

PROTECTION OF DEVELOPING SEEDS IN NEOTROPICAL ARACEAE

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In flowering plants with animal pollination and seed dispersal the reproductive cycle can be considered to consist of four stages, representing alternating phases of protection and display. In the protective phases immature flowers and fruits are safeguarded from predation and parasitism, while in the display phases pollinators and dispersal vectors are attracted.

This alternation of protection and display is accomplished by a variety of mechanisms. Initially the developing flowers are protected by bud scales, stipules, bracts, or the calyx and by cryptic coloration. As the flowers mature bud scales or stipules abscise and the pedicels or peduncles elongate, elevating the flowers to an exposed position. Heat, floral fragrances, and conspicuously colored bracts, perianth, or stamens may be elaborated; the effect of these in attracting pollinators may be enhanced by simultaneous deciduousness of the plant. Nectar or abundant pollen may be additional attractive factors. Following pollination is a second cryptic phase during which the developing fruit is protected by abscission of showy perianth parts, by rapid formation of a hard pericarp, often cryptically colored, by accretion of the calyx or bracts, and/or by elaboration of chemical defenses.

When the fruit ripens mechanisms of attraction come into play once more, including softening of the pericarp and production of colors and fragrances. In a number of tropical genera, (e.g. *Codonanthe*, *Hedychium*, *Marcgravia*, *Pittosporum*, *Carludovica*, *Myristica*) the pericarp breaks apart at maturity to reveal the seeds with brightly colored arils or embedded in a juicy, colored placenta.

Since the adaptations for protection of immature structures are often contrary to the requirements of the attractant phases, a delicately attuned sequence of developmental events is required. Most studies of reproductive biology have dealt exclusively with the attractive phases rather than considering the cycle as a whole (e.g. Ridley 1930, van der Pijl 1969, Faegri and van der Pijl 1966, Proctor and Yeo 1973), even though the adaptations of flowering plants to the protective phases are diverse and worthy of study. A notable exception is the investigations of Uhl and Moore (1973, 1977) which constitute a superb study of protective mechanisms in the reproductive structures of palms.

In this paper I report observations on the reproductive cycles of neotropical species of the family Araceae (philodendron family),

with special attention to the protection of immature seeds. This family, with about 30 genera and 1200 species in the neotropics, forms a conspicuous element of the vegetation in wet regions and includes aquatics, terrestrial herbs, lianas and epiphytes. Except for a few remarks by Engler (1920) and Ridley (1930) hardly anything has been written about the fruits of aroids. The descriptions which follow are based on observations of plants in the wild made in the course of studies carried out since 1971 in Central America and the Andes.

One of the defining features of the aroid family is the structure of the inflorescence, which consists of a spike of tiny flowers, termed the spadix, subtended by a large colored bract, the spathe. In all species the spadix is protected before anthesis by being tightly wrapped in the spathe, an additional layer of covering is provided by the sheathing base of the subtending leaf or cataphyll. The initial phase comes to an end with rapid elongation of the peduncle and unfurling of the spathe to expose the spadix. From this point a great diversity of flowering and fruiting mechanisms come into play, which are here described for each genus arranged according to the subfamilial and generic classification of Engler (1920).

POTHOIDEAE

Anthurium: *Anthurium* includes about 600 species of terrestrial herbs, climbers, and epiphytes. The flowers are perfect and have four tepals in two whorls of two; the chief pollinators are flies, sphenid wasps, and the male euglossine bees. The spathe is usually flat and

leaf-like, and in many species it serves only to protect the developing spadix, becoming reflexed as the spathe matures (Figure 1). However in some species, e.g. *A. andreanum*, it is broad and brightly colored and apparently plays a role in pollination. In a group of species allied to *A. pedatum* the spathe is shaped like an inverted canoe with the spadix pendent below (Figure 2); in this case the spathe has acquired the function of an umbrella. These species are native to very wet middle elevation forests of the western slopes of the Andes where there is a high probability of rain disturbing nectar or pollen. I have observed *Anthurium* c.f. *gualanum* in Ecuador during a heavy rain; the spadix, which was at anthesis, remained dry and was visited by flies, weevils, staphylinids, and other insects.

With the exception of the genus *Spathicarga* floral nectaries have not been reported for the Araceae. However, copious production by the pistils of stigmatic fluid, which is often sweet to the taste, may to some extent compensate for this deficiency. In *Anthurium* stigmatic fluid is often abundantly produced, and each flower elaborates about the same amount (in contrast to *Monstera* where some flowers specialize as stigmatic fluid exuders).

The developing fruit in *Anthurium* is protected by the cucullate tepals which almost entirely cover it (Figures 3, 4). A layer of sclereids below the epidermis provides a mechanical barrier around the berry. As the spadix ripens the berries soften and swell, and apparently increasing pressure in the spadix causes the berries, which abscise

from the axis, to 'pop out' from among the tepals (Figure 5). The berries do not fall to the ground, however, but dangle on four threads representing part of the epidermis of the inner two tepals. These dangling, brightly-colored berries, reminiscent of *Magnolia* seeds, are dispersed by birds, as sometimes noted on herbarium specimens. Analysis of stomach contents of *Manacus manacus* in western Ecuador showed the birds to have been feeding heavily on berries of *Anthurium dolichostachyum* (personal communication from C. H. Dodson).

In some cases the popping out of the berries exposes a previously hidden bright color. For example, in *Anthurium buenaventurae* the developing spadix is dark purple, including the tepals and protuberant apices of the berries. As the berries are squeezed out from among the tepals the lower portion, which is bright yellow, becomes exposed, apparently signalling to dispersers that the fruits are ripe.

Heteropsis: I have observed fruits only of *Heteropsis integerima*. The spathe abscises even before anthesis and the white spadix is visited by bees and small hemiptera. The developing fruit is green and the seeds are protected by a hard, sclerified pericarp. At maturity the pericarp softens and turns orange. The musty-smelling fruits are borne at the ends of elongate hanging branches, a situation suggestive of bat dispersal.

MONSTEROIDEAE

Monstera: *Monstera* includes about 25 species of scandent epiphytes, many of which have naturally perforated leaves. The spathe is white, yellow, or pink, and glo-

bose or boat-shaped; the flowers are perfect and lack a perianth, and are pollinated by *Trigona* or related bees. Though nectaries are absent, the basal flowers on the spadix are usually sterile and produce copious sweet stigmatic drops, apparently functioning as nectaries.

Since the perianth found in *Anthurium* is lacking, the developing seeds are protected by a different mechanism. The styler portion of each ovary contains numerous needle-like trichosclereids, all lying parallel to the axis of the flower (Figure 9). These tough needles, 1-2 mm long, form a considerable mechanical barrier around the developing seeds. At the time of maturity the fruit breaks in two transversely and the needle-bearing upper portion falls away, revealing the seeds in a gray or brightly colored pulp (Figure 10). The seeds are picked off by birds.

In *Monstera punctulata* the protection of developing seeds provided by the trichosclereids is augmented by a tough cap of isodiametric sclereids lying just below the epidermis of the ovary. *Monstera obliqua* lacks sclereids in the fruit altogether, and also lacks the abscission layer to discard the upper portion. This species has fruits which mature in only 6-8 weeks, while fruits of other species require up to 15 months (Madison 1977). The lack of any apparent mechanism for protection of immature fruits may be related to rapid maturation.

Stenospermatum: This genus includes about 30 species of true epiphytes with short stems and leathery leaves. The floral structure is very similar to that of *Monstera*, and the globose spathe is deciduous

after anthesis. The developing seeds are protected by needle-like trichosclereids in the apical region of the ovary. At maturity the fruits turn yellow or orange and become soft. The trichosclereids are not shed in a deciduous cap, as in *Monstera*, but remain in the mature infructescence, which is pecked apart by birds or consumed by insects.

Rhodospatha: *Rhodospatha* includes about 20 species of vines in which the spadix is composed of perfect flowers lacking a perianth. Pollination is similar to the preceding two genera. Following anthesis the spathe abscises and the developing fruits are protected by the slightly hardened pericarp. The trichosclereids found in the fruits of *Monstera* and *Stenospermation* are lacking. Predation of immature fruits of *Rhodospatha* in the wild is not uncommon, and spadices often show signs of being gnawed on or burrowed in by beetles. At maturity the fruits soften and turn white or pink.

Spathiphyllum: *Spathiphyllum* includes about 40 species of terrestrial herbs, mostly riparian. The spathe is white and broadly boat-shaped. Pollination is chiefly by male euglossine bees attracted by floral fragrances (Williams and Dressler 1976). The spathe is white at the time of flowering, and may turn green afterward. The spathe is persistent, often turning green and becoming, functionally, just another leaf. The developing seeds are protected by both a persistent perianth, as in *Anthurium*, and by trichosclereids in the styler portion of the ovary, as in *Monstera*.

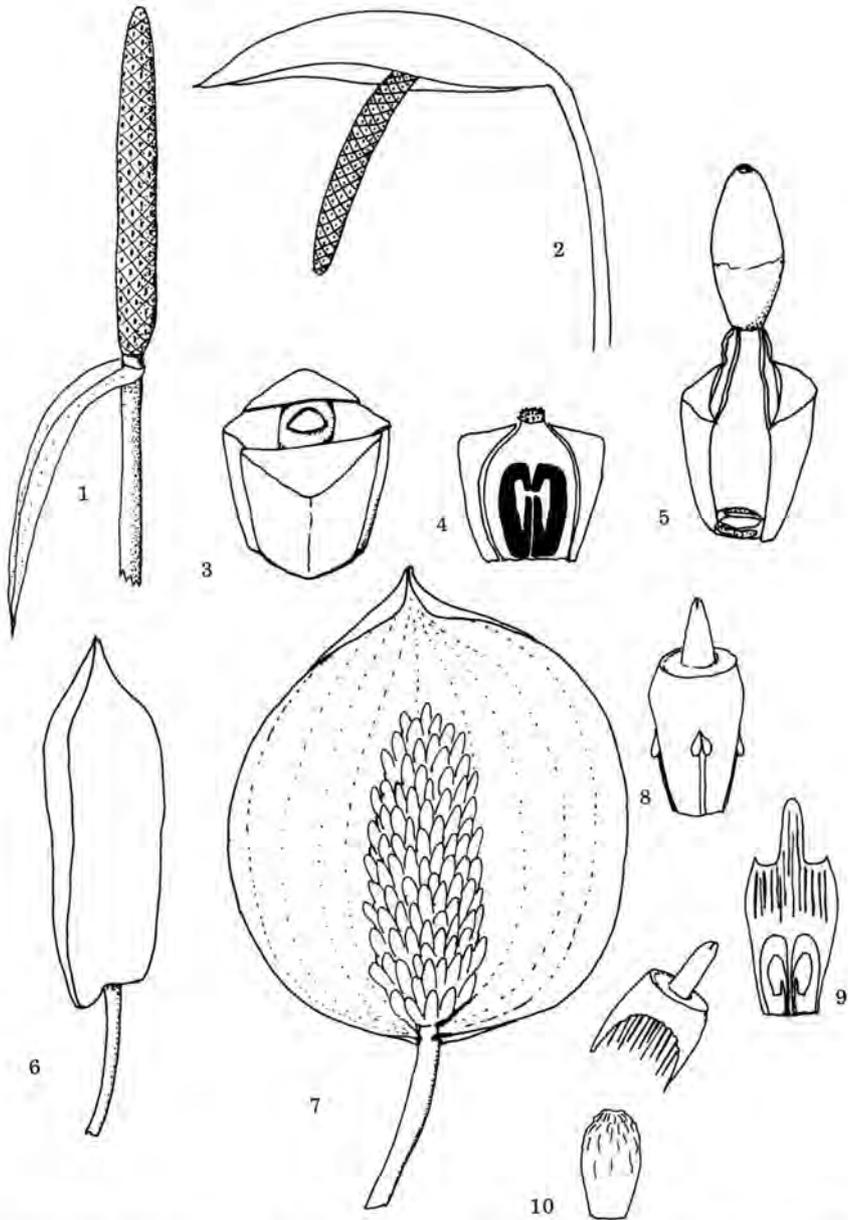
At maturity the spadix breaks apart; the tepals may abscise and the ovary breaks irregularly in two. In the Colombian species *Spathiphyllum floribundum* the seeds fall

to the ground. This species is most abundant along waterways, and since the seeds float many of them may be water-dispersed (Bunting, 1960). In addition, the swollen and juicy funiculus remains attached to the seed, and this may serve as an elaiosome in dispersal by ants which would find the seeds lying on the ground.

LASIOIDEAE

Urospatha and Dracontium: Each of these genera includes about a dozen species of tuberous herbs; both are fairly rare and poorly known. The spadix consists of perfect flowers with a biseriate perianth of 4-6 tepals. In *Dracontium* the spathe is usually dark purple and either sphaeroidally cucullate or spreading. The color and shape of the spathe and its rotten-meat odor suggest fly or beetle pollination (Croat 1975) which is typical of the whole subfamily. In *Urospatha* the spathe is much longer than the spadix and is often spirally twisted. Pollinators are unknown. In *Urospatha*, which often grows semi-aquatically in or along forest streams, the seeds have a corky epidermis which makes them bouyant, presumably an adaptation for water dispersal.

The developing fruits are to some extent protected by the persisting spathe which loosely envelops the spadix. The perianth and hard pericarp also cover the seeds. The ripe fruits are colored berries with one or a few highly sculptured seeds, which are presumably dispersed by vertebrates. In the one fruiting *Dracontium* which I have encountered in the wild the meter-long peduncle had wilted and the berries were lying on the ground.



Figures 1-10. 1. Inflorescence of *Anthurium buenaventurae*. 2. Inflorescence of *Anthurium pedatum*, in which the spathe serves as an umbrella over the spadix. 3. Flower of *Anthurium buenaventurae*. 4. Same, in section, showing the ovary covered by the sclerified tepals. 5. Ripe fruit of *Anthurium buenaventurae*, with the berries dangling from strips of the epidermis of the inner tepals. 6-10. *Monstera tuberculata* 6. Immature inflorescence wrapped in the leathery spathe. 7. Inflorescence at anthesis, the spathe open. 8. Flower. 9. Longitudinal section of the flower, showing trichosclereids in the upper part of the ovary. 10. Ripe fruit, the sclereid-containing part of the ovary falling away to expose the seed.

Montrichardia: *Montrichardia* is a monotypic genus of semi-aquatic herbs with fleshy erect stems to 8 m tall, often forming dense stands along waterways. The spadix is divided into a basal portion of carpellate flowers lacking a perianth and an upper portion of staminate flowers. At anthesis the cream-colored spathe opens slightly and an intense sweet odor is emitted which attracts various species of bees, presumably the pollinators. The spathe of *Montrichardia* is deciduous after anthesis and the developing fruits are protected by trichosclereids in the upper part of the ovary, as in *Monstera*. The mature berries are yellow, about 4 cm long, and contain abundant air-filled spongy tissue which aids in their flotation. The ripe fruits abscise and fall into the water which is the principal means of dispersal. Ridley (1930) recounts observations of feeding on ripe *Montrichardia* fruits by the Hoatzin (*Opisthocomia cristatus*).

PHILODENDROIDEAE

Philodendron: *Philodendron* includes about 300 species of lianas and epiphytes. The flowers are naked and unisexual, with the carpellate flowers aggregated at the base of the spadix and the staminate flowers at the apex. In some cases these are separated by an intervening zone of sterile staminate flowers. The spathe usually shows a constriction part way up so that it forms two chambers, the lower one enclosing the carpellate flowers and the upper one the staminate (Fig. 13).

Pollination usually occurs on two subsequent nights. On the first night the spathe unfurls and

the carpellate flowers are exposed. Beetles or flies are attracted by the fragrances, and in the case of *P. bipinnatifidum* and others, by heat produced from uncoupled oxidation of starch (Nagy et al. 1972). The spathe closes somewhat after the first night, but usually not enough to fully trap the insects, as in some other aroids, e.g. *Arum maculatum*. Nonetheless, dozens of beetles, especially ruteline scarabs, may be found crammed in the lower chamber of the spathe after the first night of its opening. On the second night fragrances and heat are again produced and pollen is shed. At this stage the stigmas are no longer receptive so that outcrossing is insured.

The beetles consume pollen and large fleshy stigmas which decompose to a slimy mass. However, if the beetles remain too long in the inflorescence they will also eat the flowers, which not infrequently happens. Two mechanisms serve to force the beetles from the inflorescence after pollination. In a number of species the spathe once again closes around the spadix, orientating itself so as to fill up with rain water. In *P. cruentospathum* the inflorescence sheds water at anthesis, but rotates 90° after flowering to become a water-holding structure (personal communication from C.H. Dodson). Many other species when cut open are found to be full of water (e.g. *P. senatocarpium*, *P. karstenianum*). The beetles are forced to leave the inflorescence to avoid drowning.

In *Philodendron acuminatissimum* the spathe closes so tightly over the spadix after pollination that the beetles are immobilized

and may be crushed. Most escape before this stage, but the common presence of holes in the lower spathes indicates that beetles have had to chew through the tightening spathe to make an escape. In this species the spathe does not fill up with water.

The persistent leathery spathe protects the developing fruits after anthesis. In most species it breaks apart and is irregularly deciduous when the fruits mature. The aggregate of berries becomes colored, usually red or orange, and soft. The berries are eaten by birds and insects. I have observed beetles and wasps crawling on the ripe infructescences of *Philodendron karstenianum*. They were consuming the sweet juices of the pulpy fruits and at the same time becoming covered with the tiny sticky seeds, which weigh less than 1mg., and which were apparently being dispersed by the insects.

In *Philodendron senatocarpium* the spathe does not abscise at maturity but is persistent and turns a deep burnt orange color. On many of these the peduncle decays and the entire ripe infructescence falls to the ground. I have not observed how these are finally dispersed.

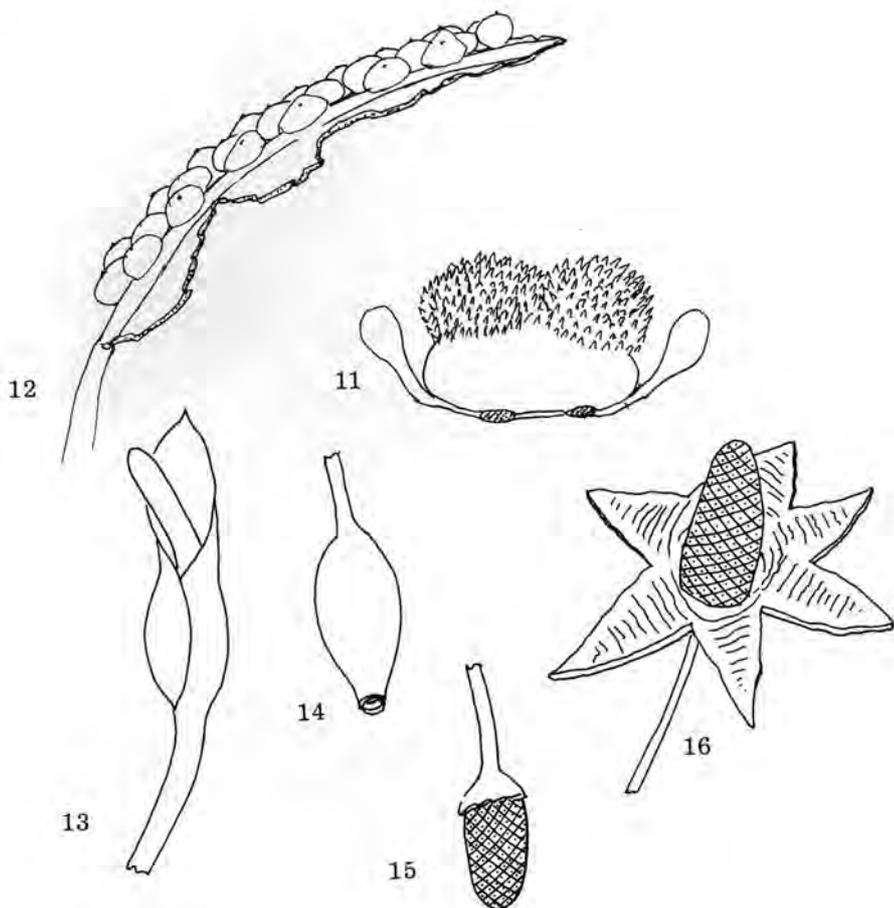
Dieffenbachia: *Dieffenbachia* includes about 30 species of terrestrial herbs occurring in the dark understory of wet forests, mostly at lower elevations. The spathe is green and tightly wrapped around the spadix, to which it is fused. The upper part of the spadix is composed of staminate flowers and the lower part of carpellate flowers surrounded by starch-filled claviform staminodia. At anthesis the spathe unfurls somewhat, allowing the entrance of flies or

beetles which are attracted by foul, or in a few cases sweet, odors. Following pollination the spathe once again wraps tightly around the spadix, and serves to protect the developing fruits from predation.

Generally the pollinators lay eggs among the *Dieffenbachia* flowers, which after anthesis become immersed in slime from the disintegration of the large stigmas and accumulation of rain water. The larvae feed on the club-shaped staminodia which surround each ovary and which have a high content of starch. Maturation of the flies apparently precedes maturation of the berries; often tiny holes may be seen in the spathe, presumably where adult flies (or beetles) have made their escape. With maturation of the fruits the spathe turns orange and breaks apart. Its disintegration is aided by the sharp backward curvature of the spadix which occurs at this time. A double row of bright red berries is thus exposed to the dispersing agents, probably birds and small mammals.

COLOCASIOIDEAE

Xanthosoma: *Xanthosoma* is a genus of about 50 species of terrestrial herbs, many of them massive 'elephant ear' plants with weedy habits. The spadices have separate carpellate and staminate portions, the junction of which is indicated by a constriction in the spathe. The spathe unfurls at anthesis and a profusion of insects visits the flowers, including hemiptera, trigonid bees, staphylinids, weevils, and ruteline scarabs, the last of which are the most likely pollinators.



Figures 11-16. 11. Carpellate flower of *Dieffenbachia seguine*, showing the ovary and two of the six staminodia. 12. Fruiting spadix of *Dieffenbachia seguine*; the curvature of the spadix helps to break away the brittle spathe, exposing the berries. 13. Inflorescence of *Philodendron*. 14. Developing fruit of *Xanthosoma sagittifolium*, the berries protected by the spathe. 15. Ripe fruit of *Xanthosoma sagittifolium*, the berries exposed. 16. Ripe fruit of *Xanthosoma* sp., the spathe splitting and reflexing to make a pseudo-flower.

After pollination the spathe closes and the lower portion may fill with slimy water representing accumulation of rain and disintegration of the stigmas. This is apparently the same 'drowning' mechanism found in *Philodendron* to get rid of potentially destructive pollinating beetles after anthesis. However, at least in *X. sagittifolium* it does not seem to be as effective;

destruction of developing fruits by beetles is fairly common.

In most species of *Xanthosoma* the staminate portion of the spadix and upper part of the spathe abscise or deliquesce soon after anthesis. The lower part remains erect and full of water for a time, but soon droops to a pendent position. As the fruits mature the remaining part of the spathe

abscises, exposing the cream to orange berries which become soft and juicy.

In one unidentified species from eastern Ecuador the spathe splits into five or six triangular segments which become reflexed at maturity. These reveal a pink adaxial surface with brown markings, and the infructescence constitutes a striking 'pseudo-flower' (Fig. 23).

Syngonium: *Syngonium* includes about 30 species of scandent herbs and is primarily circum-Caribbean in distribution. The inflorescences are similar to *Xanthosoma*, but are often sweet-smelling and are probably pollinated by bees. Following anthesis the upper part of the spathe and the staminate part of the spadix and the inflorescence becomes pendent. The developing fruits are protected by the persistent enveloping spathe, which is green. As the berries mature they coalesce into a soft syncarpium held together by a brown skin. The spathe does not abscise at maturity but becomes red and serves as the attractive part of the fruit. It is probably pecked apart by birds or other vertebrates in search of the soft sweet pericarp surrounding the seeds. In south Florida fruits of naturalized *Syngonium auritum* are eaten by a variety of birds as well as squirrels.

Of the neotropical aroids *Syngonium* exhibits the greatest development of the spathe which functions sequentially in protection of the immature inflorescence, pollination, protection of developing fruits, and finally in dispersal.

DISCUSSION

In the neotropical species of Araceae at least nine distinct mechanisms are found for protection of developing seeds:

- 1) covering of the fruits by accrescent tepals with a sclerified surface (*Anthurium*)
- 2) hardening of the pericarp (*Heteropsis*)
- 3) changes of pericarp color from white, yellow or orange to green after anthesis (many species)
- 4) surrounding the seeds with a barrier of needle-like trichosclereids in the upper part of the ovary (Monsteroideae, *Montrichardia*)
- 5) rapid maturation (*Monstera obliqua*)
- 6) envelopment of the entire infructescence by a leathery spathe (Philodendroideae, Colocasioideae)
- 7) orientation of the enveloping spathe to fill with rain water (*Philodendron*, *Xanthosoma*)
- 8) distraction of potentially destructive pollinator larvae by provision of starch-filled food bodies (*Dieffenbachia*, *Homalomena*)
- 9) presence of bundles of calcium oxalate raphides in the unripe pericarp (all genera).

In most cases the function of these mechanisms is contrary to the requirements of dispersal, so that a corresponding array of adaptations is required to reverse them when the fruits ripen. Thus we find extrusion of the berries from among the tepals in *Anthurium*, shedding of trichosclereids in the Monsteroideae, and in many genera abscission of persistent spathes and softening and coloration of the pericarp, often accompanied by production of fragrances and sugars.

Until recently investigations of the adaptive significance of reproductive structures in tropical plants were greatly overshadowed by morphological studies for strictly taxonomic purposes. The expansion of studies of pollination biology (e.g. vanderPijl and Dodson 1969, Faegrei and vanderPijl 1966) and of fruit dispersal (e.g. vanderPijl 1969) have stimulated a reexamination of reproductive structures from an ecological point of view. These new studies have emphasized the phases of reproduction in which animal agents are attracted to the plants. However, the attractant phases are separated by an intervening period in which protection of developing seeds and repulsion or evasion of predators and parasites are primary requirements. The wide variety of mechanisms here reported for the neotropical species of a single family, the Araceae, suggests that adaptations to the cryptic phases may be quite diverse, and that investigation of this in other plant families will be worthwhile.

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