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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*), lithopytes, 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 risinf 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 restiong 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 Spathiphylleae (*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) *Nephthytis* 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 Nephthytideae. 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; *Steudnera* 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