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A SURVEY OF FLORAL ANATOMY IN ARACEAE[1]

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ABSTRACT

Flowers of 23 species representing six subfamilies of Araceae were studied by means of serial cross sections, special attention being given to vascular patterns and to taxa of supposed phylogenetic importance. Floral structure is shown to be extremely diverse with no unifying pattern common to all subfamilies. Conclusions include the following: (1) *Lysichiton* has a specialized gynoecial vascular pattern which differs from others encountered in the survey and which weighs against the primitive position attributed to this genus by Hutchinson. (2) *Philodendron*, with its multiple stylar canals, cannot have originated from subfamily Pothoideae, as Engler's phylogenetic concept would require of all Araceae; instead, it appears that several syncarpous evolutionary lines have evolved independently from extinct apocarpous members of the family. (3) In *Acorus*, stamens are introrse and dorsal carpellary bundles are lacking; these characters and others justify the recognition of *Acorus* as a separate subfamily Acoroideae. In addition, the survey revealed a peculiar deterioration of the inner ovary wall and the septa in several taxa, apparently a normal feature of floral development. *Spathiphyllum solomonense* Nicolson is described in an appendix.

Literature on comparative anatomy of flowers has accumulated over the past several decades into a sizeable body of information; in Rao's (1961) bibliography of more than 800 entries, most families of angiosperms are represented by at least one publication. It appears, however, that no modern botanist has undertaken a special investigation of vasculature and histology in flowers of Araceae. This is rather surprising, because the family is large and widely distributed with many familiar ornamental species. Moreover, most of the families commonly suggested as allies of Araceae have been studied, at least in an introductory way, from the standpoint of floral structure: al-Rawi (1945), Bosch (1947), and Morrow (1963, 1965) investigated the palms; Harling (1946, 1958) and Garcin (1958), the Cyclanthaceae; Gatin (1920), Anderson (1940), and el-Hamidi (1952), the Liliaceae.

The anatomy of araceous flowers is not totally unknown, for the authoritative monographs of Engler (1905, 1911, 1912, 1915, 1920a, 1920b), Krause (1908, 1913), and Engler and Krause (1908, 1920) are replete with drawings and descriptive comments relating to floral structure. For the most part, however, these observations are derived from the earlier works of Schott (in particular his *Genera Aroidearum*, 1858) and Engler (see especially his 1884 contribution on floral morphology), in which no information is given on vascular patterns. Apparently, the only 19th century worker to examine floral vasculature of Araceae was van Tieghem (1867), who reported on the arrangement of bundles in pistillate flowers of *Zantedeschia, Alocasia,* and *Aglaonema,* later (1907, p. 315) offering an interpretation of the staminate flower of *Aglaonema.* Possibly the only contribution since van Tieghem's time is Saunders' (1939) brief commentary, expressed in the terms of her long discredited theory of "carpel polymorphism." We have not found that any author on Araceae has compared vascular systems and other microscopic floral characters in genera selected for possible phylogenetic interest, as we attempt to do in this paper.

Our investigation is meant to be no more than an introductory survey. It was planned as a summer project only (the laboratory work was completed during the summer of 1965, while the third author was a research assistant in the Smithsonian Summer Program for Graduate Students), and because of other research commitments we do not expect to carry it further. Our aims are to point out the diversity in internal floral structure of the Araceae, particularly in those groups claimed to be primitive by various authors, to compile pertinent literature, and to raise questions of phylogeny that should be considered in subsequent studies of the family. We hope thus to attract the attention of other investigators to an interesting and, from the anatomical standpoint, neglected group of monocotyledons. Accordingly, the second author will be happy to share his collections of inflorescences with any worker who wishes to use them for further anatomical research.

Materials—Specimens used in this investigation were selected from an assemblage of about

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500 araceous inflorescences collected by the second author, mostly in Southeast Asia, and preserved in various solutions of formaldehyde, paraformaldehyde, and ethanol. Except for two collections (*Lysichiton* and *Orontium*), all are documented by pressed specimens in the U. S. National Herbarium. In most cases duplicates have been deposited at herbaria in the country of origin, also in the Bailey Hortorium, the Rijksherbarium in Leiden, the Herbarium of the Royal Botanic Gardens at Kew, and in other institutions, depending on the number of duplicates available for distribution.

Observations were made on representatives of six of Engler's eight subfamilies. We did not include members of the Aroideae or the Pistioideae (comprising *Pistia* only), for these are generally agreed to be advanced members of the Araceae, and we preferred to examine those groups that seemed mostly likely to retain primitive floral characters.

METHODS—In order to avoid difficulties in orientation and interpretation that might result from sectioning the entire inflorescence, we excised individual flowers or, in some cases, a few adjoining flowers. Flowers were chosen from the central portion of the spadix or, in the case of species with separate clusters of unisexual flowers, from the center of a sexual grouping. We reasoned that in this way we could avoid the structurally aberrant flowers that occur with greater frequency at the edges of the clusters. It was necessary to rehydrate some of the specimens that had dried out during several years of storage. This was accomplished by immersing the material overnight in a 5% aqueous solution of NaOH in a 55 C warming oven. The NaOH treatment cleared the tissues sufficiently to reveal some of the larger and more thick-walled xylem elements in whole flowers. We were, however, unable to clear any flowers sufficiently to see the entire gynoecial vascular pattern, not even by bleaching with $NaClO_2$ (Barghoorn, 1948) or by adding a supplementary treatment with chloral hydrate. Contributing to this difficulty is the fact that vascular strands in some of the flowers are poorly differentiated and very slender. Mucilaginous content of the flowers presents an additional problem.

Since clearing of whole flowers proved unsatisfactory, we were obliged to base our observations entirely on serial cross sections. Under such circumstances, one would ideally section many flowers of each species in order to report on the variability of the vascular system in each. We elected instead, since this survey is the first of its kind, to section flowers from as many different taxa as possible in the period available for the research. Consequently, we have based many of our observations on complete series from only one–three flowers for a species; however, we were also able to examine several partial series for most species, and it seems unlikely that major anatomical differences among the taxa have been obscured by this shortcoming.

The photographs are the work of Smithsonian photographer Victor Krantz. *Gymnostachys anceps* was a difficult photographic subject because we had bleached the flowers severely to get good sections, thus affecting the staining unfavorably. After three sessions with the photographer, we could not improve the image shown in Fig. 21. Nevertheless, we decided to include it because it demonstrates the location of vascular tissue in the ovary wall of *G. anceps*, an important point in our taxonomic discussion.

OBSERVATIONS—*General comments*—The characteristic inflorescence of Araceae, the spadix with its subtending spathe, is familiar to all botanists, and a discussion of its various modifications is beyond the scope of our paper. The component flowers of the spadix are typically bisexual in some genera, unisexual in others; this difference, along with the presence or absence of a perianth, is important in the systematic treatments of both Engler and Hutchinson. Tepals or stamens are commonly connate in certain genera. Our observation is that where the appendages are distinct, each contains one vascular bundle, but where connation occurs, the vascular bundles do not necessarily correspond in number and position to the component units. The gynoecium, composed of two–several carpels (pseudomonomeric in many genera), has a superior ovary in certain taxa and a partially or completely inferior ovary in others. Differences in form of stylar canals and the degree of closure of the carpel margins within the ovary are of potential taxonomic significance. We emphasize these differences in our observations and discussion. An apparently constant feature of the araceous ovary is the mucilaginous content that often persists through the dehydration and embedding treatment and thus can be seen in some of our photographs. In most cases, this material is derived from the breakdown of glandular stigmatic cells and of the transmitting tissue of stylar canal and placental region. In others, as our observations on *Lasia* show, several cell layers lining the entire locule are also involved. The function of this mucilaginous material is a mystery. Knoll (1926) suggested that in *Arum nigrum* Schott it plays a role both in the germination of pollen (p. 402) and in the nourishing of insect pollinators while they are trapped within the spathe (p. 434). Hubbard (1895) observed that beetles visiting an unidentified West Indian araceous plant became coated with a paste of pollen mixed with mucilaginous material; this presumably contributes to cross pollination by insects that are not otherwise adapted for the transport of pollen. It occurs to us that the material may also aid in the protection and germination of seeds. Buell (1935) noticed that the seeds of *Acorus calamus* are ensheathed in "a clear, transparent mucilage, hard and brittle in the mature dry fruit but rapidly absorbing water and swelling into a soft gelatinous mass when dampened."

The descriptions that follow are arranged according to Engler's classification in preference to Hutchinson's (1959), for reasons discussed elsewhere (Nicolson, 1960a).

Pothoideae—In separating this subfamily of 6 tribes and 10 genera from the Monsteroideae, Engler emphasized the rarity of trichosclereids (Spicularzellen) in vegetative tissues. These conspicuous elongate elements, abundant in monsteroids, are known in only two pothoid species (Nicolson, 1960b).

Flowers of Pothoideae are usually bisexual and tepalate. Those of *Pothos* have six tepals, all identical in form but separable into an inner whorl of three and an outer whorl of three by the arrangement of their overlapping edges (Fig. 1). Among our specimens of *P. rumphii* (Presl Schott var. *rumphii* (*Nicolson 1572*) are some flowers with tepals united for their entire length into a cup-like perianth; apparently this variation has not previously been reported for the species. There are six stamens, some abortive, in a single whorl, each opposite one of the tepals. The gynoecium is usually three-carpellate with three locules opposite the outer tepals; however, one of our flowers of *P. rumphii* var. *dolichophyllus* (*Nicolson 804*) was two-locular. The locules each contain one ovule, and placentation is axile. Each carpel is closed for its whole length. Sections distal to the placentae show a central stylar canal, circular in outline and lined with secretory cells.

The gynoecium of *P. rumphii* is partially inferior, that is, the tissue of the ovary wall merges indistinguishably at the placental level and below with tissues of adjoining flowers (Fig. 4). In contrast, the gynoecium of *P. latifolius* Hooker f. (*Nicolson 1070*) is completely superior.

In both species of *Pothos* vascularized appendages occur between some of the flowers (Fig. 2, 3). The inference that these are vestigial floral bracts seems inescapable, and we are not aware that such appendages have previously been reported for the family. Indeed, Engler (1884, p. 162) expressed puzzlement at the total absence of floral bracts, rejecting the notion that the bractless condition necessarily arises when flowers are closely spaced. Short epidermal trichomes or papillae occur on the exposed surfaces of tepals and gynoecium wherever the surfaces are not tightly covered by other organs (Fig. 5). For the most part the trichomes are one-celled, but some contain thin cross-walls. The dense staining reaction of the epidermis and subjacent tissues in such areas suggests that this part of the flower may serve as an osmophor (Vogel, 1962). The entire inner lining of the carpels seems to contribute cell fragments and cytoplasm to the mucilaginous content of the locules. Tissues of the gynoecium, androecium, and perianth in both species of *Pothos* contain crystal idioblasts. Greatly enlarged raphide-containing cells are conspicuous, but druses are also very numerous, even occurring in the inner and outer epidermis of the ovary. In addition, we have observed a few brachysclereids in the tepals of *P. latifolius*.

The floral vascular pattern of *Pothos* seems relatively simple, but individual strands are difficult to follow, especially in the gynoecium. This is because the bundles are not very large in cross section and often little differentiated beyond the procambial stage. Many bundles appear to be entirely without xylem elements; moreover, the ovary wall and the septa are very thin in places, and rupturing of these tissues adds a further impediment to following the vascular strands. It is clear, however, that each stamen and each separate tepal contains only one bundle, centrally located. (The cup-like perianth of our one flower with united tepals has numerous slender vascular strands, none of which is identifiable as a midvein.) In our best cross sections of a three-carpellate gynoecium we can see six major bundles external to the locules. Since they are not conspicuous enough to show up in our photographs, we have indicated them with arrows in Fig. 1. The position of three of these identifies them as the dorsal bundles of the carpels. The other three are located opposite the septa, and a consideration of the vascular pattern in flowers of other families with similarly situated bundles suggests that they result from "phylogenetic fusion" of two bundles belonging to adjacent carpels. All six bundles connect at the base of the flower. Cross sections taken from the proximal part of the flower show a solid vascular cylinder connecting with the six outer bundles below the locules and separating into three bundles—one for each ovule—at the placental level. In addition, there are minor bundles in the outer part of some gynoecia that are of such irregular occurrence as to merit no interpretation.

Engler considered the monotypic genus *Pothoidium* the closest relative of *Pothos*, and our limited observations do not contradict this view. The flowers of *Pothoidium* have six distinct tepals in two whorls, like those of *Pothos*. Our sectioned flower of *Pothoidium lobbianum* Schott (*Nicolson 802*) lacks fertile stamens, the androecium being made up of six short staminodes rather than the three reported by Engler (1905, p. 46). Another irregularity is that one inner perianth member is united to an adjacent outer member for its entire length. The one-locular superior ovary encloses a solitary basally attached ovule, in accordance with published descriptions. The stylar canal of *Pothoidium* differs from that of *Pothos* in that it connects through a broad opening with the ovarian cavity; our sections show this opening to be somewhat excentric in the direction of the placenta (Fig. 6–8). Raphides are plentiful in the gynoecium of *Pothoidium* but not elsewhere in the flower; druses are present in both gynoecium and perianth. In sections through the stylar region,[2] six vascular bundles are readily discernible (Fig. 6). Following these through successively lower sections, one observes that two of the bundles divide, so that there are eight major strands in the ovary wall at the placental level. Of these, five bundles are located on the placental side of the ovary, but it is not possible to ascertain from our sections how many strands actually connect with the placental vascular supply. In view of the vascular pattern and the position of the stylar canal, the interpretation that the *Pothoidium* flower is one-locular by reduction from the plurilocular condition of *Pothos* seems incontestable.

The perianth and androecium of *Anadendrum microstachyum* (Vr. et Miq.) Backer et Alderw. (*Nicolson 1718*) are four-merous with adjacent tepals united to varying degrees. The four fertile stamens surround a one-locular superior gynoecium that contains a solitary basal ovule. Somewhat unusual is the fact that the basal part of the flower is elongate parallel to the axis of the spadix, but the stigma is elongate at right angles to that axis. Stigmatic secretory tissue is very well developed in this species, and raphides and druses are plentiful in gynoecium and perianth. Our sectioned flower has 11 longitudinal bundles in the ovary wall; this suggests that careful study of more extensive material might permit the identification of two or more carpels, but we shall not attempt an interpretation on the basis of this one example.

The flower of *Epipremnopsis media* (Zoll. et Mor.) Engler (*Nicolson 1701*) has four stamens and a one-locular gynoecium like that of *Anadendrum*; however, tepals are absent and there are two ovules attached at about the median level to a prominent placental ridge. The latter corresponds in position and form to a part of the septum in *Pothos* or *Pothoidium.* The pulvinate stylar region of *Epipremnopsis* contains a broad stylar canal, elliptical in cross section and filled with a conspicuous transmitting tissue of radially elongate cells (Fig. 9). Druses and abundant raphides are present in the gynoecium wall and to a lesser extent in the stamens. The gynoecium wall contains 9–12 longitudinal bundles, roughly equidistant from each other and converging apically in a bilateral pattern typical of many two-carpellate gynoecia (Fig. 9); a single additional strand (arrows in Fig. 10–15) passes longitudinally through the placental ridge near its junction with the ovary wall. There are also about six longitudinal strands in the inner part of the ridge supplying the ovules (Fig. 15). This inner vascularized portion of the ridge corresponds to the central axis in many other araceous flowers, a point which can be verified by following the ovule-bearing margin of the ridge distally (in reverse order in our figured cross sections) until it encloses the base of the stylar canal (Fig. 11–15). At the extreme apex of the gynoecial cavity the placental ridge becomes a complete septum, and two locules appear in the sections (Fig. 10). This type of floral structure is unusual, in that one of two placentae has been lost completely while the other remains with no reduction in size.

Recognizing that *Acorus*, comprising (in most treatments) two species of northern temperate regions, differs in many respects from *Pothos* and its nearest allies, Engler placed it in a separate tribe Acoreae, including with it the monotypic *Gymnostachys* of Australia. Hutchinson's generic arrangement also unites *Acorus* and *Gymnostachys* as a separate tribe, emphasizing the absence of a spathe in the two genera.

Flowers of *Acorus* are bisexual with six-merous perianth and androecium. In our examples the latter comprises fertile stamens as well as staminodes, and the stamens, being introrse, differ from all others encountered in this survey (Fig. 17). Gynoecia are three-carpellate and three-locular (Fig. 18); the septa between carpels are continuous for the entire length of the ovary and their positions are marked externally by three shallow grooves in the upper part of the ovary wall. The gynoecium is slightly inferior, i.e., the ovary wall at the base of locules is continuous with extracarpellary tissue. Each locule contains three–five pendent ovules, attached near the apex in *A. calamus* L. (*Nicolson 2181*) but nearer the median level in *A. gramineus* Aiton (*Nicolson 1675*). Sections through the narrow apical part of the gynoecium are markedly three-lobed (Fig. 16, 17) because of a relative deepening of the three external grooves. Each lobe contains a narrow stylar canal that is continuous with the locule below

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[2] We use "stylar region" loosely to indicate the distal portion of the gynoecium, even though this region is not shaped like a stylus in most Araceae. Also, we call the pollen-transmitting tract that passes through this region a stylar canal whether or not it includes an open passage. In this family a canal completely filled with transmitting tissue at an early floral stage may open later as that tissue deteriorates.

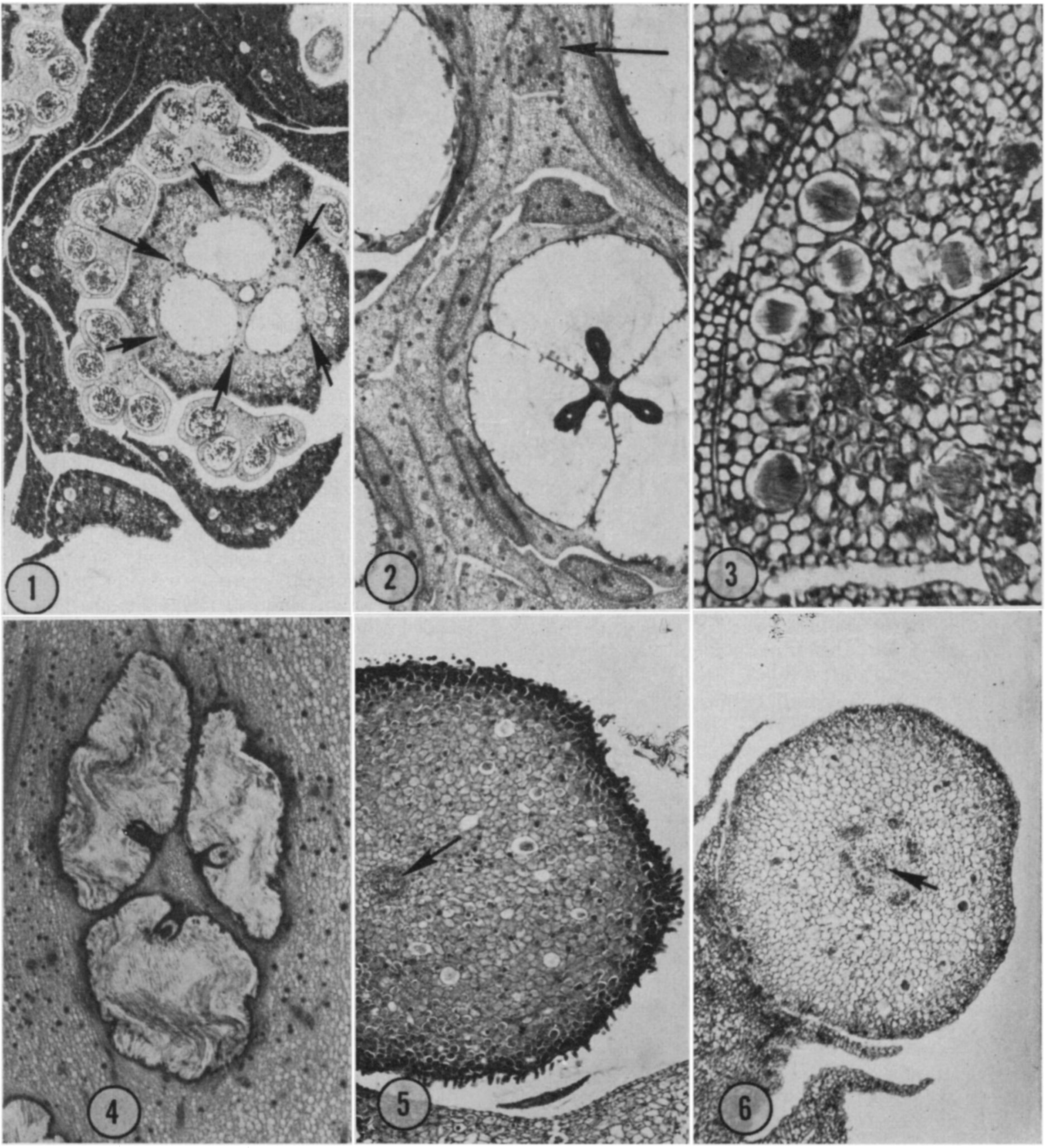
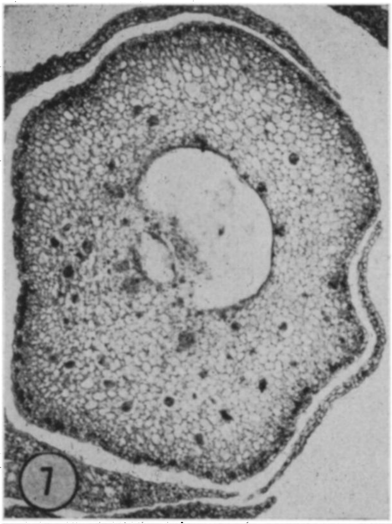


Fig. 1–6.—Fig. 1–3. *Pothos rumphii* var. *dolichophyllus.*—Fig. 1. Cross section of flower, showing stylar canal, arrangement of appendages, six gynoecial bundles (arrows), ×30.—Fig. 2. Lower section, showing interfloral appendage (arrow), insertion of ovules, deterioration of septa and ovary wall, ×30.—Fig. 3. Enlargement of interfloral appendage, showing raphide idioblasts and central vascular strand (arrow), ×190.—Fig. 4. *P. rumphii* var. *rumphii*; cross section showing insertion of ovules in inferior part of gynoecium; locule of adjoining flower can be seen in lower left corner; ×30.—Fig. 5. *P. latifolius*; oblique section through apex of gynoecium, showing stylar canal (arrow) and epidermal papillae, ×55.—Fig. 6. *Pothoidium lobbianum,* cross section through apical part of gynoecium, showing stylar canal (arrow), six vascular bundles, ×40.

Fig. 7–15.—Fig. 7, 8. *Pothoidium lobbianum.*—Fig. 7. Same flower as in Fig. 6, slightly lower section showing excentric stylar canal, ×40.—Fig. 8. Lower section showing internal opening of canal, ×40.—Fig. 9–15. *Epipremnopsis media*; progressively lower cross sections of gynoecium; arrows indicate vascular bundle of unknown significance; see text for further comments, ×25.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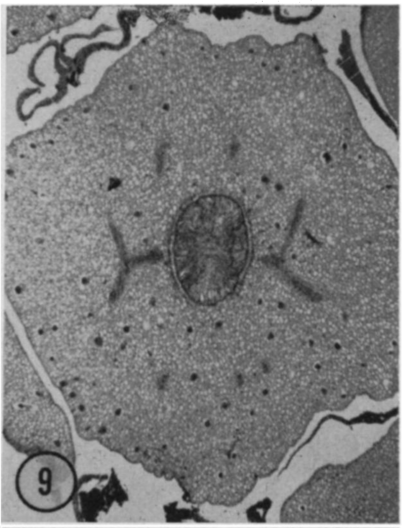
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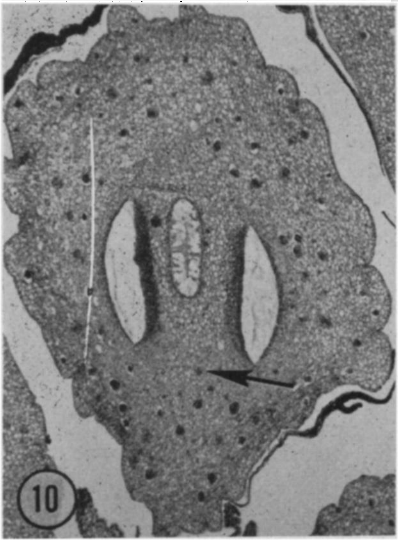
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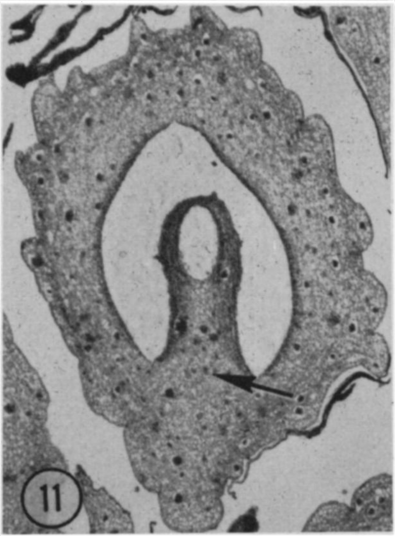
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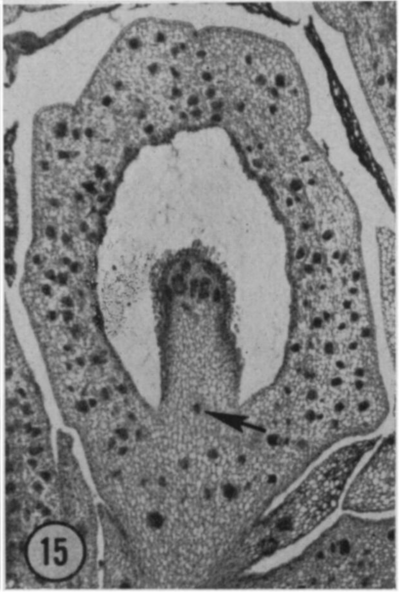
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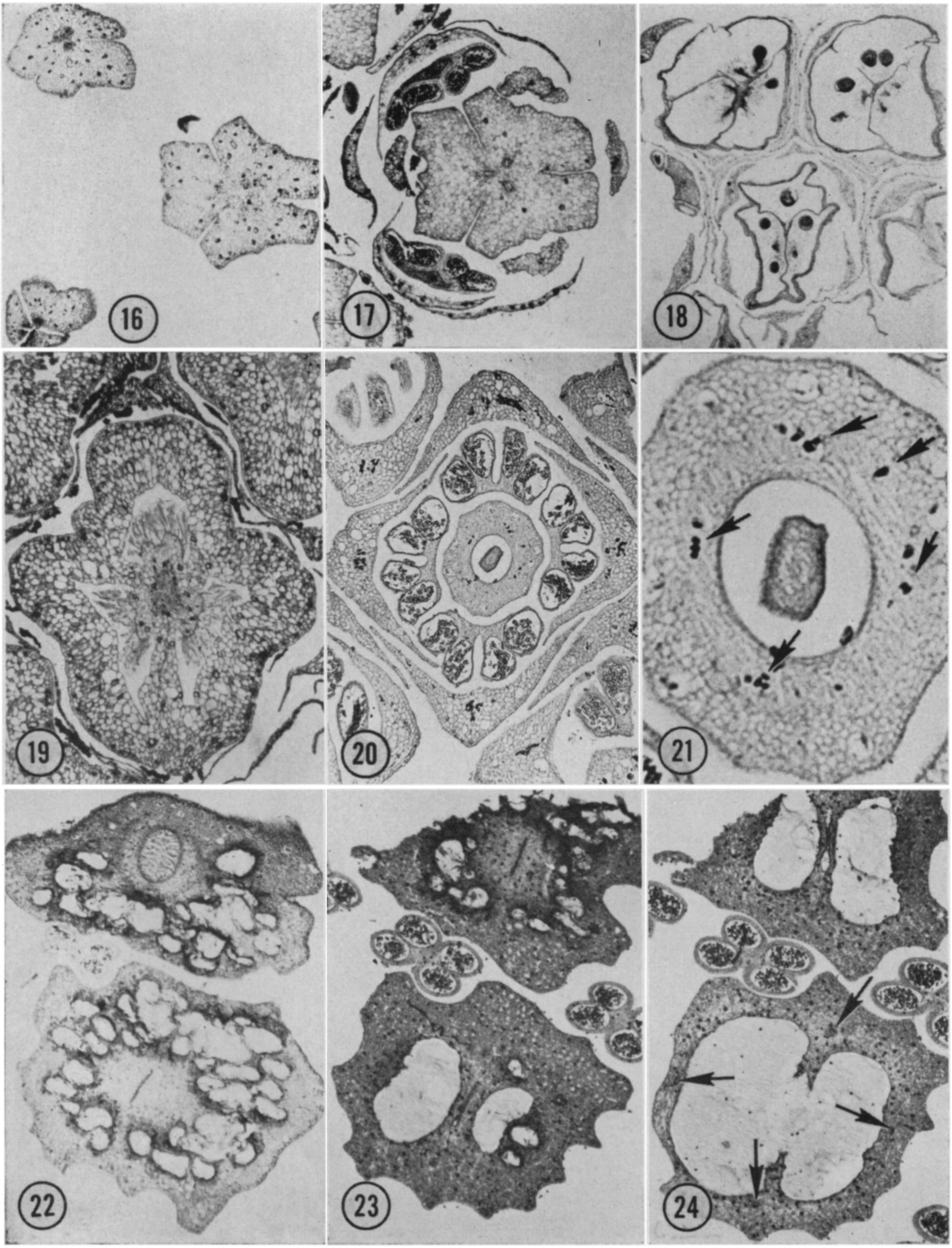


Fig. 16–24.—Fig. 16. *Acorus calamus*; cross section through flower cluster; note convergence of stylar canals in two flowers on left, ×25.—Fig. 17. *A. gramineus*; similar cluster showing introrse stamens, lobed gynoecium with three stylar canals, ×30.—Fig. 18. *A. gramineus*; same cluster, lower section showing rupture of septa, believed to be a common developmental feature, ×20.—Fig. 19. *A. calamus*; cross section through upper part of gynoecium, showing central vascular tissue; bundles are absent from septa and ovary wall, ×30.—Fig. 20, 21. *Gymnostachys anceps.*—Fig. 20. Cross section of flower showing extrorse stamens, one-locular gynoecium, ×35.—Fig. 21. Gynoecium enlarged to show vascular tissue (arrows), in ovary wall, ×140.—Fig. 22–24. *Rhaphidophora sylvestris*; successively lower cross sections through stylar canal and gynoecium of two flowers, continued on next plate. Arrows

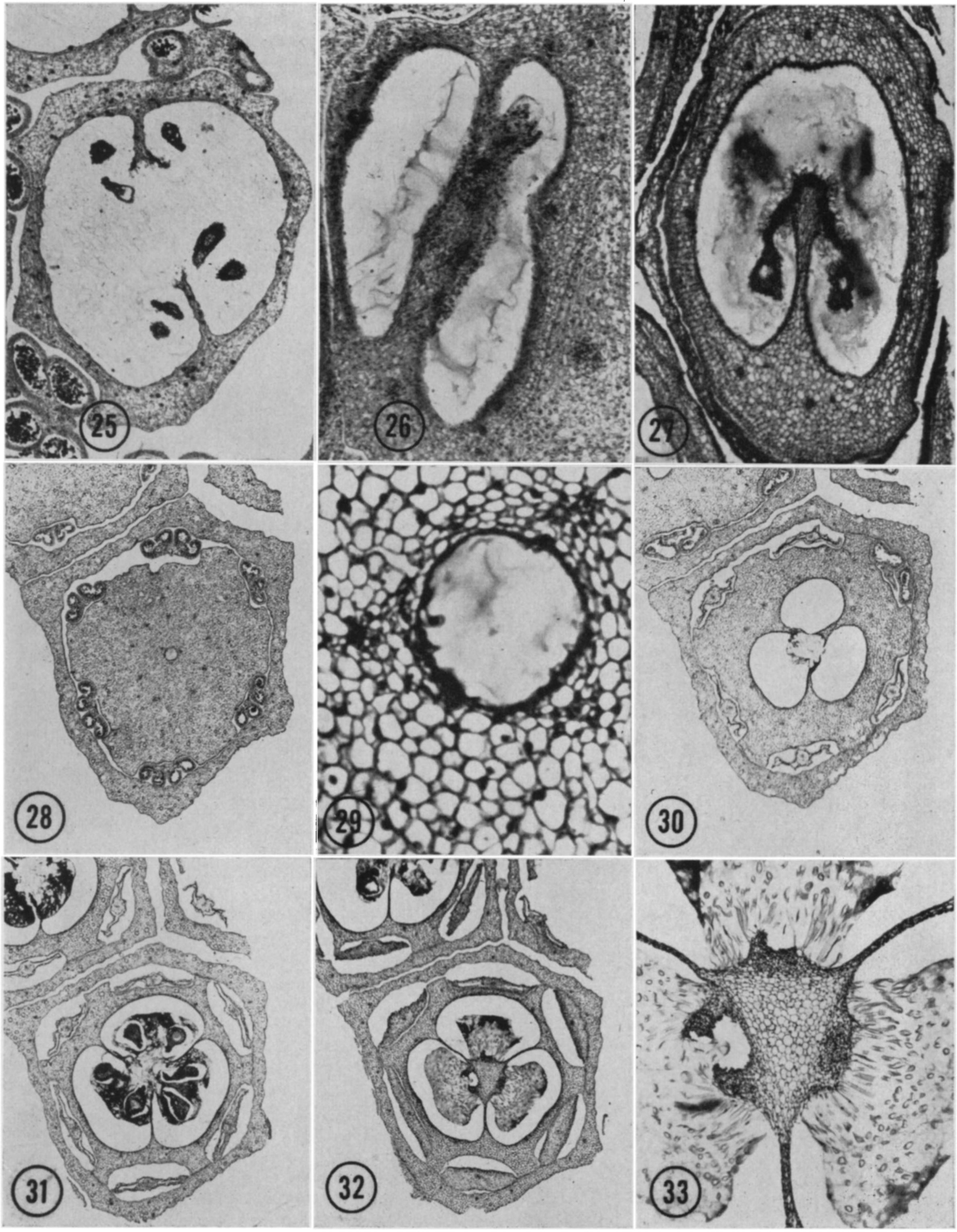


Fig. 25–33.—Fig. 25, 26. *Rhaphidophora sylvestris.*—Fig. 25. Same flower as in previous figure, fertile part of gynoecium, ×25.—Fig. 26. Basal section through a different flower; septum is complete at this level, ×55.—Fig. 27. *Amydrium humile*; cross section through gynoecium, showing attachment of ovules; note similarity to Fig. 14, ×35.—Fig. 28–33. *Spathiphyllum solomonense* sp. nov.—Fig. 28. Cross section of flower showing cupular perianth, circle of nine vascular bundles in gynoecium, ×12.—Fig. 29. Further enlarged to show three vascular strands around stylar canal, ×300.—Fig. 30. Lower section showing internal opening of canal, ×12.—Fig. 31. Section through fertile central part of gynoecium, ×12.—Fig. 32. Section below ovules showing central axis in gynoecium, ×12.—Fig. 33. Central axis further enlarged to show vascular tissue and transmitting tissue, ×40.

(Fig. 17). These canals unite only at the very apex of the gynoecium (Fig. 16), where specialized stigmatic tissue is almost totally lacking. In contrast, the placental area is covered with a transmitting tissue of long, club-shaped, densely staining cells. The tissues do not contain the raphide idioblasts found in other members of Engler's Pothoideae, but crystal sand and small druses occur in the floral tissues of *Acorus,* and tannin-containing cells are conspicuous in the perianth, androecium, and gynoecium. Vascular strands in the *Acorus* flower connect basally with a compact vascular cylinder in the inflorescence axis. Sections from immediately below the locules show the separation of this cylinder into 18 bundles, 6 of which enter the axis of the gynoecium; the other 12 can be followed in higher sections into the 12 members of perianth and androecium. With one vascular bundle in each tepal and in each stamen, the vasculature of *Acorus* resembles that of *Pothos* and other Pothoideae, but gynoecial vasculature is quite different. The six central bundles are united in a central vascular column well below the level at which the placental bundles diverge, and in sections taken near the gynoecial apex they are again recognizable as six discrete bundles. In such sections the strands are seen in three pairs, each pair accompanying one of the stylar canals (not visible in our photographs). These central strands could be called ventral carpellary bundles because of their position and their connection with the placental supply. The peculiar feature of *Acorus* vasculature is that there are no dorsal bundles; indeed, we have found no bundles at all in either the septa or the ovary wall (Fig. 19; see also descriptive comments of Saunders, 1939, p. 550).

In *Gymnostachys anceps* R. Br. (*Nicolson 1382*), the flowers have a four-merous perianth and androecium and a one-locular superior gynoecium with one pendent, apically attached ovule. Stamens are extrorse (Fig. 20) and the stylar region pulvinate with little or no specialized stigmatic or transmitting tissue. Abundant raphides are present with the druses in floral tissues. Tepals and stamens have one vascular strand each; however, in the distal third of the tepals the bundles divide into several fine strands. There are four–six bundles throughout most of the ovary wall, but sections through the distal part show a proliferation of these into many strands (Fig. 21).

Monsteroideae—An important character in Engler's recognition of this subfamily is the presence of trichosclereids in vegetative tissues. The subfamily comprises 2 tribes, 13 genera, and about 200 species, the flowers of which, like those of most pothoids, are bisexual. The tribe Monstereae, from which we have chosen two species for examination, differs from the Spathiphylleae in vegetative characters and in the absence of a perianth.

In flowers of *Rhaphidophora sylvestris* (Bl.) Engler (*Nicolson 894*) four extrorse stamens surround a completely superior two-carpellate gynoecium. Cross sections of the latter show one cavity in the median region (Fig. 24, 25) and two cavities in the basal and apical portions, where the two placental ridges are united into a continuous septum (Fig. 23, 26). Numerous ovules are borne parietally in the fertile median portion of the gynoecium. The stylar canal descends through a tubular external apical projection and at its lower end changes in transectional outline from a broad ellipse to a tightly closed slit (Fig. 22, 23). The apical portion of the ovary wall contains many cavities filled with a mucilaginous material derived from the complete deterioration of groups of cells (Fig. 22); larger cavities are formed by the union of smaller ones when intervening tissue breaks down. Solereder and Meyer (1928, p. 115, 116) mention similar cavities in the vegetative organs of *Rhaphidophora.* Raphides are present in the ovary wall, but examination of sections with polarized light shows that druses are far more plentiful; small trichosclereids can also be found. Dorsal bundles of the two carpels are readily identifiable in cross sections by their location at right angles to the plane of the placentae; two other prominent bundles occur approximately where the placental ridges join the ovary wall (Fig. 24, 25). The placentae are supplied by a vascular complex that can be traced to a group of five or six discrete strands in the central part of the basal septum, and all of the major carpellary bundles can be followed basally to their common origin below the flower.

Flowers of *Amydrium humile* Schott (*Nicolson 878*) are similar externally and internally to those of *Epipremnopsis,* thus bringing into question Engler's assignment of the two genera to different subfamilies. *Amydrium* has four stamens (all abortive in the two flowers that we sectioned) and a one-locular superior gynoecium. The stylar region resembles that of *Rhaphidophora* in that the stylar canal passes through a small apical protuberance, but the ovary of *Amydrium* does not have the mucilage-containing cavities of *Rhaphidophora.* Moreover, druses are not so abundant in *Amydrium* as in *Rhaphidophora*; instead, raphides predominate in the floral tissues. A major point of resemblance with *Epipremnopsis* is the single placental ridge bearing two ovules (Fig. 27). The gynoecial vascular pattern is also rather similar in the two genera. There are eight longitudinal bundles in the ovary wall of *Amydrium* and several additional strands in the placental ridge. Our preparations do not, however, show a conspicuous bundle in the placental ridge where it joins the ovary wall, as in *Epipremnopsis,* but this difference may be of little importance.

The cupular perianth of *Spathiphyllum solomonense* (newly described by the second author in an appendix to this paper), completely undivided and without lobes at its apical edge, surrounds a whorl of six fertile stamens. The superior gynoecium, shaped like an inverted pyramid, comprises three united carpels, each having one or two ovules. At the level of ovular attachment, there are three deeply intrusive placentae (Fig. 31) that merge below the ovules as a thick, vascularized axis (Fig. 32). A notable feature of the axis is its dense covering of club-shaped secretory cells, around which a mucilaginous residue persists, even after dehydration and sectioning (Fig. 33). Above the level of ovular attachment the vascular axis disappears, and the three septa are separate (Fig. 30, 31). A hollow, tubular stylar canal leads from the ovarian cavity to the more or less flattened apex of the gynoecium. Longitudinal trichosclereids are abundant in the perianth and in carpellary tissues of the new species, but druses and raphides are not plentiful. The perianth contains about 18 more or less equal vascular bundles, perhaps three for each of six united perianth members. There are three pairs of vascular bundles in the central axis of the ovary; these supply the ovules and are clearly inverted, that is, the xylem elements are on the side nearest the locules. The strands comprising a pair are variously united to each other for a part of their length. At all levels the ovary wall has nine evenly spaced longitudinal bundles (Fig. 28). This suggests a basic pattern of five bundles per carpel: a midvein, paired ventrals in the axis, and an additional pair of bundles in the ovary wall near each septum. In one of our two examples, however, the nine bundles are not arranged as symmetrically with the locules as this pattern would require. An interesting feature of the floral vasculature is the occurrence of three additional strands equidistantly spaced around the stylar canal (Fig. 29). Apparently these bundles do not extend below the canal nor do they connect with any other bundles.

We included two species of *Holochlamys* in our survey, because the opinions of Engler and Hutchinson differ greatly concerning the affinities of this New Guinean genus. Unfortunately, sectioning of the flowers was made difficult by numerous trichosclereids, and our preparations are therefore not of a quality to show complete vascular patterns and other details. It is clear, however, that the four stamens are extrorse, and not introrse as Engler and Krause (1908, p. 134) supposed. Perianth parts of *Holochlamys* are united as in *Spathiphyllum solomonense.* The stylar canal in *H. beccarii* (Engler) Engler (*Nicolson 1383*) is prominently four-lobed and filled with a conspicuous transmitting tissue. In our example of *H. guineensis* Engler et Krause (*Nicolson 1555*) this tissue is not so well developed, and the canal is three-lobed. The ovary wall in both species contains abundant raphides and druses. Although the gynoecium of *Holochlamys* has been described as one-locular with several basally attached ovules, our sections of *H. beccarii* are adequate to show a vascularized septum at the base of the ovary: the funiculi are attached to the septum and not directly to the floor of the cavity.

Calloideae—Engler distinguished this small subfamily (four genera, five species) from the preceding on the basis of the tube-like laticifers in vascular bundles of stems and petioles. He separated the Calloideae from succeeding subfamilies on the basis of their bisexual flowers, emphasizing also that the leaves are never sagittate. Hutchinson, although he does not recognize a taxon corresponding to Engler's Calloideae, agrees that two of the genera, *Lysichiton* and *Orontium,* are closely related.

Flowers of *Lysichiton americanum* Hultén et St. John have four tepals, four fertile stamens, and a two-carpellate, partly inferior gynoecium. Sections through the basal part of the ovary show two locules, each with a pair of ovules (Fig. 37) and axile placentation. Sections taken above the level of ovular attachment show that the septum is not complete in this region; that is, the locules connect in the upper part of the ovary (Fig. 35, 36). Transmitting tissue extends from the ovules into the narrow tubular stylar canal, but there is no external stigmatic area at the apex of the gynoecium. Raphides and druses are present in various parts of the flower. Tannin-containing cells occur sporadically in the gynoecium, and they are quite numerous in the stamens. We found no tube-like laticifers anywhere in the flower of this species or of any other species in our survey, however. Internal tissue of tepals, ovary wall, and septum are composed of schizogenous aerenchyma.

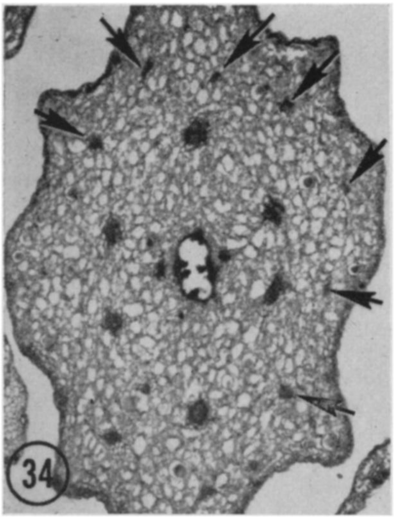
The gynoecial vascular bundles of *Lysichiton* are conspicuous and easily followed in serial cross sections. Near the apex the stylar canal is surrounded by an almost unbroken ring of vascular tissue, and in lower sections the ring is divided by parenchyma into a circle of five–eight discrete bundles (Fig. 34). The dorsals are readily identified among these bundles because of their median position relative to the locules. When the other bundles of the circle are followed through the ovary in a basal direction, two of them are found to be associated with the septum (Fig. 35, 36). In cross sections taken from the middle of the flower, these two bundles are located in the outer part of the septum near its junction with the ovary wall; a pair of internal branches of these septal bundles vascularize the two ridges that form the distal continuation of the septum. The ovular supply consists of broad, transversely oriented vascular strands connecting with the two main (outer) septal bundles (Fig. 37). Thus the *Lysichiton* flower differs from other septate flowers described in this paper in that the ovular supply does not run longitudinally through the axis. Longitudinal vascular bundles extend, however, from the funiculus to the region of the stylar canal; these distal continuations of the ovular supply are four in number at the placental level, distally uniting to form two. Another unusual feature is the presence in distal sections of an outer circle of bundles that are less prominent than the main circle and unconnected with any other bundles, either above or below (Fig. 34).

The foregoing description is based upon an examination of sections from nine flowers, part of a collection from the Netherlands (not vouchered). In addition, we examined serial sections of one flower from the state of Washington (*Nicolson 682*). The latter proved to be somewhat different in structure: the locules each contain only one ovule; vascular bundles are fewer at all levels; and the unusual "extra" outer circle of vascular strands is absent.

The familiar golden-club of eastern North America, *Orontium aquaticum* L., has as many as six tepals and six fertile stamens (see Schaffner, 1937, for other combinations). The gynoecium differs from that of *Lysichiton americanum* in being completely superior and one-locular at all levels with a solitary basal ovule. To judge from the appearance of the only example that we sectioned (from the Netherlands, not vouchered), which turned out to be a developing fruit, the inner layers of the ovary wall are absorbed by the ovule during its growth into a seed. The locular outline in this specimen is irregular; some of the cells lining the locule are ruptured, and others contain larger than normal nuclei. Consequently, vascular strands near the locule are not easily identified, but there seem to be 10–12 major longitudinal bundles, arranged in a circular pattern in most cross sections and converging distally as a vascular arc around the stylar canal. The latter is elliptical in cross section in our specimen, not triangular as Guéguen (1901, p. 279) figured the stylar canal of *"Orontium italicum."* Thick strands supplying the ovule pass transversely across the base of the ovary in a pattern similar to the transverse path of the ovular traces through the septum of *Lysichiton americanum.* Further similarities of *Orontium* to *Lysichiton* are the raphides, druses, and aerenchymatous tissues of perianth and gynoecium, and the copious tannin-containing cells in the stamens. We find no reason to doubt the prevailing opinion that the two genera are closely related.

Lasioideae—The 18 genera comprising this subfamily have unbranched laticifers, sagittate leaves with reticulate venation, and flowers either bisexual or unisexual. Engler recognized four tribes; the three genera included in our study belong to the Lasiae. Flowers of *Cyrtosperma* are bisexual, and a perianth, usually consisting of six or fewer tepals, is present in all species. Our preparations of *C. lasioides* Griff. (*Nicolson 977*) show seven tepals and seven fertile stamens in contrast to the six tepals and six abortive stamens of *C. johnstonii* (Bull) N. E. Br. (*Nicolson 1012*); otherwise the two species are very similar in floral structure. A glandular hemispherical stigmatic area tops the one-locular partially inferior gynoecium, in which (in our material) one ovule is attached by a long funiculus to a prominent vascularized placental ridge. Druses are present in the floral tissues, and large raphide-containing cells are very abundant, especially near the apex of the gynoecium. Tanniniferous cells are conspicuous in perianth, gynoecium, and androecium. Almost all of the cells of the filaments are filled with a darkly staining substance in some sections. During floral development the cell layers around the locule deteriorate, leaving intact only the outer part of the ovary wall, while cell fragments derived from the locular lining accumulate in the concave base of the cavity. The characteristic rupturing of the gynoecium and resultant exposure of seeds in the mature fruit of *Cyrtosperma* species probably begins with this developmental deterioration of the ovary wall. Tissues of the gynoecium

Fig. 34–42.—Fig. 34–37. *Lysichiton americanum* (cult. Netherlands).—Fig. 34. Cross section through gynoecium showing vascular pattern around stylar canal; arrows indicate some of the "extra" peripheral bundles that occur at this level, ×25.—Fig. 35. Lower section showing internal opening of canal; note absence of peripheral bundles, ×30.—Fig. 36. Section through upper level of placentae, ×30.—Fig. 37. Cross section (slightly oblique) through different flower, showing insertion of ovules; note that ovary is inferior at this level; note also conspicuous aerenchymya and transverse path of ovular supply through septum on left, ×25.—Fig. 38, 40. *Lasia spinosa.*—Fig. 38. Cross sections through upper part of flower showing attachment of ovule, ×35.—Fig. 39. Lower section; note slight indication of second placental ridge in lower half of photo; note also that the wall surrounding the locule deteriorates as clusters of cells slough off into the cavity, ×55.—Fig. 40. Section through base of cavity showing base of placental ridge and cellular debris that accumulates as wall deteriorates, ×100.—Fig. 41–42. *Dracontium polyphyllum.*—Fig. 41. Cross section through upper part of flower showing single stylar canal. Flower has six tepals, not all seen in this section, ×20.—Fig. 42. Slightly lower section, showing three canals; arrows indicate a dorsal (left) and a septal (right) bundle, ×50.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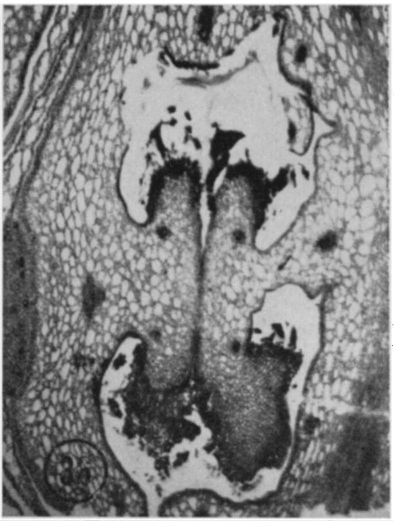
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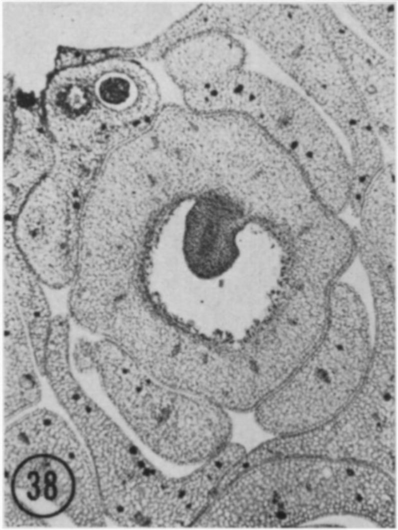
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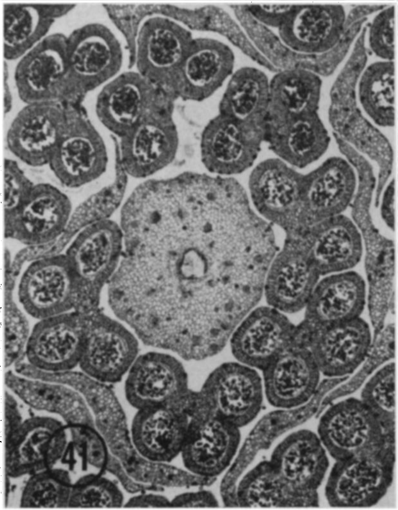
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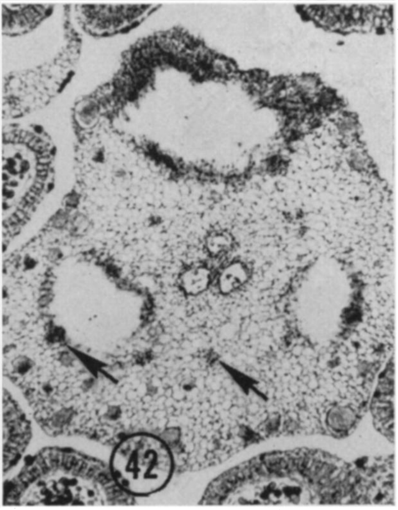
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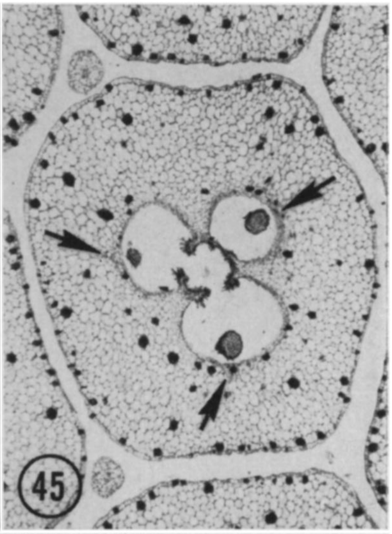
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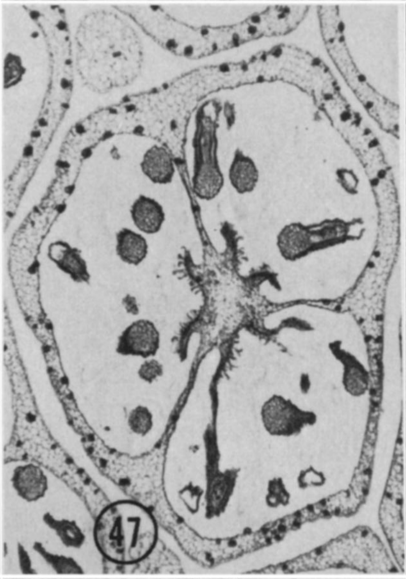
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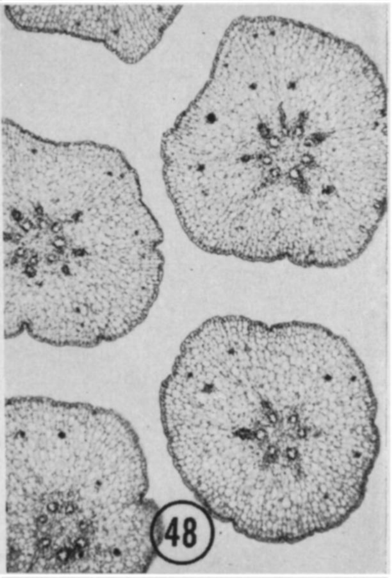
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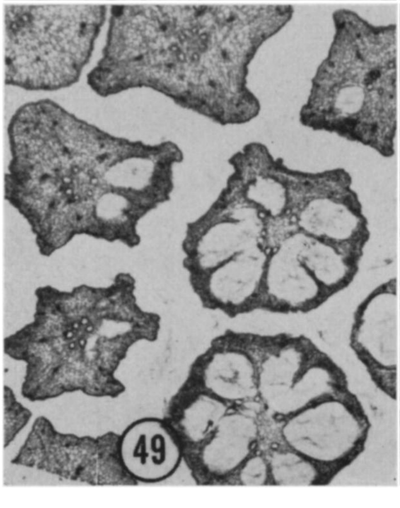
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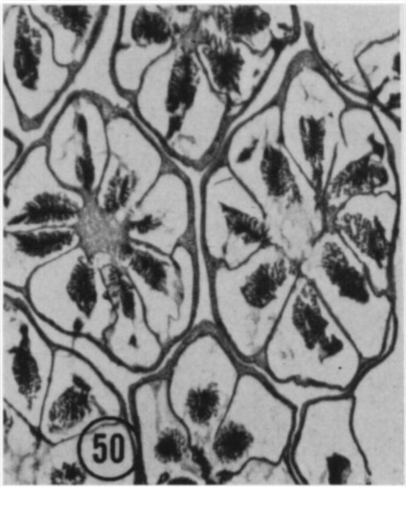
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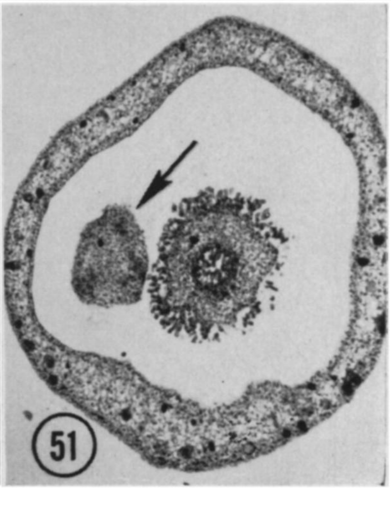
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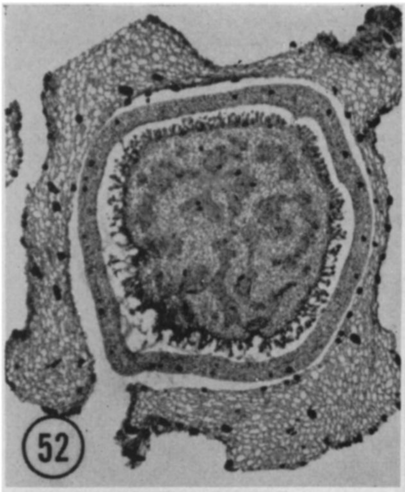
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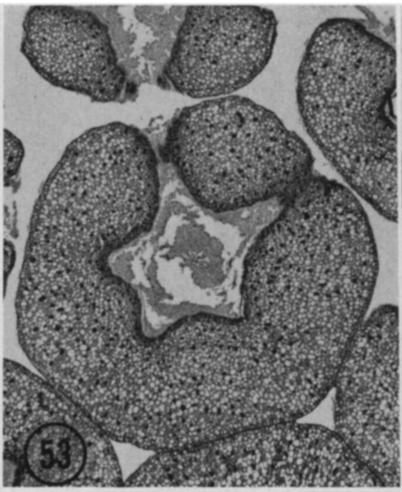
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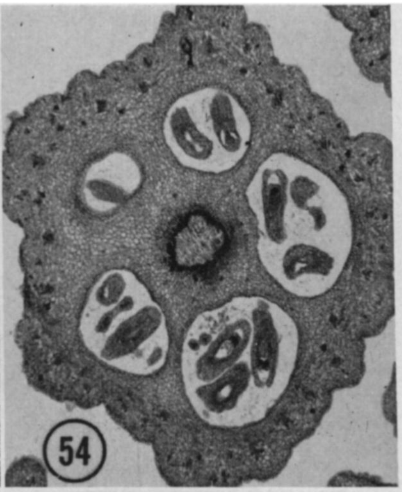
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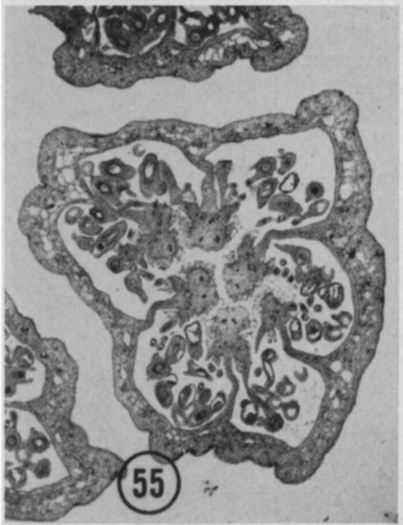
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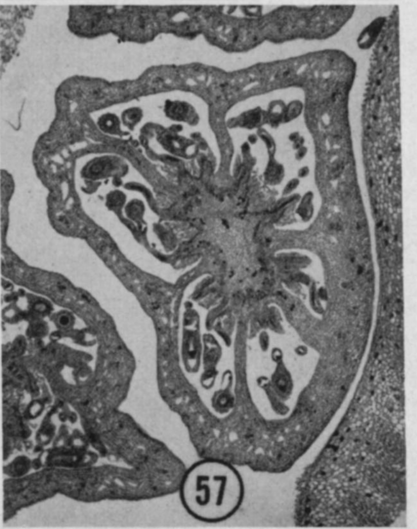
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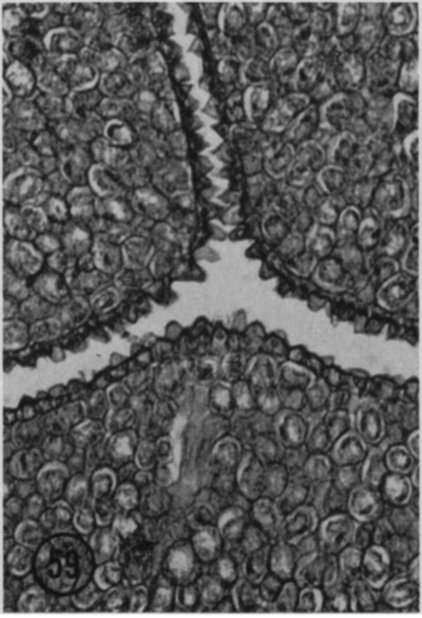
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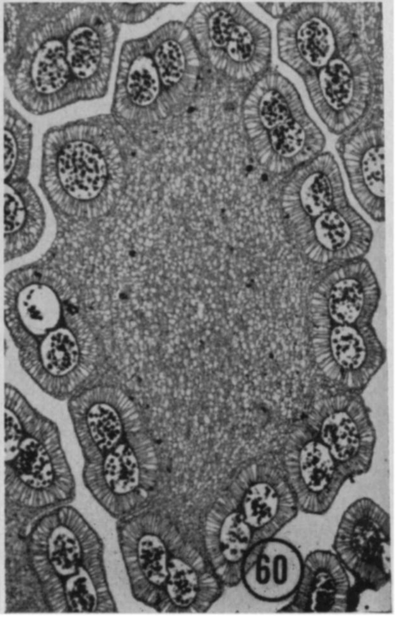
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are so distorted in our material that almost nothing can be seen of the vascular pattern.

Engler and Hutchinson agree that *Lasia* is closely related to *Cyrtosperma,* and our observations lend support to this opinion. Our preparations of *L. spinosa* (L.) Thw. (*Nicolson 1085*) include one flower with five-merous perianth and androecium and several flowers with four-merous whorls. Raphides and tannin-containing cells are common, druses rare. The gynoecium is one-locular as in *Cyrtosperma,* but the placental ridge is less intrusive, and the solitary ovule is attached near the apex; whereas in *Cyrtosperma* it is at the mid-locular level. Some of our sections show a slight indication of a second (sterile) ridge directly opposite the first (Fig. 39). Stamens and tepals are adnate to the base of the ovary wall. Although our material of *L. spinosa* was collected at an early stage of development, while the anthers still contained microsporocytes, sections show that the inner cell layers of the ovary wall had already begun to disintegrate (Fig. 38–40). Since changes in the ovary wall had not yet obscured the vascular pattern, we could establish that there are 10–12 longitudinal bundles in a circle around the locule. The ovular supply, a thick cylinder of vascular bundles, is located internal to these and accompanies the placental ridge.

In Hutchinson's classification *Dracontium* is removed from the Lasiae because of its hooded spathe, and we have found that the genus differs somewhat from *Cyrtosperma* and *Lasia* in floral structure. Our specimens of *D. polyphyllum* L. (*Nicolson 1119*) have six tepals, six fertile stamens, and a superior three-locular gynoecium. Each locule contains one ovule, inserted on the axis at about mid-locular level. Sections through the distal part of the locules show a separate stylar canal for each carpel (Fig. 42). In higher sections the three canals converge into one (Fig. 41), and in lower sections each canal opens independently into its own locule (Fig. 43). Raphides are many in the tepals and gynoecium, druses large and few. Tannin-containing cells are conspicuous, especially in the stamens. Inner layers of the ovary wall have deteriorated in our specimens; thus the vascular system is not completely clear. Surrounding the upper part of the stylar canal, there are several longitudinal bundles. At lower levels strands are discernible in the septa and in the axis of the ovary.

Philodendroideae—A subfamily of 7 tribes and 17 genera, the Philodendroideae are characterized by unbranched laticifers, parallel leaf venation, monoecism, and naked flowers. Male flowers of *Homalomena cordata* (Houtt.) Schott (*Nicolson 1112*) comprise three or four stamens; as in other members of Engler's tribe Philodendreae the stamens are distinct. Most pistillate flowers bear a single club-shaped staminode, tapering proximally to its basal union with the gynoecium (Fig. 45–47). Staminodes and fertile stamens have the histologic composition of the osmophors that Vogel (1962; see also Esau, 1965, p. 315) found in certain other Araceae; i.e., parenchyma cells in the apical portion of these appendages are filled with dense cytoplasm, and the papillose epidermal cells have thin outer walls with very little cuticle (Fig. 58, 59). The gynoecium of *H. cordata* is three-carpellate, superior, and multiovulate. Serial sections from apex to base pass first through a stigmatic region in which abundant epidermal hairs surround a triangular stylar canal (Fig. 44); next through a short stylar region where the canal narrows, becomes circular in outline, and opens into three locules (Fig. 45); then through a median region in which septa are incomplete and

Fig. 43–51.—Fig. 43. *Dracontium polyphyllum*; same flower as in two preceding photos; cross section shows internal opening of stylar canals, extreme deterioration of septa and ovary wall, ×40.—Fig. 44–47. *Homalomena cordata.*—Fig. 44. Cross section through group of flowers, showing two stylar canals, one staminode, ×30.—Fig. 45. Lower section showing opening of canal into three locules; staminode in upper left of photo joins this gynoecium at its base; arrows indicate positions of dorsal bundles, ×35.—Fig. 46. Lower section showing parietal placentation, ×35.—Fig. 47. Sectioned still lower to show axial placentation, ×40.—Fig. 48–50. *Philodendron erubescens.*—Fig. 48. Cross section through group of gynoecia showing multiple stylar canals; note that vascular bundles lie in same radii as stylar canals, ×30.—Fig. 49. Slightly lower section showing developmental extension of locules through deterioration of septa and ovary wall, ×25.—Fig. 50. Section through funicular region showing developmental rupture and distortion of septa, ×40.—Fig. 51. *Peltandra virginica*; cross section through upper part of female flower; at center of ovarian cavity is internal protrusion with stylar canal; section includes a bit of the ovule (arrow), ×30.

Fig. 52–60.—Fig. 52. *Peltandria virginica*; same flower as in previous photo, sectioned near base to show staminodial cup, massive placenta, ×30.—Fig. 53–57. *Xanthosoma sagittifolium.*—Fig. 53. Apex of gynoecium, showing star-shaped cross section of stylar canal, ×15.—Fig. 54. Lower section showing tops of locules, roughly circular outline of stylar canal, ×25.—Fig. 55. Another gynoecium, slightly oblique section from median region showing interconnecting locules; note air spaces in ovary wall, ×15.—Fig. 56. Placenta further enlarged to show six vascular bundles, ×70.—Fig. 57. Section through central axis, ×18.—Fig. 58, 59. *Homalomena cordata.*—Fig. 58. Cross section of stamen with only two locules, ×45.—Fig. 59. Junction of three stamens showing presumably osmophoric epidermal structure, ×135.—Fig. 60. *Peltandra virginica*; cross section through staminate flower showing 11 anther lobes, 1 with a single locule, ×25.

locules interconnect (Fig. 46); and finally through a basal region where septa meet in a broad central axis (Fig. 47). Ovules are attached in both the basal and the median levels; placentation is axile below and parietal above.

Tannin-containing cells are plentiful in carpellary tissues and also occur in the vascular bundle of each stamen. Druses are present in staminodes, stamens and ovary; raphides are few in the stamens, more plentiful in the gynoecia. The gynoecial vascular system is rather simple, consisting of three bundles for each carpel. Sections through the base of the ovary show a very slender dorsal bundle in the ovary wall opposite each locule and three pairs of heavier strands in the axis. At higher levels the members of each central pair are united in a single strand that passes through a parietal placenta into the stylar region. There are no vascular bundles opposite the septa in the ovary wall.

Staminate flowers of *Philodendron erubescens* C. Koch et Augustin (*Nicolson 1460*) usually comprise three fertile stamens and are borne at the apical end of the spadix. Below them are the female flowers, each consisting of a gynoecium of six–eight carpels with a stylar canal for each carpel. Locules are one-ovulate with the ovule attached basally to a long funiculus, the latter bearing a dense covering of secretory hairs. The locules do not interconnect, as they do in *Homalomena*; i.e., the septa are uninterrupted for the entire length of the ovary. Our specimens show the breakdown of inner layers of the ovary wall and resultant distortions (Fig. 49, 50; see also Fig. 18, 43) that we have observed in several other genera of Araceae. *P. erubescens* resembles *Homalomena* in its apical covering of stigmatic hairs and in the predominance of druses over raphides in the gynoecium, but tannin-containing cells are absent from gynoecial tissues of the *Philodendron* species. On the other hand, tannins are abundant in the male flowers of *P. erubescens,* and raphides are the commoner crystal type. Insofar as we can tell from our distorted material, the vascular pattern in gynoecia of *P. erubescens* is similar to that of *Homalomena,* except that the axis contains only one bundle for each carpel rather than two. Accordingly, for an eight-merous gynoecium there are eight axial strands. As in *Homalomena* a dorsal bundle extends longitudinally through the ovary wall opposite each locule; the dorsals continue distally into the stylar region, where they are conspicuous opposite the stylar canals (Fig. 48). Capus (1878) published a drawing of the stylar region of a related species, *P. cordatum* (Vell.) Kunth, in which the vascular strands are shown alternate with the canals; our observations suggest that this figure is in error.

Engler made *Peltandra,* with two species, the only genus of a tribe Peltandreae, while Hutchinson considers it a member of the Colocasiae. As the name indicates each male flower is a mass of connate stamens, more or less peltate in form. We sectioned one staminate flower of *P. virginica* (L.) Kunth (*Nicolson 2182*) and found that the component stamens are not clearly demarcated. Our example has 11 anther lobes, one of them with only a single locule (Fig. 60), and the several vascular bundles seem to have no symmetrical relationship to the lobes. In female flowers staminodes are united to varying degrees into a lobed urceolate structure, which may have little or no resemblance to stamens (Fig. 52). The staminodial identity of this structure is confirmed, however, by the presence of appendages that are intermediate in appearance in transitional flowers where the male and female parts of the inflorescence come together (Goldberg, 1941, p. 650). The superior gynoecium is one-locular with several ovules inserted on a large mound-like subbasal (subparietal) placenta. The latter is heavily vascularized by anastomosing bundles and covered densely with glandular hairs (Fig. 52). Similar hairs are found in a prominent internal protrusion (an inward extension of the conical style) that is centrally situated at the apex of the locule and carries the lower part of the stylar canal (Fig. 51). Tissues of the female flower, including the staminodial cup, contain scattered druses and raphides; in male flowers we have found only raphides. Tanniniferous cells are present in both. A ring of vascular tissue occurs in the stylar region; in successively lower sections this ring is seen to separate into about eight slender longitudinal bundles, which are too indistinct to be followed to the base of the flower. The staminodial cup contains almost no vascular tissue.

Colocasioideae—Like most Philodendroideae, the Colocasioideae have naked unisexual flowers, but this subfamily differs from the preceding in its usually anastomosing laticifers and its predominantly reticulate leaf venation. We included only one species, *Xanthosoma sagittifolium* (L.) Schott (*Nicolson 1408*), in our survey. The male flowers, which we did not section, are synandria with four–six stamens in each, according to the generic description of Engler and Krause (1920; see also sectioned flower of *X. robustum* Schott figured by Troll, 1928). Of the two female flowers that we sectioned, one was five-carpellate and the other six-carpellate (Engler and Krause described the ovary of *Xanthosoma* as two–four-locular). Locules are completely separated from each other in sections through the lower part of the ovary (Fig. 57), the septa being united in a vascularized axis. At higher levels the septa are not centrally united but intrude deeply into the ovarian cavity as parietal placentae (Fig.

55). Numerous ovules are borne on the axis below as well as on the parietal placentae. At the apex of the ovary the placentae are united around a stylar canal, star-shaped in cross section with each point of the star corresponding to the closed suture of one of the carpels. At still higher levels the canal is more or less circular in outline (Fig. 54), becoming star-shaped again as it opens externally (Fig. 53). A dense covering of glandular hairs lines the stigmatic region, the canal, and the inner edges of the parietal placentae. As is characteristic of *Xanthosoma* species the distal part of the gynoecium is broad and disk-like, cohering to similar structures of adjoining flowers (Fig. 53). Calcium oxalate occurs predominantly as crystal sand; a few druses can be found but no raphides. Tanniniferous cells are present in the ovary wall along with many large intercellular spaces. Vascular bundles are more numerous in *Xanthosoma* than in any other genera of our survey. Sections through the lower part of the locules show an inner circle of bundles (several for each carpel) in the axis and an outer circle in the ovary wall of 30–40 or more strands. In higher sections the central strands (ovular supply) accompany the parietal placentae as they separate. Each placenta receives several bundles, six being perhaps the most common number in the pattern shown in Fig. 56. It is usually possible to distinguish the dorsal bundles by their larger size and their position opposite the locules. In some sections other bundles of particular prominence can be seen at the junctions of septa and ovary wall. Above the ovarian cavity the central system of bundles diminishes and disappears, and the outer strands merge in an almost continuous vascular ring around the stylar canal. In still higher sections the ring becomes five or six discrete bundles, these alternating with the points of the star-shaped orifice of the stylar canal (not clear in our photos).

DISCUSSION AND CONCLUSIONS—*Taxonomy*—Perhaps the most interesting systematic conclusion to be drawn from our survey is the distinctness of *Acorus*. Taxonomists since Reichenbach (1828) have linked this genus with *Gymnostachys*, in spite of the fact that stamens are introrse in the former, extrorse in the latter, a striking difference reported by Eichler in his *Blüthendiagramme* (1875) but apparently overlooked by all subsequent investigators. When gynoecial characters (multiple stylar canals, absence of vascular bundles in ovary wall) and crystal complement (raphides absent) are considered along with the orientation of stamens, it is evident that *Acorus* is not properly assigned to Engler's Pothoideae. To this list may be added the presence, in vegetative parts, of ethereal oil cells (Schantz, 1958; Hegnauer, 1963). In combination these characters isolate *Acorus* quite sharply from all other Araceae; therefore, we propose the recognition of Acoroideae (Agardh, 1822, p. 133) as a separate subfamily of Araceae, with *Acorus* the only genus.

The resemblance of *Amydrium humile* to *Epipremnopsis media* is impressive. No two authorities seem to have agreed concerning the placement and affinities of these species. Prior to the completion of Engler's monograph, *E. media* had been assigned to *Epipremnum*, *Rhaphidophora*, *Anadendrum*, and *Scindapsus* (see Engler, 1905, for references). Schott (1863–64) considered *Amydrium humile* close to *Anadendrum*, and Engler (1879) originally allied it with *Heteropsis*, another pothoid. Hooker (1894) transferred it to *Epipremnum* (simultaneously suggesting that *Epipremnum* might better be united with *Rhaphidophora*!) and Engler and Krause (1908), maintaining a separate genus *Amydrium*, reassigned it to a position adjoining *Monstera*. A related complication is Alderwerelt van Rosenburgh's (1922) transfer of several *Epipremnum* species to *Epipremnopsis*. It therefore appears that a satisfactory taxonomic treatment of *Amydrium humile* and *Epipremnopsis media* will require the critical re-examination of a complex of species currently assigned to several genera, and it may be found necessary to recast the distinctions between the subfamilies Monsteroideae and Pothoideae.

We see no close anatomical similarity between *Pothos* and *Rhaphidophora* to match the cytological similarity reported by Mookerjea (1955), nor can we support Hutchinson's alliance of *Holochlamys* with *Lasia* and *Cyrtosperma*. Indeed, our observations of floral trichosclereids and a basal septum in the gynoecium of *Holochlamys* give additional weight to Engler's linking of the genus with *Spathiphyllum*.

The correct placement of *Peltandra* remains an open question, for our survey did not include flowers of *Alocasia* with which Hutchinson allies it. *Alocasia* is a member of Engler's Colocasioideae, a subfamily with predominantly reticulate leaf venation, whereas the leaves of Philodendroideae are generally characterized by "parallel" venation. The vascular pattern in *Peltandra* is intermediate but could be interpreted as derived from the colocasioid pattern. Colocasioideae more commonly have connate stamens; on the other hand, the gynoecium of *Alocasia* species, three–four-cleft in illustrations, may turn out upon examination to have a distinctly three–four-merous vascular pattern. If so, this would weigh against a close relationship to the poorly patterned gynoecial vasculature of *Peltandra*.

The occurrence of multiple stylar canals and completely isolated locules in *Philodendron* leads us to question whether *Homalomena*, with its single canal and connecting locules, is correctly placed in the same subfamily. A firm answer to this question would require a careful anatomical comparison of flowers in many genera of Philodendroideae and possibly a search for flowers of intermediate character among the various sections of *Philodendron,* a genus of more than 200 species.

Phylogenetic considerations — Although it would be foolhardy to attempt a phylogenetic arrangement of the Araceae on the basis of our limited survey, the observations suggest some comments concerning Engler's phylogenetic concepts. Early in his studies of the Araceae, Engler (1884, p. 331) proposed Pothoideae as the group from which other subfamilies arose, and this opinion had not changed substantially when he completed his series of monographs (1920b, p. 63). He was apparently aware that the multicarpellate ovaries of *Philodendron* (up to 15 carpels in subgenus *Meconostigma*) would appear more primitive to many botanists than the oligomerous gynoecia of Pothoideae, but the totality of characters in *Philodendron* seemed to him so clearly derived that he was led to explain the greater number of carpels as a specialization accompanying an evolutionary increase in available space on the thick spadix (". . . ich sehe daher in der Pleiomerie des Fruchtknotens nur eine Steigerung, die durch den grösseren Raum bedingt ist, den hier die einzelnen Blütenanlagen an dem mächtigen Kolben für sich in Anspruch nehmen können." 1884, p. 169). Today, when fairly rigorous arguments can be adduced for progressive oligomery in the gynoecia of many angiosperms, it would strain credulity to argue in this case that an increase in number of carpels has accompanied the derivation of one syncarpous group from another. Moreover, the ovular supply in *Pothos* consists of only one strand in the floral axis, clearly a more reduced condition than that of *Philodendron.* On the other hand, few contemporary botanists would suggest the converse—that the bisexual, tepalate flowers of the Pothoideae are derived from the naked, unisexual flowers of *Philodendron.* We are led to conclude that at least these two groups within the Araceae have evolved independently from an extinct ancestral complex. The multiple stylar canals of *Philodendron* contrast markedly with the single canal of *Pothos,* leading us further to conjecture that the divergence of these separate evolutionary lines began before the development of syncarpy. In the pothoid line one can visualize that the open distal stigmatic areas of the carpels of each flower united (in an evolutionary sense) around a common canal; whereas the evolutionary closure of carpels in *Philodendron* was complete except for an apical pore and thus left no open margins for the formation of a central canal. The concept of a direct derivation of *Philodendron* from apocarpous ancestors finds support in Schott's illustration (Peyritsch, 1879, Pl. 37, Fig. 11, 15), copied by Engler (1884, Pl. 5, Fig. 56, 57), of a partially apocarpous gynoecium in *P. brevilaminatum* Schott. Dismissed by Schott as "wahrscheinlich eine Monstrosität," the condition could be interpreted alternatively to indicate a direct and relatively recent evolution to syncarpy.

It appears to us that the evolution of syncarpy has occurred independently in the Araceae, not only along those lines leading to *Pothos* and *Philodendron,* but along other lines as well. *Acorus,* for instance, has separate stylar canals yet seems as remote from *Philodendron* as from *Pothos* and *Gymnostachys.* The interconnecting locules of *Xanthosoma* suggest that the syncarpous condition of this genus was attained by a different pathway from that of either *Philodendron* or *Pothos* with their completely isolated locules. An independent origin of syncarpy in several evolutionary lines within the family would explain much of the diversity in gynoecial vascular patterns (for instance, the atypical ovular supply in *Lysichiton*), for it would allow for varying degrees of specialization prior to the union of carpels. Our remarks should not be taken as a proposal that the Araceae be broken up into smaller families, however, for there are plant families with both apocarpous and syncarpous members (e.g., Palmae), and we therefore see no threat to the basic unity of the Araceae in conjecturing that the syncarpous condition has arisen within it more than once.

The foregoing commentary, though directed at Engler's phylogenetic scheme, contravenes Hutchinson's views as well. Hutchinson envisions a phylogenetic relationship between *Lysichiton* and *Orontium* on the one hand and the tribe Aspidistreae (Liliaceae) on the other, a view that requires the derivation of all Araceae from ancestral forms resembling *Lysichiton* and *Orontium.* As far as we know, no other author has accepted Hutchinson's opinion. The oligomery and peculiar vascular pattern in gynoecia of *Lysichiton* (Fig. 37) make this genus particularly unconvincing as a primitive member of Araceae.

Our survey did not include members of other monocotyledonous families; so we can contribute little toward the solution of the extrafamilial affinities of the Araceae. Except for the generally accepted relationship of Lemnaceae to advanced araceous genera (Maheshwari, 1958), there has been little agreement on this subject. Some authors, like Hutchinson, have proposed a close phylogenetic connection with the Liliaceae; others have suggested the "Helobiae" (for discussion, see Jüssen, 1928; Kimura, 1956). Hill

(1906), Lotsy (1911, p. 514, 863), and Emberger (1960, p. 1021) suggested an affinity with Piperales, and Meeuse (1965, p. 123, 156, 186) views the Araceae as having originated from a hypothetical "protomonocotyledonous group which resembled the Pandanales in several respects." Perhaps the most frequently quoted opinion is that the Araceae have evolved from the Palmae via the Cyclanthaceae. This idea (usually attributed to Engler, but we have not found the source) is clearly an oversimplification, for the highly complicated inflorescences of Cyclanthaceae can hardly have given rise to the more generalized inflorescences of many Araceae. Furthermore, the anthers of Cyclanthaceae are either introrse or latrorse, and the pistillate flowers are four-merous; it stretches the imagination too far to seek the origin of the Araceae in this combination of characters. The extant palms are equally unconvincing as ancestors of the Araceae, because, among other characters, the ovules are solitary in each locule throughout the family, and the gynoecia have only three carpels. On the other hand, we have no reason to doubt the often-advanced opinion that the Araceae, the Palmae, and perhaps also the Liliaceae share a common ancestry. In our opinion the extinct ancestral group would necessarily have been apocarpous, with many ovules in each carpel.

APPENDIX

Dan H. Nicolson

New names:

Pothos rumphii (Presl) Schott var. **dolichophyllus** (Merr.), comb. nov.

Pothos dolichophyllus Merr., Philipp. J. Sci., Bot. 11: 4. 12 Jun 1916.

In the Philippines and nearby islands a number of species belonging to what is best called the *Pothos rumphii* complex have been segregated primarily on leaf shape. It is beyond the scope of this paper to discuss all of them, but it is necessary to establish the correct name for the material used in this study. Field studies in the Philippine Islands showed that leaf shape has little taxonomic value but that the presence or absence of a stipe on the spadix is useful in distinguishing varieties of *P. rumphii*. Accordingly, I am establishing the trinomial *P. rumphii* var. *dolichophyllus* for plants with a sessile spadix.

Spathiphyllum **solomonense** Nicolson, sp. nov.

Caudex subrepens. Foliorum petiolus 35–40 cm longus ad laminae basin usque vagina subcoriacea persistente instructus; lamina lanceolata, 100–130 cm longa, 24–32 cm lata, apice apiculo 5–7 cm longo instructa. Pedunculus 45–50 cm longus, pulvinatus. Spatha persistens, spadicem amplectens, libera, usque ad 38 cm longa et ad 10 cm decurrens, 16 cm lata. Spadix 22–25 cm longus, 5–6 cm crassus. Perigonii tepala connata. Stamina 6.

Types: Cultivated, Territory of New Guinea, Bougainville Island, Arawa Plantation (10 km west of Kieta), 30 October 1961, *Nicolson 1508* (holotype: US; isotypes to be distributed to: A, B, BH, BISH, BM, BO, BRI, BSIP, CANB, G, K, KYO, L, LAE, NY, P, PNH, SING, W).

Mr. Francis McKillup, owner of Arawa Plantation, who cultivated this plant, reported that he collected it at 300 m in a moist gully of the Bovo [Borvi?] Valley in the interior of Bougainville Island. Unfortunately no wild material could be located during my visit, but the plant is so distinctive that I have no reservations in reporting it as a new species. Superficially it does not look like a *Spathiphyllum* with its spathe clasping the spadix and petioles shorter than the leaf-blades; however, structure of the flower shows that it belongs to section *Massowia*. It is quite distinct from the other species of section *Massowia*: *S. commutatum* Schott, *S. cannifolium* (Dryander) Schott, and *S. laeve* Engler, as described in Bunting's (1960) revision of *Spathiphyllum*. Interesting peculiarities in the distribution pattern of the genus were discussed by van Steenis (1962).

LITERATURE CITED[3]

Agardh, C. A. 1817–1826. Aphorismi botanici. Lundae, literis Berlingianis.

Alderwerelt van Rosenburgh, C. R. W. K. van. 1922. New or noteworthy Malayan Araceae 2. Bull. Jard. Bot. Buitenzorg, 3. 4: 163–229.

al-Rawi, A. 1945. Blütenmorphologische und zytologische Untersuchungen an Palmen der Unterfamilie der Ceroxyloideae. Arb. Inst. Allg. Bot. Univ. Zürich, 3 Ser., No. 6.

Anderson, C. E. 1940. Some studies on the floral anatomy of the Liliales. Ph.D. thesis, Cornell Univ.

Barghoorn, E. S. 1948. Sodium chlorite as an aid in paleobotanical and anatomical study of plant tissues. Science 107: 480–481.

Bosch, E. 1947. Blütenmorphologische und zytologische Untersuchungen an Palmen. Ber. Schweiz. Bot. Ges. 57: 37–100.

Buell, M. F. 1935. Seed and seedling of *Acorus calamus*. Bot. Gaz. 96: 758–765.

Bunting, G. S. 1960. A revision of *Spathiphyllum* (Araceae). Mem. N. Y. Bot. Gard. 10: 1–53.

Capus, G. 1878. Anatomie du tissu conducteur. Ann. Sci. Nat. Bot., Ser. 6, 7: 209–291; Pl. 18–24.

Eichler, A. W. 1875. Blüthendiagramme construirt and erläutert. Vol. 1. W. Engelmann, Leipzig.

el-Hamidi, A. 1952. Vergleichend-morphologische Untersuchungen am Gynoeceum der Unterfamilien Melanthioideae und Asphodeloideae der Liliaceae. Arb. Inst. Allg. Bot. Univ. Zürich, Ser. A, No. 4.

Emberger, L. 1960. Les végétaux vasculaires, tome II.

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[3] For additional references, see the excellent bibliographies in K. A. Wilson's "The genera of the Arales in the southeastern United States," J. Arnold Arbor. 41: 47–72. 1960.

In M. Chadefaud and L. Emberger [ed.], Traité de botanique (systématique). Masson et Cie., Paris.

ENGLER, A. 1879. Araceae, Vol. 2. *In* A. de Candolle and C. de Candolle [ed.], Monographiae Phanerogamarum. G. Masson, Paris.

———. 1884. Beiträge zur Kenntniss der Araceae V. 12. Über den Entwicklungsgang in der Familie der Araceen und über die Blütenmorphologie derselben. Bot. Jahrb. 5: 141–188, 287–336; Taf. I–V.

———. 1905. Araceae-Pothoideae. *In* A. Engler [ed.], Das Pflanzenreich IV. 23B (Heft 21): 1–330.

———. 1911. Araceae-Lasioideae. *In* A. Engler [ed.], Das Pflanzenreich IV. 23C (Heft 48): 1–130.

———. 1912. Araceae-Philodendroideae-Philodendreae; Allgemeiner Teil, Homalomeninae und Schismatoglottidinae. *In* A. Engler [ed.], Das Pflanzenreich IV. 23Da (Heft 55): 1–134.

———. 1915. Araceae-Philodenroideae-Anubiadeae, Aglaonemateae, Dieffenbachieae, Zantedeschieae, Typhonodoreae, Peltandreae. *In* A. Engler [ed.], Das Pflanzenreich IV. 23Dc (Heft 64): 1–78.

———. 1920a. Araceae-Aroideae und Araceae-Pistioideae. *In* A. Engler [ed.], Das Pflanzenreich IV. 23F (Heft 73): 1–274.

———. 1920b. Araceae; pars generalis et index familiae generalis. *In* A. Engler [ed.], Das Pflanzenreich IV. 23A (Heft 74): 1–71.

———, AND K. KRAUSE. 1908. Araceae-Monsteroideae. *In* A. Engler [ed.], Das Pflanzenreich IV. 23B (Heft 37): 4–138.

———, AND ———. 1920. Araceae-Colocasioideae. *In* A. Engler [ed.], Das Pflanzenreich IV. 23E (Heft 71): 1–132.

ESAU, K. 1965. Plant anatomy. Ed. 2. John Wiley, New York.

GARCIN, H. 1958. Contribution à la connaissance de la structure florale des Cyclanthacées. Nat. Monspeliensia, Bot. 10: 7–32.

GATIN, V. C. 1920. Recherches anatomiques sur le pédoncule et la fleur des Liliacées. Rev. Gén. Bot. 32: 369–437, 460–528, 561–591.

GOLDBERG, B. 1941. Life history of *Peltandra virginica*. Bot. Gaz. 102: 641–662.

GUÉGUEN, F. 1901, 1902. Anatomie comparée du tissu conducteur du style et du stigmate des phanérogames. J. Bot. 15: 265–300; 16: 15–30, 48–65, 138–144, 167–180, 280–286, 300–313.

HARLING, G. 1946. Studien über den Blütenbau und die Embryologie der Familie Cyclanthaceae. Svensk Bot. Tidskr. 40: 257–272.

———. 1958. Monograph of the Cyclanthaceae. Acta Horti Berg. 18(1): 1–428.

HEGNAUER, R. 1963. Chemotaxonomie der Pflanzen. Bd. II, Monocotyledoneae. Birkhäuser Verlag, Basel.

HILL, A. W. 1906. The morphology and seedling structure of the geophilous species of *Peperomia*, together with some views on the origin of monocotyledons. Ann. Bot. 20: 395–427; Pl. XXIX–XXX.

HOOKER, J. D. 1894. Aroideae. Flora of British India 6: 490–556.

HUBBARD, H. G. 1895. Insect fertilization of an aroid plant. Insect Life 7: 340–345.

HUTCHINSON, J. 1959. The families of flowering plants. Ed. 2. Vol. 2, Monocotyledons. Clarendon Press, Oxford.

JÜSSEN, F. J. 1928. Die Haploidgeneration der Araceen und ihre Verwertung für das System. Bot. Jahrb. 65: 155–283; Taf. XIV–XXIV.

KIMURA, Y. 1956. Système et phylogénie des monocotylédones. Notulae Syst. 15: 137–159.

KNOLL, F. 1926. Die *Arum*-Blütenstände und ihre Besucher. Abhandl. Zool.-bot. Ges. Wien 12: 381–481; Taf. 10.

KRAUSE, K. 1908. Araceae-Calloideae. *In* A. Engler [ed.], Das Pflanzenreich IV. 23B (Heft 37): 140–155.

———. 1913. Araceae-Philodendroideae-Philodendreae; Philodendrinae. *In* A. Engler [ed.], Das Pflanzenreich IV. 23Db (Heft 60): 1–143.

LOTSY, J. P. 1911. Vorträge über botanische Stammesgeschichte. Bd. 3. G. Fischer, Jena.

MAHESHWARI, S. C. 1958. *Spirodela polyrrhiza*: the link between the aroids and the duckweeds. Nature 181: 1745–1746.

MEEUSE, A. D. J. 1965. Angiosperms—past and present. Phylogenetic botany and interpretative floral morphology of the flowering plants. Adv. Frontiers Plant Sci. 11: 1–228.

MOOKERJEA, A. 1955. Cytology of different species of aroids with a view to trace the basis of their evolution. Caryologia 7: 221–291.

MORROW, L. O. 1963. Floral morphology and vascular anatomy in *Serenoa repens* (Palmae). Amer. J. Bot. 50: 622 (Abstr.).

———. 1965. Floral morphology and anatomy of certain Coryphoideae (Palmae). Ph.D. thesis, Cornell Univ.

NICOLSON, D. H. 1960a. A brief review of classications in the Araceae. Baileya 8: 62–67.

———. 1960b. The occurrence of trichosclereids in the Monsteroideae (Araceae). Amer. J. Bot. 47: 598–602.

PEYRITSCH, J. 1879. Aroideae Maximilianae. C. Gerold, Wien.

RAO, V. S. 1961. Floral anatomy. Scholar's Library, New York.

REICHENBACH, H. T. L. 1828. Conspectus regni vegetabilis per gradus naturales evoluti. Lipsiae, C. Cnobloch.

SAUNDERS, E. R. 1939. Floral morphology; a new outlook with special reference to the interpretation of the gynaeceum. Vol. 2. W. Heffer, Cambridge.

SCHAFFNER, J. H. 1937. The flowers of the golden-club. Amer. Bot. 43: 98–103.

SCHANTZ, M. VON. 1958. Über das ätherische Öl beim Kalmus, *Acorus calamus* L. Acta Bot. Fenn. 59: 1–138; Pl. 1–16.

SCHOTT, H. W. 1858. Genera Aroidearum exposita. Vindobonae, typ. Uebereuter, Olomucii, Hölzel.

———. 1863–64. Araceae. *In* F. A. G. Miquel [ed.], Ann. Mus. Bot. Lugduno-Batavi 1: 122–131, 221, 278–286.

SOLEREDER, H., AND F. J. MEYER. 1928. Systematische Anatomie der Monokotyledonen. Heft III. Principes-Synanthae-Spathiflorae. Gebrüder Borntraeger, Berlin.

STEENIS, C. G. G. J. VAN. 1962. The land-bridge theory in botany. Blumea 11: 235–372.

TIEGHEM, P. VAN. 1867. Recherches sur la structure des Aroidées. Ann. Sci. Nat., Bot., Ser. 5, 6: 72–210.

———. 1907. Remarques sur l'organisation florale et la structure de l'ovule des Aracées. Ann. Sci. Nat., Bot., Ser. 9, 5: 312–320.

TROLL, W. 1928. Über *Spathicarpa sagittifolia* Schott. Mit einem Anhang über die Stellung der Spathicarpeen im System der Araceen. Flora 123: 286–316.

VOGEL, S. 1962. Duftdrüsen im Dienste der Bestäubung; über Bau und Funktion der Osmophoren. Akad. Wiss. Lit. Mainz, Abhandl. Math.-naturwiss. Kl. 10: 601–763.