

**PHYLOGENETIC AND SYSTEMATIC STUDIES OF THE
SCHISMATOGLOTTIDEAE (ARACEAE: AROIDEAE)**

by

WONG SIN YENG

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**KAJIAN FILOGENETIK DAN SISTEMATIK DALAM
SCHISMATOGLOTTIDEAE (ARACEAE: AROIDEAE)**

ABSTRAK

Tribus Schismatoglottideae merupakan keladi hutan yang paling pelbagai di Borneo dengan lebih 100 spesies dan lebih 95% daripadanya adalah endemik. Selain daripada *Schismatoglottis* Zoll. & Moritzi, yang merupakan genus terbesar, tribus ini juga merangkumi empat genera satelit yang kecil, *Aridarum* Ridl., *Bucephalandra* Schott, *Phymatarum* M. Hotta dan *Piptospatha* N.E. Br. yang endemik kepada Borneo kecuali yang terakhir yang tertabur hingga ke Semenanjung Malaysia dan Semenanjung Selatan Thailand. Penyelidikan terkini dan yang sedang dijalankan tentang tribus Schismatoglottidae merangkumi alfa-taksonomi, fenologi dan kajian ekologi telah menyediakan pelantar spesies yang stabil supaya spesies baru yang masih wujud dihuraikan dan ini membolehkan ujian hipotesis infra-tribus dan filogenetik intergenerik dapat dijalankan. Di samping itu banyak penyelidikan perlu dijalankan untuk menentukan batas generik dalam tribus ini. Kajian ini dilaksanakan untuk: (1) menjalankan kerja lapangan yang ekstensif, merangkumi penyediaan spesimen herbarium untuk populasi yang disampelkan dalam tribus Schismatoglottideae; (2) menyelesaikan filogenetik dalaman tribus dengan menggunakan kaedah molekul; (3) menyiasat dengan menggabungkan kerja lapangan dan pemerhatian makmal tentang morfologi bunga, pendebungaan, penyebaran dan pembentukan anak benih, serta memetakan ciri-ciri ini kepada pokok filogenetik untuk menghasilkan hipotesis evolusi

kepada penyesuaian tersebut. Analisis molekul filogenetik yang menggabungkan data jujukan DNA *matK*, bahagian 3' di intron *trnK* dan *trnL-F* telah dijalankan untuk 78 taksa yang mewakili semua genus di dalam tribus, semua kumpulan yang tak formal di dalam *Schismatoglottis*, bersama-sama dengan ‘adik’ tribus *Cryptocoryneae* dan kumpulan luar dari Araceae. Analisis data DNA yang digabungkan dengan menggunakan kaedah-kaedah parsimoni, *likelihood* maksimum dan Bayesian telah menunjukkan tribus Schismatoglottideae sebagai polifiletik. *Schismatoglottis* neotropika merupakan ‘adik’ kepada Schismatoglottideae palaeotropika + *Cryptocoryneae*. *Schismatoglottis acuminatissima* merupakan cabang ‘adik’ kepada ahli Schismatoglottideae yang selebihnya. *Schismatoglottis* palaeotropika tidak disokong sebagai genus yang monofiletik. Satu tribus neotropika yang baru untuk Araceae: Aroideae, Philonotieae S.Y. Wong & P.C. Boyce telah dicadangkan. Philonotieae, bersama-sama dengan Schismatoglottideae + *Cryptocoryneae* membentuk gabungan schismatoglottid. *Apoballis*, *Hestia*, *Pichinia* dan *Schottarum* dipindahkan daripada *Schismatoglottis sensu stricto* kepada genus yang baru. *Bakoa* dan *Ooia* dipindahkan daripada *Piptospatha* dan dicadangkan sebagai genus baru. Ciri-ciri morfologi yang menyokong sifat reofitik adalah: (1) Keupayaan untuk pematahan dahan/akar; (2) Kelopak ligul yang bebas dan cepat bertukar kepada warna perang; (3) Kehadiran apendaj mikropil dan, (4) Kehadiran cawan sembur.

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SCHISMATOGLOTTIDEAE (ARACEAE: AROIDEAE)**

ABSTRACT

The tribe Schismatoglottideae is the most diverse aroid taxon in Borneo, comprising in excess of 100 species of which over 95% are endemic. Besides *Schismatoglottis* Zoll. & Moritzi, the largest genus within the tribe, the tribe includes four small satellite genera, *Aridarum* Ridl., *Bucephalandra* Schott, *Phymatarum* M. Hotta dan *Piptospatha* N.E. Br. that are endemic to Borneo, except the last which extends to the Malay Peninsular and Southern Peninsular Thailand. Recent and ongoing research of the Schismatoglottideae includes alpha-taxonomy, phenological and ecological studies have provided a stable species platform from which to describe the considerable novelties still known to exist, and from which to test hypotheses of infra-tribal, and intergeneric phylogenetic processes. In addition, considerable research remains to be done to resolve generic boundaries within the tribe. This study was carried out to: (1) undertake extensive field studies including vouchering of sampled populations belonging to tribe Schismatoglottideae; (2) resolve by use of molecular methodologies the internal phylogeny of the tribe using molecular methodologies; (3) investigate, by field and laboratory observations on inflorescence morphology, pollination, dispersal and seedling establishment processes, and by mapping relevant features onto phylogenetic trees to produce an hypothesis of the evolution of these adaptations. A combined molecular phylogenetic analysis of *matK*, the 3' portion of the *trnK* intron, and *trnL-F* DNA

sequence data was carried out on 78 taxa representing all genera in the tribe, all informal groups in *Schismatoglottis*, together with sister tribe Cryptocoryneae, and outgroups from Araceae. Analyses of combined DNA datasets with parsimony, maximum likelihood, and Bayesian methods revealed tribe Schismatoglottideae to be a polyphyletic assemblage. Neotropical *Schismatoglottis* is shown to be sister to the palaeotropical Schismatoglottideae + Cryptocoryneae. *Schismatoglottis acuminatissima* is a sister clade to the rest of the Schismatoglottideae. Palaeotropical *Schismatoglottis* is unsupported as a monophyletic genus. A new neotropical tribe of Araceae: Aroideae, Philonotieae S.Y. Wong & P.C. Boyce, is proposed. Philonotieae is sister to Cryptocoryneae + palaeotropical Schismatoglottideae, with these three tribes comprising the schismatoglottid alliance. *Apoballis*, *Hestia*, *Pichinia* and *Schottarum* are removed from *Schismatoglottis sensu stricto* into separate genera. *Bakoa* and *Ooia* are removed from *Piptospatha*, proposed as new genera. The morphological characters that facilitate rheophytism are: (1) Ability for shoot/root disarticulation; (2) Free ligular sheath soon becoming marcescent; (3) Presence of micropylar appendage and, (4) Presence of splash cup.

CHAPTER 1

INTRODUCTION

1.1 General

Araceae Juss. is a family of perennial evergreen to seasonally dormant monocotyledonous herbs defined at the macromorphological level by an inflorescence consisting of a spike of small bractless flowers on a fleshy unbranched axis (spadix) subtended by a bract or modified leaf (spathe). Vegetatively, the aroids range in size from minute to gigantic, and in habit from lianescent or subshrubby hemiepiphytes, to epiphytes, lithophytes, terrestrial mesophytes, geophytes, rheophytes, sometimes helophytes, and true or free-floating aquatics. They are predominantly tropical in distribution, with 90% of the 110 currently recognized genera and c. 95% of c. 4000+ species restricted to the everwet or perhumid tropics. Ecologically they are a very important herbaceous family in terms of their dominance of the understorey and inter-canopy herb layer and as indicators of forest quality. Aroids are most abundant and diverse in undisturbed perhumid habitats. The family furnishes some of the worlds most important carbohydrate food crops, notably taro (*Colocasia* Schott) and tannia (*Xanthosoma* Schott), primary carbohydrate crops in the Pacific, Pacific Rim, Caribbean, and tropical West Africa. The aroids are also globally important commercially as ornamental indoor and outdoor foliage plants, and as cut ‘flowers’. In these ways the aroids contribute significantly to the economy of many countries. In addition to numerous world-wide uses, the family has considerable localised uses among indigenous peoples of many of the countries, where they form a significant part of the local ecology.

1.2 Supra-Familial Phylogeny

The APG version 9 classification of flowering plants (Stevens, 2001 onwards), based on multi-gene analyses, places Araceae basal to the Alismatales, sister to all the other alismatid families and adjacent to the Tofieldiaceae Takht. *Acorus* L. (Acoraceae Martinov), long included in the Araceae, is excluded from the family and is now universally accepted in its own order – Acorales – as being the basal-most clade to the rest of the Monocots. Lemnaceae Gray, long considered as the closest relative to the Araceae is now included within the aroids by all phylogenetic workers (see below).

1.3 Intergeneric Phylogeny

Mayo *et al.* (1997) recognizes seven subfamilies and 32 tribes. The most striking feature is the recognition of a single clade for aperigoniate unisexual-flowered genera – the Aroideae – and the utilization of the informal term ‘Alliance’ to group related tribes where cladogram resolution allows. Despite a high level of resolution, 15 tribes remained unaligned and the perigoniate unisexual flowered genera *Zamioculcas* Schott and *Gonatopus* Engl., and *Stylochaeton* Lepr., were included, but with poor cladistic support, in the otherwise aperigoniate Aroideae as a paraphyletic group.

Succeeding Mayo *et al.* (1997), Hesse *et al.* (2001) and Bogner & Hesse (2005) proposed recognition of Zamioculcadoideae and Stylochaetonoideae. This proposal was published without additional cladistic analyses, although good morphological evidence from, in particular, pollen was provided. The recognition of an expanded

Zamioculcadoideae to include Stylochaetonoideae subsequently received strong support from molecular evidence provided by Cabrera *et al.* (2008) and is now generally accepted.

Work carried out by Barabé *et al.* (2002); Rothwell *et al.* (2004); Cabrera *et al.* (2008) has shown the Lemnaceae to be unquestionably embedded in the Araceae. Cabrera's work has placed Lemnaceae as sister to all the true Araceae with the Protoaraceae (Orontioideae and Gymnostachydoideae) basal to the whole family. This established almost conclusively that the duckweeds are bisexual-flowered, and not closely related to the unisexual *Pistia* L. which hitherto, by its free-floating habit and seedlings similar to mature Lemnaceae, had been postulated as a link between the Araceae and former Lemnaceae.

Gonçalves *et al.* (2007) produced compelling evidence for the merging of tribe Dieffenbachiae Engl. (*Dieffenbachia* Schott & *Bognera* Mayo & Nicolson) into Spathicarpeae Schott (*Asterostigma* F.E.L. Fischer, *Croatiella* Gonçalves, *Gearum* N.E. Brown, *Gorgonidium* Schott, *Incarum* Gonçalves, *Mangonia* Schott, *Spathantheum* Schott, *Spathicarpa* W.J. Hooker, *Synandrospadix* Engl. and *Taccarum* Schott).

At the present time, based on the above consensus, the extant Araceae comprises 9 or 10 subfamilies (depending on whether or not Stylochaetonoideae is recognized as distinct from Zamioculcadoideae), and 31 tribes.

1.4 Tribe Schismatoglottideae

Tribe Schismatoglottideae Nakai is the most speciose and diverse aroid taxon in Borneo, comprising in excess of 120 species of which over 95% are endemic. Besides the largest genus, *Schismatoglottis* Zoll. & Moritz, the tribe presently includes four smaller ‘satellite’ genera: *Aridarum* Ridl., *Bucephalandra* Schott, *Phymatarum* M. Hotta and *Piptospatha* N.E. Br. These four genera are all comprised of rheophytic species with free-ligular leaf sheaths, and all are endemic to Borneo except *Piptospatha*, which extends to the Malay Peninsula and Southern Peninsular Thailand. *Schismatoglottis* itself extends from Myanmar (Burma) to Vanuatu, and Southern China to New Guinea but nowhere is it more abundant and diverse than in Borneo.

Recent and on-going research of the Schismatoglottideae includes alpha-taxonomy (Bogner & Boyce, in press; Bogner & Hay, 2000; Boyce & Wong, 2006; Boyce & Wong, 2008a; Wong *et al.*, in press; Hay, 2002; Hay & Herscovitch, 2003; Hay & Yuzammi, 2000; Okada *et al.*, 1999; Wong & Boyce, 2007a; Wong & Boyce, 2008; phenological (Boyce & Wong, 2007; Ooi *et al.*, in prep.) and ecological studies (Boyce 2007a; Boyce, 2007b; Wong, 2007a; Wong, 2007b; Wong & Boyce, 2007b).

This research is providing a better understanding of morphological adaptation under the rigorous selective forces involved in the evolution of rheophytes in their very demanding habitat.

Tribe Schismatoglottideae is dominant in SE Asia but presents numerous problems in the delimitation of the genera as presently defined. Hitherto, one of the primary problems facing taxonomists utilizing morphological methodologies within the

Schismatoglottideae is that the satellite genera and a percentage of *Schismatoglottis* itself show multiple morphological adaptations linked to a rheophytic habitat. They also exhibit complex pollination and dispersal syndromes and it is very difficult to ascertain whether these represent shared derived characters indicative of relationship, or are independent adaptations in otherwise-related genera. A powerful tool to investigate these issues is to undertake a molecular study of generic boundaries utilizing as many species as possible, and then to map morphological characteristics onto the resulting tree in order to produce a hypothesis of morphological/evolutionary processes in the tribe.

1.5 Objectives

The objective was to produce an established and testable phylogeny for *Schismatoglottis* and the current recognized satellite genera *Aridarum*, *Bucephalandra*, *Phymatarum* and *Piptospatha*. This process has produced a hypothesis for the occurrence of the vegetative and reproductive features linked to their phylogenetic significance.

The objectives were as listed below:

- to undertake extensive field studies including vouchering of sampled populations belonging to tribe Schismatoglottideae.
- to resolve the internal phylogeny of the tribe using molecular methodologies.
- to investigate, by field and laboratory observations on inflorescence morphology, pollination, dispersal and seedling establishment processes, and by mapping

relevant features onto phylogenetic trees to produce an hypothesis of the evolution of these adaptations.

No hypothesis for the evolution of rheophytism in tribe Schismatoglottideae had been tested before using molecular-based phylogenies. Therefore, resolving the phylogenetic relationships within the tribe Schismatoglottideae was of interest because it provided an opportunity to study the evolution of rheophytism in both *Schismatoglottis* and its satellite genera.

CHAPTER 2

LITERATURE REVIEW

2.1 Araceae

2.1.1 Overview

Araceae Juss. consists of 110 genera and c. 4000 species with the inclusion of the Lemnaceae (the duckweed family). Most aroids are tropical and include members from terrestrial, aquatic, and epiphytic habitats although there are many aroids indigenous to temperate climates. Only a few of the genera from the Americas also occur in the Palaeotropics. Asia has more genera than America, but America has more species, with well over half of all the species in the world (Mayo *et al.*, 1997).

The family Araceae is most easily diagnosed by the inflorescence which is a spadix - an unbranched spike bearing small bractless flowers - subtended by a modified leaf called a spathe.

2.1.2 Vegetative Morphology

The Araceae is vegetatively hugely diverse with stem-tubers, climbers, and hemiepiphytes, true epiphytes, submersed or emergent, and free-floating aquatics all being represented. Among the climbing species, various kinds may be observed, i.e., shingle climbers (e.g., *Rhaphidophora korthalsii* Schott), huge trunk climbers (e.g., *Scindapsus latifolius* M.Hotta), and litter-basket climbers displaying differentiation

of stem function (e.g., *Scindapsus beccarii* Engl.). Young *Scindapsus beccarii* plants are straggling climber attached by short roots to a tree trunk and bearing small, scattered leaves. Once the plant reaches a certain age and height the growth alters to form a congested litter-basket comprised of large overlapping leaves. The litter basket produces several inflorescences and then sends out another straggling shoots that continue climbing for a few metres before the process is repeated.

The Araceae also contain many creeping or tufted forest floor herbs, (e.g., a large number of *Alocasia* G.Don, *Schismatoglottis* Zoll. & Moritz) while others, termed rheophytes, are adapted to streamside habitats where sudden flash floods following tropical rains exists are regular events. Rheophytic aroids are especially abundant in Borneo (e.g., *Bucephalandra* Schott, *Aridarum* Ridl. and *Piptospatha* N.E.Br.). Other wetland species vary from swamp plants such as the spiny, clump-forming *Lasia spinosa* (L.) Thwaites, to aquatics such as *Cryptocoryne* Fisch ex Wydler. The family also contains free-floating aquatics such as the water lettuce, *Pistia stratiotes* L., which can be an aggressive weed in warm countries, and the genera formerly placed in the family Lemnaceae Gray, known as duckweeds. Tuberous-stemmed genera are frequent, especially in genera occurring in habitats subjected to a seasonal dry or cold climate. *Amorphophallus* Decne. is especially noteworthy because of the enormous tubers produced by certain species. The largest species, *Amorphophallus titanum* (Becc.) Becc., can produce tubers weighing approximately 70 kg.

2.1.2.1 Root

Overview

Roots in Araceae are always adventitious, and dimorphic roots are often found in climbing hemiepiphytes, e.g., many *Monstera* Adans. and *Philodendron* Schott species. In some genera, e.g., *Arisarum* Mill., *Arum* L, *Biarum* Schott and *Cryptocoryne*, specialized contractile roots occur which prevent the stem from rising too near to the soil surface. Many rheophytes have roots with highly adhesive properties.

Anchor and feeder roots

Roots of epiphytic and climbing Araceae are often specialized into anchor roots that serve to attach the plant to the substrate providing support, and feeder roots which when aerial, extend down to the soil and supply water and dissolved nutrients to the rest of the plant (Went, 1895). Rheophytes species also have strongly clasping roots, although root-dimorphism in these taxa has not been studied.

The morphology and physiology of anchor and feeder roots are markedly different. The former are typically relatively narrow, agravitropic and appear to be negatively phototropic, which tends to bring them into contact with the substrate. Numerous root hairs are typically produced on the side adjacent to the substrate, but may develop all over the root (Troll, 1941). Anchor root growth is relatively limited and often dependent upon contact with a substrate. With no contact, growth ceases precociously, whereas prolonged contact stimulates elongation. Anchor roots never attain the enormous lengths of feeder roots. In *Monstera* (Madison, 1977) the stems

not in contact with a substrate produce only a tuft of dried anchor roots, while those in contact produce anchor roots 20 – 30 cm in length and these may surround tree trunks. Root hairs serve to attach the root to a substrate. Some anchor roots may lack root hairs and appear to be cemented by dried mucilage as in *Syngonium* Schott and *Rhaphidophora* Hassk. while in some non-lianescent genera (e.g., *Piptospatha* N.E.Br., *sensu* Bogner & Hay, 2000) there is compelling evidence that root adhesiveness is linked to mucilage production from the active root tip.

In lianescent and epiphytic genera, feeder roots are thicker than the associated anchor roots and are capable of considerable elongation. Conversely, in rheophytic genera studied to date the anchor roots are considerably more robust than the associated feeder roots.

Nest roots

Another type of aerial root characteristic of many other species of *Anthurium* sect. *Pachyneurium* Schott (the ‘bird’s nest’ or ‘litter basket’ *Anthuriums*) and in *Scindapsus* Schott. is the so-called nest root (Schimper, 1888; Bruhn, 1910). These exhibit negative gravitropism (Troll, 1941) and branch profusely forming an ‘impenetrable’ nest. The development of these roots was studied by Bruhn (1910) who found that their formation was typically inhibited when the roots were surrounded by moist moss or earth. Bruhn concluded that they resulted from damage to the root apex. In epiphytes the rosulate leaves form a ‘basket’ into which leaves, twigs and other detritus gather. The nest roots seem to be especially adapted to exploit this food resource, growing directly up into the mass of detritus and

ramifying within it (Croat, 1991). The presence of such nest roots is not restricted to Araceae. Homologous structures occur in the Orchidaceae, where they are termed “basket roots”.

Contractile roots

Specialized contractile roots seem to prevent the stem of geophytic and some aquatic species from rising too near to the soil surface. Contractile roots occur in numerous Araceae which possess a tuberous habit, for example *Typhonium* Schott (Banerji, 1947), *Arum* L. (Rimbach, 1897), other genera of subfamily Aroideae sensu Mayo, Bogner & Boyce (Rimbach, 1898), subfamily Orontioideae Mayo, Bogner & Boyce (*Lysichiton* Schott, *Orontium* L., *Symplocarpus* Salisb. ex Nutt.), some genera of subfamily Lasioideae Engl. (Hotta, 1971), and some other aquatic species, as in *Cryptocoryne* Fisch. ex Wydler, but not *Calla* L. (Dudley, 1937). Detailed studies of root contraction have been made in two species of *Arum*, *A. maculatum* L. (Rimbach, 1897) and *A. italicum* Mill. (Lamant & Heller, 1967)

2.1.2.2 Stem

The stem varies from an aerial elongated axis with extended internodes, as in the many climbing hemiepiphytes, to a hypogean rhizome or tuber. Climbing genera with long internodes are most common in the more primitive tribes, i.e., those with bisexual flowers. Geophytes are found throughout the family but are especially common in the most advanced subfamily, the Aroideae. Abbreviated aerial stems, resulting in rosulate plant forms, are also commonly found, as in many epiphytic

species of *Philodendron* and *Anthurium* Schott and many of the rheophytic genera of Schismatoglottideae. Some, generally larger, species have an arborescent habit, in which the main axis is a fleshy (*Alocasia* (Schott) G.Don, *Xanthosoma*) or fibrous (*Philodendron*) stem, or a pseudostem of petiolate sheaths (*Arisaema* Mart., *Typhonodorum* Schott). Shoot types apparently specialized for vegetative reproduction occur in various forms. Flagelliform shoots, or ‘flagellae’, equivalent to aerial stolons, have been observed in *Amydrium* Schott, *Cercestis* Schott, *Monstera* Adans., *Pedicellarum* M.Hotta, *Philodendron* Schott, *Pothos* L., *Rhaphidophora* Hassk., *Rhodospatha* Poepp., and *Syngonium* Schott, among others. They consist of branches (usually in the form of continuation shoots) in which the internodes become very much longer and more slender than in the flowering zone of the stem. The leaves often become reduced in size, sometimes to small, scale-like cataphylls. Flagelliform shoots grow rapidly, and thus encounter new host trees on which flowering stems later develop. Bulbils, which appear to be dispersed by birds, occur in *Remusatia* Schott, while tubercles occur in *Amorphophallus bulbifer* (Roxb.) Blume, *Dracontioides* Engl., *Dracontium* L., *Pinellia* Ten., and many *Alocasia*, while hypogean stolons are found in *Colocasia*, *Cryptocoryne* Wydler, some *Spathiphyllum* Schott and *Lasimorpha* Engl.

Shoot organization shows a range of interesting variations within the family and can be taxonomically useful (Engler 1877; Blanc 1977a,b, 1978, 1980, Ray 1986, 1987a–c, 1988, 1990). In virtually all genera the mature stem is a sympodium composed of sympodial units (modules) each of which has a more-or-less determinate structure, beginning with a prophyll and ending with an inflorescence or aborted inflorescence. Foliage leaves and cataphylls (reduced sheath-like leaves) occur in a sometimes very

regular sequence within each unit. In pleionanthic taxa continued growth of the stem takes place in most genera via the development of a ‘continuation shoot’ in the axil of the leaf (foliage leaf or cataphyll) situated at the second node below the spathe insertion. In subfamily Orontioideae it arises at the first node below the spathe. In hapaxanthic taxa the continuation shoot arises from the base of the active shoot but its relation to reiterative points in pleionanthic taxa has yet to be studied.

The production of more than one inflorescence to form a floral sympodium commonly takes place by the development of short units consisting of a prophyll, a spathe and a spadix. The first unit arises in the axil of the leaf immediately below the spathe and succeeding ones in the axils of the prophylls. These floral sympodia have a range of structural variation which may be quite complex; and some extreme forms are found in *Homalomena* Schott (Ray, 1988). Anomalous shoot organization of an apparently unique type occurs in *Gymnostachys* R.Br., while in most tribe Potheae and *Heteropsis* the flowering axes occur as lateral short shoots on monopodial main vegetative axes of apparently indeterminate growth.

2.1.2.3 Leaf

General

In virtually all genera the leaf is clearly differentiated into an expanded lamina, petiole and variously attached petiolar sheath. Exceptions are *Gymnostachys* and some *Biarum* species. The petiolar sheath normally clasps the subtended internode, at least basally, and has an annular insertion (except many Potheae and most *Heteropsis*). The foliage leaves that occur nearest the end of sympodial shoot

modules (sympodial leaves) often have short or very reduced sheaths, particularly when the module apex aborts and fails to develop an inflorescence, e.g., in *Philodendron* Schott.

For descriptive purposes, the leaf is divided into the anterior division, corresponding to that part of the lamina surrounding the midrib, and two posterior divisions, which, when present, are those portions of the leaf lamina which extend basally on each side of the petiole insertion. In many genera, e.g., those comprising the Monsteroideae, there are no posterior divisions and the lamina is composed entirely of the anterior division. In other taxa, such as the Lasioideae, many species have deeply sagittate or hastate leaves with very strongly developed posterior divisions, sometimes greatly exceeding the anterior division in length. In strongly sagittate leaves, each posterior division usually has a well developed basal rib, which performs the same mechanical support role as the midrib does for the anterior division. In cordate and cordatosagittate leaves the basal ribs may be short or even absent, with the individual primary lateral veins arising independently at the base of the midrib. On the other hand, pedately divided leaves, as seen for example in *Philodendron goeldii* G.M.Barroso, *Dracunculus* Mill., many *Arisaema* Mart., some *Syngonium* Schott and some *Typhonium* Schott, have a central, undivided anterior division while the posterior divisions are represented by the lateral series of pedate segments on either side. Here the basal ribs are represented by the ‘arms’ on which the segments of the posterior divisions are inserted and which arch back from the midrib insertion at the apex of the petiole. Leaf lamina size and shape is exceedingly diverse. Size may range from diminutive (e.g., *Ambrosina*) to gigantic (e.g., *Alocasia*, *Amorphophallus*, *Anchomanes* Schott, *Cyrtosperma* Griffith, *Xanthosoma* and *Typhonodorum* Schott).

Shape varies from linear (*Biarum*, *Jasarum*) to ‘dracontoid’ (tribes Thomsonieae, i.e., *Amorphophallus* and Nephythytideae, i.e., *Anchomanes* Schott and *Pseudohydrosme* Engl. and Lasioideae, i.e., *Dracontium* L. and *Pycnospatha* Gagnep., through elliptic, ovate, cordate, sagittate, hastate, trifid or trisect, pedatifid, pinnatifid, pedatisect, pinnatisect and radiatisect. Sometimes the posterior divisions of pedatifid and pedatisect leaves are twisted spirally so that the leaf segments resemble a spiral staircase ‘Wenteltrappenblätter’ (*Eminium* (Blume) Schott, *Helicodiceros* K.Koch). Bipinnatifid, tripinnatifid and partially quadripinnatifid leaves also occur.

Decompound Leaves

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

Dracontoid Leaves

‘Dracontoid’ leaf – elaborated forms of sagittate, hastate or trisect leaves in which the anterior and posterior divisions are highly dissected and subdivided, highest order divisions entire, often fenestrated, or lobed and with two tips or more tips; see *Pycnospatha* & q.v., decompound leaf (Boyce & Hetterscheid, pers. comm.).

Heteroblasty, perforated and peltate leaves

Heteroblasty is a striking and sometimes taxonomically useful feature (e.g. Madison, 1977) of a number of climbing genera (*Cercestis* Schott, *Monstera*, *Philodendron*, *Pothos* L., *Rhaphidophora* Hassk., *Rhodospatha* Poepp., *Syngonium*). It occurs both in ontogeny from seedling to the mature plant and in association with the development of flagelliform shoots. A very striking form of heteroblasty is shown in certain genera (e.g., *Monstera*, *Rhaphidophora* and *Pothos*) where the juvenile leaves have very short petioles and their laminae are held flat against the host tree in a regular, overlapping sequence giving the appearance of roof shingles or tiles. These are consequently known as shingle plants.

Perforated (fenestrate) leaves are another peculiarity of Araceae in genera such as *Dracontiodes* Engl., *Monstera*, *Rhaphidophora*, and in juvenile leaves of *Anchomanes* and certain species of *Cercestis*. Interesting work has been carried out by Gunawardena (2008) which argues that the perforations in the leaf laminae in *Monstera* species arise through programmed cell death early in leaf development.

A number of genera have species with peltate leaves (tribe Colocasieae Engl., *Anthurium*, *Caladium* Vent., *Homalomena*), in which the petiole is attached from the underside of lamina in the manner of a lotus.

The midrib is almost always present, being absent only in *Gymnostachys* and *Pistia*. The major veins which comprise the midrib and basal ribs and which branch laterally from them are termed primary lateral veins. Secondary, tertiary and higher orders of lateral veins are recognized by their relative thickness and/or their hierarchical level

of branching. The primary lateral veins may be arcuate-parallel (e.g., *Ambrosina*), pedate (e.g., *Typhonium*) or radiate (e.g., many *Arisaema*), but most commonly are pinnately arranged. Even in pedatifid (-sect) and radiatisect leaves, the primary lateral veins of each segment are generally pinnate. Except in deeply divided leaves, the primary lateral veins always run throughout the leaf lamina, ultimately joining together at the leaf apex (Ertl, 1932).

Venation

The primary lateral veins generally run to the margin first, where they form a marginal vein and this then runs to the leaf apex. In some species, most primary lateral veins curve arcuately within the margin to fuse together at the apex, and in these cases only the lowermost primaries run into the margin to form a marginal vein. In other genera either one or several of the primary lateral veins form a submarginal collective vein (brochidodromous pattern) which lies parallel to the marginal veins.

The finer venation may be variously reticulated (e.g., *Anthurium*, and many *Schismatoglottis*) or may run essentially parallel to the pinnately arranged primary lateral veins (e.g., *Philodendron*, *Homalomena*). This latter venation type is termed parallel-pinnate or striate, to distinguish it from true, grass-type parallel venation, which in Araceae occurs only in *Gymnostachys*.

A third type of fine venation ('colocasioid venation') has been recognized for tribes *Colocasieae* and *Caladieae* and analogies occur also in *Schismatoglottis*. In this

pattern, the finer veins branch almost at right angles from the primary lateral veins and then arch strongly towards the leaf margin, often fusing on the way to form a more-or-less sinuose interprimary collective vein. The fine veins finally join into a submarginal collective vein. Intermediates occur between most recognized types.

2.1.3 Floral Morphology

2.1.3.1 Overview

Araceae is characterized at a macro morphological level by it bearing small bractless flowers on a fleshy unbranched axis (spadix) subtended by a modified leaf (spathe). The flowers are usually numerous, small to very small and sessile in all genera except *Pedicellarum* M.Hotta and some *Arisaema*. They are generally spirally arranged and usually tightly packed, although in some species of the Goniurid *Pothos* (*Goniurus* Group), *Pedicellarum*, *Amorphophallus* (male and female flowers), tribe Spathicarpeae (female flowers) and most species of *Arisaema* and *Arisarum* (male flowers), they may be somewhat distant from one another. The spathe is, strictly speaking, the last leaf of a flowering module. It is usually a specialized attractive organ, although in a few genera (*Gymnostachys*, *Orontium*) is inconspicuous. The internode between spathe and spadix (spadix stipe) is usually very short or absent, while the peduncle – the internode between spathe and last foliage leaf or cataphyll – is usually much longer. In some primitive genera, however, it is the stipe which is longest (*Gymnostachys*, subfamily Orntioideae (*Lysichiton* and *Orontium*) [in *Symplocarpus* with a peduncle and the spadix with a short stipe], and some *Pothos* species).

The typical aroid inflorescence architecture has given rise to a wide range of variant forms in different genera. These can be seen to represent an evolutionary trend of increasing integration towards a synflorescence or pseudanth. The major phyletic modifications are: 1) loss of perigone in the flowers; 2) specialization of flowers on the spadix into a lower female zone, upper male zone and, often, one or several zones of sterile flowers, entirely naked axial zones and smooth or staminodial terminal appendices; 3) differentiation of the spathe into a lower, convolute tube and an upper, expanded lamina. Spathe and spadix modifications are closely related so that the spathe may be seen evolutionarily as becoming increasingly integrated into the inflorescence itself, until in extreme cases, such as tribe Cryptocoryneae, *Ambrosina*, *Pistia*, some *Typhonium*, and *Pinellia* Tenore, fusion and still more elaborate modifications have brought about division of the spathe into separate chambers. All flowers are adnate to the spathe in *Spathicarpa* and *Spathantheum*. Other notable specializations of the inflorescence include the wide range of odours found in different genera, colour patterns, especially on the spathe, the relative persistence of different regions of the spathe, notably the lower persistent part in many genera that is linked to fruit and seed dispersal mechanics, and a wide range of floral adaptations, many seemingly linked to ‘managing’ pollinators.

Terminal appendices of the spadix are found in tribes Areae, Arisaemataee, Colocasieae, Schismatoglottideae, Thomsoniae and Zomicarpeae, and sporadically elsewhere in the family. The function of the appendix, where investigated, is to produce odours to attract pollinators (Vogel, 1990).

The appendix is either clearly composed of staminodes (e.g., many *Schismatoglottis*, some *Amorphophallus*) or is partially composed of staminodes, or entirely smooth with no vestiges of floral organs (e.g., *Arum*, most *Amorphophallus*).

The sex of the individual flowers and their arrangement on the spadix are two of the characters used to define taxonomic groups. Depending on the genus the spadix may be either unisexual or bisexual flowers. When the spadix bears bisexual flowers then these are uniformly arranged over the spadix. Bisexual flowers have an envelope of reduced tepals termed a perigone or tepals are lacking (e.g., Monstereae). If unisexual, the flowers are usually arranged with the females at the base of the spadix and the males above, with the zones occasionally separated by a zone of sterile flowers and the spadix occasionally terminated by a sterile appendix. In *Arisaema*, the sex of the inflorescence of most species is usually 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 mature plants growing in a less than ideal habitat will produce male inflorescences. 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 are naked, i.e., lacking a perigone. Only three genera (*Zamioculcas*, *Gonatopus* and *Stylochaeton* have unisexual flowers with a perigone.

2.1.3.2 Flowers

Overview

Flowers in Araceae may be 2- or 3-merous, sometimes more, very rarely less. In perigoniate flowers the tepals, when free, are organized in two whorls. The tepals are usually more-or-less fleshy and fornicate and truncate apically (except subfamily Pothoideae) and in some genera or sections (*Anadendrum*, *Holochlamys*, *Pedicellarum*, *Spathiphyllum* sect. *Massowia*, *Stylochaeton*) they are fused into a cup-like structure. Stamens in perigoniate flowers and in the naked bisexual flowers of most Monsteroideae have essentially the orthodox structure of distinct (usually flattened) filament, basifixated anther and slender, inconspicuous connective. In the unisexual flowers of many tribes of subfamily Aroideae, however, filaments are typically very short or lacking, and there is a thick, fleshy connective which perhaps acts as an osmophore (Aglaonemateae, Culcasieae, Homalomenae, Montrichardieae, Nephthytideae, Philodendreae, Zantedeschiae). Stamens of tribes Anubiadeae, Caladieae, Colocasieae, Spathicarpeae, and Peltandreae are essentially similar but are always fused into synandria. Filaments of the stamens are connate in a different degree in the tribe Spathicarpeae.

Stamens

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*, *Stylochaeton*) or by apical or subapical pores either directly on the thecae, or via an elongated needle-like structure (e.g.,

Cryptocoryneae, *Aridarum*, *Bucephalandra* and *Phymatarum*) or short slits. In many genera of subfamily Aroideae dehiscence of each thecae is by a subapical stomial pore and this morphology is frequently correlated with the extrusion of pollen in strands. Similar structures occur in *Amorphophallus* and *Dracunculus*.

Pistils

The gynoecium usually varies between 1- and 3- locular, and when unilocular it 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 are found 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*, *Helicodiceros*, 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., *Caladium*, *Xanthosoma*, 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*) 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, 1989). In tribe Monstereae this stylar region is especially well developed and densely filled with trichosclereids. Here the style seems to substitute functionally for a perigone in protecting the sexual organs of the flower and certainly plays a role in protecting the developing fruits after. Stigmas

are always wet in Araceae and in some genera (*Anthurium*, *Arum*, 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.

2.1.4 Fruit and Seed Morphology

2.1.4.1 General

The fruits of Araceae are typically juicy berries, rarely dry and leathery less often dehiscent syncarps. The infructescence is usually variously cylindric or sometimes globose. Berries are most commonly red or orange but also dirty white, green or yellow and even blue are also common. Berries are almost always free with notable exceptions in *Syngonium*, in which the berries form an indehiscent syncarp, and *Cryptocoryne* which has an apically dehiscent syncarp. In *Lagenandra* the free berry actively opens at the base to release the seeds, but aroid berries are otherwise indehiscent. The distinctive sloughing-away of the stylar tissue in the Monsteroideae makes such fruits arguably dehiscent although their status as berries is very much open to question. Madison (1979) uses the term fruit but without further elaboration; in all likelihood a new descriptive term is needed for this fruit type. Monstero carp has been adopted for the forthcoming Flora of Thailand account (Boyce, pers comm.)

2.1.4.2 Fruit Protection

The various mechanisms observed for protection of the developing fruits and seeds have been discussed by Madison (1979). In the Monstereae, which have bisexual but non-perigoniate flowers, the thick stylar region is filled with trichosclereids which protect the developing seeds. At maturity the stylar region is shed to reveal the seeds.

In perigoniate genera such as *Anthurium* the perigone clearly plays a protective role and keeps pace during growth of the developing berry. The latter only becomes fully exposed at maturity by extrusion from the flower. In *Lysichiton*, also perigoniate, the stylar region and tepal apices protect the young berry, eventually breaking off to reveal the ripe seeds (Hultén & St. John, 1931).

In many unisexual-flowered genera the protective function is assumed by the persistent spathe or spathe tube. Spathe growth continues around the developing fruits until maturity when the spathe may split open either basiscopically (*Alocasia*, *Dieffenbachia*, *Schismatoglottis*) or acroscopically (*Homalomena*) or absciss 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., *Arum*) protection may possibly be through the presence of toxic chemical compounds in the berries.