Ecology and Life Forms of Araceae

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INTRODUCTION

Araceae, a family of herbaceous monocotyledons with 106 genera, is a complex group in terms of life form and ecology. The family is widespread, with almost an equal number of genera in both the Old and New Worlds, but with the majority of species occurring in the New World tropics. A few genera range into north temperate regions with one species ranging to at least 63 degrees north latitude. Few aroids range into temperate regions of the southern hemisphere; the most southernly being *Pistia stratiotes* L., which can be found through 36 degrees south latitude in Argentina. The family occupies a wide variety of life zones and habitats throughout its range, extending from tropical dry to pluvial rainforest, but also ranges into subarctic marshes, tropical swamps, cloud forests, cold windswept montane plains and semi-arid to arid coastal plains. The family has many species which will not tolerate any degree of frost or cold such as *Anthurium brownei* Masters, as well as some, like *Symplocarpus foetidus* (L.) Nutt., which actually emerge from snow-covered ground.

The most interesting aspect of the family's ecology is the diversity of adaptive life forms. These range from submerged to free-floating, and emergent aquatics to terrestrial plants and to epilithic or epiphytic forms which may be true epiphytes or hemiepiphytic (growing on trees but rooted in soil). Hemiepiphytism is diverse itself, with some species beginning their lives as terrestrial seedlings, then growing skototropically (toward darkness) until they arrive at the nearest suitable tree (usually a relatively large one which casts a darker shadow) where a physiological change takes place allowing them to grow toward light (Strong & Ray, 1975). They grow as appressed epiphytes on trees or as vines in the canopy. Others begin their lives as true epiphytes, some reconverting to hemiepiphytes by producing long, dangling roots contacting the forest floor below.

Some species, especially members of subfamily Monsteroideae, have heteroblastic development with leaf and stem morphology reflecting the differences in their growth phases. Juvenile plants may produce a small terrestrial rosette of leaves, then grow rapidly, producing a few small leaves on long internodes. The preadult leaves of the first hemiepiphytic phase of such plants are often very distinct from the adult leaves. Many such species are able to convert again and again from adult growth (consisting of short, thick internodes) back to juvenile growth (with elongate internodes bearing smaller leaves), either to establish more adult plants with a rosette of leaves or to survive the dynamics of an ever-changing forest, complete with treefalls and falling branches (Ray, 1987). Other hemiepiphytic species are vines which branch and produce growth throughout the lower and middle levels of the canopy. These species (e.g., *Philodendron scandens* K. Koch & Sellow) accomplish long-term survival by having a portion of their biomass in a part of the canopy which survives any particular treefall (Peñalosa, 1975). Even true epiphytes rarely succumb promptly to a fall from their host tree, but instead continue to flower and fruit on the ground for a limited time.

DISCUSSION

The following is an outline and discussion of life form diversity in the Araceae (see Appendix III for a glossary of terms):

1. Aquatic plants
- 1.1 Submerged aquatics
- 1.2 Free-floating aquatics
- 1.3 Emergent aquatics

2. Terrestrial plants

3. Epilithic plants

4. Epiphytic plants
- 4.1 Hemiepiphytes
  - Vines
  - Appressed climbers
- 4.2 Epiphytes

1.1 Submerged Aquatics

Jasarum steyermarkii Bunting has permanently submerged leaves and is the only true example of this life form among neotropical Araceae. It grows rooted in moving streams on the escarpment of the Guayana Highland where it is endemic (Bogner, 1985). When it flowers, the scape is protruded above the level of the water. Many rheophytes, however, may spend a portion of their lives underwater with no apparent harm, but flowering occurs when the plants are mostly emerged and have only their short stems below water. Species of *Acorus*, *Anubias*, *Lagenandra*, *Spathiphyllum* and especially *Cryptocoryne* are used as aquarium plants and may be submerged completely for indefinite periods of time without apparent injury. Even *Dieffenbachia* has been used in aquaria (D. Nicolson, pers. comm.)

The Asian tropics, in contrast to the American tropics, have large numbers of submerged aquatics, the most important being the genus *Cryptocoryne*. Members of this genus spend most of their lives in shallow water, but typically flower at periods of low water (when their leaves have emerged above water level) or when the water level is low (Jacobson, 1980, 1982; J. Bogner, pers. comm.).

1.2 Free-floating Aquatics

Free-floating aquatics are represented by only one genus, with one pantropic and variable species. *Pistia stratiotes* L. has a short stem and a rosette of aerenchymatous, buoyant leaves, with a cluster of fine, hair-like roots below. It occurs mainly at lower elevations and inhabits mostly open, fresh waters at the edges of slow-moving streams, lakes and ponds. This species is remarkably successful in using mostly vegetative reproduction, often totally clogging small to large waterways in a short period of time.

1.3 Emergent Aquatics

Emergent aquatics make up a very large group within Araceae. Many genera have at least some species which spend all or part of their lives rooted in standing or moving water. Temperate North America is particularly rich in aquatic or semiaquatic genera. Most, including *Acorus*, *Calla*, *Lysichiton*, *Orontium*, *Peltandra* and *Symplocarpus*, grow in swampy or marshy areas, lakes, ponds, or along the edges of creeks. *Arisaema triphyllum* (L.) Torr. is also reported as sometimes occurring in swampy areas (Small, 1933; Correll & Correll, 1972).

Some emergent aquatics, e.g., *Montrichardia arborescens* (L.) Schott, *Peltandra virginica* (L.) Kunth, *Cryptocoryne ciliata* (Roxb.) Fischer ex. Schott (D. Nicolson, pers. comm.) and *Typhonodorum lindleyanum* Schott (J. Bogner, pers. comm.), occur in tidal zones.

While most emergent aquatic genera in the neotropics are well-rooted, terrestrial plants, some are epilithic, such as a rheophytic group of *Anthurium* (*A. andicola* Liebm., *A. sytsmae* Croat, *A. rupicola* Croat and *A. antioquiense* Engl.) and *Spathiphyllum* (*S. quindiuense* Engl.), although the percentage of rheophytic species for each genus is low.

The Asian tropics, on the other hand, are much richer in rheophytic plants. *Aridarum*, *Bucephalandra*, *Cryptocoryne*, *Furtadoa*, *Heteroaridarum*, *Hottarum*, *Lagenandra*, *Phymatarum*, *Pipto-*

spatha, some *Homalomena* and some *Schismatoglottis*, have the majority, or all, of their species occurring along or in streams, frequently clinging to rocks on stream banks (van Steenis, 1981).

The majority of emergent aquatic plants are not rheophytic, but rather occur in flowing or standing water. Among the New World genera, which are nearly always found growing in water, are *Dracontioides*, *Montrichardia* and *Urospatha*. Other genera, such as *Dieffenbachia*, *Philodendron* and *Spathiphyllum* have some species growing in aquatic or marshy situations. *Anaphyllopsis* (A. Hay, 1989) grows along streams or in swampy areas in the understory and survives partly underwater part of the year. *Homalomena* sometimes occurs in varzea forest in the Amazon basin, and survives underwater conditions for long periods, then tolerates swampy situations until the water fully recedes.

In addition to the rheophytic genera mentioned above, there are a number of other, chiefly emergent aquatics in Asia usually growing along streams or in swamps. They differ in that they are not usually clinging to rocks or to steep banks, but are rooted along the edges of water courses and usually have subterranean root systems. These include most species of *Cryptocoryne*, *Cyrtosperma*, as well as *Anubias*, *Aglaodorum* (in brackish water), *Lagenandra*, *Lasia* and *Podolasia*.

Africa, a generally much drier continent than Asia or America, has relatively fewer exclusively aquatic genera, although *Anubias* has species which are principally aquatic. *Lasimorpha senegalensis* Schott from tropical West Africa is also an emergent aquatic. In Madagascar (also introduced in surrounding islands), *Typhonodorum* is almost always found in standing water.

Many other genera, in both the Old and New Worlds, frequently grow on stream banks but rarely come in direct contact with the water and cannot be considered aquatic in the true sense. Many are, in fact, principally epiphytic genera which find steep, well-drained stream banks good substitutes for the normal epiphytic habit (see below).

2. Terrestrial Plants

The terrestrial habit is predominant for aroids on a world-wide basis. Terrestrial genera are the most diverse ecologically, occurring in humid to very dry habitats, in secluded forest understory and in open, exposed areas. While most genera comprise mainly understory plants in primary forest, some range into savannas, exposed steppes, alpine meadows and even into semidesert areas. Terrestrial aroids range in habit from caulescent plants (*Dieffenbachia* and *Aglaonema*) to tuberous plants (*Amorphophallus*, *Arum* and *Dracontium*), to rhizomatous (rarely also reported as cormose — see *Colocasia*, *Theriophonum* or *Typhonium* in Appendix II.) and to subscandent plants (*Cercestis* and *Culcasia*).

A large percentage of terrestrial aroids have rhizomes, or short stems with short internodes, which usually creep over the surface of the soil or just beneath the soil surface. Rhizomes may be deeply rooted, as in *Cyrtosperma* and *Spathiphyllum*, but most are weakly or loosely rooted. A few species of *Anthurium* (e.g., *A. ochranthum* K. Koch, *A. pluricostatum* Croat & Baker) and *Philodendron* (e.g., *P. grandipes* K. Krause) are deeply rooted terrestrial plants, although these genera are typically epiphytic.

Most of the rhizomatous creeping genera, as well as caulescent plants like *Dieffenbachia* and *Aglaonema*, have the apical portion of their stems erect with the older part reclining. Typically, when a plant reaches a certain height, the weight of the added growth causes the lower part of the stem to recline. As a result, older plants of *Dieffenbachia*, *Xanthosoma* and terrestrial *Rhodospatha* may have stems extending for more than a meter over the forest floor.

Paleotropical terrestrial aroids are often direct ecological and growth form counterparts of neotropical genera without necessarily being phylogenetically related. For example, *Amorphophallus* (Aroideae) and *Anchomanes* (Philodendroideae) of the paleotropics look superficially like *Dracontium* (Lasioideae) of the neotropics and behave in the same manner, i.e., an inflorescence being produced before the single large leaf is produced.

Among the temperate North American genera, all except *Arisaema*, are associated with the aquatic habitat, though most, including *Acorus*, *Calla*, *Lysichiton*, *Peltandra* and *Symplocarpus* may sometimes be found on dry land but rarely far from water. *Orontium* is always aquatic. Even some species of *Arisaema* (*A. dracontium* (L.) Schott) are most frequent in swamp forest and riparian habitats (M. Grayum, pers. comm.).

Most neotropical terrestrial species are understory plants occurring in humid to wet primary forest, at the edges of primary forests or in open areas in forests, or along stream banks. The genera involved are *Anaphyllopsis*, *Caladium*, *Chlorospatha*, *Dieffenbachia*, *Dracontium*, *Filarum*, *Spathiphyllum*, *Ulearum*, *Xanthosoma* and *Zomicarpa* as well as some species of *Anthurium*, *Philodendron*, *Rhodospatha* and *Stenospermation*. The habit of *Zomicarpella* is also that of an understory herb. A few other genera, including *Stenospermation*, may occur on steep banks, where drainage is good and the ecological situation closely matches the epiphytic habit, but this is commonly true only in areas of disturbance, such as along eroding river banks and roadcuts.

At higher elevations on steep slopes, and especially in cloud forests, the distinction between the epiphytic and terrestrial habit may break down altogether. The general accumulation of debris on the forest floor and good drainage makes such situations virtually identical to the conditions an epiphyte encounters while growing on tree trunks. The distinction between an epiphyte and an epilithic plant is often blurred as well (see below).

In the neotropics, there is a total of 22 strictly terrestrial genera with 267 terrestrial species (including emergent aquatics), with perhaps an additional 250 species in the genera *Anthurium*, *Philodendron* and *Rhodospatha* (genera which are largely epiphytic). The majority are inhabitants of the humid, warm, tropical areas, which contribute 14 genera and almost 500 species. Ten additional genera with 25 species occur principally in cooler or drier habitats in mostly subtropical or temperate South America, while temperate North America contributes an additional six genera and 13 species (see Appendix I for the estimated number of terrestrial species in each group).

Many of the genera, especially in the southern part of the neotropics, are better adapted to growing in harsher conditions. Because of the latitudes or elevations at which they occur, they are adapted to relatively extreme conditions of drought or cold. These genera include *Asterostigma*, *Gorgonidium*, *Mangonia*, *Scaphispatha*, *Spathantheum*, *Spathicarpa*, *Synandrospadix* and *Taccarum*, as well as some species of *Xanthosoma*. All are tuberous, and most have an interrupted growth period due to conditions of cold (as is the case of those in Argentina or at high elevations in the Andes) or to drought, when leaves are deciduous. While some genera usually occur as understory plants, (*Asterostigma*, *Spathantheum*, *Spathicarpa* and some species of *Taccarum*), other genera frequently occur in more open habitat (*Mangonia*, *Gorgonidium*, *Scaphispatha*, *Synandrospadix* and some species of *Taccarum* and *Xanthosoma*).

A higher percentage of paleotropical, as opposed to neotropical, genera are terrestrial and are more ecologically

diverse. Most of the endemic African genera are terrestrial in habit. On mainland Africa these include *Anchomanes*, *Anubias*, *Callopsis*, *Gonatopus*, *Nephthytis*, *Pseudohydrosme*, *Stylochaeton*, *Zamioculcas* and *Zantedeschia*, as well as some species of *Cercestis* and *Culcasia*. In the Malagasy area, terrestrial genera include *Arophyton*, *Carlephyton*, *Colletogyne* and *Protarum* (Seychelles). As in the neotropics, most of the species in these genera occur in the understory of primary, mostly humid forests. Indeed, with the exception of a few species of two genera, *Pothos* and *Rhaphidophora*, most of which occur in Asia, all of the African genera are basically terrestrial. The genus *Anubias* has some species which are aquatic at least part of the time, and both *Cercestis* and *Culcasia* have species which are hemiepiphytic.

A high percentage of the endemic African genera are adapted to a dry season and have developed tuberous stems or rhizomes. These include *Anchomanes*, *Arophyton*, *Carlephyton*, *Colletogyne*, *Gonatopus*, *Protarum* and *Remusatia*. In addition, all of the north African genera of Mediterranean climate areas (see below) are tuberous, as are the three genera which also occur in Asia, namely *Amorphophallus*, *Sauromatum* and *Typhonium* (the last naturalized in Africa). *Stylochaeton*, though not tuberous, accomplishes the same ability to survive long periods of drought by having a short rootstock with thick succulent underground roots.

Not surprisingly, all species occurring in Europe and in the Mediterranean region are terrestrial and most (except *Arisarum*, *Calla* and the introduced *Acorus*, which are rhizomatous) are always tuberous. Most species of *Arum* are adapted to dormancy during the northern winters or during the hot, dry Mediterranean summers. The tuberous genera include *Ambrosina*, *Arum*, *Biarum*, *Dracunculus*, *Eminium* and *Helicodiceros*. See Appendix II for ecological requirements of these genera.

Australia has seven indigenous terrestrial genera, each with only one or two species. These are *Alocasia*, *Amorphophallus*, *Colocasia*, *Gymnostachys*, *Remusatia* (also epiphytic), *Sauromatum* and *Typhonium*. Only *Gymnostachys* is endemic at the generic level (*Amorphophallus*, *Alocasia* and *Typhonium* have endemic species). Aside from the terrestrial species, there is one aquatic (*Pistia*), one epiphytic (*Remusatia vivipara* (Roxb.) Schott) and six hemiepiphytic species, so that sixty percent of the araceous flora is terrestrial.

Ecologically, the Asian terrestrial species are more complex than those in Africa. As is the case in the American tropics, the majority of the terrestrial species are understory plants occurring in humid primary forests, but a higher percentage of Asian genera occur in marshy areas. The greatest concentration of genera is in the Malesian region, mostly in evergreen forests, but large numbers of species also occur in monsoon forests further to the north, with a respectable number of species ranging as far north as China and Japan. Asian understory genera include *Aglaonema*, *Alocasia*, *Amorphophallus*, *Anaphyllum*, *Arisaema*, *Colocasia*, *Cryptocoryne* (usually in dried out pools and also included under "rooted aquatics"), *Cyrtosperma*, *Hapaline* (usually terrestrial, rarely epiphytic), *Holochlamys*, *Homalomena*, *Remusatia* (also included among "hemiepiphytes"), *Sauromatum*, *Schismatoglottis*, *Spathiphyllum*, *Steudnera* and *Typhonium*. *Pycnospatha* is also an understory herb.

The majority of the terrestrial Asian genera have rhizomatous stems, though some (*Amorphophallus* and *Pycnospatha*) have tuberous stems and are adapted to short to relatively long periods of dormancy. Most Asian species of *Amorphophallus* occur in closed primary or secondary forest undergrowth (van Alderwerelt van Rosenburgh, 1920, Hu, 1968, Johns & Hay, 1981), but

sometimes also in open areas (see Appendix II).

While some terrestrial aroids have relatively long, erect stems, the majority have short internodes and are tuberous or rhizomatous. A few genera are reported as cormose and there are differences of opinion as to whether they are tuberous or cormose (see *Colocasia*, *Theriophonum* and *Typhonium* in Appendix II). Although standard definitions of corm and rhizome give distinct differences (see glossary, Appendix III) it is not entirely clear how these are reflected in the Araceae. Engler (1905-1920) defines the stem types of Araceae in some detail (see especially the "Pars Generalis," Engler, 1920), but he does not include cormose as a stem type for Araceae. By the strictest definition of terms presented in a variety of glossaries and textbooks there is no question that genera like *Amorphophallus* produce tubers. It is less apparent from the definitions of corms that this stem type exists among the Araceae. Two fairly recent works have reported cormose plants for the Araceae. These include reports for *Theriophonum* (Sivadasan & Nicolson, 1982) and for *Colocasia* and *Typhonium* (Pate & Dixon, 1982). Burnett (1984) also mentions corm production from the rhizomes of *Alocasia*. The stem types mentioned in Appendix III have been taken from Engler (1905-1920) and also from the sources quoted in the text. For a few poorly known genera the stem type was deduced from closely related genera.

3. Epilithic Plants

Epilithic plants do not show a great preference for the surface on which they grow. Many species grow as appressed plants on tree trunks or on boulders. Porous limestone is particularly suitable for epilithic plants because of its ability to catch debris and to provide many interfaces for adequate rooting sites. Rarely is a species found only on limestone (e.g., *Anthurium reflexinervium* Croat sp. nov. ined., *Colocasia gigantea* Hook. f., *Typhonium albispathum* Bogner and *Amorphophallus putii* Gagnepain), but more commonly, species occur both on the limestone and on the trees growing over and in between limestone rocks. In the neotropics, as well as in Asia, craggy limestone areas are invariably good aroid sites, and depending on the amount of rainfall in the region and the exposure, they may be species-rich sites as well. For example, in the region northeast of Tuxtla Guttierrez in the state of Chiapas, Mexico, shady limestone cliffs may be the only areas which are rich in species. The area is relatively dry, and shady limestone cliffs are substantially less arid than tree trunks. Limestone rocks and granite boulders in forests are also important since they represent obstacles to normal tropical agriculture and are usually not cleared to grow crops. Aroids in disturbed areas are thus more likely to be found growing on rocks. Steep road banks also often have an established aroid flora, presumably established soon after the roadcut was made and before the remaining forest in the region was cleared. The same situation exists for epiphytic species which persist in deep ravines passed over by farmers (see below).

The epilithic habitat is as particularly important for rheophytes (see above under "rooted aquatics") as it is for many genera which generally occur on the forest floor (see Appendix I). Many loosely-rooted species occur on the forest floor or along the edges of forest just as commonly as on rocks. In Appendix I, there are 18 genera (16% of the total) classified as both terrestrial and epilithic and the percentage is possibly much higher. The percentage of epiphytic genera which occur both on tree trunks and on rocks is higher still (see below under "epiphytic plants").

4. Epiphytic Plants

Plants which are true epiphytes are naturally restricted to growth on trees or shrubs and thus generally occur in

forests. They are almost invariably restricted to primary forest or regrowth in primary forest, typically in humid to wet areas, and commonly persist in large trees, even after virtually all remaining forest is removed, but in such cases they often do not reproduce sexually. However, vegetative reproduction is so successful in many epiphytic species that they may become more abundant in such situations than they were in the primary forest. Even in primary forest areas, sexually reproducing plants may be rare, while vegetative reproduction is very successful. For example, on Barro Colorado Island in Panama (Croat, 1978), some species, such as *Monstera dilacerata* (K. Koch & Sellow) K. Koch and *Syngonium erythrophyllum* Birdsey ex Bunting, are both rare as adults (only one collection of an adult plant known for each on the island) while juvenile plants are abundant, in general found throughout much of the trail system and covering the ground virtually everywhere.

Epiphytic plants, at least in their early stages of growth, show little preference for either rocks or trees (commonly they are referred to as epilithic, lithophytic or rupicolous when occurring on the former). Most genera have been reported as occurring on rocks, and those not previously reported as epilithic will probably prove to occur on rocks, at least in their initial developmental stages. Since all hemiepiphytic genera begin their development in the soil (except a few species of *Philodendron* which germinate on trees and later produce roots which reach the ground), rocks or boulders are often the first flat upright surface they encounter. Among climbing aroids there are no known cases where rocks are preferred to trees as the principal habitat.

Generally speaking, epiphytic plants prefer to grow on larger trees. The reasons for this are unknown; perhaps the perching behavior of birds dispersing the fruits is the cause. Occasionally, juvenile plants of species which will become large are found on shrubs, without the strong support needed for further development, but they rarely persist there. Appressed hemiepiphytic climbers such as *Monstera*, *Philodendron*, *Rhodospatha* and *Syngonium* remain in a juvenile or preadult condition in shrubs since the right conditions of adequate support and availability of light are not met. The stems of such plants commonly fall free after a time, return to the ground and seek a larger support. Alternatively, some species of *Anthurium* (e.g., *A. kunthii* Poeppig, *A. brevispadix* Croat, *A. pentaphyllum* (Aubl.) G. Don and *A. flexile* Schott) normally occur on smaller trees, including small palms, and on shrubs. Again the reasons are not obvious, but they are species which do not need to attain much height to flower and are generally small in overall size. *Philodendron* section *Pteromischum* also has species which appear to be restricted to shrubs, e.g., *P. aurantiifolium* Schott and *P. viaticum* Croat & Grayum sp. nov., ined.

Most epiphytes (including hemiepiphytes) prefer to grow on the lower part of tree trunks, commonly from one to four meters above the forest floor, probably because conditions of light are generally adequate and humidity is high. Perhaps even more important, the amount of available nutrients and water increase toward the base of the tree, as all nutrients for true epiphytes are derived from runoff from above. Not surprisingly, the only epiphytes which occur very high in the canopy are unusual, either in their ability to withstand the effects of drought (e.g., with thicker, generally more succulent leaves and/or roots), or in their ability to acquire nutrients. Some members of *Philodendron* subgenus *Meconostigma*, for example, may grow very high in trees and eventually produce adventitious roots which extend to the ground. *Anthurium gracile* (Rudge) Lindley often occurs high in the canopy, but

when found there it is generally associated with ant nests, which provide an alternate source of nutrients from detritus accumulated by the ants. It is also a species with roots having a velamen, thus enabling it to better utilize atmospheric humidity as a water source. Some members of *Anthurium* sect. *Pachyneurium* are capable of growing relatively high in the canopy or even on rocks in areas where there is little overhead canopy to provide an adequate nutrient supply. This group is ideally suited to conditions of low rainfall (and consequently low nutrient availability) and has short stems with a large, dense root mass, better able to catch rainfall when it occurs and generally has rosulate leaves to catch and hold fallen debris. The debris accumulates in the "basket" formed by the leaves and the upper, younger roots grow into this debris, providing nutrients and water-holding capacity not available to most other epiphytic aroids.

The epiphytic habit is perhaps even more diverse in form than the terrestrial habit, with both true epiphytes (those which never have contact with the ground), and hemiepiphytes (those which rely on a support on which to grow, but are also rooted in the ground). True epiphytes may on occasion become hemiepiphytes by producing roots which reach the ground, and hemiepiphytes may become true epiphytes by losing their connection with the ground. The different classes of epiphytism will be discussed in turn.

4.1 Hemiepiphytes. This discussion of hemiepiphytes makes no distinction between plants occurring on trees and those occurring on rocks or on stones, even though the term "epiphytes" refers specifically to the former. Perhaps a new term needs to be coined, such as "hemiepilythiphytes", to describe plants using rocks as their support but which are rooted in the ground. From the standpoint of the plant (as already mentioned above) there seems to be little distinction made by most appressed-climbing plants between rocks and trees. However, appressed climbers are rarely seen on rocks, except at forest edges or in open areas in the forest, unless the rock is a very large one; this no doubt due to the unavailability of light where smaller rocks occur. Alternatively, along stream banks, rocks provide a more suitable habitat (permanency, better drainage) than steep banks. The occurrence of appressed-climbing plants located there is much more frequent.

Hemiepiphytic Araceae are of two types. Primary hemiepiphytes, the first type, are those which start their lives as true epiphytes and later make connection with the ground by means of long roots which grow down from the plant and make contact with the ground. Examples of this type are species such as *Philodendron solimoesense* A. C. Smith and *P. megalophyllum* Schott.

The second type start their lives on the ground and climb trees where they become adults and may lose their connection with the ground. These are referred to as secondary hemiepiphytes (Putz & Holbrook, 1986). Most *Anthurium* and *Philodendron* species, as well as *Anadendrum*, *Heteropsis*, *Pothoidium*, *Pothos*, *Syngonium*, many species of *Cercestis*, *Culcasia* and the tribe Monsteroideae are secondary hemiepiphytes.

Most hemiepiphytes must attain a certain stem girth before assuming adult growth and flowering. About half of all hemiepiphytes, including *Alloschemone*, *Amydrium*, *Epipremnum*, *Monstera*, *Rhaphidophora*, *Scindapsus* and *Syngonium*, have heteroblastic leaf development (leaf blades of radically different shapes at different stages of development). One of the most radical examples of heteroblasty occurs in *Monstera* where some juvenile leaves (sect. *Marcgraviopsis*) are tightly appressed ("shingle leaves") and others are free and spreading. In time, this growth form gives way to intermediate, pre-adult

leaves which are more nearly shaped like the adult blades, but which usually are entire, not perforate or lobed (see photographs). Higher up on the stem adult leaves are later formed. This generally means genera with heteroblastic leaf development must attain a suitable height on the tree trunk (generally 2.5 to 5 m) to pass through the juvenile and preadult phases. Light availability appears to be the most important criterion for a plant converting from juvenile to preadult leaves (Ray, 1987). Adult plants may flower even on short tree stumps in forest regrowth, or on rocks in open areas. Substrate is equally important since some plants, under greenhouse conditions with adequate light but without adequate support, have never been observed to change to their adult forms. Even if a concrete wall of adequate height (5 meters or more) is provided, some species grow upon the wall endlessly without becoming adult plants.

Species of hemiepiphytes that do not undergo heteroblastic development have leaves which become increasingly larger in size as the plant matures, but do not undergo marked changes in leaf morphology. Commonly, however, there are minor differences in shape and often coloration and texture as well. The non-heteroblastic genera of hemiepiphytic aroids include *Anadendrum*, *Cercestis*, *Culcasia* (both of the latter sometimes merely terrestrial), *Heteropsis*, some *Monstera*, *Philodendron*, *Pothoidium*, *Pothos*, *Rhodospatha* and *Spathiphyllum* (the last almost always terrestrial). The height at which these genera reach flowering size varies greatly, but is generally much lower than those genera with heteroblastic development. *Rhodospatha* usually flowers at heights similar to those of heteroblastic genera (above 2.5 m), while *Philodendron* is variable, with some species flowering near the ground or even on terrestrial plants about one meter above the forest floor (e.g., *P. luteynii* Croat & Grayum, sp. nov. ined.) and others, especially vines, often occurring in the canopy of the forest (e.g., *P. davidsonii* Croat and *P. scandens* K. Koch & Sellow). *Cercestis* and *Culcasia* often flower very near the ground, as do *Anadendrum*, *Pothoidium* and *Pothos*. *Spathiphyllum commutatum* Schott, and *S. solomonense* Nicolson, both of which may be hemiepiphytic, flower near the ground.

Internode length plays an important role in defining growth behavior of epiphytes, especially hemiepiphytes. Among hemiepiphytes, there are relatively few vines or plants that are markedly scandent. Species generally have relatively long internodes when they are young and in an establishment phase. As the plant approaches maturity, internodes become shorter and thicker. The transition may be fairly abrupt, but generally occurs over a long succession of internodes. Once sexual maturity is reached, and assuming no such major disruptions as a treefall (which will greatly affect the available light or the plant's disposition), most plants indefinitely produce short internodes which grow slowly up the side of their support. There are a number of exceptions to this rule. Some species of *Philodendron*, e.g., *P. linnaei* Kunth, produce a series of short internodes with a tight rosette of leaves alternating with a series of long internodes, which carries the plant apex higher up the tree where another rosette of leaves is produced (Blanc, 1980). This process can be repeated indefinitely. *Philodendron fragrantissimum* (Hook.) Kunth has the same manner of growth but its rosettes are more widely spaced and are even sometimes found on different trees.

Other important exceptions to the rule that hemiepiphytes remain in the "short internode stage" once they have reached this developmental stage are those exhibiting heteroblasty (*Syngonium* and genera in the tribe Monsteroideae). These genera have the ability for repeated conversions from adult growth

with short, thick internodes to juvenile growth with long, slender internodes (Ray, 1983a, 1983b, 1986, 1987).

Scandent hemiepiphytes begin their growth in usually the same manner as short stemmed appressed-climbers, but differ in that the production of longer internodes continues perpetually. As the plant matures, the stems usually also increase in diameter with only moderate decrease in length of internodes.

On appressed-climbers, usually only the uppermost nodes (commonly fewer than ten) are leaf-bearing, but much of the non-leafy stem is intact and acts as continued physical support and probably will also have still active roots for absorbing water and nutrients. The most active roots are always borne on the leafy portion of the plant. However, hemiepiphytic vines are leafy throughout all or much of their length and their roots are likewise more scattered and occur only at the nodes. They are not aggregated in a manner allowing debris to be easily trapped among them, and are therefore less successful in providing themselves with a nutrient supply. Perhaps for this reason the number of hemiepiphytic vines is relatively low compared to the number of appressed epiphytes. Still, it cannot be denied that many hemiepiphytic vines (e.g., *Philodendron scandens* K. Koch & Sellow, *Epipremnum pinnatum* (L.) Engl. and *Pothos scandens* L.) are among the most widespread and successful species.

In the New World all of the hemiepiphytic genera occur principally in primary, mostly humid to wet forests. These genera include *Alloschemone*, *Anthurium* (few species), *Heteropsis*, *Monstera*, *Philodendron*, *Rhodospatha* and *Syngonium*. Some species, especially of *Monstera* and *Syngonium* and also of *Philodendron*, may be abundant in weedy situations, commonly along fence rows and on trees in coffee plantations. In natural habitats they generally begin their growth in areas of natural disturbance and so are preadapted for such conditions; they are often much more abundant in weedy habitats.

The same situation often applies to areas where part of the forest has been cut away, such as a new road. Most hemiepiphytes thrive particularly well in these partially-shaded forest edges. Open areas along rivers and smaller streams offer similar growing conditions.

The neotropics have a much higher percentage of hemiepiphytic genera that are than do the paleotropics. Of all the genera which are predominantly epiphytic, only *Stenospermation* is never hemiepiphytic. *Anthurium*, though it has numerous terrestrial species and a few hemiepiphytic members, largely consists of true epiphytes. *Philodendron* is largely hemiepiphytic, with only a few true epiphytes which start their lives as epiphytes and remain epiphytic (e.g., *P. wendlandii* Schott and *P. davidsonii* Croat).

In contrast to the American tropics, Africa and the Malagasy region have no true epiphytic genera (*Remusatia* is sometimes epiphytic in Asia and Madagascar) and only four hemiepiphytic genera: *Cercestis* and *Culcasia* (endemic), *Pothos* and *Rhaphidophora*, which are indigenous but better represented in Asia.

Four epiphytic genera occur in Australia: *Epipremnum*, *Pothos*, *Pothoidium* and *Rhaphidophora*. All are hemiepiphytes. The percentage of hemiepiphytes in the Australian flora is rather high (five out of 17). All Australian genera (and most of the species as well) except *Gymnostachys*, are widespread in Asia. Asia has eight indigenous genera of epiphytes, and all are hemiepiphytic. These include *Amydrium*, *Anadendrum*, *Epipremnum*, *Rhaphidophora*, and *Scindapsus*. *Spathiphyllum commutatum* Schott (based on Croat 33032) has been observed as an incidental hemiepiphyte in the Philippines. Most are members of the understory or they occur along primary forest edges or in

regrowth in humid to wet areas. Several genera, including *Amydrium*, *Epipremnum*, *Rhaphidophora* and *Scindapsus*, are members of the subfamily Monsteroideae and have heteroblastic leaf development and alternating adult-juvenile growth phases. The only remaining hemiepiphytic genus, *Anadendrum*, has short to moderately long internodes and is (often somewhat) scandent. Of the estimated 700 indigenous Asian species only about 22% are generalized epiphytes (about 160 species, nearly all of which are hemiepiphytic) while of the estimated 2,206 indigenous neotropical species, an estimated 86% (1,000 hemiepiphytes and 910 true epiphytes) are generalized epiphytes. This astounding difference between the araceous flora of the neotropics and the paleotropics is mostly due to *Anthurium* and *Philodendron*, the two largest genera in the family. Both are restricted to the neotropics and both are chiefly epiphytic.

4.2 True epiphytes. This life form group constitutes the largest single group of aroids in the neotropics (about 620 species). The true epiphytes in the neotropics consist largely of *Anthurium* species, but also include all species of *Stenospermation* and some species of *Philodendron*. Hemiepiphytic genera are sometimes disconnected from the soil and thus become true epiphytes, since they are capable of persisting in that state indefinitely. An unusual situation with a few true epiphytes is their ability to eventually send roots to the ground and become hemiepiphytes (e.g., *P. radiatum* Schott and *P. solimoesense* A. C. Smith). These plants often grow very slowly for years before being large enough to send roots to the ground. Particularly surprising in this respect is *P. solimoesense*, as it often grows in very exposed situations high in the canopy where falling debris is more limited.

Most true epiphytes have short internodes and grow more slowly than the average hemiepiphyte. Some species of *Anthurium* (e.g., *A. scandens* (Aubl.) Engl. and *A. interruptum* Sodiro) have elongate internodes, but with the lowermost internodes short and densely rooted for support and for debris collection.

The overwhelming majority of true epiphytes are neotropical; the paleotropics having comparatively few epiphytic species (see above).

As in the case of hemiepiphytes, many true epiphytes are also found on rocks or boulders, when growing in or at the edge of a primary forest. Epiphytic species of *Anthurium*, *Philodendron* and *Stenospermation* may sometimes occur epilithicly.

At higher elevations, many epiphytic species are frequently found in situations where they are neither on trees nor on rocks. These habitats could theoretically be classified as terrestrial, and indeed in these situations the plants are often actually rooted into the soil. Nevertheless, these rarely constitute terrestrial habitats as found in the hot, lowland tropics, where little debris is present on the ground except at the end of the dry season. Instead, these plants are usually rooted in a deep mat of debris due to slow humus breakdown at higher elevations. Bryophytes may be abundant as well, contributing further to substrate formation for the root systems of aroids and other plants. In most cases, such "terrestrial plants", which are normally epiphytic, are also found on steep slopes where drainage is good and where the habitat duplicates the normal epiphytic habitat. As mentioned earlier, normally epiphytic species may also inhabit steep banks of streams or occur on roadcuts, where drainage is good and light is not too intense throughout the day.

Comparison of Different Phytogeographic Regions:

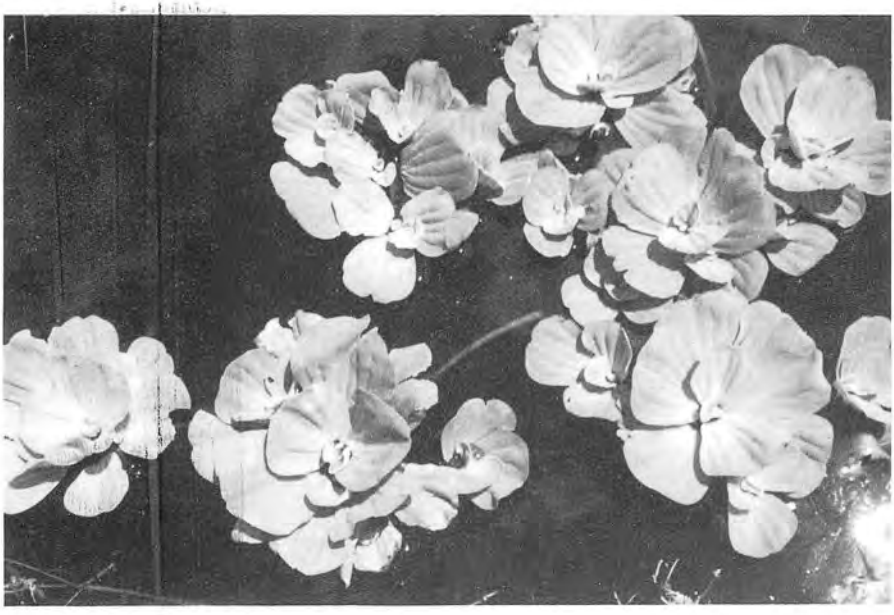
While representation of most life forms of Araceae are found in each major continental area of America, Africa and Asia, there are certain significant similarities and differences. The Mediterranean

region and Europe have only terrestrial, mostly tuberous life forms. North America has only terrestrial, principally aquatic life forms. Temperate and subtropical South America has principally tuberous life forms. Tropical Africa has predominantly tuberous life forms. Tropical America, as well as tropical parts of Africa and Asia, has species primarily inhabiting primary forest, while America overall has a preponderance of hemiepiphytic and epiphytic life forms. Among hemiepiphytic plants, appressed-climbers predominate, while true vines are a minor component. Appressed epiphytes are dominated by genera which have heteroblastic leaf development. In strong contrast to the neotropics, Asia has only a few true epiphytes (probably fewer than six). Tropical America has relatively few rheophytic genera, while Asia has many. Africa has principally terrestrial life forms, no true epiphytes, and few appressed hemiepiphytes or hemiepiphytic vines. Asia has more rooted aquatic genera, and especially species, than does America. Africa has few rooted aquatic plants but a moderately rich assortment of tuberous genera. African genera are rich in plants adapted to dry conditions, with no pronounced diversity in any genus. Although rich in genera, Asia has only moderate speciation in many genera. Asia has more medium-sized genera (60 or more species) than America (*Alocasia*: 70, *Amorphophallus*: 100, *Arisaema*: 150, *Homalomena*: 140 and *Rhaphidophora*: 60), but has no truly large genera like *Anthurium* (1,000) or *Philodendron* (700) in the American tropics. Aside from these two large genera, the neotropics have few genera with as many as 60 species, though a few genera have a moderate number, including *Dieffenbachia* (50), *Monstera* (60), *Rhodospatha* (67), *Syngonium* (36) and *Xanthosoma* (45).

SUMMARY

The Araceae comprises a complex group in terms of life forms and ecologies. Life forms range from submerged to free-floating, from emergent aquatics to terrestrial plants, and from epilithic to epiphytic forms. Life zones range from tropical dry through tropical swamps, cloud forests, cold, windswept montane plains, and semi-arid to arid coastal plains.

The family is widespread with almost equal numbers of genera occurring in the Old and New Worlds, although the majority of species are found in the New World tropics. Distinct differences are shown phytogeographically as well as at the suprageneric taxonomic level. □



Pistia stratiotes L.; a free-floating aquatic, Las Alaotra, Madagascar. Photo: J. Bogner.

Aridarum nicolsonii Bogner; a typical rheophyte growing on sandstone rocks in the Sungai Tambak, Mt. Santubong, Sarawak. Photo: J. Bogner.

Philodendron scandens K. Kock and Sellow; hemiepiphyte appressed-climbing.

Anthurium clidemioides Standl. ssp. *pacificum* Croat and Grayum; hemiepiphyte appressed-climbing.

Rhodospatha moritziana (Schott) Croat; caulescent terrestrial.

Carlephyton diegoense Bogner; terrestrial tuberous, growing in humus collections of limestone in the Montagne des Français, Madagascar. Photo: J. Bogner.

Bognera recondita (Madison) Mayo and Nicolson; acaulescent terrestrial, growing in sandy soil in the rainforest in terra firme at the Rio Javarí near Lago Cauxi, Amazonas, Brazil. Photo: J. Bogner.

Spathicarpa gardneri Schott; tuberous terrestrial, growing on the forest floor in northern Goiás, Brazil. Photo: J. Bogner.

Dracontium pittieri Engl.; tuberous terrestrial.

Zomicarpella amazonica Bogner; tuberous terrestrial, growing in loamy soil in the rainforest in terra firme at the Rio Javarí, Amazonas, Brazil. Photo: J. Bogner.

Syngonium hoffmanii Schott; hemiepiphyte appressed-climber.

APPENDIX I

ARACEAE

Estimated number of species per genus of Araceae.

Neotropical

Alloschemone	1
Aphyllarum = Caladium	
Anthurium	1000
Asterostigma	5
Bognera	1
Caladium	17
Chlorospatha	15
Dieffenbachia	50
Dracontioides	1
Dracontium	18
Echidnium = Dracontium	
Filarum	1
Gearum	1
Gorgonidium	3
Heteropsis	13
Homalomena	17
Jasarum	1
Mangonia	2
Monstera	60
Philodendron	700
Pistia	1
Rhodospatha	67
Spathantheum	1
Spathicarpa	7
Spathiphyllum	60
Stenospermation	60
Synandrospadix	1
Syngonium	36
Taccarum	5
Ulearum	2
Urospatha	20
Urospathella = Urospatha	
Xanthosoma	45
Zomicarpa	3
Zomicarpella	1

Extraneotropical Genera

Acorus	2
Aglaodorum	1
Aglaonema	21
Alocasia	70
Ambrosina	1
Amorphophallus	100
Amydrium	4
Anadendrum	9
Anaphyllum	2
Anaphyllopsis	3
Anchomanes	10
Anubias	8
Aridarum	7
Ariopsis	1
Arisaema	150
Arisarum	3
Arophyton	7
Arum	26
Biarum	21
Bucephalandra	2
Calla	1
Callopsis	1
Carlephyton	3
Cercestis	10
Colletogyne	1
Colocasia	8
Cryptocoryne	50
Culcasia	20
Cyrtosperma	11
Diandriella = Homalomena	
Dracunculus	2
Eminium	6
Epipremnum	15
Gonatanthus	1
Gonatopus	5
Gymnostachys	1
Hapaline	5
Helicodiceros	1
Heteroaridarum	1
Holochlamys	3
Homalomena	130
Hottarum	4
Lagenandra	14
Lasia	2
Lysichiton	2
Nephthytis	5
Orontium	1
Pedicellarum	1
Peltandra	3
Phymatarum	2
Pinellia	7
Piptospatha	10
Pistia	1
Podolasia	1
Pothos	50
Plesmonium = Amorphophallus	
Pothoidium	1
Protarum	1
Pseudodracontium	7
Pseudohydrosme	2
Pycnospatha	2
Remusatia	3
Rhaphidophora	60
Rhektophyllum = Cercestis	
Sauromatum	2
Schismatoglottis	100
Spathiphyllum	3
Steudnera	8
Stylochaeton	21
Symplocarpus	2
Scindapsus	25
Theriophonum	5
Thomsonia = Amorphophallus	
Typhonodorum	1
Xenophya = Alocasia	
Zamioculcas	1
Zantedeschia	6

APPENDIX II

ECOLOGY OF ARACEAE
[Suprageneric classification based on Grayum (1984)]

NEW WORLD

Subfamily Pothoideae
Tribe Spathiphylleae
Spathiphyllum

Principal Life Form:
terrestrial
Alternate Life Form:
hemiepiphytic
epilithic

Ecology: Understory terrestrial, rhizomatous herbs in primary forest or regrowth, usually in wet to swampy areas or along streams in full sun or partial shade, on rocks in streams, rarely on well-drained slopes; open, swampy areas; rarely somewhat hemiepiphytic (Croat & Grayum, in press). *Spathiphyllum* spp. are facultative rheophytic (van Steenis, 1981).

Tribe Anthurieae
Anthurium

Principal Life Form:
epiphytic
Alternate Life Form:
terrestrial
epilithic
hemiepiphytic

Ecology: Mostly appressed-climbers on trees in understory of primary forest, less frequently on higher branches; rarely terrestrial in the understory, frequently on rocks, especially abundant in open areas, along roadcuts, streams and at the edges of treefalls; less frequently terrestrial under shrubs in dry forest or in open sandy areas; rarely along stream banks; common at lower and middle elevations and especially common in cloud forests compared with other aroid genera at middle elevations (Croat & Grayum, loc. cit.).

Tribe Monstereae
Subtribe Heteropsidinae
Heteropsis

Principal Life Form:
hemiepiphytic

Alternate Life Form:
epilithic

Ecology: Scandent plants on trees or less frequently on rocks, usually in the lower canopy or on tree trunks in primary forest (Croat & Grayum, loc. cit.). Sometimes producing slender roots which hang down toward the ground; the subterete seeds germinate in the soil (M. Grayum, pers. comm.).

Subtribe Monsterinae
Monstera

Principal Life Form:
epiphytic
hemiepiphytic

Alternate Life Form:
terrestrial
epilithic

Ecology: Appressed-climbers with usually short internodes as adults, reverting to juvenile or preadult growth upon disturbance; usually on trees in understory of primary forest, less frequently canopy vines with pendent flowering branches; occasionally in regrowth, on fence rows; more abundant in open areas along forest edges (Croat & Grayum, loc. cit.); seeds germinate in soil, juvenile plants terrestrial and skototropic.

Alloschemone

Principal Life Form:
hemiepiphytic

Ecology: Appressed-climbers on trees in understory of primary forest (Croat & Grayum, loc. cit.).

Stenospermation

Principal Life Form:
epiphytic

Alternate Life Form:
terrestrial
epilithic

Ecology: Appressed growth with usually short internodes, rarely somewhat scandent or terrestrial on steep banks; usually in primary cloud forest at mid to high elevations, usually on tree trunks and lower branches, sometimes on rocks; less frequently in lowland rainforest; sometimes on steep road banks in cloud forest areas; germination of seeds in trees (Croat & Grayum, loc. cit.).

Rhodospatha

Principal Life Form:
hemiepiphytic

Alternate Life Form:
terrestrial
epilithic

Ecology: Appressed-climbers, usually in primary lowland to mid-elevation forests, usually on tree trunks; less frequently terrestrial on steep banks, especially on stream banks; germination of seeds in soil with juvenile plants often blanketing much of the forest floor (Croat & Grayum, loc. cit.).

Subfamily Philodendroideae
Tribe Calleae
Calla

Principal Life Form:
terrestrial

Ecology: Herb with long creeping rhizomes growing usually in cold water bogs, pond margins or swampy grasslands from sea level to 1,300 m (Hegi, 1909; Fernald, 1950; Hotta, 1970). The boggy areas may be open to full sunlight or beneath a tree layer (Croat & Grayum, loc. cit.).

Tribe Montrichardieae
Montrichardia

Principal Life Form:
rooted aquatic

Ecology: Shrub-like herb with stems erect and spongy, occurring in warm standing or slowly moving fresh water at low elevations, often forming dense to solid stands along the margin of water courses; sometimes stranded above water levels during the dry season; fruits water-dispersed (Croat & Grayum, loc. cit.).

Tribe Zomicarpeae
Filarum

Principal Life Form:
terrestrial

Ecology: Tuberous understory herb of primary forest.

Ulearum

Principal Life Form:
terrestrial

Ecology: Understory rhizomatous herb growing on leaf litter on "terra firme" of primary forest.

Zomicarpella

Principal Life Form:
rhizomatous

Ecology: Tuberous creeping rhizomatous understory herb in leaf litter on "terra firme" (unflooded areas) of primary forest?

Zomicarpa

Principal Life Form:
terrestrial

Ecology: A tuberous herb occurring in the understory of seasonal forest in Ceará, otherwise in Bahia; where it grows in the rainy season and is dormant in the dry season (J. Bogner, pers. comm.).

Tribe Homalomeneae

Homalomena

Principal Life Form:
terrestrial

Ecology: Usually understory with short, erect (sometimes creeping) stems occurring in primary forest, frequently in wet areas such as along small forest streams. Often on roadbanks in partial shade; less frequently on well-drained slopes in tropical moist forest (*H. wendlandii* Schott) (Croat & Grayum, loc. cit.).

Tribe Spathicarpeae

Mangonia

Principal Life Form:
terrestrial

Ecology: Tuberous herb occurring in seasonally dry areas (Croat & Grayum, loc. cit.).

Asterostigma

Principal Life Form:
terrestrial

Ecology: Tuberous herb occurring usually as an understory plant in primary forest occurring in cool mountain valleys (Madison, 1978), often on steep slopes, ranging from near sea level to 2,300 m.

Synandrospadix

Principal Life Form:
terrestrial

Alternate Life Form:
epiphytic

Ecology: Tuberous herb in dry shrub forest, sometimes in sandy soil with little other vegetation (E. Zardini, pers. comm.), occurring up to 2,000 m; flowering and leafing out in September and early October at the beginning of the rainy season.

Taccarum

Principal Life Form:
terrestrial

Ecology: Tuberous; growing in damp soil in understory or on roadsides, in humid but often seasonally dry areas; sometimes in open areas of "campo cerrado" (a type of shrub forest) (Chodat & Vischer, 1920).

Gorgonidium

Principal Life Form:
terrestrial

Ecology: Tuberous; occurring in seasonally dry areas at 2,500-3,000 m; *G. vargasii* Bogner & Nicolson has been collected in stony cultivated fields near fences (J. Bogner, pers. com.).

Gearum

Principal Life Form:
terrestrial

Ecology: Plants with rhizomatous tubers growing in inundated areas (probably after heavy rains) and with hysteranthous flowering (J. Bogner, pers. comm.).

Spathantheum

Principal Life Form:
terrestrial

Ecology: Tuberous; usually loosely rooted in the understory, growing on deposits of humus on rocks, or under the edges of cliffs and in rock crevices along road banks in shady areas in Bolivia (Croat & Grayum, loc. cit.) or in mountain prairies up to 2,400 m in northern Argentina (J. Crisci, pers. comm.).

Spathicarpa

Principal Life Form:
terrestrial

Ecology: Tuberous plants with tubers, rhizomes or rhizomatous tubers occurring in the understory of humid or marshy forests; *S. hastifolia* Hook. has a wide range of ecological preferences including dry forest (caatinga) where the vegetative parts may die back during periods of drought (J. Crisci, pers. comm.).

Tribe Philodendreae
Philodendron

Principal Life Form:
hemiepiphytic

Alternate Life Form:
epiphytic
terrestrial
epilithic

Ecology: Rhizomatous to scandent herbs with a broad range of ecological requirements; mostly appressed-climbers on trees (less frequently on rocks) in the understory, especially in humid forests at low to middle elevations; sometimes vines growing over low vegetation, especially along edges; rarely as terrestrial herbs in deep shade or as high canopy vines; infrequently in aquatic situations (e.g., *P. brevispathum* Schott, *P. muricatum* Willd. ex Schott, *P. undulatum* Engl.); some groups (e.g., many sect. *Meconostigma*) as erect pachycaulous tree-like plants in open, usually dry areas, especially on pure sand deposits; more frequently as decumbent plants on rocky exposed areas (e.g., *P. callosum* K. Krause) or on rocky cliffs (e.g., *P. henripittieri* Bunting) (Croat & Grayum, loc. cit.). Also some species (*P. wendlandii* Schott) are true epiphytes with a rosulate growth pattern. Still others, e.g., *P. solimoesense* A.C. Smith, begin their life as true epiphytes and eventually produce long roots which reach the ground (thus becoming hemiepiphytes). At least one species has adopted to dry conditions by rooting into tank bromeliads (Mayo & Barroso, 1979).

Tribe Dieffenbachieae
Dieffenbachia

Principal Life Form:
terrestrial

Alternate Life Form:
rooted aquatic

Ecology: Caulescent herb usually in the understory and along clearing edges or stream banks in humid to wet forest; often colonial, forming dense local stands, frequently on well-drained slopes or in rocky areas along streams; rarely in standing water in almost permanently swampy areas in ditches or areas that are annually flooded for a large part of the year (Croat & Grayum, loc. cit.).

Tribe Bognereae
Bognera

Principal Life Form:
terrestrial

Ecology: Rhizomatous understory herb growing on leaf litter or sandy soil (J. Bogner, pers. comm.) in dark, humid forests (Madison, 1980).

Subfamily Colocasioideae
Tribe Caladieae
Subtribe Jasarinae
Jasarum

Principal Life Form:
submerged aquatic

Ecology: Totally submerged in moderately slow moving black-water streams with a pH of 5.0-5.4 in shade or in full sun; flowering scapes emerging from the water for pollination (Bogner, 1977; 1985); mostly *Jasarum* grows in the mud on the stream floor, occasionally between rocks (J. Bogner, pers. comm.).

Subtribe Scaphispathinae
Scaphispatha

Principal Life Form:
terrestrial

Ecology: Tuberous herb occurring in dry, open, grassy areas or in temporary wet spots; appearing after heavy rains and flowering and fruiting promptly (J. Bogner, 1980a).

Subtribe Caladiinae
Caladium

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Usually an understory tuberous herb in open areas in the forest, on creek banks, being especially common in areas of semideciduous forest, where they lose their leaves during the dry season and go dormant; occasionally epilithic with tubers wedged into rocks along creeks or on steep slopes. *Caladium* is well adapted to disturbance, often proliferating in areas along roads in partial shade; ranging from near sea level to at least 1,000 m. (Croat & Grayum, loc. cit.).

Xanthosoma

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Rhizomatous or tuberous; ecologically variable, with some species being understory herbs in moist to wet forests, especially along and in ravines (e.g., *X. robustum* Schott, *X. peltatum* Bunting, *X. tarapotense* Engl.) and others occupying areas of tropical moist to tropical dry forest and losing their leaves during all or part of the dry season; some species occur in open marshy areas in full sun or partial shade (Croat & Grayum, loc. cit.); rarely epilithic in *X. caladioides* Grayum (Grayum, 1986).

Chlorospatha

Principal Life Form:
terrestrial

Ecology: Rhizomatous understory plants in wet ravines, well-shaded creek beds or in boggy areas in the forest, generally at middle to low elevations.

Subtribe Syngoniinae
Syngonium

Principal Life Form:
hemiepiphytic

Alternate Life Form:
epilithic
epiphytic

Ecology: Usually appressed-climbers on tree trunks in the understory of usually moist to wet (rarely dry) primary forest; frequent in disturbed areas such as regrowth or even weedy areas such as in fence rows and on road banks; juvenile plants terrestrial, growing skototropically to the nearest large tree; adult plants converting to juvenile form on disturbance (Ray, 1983b, 1986, 1987).

Subfamily Lasioideae
Tribe Oronteae
Subtribe Symplocarpiinae
Symplocarpus

Principal Life Form:
terrestrial

Ecology: Subterranean rhizomatous herbs occurring principally in wet areas in meadows, woods, swamps, peat bogs, usually on level ground or sometimes on steep slopes or in ravines, often on rich soil in forest or in regrowth (Li, 1979; Croat & Grayum loc. cit.); sometimes in sunny open areas (Nasir, 1978), open steppe or subdesert (Li, 1979).

Lysichiton

Principal Life Form:
terrestrial

Ecology: Rhizomatous; occurring in swampy hardwood forests or occasionally in disturbed forests (Hulten & St. John, 1931); often in broad marshy creekbeds or swampy meadows (Croat & Grayum, loc. cit.).

Subtribe Orontiinae
Orontium

Principal Life Form:
aquatic

Ecology: Herbs on sandy, muddy and peaty shores or rooted in the bottom of shallow fresh water in swamps and lakes (Fernald, 1950); having a broad ecological amplitude from the standpoint of temperature as it ranges from Florida to Massachusetts; the plant is submerged, with most of the leaves exerted; inflorescences protrude above the water at flowering, usually in the spring.

Tribe Lasieae
Subtribe Dracontiinae
Anaphyllopsis

Principal Life Form:
terrestrial

Alternate Life Form:
aquatic

Ecology: Rhizomatous understory herb in primary forest, especially in swampy, sandy areas along streams; the short erect stems are at least partly underwater for part of the year (Bogner, pers. com.). Hay (1988) reported *A. americana* (Engl.) A. Hay to grow in the shade of swamp forests and in a partially flooded area along a road.

Urospatha

Principal Life Form:
aquatic

Ecology: Rhizomatous herb in coastal swamps along the Caribbean coast of Central America and in lowland Amazonia; rarely in areas which are occasionally not wet (Engler, 1911).

Dracontioides

Principal Life Form:
aquatic

Ecology: Swampy herb with spongy rhizome occurring in standing water (Mayo, 1978; Croat & Grayum, loc. cit.).

Dracontium

Principal Life Form:
terrestrial

Ecology: Tuberous herb in seasonally dry areas; leaves deciduous annually; principally occurring in tropical moist and tropical dry forest life zones, less frequently in wetter areas; locally abundant but infrequently seen; plants usually flowering hysteranthously, then producing usually a single leaf (Croat & Grayum, loc. cit.).

Subfamily Aroideae
Tribe Pistieae
Pistia

Principal Life Form:
free-floating aquatic

Ecology: Floating aquatic, reproducing principally vegetatively; growing along water courses (drainage ditches and ricefields, etc.) in mostly fresh water systems at low elevation, occasionally completely covering the surface of the area inhabited (Croat & Grayum, loc. cit.).

Tribe Arisaemateae
Arisaema

Principal Life Form:
terrestrial

Ecology: Tuberous or rarely rhizomatous tuber; New World species usually occurring in primary forest areas as an understory plant in open woodlands,

edges of forest, wet woods or boggy areas or on slopes, usually in deep alluvium or rocky areas (Fernald, 1950; Steyermark, 1963; Correll & Correll, 1972; Croat & Grayum, loc. cit.).

OLD WORLD

AFRICA (Endemic genera only)

Subfamily Pothoideae
Tribe Potheae
Pothos (discussed under Asia)

Tribe Zamioculcadeae
Zamioculcas

Principal Life Form:
terrestrial

Ecology: Seasonally dormant herbs with a more or less rhizomatous tuber (Mayo, 1985); occurring in spreading clumps in the understory of coastal forest, in sandy soil rich in humus or in humus deposits between rocks (Obermeyer & Strey, 1969); adapting locally to either open sunny areas or to dark understory (M. Bleck, pers. comm.).

Gonatopus

Principal Life Form:
terrestrial

Ecology: Tuberous understory herbs in dune forest in northern Natal; *G. angustus* N.E. Br. occurs in shady rocky pockets in low-lying "bushveld" area of eastern Transvaal (Obermeyer, 1977); *G. boivinii* (Decne.) Hook.f. occurs at the edges of virgin forest and within the forest along ravines (Peter, 1930).

Subfamily Philodendroideae
Tribe Culcasieae
Culcasia

Principal Life Form:
hemiepiphytic

Alternate Life Form:
terrestrial
epilithic

Ecology: Rhizomatous to somewhat scandent herbs, mostly with elongate internodes; occurring mostly in lowland primary vegetation in the understory; sometimes in secondary forest, gallery forest, clearings, shallow streams (on rocks) or in wet areas along streams (Hepper, 1968; Knecht, 1983; Croat & Grayum, loc. cit.). Growth forms vary from erect to semierect terrestrial plants to hemiepiphytic climbers (Knecht, 1983).

Tribe Nephtytideae
Nephthytis

Principal Life Form:
terrestrial

Ecology: Understory herbs with creeping rhizomes, growing in dense shade, in lowland primary forest, secondary forest or gallery forest, sometimes occurring on granitic rocks (Knecht, 1983); *N. hallaei* (Bogner) Bogner grows on a layer of humus in sandy soil; *N. swainei* Bogner occurs on acidic, nutrient poor soil (Bogner, 1980b).

Cercestis

Principal Life Form:
hemiepiphytic

Alternate Life Form:
terrestrial

Ecology: Rhizomatous or climbing understory herbs, mostly appressed hemiepiphytic, (sometimes terrestrial) or scandent; *C. ivorensis* A. Chev. occurs in dense shade, while *C. afzelii* Schott requires more light and occurs in secondary forest (Knecht, 1983).

Tribe Callopsidae
Callopsis

Principal Life Form:
terrestrial

Ecology: Small rhizomatous herbs in

the understory of lowland evergreen forest, bearing thick spreading roots; occurring at 45-800 m (Mayo, 1985).

Tribe Anchomaneae
Anchomanes

Principal Life Form:
terrestrial

Ecology: Rhizomatous sparsely leaved herbs usually in open areas in humid forests, along edges of forest or in clearings; sometimes in savanna forest (Hepper, 1968), the bases of isolated hills (Knecht, 1983), abandoned fields and on roadbanks. Plants seasonally die back and go dormant (Mayo, 1985). Engler (1911) described *Anchomanes* as having tubers rather than rhizomes.

Pseudohydrosme

Principal Life Form:
terrestrial

Ecology: Tuberous; in understory in deep shade in the humus layer over sandy loam soils; occurrence extremely rare. (Bogner, 1981a).

Tribe Anubiadeae
Anubias

Principal Life Form:
terrestrial

Alternate Life Form:
aquatic

Ecology: Rhizomatous herb in wet, shady areas of the understory in forest, especially on stream banks, in river beds in either rocky areas or mud (Croat & Grayum, loc. cit.); plants may be completely submerged (Hutchison & Dalziel, 1936; Crusio, 1979) or on rotting logs (Crusio, loc. cit.). Three species are possibly truly rheophytic (van Steenis, 1981).

Tribe Zantedesheae
Zantedeschia

Principal Life Form:
terrestrial

Ecology: Well-rooted rhizomatous or tuberous herbs (Mayo, 1985) perennials with variable ecological requirements; *Z. rehmannii* Engl. occurs on dry, rocky hills (Traub, 1949), or in swampy ground, along forest edges or roadsides usually in sunny areas (Jeppe, 1975); *Z. aethiopica* (L.) Spreng. prefers swampy areas (Jeppe, loc. cit.).

Tribe Peltandreae
Typhonodorum

Principal Life Form:
aquatic

Ecology: Robust rhizomatous aquatic in standing fresh water swamps occurring from near sea level to 900 m; fruits develop and germinate prematurely within the spathe, giving the capability of prompt establishment after dispersal. Engler (1915) reports the genus to have oblong horizontal tubers.

Tribe Arophyteae
Arophyton

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic
epiphytic

Ecology: Tuberous; growing in humus deposits in the understory of forests, sometimes in humus deposits over limestone (*A. crassifolium* (S. Buchet) Bogner) or over granite or gneiss, less frequently as an epiphyte (*A. buchetii* Bogner and sometimes *A. tripartitum* Jum.)(Bogner, 1975).

Carlephyton

Principal Life Form:
terrestrial

Ecology: Tuberous; occurring in shady places in moderately acidic humus deposits (pH 5.4-5.8) over limestone or basalt in deciduous forests (Bogner, loc. cit.).

Colletogyne

Principal Life Form:
terrestrial

Ecology: Tuberous; occurring in shady places in moderately acidic humus deposits overlaying calcareous rocks (Bogner, loc. cit.).

Subfamily Colocasioideae
Tribe Colocasieae
Subtribe Protarinae
Protarum

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Tuberous; growing in the forest understory on hills where it protrudes from the humus layer on or between granitic rocks (Bogner, 1973b) in a region with an evenly distributed rainfall of 250 cm per year and relatively constant temperature of 18 degrees Centigrade.

Subtribe Remusatiinae (see Asia)

Subfamily Lasioideae
Tribe Lasieae
Subtribe Dracontiinae
Cyrtosperma (see Asia)

Lasimorpha

Principal Life Form:
terrestrial

Ecology: Rhizomatous; inhabiting forest edges and in swamps and ravines in savanna country (Hepper 1968); Bogner (1987) reports that this species produces long underground stolons several meters long and may quickly invade areas by this manner.

Tribe Stylochaetoneae
Stylochaeton

Principal Life Form:
terrestrial

Ecology: Seasonally dormant rhizomatous herbs, sometimes with stems stoloniferous (Mayo, 1985). Engler (1920) reports it to have rhizomatous tubers.

Subfamily Aroideae
Tribe Thomsonieae (Amorphophalleae)
Amorphophallus (see Asia)

Tribe Arisareae
Arisarum (see Mediterranean Region)

Tribe Ambrosineae
Ambrosina (see Mediterranean Region)

Tribe Arisaemateae
Arisaema

Principal Life Form:
terrestrial

Alternate Life Form:
epiphytic

Ecology: Growing as a terrestrial tuberous herb principally in damp shady sites in forested areas in bamboo thickets along field borders, margins of thickets or hedges, sometimes over limestone for *A. flavum* (Forssk.) Schott, frequent on rocky slopes (*A. enneaphyllum* Hochst. ex A. Rich.) infrequently epiphytic for *A. schimperianum* Schott and *A. ruwenzoricum* N.E. Br. (Mayo & Gilbert, 1986).

Tribe Areae
Dracunculus (see Mediterranean Region)

Sauromatum (see Asia)

Eminium (see Mediterranean Region)

Biarum (see Mediterranean Region)

ASIA & AUSTRALIA

Subfamily Gymnostachydoideae
Gymnostachys

Principal Life Form:
terrestrial

Ecology: An evergreen herb occurring in open shrublands, usually at the border of shrubs (Bailey, 1902) or in sheltered gullies, rain forests (Beadle, Evans & Carolin, 1982) and in wetter types of Eucalypt forests (Cribb & Cribb, 1981). It is also reported from wet sclerophyll forest, preferring shales and basalt soils but soils are fairly deep (Shelton, 1980). Williams (1979) reports *Gymnostachys* to be common on cool southerly slopes and in cool moist gullies "in areas of sandstone ridges where soils are derived from the weathering of the sandstone."

Subfamily Pothoideae
Tribe Spathiphylleae
Spathiphyllum (see New World)

Holochlamys

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Small herbs with short creeping fusiform tubers occurring in primary forest understory, particularly along small streams, on rocks in streams or on river banks (Johns & Hay, 1981; Croat & Grayum, loc. cit.).

Tribe Potheae
Pothos

Principal Life Form:
hemiepiphytic

Ecology: Generally scandent herbs usually occurring in primary forest or regrowth (Johns & Hay, 1981), usually in humid areas; less frequently on steep banks (Ridley, 1925); usually occurring at low to moderately low elevations but ranging up to 2,400 m in southwestern China (Li, 1979).

Pothoidium

Principal Life Form:
hemiepiphytic

Ecology: Scandent herb occurring in the understory of humid primary forest.

Tribe Anadendreae
Anadendrum

Principal Life Form:
hemiepiphytic

Alternate Life Form:
epilithic

Ecology: Scandent; rooting on trees, shrubs or on rocks in moist to wet forests, often along streams (Ridley, 1925).

Tribe Monstereae
Subtribe Monsterinae
Amydrium

Principal Life Form:
hemiepiphytic

Alternate Life Form:
terrestrial

Ecology: Appressed low climbers on trees or terrestrial plants on steep banks (Ridley, 1925), occurring primarily in primary forest (Li, 1979; Croat & Grayum, loc. cit.) or in late secondary forest regrowth (Johns & Hay, 1981).

Rhaphidophora

Principal Life Form:
hemiepiphytic

Alternate Life Form:
terrestrial
epilithic

Ecology: Appressed-climbing hemiepiphytes occurring from sea level to 2,200 m. in humid to wet, evergreen to deciduous primary forests or in regrowth (Croat & Grayum, loc. cit.). Van Steenis (1987) lists *R. angustata* Schott and *R. beccarii* Engl. as new specific records for the rheophytic habit.

Epipremnum

Principal Life Form:
hemiepiphytic

Alternate Life Form:
terrestrial
epilithic

Ecology: Appressed-climbing hemiepiphytes, occurring principally in humid primary forests or in regrowth on trees or rocks (Ridley, 1925).

Scindapsus

Principal Life Form:
hemiepiphytic

Alternate Life Form:
terrestrial
epilithic

Ecology: Appressed-climbers occurring principally in primary forest understory in humid to wet areas but also in mixed deciduous to dry deciduous forests (Hu, 1968); less frequently in secondary forests (van Alderwerelt van Rosenburgh, 1922a); often terrestrial in sandy soil when juvenile (Croat & Grayum, loc. cit.).

Subfamily Philodendroideae
Tribe Aglaonemateae
Aglaonema

Principal Life Form:
terrestrial

Ecology: Herbs with erect stems or creeping rhizomes, occurring principally in the understory in humid to moist, evergreen or occasionally deciduous forest or in regrowth (Johns & Hay, 1981); occasionally occurring on limestone, on humus deposits on limestone, in peat deposits, fresh water peatswamps or on volcanic soils. Though species chiefly have erect stems, some are epigeal, creeping over the surface of the soil and becoming covered with humus (Nicolson, 1969).

Aglaodorum

Principal Life Form:
aquatic

Alternate Life Form:
terrestrial

Ecology: Stout rhizomatous herbs growing in tidal swamps among *Nypa* palms (Ridley, 1925) (Sumatra & Borneo).

Tribe Homalomeneae
Furtadoa

Principal Life Form:
epilithic

Ecology: Rheophytes with rhizomatous stems growing on wet rocks along streams (Hotta, 1981).

Homalomena

Principal Life Form:
terrestrial

Ecology: Rhizomatous to erect short-stemmed herbs occurring principally in the undergrowth of lowland primary forest (van Alderverelt van Rosenburgh, 1922a, 1922b; Rataj, 1975; Johns & Hay, 1981) especially along streams (Ridley, 1925; Hu, 1968) or along edges, especially on roadbanks in semi-shade (Croat & Grayum, loc. cit.). Four species are listed as possible rheophytes and *H.*

paucinervia Ridley as a typical rheophyte by van Steenis (1981).

Tribe Cryptocoryneae
Subtribe Cryptocoryninae
Cryptocoryne

Principal Life Form:
aquatic

Alternate Life Form:
terrestrial
epilithic

Ecology: Usually small, rhizomatous thin-leaved herbs growing in swampy, mostly open areas or along the edges of streams, ditches or ponds, sometimes on rocks at edges of streams, in gravely stream beds, in cracks of rocks along streams or in densely forested areas (Ridley, 1925; Henderson, 1954; Bennet, 1979; Jacobsen, 1982); some species are found in the fresh water tidal zone in coastal rivers where flowering may be correlated with action of the tide (Jacobsen, loc. cit.), while others are embedded in sand flats along rivers during the rainy season and are exposed during the dry season when they flower (Li, 1979). Eleven species are listed as 'confirmed' rheophytes (van Steenis, 1981) and an additional six species are listed as 'possible candidates' as true rheophytes and others "often occur in slow or stagnant water of ditches and forest pools, on river foreshores, or in small forest rivulets....also certain species are confined to swift-running water and can form submerged mats on rocky or gravely bottoms. Leaves occur tufted on a rhizome which produces runners. Plants root between rocks and boulders, in clefts and in sand; they do not occur mat-rooted on rocks."

Lagenandra

Principal Life Form:
aquatic

Alternate Life Form:
terrestrial

Ecology: Moderately small, thick-leaved helophytes (swamp plants) or a facultative rheophyte with stoloniferous rhizomes occurring mostly in wet places in low country and in shallow water along streams or on stream banks (Trimen, 1898; Fischer, 1931; sometimes being overflooded by high water (Manilal and Sivarajan, 1982). Van Steenis (1981) says *L. undulata* Sastry. "forms dense, submerged patches on partly submerged rock in streambed (Assam). The nine Ceylon species occur apparently mostly in rivers, but do not seem confined to swift-running water."

Subtribe Schismatoglottidinae
Schismatoglottis

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Herbs with short stems or stoloniferous rhizomes occurring in the understory of primary forest along streams, among rocks, in damp areas or on well-drained slopes (Ridley, 1925), often forming dense colonies; sometimes occurring as rheophytes (Croat & Grayum, loc. cit.). Three species are listed as possible rheophytes and two as typical ones by van Steenis (1981).

Piptospatha

Principal Life Form:
epilithic

Ecology: Small herbs with short creeping rhizomes, occurring as rheophytes on rocks or in cracks of rocks along streams in forest understory (Ridley, 1925). Five species are listed by van Steenis (1981) as possibly true rheophytes, and *P. elongata* (Engl.) N.E. Br. as a true rheophyte.

Hottarum

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Small rheophytes with short, creeping rhizome on rocks in and along streams and on nearly vertical mossy banks of streams (Bogner, 1983a; Bogner & Hotta, 1983). *H. truncatum* (Hotta) Bogner & Nicolson is possibly a rheophyte, while *H. lucens* Bogner is a confirmed "typical" rheophyte (van Steenis, 1981, 1987).

Bucephalandra

Principal Life Form:
epilithic

Ecology: Small rheophytes growing (especially sandstone) and in crevices, in and along forest streams (Bogner, 1980c). True rheophyte (van Steenis, 1981).

Phymatarum

Principal Life Form:
terrestrial

Ecology: Small rheophyte with a short, creeping rhizome growing on steep alluvium banks and on alluvium deposits on the forest floor near streams in shady areas in the understory of primary riparian forest (Bogner, 1984). Listed as a 'typical' rheophyte, without comment, by van Steenis (1981).

Aridarum

Principal Life Form:
epilithic

Alternate Life Form:
terrestrial

Ecology: Small rheophytes with short creeping rhizomes occurring on wet rocks (especially sandstone), along and in shallow streams in shady forested areas (Bogner, 1979; 1981b; 1983b). "Five species, all in Sarawak. At least three taxa are rheophytes" (van Steenis, 1981). *A. hansenii* Bogner is listed as a new specific record for true rheophytes by van Steenis (1987).

Heteroaridarum

Principal Life Form:
epilithic

Alternate Life Form:
terrestrial

Ecology: Short-stemmed rhizomatous, monotypic rheophyte occurring as an understory herb along streams in Borneo (van Steenis, 1981).

Subfamily Colocasioideae
Subtribe Steudnereae
Steudnera

Principal Life Form:
terrestrial

Ecology: Herbs with short ascending stems occurring in the understory in wet areas along streams; *S. colocasiifolia* K. Koch occurs in taller forest from 650-1,400 m (Hu, 1968), while *S. griffithii* (Schott) Hook f. occurs in shrub forest at 100-500 m (Li, 1979).

Subtribe Remusatiinae
Remusatia

Principal Life Form:
epiphytic

Alternate Life Form:
terrestrial
epilithic

Ecology: Tuberous herbs occurring mostly in the understory in seasonally dry areas where plants may lose all their leaves during the dry season. Plants grow chiefly as epiphytes (Cooke, 1906; Craib, 1912; Li, 1979; Bogner, 1975; Knecht, 1983), but may also occur in rock crevices (G. Thanikaimoni, pers. comm.), in rocky places in the forest (Fischer, 1931; Hu, 1968), in the under-

story of open forest or in shrub forest on rocks (Li, 1979).

Gonatanthus

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Tuberous; occurring in mossy, moist evergreen forest on deposits of humus on trees (Li, 1979); most common in the rainy season (D. Nicolson, pers. comm.).

Subtribe Colocasiinae
Colocasia

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Often large coarse herbs with caudex short and erect or tuberous (Engler & K. Krause, 1920) to cormose (Pate & Dixon, 1982), the majority occurring in shady places along edges of forest, frequently along streams, often in dark humid situations below 1,300 m (Hu, 1968; Li, 1979) or sometimes on steep, rocky places (Hu, 1968). The weedier species, such as *C. esculenta* (L.) Schott, may occur in moist open areas in undisturbed forest, but more often occur in areas along water courses, roadside ditches and in marshes (Nicolson in Saldanha and Nicolson, 1976); *C. gigantea* Hook. f. is frequent on limestone outcrops in creek valleys in the understory (Ridley, 1925; Hu, 1968; Li, 1979) but also in areas away from limestone deposits (Henderson, 1954).

Alocasia

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Rhizomatous or caulescent herbs, often large, occurring principally in open or semi-open forest, or along streams in partially shaded areas or in full sun. Two basic growth types occur: the terrestrial species tend to be large, often solitary or in small clumps and may prefer open boggy areas (Johns & Hay, 1981; Burnett, 1984); lithophytic species tend to be smaller, generally clustered and grow in rock crevices, or over humus deposits on rocks, especially limestone (Burnett, 1984; Croat & Grayum, loc. cit.), with their stems mostly repent with only the roots covered by soil. Burnett (1984) states that *Alocasia* produces corms which grow on stolons off the root system and by offshoots which emerge from the side of the rhizome.

Subtribe Hapalininae
Hapaline

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: *H. appendiculata* Ridley is a tuberous understory herb (Ridley, 1908) found in humus deposits along paths with basalt rock (Bogner, 1984); *H. benthamiana* Schott occurs in open dipterocarp forests (Hu, 1968). *H. kerrii* Gagnepain occurs in crevices in limestone rock (Gagnepain, 1941).

Subfamily Lasioideae
Tribe Lasieae
Subtribe Dracontiinae
Cyrtosperma

Principal Life Form:
aquatic

Alternate Life Form:
terrestrial

Ecology: Coarse, short-stemmed to tu-

berous (Engl. & K. Krause, 1911), usually solitary herbs with underground rhizomes (Johns & Hay, 1981) occurring in wet areas in the understory of open woods, in regrowth or in marshy open areas (Ridley, 1925; Johns & Hay, 1981). In New Guinea the genus usually occurs in the lowlands and in the "Lower Montane" zone (Johns & Hay, loc. cit.).

Lasia

Principal Life Form:
aquatic

Alternate Life Form:
terrestrial

Ecology: Short-stemmed coarse herbs with underground rhizomes (Johns & Hay, 1981), usually occurring in open marshes or wetlands, usually in permanently standing water (Bennett, 1979; Johns & Hay, loc. cit.), in marshes, at edges of bogs, or along streams in primary or cut over forest (Hu, 1968), sometimes in river mud, usually in tidal flats (Ridley, 1925); in ridges in rice fields, in wet bamboo forests or in tropical and seasonal rain forest regions (Li, 1979); Johns & Hay (loc. cit.) report the genus to prefer areas which are markedly to somewhat seasonal and to be tolerant of somewhat saline situations.

Anaphyllum

Principal Life Form:
terrestrial

Ecology: Rhizomatous herbs in humus deposits of evergreen and semievergreen forests (Croat & Grayum, loc. cit.); sometimes on wet places (J. Bogner, pers. comm.).

Podolasia

Principal Life Form:
aquatic

Ecology: Herbs occurring in swampy places along streams (Croat & Grayum, loc. cit.). Engler (1911) reported it to have a short, erect caudex, but Hay (1988) reported the stem of *Podolasia* to be rhizomatous.

Subtribe Pycnospathinae
Pycnospatha

Principal Life Form:
terrestrial

Ecology: Tuberous herbs occurring in sandy loam in shady places under shrubs, trees or bamboos (Bogner, 1973a). The tuber is subterranean, usually 10 to 12 cm deep in the soil (Bogner, loc. cit.).

Subfamily Aroideae
Tribe Thomsonieae
(Amorphophalleae)
Amorphophallus

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Tuberous; the majority of the species in the genus are Asian, principally terrestrial but occasionally on rocks, especially limestone (usually with a humus covering). They may occur in the understory or along the margins of primary evergreen or deciduous forest and usually spend at least some time in a dormant state (e.g., *A. galbra* F.M. Bailey in Australia, which flowers hysteranthously. Most Asian species occur in closed primary or secondary undergrowth (van Alderwerelt van Rosenburgh, 1920; Hu, 1968; Johns & Hay, 1981). Most are heavily rooted in soil, often associated with humus or rocks (Hu, 1968). A few species are reported from open pastures, grassy fields (Ridley, 1925), waste places or savannas (Johns & Hay, 1981) or in areas of human habitation (Mayo, pers. comm.).

Tribe Atherurinae
Pinellia

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Tuberous herbs occurring principally in shady wet areas along creeks or rivers, on rocks in forests, in rock crevices or rocky slopes by streams and as forest floor herbs (Hotta, 1970; Li, 1979) but also in waste fields, roadsides and cultivated lands (Hotta, loc. cit.).

Tribe Pistieae (see New World)

Tribe Ariopsideae
Ariopsis

Principal Life Form:
terrestrial

Alternate Life Form:
epilithic

Ecology: Tuberous herb occurring in crevices or on forest floor, flowering during the rainy season and becoming leafless during the dry season (Manilal & Sivarajan, 1982).

Tribe Arisaemateae
Arisaema

Principal Life Form:
terrestrial

Ecology: Tuberous (or rarely rhizomatous) herbs usually occurring in understory, in Asia (as in the New World), often at the base of slopes, on rocky slopes or in ravines (Li, 1979), occasionally in wet areas, swamps or in peat bogs; occasionally in open areas near forest or in regrowth in rich soil (Li, pers. comm.), sometimes in sunny open areas (Nasir, 1978), open steppe or subdesert (Li, loc. cit.).

Tribe Areae
Theriophonum

Principal Life Form:
terrestrial

Ecology: Tuberous (Engler, 1920) or cormose herbs (Sivadasan & Nicolson, 1982) occurring in moist, shady areas on rocky, lateritic soil (Manilal & Sivarajan, 1982) or in grassy areas of dry country (e.g., *T. crenatum* Blume in Sri Lanka) (Trimen, 1898).

Typhonium

Principal Life Form:
terrestrial

Ecology: Tuberous (Engler, 1920) to cormose (Pate & Dixon, 1982) perennial herbs occurring from near sea level to 4,000 m (e.g., in alpine and subalpine meadows in southwest China (Li, 1979) and principally in shady areas in thickets near hedges and in fence rows, open areas in shade, along streams, ponds and grassy areas (Bennet, 1979; Manilal & Sivarajan, 1982), in waste ground, along roads (Ridley, 1925; Henderson, 1954), sometimes in evergreen forest, frequently in deep humus (Hu, 1968), on limestone rocks in damp areas (Ridley, loc. cit.) or in bamboo forests (Li, 1979).

Sauromatum

Principal Life Form:
terrestrial

Ecology: Tuberous; occurring in shady damp places in riverine forests, upland areas in Africa (Hepper, 1968; Mayo, 1985); in Asia, Nasir (1978) reported its occurrence in the understory as well as in sunny, open places. Peter (1930) found *Sauromatum* in banana fields.

Eminium (see Mediterranean Region)

EUROPE & MEDITERRANEAN REGION
(Endemic genera only)

Subfamily Aroideae
Tribe Areae
Subtribe Arinae
Arum

Principal Life Form:
terrestrial

Ecology: Tuberous herbs adapted primarily to a Mediterranean climate with hot, dry summers and cool, wet winters, but occurring much further north in Europe where seasonality is in tune with normally hot, moist summers and cold winters. In both cases, plants spend a significant part of their life cycle in a dormant, leafless condition. Growing under a wide variety of situations, including shady, woody areas along rivers and swamps in both lowlands and uplands (Prime, 1960), in beech forests on limestone, as well as open bush vegetation, in moist loamy soil in open country, and in hedges (H. Riedl, pers. comm.), as well as in pastures and abandoned areas, especially in deep soil with small rocks (Mouterde, 1966).

Dracunculus

Principal Life Form:
terrestrial

Ecology: Tuberous herbs growing in shady places (Boissier, 1884), usually in shrubby thickets (Hegi, 1909) in areas of Mediterranean climate.

Helicodiceros

Principal Life Form:
terrestrial

Ecology: Tuberous herb of Mediterranean climate; dormant during the hot dry summers.

Eminium

Principal Life Form:
terrestrial

Ecology: Tuberous herbs of principally Mediterranean or monsoon climates with a distinct dry and wet season, growing among stones, or in sand, principally in open areas or in waste ground (Mouterde, 1966; L. Boulos, pers. comm.).

Biarum

Principal Life Form:
terrestrial

Ecology: Tuberous herbs in Mediterranean climates, growing in hilly areas in fields and pastures, vineyards or limey fields in dry, sandy areas and among rocks (Boissier, 1884; Mouterde, 1966). Flowering occurs in the fall usually just before the leaves emerge and the leaves die off in late spring when the plant becomes dormant (Mayo, 1980).

Subtribe Arisarinae
Arisarum

Principal Life Form:
terrestrial

Ecology: Tuberous or rhizomatous herbs in Mediterranean climates, growing in lanes and sheltered roadsides (Prime, 1960). In Israel, *A. vulgare* Targ.-Tozz. occurs on the coastal plains, in the inland valleys and in mountains, growing on a wide variety of soil types with the exception of pure sand or in marshlands (Galil, 1978).

Subtribe Ambrosiinae
Ambrosina

Principal Life Form:
terrestrial

Ecology: Tuberous herbs in Mediterranean climates, growing principally along coasts on north facing slopes in depressions and in sandy or rocky areas in "grassy vegetation, degraded forests, hedges and especially in machia-like shrubs" (Riedl, 1980).

APPENDIX III

GLOSSARY

Life Forms

APPRESSED-CLIMBING An epiphytic (usually hemiepiphytic) plant, which grows tightly appressed up the side of tree trunks, cliffs or stones, typically with the internodes getting shorter and broader in age.

AQUATIC Growing wholly or partly submerged in water for most of its life. Wholly "submerged aquatics" are those, like *Jasarum*, which are continuously immersed except for the inflorescence which protrudes above the water. A "free-floating aquatic", like *Pistia*, is not rooted in soil and plants are largely above the water surface owing to the buoyancy of the leaves. "Emergent aquatics" like *Urospatha* and *Montrichardia* have, in general, only the roots and lower part of the stems beneath the water but usually will not survive long without being in standing water.

EPILITHIC Growing on rocks, sometimes in shallow deposits of soil but not rooted into the ground.

EPIPHYTIC Growing on trees and not rooted into the ground; in a general sense often used for those growing also on rocks, fence posts, etc.; in the strictest sense those growing on trees only; seeds germinating on support, not in soil on the ground.

HEMIEPILITHIC Growing on rocks but rooted in the soil (constitutes previously unused term).

HEMIEPIPHYTIC Growing on trees but rooted into the ground; may be either: 1) primary epiphytes (Putz & Holbrook, 1986) which have seeds germinating on the tree and later send roots to the ground, or 2) secondary epiphytes, those which have seeds germinating in the soil on the ground and later grow up the tree and frequently (always?) lose their connection with the ground. In addition hemiepiphytes show variation in the degree of attachment with the majority being "appressed-climbers" (also sometimes referred to as "root-climbers"), plants with short internodes which are growing very slowly up their support. The second growth type, featured by such species as *Philodendron scandens* K. Koch & Sellow, begin their life as appressed-climbers but later become scandent or even pendent.

RHEOPHYTIC Growing along the edges of moving streams, either those rooted in deep soil or those occurring on rocks.

TERRESTRIAL Growing in soil, even rocky soil but not in swampy or inundated soils.

Storage Organs

CORM A swollen base of a stem enclosed by the dry scale-like leaves, a solid structure with distinct nodes and internodes (Hartmann & Kester, 1975); a bulb-like fleshy stem or base of a stem; a "solid" bulb (Jackson, 1965); an underground stem that "is vertically compressed but expanded horizontally" (Dodd, 1962); the corm "in dormant condition carries a well-defined, apical meristem, and various forms of scar tissue marking points of attachment of previous leaves, inflorescences and roots" (Pate & Dixon, 1982); each growing season the apical meristem of the corm produces a set of aerial leaves; "a flowering stem then becomes reproductive, storage tissue arises through the swelling of new nodal and internodal tissue" (Pate & Dixon, loc. cit.); in a comparison with the tuber, Starr &

Taggart (1984) define a corm as developing new plants from "an axillary bud on short, thick, vertical underground stem" whereas tubers produce new shoots "from buds on tubers (enlarged tips of slender underground rhizomes)."

RHIZOME The rootstock or dorsiventral stem, of root-like appearance, prostrate on or underground, sending off rootlets, the apex progressively sending up stems or leaves (Jackson, 1965).

TUBER A modified stem which develops below the ground as a consequence of the swelling of the subapical portion of a stolon and subsequent accumulation of reserve materials (Hartmann & Kester, 1975). A class of storage organs divided into stem tubers and root tubers (Pate & Dixon, 1982); see respective definitions.

STEM TUBER "Any globoid, thick-cylindrical or jointed swelling of underground fleshy stem tissue" (in the broadest sense) (Pate & Dixon, loc. cit.). "In one type the tubers consist of swollen, underground lateral shoots of vertical or horizontal orientation, whose storage potential is increased by extension and thickening of existing tubers or by development of new tubers" (Pate & Dixon, loc. cit.). A "second, more closely-prescribed form of stem tuber is one in which each storage unit arises separately as a highly modified swollen lateral shoot on an otherwise unswollen shoot system" (Pate & Dixon, loc. cit.). Tubers may be perennial and added to seasonally or they may be seasonally replaced as in the case of *Amorphophallus*.

ROOT TUBER Storage organs derived from roots either arising on existing "true" roots or arising on "adventitious" roots which have arisen from stem tissue as opposed to already existing tissue (Pate & Dixon, loc. cit.).

"Shingle" leaf of *Monstera spruceana*.

Xanthosoma robustum Schott; caulescent terrestrial.

Stenospermation marantaefolium Hemsl.; epiphyte.

Philodendron wendlandii Schott; epiphyte.

Montrichardia linifera (Arruda) Schott; emergent aquatic.

Orontium aquaticum L.; emergent aquatic.

Lasia spinosa Thwaites; emergent aquatic.

Urospatha sagittifolia (Rudge) Schott; emergent aquatic.

Anthurium schlechtendalii ssp. *schlechtendalii* Kunth; epilithic.

Anthurium nizandense Matuda; epilithic.

Philodendron radiatum Schott; hemiepiphyte, growing on lateral branch.

Syngonium hoffmanii Schott; hemiepiphyte appressed-climbing.

Epipremnum amplissimum Engl.; hemiepiphyte appressed-climbing.

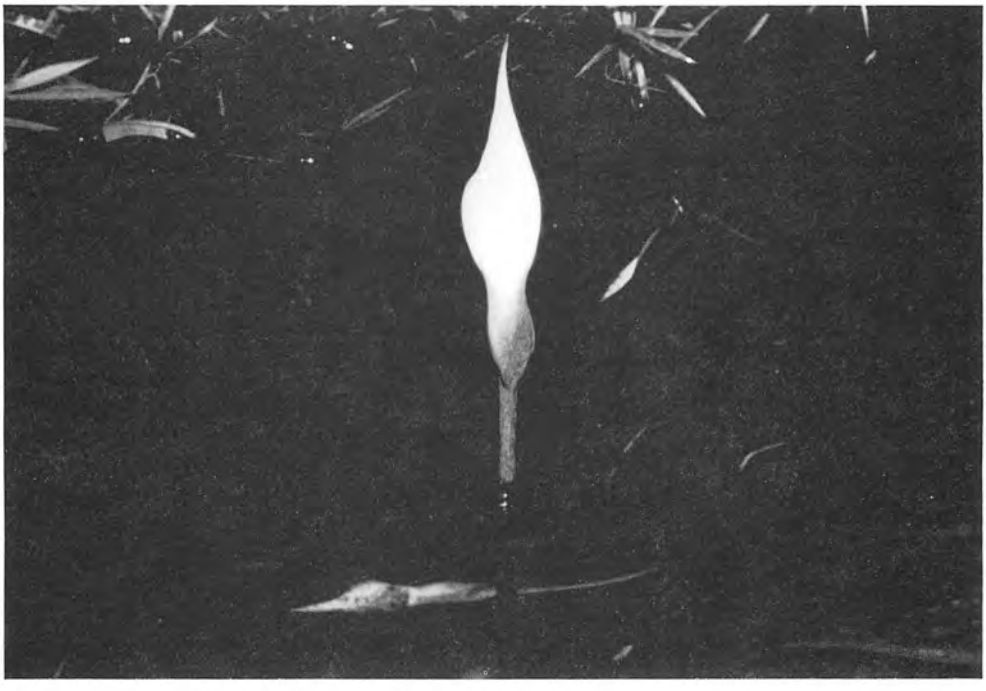
Juvenile and adult leaf forms on *Rhaphidophora pinnata*.

Dieffenbachia seguine (Jacq.) Schott; caulescent terrestrial.

Xanthosoma helleborifolium (Jacq.) Schott; tuberous terrestrial.

Philodendron rigidifolium K. Krause; hemiepiphytic vine.

Anthurium hacumense Engl.; epiphyte .



Jasarum steyermarkii Bunting; submerged aquatic.

Ambrosinia bassii L.; tuberous terrestrial. Photo: J. Bogner.

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