia.

20. *Furtadoa* M.Hotta, *Acta Phytotax. Geobot.* 32: 142 (1981).

21. *Homalomena* Schott in H.W.Schott and S.L.Endlicher, *Melet. Bot.*: 20. (1832).

Tribe Cryptocoryneae

Cryptocoryneae comprises two genera, *Cryptocoryne* Fisch. ex Wylder and *Lagenandra* Schott; the latter is restricted to India, Bangladesh and Sri Lanka.

One genus and ca 60 species in Malesia.

22. *Cryptocoryne* Fisch. ex Wylder, *Linnaea* 5: 428. (1830).

Tribe Schismatoglottideae

Schismatoglottideae is a diverse group of terrestrial, rheophytic, lithophytic or chasmophytic rainforest herbs centred on Borneo. *Schismatoglottis* Zoll. and Moritzi is by far the largest genus, extending throughout Malesia to the tropical western Pacific, north through much of Indochina and into SW China and Taiwan. The remaining genera are relatively small to monospecific and with the exception of *Hestia* S.Y.Wong and P.C.Boyce, *Apoballis* Schott, and *Piptospatha* N.E.Br. are endemic on Borneo. *Schismatoglottis* is predominantly non-rheophytic, although it does comprise some rheophytic species, most of which are notable for the petiolar sheath being attached only at the very base, with the remainder forming a long, variously persisting, free-ligular portion. This peculiar morphology, while present in a minority of *Schismatoglottis*, is common to all except two of the remainder of the tribal genera, which are in turn almost all obligate or facultative rheophytes.

13 genera and at least 200 species in Malesia.

23. *Apoballis* Schott, *Oesterr. Bot. Z.* 8(10): 318. (1858).

24. *Hestia* S.Y.Wong and P.C.Boyce, *Bot. Stud. (Taipei)* 51: 250. (2010).

25. *Schottariella* P.C.Boyce and S.Y.Wong, *Bot. Stud. (Taipei)*: 50:269. (2009).

26. *Piptospatha* N.E.Br., *Gard. Chron.*, n.s., 1879(1): 138. (1879).

27. *Ooia* S.Y.Wong and P.C.Boyce, *Bot. Stud. (Taipei)* 51: 545. (2010).

28. *Phymatarum* M.Hotta, *Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol.* 32(1):29. (1965).

29. *Bucephalandra* Schott, *Gen. Aroid.*: t. 56. (1858).

30. *Aridarum* Ridl., *J. Bot.* 51: 201. (1913).

31. *Pichinia* S.Y.Wong and P.C.Boyce, *Gard. Bull. Singapore* 61(2): 544. 2010.

32. *Bakoa* P.C.Boyce and S.Y.Wong, *Bot. Stud. (Taipei)* 49(4):398. (2008).

33. *Hottarum* Bogner and Nicolson, *Aroideana* 1(3): 72. ("1978" – 1979).

34. *Schottarum* P.C. Boyce and S.Y. Wong, *Bot. Stud. (Taipei)* 49(4): 393. (2008)

35. *Schismatoglottis* Zoll. and Moritzi, *Syst. Verz.* 83. (1846).

Tribe Thomsonieae

A highly distinctive tribe of often large, occasionally gigantic mostly tuberous geophytes, with usually solitary leaves comprising highly dissected leaf blades carried on a stout petiole. In most species the inflorescences are large and appear while the plants are leafless.

One genus and ca 60 species in Malesia.

36. *Amorphophallus* Blume ex Decne., *Nouv. Ann. Mus. Hist. Nat.* 3:366. (1834), *nom. cons.*

Tribe Caladieae

Caladieae is in the main Neotropical, with only a single indigenous Asian genus, *Hapaline* Schott. *Caladium* Vent., *Syngonium* Schott and *Xanthosoma* Schott are commonly cultivated, and not infrequently encountered as naturalized plants or weedy escapes. *Xanthosoma* is occasionally cultivated as a minor carbohydrate crop.

One genus and three or four species in Malesia.

37. *Hapaline* Schott, *Gen. Aroid.* 44. (1858).

Tribe Pistieae

Pistieae comprises one genus with one species, the ubiquitous water lettuce, *Pistia stratiotes* L., cosmopolitan in warm temperate, subtropical, and tropical freshwater aquatic ecologies. Often (e.g., Africa) becoming pestilential.

38. *Pistia* L., *Sp. Pl.*: 963. (1753).

Tribe Colocasieae

Three genera of this large and important tribe occur in Malesia, *Colocasia* Schott, *Remusatia* Schott, and *Alocasia* (Schott) G.Don. The tribe features mostly large, sometimes gigantic erect to creeping herbs with milky to almost clear latex and often distinctly undulating interprimary collecting veins.

Three genera and ca 120 species in Malesia.

39. *Colocasia* Schott in H.W.Schott and S.L.Endlicher, *Melet. Bot.* 18. (1832).

40. *Remusatia* Schott, *Melet. Bot.*: 18. (1832).

41. *Alocasia* (Schott) G.Don, *Hort. Brit.*, ed. 3:631. (1839), *nom. cons.*

Tribe Arisaemateae

Arisaema is predominantly warm temperate Asian, with the greatest number of species and highest diversity occurring in China and Japan. The majority of

Arisaema species are remarkable for their ability to change the sex of the inflorescences dependent on the size, maturity and overall vigour of the plant. Plants flowering for the first time, and weak mature individuals produce staminate inflorescences whereas robust plants in good health flower pistillate. This phenomenon is termed paradioecy.

One genus and ca 19 species in Malesia.

42. *Arisaema* Mart. Flora 14(2):459. (1831).

Tribe Areae

In tropical Asia the Areae is a predominantly continental taxon, with the largest genus, *Typhonium* Schott, particularly species-rich and diverse in monsoonal Thailand and Indochina. The Areae is notable for the often elaborate sterile flowers separating the staminate and pistillate flower zones and the often strongly malodorous spadix appendix.

43. *Typhonium* Schott, *Wiener Z. Kunst* 3: 72. (1829).

44. *Sauromatum* Schott in H.W.Schott and S.L.Endlicher, *Melet. Bot.*: 17 (1832).

ADVENTIVES

Four genera of exotic aroid (*Caladium* Vent., *Dieffenbachia* Schott, *Syngonium* Schott, and *Xanthosoma* Schott) are frequently encountered as adventives in Malesia. While usually close to habitation, on occasion exotic aroids (and, indeed other plants, notably species of Marantaceae, *Codiaeum*, *Dracaena* and even roses!) occur in areas of seemingly undisturbed forest, although an examination of the surrounding area will often reveal activity related to collection of forest produce such as rattan, durian, etc.

Caladium is represented by *C. × hortulorum*, with large stands occurring along the fringes of old rubber plantations, and in fallow areas of oil palm plantation that have escaped herbicide application. Plants seldom flower, and fruits have not been observed by either of authors.

Dieffenbachia seguine (Jacq.) Schott (or, at least hybrids involving this species) is a popular ornamental plant in *kampung*s. Its decumbent-rooting habit and the brittle nature of the stems combined with the ability of even a small portion to regenerate means that it often forms large stands in sunny, wet places. Although flowering regularly, fruit set is exceedingly uncommon.

Syngonium podophyllum Schott is perhaps best regarded as semi-naturalized weed since it fruits prolifically and the fruits are dispersed by monkeys, squirrels, and various birds, notably bulbuls, and this combined with the plants' ability to vegetatively 'invade' stands of trees via creeping flagelliform shoots and also out-compete many local vining plants means that it often forms considerable areas of detrimental growth.

At least two *Xanthosoma* species occur as adventives close to longhouses, and appear to be the result of plants cultivated as carbohydrate crops escaping via the translocation of tuberules. *Xanthosoma* does not flower regularly in Sarawak, and neither of the authors have ever witnessed fruits being developed.

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