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LIFE HISTORY OF PELTANDRA VIRGINICA

BENJAMIN GOLDBERG

(WITH FORTY-NINE FIGURES)

Introduction

A morphological study of *Peltandra virginica* Kunth was made to assemble data which would give a rather complete life history of a widespread plant and a basis for comparison within and outside the Araceae. Features neglected or incompletely ascertained in the plant and the family as a whole were studied as fully as possible.

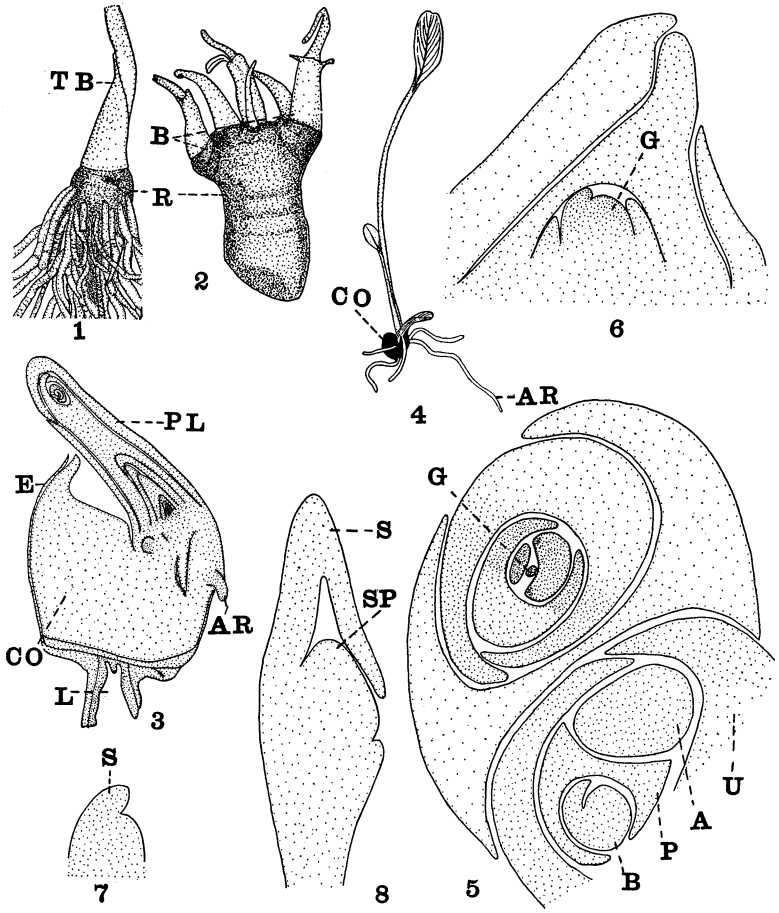
Comparative studies on the aroids (**13, 23**) have been of interest since ENGLER (**10, 11, 12**) pointed out that in spite of appreciable variation there were unifying tendencies in the group. The only detailed morphological account of *Peltandra* (**7**) deals with part of the development of the pollen. Additional reports include a microchemical study of the seed and its germination (**18**), a demonstration that the seed can germinate in almost total absence of oxygen (**8**), and an account of seed frequencies (**9**).

Observations

Peltandra is found throughout the eastern United States and has been reported west of the Mississippi River. It is an inhabitant of fresh water marshes, especially along the banks of tidal rivers. The stem is a subterranean vertical rhizome (figs. 1, 2*R*), cylindrical, and with a diameter in mature, unbranched specimens of 8 cm. The leaves are so compactly arranged that internodes appear nonexistent. The rhizome sometimes branches (fig. 2*B*) and the branches become separated from the parent plant as the basal portion of the rhizome decays. Since branches as well as parent axis form erect rhizomes, there results characteristically a cluster of plants.

Some rhizomes bear 100 or more adventive roots, which reach a diameter of

about 7 mm. in their proximal portions. Roots arise acropetally on the rhizome (fig. 1) and sometimes pierce the sheathing leaf bases. Wrinkling of the outer cortical tissues of roots of seedlings and older plants occurs, sometimes contracting to almost 50 per cent of the original length in some regions.



FIGS. 1–8.—Fig. 1, plant collected in October. Fig. 2, branched plant in dormant state with roots removed. Fig. 3, longisection of germinating seed (*CO*, cotyledon; *L*, lumen of haustorial cell). Fig. 4, seedling 16 days old with cotyledon (*CO*) still within pericarp. Figs. 5, 6, transverse and longisections through apex of mature rhizome. Figs. 7, 8, longisections of young inflorescences.

Above the concave top of the rhizome during most of the year is a large conical terminal bud (fig. 1*TB*) about 15 cm. long, extending from the top of the rhizome to the soil surface. From this bud, containing rudiments 15 cm. to 50 μ long, only a part of the outer, older, and larger rudiments emerge in late spring; the remaining ones, excluding those which abort during the interim, emerge during the fol-

lowing year. The various regions of the leaf are clearly defined. Leaves of mature form and size have a sheath 4.5–6.5 dm. long (including the subterranean portion extending from the soil surface to the apex of the rhizome), a stalk 2–4 dm. long, and a sagittate to hastate lamina reaching at times a length of 5 dm. (from the acuminate apex to the rounded basal lobes) and a width of 2 dm.

The larger inflorescences are about 70 cm. long, from the subterranean proximal region of attachment of the peduncle to the distal end of the spathe. The dark green spathe is 20–30 cm. long and extends a few centimeters beyond the inclosed spadix. While there is much variation, most plants in Maryland are at the height of their vegetative and flowering activity by the end of May or early June. After pollination, which occurs at this time, the distal part of the spadix, covered with staminate flowers, disintegrates, together with the distal part of the spathe, marked off by a slight invagination. The erect inflorescences bend below the attachment of the spathe to the peduncle, the fruiting spadix finally pointing toward or resting on the soil. The fruits, surrounded by the enlarged basal part of the spathe, ripen in August or September.

Seed and seedling

The dark green to brown obovoid fruits measure about 1.5 cm. long and 1 cm. wide, and show an apical scar marking the former position of the style. Within the membranous pericarp lies usually one, but sometimes as many as three, seeds imbedded in a colorless jelly-like material.

To the conspicuous, flattened-globular, micropylar portion of the seed is attached an obovoid chalazal appendage about 2–2.5 mm. long, which marks the position of the large haustorial cell of the endosperm. Within the seed lies the large embryonic sporophyte enveloped by the residual endosperm and the almost entirely withered parent sporophytic tissue. The layer of remaining endosperm surrounding the embryo is one cell thick, except in the region nearest the empty haustorial cell, where it is about seven cells thick. The integuments have become brownish and shriveled, but the parent sporophytic tissue in the chalazal region forms a thick coat around the empty haustorial cell.

The pale green cotyledon forms the greater part of the embryo, and has almost the same size and shape as the more conspicuous micropylar portion of the seed. In a deep groove of the cotyledon near the apex of the seed lies the narrowly conical, green plumule, about 9 mm. long and 3.5 mm. in diameter at its base. It contains six or seven foliar structures. Since it is partly encircled by the upgrowth of cotyledonary tissue, it forms with the cotyledon a compact body. The radicle does not form a group of tissues topographically delimited from the surface of the rest of the embryo. Occasionally the hypocotyledonary portion of the radicle appears on the side of the cotyledon as a poorly defined swelling, 1.5 mm. thick and 4–5

mm. wide. About 1.5 mm. below the base of the plumule on its exposed side lies the primary root, a slight rounded protuberance less than 1 mm. in diameter. Around the primary root the surface of the hypocotyl is marked by three to five small, circular, partially hyaline areas which indicate the position of adventive root primordia.

Usually the seeds germinate in April, but in some cases they germinate in the late summer of the year the ovules were fertilized, and while the fruits are still attached to the parent plant. By the time germination occurs the ovary wall is usually so decayed that it presents no mechanical obstacle to germination. As the plumule rises from its cotyledonary groove (fig. 3*PL*), the membranous envelope (*E*), consisting of the remains of endosperm and integuments, is ruptured. Although the primary root generally fails to elongate, it may attain a length of 2.5 cm. before withering. The adventive roots (fig. 3*AR*) grow and elongate rapidly; the first ones are small and short-lived, those formed later approach by degrees the mature size. Figure 4 shows a seedling, with a few adventive roots (*AR*) and the first three cauline foliar structures, 16 days after germination began. The first emergence was a bladeless sheathlike structure about 2 cm. long, the second and third possessed elliptical laminae, and the third alone a distinct stalk below the lamina. The primary axis increases rapidly in diameter, so that the young rhizomes show an obconical tapering.

Mature plant

Branching.—The seedling behaves as a monopodium until initiation of the first inflorescence, which is developed directly from the apex of the primary axis. Apical growth is then carried on by a bud which develops in the axil of the penultimate leaf. In the axil of the ultimate leaf a second bud is formed, which gives rise only to a basal acroscopic, two-keeled prophyll and a second inflorescence at its apex. The bud in the axil of the penultimate leaf completely displaces the original apex of the shoot in prominence and central position, so that outwardly the branching system appears unchanged, and the branch developing from this bud also ceases its apical growth with the formation of an inflorescence, after it has given rise to its share of leaves. Apical growth of the plant is then maintained by a bud in the axil of the penultimate leaf of the branch. The process is continued; and though a mature plant has an erect vertical rhizome, it is actually composed of superposed branches of increasingly higher rank. Engler (10), recognizing the sympodial nature of the shoot in practically all the Araceae, regarded the shoot corresponding to the one arising from the bud in the axil of the penultimate leaf of the *Peltandra* shoot as a unit in the structure of the plant and called it a *Fortsetzungspross* (continuation shoot).

As in the primary axis of the seedling, a second inflorescence (fig. 5*B*), together with a two-keeled prophyll (*P*), is borne in the axil of the ultimate leaf (*U*) of each

continuation shoot. In several hundred plants examined in 5 years, inflorescences were never observed in other positions on the continuation shoot. The second, or lateral, inflorescence originates after the first (fig. 5*A*) and always lags behind it in development. Both inflorescences of a continuation shoot, because of their position in initiation and development, are enveloped by the ultimate leaf.

Frequently the antepenultimate leaf of a continuation shoot bears an axillary bud, the *Vermehrungsspross* (**12**) or vegetative bud (**28**). In a series of plants collected in 1939, the vegetative bud was found on 118 out of 188 continuation shoots. Some plants bear no vegetative buds whatever; others show them only in part; and still others bear one in the axil of every antepenultimate leaf or leaf rudiment. Vegetative buds, if they develop at all, result in the branching of the rhizome and subsequent vegetative multiplication of the plant. In *Symplocarpus* and *Lysichiton* (**28**) the vegetative buds occur in a definite position, that is, in the axil of the lowest leaf of the continuation shoot, but do not develop into branch shoots. In *Peltandra* the buds often do not develop, but many do, some after lying dormant for a time and after the surrounding organs have emerged and disintegrated.

In a series of plants collected from 1937 to 1939, 207 out of 300 continuation shoots showed vegetative buds in the axils of the antepenultimate leaves; two of the 207 also showed them in the axils of the ante-antepenultimate leaf. None were observed in the axils of older leaves, except on the primary axes of seedlings. In one such case thirteen vegetative buds were found, one in the axil of each of thirteen leaves. Vegetative buds were never observed in the axils of the ultimate or penultimate leaves of a shoot.

Morphologically both the vegetative bud and the continuation shoot arise as buds of equal rank, but they differ in appearance and composition as well as in development. Both start with two-keeled, acroscopic prophylls. On the continuation shoot the next foliar structure is a leaf with a lamina of mature form and size; on the vegetative bud one or two more bladeless leaves are borne, while the laminae on subsequent leaves attain only by degrees the mature form and size. The vegetative bud is flattened dorsiventrally much more than the bud of the continuation shoot. After initiation, development of the bud of a continuation shoot is rapid, while that of the vegetative shoot is much slower and sometimes even appears to cease.

Number of leaves per continuation shoot.—Engler pointed out that the number of laminated structures appearing in a growing season, or on a continuation shoot, is often limited in the Araceae, only one being formed in species of *Amorphophallus* and *Philodendron*. In *Peltandra* the number in general decreases with increase in size and with maturity of the plant. On the other hand, branching of the rhizome, through development of vegetative buds, is apparently associated with an increased number of foliar structures on a continuation shoot.

The minimum number of foliage leaves found on a continuation shoot was three.

Once attained, subsequent shoots do not continue bearing this number exclusively, although in one case three foliage leaves were found retained for three consecutive shoots. There was no regularity in the succession of shoots bearing three, four, and five or more foliage leaves in specimens collected over a period of 4 years.

The following diagram is based on ENGLER'S method of summarizing shoot structure types in the Araceae (10), and has been modified to represent the complete record of a single specimen at the height of its activity. A continuation shoot and a vegetative bud of equal rank are represented by one horizontal row, and each is connected by a vertical line with the leaf in whose axil it is borne. Lateral inflorescence branches are similarly connected by vertical lines, but placed above their parent axes for clearness. Horizontal lines connect organs at successively higher levels, as read from left to right, on the same shoot.

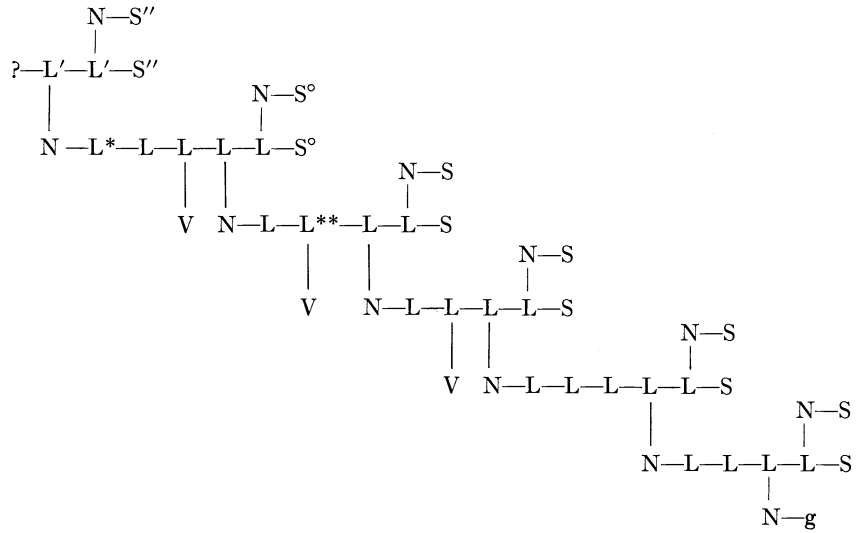


Diagram of mature plant of *P. virginica* collected June 9, 1939, dissected to show number and arrangement of organs, emerged and in rudimentary state. L, leaf; N, two-keeled prophyll; V, vegetative bud (constituent rudiments not indicated); S, spathe and spadix; S″, inflorescence already flowered; S°, inflorescence about to flower; ′, degenerate organs emerged or aborted in 1938; *, first emerged leaf; **, first rudiment of terminal bud (all organs following also exist in bud as rudiments); g, apical growing point of rhizome.

ESTIMATED AGE OF RUDIMENTS AT TIME OF EMERGENCE.—Characteristics of mature plants such as that diagramed may be enumerated as (*a*) small number of leaves (3–5) on a continuation shoot; (*b*) large number of inflorescences for time of year in which examined; (*c*) mature form and large size of leaf (not so reliable an index as the others); (*d*) unbranched rhizome with large diameter; and (*e*) vegetative buds either not initiated or arrested in development after attaining position

for emergence of rudiments. Plants selected by these criteria as mature agreed, to a certain extent, in number of leaf and inflorescence rudiments contained in the terminal bud during the dormant season, in number of organs emerging during the growing season, and in number of primordia added to the bud in summer by activity of growing points of successive continuation shoots. In view of this uniformity, periodic examinations of this type of specimen should reveal, within limits, details of sequence of the emergence of rudiments and their initiation, and the time elapsed from formation to emergence of a leaf or an inflorescence. The numerical range of leaves and inflorescences in mature, rudimentary, and aborted condition

TABLE 1

NUMBER OF LEAVES AND INFLORESCENCES FOUND IN MATURE, RUDIMENTARY, AND ABORTED CONDITION ON MATURE PLANTS THROUGHOUT THE YEAR

MONTH	CONDITION OF PLANT	SPADICES IN BUD	LEAVES IN BUD	SPADICES IN FLOWER OR FRUIT	EMERGED LEAVES	ABORTED SPADICES	LEAVES PER CONTINUATION SHOOT
Jan.	Dormant	9–10	.....	0	0	0–1	.....
Feb.	Dormant	10	.....	0	0	0–2	4
Apr.	Dormant	10–11	.....	0	0	0–1	.....
May	Dormant	10–12	20–25	0	0	0–2	3–5
June	In flower, fruit, and foliage	6–8 (10)*	15–18	3–5 (6)†	6–8	0–1	3–5
July	In foliage and fruit	7–9	17–21	3–5	5–9	0–1	3–5
Aug.	In foliage and fruit	8–11	21–25	2–4	5–6	0–2 (3)†	3–5
Sept.	Dormant	10–11	ca. 23	0	0	0–2	4–5
Oct.	Dormant	10–12	20–22	0	0	0–2	3–5

* Only one specimen found with ten rudimentary inflorescences at this period; the two oldest seemed about to flower.
† Only case of its kind found.

found on mature plants at various times during the year is shown in table 1. In an average mature specimen, five to nine of the twenty-odd leaves in the terminal bud at the beginning of May, together with three or four of the ten to twelve inflorescences present, emerge by the early part of the summer. Usually one to three leaves and not more than two inflorescence rudiments (the oldest and outermost of the terminal bud) abort between yearly emergences, and are found outside the terminal bud after the yearly crop of organs has emerged and degenerated. Thus about half the rudiments in a terminal bud early in May remain intact in the bud during the subsequent summer and dormant season.

Rudiments initiated during the summer (July–October) are added to those already present in the terminal bud, while the latter increase in size and assume the relative positions occupied by the recently emerged organs before emergence. By October, formation of new rudiments has apparently ceased, since the number re-

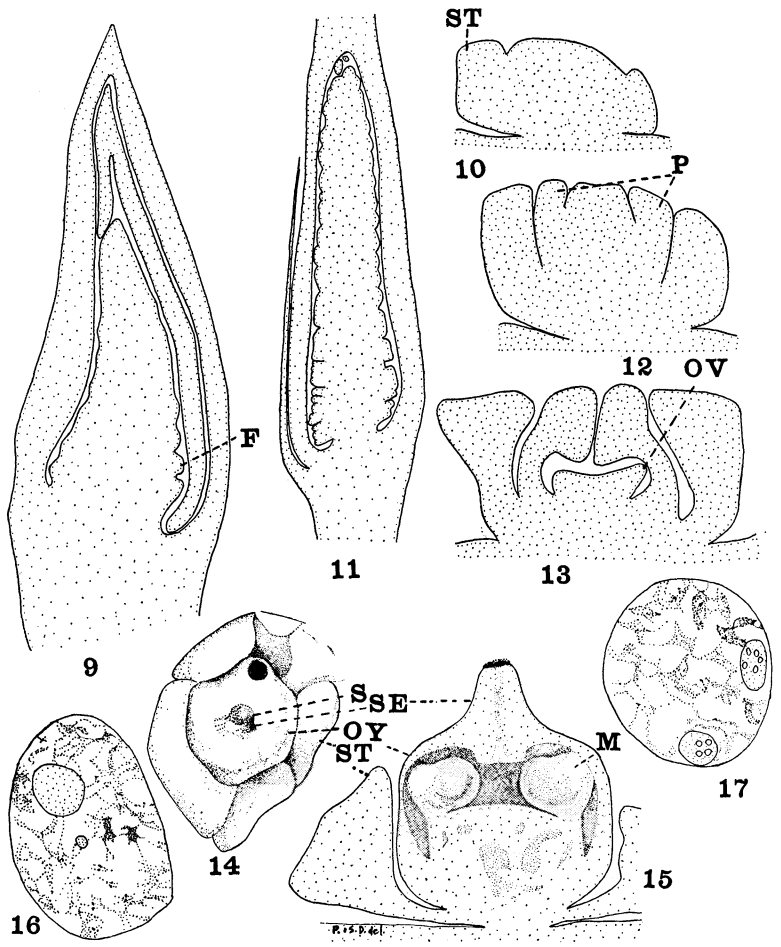
mains the same from October to May and no abortions were observed during this period. It appears that rudiments initiated prior to October of one year do not emerge until about 20 months later (cf. *Symplocarpus* **27**), shortly before the second succeeding summer.

APEX OF SHOOT AND ORGAN INITIATION.—The growing point of the rhizome and the youngest organ primordia lie in a slight apical depression, at the center of which the growing point of the youngest continuation shoot (figs. 5, 6, *G*) can be seen as a dome-shaped structure, overarched and enveloped by leaf primordia. First indications of a leaf are periclinal divisions in the hypodermal layer of the apical region. Very early the tip of the young primordium is marked off by its less meristematic appearance. In the young leaf it is disproportionately large as compared with its relatively insignificant size (about 5 mm.) in the mature organ.

The spathe appears to originate just as a leaf does, although a detailed study of this was not made. Its nature is soon revealed by failure to show the adaxial thickening that characterizes the early stages of petiole-midrib development, by elongation of the axis below its insertion in the formation of the peduncle, and by its position relative to the rapidly developing bud in the axil of the penultimate leaf. If a vegetative bud is to be formed in the axil of the antepenultimate leaf, it appears about the same time as the bud which gives rise to the new continuation shoot. The bud which gives rise to the lateral inflorescence is initiated later. Like the leaf, the spathe early surpasses and envelops the former growing point (figs. 7, 8, *S*) and forms a conspicuous tip, although it develops neither a stalk nor a blade. As the axis below the insertion of the spathe elongates, the former shoot apex develops directly into the spadix (fig. 8*SP*), the outline of which soon becomes slightly undulate. The number of swellings increases acropetally as those more basally situated become pronounced and flattened (fig. 9*F*).

As a result of continued distal flattening, the floral primordia appear in section as inverted truncate wedges. The primordia on the basal part of the spadix give rise to lateral members (fig. 10*ST*), appearing usually as incomplete or infrequently as complete rings, which mark the beginning of the staminodes. Later the primodia give rise to a ringlike lateral growth just within the staminodes (figs. 11, 12*P*). At first the staminodes, the newly formed ring, and the central truncate portion of the primordium develop at about the same rate. Subsequently the ring surpasses the other elements, curving centripetally as it envelops the central region. The edges of the ring, as they grow toward each other, flatten in a direction perpendicular to the long axis of the spadix and form the narrow, slitlike, stylar canal (fig. 13). The proximal part of the former ringlike structure extends centrifugally (fig. 13), forming the ovary; and the central truncate part of the floral primordium becomes the flattened basal placenta which gives rise to the ovules at points around its edge (fig. 13*OV*).

The more apical and by far the larger number of floral primordia do not give rise to lateral members (fig. 11); the flattened protuberances merely increase in bulk. Eventually these primordia, which give rise to the staminate flowers, be-



FIGS. 9–17.—Figs. 9, 11, longisections of young inflorescences. Figs. 10, 12, 13, same of young pistillate flowers. Fig. 14, mature pistillate flower from above. Fig. 15, longisection of same. Figs. 16, 17, early meiotic stages in microsporocyte nuclei.

come roughly rhomboidal to hexagonal when viewed in a section tangential to the surface of the spadix. Undulations arise along the edges of these staminate flowers and mark the origin of individual microsporangia, which usually occur in pairs. As development proceeds, adjacent pairs of microsporangia often become separated by sharp invaginations. This compact structure, bearing usually

sixteen to twenty microsporangia and representing a staminate flower, is the synandrium.

While the spadix may bear staminate flowers almost to the tip, sometimes its distal end is sterile. The synandria are usually flat-topped but sometimes show centrally located depressions of varying extent, which on evidence from transition forms are regions where pistils would be located.

Both ENGLER and BENTHAM and HOOKER described the staminodes as fused into a ring around the ovary. While this condition has been found, more often one to five separate staminodes to a pistillate flower were noted (fig. 14*ST*). Sometimes the staminodes were so large as completely to fill the spaces between pistillate flowers; at other times they were so inconspicuous as to be covered by the bulging sides of the pistils, and sterile regions of the spadix were then visible between the flowers. Rarely the staminodes of the more distal pistillate flowers bear apparently normal pollen. Staminate flowers may abut directly on the pistillate, but sometimes a transition zone is indicated by relatively few and scattered flowers, or flowers consisting exclusively of staminodes.

The normal pistil (figs. 14, 15) has a slightly flattened globular ovary (*OV*) with a short style (*SE*) and a terminal stigma (*S*), but various types of incompletely developed pistils occur between staminate and pistillate parts of the spadix. In addition to ovules borne normally on the placenta, they were sometimes borne at the base of the style on the protuberance into the ovarian chamber below the top of the ovary. Six substylar ovules were found in an ovary which contained also seven placental ovules.

DEVELOPMENT OF POLLEN

DUGGAR'S observations (**7**) on development of the pollen in *Peltandra* did not cover some of the earlier stages of meiosis, and the writer differs with him on some interpretations. As noted elsewhere (**6**), the chromosome number 22 given by DUGGAR does not appear to refer expressly to either *Peltandra* or *Symplocarpus*.

When preparations made from staminate flowers fixed without previous dissection showed the synizetic phenomenon in the earlier stages of meiosis, it was found necessary to dissect out contents of individual microsporangia in the fixing fluids in order to avoid clumping of the nuclear material. Sporocytes fixed in this way for temporary aceto-carmine mounts, or for imbedding and sectioning by the alcohol-xylol-paraffin method, gave about the same results as fresh untreated sporocytes dissected and mounted in paraffin oil. While it is evident that artifacts may be produced in the material during dissection, and indeed the instances of cytomixis observed are probably the result of tension and pressure, yet the frequent absence of distortion in all the stages, and another aspect of nuclear behavior to be discussed later, encourage confidence in the results obtained.

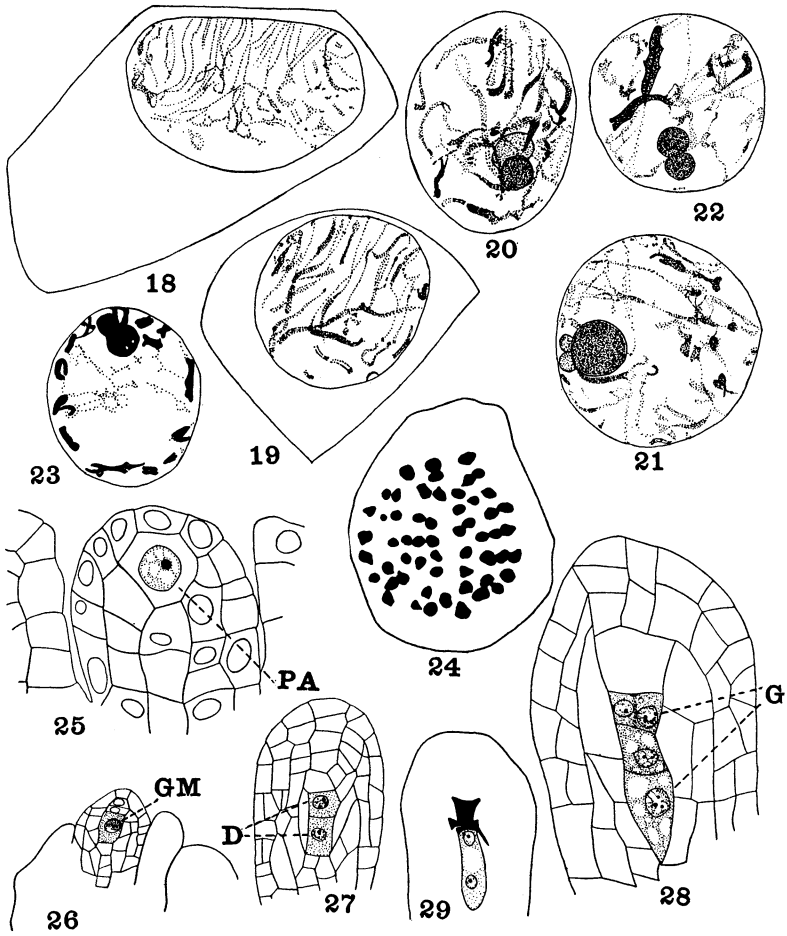
In the microsporangium, as in the ovule, the definitive sporogenous tissue is not marked off until the spring in which the meiotic divisions and flowering occur. Within a month of the occurrence of meiosis, the tapetal, wall, and sporogenous layers can be distinguished. Somatic mitoses occur in the sporogenous cells during the same season that the meiotic divisions occur. The wall is four to seven cells thick, the tapetum two to three, and the sporogenous region four or five in cross section. At length the cells of the sporogenous tissue enlarge, containing larger nuclei and denser cytoplasm than cells of surrounding tissues.

At first the large resting nuclei of the microsporocytes contain four or more nucleoli, stain lightly with Heidenhain's haematoxylin, and appear to contain fine filamentous structures with scattered, more chromatic material (fig. 16). As the nuclei enter the meiotic prophase, bodies similar to prochromosomes are formed; that is, vaguely limited bodies, roughly rectangular in section, and composed—in part at least—of filamentous structures (fig. 17). The delicate chromonemata observed in early meiosis seem to arise from the prochromosome bodies, and later stages show their gradual evolution and the initiation of their orientation. The few denser-staining regions evident in the resting nucleus give way to scattered, darkly staining structures which seem to become incorporated with the fine threads. The nucleoli tend to fuse in pairs. At this point, while dissected material showed a polarization of the threads, other material showed the familiar synizetic ball. Eventually a majority or all of the threads become polarized ("bouquet" stage) and extend parallel to each other from one side of the nucleus. Toward the periphery of the nucleus the chromonemata curve outward. The threads at this stage do not stain deeply and no structure could be discerned inside them, but their arrangement (fig. 18) indicates that they may be pairing. Sometimes there is a definitely thicker strand, which may be an already synapsed thread. More definite conclusions concerning behavior at pairing cannot be formed as yet.

In preparations showing polarization of the chromonemata, orientation of the threads in different nuclei was more or less random, except that frequently in two neighboring nuclei the chromonemata were oriented toward each other, perpendicular to a common cell wall separating them. This tends to emphasize the validity of the method of fixation, since it suggests that the chromonemata may be oriented with respect to the last somatic metaphase plate. The random orientation otherwise observed in any sporogenous mass seems to invalidate the suggestion that the arrangement is the result of an external mechanical disturbance, since if the latter were true, orientation of chromonemata in different nuclei would tend to be uniform and the nuclei otherwise distorted. A similar bouquet stage has been observed in various animals and plants (**4, 5, 14, 19, 24, 31, 32**).

The next stage was frequently observed. The threads, thicker in diameter and

staining more readily and sharply, still show in part the polarized arrangement of the bouquet. Clearly they are fewer in number. Their dual nature is sometimes obvious (fig. 19). The chromonemata do not appear homogeneous but are composed of densely staining granules (chromomeres) separated by less chromatic



FIGS. 18–29.—Figs. 18–24, stages in meiosis in microsporocytes. Fig. 24, polar view of metaphase. Figs. 25–29, longisections of nucellus or distal portion of ovule, showing development of female gametophyte.

regions. Although such bodies were not found in general, their presence was clear in a few cases. The chromonemata at this stage did not show uniform diameter throughout their length. This phenomenon, called first "partial contraction" and more recently "differential condensation," has been noted in animals and plants (4). In *Peltandra*, as in some other angiosperms, it seems to persist from

this late zygotene stage up to the beginning of diakinesis (figs. 19–23). From this time on the nucleoli are usually fused into one body, or closely associated, and contain few to many vacuolar spaces. With this, zygotene is complete and pachytene is gradually entered. It is clear from the number of ends evident in the ensuing stages that the chromonema is not a continuous thread, although the number of elements could not be ascertained. As the chromonemata grow shorter, the so-called spireme stage is reached. Material used for study of this and subsequent stages was not fixed with the same precaution for most rapid penetration as material for preceding stages; hence observations will be reported briefly.

The last traces of polarization vanish and the threads extend throughout the nucleus as the spireme or pachytene stage progresses. Following pachyphase, the chromonemata begin to show marked differences in chromaticity in some regions (figs. 20–22), and as they shorten tend to come into contact. These phenomena are more marked through the diplotene stage. With advanced diplophase (fig. 21) the contracting chromonemata migrate toward the periphery of the nucleus, and their dual nature is plain (fig. 22). Characteristic tetrad shapes appear (fig. 23).

After disappearance of the nuclear membrane the spindle, at first multipolar, becomes bipolar (cf. **7**). The haploid number of chromosomes, as ascertained by the various stages of the heterotypic (fig. 24) and homoeotypic divisions, is 56. The meiotic divisions are "successive." Localization of chromatic material never entirely disappears from the chromosomes at interkinesis, although irregularly outlined nucleoli, one or more per dyad, appear.

As the tetrads of microspores become established, the walls of the tapetal cells disappear and their cytoplasm appears to migrate throughout the locule and to separate the tetrads. Later the nuclei of the tapetal cells leave their peripheral position and become distributed throughout the microsporangium. The individual microspores become rounded off and invested with a heavy, at first unsculptured, wall. The periplasmodial nuclei are amoeboid in form. At maturity, just before the pollen grains are shed, they measure about 25μ in diameter, are sculptured with short, pointed spines, and contain a large nucleolated pollen tube nucleus and two smaller (male) nuclei devoid of nucleoli and staining densely. The wall of the mature pollen grain is pitted. The pollen-tube nucleus, which becomes lightly staining, irregular in outline, and apparently degenerate, may precede or follow the male nuclei into the pollen tube. Tests showed abundance of starch grains in mature pollen grains and pollen tubes. The male nuclei usually have surrounding hyaline areas clearly delimited from the granular cytoplasm of the tubes (cf. **29**). The possibility that these hyaline areas are artifacts has not been overlooked. Sometimes a distinct granular cytoplasmic layer can be seen surrounding each male nucleus, and this in turn is surrounded by the clear areas.

At maturity the sessile, staminate flowers consist of an angular disk 3–5 mm.

long, 2–3 mm. wide, and about 1 mm. high. In a tangential section of the spadix a sharp cusp appears between the upper portions of the sporangia of each of the pairs arranged around the periphery of the floral disk. This cusp marks the sole region in which the cells of the hypodermal layer of the theca remain small, with walls unthickened. The one-cell layer envelope of mechanically strengthened cells also occurs on the side of the loculus attached to the floral disk. As the periplasmodium of each microsporangium and the septum separating the microsporangia of each theca disappear in the course of development, the pollen masses become confluent. The wall of the theca ruptures in the region of the unstrengthened hypodermal cells. At first the freshly shed pollen tends to remain in vermiform masses near its place of exit on the outer surface of the synandrium, but on being disturbed most of it falls into the dilated proximal part of the spathe.

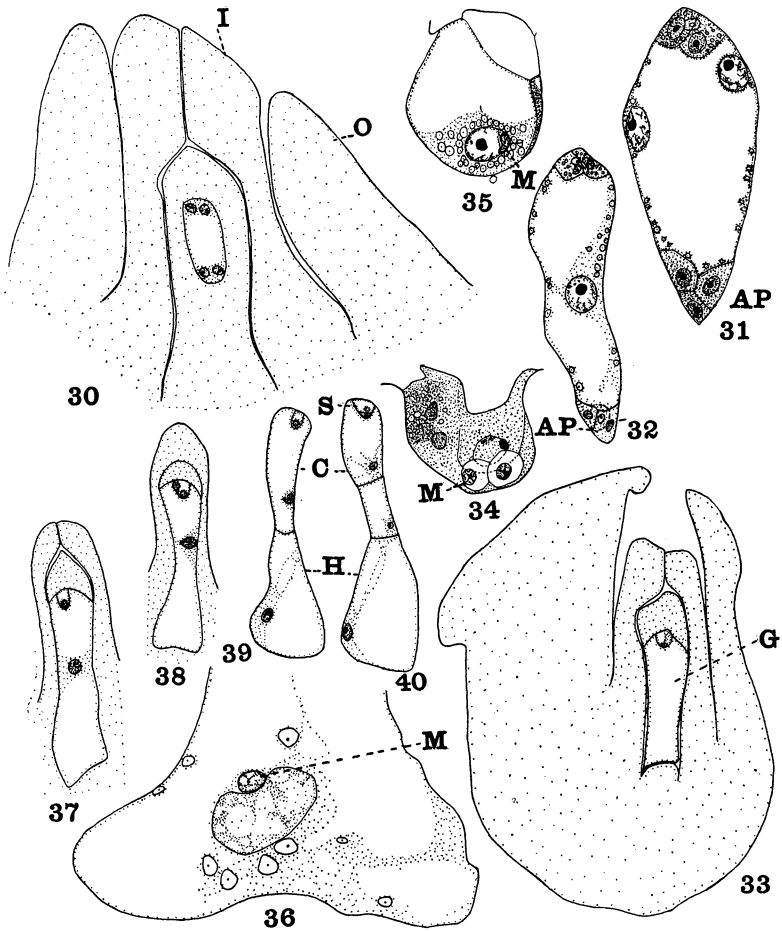
Development of megagametophyte

The primordia from which the one to ten ovules arise grow upward and outward from the edge of the basal placenta and eventually approach the wall of the ovary in its upper regions. At the first sign of the integuments, the primary archesporial cell is not clearly marked off. The inner integument differentiates more rapidly than the outer. A median hypodermal cell of the nucellus is differentiated as the primary archesporial cell (fig. 25*PA*). The megaspore mother cell (fig. 26*GM*) can be seen with two overlying tapetal cells, which were probably formed by division of the sister cell of the megaspore mother cell. *Symplocarpus* (**27**) and *Calla* (**23**) also show tapetal cells, but other aroids—for example, *Acorus calamus* (**1**)—form none. Throughout development of the ovule, the portion of the outer integument on the side next to the funiculus is larger than that diametrically opposite. The micropylar end of the hemianatropous ovules is consistently directed outward toward the wall of the ovary (fig. 15*M*).

By the time the first meiotic division has occurred the megaspore mother cell is well surrounded by nucellar tissue, and the distal part of the inner integument is growing contripetally and overarching the nucellus, forming the narrow micropyle. At first the outer integument does not keep pace in growth longitudinally with the inner, but it is broader than the inner integument, which is two or three cells thick, except at its tip. As in other aroids (**23**), the inner layer of the inner integument forms a distinct layer of cells, rectangular in outline, with their longer axes perpendicular to the longitudinal axis of the ovule (the "tapetal" layer of the megagametophyte).

The spindle in the smaller, micropylar member of the dyads (fig. 27*D*) is perpendicular to, and the spindle in the chalazal dyad (fig. 28) is parallel to, the longitudinal axis of the ovule. Of the four megaspores formed (fig. 28*G*), the chalazal one becomes conspicuously vacuolated and gives rise to the megagameto-

phyte. The outer integument has now reached the length of the inner and begins to exceed it. Centripetal growth of the distal end of the inner integument has reduced the micropylar opening. The chalazal megaspore seems to develop nor-



FIGS. 30–40.—Figs. 30–33, longisections showing development of female gametophyte. Fig. 30, section of micropylar portion of ovule perpendicular to longitudinal axis of funiculus (*O*, outer; *I*, inner integument). Fig. 33, longisection of ovule at fertilization, parallel to longitudinal axis of funiculus. Fig. 34, male nuclei beside egg cell. Fig. 35, fertilization. Fig. 36, male nucleus beside fusion nucleus in chalazal region of female gametophyte. Fig. 37, gametophyte after fertilization. Figs. 38–40, first and second divisions in endosperm.

mally into a typical 8-nucleate megagametophyte. From the 2-nucleate stage on, the megagametophyte shows a decided polarity, the nuclei being equally distributed above and below the large central vacuole (figs. 29–31). The polar nuclei were observed in the process of fusion at about the middle of the megagameto-

phyte, after formation of antipodal cells and the egg apparatus. Three antipodal cells are organized (figs. 31, 32, *AP*). They soon show signs of degeneration.

In the later stages of its development the megagametophyte contains abundant starch grains, especially in the micropylar cells and about the fusion nucleus. The nucellar tissue flanking the megagametophyte has begun to disappear (through digestion) by this time. Before fertilization occurs this part of the nucellus has been completely digested, and the sides of the megagametophyte (fig. 33*G*) are in contact with the inner layer of the inner integument.

After degeneration of the antipodals the fusion nucleus comes to lie at the chalazal end of the megagametophyte, which becomes truncate as it extends coincident with digestion of the chalazal nucellus. When ready for fertilization, the megagametophyte contains two synergids and an egg cell in the micropylar end and the fusion nucleus in the opposite end. The outer integument now extends beyond the inner. After the chalazal megaspore has begun to enlarge, or sometimes even before, a palisade of unicellular glandular hairs develops from the superficial layer of the placenta and adjacent regions of the funiculi. These hairs, together with those formed within the ovary near the base of the style, produce a jelly-like, colorless material that fills the ovary before fertilization and persists until after the seed germinates.

POLLINATION AND FERTILIZATION

Prior to pollination the spathe remains tightly wrapped about the spadix, one edge overlapping the other. The upper part of the spathe surrounding the staminate flowers becomes marked off from the lower surrounding the pistillate flowers. While the upper two-thirds of the spathe is dark green and tapers gradually toward the tip, the lower part is yellowish to light green and of greatest diameter at the middle. Opening in both regions is preceded by longitudinal extension of first the inner and then the outer margin of the spathe, both margins being thrown into wavelike folds. The lower part of the spathe opens first, but the opening is small and only a few pistillate flowers can be observed from without. Each pistillate flower consists of one to five whitish, fleshy staminodes surrounding a flask-shaped pistil about 3 mm. high with a subglobose, one-celled ovary about 2.5 mm. in diameter; a comparatively thick style 0.8–1.5 mm. long, having a central canal lined with hairs; and an inconspicuous terminal stigma of short unicellular hairs (figs. 14, 15). The upper portion of the spathe opens later. Sometimes it opens completely, freely exposing the tip of the spadix; but it may only loosen a little, without actually exposing the staminate flowers.

The behavior of the spathe and other circumstances make cross-pollination feasible and probable. Insects (Syrphidae, Chloropidae, and others) were seen entering the spathe, frequently laden with *Peltandra* pollen. Eggs of insects are

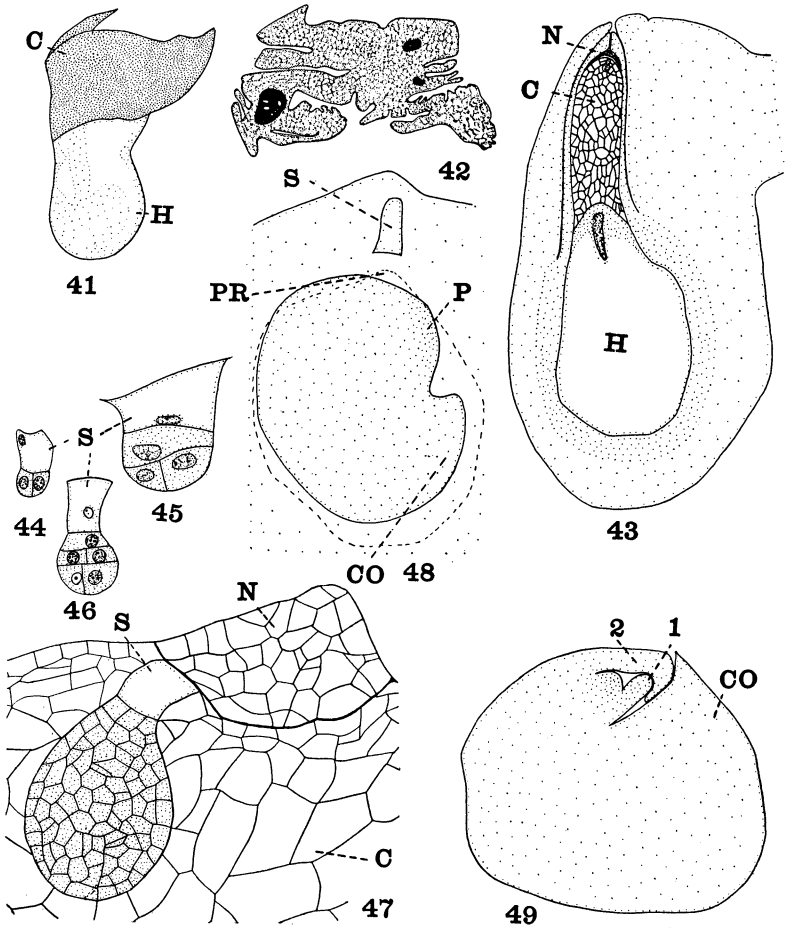
often found on the inner surface of the spathe, and insect larvae develop in and feed on the immature fruiting spadix. In several instances, when only the lower part of the spathe surrounding the pistillate flowers was open, germinated pollen grains were observed on the stigmas of the pistils before there was any sign of dehiscence and liberation of pollen from the loculi of the synandria on the same spadix. Apparently the pistillate flowers can be and are pollinated before the staminate ones on the same spadix liberate pollen. Should cross-pollination of any pistillate flower fail to occur, self-pollination is still possible, if the stigma remains receptive; for large amounts of pollen from the overlying synandria are liberated and reach the lower region of the spadix (by means of insects or force of gravity) after fertilization has occurred in some of the pistillate flowers on the same spadix.

Germinated pollen grains have been observed on the stigma; pollen tubes have been found in the stylar canal, in the jelly-like material within the ovary, entering the micropyle, and traversing the micropylar nucellus. As recorded for several other plants (**29**), more than one pollen tube may enter the megagametophyte. In one case three pollen tubes entered a single micropyle. In some instances clear areas, like those observed in the pollen tubes, surround the male nuclei in the megagametophyte (fig. 34*M*). One male nucleus (fig. 35*M*), lacking a nucleolus and staining densely, fuses with the egg nucleus; a second fuses with the fusion nucleus (fig. 36*M*). Among aroids double fertilization has also been recorded for *Arum maculatum* (**21**) and *Arisarum vulgare* (**22**), and suggested for *Dieffenbachia picta* var. *baraquiniana* (**16**). The fusion nucleus contains a large vacuolated nucleolus. Upon fusion with a male nucleus, the resulting endosperm nucleus finally comes to possess several smaller nucleoli, and the rather irregular chromatic reticulum is replaced by a more threadlike structure.

Development of endosperm

So far as observed, the endosperm nucleus always divides before the oospore nucleus. Usually this nucleus migrates from its chalazal position toward the micropyle (fig. 37), dividing at a position somewhat more than half way (fig. 38). Cytokinesis follows this karyokinesis (fig. 39). In this respect *Peltandra* resembles some aroids (**1, 20, 23**) but differs from others (**15, 23, 26, 27**). The micropylar endosperm cell thus formed gives rise to a cellular endosperm (figs. 39, 40, 43, *C*). The chalazal cell (*H*) never divides again and eventually reaches a tremendous size (figs. 41, 43, *H*), 2.4 by 1.6 mm. or more (cf. **26**). Its nucleus also fails to divide again, increases greatly in size, and becomes very much lobed (fig. 42). After attaining a large size, the nucleolus fragments and the pieces become highly vacuolated. When endosperm with the chalazal cell still intact was dissected from ovules, mounted in tap water, and observed with the microscope, large coarse strands of cytoplasm were noted traversing the cell vacuole of the giant haustorial

cell. Within these strands the middle regions could be seen in streaming motion. Large haustorial cells, similar in origin and possessing large and intricately lobed nuclei, have been reported for other aroids, but the number found in different species varies from one to eight.



FIGS. 41–49.—Fig. 41, endosperm dissected from ovule, with haustorial cell intact. Fig. 42, section of nucleus of haustorial cell. Fig. 43, longisection of maturing ovule in plane of funiculus. Figs. 44–49, development of embryo (*N*, nucellar cap).

The second nuclear division in the endosperm, that is, the division of the nucleus of the micropylar daughter cell, is also accompanied by cytokinesis (figs. 39, 40); hence development of the endosperm is cellular. The occurrence of cellular endosperm has been suggested or reported several times for aroids (**23, 29, 30**). Usually the reports are uncertain or the necessary sequence of stages has not been

obtained. On the other hand, the reports indicate that if the endosperm (especially the micropylar portion) is not cellular from the start, the non-cellular condition is of brief duration (**1, 25**).

The third division in the endosperm was not observed. Soon walls, perpendicular to those first formed and parallel to the long axis of the ovule, appear in the chalazal region of the cellular endosperm. Eventually the micropylar endosperm cells also undergo divisions in this plane.

In the development of the ovule after fertilization, the haustorial cell at first enlarges more rapidly than the cellular endosperm, especially in a direction perpendicular to the long axis of the ovule. Consequently the products of the megagametophyte (and the entire ovule) assume, as a whole, a pyriform shape, the micropylar end being narrower (fig. 43). In subsequent development of the ovule, the haustorial cell, after attaining relatively great dimensions, ceases to enlarge; it is overtaken and finally surpassed in cross-sectional area, as well as in longitudinal extent, by the cellular endosperm. By the time the embryo sporophyte becomes fairly conspicuous the form of the maturing seed is again pyriform, but this time the chalazal region housing the haustorial cell is the narrower. In the ripe seed the micropylar portion containing the large embryo is by far the more conspicuous; the haustorial cell with its surrounding coat of parent sporophytic tissue becomes a mere withered protuberance of the chalazal region.

Development of embryo

When the endosperm is in the 2- or 3-cell stage, the oospore nucleus divides and a wall perpendicular to the longitudinal axis of the ovule is formed (fig. 40). The micropylar cell is the larger, and with the possible exception of one preparation was not observed to undergo further nuclear or cellular divisions (figs. 40, 44, 45, 46, 47, 48, *S*). It becomes the one-celled suspensor, and although relatively large attains no striking dimensions or differentiation. The smaller distal cell gives rise to the embryo proper, and next divides by a wall perpendicular to the first (fig. 44).

A review of studies on aroids reveals that while the suspensor does not become conspicuous, its origin and the fate of the micropylar cell of the 2-celled proembryo vary in different species. *Pistia* (**20**) has no suspensor; in *Arum orientale* and *A. maculatum* (**20**) the suspensor arises from the micropylar cell of the 2-celled proembryo; in *Acorus* (**1**) and *Antherurus* (**17**) the micropylar cell divides by a transverse wall; in *Calla* (**23**) and *Arisaema* (**26**) cellular suspensors arise from the micropylar cell.

The first and second cell walls to be formed in the embryo are in some cases parallel to each other and perpendicular to the long axis of the ovule, for example, in *Aglaonema* (**2**) and others. In *Peltandra*, *Arisaema* (**26**), and *Spathicarpa sagit-*

taefolia (3) the second wall in the proembryo is perpendicular to the first and parallel to the long axis of the ovule. The immediately succeeding divisions were not seen, but the 7-cell stage (fig. 45) indicates that the next walls formed are parallel to the first and hence perpendicular to the second. Figure 46 is a longitudinal section of the 10-cell stage.

The embryo proper now proceeds to form a globular to ovoid body (fig. 47). Later a groove appears on one side of the embryo and separates the terminal cotyledon (fig. 48*CO*) from the lateral plumule primordium (fig. 48*P;* dotted line is outline of embryo in region of primary root, *PR*). Except in the region separating the plumule from the cotyledon, the surface of the latter is evenly continuous with the rest of the embryo at this as well as at later stages of embryonic development, for the radicle does not form a distinct protuberance. Initiation of the primary root begins shortly after the cotyledon and plumule primordia have been differentiated.

While the radicle seems to undergo an abortive development, the terminal cotyledon enlarges so rapidly and extensively that the plumule comes to lie roughly at the micropylar end of the embryo as a whole. The growing point of the plumule always points laterally, is usually distinct; and as the cotyledon enlarges, gives rise to the first cauline foliar organ on its micropylar side (fig. 49, *2*). The next leaf arises on the chalazal side (fig. 49, *1*). At maturity the embryo possesses a relatively large plumule with six or seven cauline leaf rudiments and several rudimentary adventive roots.

In the late summer and fall the lower parts of the spathes around the ripening fruits disintegrate, together with the remaining axial part of the spadix. Since the released fruits are buoyant and the marshes occasionally flooded, they were observed dispersed by flowing water in Maryland.

Summary

1. The subterranean vertical rhizome of *Peltandra virginica* is built up sympodially from branches arising in the axils of the penultimate leaves of continuation shoots of successively higher rank. Each continuation shoot, as well as the primary axis, terminates in a spadix. A second spadix arises in the axil of the ultimate leaf.

2. Usually vegetative buds, which sometimes result in vegetative multiplication of the plant, arise in the axils of only the antepenultimate leaves.

3. There is a tendency to limit the number of foliage leaves formed on a continuation shoot. The minimum number was three.

4. Leaves and inflorescences appear to be initiated about 20 months before they actually emerge from the terminal bud.

5. Development of the staminate flowers differs from that of the pistillate in that the latter alone show a distinct segmentation of the floral primordia.

6. A "bouquet" stage was found in early meiosis. The haploid number of chromosomes was 56.

7. Periplasmodium formation was found in the microsporangium, and the pollen is 3-nucleate before it is shed. Evidence for the occurrence of cross-pollination was found. "Double" fertilization occurs.

8. The endosperm is cellular from the start; the large haustorial cell in the maturing ovule is the chalazal daughter cell formed upon division of the endosperm cell.

9. The embryo contains a large, well-developed plumule and a small, poorly-developed primary root.

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2707 PENNSYLVANIA AVENUE
BALTIMORE, MARYLAND

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