Morphological Variation in Aroids

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INTRODUCTION

The Araceae or aroids are a large family of about 2400 species, grouped in 107 genera and these again in nine subfamilies. The aroids are mainly a tropical family and are distributed world-wide. They show great variation in their morphological characters, which will be described in this paper along with some other data.

USES

Many aroids are very handsome ornamental plants and often cultivated, to mention just a few: *Monstera deliciosa* Liebm., *Dieffenbachia maculata* (Ladd.) G. Don, *Epipremnum aureum* (Linden & André) Bunting, many Philodendron species etc. *Monstera deliciosa* also has a delicious fresh infructescence tasting like pineapple. Others are important food plants, like *Colocasia esculenta* (L) Schott, the Taro, in which the tuberous stems and the leaves are eaten cooked; *Amorphophallus paeoniifolius* (Dennst.) Nicolson is cultivated for its starch-rich tubers in tropical Asia, mainly India. *Cyrtosperma merkusii* (Hassk.) Schott var. *chamissonis* (Schott) A. Hay is grown in Southeast Asia and a few Xanthosoma species, originally from tropical America, are cultivated in the Neotropics, tropical Africa and Asia. Some others are also used by indigenous people, like seeds of *Typhonodorum lindleyanum* Schott in Madagascar and the roasted seeds of Montrichardia by Indians in tropical South America. Many aroids are poisonous in the fresh stage, including those mentioned above which are used as food plants (Colocasia, Xanthosoma, Cyrtosperma, Amorphophallus). Their stems, rhizomes, tubers or leaves must be cooked

or roasted (or otherwise heated) to become edible. Essentially, plants have produced poisons to protect themselves from being eaten by animals. Several aroids also have uses in folk-medicine. For instance, *Acorus calamus* has been used since ancient times for stomach ailments. *Typhonium blumei* Nicolson & Sivadasan is used to treat diarrhea in tropical Asia and was brought by man (probably from India) to Africa, Madagascar and to the Neotropics (Brazil, Venezuela), where it is naturalized today. The Indians in Colombia use *Urospatha antisylleptica* R. E. Schultes, *Philodendron dyscarpium* R. E. Schultes and *Anthurium tessmannii* Krause for contraceptive purposes. Roots of *Heteropsis spruceanum* Schott are used for basket-weaving and certain aroids as arrow poisons for hunting by indigenous people. These are just a few examples of the uses of aroids, about which much more is known.

ECOLOGY

The aroids are adapted to many habitats and more than 90% are tropical. The majority prefer warm and humid conditions, but aroids have also conquered periodically dry areas, where they have a resting period with dormant rhizomes, tubers or very fleshy roots (Stylochiton). But nearly all of these prefer shady places, at least under trees or shrubs or between rocks. One, Zamioculcas, is a succulent plant and stores the water in its thick petioles. Aroids also grow in very special ecological niches, like rheophytic habitats; true rheophytes are Aridarum, Bucephalandra, Piptospatha, etc. Others grow permanently submerged (Jasarum,

many Cryptocoryne species) or float on the water surface (Pistia). Some aroids (Aglaodorum, several Cryptocoryne, e.g. *C. ciliata*, tolerate brackish water and occur in fresh water tidal zones in tropical Asia). But no aroids occur in true deserts; some grow in very dry areas (Arum and Eminium in Central Asia, Arum and Biarum in North Africa and the Orient, Arisaema in the Arabian Peninsula and East Africa, a few Stylochiton species reaching the Sahel zone), but all of these areas have a certain rainy season each year, during which they can grow vegetatively. Temperate areas are poor in aroids, but contain some old isolated genera (Calla, Symplocarpus, Orontium, Lysichiton, all of which are swamp plants). Calla and Lysichiton are distributed northwards to the subarctic zone (Calla to northern Scandinavia, Lysichiton to Alaska). A few of the other mainly temperate genera (Arum, Arisaema, Pinellia) grow on the forest floor or at least in shady places under trees or shrubs, but in all these cases their rhizomes or tubers are dormant during the cold season. Some aroids go high up into the Andes (Gorgonidium ca. 3000 m) or African mountains (*Arisaema ruwenzoricum* up to 3200 m on the Ruwenzori), where a warm temperate climate exists. The highest altitude is reached by the genus Arisaema in the Himalaya, where *Arisaema lobatum* Engler and *A. jacquemontii* Blume are growing up to an elevation of 4500 m, *Arisaema flavum* Schott up to 4400 m and for some other species an altitude up to 4000 m is reported. Some aroids grow under semi-epilithic conditions, with their stems, rhizomes or tubers growing in humus deposits in holes or crevices of steep rocks (limestone hills in Malay peninsula with *Colocasia gigantea* Hook. f., Amorphophallus; washed out holes in limestone in Madagascar with Carlephyton, Colletogyne; or granitic hills in Eastern Brazil with a few hard-leaved Anthurium species). The rheophytes grow mostly directly on rocks under very humid conditions.

GROWTH FORMS

Aroids have many different growth forms. Most are terrestrial plants growing in the soil or high climbers which can become disconnected from the forest floor and then send down long feeding roots to the soil (= hemiepiphytes). It can be expected that all climbers exhibit skototropism, but this has so far been proven for only a few species to date. There are also true epiphytes (many Anthurium species, Remusatia), swamp plants, true submerged aquatic plants (Jasarum, most Cryptocoryne species) and a free-floating species, *Pistia stratiotes* L.

MORPHOLOGY

Vegetative Parts (shoots, vegetative propagation)

Aroids are herbaceous, perennial herbs, some very large, or subshrubby climbers with somewhat woody older stems. The leaves are arranged in rosettes or the internodes may be long, especially in the root climbers, where some groups (Monstereae, Cercestis) flagelliform shoots (= flagelles), with very long internodes and cataphylls only, also occur. Some aroids have upright short stems with the leaves at their apex (Alocasia, Xanthosoma sect. Xanthosoma), pseudostems (Typhonodorum), creeping rhizomes or tubers; rarely they may be tree-like (Montrichardia with stems up to 6 m, some species of Xanthosoma with trunks to 3 m tall and some species of Alocasia such as *A. portei* Becc & Engl., *A. macrorrhiza* (L.) G. Don, *A. odora* C. Koch). The ramification of aroids is usually sympodial, rarely monopodial (Potheae). Vegetative propagation usually occurs. There are shoots, often specially formed as long runners (stolons) with a rosette of leaves (Cryptocoryne) or a tuber at their apex (some Alocasia, few Amorphophallus). Some produce underground runners several metres long (*Lasiomorpha senegalensis* Schott), quickly occupying large areas. The flagelles (with their very long internodes) of

Fig. 1 *Aridarum nicolsonii* Bogner. A typical rheophyte growing on sandstone rocks
        at Sungai Tambak, Mt. Santubong, Sarawak. J. Bogner
Fig. 2 *Cryptocoryne pontederiifolia* Schott growing in a *Nypa fruticans* swamp near
        Tabakis, Sumatra, Indonesia. J. Bogner
Fig. 3 *Lagenandra ovata* (L.) Thwaites, in Sri Lanka (Ceylon). J. Bogner
Fig. 4 *Lasia concinna* V. A. V. R. This very rare aroid from Kalimantan, growing in the
        Kebun Raya, Bogor (Java). W. Herrmann

several Monstereae and Cercestis enable them to quickly reach another branch or tree. Peculiar erect or horizontal above-ground shoots with many small bulbils also occur in Remusatia and Gonatanthus. One bulbil is produced on the upper part of each petiole in *Pinellia ternata* Makino (syn.*P. tuberifera* Ten. and a few on the leaf-blade of *Amorphophallus bulbifer* (Roxb.) Bl. Much more common are tubercles produced sometimes in large quantities around the apex of an old tuber (Dracontium), or in lower numbers in many other tuberous species (Arisaema, Typhonium). Another unusual type of vegetative propagation is by broken leaflets, in Zamioculcas and Gonatopus; the leaflets fall down by a slight touch, then root in the soil and form a tubercle from which a new leaf will develop.

Leaves

Aroid leaves show very great variation. The leaves are usually arranged spirally, only rarely distichously or solitarily (Amorphophallus, Dracontium). The petiole is usually well developed and has a sheath, which protects the young, still furled leaf; only rarely are leaves subsessile. Some aroids (Anthurium, Monstereae) have a geniculum which enables them to move the leaf-blade into an optimal position relative to the light.

Although ensiform leaves (unifacial in Acorus, bifacial in Gymnostachys) rarely occur, most leaf-blades range from filiform (certain stages in *Cryptocorne retrospiralis* Kunth and *C. consobrina* Schott), linear (Jasarum), elliptic, ovate, oblong to sagittate, hastate and tripartite; compound leaf-blades also occur and may be of the pedate, radiate or the dracontioid type, the latter with three main parts, each of which can be divided two or three times again. True pinnate leaves (Zamioculcas, somewhat intermediate in *Gonatopus petiolulatus* (Peter) Bogner and Anaphyllum), are also known, as well as pinnatifid to pinnatisect and laciniate leaf-blades, sometimes with holes (many Mon-

stereae). There is often a great difference between juvenile and adult leaves. In most cases, the first foliage leaf (of a seedling), is entire; subsequent leaves may become increasingly divided, sometimes ending up highly compound; between the extremes, all intermediate leaf-forms exist. There are species, for instance in the genera Syngonium and Xanthosoma, in which juvenile and adult leaves are always entire, yet other species in the two mentioned genera have compound (pedate) leaves in the adult stage. But there are other genera, like Gonatopus and Amorphophallus, in which the first foliage leaf (of a seedling) is already divided; they never have entire leaves.

Leaf venation in aroids is parallel or reticulate, but in both types we can find some variation in certain groups, like Pothos or Colocasioideae; also somewhat intermediate types exist, where the (primary) lateral veins of the first order are parallel, but the lateral veins of the second order are reticulate (some Monstereae, Spathiphyllum). One (or two) collecting veins running along the margin of the leaf-blade are quite common, where the lateral veins of the first order turn upwards and then connect (anastomose) along the margin.

Aroid leaves, as well as all other parts of the plant, are usually glabrous, but hairy leaves aare also known. These are mostly pubescent, tomentose, villous or with trichomes on the petioles and the veins on the lower surface of the leaf-blade only. *Pistia stratiotes* is well known as a hairy species; the other species with trichomes occur in disparate, often completely unrelated genera (Schismatoglottis, Cryptocornye and Lagenandra, Arisaema, Stylochiton, Xanthosoma, Philodendron). Spiny petioles occur in many Lasioideae. Some aroid species have leaves that are naturally colored, either on the entire lower or upper surfaces or as spots or stripes. These species have been used especially for selection and crossing of nicely colored cultivars (some Aglaonema Caladium, Dieffenbachia).

Development, juvenile and adult stages

Cataphylls are leaves in which the blade is not developed or is reduced, and in certain cases (stolons), all intermediates can be found, beginning with a minute blade at the apex of the cataphyll, and so on. Cataphylls can be found on stolons, flagelles, seedlings or on adult shoots in association with ramification. Cataphylls are usually membranaceous, though sometimes weathering to fibers persisting for a long time on the stem (some Philodendron, Anthurium); usually however they rot away quickly, soon drying or falling off. Seedlings start with one or a few cataphylls before the first foliage leaf appears. Sympodial ramification terminates in an inflorescence and the new shoot always starts with one or a few (depending on the group) cataphylls. In several cases (Anthurium, Philodendron, Cryptocoryne) cataphylls appear but not inflorescences, which are actually suppressed. But it is then easy to see that such a plant has already reached the adult stage, even if juvenile and adult leaves are not different. For example, if a Philodendron with uniform leaves (some have different leaf forms in the juvenile and adult stage) produces one foliage leaf after another then it is in juvenile stage; if foliage leaves and cataphylls are produced alternately then it is in the adult stage, but this does not automatically mean that such a plant will produce inflorescenes. The length of the sheath also usually changes from the juvenile to the adult stage.

Inflorescences

The flowers of aroids are usually very numberous and small, rarely few by reduction, and are generally arranged on a fleshy axis, the spadix, only rarely in a (non fleshy) spike (Pedicellarum, some Pothos). Not much is left of the spadix in the very reduced Pistia, and in the related Lemnaceae, the Duck Weeds, the spadix is completely lacking.

Spathes

The aroid spadix is subtended by a modified leaf or bract, the so-called spathe. The spathe has undergone great modifications in its evolution, from an inconspicuous green, leaf-like organ to a colored, spreading and very showy one. The most highly specialized spathes are constricted between the female and male flowers or above the fertile flowers, with a tube below and a showy lamina above. But spathes may also be partly (Stylochiton, Sauromatum) or for most of their length marginally connate and forming a kettle' enclosing the flowers (Lagenandra, Cryptocoryne). Usually the spathe is adnate below the spadix, but in two genera (Lysichiton, Orontium) the spathe goes down to the rhizome and only encloses (not adnate) the peduncle; this is an unique and, in my mind, another primitive character.

Flowers

Aroid flowers are nearly always sessile (except shortly pedicelled in Pedicellarum), usually densely arranged on the spadix and are always lacking a bract below each flower. Such bracts are always present in the Liliiflorae, which are especially interesting in that they may imitate aroids in having densely flowered spikes (Rohdea, Gonioscypha). The primitive spadix in aroids is covered with perfect flowers up to its apex. Then, an evolutionary tendency toward reduction of flowers appears. The upper flowers may become sterile and, in highly advanced spadices, we find a long terminal appendage without any sign of floral rudiments. Often sterile flowers appear between the male and female parts of the spadix, and these have a characteristic form in different groups. There is great variation among sterile flowers, too. The female flowers are always situated on the lower part of the spadix, the male ones above them, except in Spathicarpa where male and female flowers are arranged in longitudi-
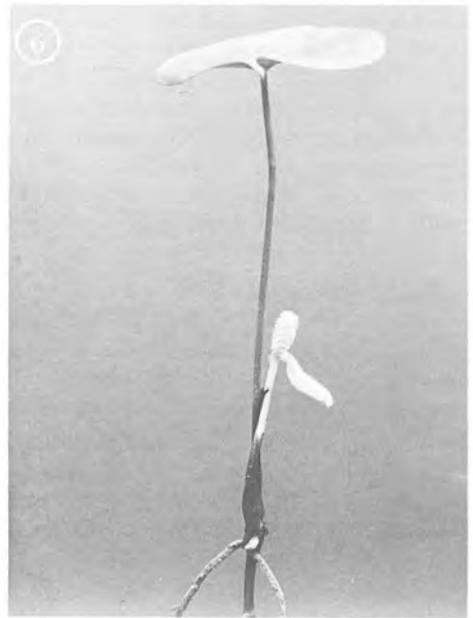
Fig. 5 *Cryptocoryne ciliata* (Roxb.) Schott, showing the limb of spathe with a ciliate
     margin; from Celebes. J. Bogner
Fig. 6 *Amydrium humile* Schott, in flower from the Malay Peninsula. J. Bogner
Fig. 7 *Anaphyllopsis americana* (Engl.) A. Hay in flower from French Guyana. J.
     Bogner
Fig. 8 *Rohdea japonica* (Thunb.) A. W. Roth. A member of the Liliaceae first
     described as an aroid (*Orontium japonicum*) by Thunberg. J. Bogner

nal rows with the spadix and spathe completely connate. But in the related genus, Spathantheum, in which the spadix is also entirely adnate to the spathe, the female flowers are below and the male ones above, as in typical aroids. The spadix in other aroids is free, but in some genera there is a partial adnation of the lower (female) part to the spathe.

The flowers themselves undergo a great evolutionary reduction from perfect flowers to naked bisexual flowers to· naked unisexual flowers, with several intermediate forms. Plants with unisexual flowers are usually monoecious, but in Arisaema most species are paradioecious. Paradioecious means that sexuality is not genetically fixed, but depends on environmental conditions; stronger and bigger plants produce female flowers only, whereas weaker or younger plants produce male flowers only. Since the tubers are formed anew in each vegetative period, it may happen that a small tuber is produced due to poor nutrients or the destruction of the leaf early in its growth; such a plant, if it flowers at all, may produce male flowers only. Arisaema species are normally either monoecious or paradioecious, but occasionally in certain usually paradioecious species plants can be found with female and male flowers on the same spadix.

As already mentioned, in the evolution of aroids there has been an across-the-board trend toward reduction in flower structures. Perfect (bisexual) flowers with a perigon become naked bisexual flowers (Monstereae, Pycnospatha) or unisexual flowers with or without a perigon, with or without rudiments of the other sex. A few examples should suffice to demonstrate this; first, perfect flowers are considered.

Perfect flowers

Perfect flowers in aroids usually have four or six tepals, in two whorls of two or three, as well as the same number of stamens. The tepals are of a medium-thick

structure, very thick and truncate (Anthurium, Dracontium, Urospatha) to membranaceous (Anadendrum, in which they are also shorter than the ovary and inconspicous). Tepals may either be free, partly connate (some Pothos) or completely connate and forming a cup (Pedicellarum, Spathiphyllum sect. Massowia, Holochlamys). The number of tepals of the perigon in the genera Urospatha and Dracontium is inconstant. *Urospatha sagittifolia* (Rudge) Schott has flowers with four, sometimes five or six tepals as well as stamens on the same spadix. The same situation is found in the genus Dracontium, where up to eight tepals may occur and often the same number of stamens, though the latter may have up to nine or twelve, and then do not correspond with the number of tepals. This example shows that the question of whether aroid flowers are basically di- or trimerous should not be overemphasized.

Unisexual flowers

Unisexual flowers with a well developed perigon are found in the genera Zamioculcas and Gonatopus; both have female flowers without rudiments of the other sex, but the male flowers have a pistillode in the center. In Zamioculcas the stamens are free, whereas in Gonatopus the stamens are connate with the fused filaments forming a ring around the pistillode. The unisexual flowers of Furtadoa are naked; each male flowers consists of single stamen and one pistillode and each female flower of a pistil with one staminode. Taccarum and Gorgonidium have male flowers with completely or partly connate stamens, but the central part of each synandrium is clearly of pistillodial origin. Most species of Stylochiton have a small, inconspicuous pistillode in the center of the male flower, but their male flowers have free stamens with filiform filaments and each male flower is surrounded by a saucer-like perigon; each female flower is surrounded by a cup-like perigon covering the whole ovary, and staminodes never present. The

flowers of the Arophyteae are naked and the very similar cup-like organ around the pistil of the female flower is clearly of staminodial origin, as it is proven by the existence of bisexual flowers between the female and male flowers in some species; other species have sterile flowers (= sterile male flowers) of the same structure in this region and form a so-called synandrodium (lacking the anthers). A similar situation can be found in the genus Asterostigma sect. Rhopalostigma, in which the staminodes around the pistil are connate. Usually, the staminodes are free and surround the pistil; they are mostly four or six in number, but there is some variation. In the genus Homalomena there is usually only one staminode beside the pistil, or else staminodes are lacking altogether. The staminode in Homalomena can be as long as the pistil, in which case it is often clavate, but in many cases it is much smaller and more or less conical or conoidal or sometimes minute or completely lacking. Other examples are the genera Zantedeschia and Amorphophallus. *Zantedeschia aethiopica* (L.) Spreng. has several staminodes around the pistil of each female flower, whereas all other species of this genus are completely lacking such staminodes. Another case is *Amorphophallus cirrifer* Stapf, which has filiform staminodes around the pistil, all other species lacking any staminodes in the female flowers. Some Amorphophallus species have staminodes between the female and male flowers. Two species (*A. margaritiferus* Kunth and *A. mysorensis* E. Barnes & C. E. C. Fischer) have peculiar pearl-like organs in this position. Most species of Amorphophallus have an (apical) appendix without any sign of staminodes, but a few unrelated species have an appendix with more or less well developed staminodes. The conclusion is that the presence or absence of one or more staminodes, as in the above mentioned examples, should be not overemphasized. Those species of Homalomena without a staminode in the female flower are closely related to other species on the basis of

other characters, and the same can be said in the case of *Zantedeschia aethiopica* or *Amorphophallus cirrifer*. At first, upon seeing *A. cirrifer* with its long filiform staminodes around the pistils, one thinks in terms of a separate genus, but a comparison of other characters reveals that it is closely related to other species. I think that this species is worthy of subgeneric or sectional rank; Stapf, who described it, has already established the subgenus Metandrium for *Amorphophallus cirrifer*.

Staminodes

Generally, staminodes and sterile male flowers are quite variable in form, and both are used for classification. Staminodes can be free or partly or completely connate; their form varies from filiform, cylindrical, clavate or spathulate to scale-like. These kinds of staminodes can surround the pistils or lie between the female and male flowers, or above the male flowers. Quite often synandrodia arise from connate staminodes or from synandria, become steril, and are situated between the female and male flowers or on the (apical) appendix. They are also variable in form, often resembling the synandria, but without thecae and appearing elongate or subrhombic in shape (viewed from above) and truncate in Caladieae. Synandrodia in the Arophyteae are empty only in the center where there is usually a pistil (in bisexual flowers, between the female and male flowers). But synandrodia can be also wart-like, flat, knob-like or prismatic; these kinds are mostly found on appendices.

Male Flowers

Male flowers are also distinctively formed in the different groups. The male flowers of Zamioculcas and Gonatopus have already been mentioned; these still retain a perigon. In other cases, male flowers are naked. The stamens are free or all partly or completely connate, and then forming a synandrium. Free stamens

may be in groups of two, three, four or six in a male flower, but they can also be solitary, which means that each male flower consists of only one stamen. The filaments of the stamens may be filiform, but are more often flat. They may be fused only basally or higher up, and there is often much variation on the same spadix, as in *Gorgonidium mirabile* Schott. But mostly the filaments are completely connate and the thecae are arranged laterally or apically, or even marginally on the synandrium. These synandria are mostly truncate, but may be mushroom-like, cyclindric or of other shapes. Synandria can also be reduced to one stamen only (Colletogyne). In Ariopsis, all male flowers are connate and form a single mass.

The anthers always consist of two thecae, each of which consists of two pollen sacs. The thecae open by means of a lateral slit or an apical pore or slit; the opening of each pollen-sac separately is rare. Some (Cryptocoryne, Lagenandra, Aridarum) have horned thecae, ending in a more or less long tubule with poricidal dehiscence. The stamens of Aridarum are peculiar: the thick filament is excavated and the two thecae are situated inside or outside of the cavity, depending on the species.

Pollen grains

The pollen grains of aroids are of different types and their morphology is very useful for the classification of genera or higher taxa. The pollen grains are usually shed in monads, but Xanthosoma and Chlorospatha have tetrads. The most primitive aperture is the monosulcate type; a few genera have dicolpate (Calla, Rhaphidophora, Heteropsis), periporate (Anthurium), or extensive-sulcate or zonate-sulcate pollen grains. Inaperturate pollen grains are, however, quite common. The ornamentation of the exine also shows great variation: smooth, rough, reticulate, foveolate, striate, echinulate (spiny), verrucose (warty), areolate and baculate.

Pistils

The aroid pistil usually has a slightly narrowed stylar region below the stigma, but long styles and sessile stigmas are also known. The stigma is always wet and covered with copious secretion during the receptive phase, and dries afterwards. The stigma is capitate to disc-like, or lobed to star-like. The ovary is unilocular to plurilocular, though unilocular ovaries are pseudomonomerous. Two- or three-locular ovaries are common, and some species have ovaries with numerous locules. There are one to many ovules per ovary or locule, in some species up to one hundred in an ovary. Great variation also exists in the type of placentation. Axile, parietal, apical, basal or basal *and* apical placentation all occur in aroids. The ovules can be orthotropous, hemiorthotropous, amphitropous, hemianatropous or anatropous.

Fruits

The fruits of aroids are usually berries with plenty of juice, rarely nearly juiceless, closely packed in the infructescence. Generally, the berries are free, but form an indehiscent syncarp in Syngonium and, in Cryptocoryne, a syncarp which opens apically. The berries are usually indehiscent (not opening), the ripe berries of Lagenandra open basally at maturity and release the seed or seeds. Aroid berries contain one to many seeds. The spathe can be deciduous after anthesis, drying or rotting away, or may be completely or partly persistent. In many cases, the lower part of spathe (tube) protects the young developing fruits, then decays at maturity or actively opens (Alocasia) to present the colored berries. The berries in aroids are vividly orange to red or purple-red in color, white (many Philodendron species, Stenospermation), sometimes green or yellow (Typhonodorum).
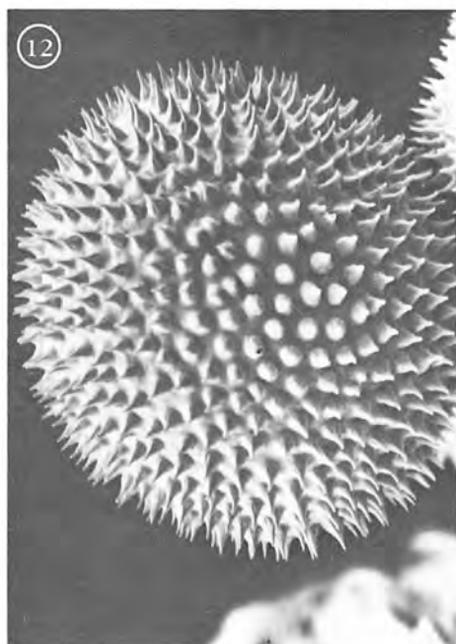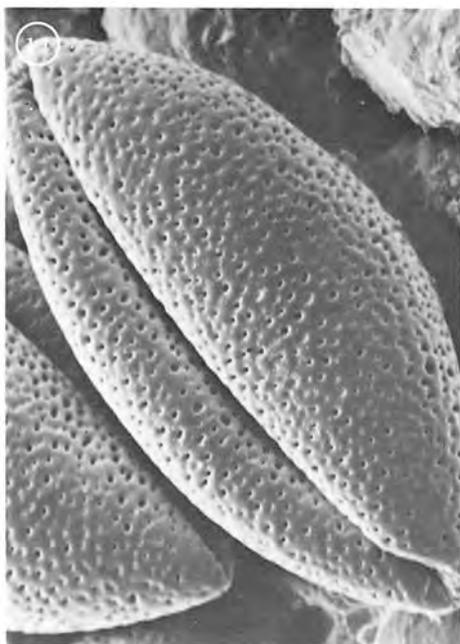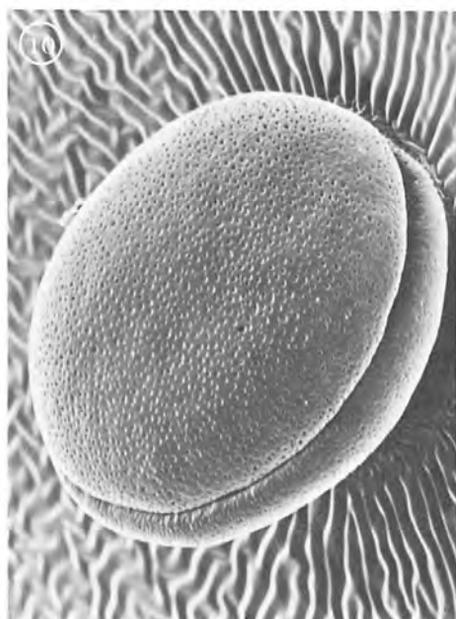
Fig. 9 Pollen grain of *Pistia stratiotes* L. W. Barthlott

Fig. 10 Pollen grain of *Gonatopus boivinii* (Decne.) Hook. f. W. Barthlott

Fig. 11 Pollen grain of *Gymnostachys anceps* R. Br. W. Barthlott

Fig. 12 Pollen grain of *Hapaline brownii* Hook. f. W. Barthlott

Seeds

Aroid seeds may or may not have en-endosperm; some have only a little endosperm, and there are all intermediates between plenty and no endosperm. The embryo is mostly straight, though in some genera it is curved; it is usually not differentiated, or rarely with a highly developed plumula with several leaf primordia. Seeds with a highly developed plumula of the embryo always lack endosperm. The outer integument is usually fleshy. The testa can be smooth, rough, verrucose or striate. Genera with a highly developed embryo (Nephthytis, Gonatopus) have a thin papery testa, but such large embryos already contain chlorophyll.

DISPERSAL OF SEEDS

The dispersal of aroid fruits appears to be done mostly by birds (ornithochory). Often the mature berries stay fresh for a relatively long time (Arum, Nephthytis), just 'waiting for their dispersers.' Many aroid fruits (Philodendron, Dieffenbachia, Syngonium) are markedly ephemeral, disappearing almost as soon as they are exposed. Dispersal by water is known (Montrichardia, Lagenandra, Cryptocoryne, Pistia) as well as by bats (*Xanthosoma robustum* Schott, maybe others). The seeds of aroids do not remain viable for a long time, and therefore long-distance transport by natural vectors is probably not possible.

POLLINATION

The flowers of aroids are entomophilous. The pollinators are mostly Diptera or Coleoptera, in a few genera also Hymenoptera (euglossine bees in Spathiphyllum). The flowers are proterogynous which favors a cross-pollination. Receptive stigmas and ripe anthers can overlap on one spadix (*Lysichiton americanus* Hulten & St. John, some Anthurium). Apomyxis has only rarely been reported, but is probably more common than believed. Insects are primarly attracted by smell, but also by the color and structure of the inflorescence (spathe and spadix).

CHROMOSOMES

Chromosome numbers in aroids are variable, and polyploidy occurs frequently. A primary base number of $x = 7$ can be estimated, but higher secondary basic numbers must be accepted. The highest number known is well over one hundred chromosomes. Some groups have a certain characteristic number, sometimes a doubling of the genome; others have quite different numbers even within a single genus, where aneuploidy may occur (Cryptocoryne).

PHYLOGENY

A personal conclusion about aroid phylogeny must be allowed, without discussing this in detail. In my opinion the ancestors of the aroids must be sought in an old group near the Liliiflorae, but not among recent species. Unfortunately the known fossil records of both groups do not help in this matter. The idea of an origin of the aroids in the Liliiflorae is not new; several authors (Hallier, 1912; Bessey 1915; Hutchinson, 1934, 1959; Novak, 1954; Kimura, 1956; Takhtajan, 1959) have suggested it. Engler (1920, p.47) briefly expressed a similar opinion. Hutchinson (1934) hypothesized that the aroids could be derived directly "from the stock of tribe Aspidistreae of Liliaceae, in which the flowers are arranged in dense spikes (Tupistra, Rohdea, Gonioscypha)." In my mind, there has certainly been convergent evolution in this group toward an aroid-like habit.

An interesting question is what would the ancestral aroid have looked like, and what ancestral characters would it have combined? The very small flowers must have had two whorls of three free tepals, two whorls of three free stamens and a superior, three-locular ovary. These flowers must have lacked any bract below each flower; the flowers could have been

laxly or densely arranged on a spike (not necessarily a "fleshy" flower axis or spadix). They must have had an inconspicuous spathe (bract) below the flower axis (spike), somewhat like a foliage leaf and not distinctively colored or formed. The venation type of the leaves could have been either reticulate or parallel. The leaf-blade must have been well developed (the ensiform leaves of Acorus and Gymnostachys could have evolved via neoteny). These hypothetical ancestral plants must not have been climbing (like today's Pedicellarum or Pothos), but probably had short, upright stems. Other primitive characters must have been present, such as monosulcate pollen grains and endospermous seeds. Of course, we cannot expect to find such an ancestral aroid still living today, but neverthelesss several aroids have retained one or a few such primnitive characters. Such ancestral plants may have existed for only a short geological period, died out quickly and were succeeded by better adapted ones.

EXPLANATION OF SOME BOTANICAL TERMS

Anther: the apical fertile portion of a stamen, consisting of two thecae, connected by the connective, and each theca with two pollensacs (exceptions from this basic structure are rare.) The anthers contain the pollen.

Appendix: sterile terminal part of spadix.

Cultivar: variety originated in cultivation by selection, crossing or mutation.

Epilithic (Semiepilithic): growing on rocks (like some rheophytes); semiepilithic: growing on rocks covered with mosses etc., or very little humus.

Epiphyte: a plant which grows on other plants, but not parasitically.

Geniculum: a knee-like, thickened joint in the petiole, usually at the apex.

Inflorescence: the disposition of the flowers on the floral axis.

Integument: the envelope of an ovule.

Ovary: that part of pistil which contains the ovules.

Ovule: the organ which develops after fertilization into a seed. An orthotropous ovule has a straight axis with the hilum and micropyle on the opposite ends; an anatropous ovule is reversed, with the micropyle close to the side of the hilum.

Perigon: a perianth consisting of equal parts, these called tepals (not differentiated into calyx and corolla).

Pistil: the female organ of a flower, consisting of ovary, style and stigma.

Pistillode: a sterile (rudimentary) pistil.

Placentation: the disposition of the placenta or placentae. (Placenta: the organ which bears the ovules in an ovary).

Pseudomonomerous: an unilocular ovary that originates evolutionarily from an ovary with more than one carpel.

Pseudostem: a false stem formed by overlapping sheathed petioles only; typical example banana.

Rheophyte: flood-resistant plant growing in and along swift running streams or rivers up to flood-level.

Skototropism: an orientation movement towards a dark area. The seedlings of certain climbers grow towards darkness, which in forest is nearly always a tree trunk.

Stamen(s): the male organ(s) of a flower.

Staminode: a sterile or abortive stamen (without an anther).

Synandrium: the stamens of a male flower that are all connate.

Synandrodium: structure formed by staminodes that are connate or a synandrium that becomes sterile (lacking the anthers).

Syncarp: a multiple or fleshy aggregate fruit-like structure formed of numerous small fruits that are themselves connate; typical examples are pineapple or mulberry.

Tepals: units of a perigon.

Testa: seed-coat.

Theca: an anther half.

Trichome: hair or any hair-like outgrowth of the epidermis.

CITATED AND RECOMMENDED LITERATURE

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Engler, A., in part with Krause, K., 1905-1920: Araceae. — In A. Engler, Das Pflanzenreich IV. 23-A-F (Heft 21, 37, 48, 55, 60, 64, 71, 73, 74). — Leipzig: Engelmann. This monograph contains also a comprehensive morphology of the different subfamilies and in its general part (par generalis) in Heft 74, the latter published 1920 (contains the reference "Engler (1920, p. 47")).

Hutchinson, J. 1934: The Families of Flowering Plants, II. Monocotyledons. — London: Macmillan & Co. Ltd.

Takhtajan, A. 1959: Die Evolution der Angiospermen. — Jena: VEB Gustav Fisher. This book, contains a comprehensive treatment of the evolution and phylogeny of flowering plants and gives a large reference for the literature (see there for further reference).

Amorphophallus paeoniifolius (Dennst.) Nicolson.   Photo by J. Banta