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THE DEVELOPMENT OF MAGNOLIA AND LIRIODENDRON, INCLUDING A DISCUSSION OF THE PRIMITIVENESS OF THE MAGNOLIACEAE[1]

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(WITH PLATES I–III)

The recently announced theories of ARBER and PARKIN, especially as developed in their paper "On the origin of angiosperms" (2), make it desirable that more detailed work be done on the Magnoliaceae and related groups. Besides, as the embryo sac of only one species of the Magnoliaceae, *Drimys Winteri* (29), has ever been studied, it seemed probable that an investigation of other genera of this family, from this point of view, might be of value in several ways, but especially in furnishing either positive or negative evidence concerning the primitiveness of this family.

In the present study of *Magnolia virginiana* L. and *Liriodendron Tulipifera* L. two objects have been kept in mind: (1) the determination of the course of development of the sporogenous tissues and of the mature gametophytes, and also the examination of certain points concerning the gross structure and anatomy of these forms; (2) a consideration of the primitiveness of the Magnoliaceae on the basis of the evidence gained by such investigation, and of present prevailing theories respecting the origin of angiosperms.

The collection of material was begun in December of 1910 and was continued at intervals of generally two or three weeks until

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[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, no. 34.

September 1911. Material for the study of *Liriodendron* was obtained at Homewood, the new site of the Johns Hopkins University, and that for *Magnolia* in a swampy region at Glen Burnie, Maryland, a typical habitat for the so-called swamp magnolia. Most satisfactory results were obtained by using a chromacetic solution for fixing, although acetic alcohol worked well also. The principal stains used for sporogenous tissues and young embryo sacs were iron-hematoxylin and orange G; and for older sacs safranin and Delafield's hematoxylin, or for embryos hematoxylin alone.

The writer is greatly indebted to Professor DUNCAN S. JOHNSON, and desires to express thanks for many suggestions and much helpful criticism during the progress of the work.

As the course of development is very similar in *Magnolia* and *Liriodendron*, in the following description attention will be directed mainly to the former, differences between the two species being pointed out where they occur.

The stamens of *Magnolia* and *Liriodendron* have elongated anthers on short filaments, the connectives extending beyond the anthers. The anthers contain four locules, with walls of 3 or 4 layers of cells, and dehisce longitudinally. In *Magnolia* the sporogenous tissue in the stamens is already differentiated early in December (fig. 15), and in *Liriodendron* early in January. Little change occurs in this tissue until March, when the sporogenous cells enlarge considerably and divide. The nuclei of the microspore mother cells are found in synapsis from April 20 to May 1 (fig. 16). The first mitosis in both species usually occurs during the first week in May (fig. 2), and tetrads are developed by the simultaneous method about May 10 (fig. 18).

After the first and second mitosis of the nuclei of the microspore mother cells the number of chromosomes is 19 (figs. 3 and 19). The actual number in the microspore mother cells, or in the vegetative tissues, was not determined, but is much greater than 19; therefore, as the usual heterotypic division occurs in the microspore mother cells, and after this division a smaller number of chromosomes than before is present, there can be little doubt that in microspore formation reduction takes place, and that the x and $2x$ generations are characterized respectively by 19 and 38 chromosomes. Neither STRASBURGER (29) nor ANDREWS (1) determined the exact number of chromosomes in the forms studied by them.

The mature pollen grains are oval in shape, with rather thick walls. In the case of *Magnolia* they are binucleate (fig. 21), while those of *Liriodendron* are two-celled (fig. 4). This condition is found in the anthers before dehiscence occurs, which, in the latter species, is between May 15 and 18, and in the former about May 30.

In early stages of development it is evident that the tapetum arises from the sporogenous tissue (fig. 15), later differing from it especially in size of cells and nuclei (fig. 17). Still later, when tetrads are forming, the tapetum consists of 2 or 3 layers of large, binucleate cells lining the walls of the loculi (fig. 1). Finally, as the pollen grains mature, the tapetum gradually disappears, but there is no evidence of migration of its nuclei among the developing pollen grains (fig. 18). The walls of the loculi consist of 3 or 4 layers of cells. As the anthers mature, the subepidermal layer of cells becomes differentiated into the usual type of cells which are active in dehiscence.

The ovules in both *Magnolia* and *Liriodendron* are marginal in origin and anatropous, but there is considerable difference in the time of initiation of these organs. It occurs in the former as early as the first two weeks in December or earlier, while in the latter not until after the middle of March. Early in April, however, the condition attained is about the same in both, and the two develop at the same rate until the completion of the embryo sac. The first rudiment of the inner integument appears when the megaspore mother cell is well differentiated (April 20), and soon afterward the outer integument is initiated (fig. 5). From the archesporial cell (fig. 22) a tapetal cell is cut off (fig. 23), apparently in both species, and the mother cell soon becomes deeply buried within the nucellus (fig. 24). By two successive divisions of the megaspore mother cell 4 megaspores are formed (figs. 6, 7, 25, 26, 27), the innermost of these in each case being functional, while the others degenerate. By the time the 4 megaspores have developed the innermost one comes to lie very deep within the nucellus (fig. 7).

The development of the embryo sac is normal throughout.

Even in the binucleate condition the sac is considerably elongated (fig. 28); it continues to grow more in length than in breadth; finally it becomes slightly curved and also somewhat enlarged at the ends. The tetranucleate sac is shown in fig. 29. The mature sac is of the ordinary type, containing an egg and two beaked synergids at the micropylar end, three antipodals at the opposite end, and two endosperm nuclei somewhat above the middle (figs. 8, 9, 10, 30).

While fertilization was not observed in either species, there can be little doubt of its occurrence in both. The evidence for this is that when material of a certain age is examined the remains of the pollen tube are invariably found in the micropyle and also within the embryo sac (fig. 31).

In all the sacs of *Magnolia* in which the polar nuclei were found, partial fusion had already occurred (fig. 30). After fusion the endosperm nucleus moves close to the egg apparatus, and then, before division of the (presumably fertilized) egg, the first division of the fusion nucleus takes place. At this division a wall is formed transverse to the long axis of the embryo sac (fig. 31), hence the endosperm is cellular from the start, differing from *Drimys* (**29**) in this respect. Both of the resulting cells participate in the formation of the endosperm, that part of the sac surrounding the egg becoming filled with endosperm much more rapidly than the antipodal end. In early stages the endosperm is quite compact (fig. 32), but later the cells seem to enlarge; finally, in the mature condition, the nucellar tissue disappears completely and an abundant supply of compact endosperm fills the seed.

In the development of the embryo of *Magnolia* the first division is transverse, the second longitudinal to the long axis of the embryo sac (fig. 33). A second longitudinal wall separates the young embryo into octants (fig. 34), and soon thereafter the divisions apparently become quite irregular (fig. 35). There is much difference in the form of different embryos of approximately the same age, some being nearly globular (fig. 35) and others considerably elongated. A well defined suspensor (fig. 36) appears somewhat late and may persist until the embryo is mature. The cotyledons are initiated after the embryo has enlarged considerably.

They appear simultaneously and are independent from the start, there being no evidence of a pseudo-monocotyledonous habit such as occurs in various other members of the Ranales. In the mature seed the embryo is typically dicotyledonous, with a short radicle and well developed hypocotyl and cotyledons (fig. 37).

The seed coats of *Magnolia* have been described by different botanists, probably the earliest correct description being that given by ASA GRAY (10). In the mature seed the outer integument is differentiated into two layers, an outer fleshy one well filled with oil receptacles, and an inner stony layer of bony hardness. The inner integument forms only a thin layer in the ripe seed. After dehiscence of the carpels the seeds remain suspended a few days by means of an elastic thread formed from the spiral thickening bands of the xylem elements of the raphe. Finally the threads may be broken and the seeds fall to the ground; or sometimes the entire cones with most of the seeds still attached are shed. This shedding of the cones results from a break across the base of the peduncle, but without the formation of a definite absciss layer.

In the case of *Liriodendron* the development of the endosperm and embryo were not investigated.

Before discussing the embryo sac and certain other points mentioned above, several features of gross structure and anatomy deserve attention. ARBER and PARKIN (2) define the term flower as "a special form of a type of strobilus common to angiosperms and certain mesozoic plants," and propose to designate it as an anthostrobilus. The anthostrobilus differs from all other strobili in that it is typically amphisporangiate, with the megasporophylls above the microsporophylls on an elongated axis, and below the sporophylls a distinct perianth which is wholly or partially protective. The angiospermous type of anthostrobilus is called a euanthostrobilus, and is believed by them primitively to have possessed among others the following characteristics: a large or indefinite number of parts arranged spirally; ovules orthotropous, several in each ovary, with two integuments; marginal placentation; filaments short, bearing long anthers with the connectives prolonged beyond them; members of the perianth all similar, or more or less differentiated; entomophilous. The flowers of

Magnolia and *Liriodendron* differ from the above type only in having anatropous ovules and two-seeded carpels. In the proanthostrobilus or Bennettitean type of "flower" corresponding parts occur with a similar arrangement. ARBER and PARKIN hold that "its parts are homologous with the carpels, stamens, and perianth of a typical amphisporangiate angiospermous flower." It differs from this, however, "especially in the presence of a seminal pollen-collecting mechanism, and in the form of the microsporophylls," which are decidedly fernlike. More details regarding the proanthostrobilus cannot be included here, but may be found in the well known work of WIELAND (**32**).

The seedling structure of *Liriodendron* has been described by Miss THOMAS (**30**). She finds here a form intermediate between the normal tetrarch and diarch types of transition from cotyledons and hypocotyl to root as found in the Ranales, Rhoedales, and various other dicotyledons. The writer has confirmed Miss THOMAS' descriptions. The peculiarity in *Liriodendron* is that while in the cotyledons and upper part of the hypocotyl the structure is that ordinarily occurring in connection with the tetrarch type of root (figs. 13, 14), lower down in the hypocotyl certain elements disappear so that the root is diarch (fig. 12). On account of lack of material the seedling of *Magnolia* has not yet been studied.

In both gross structure and anatomy *Magnolia* and *Liriodendron* afford many points of similarity, possessing certain characters common to all Magnoliaceae and others which are peculiar to the Magnolieae (**28, 21**). Among the former are woody stems, alternate leaves, secretory cells, a characteristic type of stoma, and more or less abundant endosperm in the seed; the latter include foliar stipules, sclerenchymatous diaphragms in the pith, and the bundles of the petiole more or less fused in an irregular ring.

The arrangement of the vascular bundles in the peduncle of *Magnolia* and in the petioles of *Magnolia* and *Liriodendron* is shown in figs. 11, 38, and 40, and details of the petiolar bundle of *Magnolia* are represented in fig. 39. Considering the Magnoliaceae as a whole, the petiolar bundles are distributed either as in these two species or in the form of a crescent. PARMENTIER (**21**) regards the different arrangements as correlated with the size of the leaves. WORSDELL (33) finds medullary bundles in the petioles of various species of *Magnolia*, and interprets these as reminiscences of a primitive, more scattered system in their ancestors. He believes also that the somewhat irregular system of bundles in the peduncle of *Liriodendron* and *Magnolia* indicates the same thing. If we accept the view that dicotyledons have been derived from monocotyledons, this explanation might seem more or less plausible; however, on the theory that monocotyledons are secondary, this interpretation could hardly be correct.

Present theories concerning the primitiveness of various types of angiospermous embryo sac will now be discussed. According to the archegonium theory of PORSCH (22), the 8-nucleate embryo sac is to be interpreted as the equivalent of two archegonia, a micropylar one represented by the egg apparatus, and a chalazal one represented by the three antipodals. Accepting this view, as has been pointed out by BROWN (3), "we might conceive of the embryo sac of *Peperomia* as really composed of four sacs, each of which gives rise to one archegonium." A similar explanation might hold also for certain other anomalous embryo sacs such as are found, for example, in the Pennaeaceae. PORSCH, however, in his paper considers only the 8-nucleate type.

This theory has been criticized from various standpoints. In the gymnosperms, for instance (3), in all species that form archegonia, the megaspore first produces a non-cellular stage of the gametophyte, and subsequently a cellular stage in all species that form archegonia; and it is in this cellular tissue that the archegonia are initiated and formed. So if we homologize the first two divisions of the ordinary angiospermous embryo sac with the free nuclear divisions of the gymnospermous prothallus, the shifting of the archegonia from the cellular to the non-cellular stage of the prothallus must be explained.

ERNST (9) admits that the archegonium theory would be *sehr bestechend* if within the 8-nucleate embryo sac the two groups of nuclei were always of nearly the same form. The numerous variations from the "normal" type, not only in the form of the egg apparatus and of the antipodal apparatus, but also in the behavior of the polar nuclei, serve, he believes, better to refute than to support PORSCH's theory.

Other valid criticisms might be offered, but we need not do this here, since, even if we were to accept the theory, the question as to the most primitive type of angiospermous embryo sac would still remain unsolved.

In a recent publication (9) ERNST, after considering the course of development of the ordinary angiospermous embryo sac, as well as of such peculiar types as occur in *Gunnera macrophylla*, *Peperomia pellucida*, *P. hispidula*, and the Pennaeaceae, arrives at conclusions quite different from those published slightly earlier by COULTER (5). According to COULTER, the most important of the five nuclear divisions in the development of the ordinary embryo sac are the first two, which result in the formation of tetrads. COULTER asserts that, so far as we know, if fertilization is to occur later, the reduction divisions are not omitted; and that whether the number of divisions of the embryo sac mother cell is reduced from 5 to 4, or even to 3, the reduction divisions are never omitted. In such forms as *Peperomia*, in spite of the fact that the embryo sac contains 16 nuclei, there are only 4 divisions of the embryo sac mother cell, instead of 5 as in the ordinary 8-nucleate type of embryo sac.

To this view ERNST replies: "Die Entwicklungsvorgänge im Embryosack scheinen mir unabhängig von seiner Entstehung betrachtet werden zu müssen." So ERNST holds that although the omission of tetrad formation is a reduction of the course of development and not a primitive character, it has, nevertheless, no influence on the development of the embryo sac, and that the 5 divisions of the embryo sac mother cell resulting in the 8-nucleate sac belong to two entirely different phases of development; that is, formation of spores, characterized by reduction of chromosomes, and germination of spores, characterized by polarity, number of nuclear divisions, position of nuclei, development of vacuoles, and cell formation.

It is evident that COULTER regards the 16-nucleate embryo sac of such forms as *Peperomia* as derived by a reduction of the divisions of the embryo sac mother cell to 4 instead of 5. ERNST, on the other hand, sees here an omission of tetrad formation and one more than the usual number of divisions in the germination of the megaspore to the embryo sac. He therefore considers the 16-nucleate sac as an older, or at any rate an independent, form of embryo sac, not derived from the 8-nucleate type. These two views, then, are directly opposed to each other.

With respect to the nature of the 16-nucleate embryo sac of *Peperomia*, CAMPBELL (4) and JOHNSON (15, 16), as is well known, have arrived at opposite conclusions. CAMPBELL says: "*Peperomia*, in regard to the embryo sac, probably represents the most primitive form yet discovered among the angiosperms. . . . . *Peperomia* offers a basis for an explanation of the homologies of the embryo sac." JOHNSON, a little later, after studying several genera of Piperaceae, maintained that the peculiarities in *Peperomia* are of secondary origin. The latter view is supported by BROWN (3) who, in *Peperomia sintenisii* and *P. arifolia*, finds that at the first two divisions of the embryo sac mother cell typical reduction of chromosomes occurs; and also that during these divisions the nuclei are separated by evanescent cell walls. So he concludes that these phenomena seem to indicate that the sac is a compound structure derived from the nuclei of four megaspores, the primary sac nucleus being a mother cell rather than a megaspore.

Reference has been made to COULTER'S view that while the genesis of the ordinary angiospermous embryo sac from the megaspore mother cell involves 5 divisions, the essential part of the process is found in the first two divisions which, so far as we know, are necessary if fertilization is to occur. BROWN (3) maintains that we cannot make chromosome reduction the sole criterion of megaspore formation, and adds as another distinction that while a division giving rise to megaspores is characterized by a cell wall or a cell plate, the first division of a megaspore is not accompanied by a cell plate. Quite lately SMITH (27) has pointed out that this distinction does not hold in the case of *Clintonia*, where, at the first division of the megaspore nucleus, a cell plate appears, and SMITH infers it will not hold for certain other cases.

Sufficient emphasis, it seems to the writer, has never been given to the fact that while the anomalous types of embryo sac are as a rule of rare occurrence and are distributed among entirely unrelated families, on the other hand, the ordinary 8-nucleate type developed by 5 divisions of the megaspore mother cell occurs in nearly all families of angiosperms from the most primitive to the most specialized. This is significant and is hardly to be explained on any other hypothesis than that the latter type is primitive. We have in the 8-nucleate sac, it seems, a structure of marvelous constancy in development and arrangement of parts, evolved in the course of long ages, the exceptions to which only strengthen the view that it is a primitive type of embryo sac.

Another reason for regarding anomalous types of embryo sac as derived is the variability in the manner of their development. This is especially marked in the case of 16-nucleate sacs, where a peculiar method of development is found in almost every new case discovered. Of course it may be objected that these variations are of minor importance. But even if this were true, it certainly contrasts strikingly with the remarkable uniformity so very general even in minor details of the development of the ordinary angiospermous type, and is a fact to be explained.

Whether or not we consider the first 4 nuclei produced by division of the embryo sac mother cell as megaspores, and this view seems reasonable in most cases, is probably of less importance than many have believed. The genesis of the angiospermous sporophyte, aside from the exceptional cases such as those involving apogamy and budding, always begins with a perfectly definite structure, the embryo sac mother cell. If fertilization is to occur later, then, without exception, reduction of chromosomes takes place at the first two divisions of this cell. Now, considering parthenogenesis as a secondary phenomenon, we see that in the development of all normal embryo sacs (that is, those capable of being fertilized), whatever their type of mature structure, there is this common feature in development. After the reduction divisions the embryo sac may develop as the product of one-fourth, one-half, or all of the four reduced nuclei derived from the original mother cell. The ordinary 8-nucleate type develops as the product of one-fourth of these nuclei by three successive divisions; the sac of *Cypripedium* (**20**) develops as the product of one-half of these nuclei by one division; that of *Lilium* as the product of all of these nuclei by one division; and that of *Peperomia* from all of these nuclei by two divisions. The three latter cases clearly show an abbreviation in the course of development of the gametophyte, whether we regard that course as beginning with the embryo sac mother cell or after chromosome reduction.

That we cannot make chromosome behavior the sole criterion for distinguishing sporophyte and gametophyte is doubtless true. This is evident from chromosome behavior in cases of parthenogenesis such as occur in *Alchemilla* (19), and in the numerous instances of apogamy and apospory among both pteridophytes and spermatophytes. However, it is probable that no one has ever dreamed of making such unusual phenomena the basis of any theory of the nature or phylogeny of the angiospermous embryo sac. These phenomena undoubtedly are secondary. Hence the conception that chromosome behavior is the most important criterion, at least in all cases where fertilization occurs, seems well founded. So if abbreviation in the developmental history of the gametophyte in angiosperms expresses an evolutionary tendency which can be traced back as far as the gametophyte of the pteridophytes, then anomalous embryo sacs are secondary rather than primitive types.

If now the embryo sacs of those Magnoliaceae thus far investigated are considered, no clue is discovered in their development or structure as to the primitiveness of the group; and this for the simple reason that, although we regard this type as the most primitive among angiosperms, yet the same type is the common one among all angiosperms. Moreover, whatever theory we accept, the past study of the embryo sac has served mainly to emphasize the vast difference between angiosperms and lower groups of plants in this respect, and so to increase rather than to bridge the wide gap between them. It would seem then that if the problem of the origin of angiosperms is to be solved this must come about principally as a result of investigations of other features than the embryo sac.

During the last two decades the amount of purely descriptive literature dealing with embryo sacs has grown to huge proportions, but the different theories as to which type is primitive have not been reconciled. If, however, anomalous types of angiospermous embryo sacs are secondary and not primitive, as seems most reasonable, then the causes of these secondary modes of development should be investigated. This is obviously a problem presenting serious difficulties, yet they are probably not insurmountable. A key to the situation may probably be found by considering the possibility that there is some relation between anomalous types of embryo sac development and peculiar environmental conditions. This has been suggested, for example, by JOHNSON (15).

Since the strobilus theory of ARBER and PARKIN (2) is based so largely on a comparison of the flower (euanthostrobilus) of angiosperms and the proanthostrobilus of the Bennettitales, we must refer to certain views as to the nature of these structures. ARBER and PARKIN, agreeing with HALLIER (11) and SENN (26), consider the amphisporangiate flower of *Magnolia* and *Liriodendron* as made up of sporophylls and perianth borne directly on the main axis of the floral shoot rather than as a compound structure. This they regard as the most primitive type of angiospermous flower, reproducing the essential features of the Bennettitean strobilus. WETTSTEIN (31) and others, on the contrary, think that the primitive type is to be sought for among the monosporangiate Apetalae, and that the angiospermous fructification is a reduced inflorescence, derived from that of the gymnosperms. LIGNIER (17), at least, interprets the Bennettitean strobilus also as a compound structure, an inflorescence. It is clear that conclusions as to the primitiveness of different groups, as well as to the origin of angiosperms as a whole, will vary according to which of these views is accepted.

The greatest differences between the two theories have been indicated. Whether the primitive angiospermous flower was anemophilous or entomophilous is perhaps of relatively minor importance, yet this question also is involved in both of these theories. It would seem natural to imagine anemophily as the method of pollination among primitive angiosperms, yet if entomophily has played as important a rôle as many suppose in their evolution, from their very origin, then the latter must be primitive for this group.

Thus far the monocotyledons have been left out of account in looking for primitive angiosperms. Let us now turn to this group.

The remarkable uniformity in the development and mature condition of the male and female gametophytes of monocotyledons and dicotyledons has been brought forth repeatedly as the strongest argument in favor of a monophyletic theory. In spite of objections such as the claim that "similarity in structure may be the outgrowth of the changes that resulted in the evolution of seeds" (**6**), it seems that we are far from the point of even thinking of abandoning this as well-nigh irrefutable evidence of close genetic relationship between the two great classes of angiosperms.

Within the last few years the striking similarity in the seedling structure of dicotyledons and monocotyledons has been demonstrated in many forms. Although the generalization that "ontogeny repeats phylogeny" has likely been overworked, yet if there is anything at all in this rule, then the evidence from seedling structure deserves its full share of consideration.

In favor of the view that the two groups have originated independently are the differences in their anatomy, and in the development and mature condition of the embryo. As a result of recent study, however, we learn that anatomically the structure of seedlings in particular, but also of mature individuals in the two groups, offers many striking points of resemblance. Other differences, generally regarded as secondary in importance, are seen in the venation of the leaves, in the grandifoliate as opposed to the parvifoliate habit, and in floral symmetry.

The principal resemblances and differences between monocotyledons and dicotyledons on which present phyletic theories are based have been mentioned. In reviewing these theories we may recall the fact that while according to most if not all monophyletic theories proposed until recently, dicotyledons were assumed to be derived from monocotyledons, students of phylogeny today quite generally hold the opposite view. WORSDELL (**33**), however, is still inclined to the view that monocotyledons rather than dicotyledons are primitive. He believes that "angiosperms have developed directly from an ancestor belonging to the bryophytic level, and that they have not come from either gymnosperms, pteridosperms, or ferns." His conclusion is based mainly on the following insufficiently substantiated assumptions: that taking the vegetable kingdom as a whole, the grandifoliate habit is primitive, the parvifoliate derived; that the appearance of two cotyledons in dicotyledons is illusive, there really being only one which is deeply bifurcated; that in the monocotyledonous seedling there is no room for the scattered arrangement of the bundles, so we cannot on account of its absence here conclude that the scattered condition has been derived from a vascular cylinder. These points cannot be discussed here; it suffices to say that the criticism that this view assumes entirely too much seems fair. Besides, the evidence from fossils is entirely against it, the general conclusion of paleobotanists being that from the Bryophyta no higher forms have ever evolved. SCOTT (25), touching this point, says: "neither among living nor fossil plants has any indication of a structure intermediate between the plant of a vascular cryptogam and the fruit (sporophyte) of a bryophyte ever been discovered."

The view that monocotyledons have been derived from dicotyledons, doubtless at a rather early period in the history of angiosperms, and possibly by branching from several points along the dicotyledonous line, has been much strengthened by the researches of the last 15 years. Miss SARGANT (24) regards the common characters of monocotyledons and dicotyledons as too numerous and uniform to have been acquired independently, and emphasizes the fact that angiosperms are especially unique with respect to their flowers, carpels, and endosperm. The attainment of practical identity in the "germination of the embryo sac and the history of the endosperm" by independent evolution among monocotyledons and dicotyledons "would require a series of coincidences," she says, "so improbable as to be inconceivable." With respect to the flower, Miss SARGANT agrees with the view of ARBER and PARKIN given elsewhere.

Probably Miss SARGANT'S most important contribution to the monophyletic theory is based on anatomical investigations. The presence or absence of a cambium seems to account largely for the difference in detail between monocotyledonous and dicotyledonous stems, hence the great importance of any evidence as to its presence among primitive angiosperms. That a true cambium develops in certain monocotyledons (*Gloriosa*, 23) is now well known; but especially significant is the fact that while the structure of the mature stem of monocotyledons and dicotyledons generally varies greatly, the primary structure of the dicotyledonous stem, which is the same in seedlings and mature plants, is also frequent in monocotyledonous seedlings. So in the light of this evidence and also of the fact that a cambium is usually present among living gymnosperms and extinct vascular cryptogams, and is universally present, so far as known, among extinct gymnosperms, the view that primitive angiosperms possessed a cambium seems well founded.

The argument for most of Miss SARGANT'S other views cannot be included here, yet one other conclusion should be mentioned. Since among gymnosperms monocotyledonous forms are unknown, and the dicotyledonous condition prevails, one would naturally presume that the embryo of primitive angiosperms was dicotyledonous; besides, the embryological development of angiosperms points in the same direction. So the general conclusion is that monocotyledony is secondary, being the result of a fusion of two cotyledons.

ARBER and PARKIN in discussing the origin of angiosperms hold "that monocotyledons branched off from the main angiospermous line, that is, dicotyledons, at a very early period." Since the embryo of *Bennettites* was dicotyledonous, they regard the Hemiangiospermae as dicotyledonous also, and so conclude that the monocotyledonous type is the less primitive one. In their opinion Miss SARGANT'S explanation of the monocotyledonous embryo is the best yet offered. They also recognize the need of accounting for the origin of the monocotyledonous habit.

For a number of years the so-called anomalous dicotyledons have attracted students in the hope that knowledge of their embryos and anatomy would aid in solving phylogenetic problems. One of the general conclusions of such investigations is that the anomalous characters are secondary and not primitive features. MOTTIER (18), for example, says, "it is probably true without exception that dicotyledonous plants possessing anomalous embryos are either partially or wholly geophilous in habit, having stems either in the form of a rhizome, tuber, or a short, squat axis."

That anomalies not only in embryology and anatomy, but even in embryo sacs, depend largely on environmental conditions has been suggested in the past (JOHNSON 15), and seems continually to be receiving wider attention. HILL (14), for example, has discovered in the Andes, Central America, and Mexico a few geophilous species of *Peperomia* which are of great interest. Although their seedlings are described as possessing all the external characters of monocotyledons, yet they are true dicotyledons, but the cotyledons exhibit a marked division of labor, one serving for absorption, the other for photosynthesis. That these species are true dicotyledons is shown by the structure of the seed; the presence of stomata on the lamina of the absorbent cotyledon; persistence of the primary root for some time after the formation of the bulb; and the vascular structure of the seedling. Moreover, most of the members of the genus, containing some 400 species, are normally dicotyledonous. The peculiar habit of these few species is therefore interpreted as due to xerophytic conditions, resulting in the assumption of the geophilous habit, accompanied by formation of bulbs or tubers, and finally affecting even the embryonic structure of the plants so that the division of labor referred to above has resulted. Although HILL opposes Miss SARGANT'S theory as to the origin of the single cotyledon of monocotyledons, it is worthy of note that he attributes the anomalies in *Peperomia* to the geophilous habit. This is the same cause that other workers have assigned for the pseudo-monocotyledonous habit, anomalous stem structure, and so on, in the case of various other dicotyledons.

Now if it is conceivable that a pseudo-monocotyledonous habit has arisen in different ways among dicotyledons, then the possibility of the same thing happening among monocotyledons presents itself, especially if monocotyledons have branched off at several points along the dicotyledonous line. Indeed, attempts at a causal explanation of the origin of monocotyledons from dicotyledons have actually been made, one of the most important of these being HENSLOW'S theory (12).

This theory is founded mainly on the large number of coincidences among both dicotyledonous and monocotyledonous aquatic plants, and on the fact that all terrestrial monocotyledons exhibit the same coincidences. HENSLOW, as well as many others, regards the monocotyledons as degenerate (when compared with dicotyledons), although there is not always agreement as to the cause of degeneracy. HENSLOW himself believes an aquatic habit has been the principal cause, and points to a number of characteristics of monocotyledons and dicotyledons that he considers the result of adaptation to a moist or aquatic environment. Among these peculiarities are large size of leaves, water storage organs, the pseudo-monocotyledonous condition of certain dicotyledons, early loss of primary root, and "endogenous" arrangement of cauline bundles. HENSLOW remarks: "In the title of my first paper in 1892 (**13**), I used the word 'theory,' but . . . . I feel justified in abandoning the term; for I would maintain that the conclusion has passed the stage of hypothesis and probability only, to that of a *demonstrated fact.*" While it is likely that very few of us would be willing to subscribe to this conclusion, yet all must agree that such considerations are extremely suggestive, and indicate a line of work that is promising, especially if taken up experimentally.

To multiply examples would probably not add to the force of the argument. We see that various competent workers attribute anomalies among dicotyledons to a geophilous habit, response either to xerophytic or to hydrophytic conditions. Such responses result in structural peculiarities in stems, formation of various types of underground stems, a pseudo-monocotyledonous habit, or division of labor among the cotyledons. When we turn to the monocotyledons, we find these peculiarities duplicated, but as a rule they are intensified. That their production is related to environment seems clearer in the case of dicotyledons than of monocotyledons, no doubt because many monocotyledons at present live where the prevailing conditions do not seem to necessitate geophily. The persistence of these peculiarities in such environments may be interpreted as retention of past characters.

It seems then that, on account of many similarities between monocotyledons and anomalous dicotyledons, HENSLOW'S conclusion that the former have been derived from the latter as a response to the same factors that determined the geophilous habit is reasonable, at least, as a working hypothesis. Failure to recognize the fact, however, that geophily may express itself variously has sometimes led to disagreement in theories where none actually exists. This appears especially in discussions of the origin of the monocotyledonous from the dicotyledonous habit, it being held that monocotyledony has arisen in only one way. There are at least three plausible theories concerning the method by which this may have occurred: first, by suppression of one of two cotyledons; next, by fusion of two cotyledons; and, finally, by a division of labor between two cotyledons. Now since we find a difference in the behavior of the cotyledons in certain anomalous dicotyledons, it is entirely probable that the same thing has happened in the origin of monocotyledons from dicotyledons, so much the more so if there is more than one monocotyledonous branch from the primitive dicotyledonous stock.

While, as has been shown, the most generally accepted view is that angiosperms are monophyletic we must also remember the possibility of a diphyletic origin. COULTER (6) has expressed his view on this point as follows: "In our judgment the evidence is strongly in favor of the independent origin of the two groups, which have attained practically the same advancement in the essential morphological structures, but are very diverse in their more superficial features. Their great distinctness now indicates either that they were always distinct or that they originated from forms that were really proangiosperms and neither monocotyledons nor dicotyledons." Those who hold this view will have to explain more satisfactorily than has been done the similarity between monocotyledons and dicotyledons in gametophytic development and in seedling structure; the general similarity between monocotyledons and anomalous dicotyledons; and the evidence that primitive angiosperms possessed a cambium and were dicotyledonous. The monophyletic theory has been strongly reinforced in recent years and the writer finds it more acceptable than the diphyletic, but more evidence is needed before it can be unreservedly accepted.

It is evident then, from the above considerations, that we regard the Magnoliaceae, since they belong to the more primitive group of angiosperms, as more primitive than the monocotyledons. Let us next consider certain theories relative to the primitiveness of various features among the dicotyledons themselves.

Present theories on this subject are fairly well represented by the views of WETTSTEIN (31) on the one hand and those of ARBER and PARKIN (2) on the other. Both believe that monocotyledons have been derived from dicotyledons. WETTSTEIN holds, because of similarity in cotyledons, stem, floral structure, and reduction of the primary root, that monocotyledons have been derived from the Polycarpicae. He also points out that while we may think of derivation of one cotyledon from two, the reduction of a primary root, and so on, the opposite would not seem possible under any circumstances. So he concludes that we must turn to the dicotyledons in considering the phylogeny of angiosperms, but disagrees entirely with many as to which dicotyledons are most primitive.

Both theories derive angiosperms from gymnosperms. According to WETTSTEIN, primitive angiosperms should present among others the following characteristics: prevalence of woody plants and absence of vessels in the vascular bundles; prevalence of monosporangiate flowers, with either no perianth or one of simple structure; prevalence of anemophily. These are gymnospermous characters, and WETTSTEIN holds that we should regard that group of angiosperms as most primitive which exhibits these characters developed in high degree. ARBER and PARKIN (2), HALLIER (11), and others give a much longer list of characters which they believe are primitive. According to their views, amphisporangiate, actinomorphic flowers, with elongated axes bearing numerous free, spirally arranged floral parts, are primitive. Such flowers also possess a well developed, undifferentiated perianth and are entomophilous. Besides, primitive angiosperms are dicotyledonous, have small embryos and abundant endosperm, are treelike, and lack true vessels among autophytic species.

If it is granted that all the essential characters that may be regarded as primitive have been included in these lists, then it is evident that the great differences between the two theories relate to but a few points, points which involve, however, no end of difficulty. The two theories would apparently be reduced to one if we could say which of the following are primitive: monosporangiate or amphisporangiate flowers; presence or absence of a perianth; anemophily or entomophily. Of possibly less importance is the question whether the angiospermous flower is a modified simple (that is, unbranched) shoot or a modified infloresence. There is agreement as to the primitiveness of such characters as actinomorphy, freedom of floral parts, dicotyledony, lack of true vessels in the vascular strands, and prevalence of woody plants. So it seems important to discuss the differences cited.

The fact that certain characters are common to all or nearly all gymnosperms seems in many instances to be one of the strongest reasons for regarding those characters as primitive if they occur at all among angiosperms. Among these supposedly primitive characters are dicotyledony, prevalence of woody plants, and absence of tracheae in the conducting strands. For the same reason we might conclude that primitive angiosperms were anemophilous and possessed naked, monosporangiate flowers, since these characters also are common to most gymnosperms.

Before discussing this matter further, reference may be made to the possibility of there being two entirely separate lines of dicotyledons. Reasons have been given for believing that angiosperms are monophyletic. Now if the similarity between dicotyledons and monocotyledons is close enough to warrant such a conclusion, then, since the similarity is so much more striking among dicotyledons themselves, this conclusion seems all the more certain in the latter case. In the group Dicotyledoneae the diversity in the development and structure of the gametophytes and embryos is surely less marked than is the diversity among angiosperms as a whole, and so difficulties are increased accordingly if any other than a monophyletic theory is proposed for the phylogeny of dicotyledons. It is certainly true that the reproductive structures and organs of spermatophytes are among their least plastic features. While it is dangerous to emphasize too strongly the importance of even the most stable character to the exclusion of others, nevertheless, if the view that the embryo sac points unmistakably to a monophyletic origin of angiosperms is incorrect, a more satisfactory one has never been advanced. The homoplastic explanation seems well-nigh inconceivable. Besides, in the morphological and anatomical structure of seedlings and mature plants all dicotyledons are essentially alike, so most of the important differences, as has been indicated above, are in the flowers. Taking all the evidence into account then, it seems likely that all dicotyledons are of one stock, and that the monocotyledons have arisen as one or more branches of this stock.

If then dicotyledons are monophyletic, which are the most primitive? If, as ARBER and PARKIN (2), WETTSTEIN (31), and others suppose, they have been derived from gymnosperms, from what particular gymnospermous stock may they have come? The Gnetales and more recently the extinct Bennettitales have each been thus designated. Even if dicotyledons originated from a gymnospermous stock, opinions will differ as to which is the parent group, depending on whether one regards naked, monosporangiate, anemophilous flowers, or entomophilous, amphisporangiate ones with a perianth as primitive.

The entomophilous habit seems clearly associated with much in the evolution of angiosperms, but it does not necessarily follow that primitive angiosperms were entomophilous. That anemophilous angiosperms may succeed and persist in competition with entomophilous forms is well illustrated by such groups as the Amentiferae and Gramineae.

Few, if any, believe that the flower of any existing angiosperm is like the primitive angiospermous flower. Whether this primitive flower was monosporangiate or amphisporangiate it does not follow, though this is quite possible, that any particular flower of today is the direct descendant of a similar type in its ancestor. It is certain that in many instances amphisporangiate flowers have become monosporangiate, and that perianths have been more or less completely lost.

That the opposite may have occurred, however, is less easily proven. ARBER and PARKIN (2), for example, object to ENGLER'S view (8) that the monosporangiate Apetalae are primitive among dicotyledons, by saying that "it must be assumed that the perianth is evolved *de novo* and is an organ *sui generis*." But suppose we do assume that primitive angiosperms possessed a perianth, the origin of the perianth still remains to be explained. Even if we say that it is a direct derivative from a Bennettitean ancestor, its phylogenetic origin still remains a mystery. So if a perianth developed in some manner or other among the Bennettitales, might not the same thing have occurred among angiosperms, even long after they became a distinct group of plants?

The question whether primitive angiospermous flowers were monosporangiate or amphisporangiate presents even greater difficulties than that concerning the primitiveness of the perianth. If angiosperms have descended from gymnosperms we would rather expect primitive flowers to be monosporangiate. Evidence from gymnosperms that amphisporangiate flowers are primitive rests almost entirely on a single, extinct, much specialized group of plants, the Bennettitales. This group no doubt represents, as COULTER (7) suggests, "the end of a gymnosperm phylum." Moreover, that the proanthostrobilus of the Bennettitales corresponds closely to such a flower as that of *Magnolia* or *Liriodendron* still remains undecided. The resemblance is remarkable, yet if the view (17) that the Bennettitean inflorescence is a compound structure is correct, and if the flower of *Magnolia* is not compound, then the resemblance becomes only a superficial one.

If then we go back far enough in the evolution of angiosperms, the probability seems strong that the group was monosporangiate. Amphisporangiate flowers are unknown below angiosperms except in the Bennettitales and possibly *Welwitschia.* Although in a number of respects angiosperms and Gnetales have developed along parallel lines, it is now generally believed that the Gnetales are not transition forms leading to angiosperms. This view, however, does not preclude the possibility of common ancestry in the distant past. The Gnetales likely represent the end of a gymnospermous phylum just as the Bennettitales do. So neither group represents the direct progenitors of angiosperms.

COULTER and CHAMBERLAIN (7) say: "It is recognized that in the evolution of strobili among gymnosperms there were probably two distinct tendencies: a monosporangiate strobilus (Cycadales, Cordaitales, Ginkgoales, Coniferales), and a bisporangiate strobilus with the anthostrobilus arrangement of sporophylls (Bennettitales, Gnetales, and leading to angiosperms)." This view apparently involves the idea that the Bennettitales, Gnetales, and angiosperms belong to one stock, but the relationship between the three groups at their origin may have been anything but close. Even though angiosperms are prevailingly amphisporangiate today this may not have been the condition among their remote ancestors; in fact it seems probable that those ancestors possessed monosporangiate flowers.

Though primitive angiosperms possessed monosporangiate, naked, anemophilous flowers, it is evident that they did not become the dominant group of plants until they developed amphisporangiate flowers with a perianth, and became entomophilous. This view is evidently opposed to the one that the present day angiosperms have been derived from the Bennettitean stock. The main reason for this belief is that except for resemblance in the fructifications, which may be quite superficial, the two groups are entirely different in structure. Indeed, had the Bennettitean proanthostrobilus never been discovered, probably no one would have ever suspected close relationship between such widely different groups. Leaving out of consideration the nature of the inflorescence, the following may be noted with reference to the Bennettitales: their seeds are of the gymnospermous type; the microsporophylls, microsporangia, and ramentum are fernlike in character; the external appearance and anatomy of the stem and leaf indicate relationship with cycads. All these characters suggest relationship with Cycadofilicales, while their strobili alone indicate a possible connection with angiosperms. It seems on the whole much simpler and safer to conclude that the Bennettitean proanthostrobilus and the angiospermous anthostrobilus are nothing more nor less than the results of homoplastic development, and that if they indicate relationship at all, it must be of the remotest kind, dating from a time prior to the origin of the Bennettitales as a separate stock, a time when neither true Bennettitales nor angiosperms had ever existed.

If then angiosperms were primitively anemophilous with naked monosporangiate flowers, why are the present Monochlamydeae not to be regarded as the most primitive living members? This is because various features of the Monochlamydeae indicate reduction and not primitiveness. If, for example, the entire group as constituted by WETTSTEIN (31) be considered, it is found to be prevailingly syncarpous. This surely is not a primitive feature. Again, in various families there are closely related genera, even species, some of which possess a perianth, while in others it is rudimentary or entirely absent. It is difficult, in such cases at least, to conceive of the latter condition as primitive. Besides, the stamens and carpels may vary in number even in closely related genera and species. That the smaller numbers in such cases are derived seems to be a reasonable conclusion. Moreover, the inflorescences among the Amentiferae, for example, are compound structures exhibiting considerable complexity. This too can be more readily interpreted as derived and not primitive. Amphisporangiate flowers also occur in certain members of at least 7 families included by WETTSTEIN among the Monochlamydeae. Such cases add much weight to the view that the monosporangiate condition throughout the group is secondary and not primitive.

We may conclude then that considering existing angiosperms, the evidence at present available is in the main opposed to the view that they have been derived from forms at all closely related to the Bennettitales. The one striking similarity between modern angiosperms and the Bennettitales may well be a result of homoplasy. Among existing angiosperms, assuming that they are monophyletic, the derivation of forms having monosporangiate, naked flowers from those possessing amphisporangiate flowers, bearing an undifferentiated perianth, seems far simpler than the reverse. So, while agreeing with ARBER and PARKIN, HALLIER, and SENN in general with reference to those features which they believe are primitive among existing angiosperms, there seem to be no very adequate grounds for concluding that primitive angiosperms were provided with entomophilous, amphisporangiate flowers bearing a perianth. The opposite seems much more probable. If the latter is true, scarcely a suggestion of relationship with the Bennettitales remains. But even if the former is true, it would seem hazardous to hold that angiosperms are more closely related to the Bennettitean stock than to any other gymnospermous stock. COULTER and CHAMBERLAIN (7) say that "the Cycadofilicales are so fernlike in every feature except their seeds, that their derivation from some ancient fern stock (called provisionally Primofilices) is as certain as phylogenetic connections can be. The origin of the Cordaitales therefore presents two alternatives: either they arose independently from the same ancient fern stock, or they were differentiated from the Cycadofilicales very early." The same two alternatives present themselves, it seems, in the case of angiosperms. Which view we accept is of little consequence since probably neither can be proven. Either view would make the connection between angiosperms and the Bennettitales, as we know them, a most distant one.

Let us now turn to our original question concerning the primitiveness of the Magnoliaceae among existing angiosperms. While the following list of characters of the Magnoliaceae is incomplete, it doubtless includes most of the more important ones that may be considered primitive: (1) the ordinary 8-nucleate type of embryo sac; (2) dicotyledony; (3) undifferentiated perianth; (4) amphisporangiate flower; (5) entomophily; (6) elongated conical floral axis; (7) actinomorphy; (8) indefinite number of free floral organs arranged spirally; (9) hypogyny; (10) apocarpy; (11) woody stems; (12) occasional absence of tracheae in the vascular bundles.

It is quite generally agreed that the last 7 of these characters are relatively primitive wherever found among angiosperms, or if not that they are of minor importance as evidence of phylogeny. The first two characters, since they are common to nearly all dicotyledons, are valueless as criteria for determining primitiveness. There are left three characters which may be either primitive or derived, namely, undifferentiated perianth, amphisporangiate flowers, entomophily. These three characters have no doubt developed together and are closely bound up with the evolution of angiosperms. If not, then naked, monosporangiate, anemophilous flowers must indicate primitiveness where found in existing forms. We believe, for reasons previously given, that the type of flower found among the Magnoliaceae is primitive.

The present investigation adds little toward the solution of the plexus of problems involved in the origin of angiosperms and the relative primitiveness of existing groups. An opportunity was offered, however, to determine whether such a study as the present one of a possibly primitive group of angiosperms might yield any results of either positive or negative value as a contribution to present theories; to suggest new points of view and especially to emphasize certain old ones; to review briefly some of the principal theories of the present day on the primitiveness and origin of monocotyledons and dicotyledons; and finally to criticize where it seemed this might be helpful in bringing about in the future reinforcement or correction either of earlier theories or of the views expressed in this paper.

Summary

1. In both *Magnolia* and *Liriodendron* the sporogenous tissue in the anther is differentiated early in the winter. Tetrads develop by the simultaneous method and the pollen grains when mature are binucleate in *Magnolia*, two-celled in *Liriodendron*. The tapetum originates from the sporogenous tissue.

2. The x number of chromosomes in each species is 19.

3. The ovules in both species are marginal, anatropous, and provided with two integuments. The megaspore mother cell in each species, by two successive divisions, produces 4 megaspores, of which the innermost is functional. The mature embryo sacs are of the ordinary 8-nucleate type and fertilization probably occurs as usual.

4. The endosperm of *Magnolia* is cellular from the beginning of its formation and is abundant in the mature seed, surrounding a small, typically dicotyledonous embryo. The first division in the development of the embryo is transverse, the second longitudinal to the long axis of the embryo sac. The embryo has a well defined suspensor and no evidence of monocotyledony was found.

5. The seed of *Magnolia* possesses three coats: an outer fleshy

and within this a stony one, both developed from the outer integument, and a thin inner one from the inner integument.

6. The flowers of both species differ from the euanthostrobilus of ARBER and PARKIN only in having anatropous ovules and two-seeded carpels.

7. In *Liriodendron* the seedling possesses in the cotyledons and upper part of the hypocotyl the structure generally found associated with tetrarch roots, but the root is diarch.

8. All Magnoliaceae possess certain common anatomical characters, while others are peculiar to particular groups. The bundles in the petioles and peduncles of *Liriodendron* and various species of *Magnolia* are somewhat scattered, a feature the interpretations of which vary.

9. PORSCH'S archegonium theory gives no suggestion as to what type of angiospermous embryo sac is primitive.

10. A consideration of all available evidence in the light of present theories very strongly favors the conclusion that the ordinary 8-nucleate type of angiospermous embryo sac is the most primitive. But in view of its wide distribution among all groups of angiosperms, its occurrence either among the Magnoliaceae or in any other family is no evidence of the primitiveness of that family.

11. Angiosperms are believed to be monophyletic, especially on account of the uniformity in the development and mature condition of the gametophytes, and because of similarity in seedling structure of monocotyledons and dicotyledons.

12. The view that dicotyledons have been derived from monocotyledons, as advanced by WORSDELL, rests too largely on assumption.

13. The theory that monocotyledons originated from dicotyledons is supported by evidence from gametophytic development and anatomical structure of seedlings and mature plants, as well as by indications that primitive angiosperms possessed a cambium and were dicotyledonous, and by the conclusion that the peculiarities of anomalous dicotyledons are secondary. The important differences between monocotyledons and anomalous dicotyledons on the one hand, and ordinary dicotyledons on the other, are believed

by many to be due to response to the peculiar environmental conditions surrounding the former.

14. Theories differ especially as to whether amphisporangiate, entomophilous flowers bearing a perianth, or naked, anemophilous, monosporangiate ones are primitive among dicotyledons. The writer holds, for reasons given, that in the remote past the ancestors of the dicotyledons (and so of all angiosperms) possessed naked, unisexual flowers, but that among existing groups hermaphrodite flowers provided with a perianth are primitive, and that the naked, unisexual forms existing today have been secondarily derived from the latter; moreover, that the appearance of entomophily, the amphisporangiate condition, and the perianth have been very important features in the evolution of modern angiosperms.

15. The Bennettitales, Gnetales, and angiosperms may have had common ancestors if we go back to a time prior to that when the Bennettitales became a distinct line. It seems reasonable to conclude either that angiosperms were derived from the same ancient fern stock from which the Cycadofilicales originated, or else that they were differentiated from the Cycadofilicales at a very early time.

16. In conclusion, it is believed that the most primitive of existing angiosperms are to be found among the Magnoliaceae or related forms, and not among forms with naked, monosporangiate, anemophilous flowers.

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EXPLANATION OF PLATES I–III

All drawings were made with the aid of a camera lucida from microtome sections.

Abbreviations used: *a*, antipodal; *ar*, archesporium; *cb*, cortical bundle; *cc*, central cylinder; *c*, cotyledon; *e*, egg; *em*, embryo; *es*, endosperm; *fvb*, fibrovascular bundle; *ii*, inner integument; *m*, mechanical tissue; *mgmc*, megaspore mother cell; *mg*, megaspore; *mcmc*, microspore mother cell; *mp*, micropyle; *n*, nucellus; *oi*, outer integument; *p*, pith; *pc*, parietal cells; *ph*, phloem; *pn*, polar nucleus; *pt*, pollen tube; *st*, sporogenous tissue; *su*, suspensor; *sy*, synergid; *t*, tapetum; *tc*, tapetal cell; *te*, tetrad; *v*, vacuole; *x*, xylem.

Liriodendron

FIG. 1.—Part of longitudinal section of microsporangium and wall; wall somewhat diagrammatic; ×350.

FIG. 2.—Pollen mother cells dividing; ×350.

FIG. 3.—Section of pollen grain with reduced number of chromosomes; ×600.

FIG. 4.—Section of two-celled pollen grain; ×350.

FIG. 5.—Longitudinal section of young ovule; ×300.

FIG. 6.—Megaspore mother cell divided; ×350.

FIG. 7.—Longitudinal section of ovary showing tetrad of megaspores deeply buried within nucellus; ×350.

FIG. 8.—Longitudinal section of micropylar end of embryo sac; ×350.

FIG. 9.—Polar nuclei fusing; ×350.

FIG. 10.—Longitudinal section of antipodal end of embryo sac; ×350.

FIG. 11.—Transverse section of petiole showing arrangement of fibrovascular bundles; ×50.

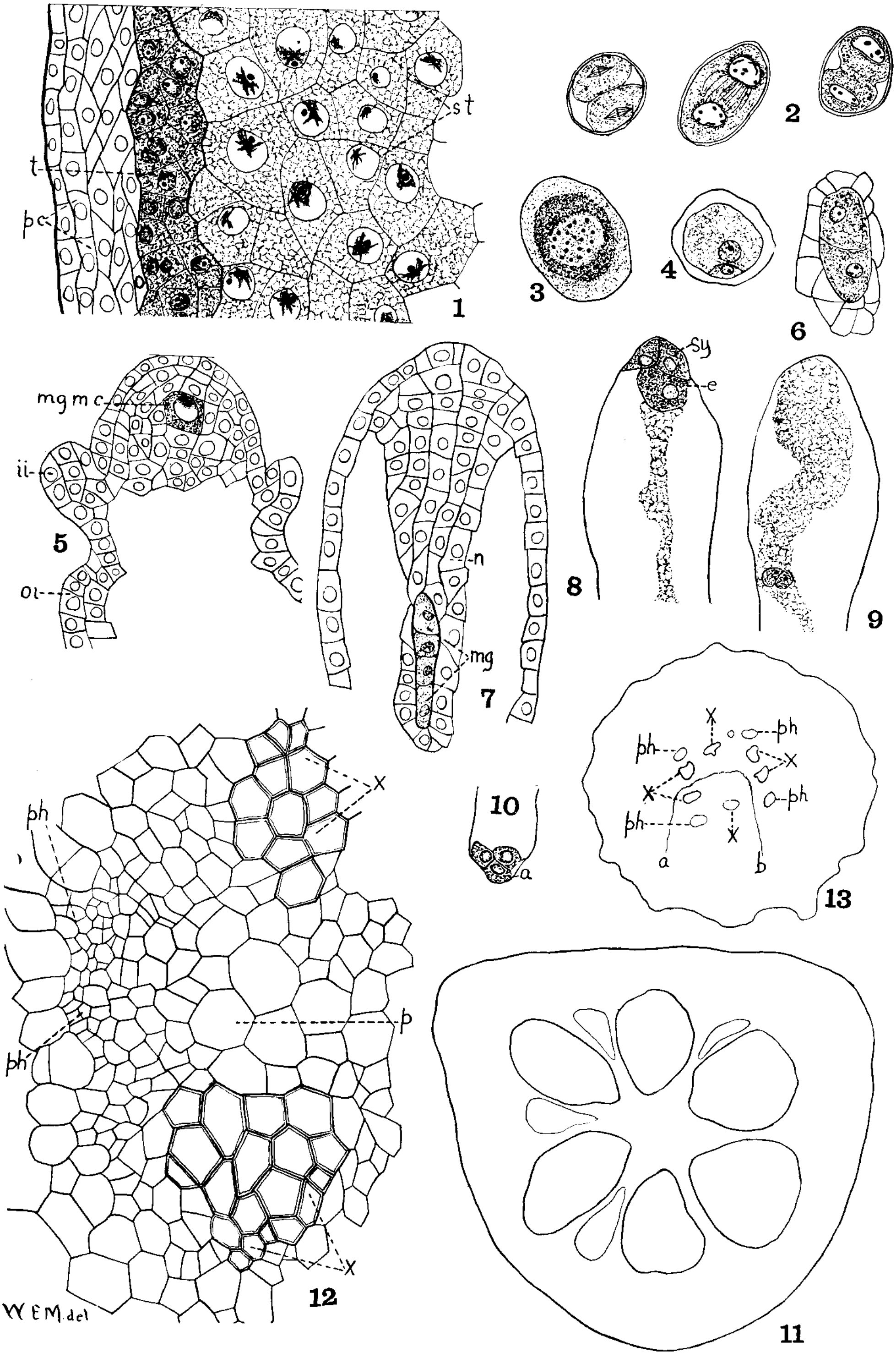
FIG. 12.—Transverse section of portion of central region of diarch root; ×590.

FIG. 13.—Transverse section of hypocotyl; ×50.

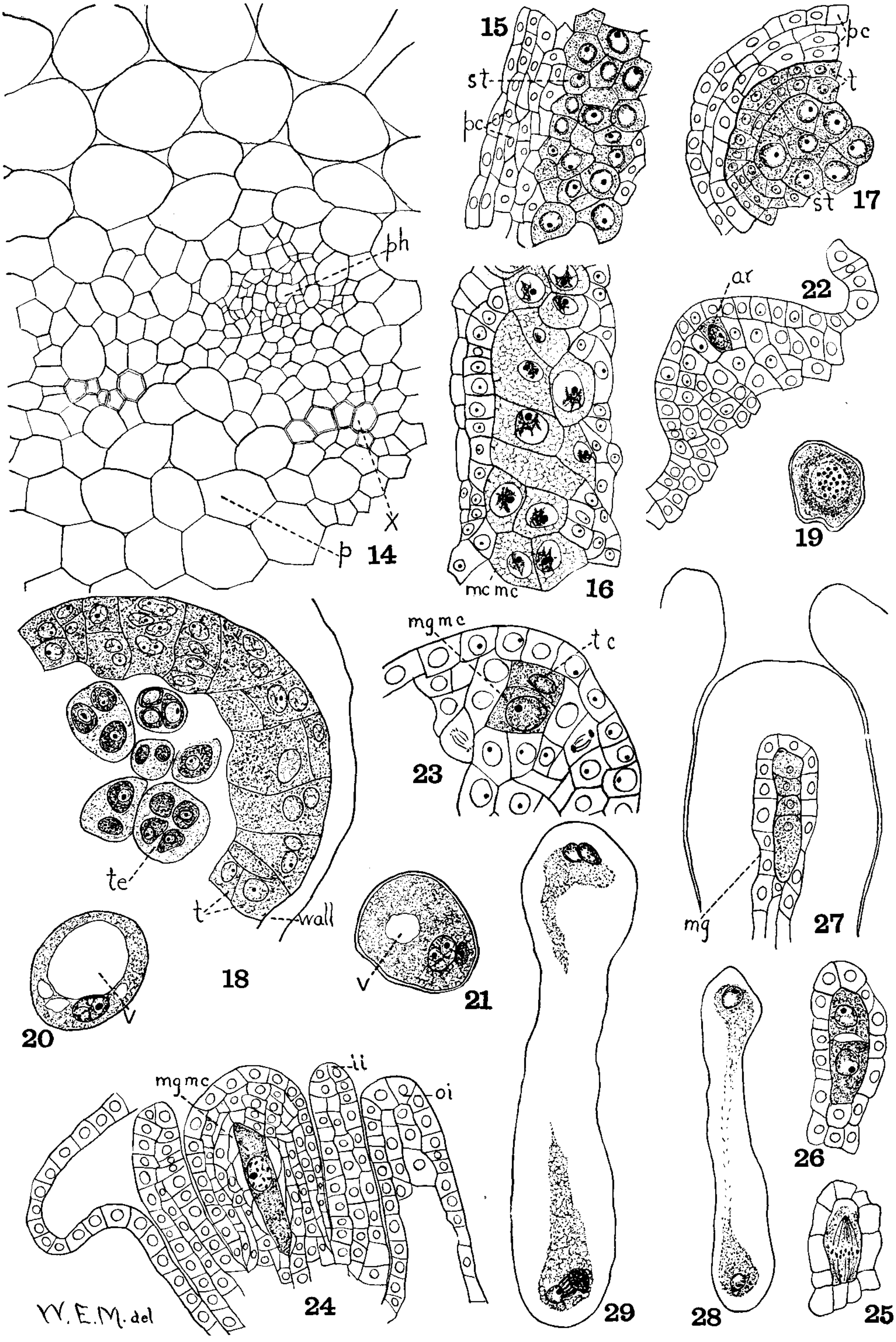
FIG. 14.—Transverse section showing details of the portion of fig. 13 indicated by line *ab;* ×300.

Magnolia

FIG. 15.—Longitudinal section of part of anther; sporogenous tissue differentiated; ×350.



MANEVAL on MAGNOLIACEAE



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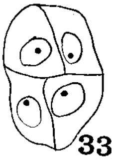
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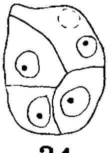
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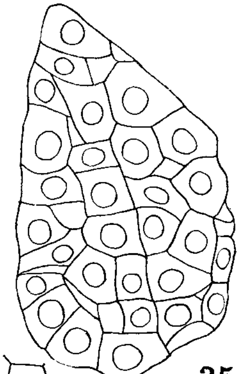
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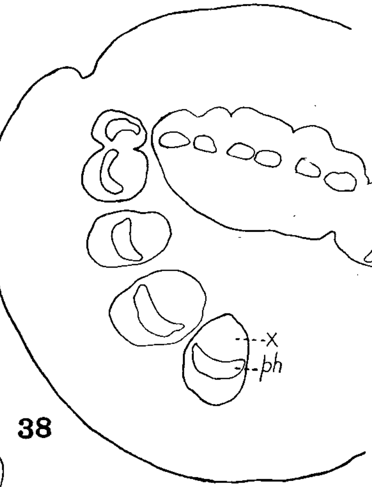
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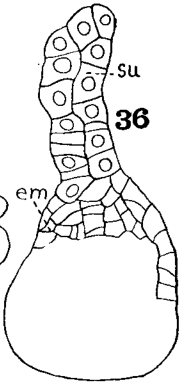
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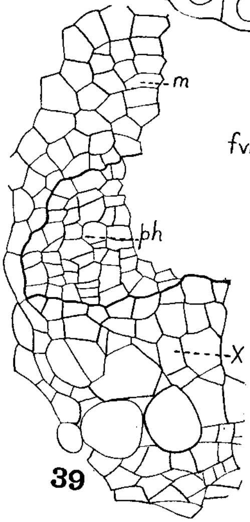
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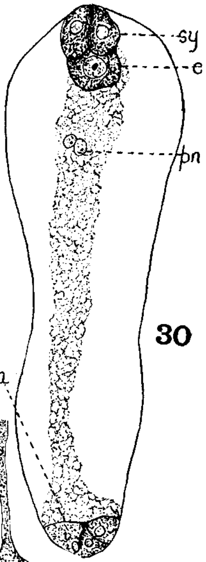
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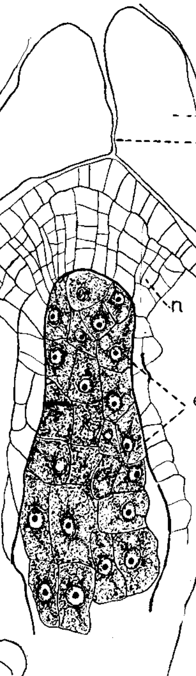
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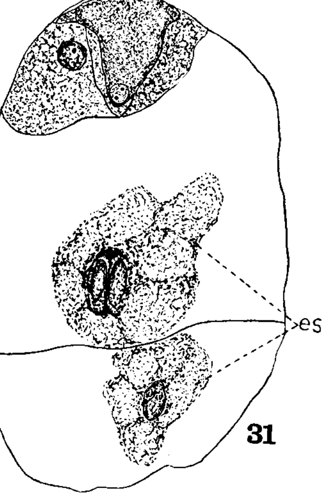
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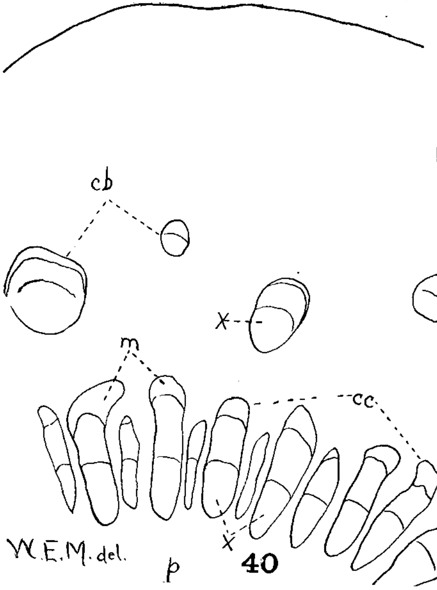
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W. E. M. del.

MANEVAL on MAGNOLIACEAE

FIG. 16.—Longitudinal section of part of anther; microspore mother cells in synapsis; ×300.

FIG. 17.—Transverse section of anther; tapetum and sporogenous tissue differentiated; ×350.

FIG. 18.—Transverse section of anther; tetrads of microspores; ×300.

FIG. 19.—Section of pollen grain with reduced number of chromosomes; ×500.

FIG. 20.—Uninucleate pollen grain; ×350.

FIG. 21.—Binucleate pollen grain; ×350.

FIG. 22.—Longitudinal section of ovule with archesporial cell; ×300.

FIG. 23.—Longitudinal section of ovule through megaspore mother cell and tapetal cell; ×500.

FIG. 24.—Longitudinal section of ovule; megaspore mother cell; integuments; ×300.

FIG. 25.—First division of megaspore mother cell; ×350.

FIG. 26.—Megaspore mother cell divided; ×350.

FIG. 27.—Tetrad of megaspores; ×350.

FIG. 28.—Longitudinal section through binucleate embryo sac; ×350.

FIG. 29.—Longitudinal section through tetranucleate embryo sac; ×350.

FIG. 30.—Longitudinal section through mature embryo sac; ×350.

FIG. 31.—Micropylar end of embryo sac; pollen tube; two-celled endosperm; ×600.

FIG. 32.—Longitudinal section of micropylar end of embryo sac showing early condition of endosperm; ×300.

FIG. 33.—Section of four-celled embryo; ×500.

FIG. 34.—Section of eight-celled embryo; ×500.

FIG. 35.—Longitudinal section through an older embryo; ×500.

FIG. 36.—Longitudinal section of embryo and suspensor; ×300.

FIG. 37.—Longitudinal section of embryo from mature seed; ×50.

FIG. 38.—Transverse section of petiole; ×50.

FIG. 39.—Transverse section of portion of a fibrovascular bundle of a petiole; ×300.

FIG. 40.—Transverse section of portion of peduncle; ×50.