MORPHOLOGICAL AND CYTOLOGICAL STUDIES OF CALLA PALUSTRIS

MARGARET G. DUDLEY

(WITH PLATES IV, V, AND TEXT FIGURES)

Introduction

Although *Calla palustris* L., the wild calla lily or water arum, has received considerable attention from systematists, and has been of interest to cytologists, certain morphological and cytological features have not yet been accorded adequate treatment.

BUCHENAU (3) reported CASPARY as citing 272 cases of *Calla* as possessing two, three, or even four spathes on a single spadix, a fact noted also by HALSTED in 1874, and verified in connection with the preparation of this paper. KOSCHEWNIKOFF (12), writing on the development of the flowers of the Araceae, included a description of the inflorescence of *Calla palustris*. His statements have been verified, except those concerning a second type of placenta found in the lower flowers only.

ENGLER (5) monographed the Aroideae and, in a short paragraph on *Calla palustris* (6), stated that it is proterogynous, that the stamens dehisce sporadically after the stigmas have nearly all withered, and that the plant has therefore to rely principally on cross pollination (by means of insects). Later ENGLER and PRANTL (7) classified *C. palustris* as a close relative of *Lysichiton*, *Symplocarpus*, and *Orontium*. The validity of this arrangement will be discussed in a subsequent section. KRAUSE (13) repeated the substance of LIERAU'S (14) description of the root of *Calla*, amplifying it somewhat.

ARBER (1) traced (in the Araceae) the "course of differentiation from the family type to the specific type," and made several scattered references to *C. palustris*, with a number of figures illustrating the vascular bundles, the circles of adventitious roots, the ligular leaf sheath, and the spathe. METOLITZKY (16) described and figured the seed of *C. palustris*.

JÜSSEN (11) discussed the haploid generation of the Araceae, devoting considerable space to *C. palustris* and to *Symplocarpus*, but unfortunately omitted *Orontium* and *Lysichiton*, the other two genera of the Calloideae. The only point in which my observations do not agree with those of JÜSSEN is that the microspores show, in a number of cases, division of the generative nucleus while within the anther; they are therefore not binucleate as JÜSSEN has described them.

MARIE-VICTORIN (15) gave an account of *Calla palustris*, with a sketch of the flowering shoot, in which there are several errors: The filaments are much too slender, at least for the species as it occurs in Minnesota. The leaf venation is not correctly drawn, thus giving the impression that the "midrib" persists to the apex of the leaf. The inflorescence arises laterally, instead of being terminal, and the spathe has the appearance of encircling the spadix, which it does not do. The second leaf has no sheath, so that the peduncle apparently arises from the axil of the first leaf.

ERTL (8) discussed the development of leaf venation of the Araceae, including that of *Calla*, but the information contained in his publication has not been checked by the writer.

Material and methods

All the material was obtained in the state of Minnesota, from Itasca State Park, Cedar Bog in northern Anoka County, and from Grand Marais on Lake Superior, and consisted of spadices, rhizomes, and mature seeds. The spadices were fixed as soon as possible in either Navashin's or Carnoy's fluid, the latter solution being used for the stages which were young enough to admit of the possibility of finding reduction division in the pollen mother cells. The rhizomes, collected in late October, were covered with damp sphagnum and left in the open until thoroughly frozen (two–six weeks). They were then thawed gradually, planted in peat, and transferred to the greenhouse, where they began to grow almost immediately, blooming six weeks later, after producing three or four leaves. Some of the fruits, gathered in August, were placed in damp sphagnum, where the pericarps and mucilage disintegrated, setting free the seeds, which were then thoroughly dried before planting. Others were allowed to dry *in situ* and stored until needed.

All the material, after being dehydrated, was transferred to chloroform and imbedded in paraffin. The celloidin method was employed in the preparation of the rhizomes, because of their spongy nature. The seeds were soaked in weak hydrofluoric acid for three or four weeks, then imbedded according to the butyl alcohol method.

The sections of the root tips were cut 6–7 μ; those of the spadices 12 μ; those of the seed, seedling, and mature embryo 15 μ; and those of the rhizome 20–30 μ. Some of the rhizomes were stained with Delafield's haematoxylin, but safranin and fast green were used for the majority of them, and also for the seeds, seedlings, and growing points. Heidenhain's iron-alum haematoxylin was used for the embryos, crystal violet for the root tip sections, and iron-alum haematoxylin and crystal violet for the pollen mother cells.

Investigation

General description

Calla palustris is found in bogs and swamps of the northern hemisphere (**13**), occurring locally in moderate abundance in Newfoundland, eastern Canada, the Maritimes, Manitoba, and northern Saskatchewan, and sporadically in Alberta and British Columbia (only one record from British Columbia[1]). In the United States it is found as far west as Minnesota and as far south as Virginia. It is fairly abundant in central and northern Minnesota, except in the western portions, and blooms freely when not too shaded. The plant spreads over the mud by means of a branching sympodial rhizome, green in color, bearing circles of adventitious roots at the nodes. A bud is formed at each node, but very few of these develop into shoots. The leaves, which are confined to the current year's growth (the last few nodes), are, like the buds, alternate in arrangement. The inflorescence, as in other Aroids, is borne on the end of a terminal two-leaved shoot. A branch shoot arises in the axil of the penultimate leaf of this flowering shoot, and grows rapidly, producing a number of leaves (six–twelve normally) the first season. After remaining dormant during the winter, this rhizome bears two more leaves and an inflorescence, which terminates its growth. The plant

[1] Henry J. K., Flora of Southern British Columbia and Vancouver Island.

axis is then continued by another shoot, arising, like its predecessor, in the axil of the penultimate leaf of the flowering shoot (fig. 1). The rhizome, since it is usually submerged, is very spongy. Its large lacunae are filled with mucilage, and often contain raphide cells, which are much larger than those composing the lacunar walls. The cells containing the raphides are usually attached by one end to the small ones bordering the lacunae, and project therefrom into the mucilage-filled canals (fig. 8). The walls of the lacunae are one cell in thickness. In cross section they are dotted with scattered amphi-

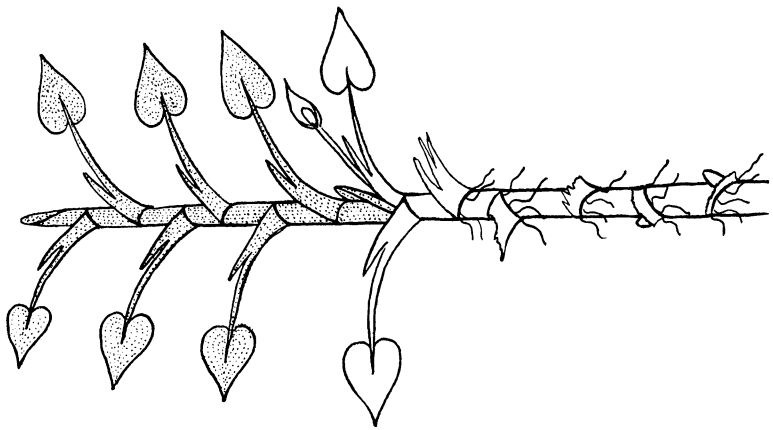


FIG. 1—Diagrammatic representation of sympodium of plant axis; continuation shoot stippled.

vasal vascular bundles, which frequently appear to be composed of two or three smaller bundles grouped together. The tracheae are few and very weakly lignified. Scattered laticiferous ducts, in connection with the vascular bundles, are evident in stained preparations (figs. 3, 8). Some of these vascular bundles form a ring at each node, outside which, in the young shoot, may be found a circle of adventitious root initials (fig. 9).

The adventitious roots are polyarch, with about seven small protoxylem vessels alternating with the sieve tubes near the periphery of the stele, and an approximately equal number of large metaxylem elements surrounding the small pith. The inner portion of the cortex is composed of radiating rows of regular, more or less

octagonal cells separated by large intercellular spaces, which are lacking between the smaller cells of the outer four or five layers.

The large, thin, cordate leaves have long spongy petioles concave on the adaxial surface. They have a divergence of one-half, and their vernation is convolute, successive leaves being rolled alternately right and left. The numerous well marked lateral veins diverge, one at a time, from the "midrib" and curve outward, parallel to one another, anastomosing just before reaching the margin of the leaf. In consequence the "midrib" gradually becomes narrower and finally disappears, its total length being about two-thirds that of the leaf blade. Each leaf possesses a ligular sheath (convolute in the bud), united with the petiole for approximately half its length and encircling the younger leaves (figs. 2, 4). The line of divergence from the rhizome being in the form of a spiral, with the ends overlapping, the nodes are in consequence not quite at right angles to the long axis of the rhizome, but are slightly slanting, the higher side of the node being alternately right and left (fig. 1).

The inflorescence appears in May (in Minnesota), when the plant has three or four leaves, two on the flowering shoot and one or two on the branch which is to continue the growth of the rhizome. As a rule there is not more than one inflorescence per year from each growing point, but there may be more than one spathe to a spadix (3).

Morphology and development of pollen grains

The anthers, which are very short in proportion to the filaments, are four-chambered and open extrorsely. The anther wall consists of three layers of cells: an epidermal, a palisade, and a tapetal layer (fig. 10), the first two of which are entirely normal in appearance and behavior.

The pollen mother cells undergo meiotic division while the archesporial cell is present in the ovule. They are large, easily stainable, and possess a conspicuous nucleolus. Previous to division the chromatin material of each nucleus becomes aggregated into a small, deeply staining sphere in close proximity to the nucleolus and very similar to it in appearance (11).

The meiotic divisions (figs. 11, 15) of the successive type take

place rapidly, and result in a considerable number of ellipsoidal pollen grains, so crowded as to be almost indistinguishable. These pollen grains are easily stainable throughout their development up to the point when they finally become separated from one another. They then apparently increase in size, without any appreciable increase of their plasma content, until the nucleus undergoes division. The pollen grain, while still uninucleate, possesses a large central vacuole, and its nucleus is often found near one end, imbedded in the peripheral layer of cytoplasm. Mitosis apparently takes place rapidly in this nucleus, since it was observed but rarely. The nuclei resulting therefrom, although at first identical, later become unequal in size, and are arranged in a line along the longitudinal axis of the pollen grain. Although JÜSSEN states that in *Calla*, division of the generative nucleus does not take place while the pollen grain is still in the anther, 2.5 per cent of the pollen examined by me was discovered to be trinucleate (fig. 16). As these pollen grains were not yet ready to be discharged, the percentage of trinucleate ones would doubtless be much higher at the time of dehiscence.

According to JÜSSEN, *Symplocarpus foetidus* has binucleate pollen, while that of *Zantedeschia aethiopica* and *Z. albomaculata* is trinucleate. In this respect, at least, no close affinity between *Calla* and *Symplocarpus* seems to be indicated.

The haploid chromosome number in *Calla*, as determined from the meiotic divisions (metaphase I, end view, and very late diakinesis) in the pollen mother cells is 18 (figs. 11, 15). The diploid number, as obtained from sections of the root tips, is 36 (fig. 13). Chromosome counts have not yet been recorded for any considerable number of the Araceae, but the basic number in the family appears to be 8 (**9**), *Spathiphyllum patinii* and *Acorus calamus* (unpublished data) being the only Aroids thus far discovered to have 9 as their haploid number. The data concerning the chromosome number in *Peltandra undulata* have apparently been misinterpreted. The haploid number is given by GAISER (**9**) as 22, on the authority of DUGGAR (**4**), but was apparently inferred from his writings to be the haploid number, since it is clearly shown by his illustrations to be the diploid number, if any. DUGGAR (**4**) states that there are about 22 chromosomes, referring to the first meiotic division, but neglects to state

whether the chromosomes occurred in *Symplocarpus* or *Peltandra*, or in both! The chromosome number for *Zantedeschia aethiopica*, as determined by OVERTON (18), is given as 16, while MICHELL (17) calculated it to be 12. OVERTON worked with greenhouse plants, however, and MICHELL with the native South African ones, which may account for the discrepancy between their results. It is obvious that much additional investigation is needed before any reliable conclusions can be drawn in regard to the basic chromosome number of the family, and as to what extent this criterion can be used as an indication of relationship and phylogeny.

In figure 16, illustrating the trinucleate pollen grain, may also be seen a smaller spherical body, which is one of the nuclei originally belonging to the tapetal layer already mentioned. The cells of this layer soon become dissociated, lose their walls, and form the periplasmodium typical of the Araceae (11), of which the nuclei only are still in evidence by the time the nucleus of the pollen grain is undergoing division. As may be seen from figure 16, the nuclei of the periplasmodium are slightly smaller than those of the pollen grains among which they are scattered, and contain a number of conspicuous chromatin granules, in addition to a nucleolus.

The mature pollen grains, in their natural condition, appear trapezoidal, with two lengthwise contraction grooves. When expanded by lactic acid and slightly stained with aceto-carmine, they are ellipsoidal and show no grooves. The exine is thick, subpunctate, and possesses three pores, one at the end of the grain slightly to one side and two near the other end, equidistant from its middle point and also from the first mentioned pore.

SEED AND EMBRYO

The seeds, of which two to fourteen are imbedded in the mucilage of each red berry-like fruit, develop from anatropous ovules[2] which bend outward from a raised circular placenta (fig. 7).

Double ovules sometimes occur, fused throughout their length (fig. 5), which develop into seeds containing normal embryos.

[2] The origin and development of the embryo and ovule have been omitted from this discussion, as a full description of the embryogeny of *Calla palustris* will be included in a later publication. Figures 14 and 19 illustrate typical stages in the development of the embryo.

The mature seed is brown, 3.7×1.6 mm. on the average, and pitted in regular horizontal rows. There are a number of dark spongy blotches at the chalazal end, possibly facilitating imbibition of water by the germinating seed (fig. 20). The pits are depressions in the epidermis, underlain by large subepidermal lacunae. The one-layered epidermis is composed of oblong palisade-like cells. The rest of the seed coat (developed from the outer integument) is formed

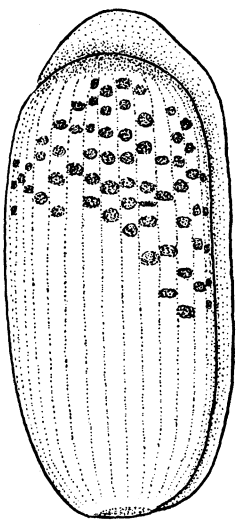


FIG. 20

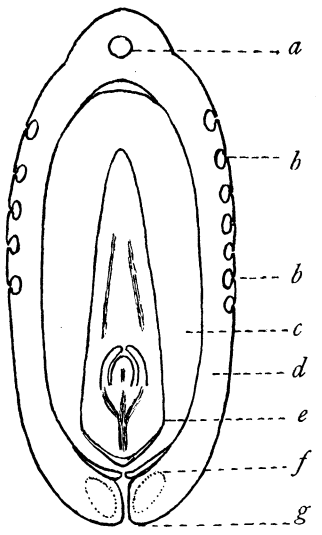


FIG. 21

FIGS. 20, 21.—Fig. 20, external view of seed showing raphe. Fig. 21, diagram of longitudinal section of seed showing embryo (*a*, vascular bundle; *b*, subepidermal lacunae; *c*, endosperm; *d*, seed coats; *e*, embryo; *f*, circum-micropylar canal; *g*, micropyle).

of about twenty rows of small isodiametric cells with intercellular spaces between them. The micropyle is practically closed, and a circular canal is plainly to be seen around it (fig. 21). The raphe possesses a large vascular bundle, and forms a ridge approximately 0.4 mm. wide, extending from the funicle to the chalaza, where it bends over and downward, expanding into a mass of tissue shaped like an inverted funnel. The abundant endosperm, which completely surrounds the embryo except at the micropylar end, is composed of starch-filled polygonal cells having no intercellular spaces. When

the hard testa is removed, the outer layer of the endosperm appears pale yellow and shiny, owing to the adherence of the crushed inner integument.

The mature embryo is green, lanceolate in shape (figs. 17, 18, 21), 2.5 mm. long and 0.6 mm. in its greatest width, central in position at the micropylar end of the seed, and often still attached to the suspensor (fig. 19).

The cotyledon, which forms the major part of the embryo, is thin at the base and sheathes the plumule. At this stage there are three longitudinal veins present which gradually converge, uniting a little below the solid apex of the cotyledon. The lateral veins sometimes unite before coalescing with the midrib, while in other cases they anastomose with the latter independently of one another.

The radicle is short and blunt, with a large central vascular strand, which divides near the apex of the hypocotyl (figs. 17, 21). Branches extend to the cotyledon, and to the leaves of the plumule, of which two are visible at this stage. The first leaf is inserted opposite the cotyledon, is curled inward at the apex over the second leaf, and usually possesses three longitudinal veins, similarly to the cotyledon, although cases were found in which there were four of these veins, two on one side of the midrib and one on the other. The second leaf is essentially similar to the first, and inserted not quite opposite it. The vascular supply to the first adventitious root leaves the main vascular strand immediately below the point where the latter divides into four branches, all of which arise at almost the same level. One of these branches supplies the midrib of the cotyledon, another all the veins of the first leaf, while the remaining two each supply one lateral vein of the cotyledon and part of the veins of the second leaf. Owing to the shortness, almost non-existence, of a hypocotylar region in the embryo, it is extremely difficult to distinguish with certainty the point of origin of the veins.

GERMINATION OF SEED

The seeds were planted on damp sphagnum in petri dishes after having been soaked overnight. Those planted on May 5 germinated on May 11. Others planted January 17 (five months after ripening) germinated within four days. Seeds gathered in August germinated

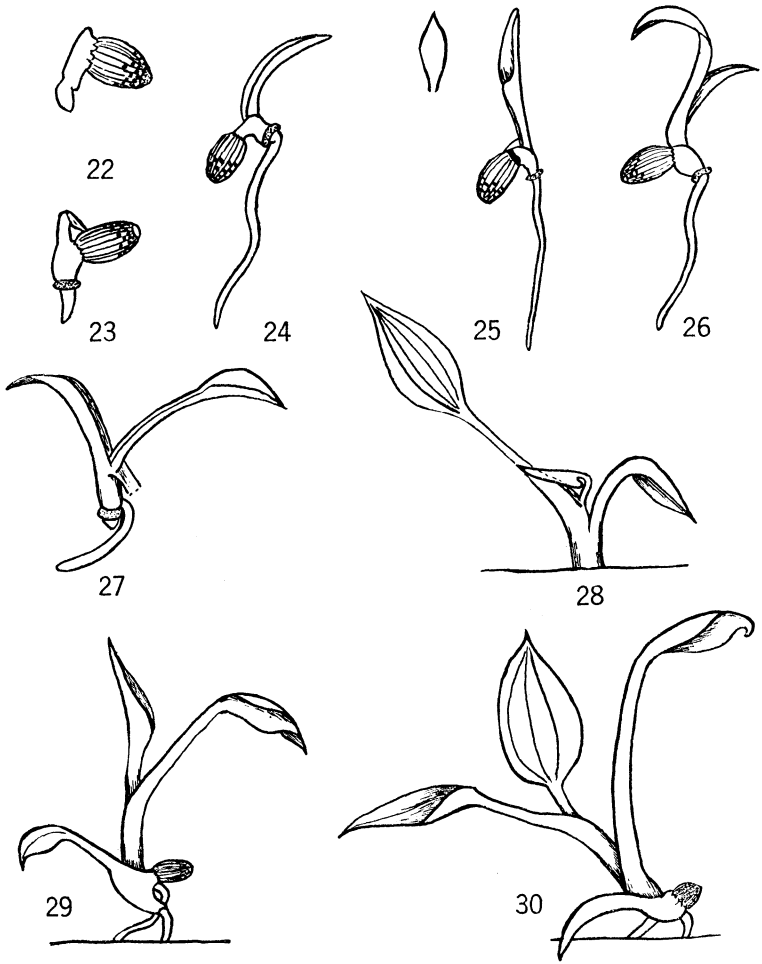
readily in October, after having been thoroughly dried, but would not germinate while still wet.

The radicle, which emerges through the annular canal, is green, massive, and blunt-pointed. It grows rapidly and turns downward, and the plumule is forced out of the seed by the extension of the base of the cotyledon (fig. 23). There is a spongy ringlike protuberance on the radicle, as shown in figures 23–27. The chief elongation of the embryo occurs above this structure, and is evidently due to growth in the basal part of the cotyledon, since in the several sections examined the upper portion still occupied its original position. Germination is evidently according to type B, as defined by BOYD (2), in which germination is hypogeal and there is a shallow collar edging the cotyledonary slit (figs. 24, 25). The three vascular strands of the cotyledon do not traverse this collar, but emerge through the "stalk" of the cotyledon close together while passing down the cotyledonary sheath, then converge to unite with the central vascular strand in the hypocotyl. The vascular supply to each petiole usually consists of three strands, which diverge, as do the cotyledonary ones, in cyclic order from the central mass of vascular tissue.

The leaves of the young seedling are similar in shape to those of the mature plant, but lack the ligular sheath. They have a divergence of one-half, their vernation is convolute, and each has a sheathing base which surrounds the younger leaves. The first leaf, which is usually small and not very well differentiated, emerges from the "collar" previously mentioned with its midrib on the side farther from the seed. Successive leaves are larger and more "*Calla*-like." Unfortunately none of the seedlings used survived beyond the four-leaved stage, so it is impossible to describe their subsequent growth (figs. 22–30).

In about half the cases studied the primary root did not develop at all, but the seedling derived its nourishment through an adventitious root, emerging from the central cylinder at a point immediately below the cotyledonary branches (fig. 12). In external view this root had its origin slightly above the spongy ring of tissue already mentioned, and marking the upper limit of the root sheath. In cases where the primary root grew and functioned, it broke through this sheath and lengthened rapidly. Unlike that of the seedling of

Zantedeschia aethiopica (3), the primary root of *Calla* bears no root hairs, but is itself short-lived, its place being taken by adventitious roots. This feature, according to BOYD, is an indication of "ad-



FIGS. 22–30.—Fig. 22, semi-diagrammatic drawing of seedling 2 days old; fig. 23, 4 days old; fig. 24, 7 days old; fig. 25, 8 days old; fig. 26, 11 days old; fig. 27, 13 days old (cotyledon broken off); fig. 28, 21 days old; fig. 29, 20 days old; fig. 30, 33 days old (same plant as no. 11).

vanced morphology" of the seedling; on the other hand, a simple tubular cotyledon, such as that possessed by *Calla*, is to be regarded

as a "primitive characteristic." *Zantedeschia* (*Richardia*) *elliottiana* is the only rhizotomous Aroid discussed by BOYD, and as that is done in a rather sketchy manner, one is not able to make comparisons. The germination of *Zantedeschia* (*Richardia*) *aethiopica*, as described by BUCHENAU, and also as attempted by the writer, seems to be very similar to that of *Calla palustris*, and if carried through might prove to be another link in the chain of evidence binding *Calla* and *Zantedeschia* together.

Systematic position of Calla

One of the more revolutionary changes in the classification of flowering plants, as set forth by HUTCHINSON (10), concerns the Araceae, and therefore a short résumé of the history of the classification of the Araceae is here given.

BENTHAM and HOOKER (1862–1883) place the Araceae together with the Pandanaceae, Cyclanthaceae, Typhaceae, and Lemnaceae, in series 5 (Nudiflorae), while the Liliaceae are in series 3 (Coronarieae). In ENGLER and PRANTL (1924 edition) the Araceae and Lemnaceae form the 7th "Reihe" (Spathiflorae), while the Liliaceae are placed in the 9th. LOTSY (1911) derives the Araceae, together with the "Spadiciflorae" (Lemnaceae, Cyclanthaceae, Palmae, Pandanaceae, Sparganiaceae, Typhaceae), from the Piperales, and the Liliaceae from the hypothetical "*Pro-ranales*." BESSEY (1915) places the Araceae in the Strobiloideae (ovary superior) and apparently considers them to be derived after the Liliaceae, although this point is not clear. WETTSTEIN (1924) unites the Araceae with the Palmae and the Cyclanthaceae in order 8 (Spadiciflorae), while the Liliaceae are in order 2 (Liliflorae). MEZ (1926) in his sero-diagnostic chart places the allied Araceae and Lemnaceae on the same branch as the Palmae and Cyclanthaceae, but the Liliaceae alone on another branch of the monocotyledons, and further from the main stem. JÜSSEN (1928), after reviewing several systems of classification, agrees with ENGLER in considering the Araceae and Lemnaceae as forming an independent order, and also cites several points of similarity between the haploid generations of the Araceae and the Helobiae (trinucleate pollen grains, periplasmodium, endosperm formation), evidently considering the Liliaceae to be unrelated to either.

HUTCHINSON (1934) places the order Arales (Araceae and Lemnaceae) in the subphylum Corolliferae (with a corolla-like perianth), and derives them directly from the Liliaceae through the tribe Aspidistreae. The Helobiae are all included in the subphylum Calyciferae (perianth biseriate). If this arrangement be correct, the cytological similarities observed by JÜSSEN must be due to parallelism.

HUTCHINSON places *Calla palustris* in the tribe Calleae (number 8 of the series of 17 tribes constituting the family), and it is therefore considered to be more highly evolved than *Acorus*, *Lysichiton*, *Orontium*, and *Symplocarpus* but less so than *Zantedeschia*, *Aglaonema*, *Arum*, and *Arisaema*. According to HUTCHINSON, the more primitive Araceae are those with a poorly developed or leaflike spathe, and hermaphrodite flowers possessing a perianth. He states (**10**, p. 119), "The more highly evolved Araceae would have unisexual flowers, an increasingly protective spathe, and owing to reduction, some part of the spadix would become barren." An examination of *Calla* readily shows that it is intermediate between these two extremes, and therefore correctly placed with regard to the principles just enunciated.

ENGLER (**6**, p. 122) likewise places *Calla palustris* in the tribe Calleae, but unites it with the tribe Symplocarpeae (*Lysichiton*, *Symplocarpus*, and *Orontium*) into the subfamily Calloideae, one of whose characteristics is said to be the possession of a creeping underground rhizome [elaborated upon by KRAUSE (**13**) and which unfortunately, as shown by ROSENDAHL, is not present in either *Symplocarpus* or *Lysichiton* (**19**)]. Another characteristic stressed by ENGLER is the presence of "simple or unbranched latex ducts in connection with the phloem of the vascular bundles" (**19**, p. 138). This characteristic, however, is not common to the four genera forming the Calloideae, but occurs in *Calla* and *Orontium* only, thus casting further doubt upon the validity of ENGLER'S disposition of these genera.

HUTCHINSON distributed the Calloideae of ENGLER among the three tribes Orontieae (*Lysichiton* and *Orontium*), Dracontieae (*Symplocarpus*, *Dracontium*, *Echidnium*, and *Dracontioides*), and Calleae (*Calla*), the last being the most advanced and distinguished

from the other two by the absence of a perianth (a characteristic shared by the Monstereae). The Dracontieae are separated from the Orontieae by reason of the possession of a well differentiated spathe (10).

KRAUSE also distinguishes *Calla* from the other three genera (Symplocarpeae) through the absence of a perianth, coupling with this characteristic the presence of endosperm and parallel lateral veins.

A comparison of the four genera seems to show more differences than similarities, and would therefore lead to the conclusion that they cannot be combined into one subfamily, and that HUTCHINSON'S arrangement (in the order of evolutionary progress) is the most satisfactory one yet proposed.

Summary

1. *Calla palustris* spreads over the ground by means of an alternately branching sympodial rhizome, which bears numerous adventitious roots at the nodes.

2. Each growing point is active for two seasons, producing several leaves the first year and two more the next spring, followed by an inflorescence, which terminates the growth of that branch of the rhizome.

3. Each principal plant axis is continued by the production of a branch in the axis of the penultimate leaf of the flowering rhizome.

4. The leaves are thin, bright green, and cordate, with ligulate sheathes. Their vernation is convolute, and they are rolled to right and left alternately.

5. The ovary is unilocular, and contains from two to fourteen anatropous ovules. Double ovules, fused longitudinally, sometimes occur.

6. A periplasmodium is formed in the anther. The pollen grains are apparently trinucleate before dehiscence occurs.

7. The seed is albuminous, and possesses a hard seed coat. The embryo is central, and germinates without a period of rest if the seed has been thoroughly dried.

8. Germination is hypogeal. The base of the cotyledon elongates, forcing the radicle and plumule down into the substratum. The

cotyledonary slit is edged by a collar, through which the plumule emerges. The vascular strands of the cotyledon are three in number, and do not traverse the collar.

9. The primary root sometimes develops, but more often does not, when its place is taken by an adventitious one. This adventitious root is very noticeable, even before germination.

10. The leaves of the young seedling have no ligular sheath, but resemble adult leaves in all other particulars.

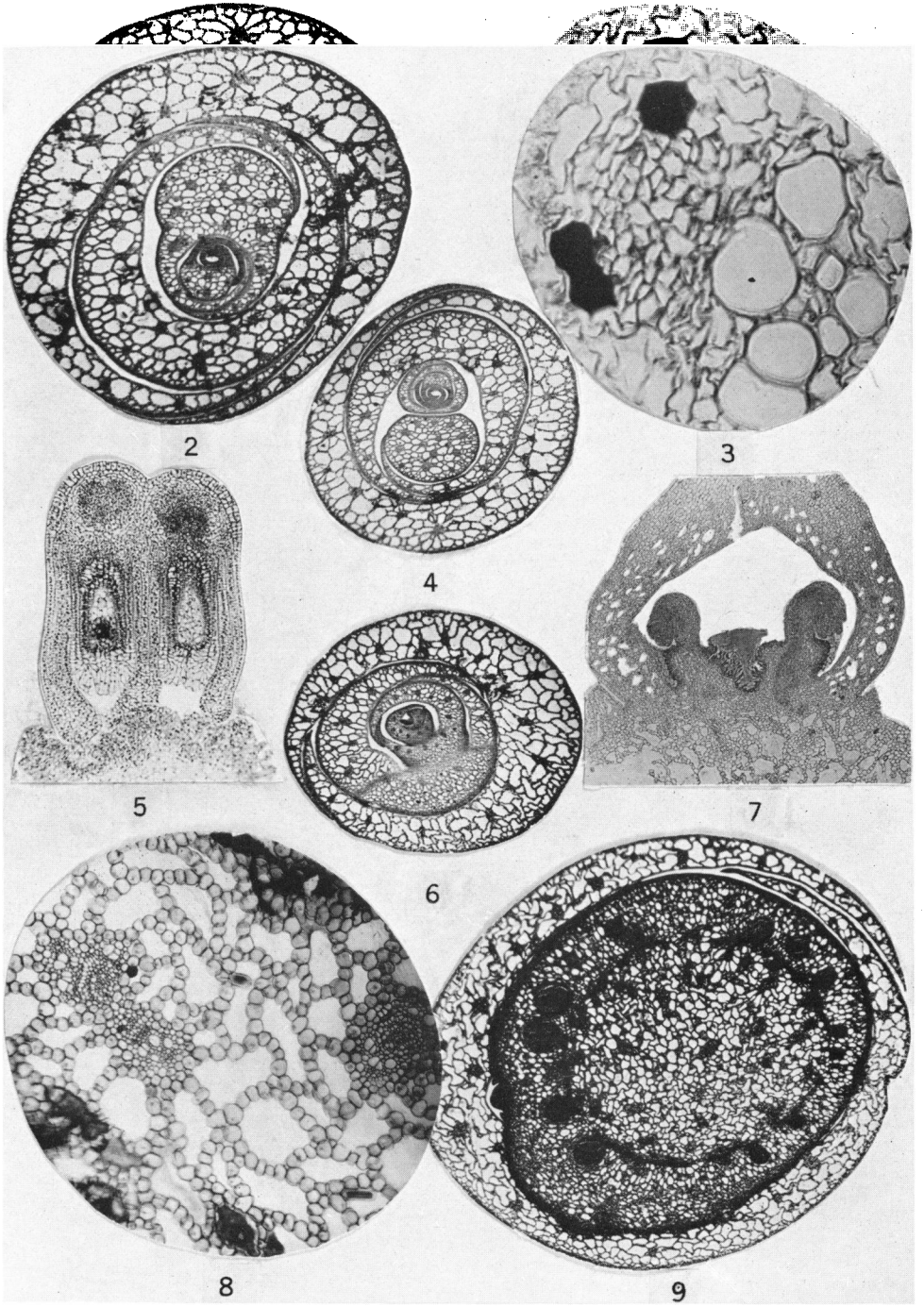
11. The haploid chromosome number, as determined from pollen mother cells at metaphase I, is 18. Metaphase plates of root tips show 36 chromosomes.

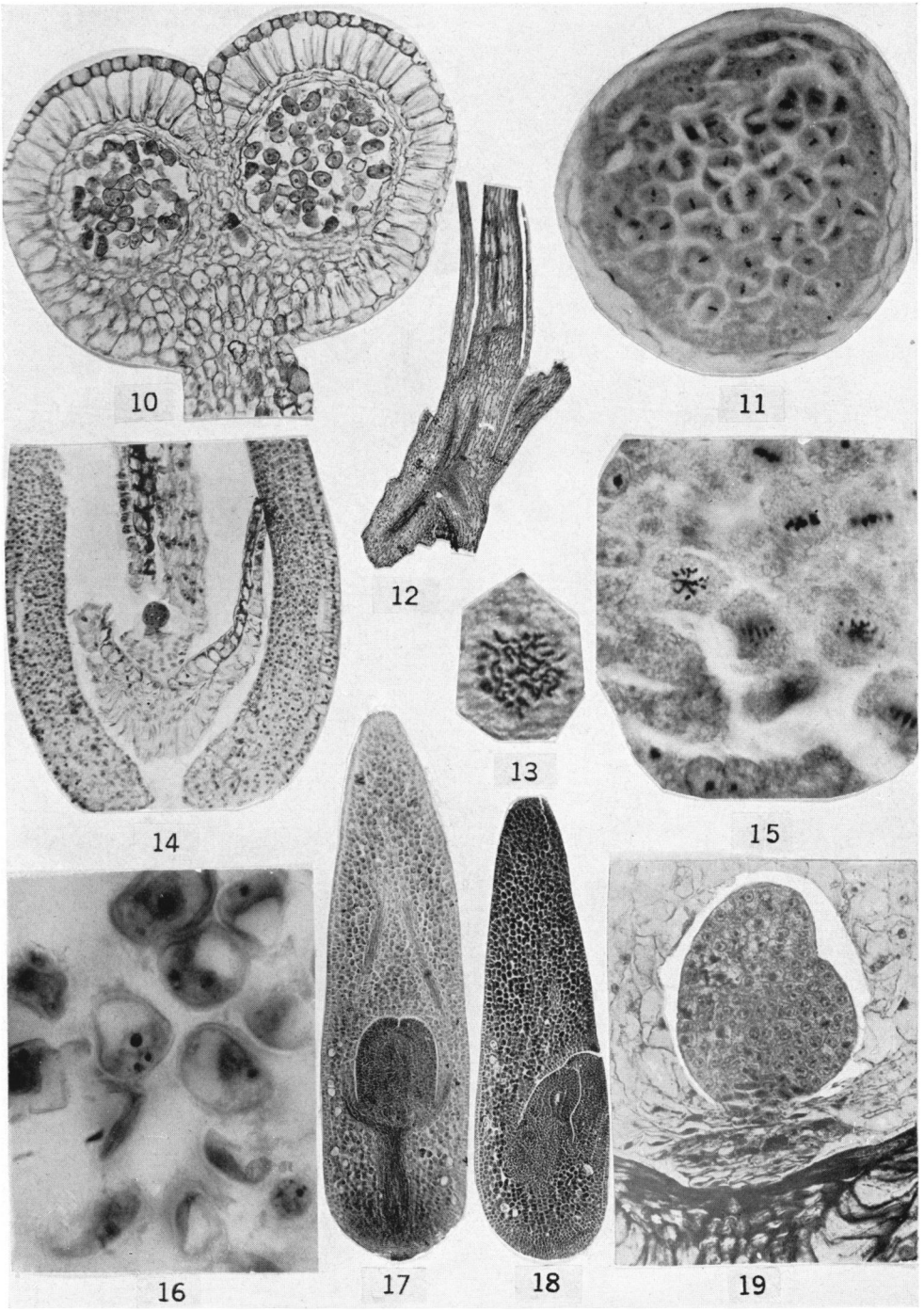
The writer wishes to thank Dr. C. O. ROSENDAHL and Dr. F. K. BUTTERS, of the University of Minnesota, for their continued interest and stimulating advice, and Mr. A. O. DAHL for his technical assistance.

DEPARTMENT OF BOTANY
UNIVERSITY OF MANITOBA
WINNIPEG, CANADA

LITERATURE CITED

1. ARBER, AGNES, Monocotyledons. Cambridge Botanical Handbooks. 1925.
2. BOYD, LUCY, Monocotylous seedlings: morphological studies in the post-seminal development of the embryo. Trans. Proc. Bot. Soc. Edinburgh **31**:5–224. 1932.
3. BUCHENAU, FRANZ, Über das Verkommen von Zwei Hüllblättern am Kolben und die Keimung von *Richardia aethiopica* (L.) Buchenau. 1866.
4. DUGGAR, B. M., Studies in the development of the pollen grain in *Symplocarpus foetida* and *Peltandra undulata*. BOT. GAZ. **29**:81–97. 1900.
5. ENGLER, A., in DECANDOLLE, Monographiae Phanerogamarum. Vol. II. Paresus. 1879.
6. ———, Beiträge zur Kenntniss der Araceae. IV. Bot. Jahrb. **4**:341–352. 1883.
7. ENGLER, A., and PRANTL, K., Araceae. Die natürlichen Pflanzenfamilien. II, **3**:102–153. 1889.
8. ERTL, P. OTTMAR, Vergl. Untersuchungen über die Entwicklung der Blattnervatur der Araceen. Flora **126**:116–148. 1932.
9. GAISER, L., Chromosome numbers in angiosperms. II. Bibl. Genet. **6**:381–384. 1930.
10. HUTCHINSON, J., Families of flowering plants. Vol. II. Monocotyledons. 1934.


2
3
4
5
6
7
8
9



DUDLEY on CALLA PALUSTRIS

11. JÜSSEN, F. J., Die Haploid-generation der Araceen und der Verwertung für das System. Bot. Jahrb. (ENGLER) **62**:155–283. 1928.
12. KOSCHEWNIKOFF, D. A., Zur Entwicklungsgeschichte der Araceenblüthe. Bull. Soc. Nat. Moscow **52**:296–299. 1877.
13. KRAUSE, K., Araceae-Calloideae. Das Pflanzenreich. **23B**:140–155. 1908.
14. LIERAU, MAX, Beiträge zur Kenntniss der Wurzeln der Araceen. Wilhelm Engelmann, Leipzig. 1887.
15. MARIE-VICTORIN, FR., Les Spadiciflores du Quebec. Inst. Bot. Univ. Montreal. no. 19. 1931.
16. METOLITZKY, FRITZ, Anatomie der Angiospermen-samen. Handbuch Pflanzen. **12**:66–68. 1926.
17. MICHELL, M. R., The embryo sac of *Richardia africana* Kth. BOT. GAZ. **61**:325–336. 1916.
18. OVERTON, J. B., On the organization of the nuclei in the pollen mother-cells of certain plants, with especial reference to the permanence of the chromosomes. Ann. Bot. **23**:19–61. 1909.
19. ROSENDAHL, C. O., *Symplocarpus* and *Lysichiton*. Minnesota Bot. Studies **2**:137–152. 1911.

EXPLANATION OF PLATES IV, V

PLATE IV

FIG. 2.—Cross section of growing point showing four leaves.

FIG. 3.—Detail of vascular bundle in rhizome showing laticiferous ducts.

FIG. 4.—Cross section of growing point, slightly below level at which fig. 13 was taken.

FIG. 5.—Double ovule, fused longitudinally.

FIG. 6.—Cross section of growing point showing node.

FIG. 7.—Longitudinal section of young ovary showing two ovules.

FIG. 8.—Cross section of rhizome showing vascular bundles, raphides, and mucilage.

FIG. 9.—Cross section of node showing bud in axil of sheathing leaf.

PLATE V

FIG. 10.—Longitudinal section of stamen.

FIG. 11.—Cross section of anther sac showing meiotic division in pollen mother cells.

FIG. 12.—Longitudinal section of 21-day old seedling showing first adventitious root, junction of cotyledon, and vascular supply to cotyledon.

FIG. 13.—Cell of root tip showing metaphase stage of mitotic division.

FIG. 14.—Multicellular proembryo showing nucellar cap.

FIG. 15.—Detail of meiotic division in anther sac.

FIG. 16.—Mature pollen grains showing one trinucleate grain and one of the nuclei of periplasmodium.

FIGS. 17, 18.—Longitudinal sections of mature embryos from ripe seeds.

FIG. 19.—Multicellular proembryo, with suspensor.