evolution from the sporangium-bearing leaf of the ferns, which is often interpreted as a modified branch system (see page 305).

The Ovule. In the development of an ovule, at first a small rounded protuberance appears (Fig. 327). This is the nucellus, or megasporangium proper. At its base an integument then arises as a ring of tissue, the nucellus meanwhile increasing in prominence. Later, if a second integument is to be formed, it arises outside the first one. The integument or integuments grow out beyond the nucellus, leaving a narrow passageway, the micropyle. In the Archichlamydeae and Monocotyledoneae two integuments are generally present, but in nearly all the Metachlamydeae there is a single massive one. As a rule, the ovule is borne on a short stalk, the *funiculus*, the part of the ovary to which it is attached being the *placenta*. The basal portion of the ovule is called the *chalaza*.

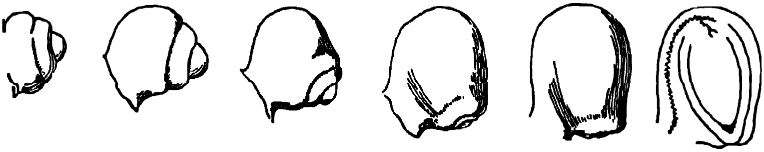

FIG 327. Successive stages in the development of an anatropous ovule, the last representing a section through a mature ovule. (*After Gray.*)

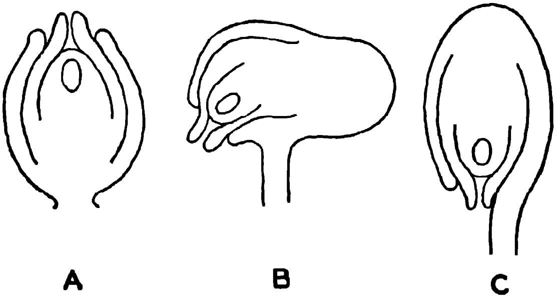

FIG. 328. Directions of ovules: *A*, orthotropous; *B*, campylotropous; *C*, anatropous. (*After Coulter.*)

When mature, ovules may be erect (*orthotropous*), curved (*campylotropous*), or inverted (*anatropous*) (Fig. 328). There are also intermediate conditions. The first represents the most primitive condition and is characteristic of most cauline ovules. It is found among the Urticaceae, Polygonaceae, Xyridaceae, and a few other relatively primitive families of Archichlamydeae and Monocotyledoneae. The second type is also uncommon, being found among the Chenopodiaceae, Caryophyllaceae, Cruciferae, and Gramineae. The third condition is most advanced and most common. Anatropous ovules are found in many of the Archichlamydeae and Monocotyledoneae, and almost exclusively in the

Metachlamydeae. In anatropous ovules having two integuments, the outer one is united on one side with the funiculus.

The development of the ovule is eusporangiate. Generally a single hypodermal initial is differentiated at the apex of the nucellus, but occasionally there are two or more initials, especially among the lower families of Archichlamydeae. Ordinarily the initial, by a periclinal division, gives rise to an outer *primary parietal cell* and an inner *primary sporogenous cell*, as in the microsporangium (Fig. 329). The parietal cell may divide periclinally once or twice again, or it may remain undivided. In practically all the Metachlamydeae, and exceptionally in the two other groups of angiosperms, wall tissue is eliminated, the hypodermal initial functioning directly as the megaspore mother cell (Figs. 330*A* and 333*A*). In all other angiosperms the primary sporogenous cell is the megaspore mother cell. It gives rise, by two successive divisions, usually to a linear tetrad, the reduction in the number of chromosomes taking place at this time (Fig. 330*B*–*D*). A T-shaped arrangement of the megaspores is not infrequent.

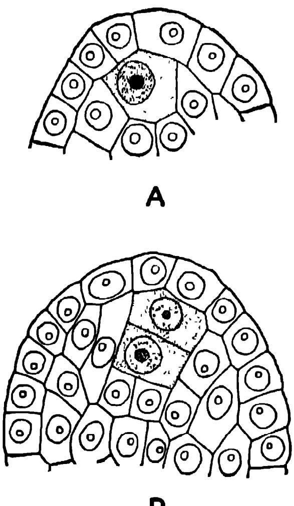

FIG. 329. Early development of the megasporangium of the willow (*Salix*), showing single hypodermal initial (*A*) and the two cells derived from it (*B*): the primary parietal cell (outer shaded one) and the primary sporogenous cell. (*After Chamberlain.*)

The Female Gametophyte. As in gymnosperms, the female gametophyte (embryo sac) develops within the tissues of the ovule and similarly is nearly always formed by the innermost megaspore, the other three degenerating. The functional megaspore greatly enlarges, encroaching upon and absorbing the abortive megaspores as well as more or less of the surrounding nucellar tissue (Fig. 330*E*). Typically the megaspore nucleus gives rise to eight nuclei by three successive divisions (Figs. 330*F*–*H* and 331). Thus, as in gymnosperms, the development of the female gametophyte is initiated by free-nuclear division, but in angiosperms the nuclei are almost always definitely eight in number. There is no wall formation at this stage, but the free nuclei exhibit a striking polarity, four being at one end of the embryo sac and four at the other end. This polarity is established after the first nuclear division, when a large vacuole appears between the daughter nuclei (Fig. 330*G*).

One nucleus from each polar group now comes to the center of the embryo sac. These two nuclei, called *polar nuclei*, come in contact with each other and generally unite at once to form the *fusion nucleus*, or some-

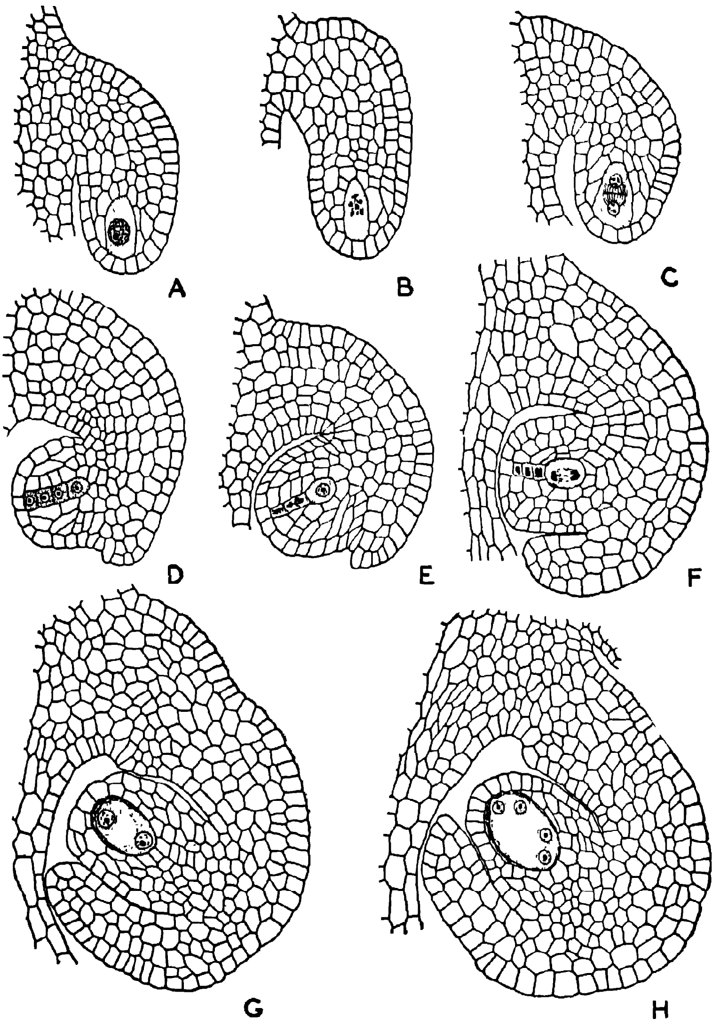

FIG. 330. Megasporogenesis and early development of the embryo sac of *Anemone patens*, ×200. *A*, young ovule with megaspore mother cell; *B*, first meiotic division; *C*, completion of first division; *D*, linear tetrad of megaspores; *E*, functional megaspore enlarging; *F*, division of megaspore nucleus; *G*, 2-nucleate embryo sac; *H*, 4-nucleate embryo sac. (*From preparations supplied by Dr. George H. Conant.*)

times remain distinct (Fig. 331). The three nuclei left at the micropylar end of the embryo sac become organized as naked cells, forming the *egg apparatus*. Of these, one is the *egg* and the two others are *synergids*. Ordinarily the egg lies between the synergids and slightly exceeds them in size; its nucleus is farther from the micropyle than their nuclei are. Usually the three cells forming the egg apparatus are pyriform. The synergids are generally interpreted as potential eggs normally incapable of being fertilized. The three nuclei at the chalazal end of the embryo sac, which is the one opposite the micropylar end, are usually organized as small naked or walled cells called *antipodals*. The antipodals, sometimes ephemeral, are usually somewhat persistent, rarely giving rise later to an extensive tissue. The antipodals are said to be nutritive in function and probably represent vegetative cells of the female gametophyte in various stages of disappearance.

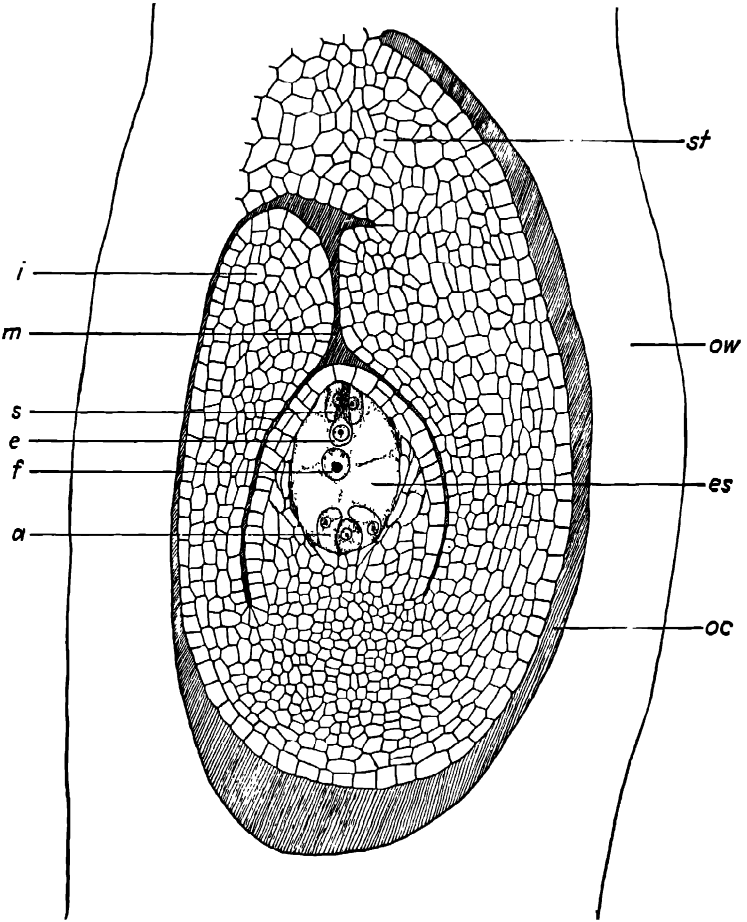

Fig. 331. Ovule of *Anemone patens* with mature embryo sac, ×200; *ow*, ovary wall; *oc*, ovary cavity; *st*, stalk of ovule; *i*, integument; *m*, micropyle; *es*, embryo sac; *s*, synergid; *e*, egg; *f*, fusion nucleus; *a*, antipodal cell.

Variations in Embryo-sac Development. The development of the ordinary type of embryo sac is characterized by two important features:

(1) Five successive nuclear divisions intervene between the megaspore mother cell and the formation of the egg. (2) The embryo sac is derived from a single megaspore, the innermost one. Numerous deviations from this type of development are seen throughout the angiosperms. The principal ones are as follows (Fig. 332):

Oenothera. In *Oenothera* and other members of the Onagraceae, a linear tetrad of megaspores is formed in the usual way but, with few exceptions, the outermost (micropylar) megaspore, rather than the innermost (chalazal) one develops into the embryo sac. Only four successive nuclear divisions intervene between the megaspore mother cell and the egg. The nucleus of the functional megaspore gives rise to two nuclei, both of which remain at the micropylar end of the embryo sac, a vacuole appearing below them. Each again divides and, of the four nuclei thus formed, three are organized into the egg apparatus, while the fourth becomes a polar nucleus. Because of the absence of a fifth nuclear division, there is no second polar nucleus and there are no antipodals.

Allium. This type of embryo sac occurs not only in certain other genera of Liliaceae, such as *Scilla* and *Trillium*, but also in numerous genera belonging to many other families. The megaspore mother cell divides into two cells of which the upper one soon degenerates, while the lower one undergoes three successive free-nuclear divisions to form the embryo sac. When mature, this displays the usual kind of eight-nucleate organization. It is apparent that only four nuclear divisions occur between the megaspore mother cell and the egg and that two megaspore nuclei participate in the formation of the embryo sac.

Peperomia. In this genus, one of the Piperaceae, all four megaspore nuclei are involved in the formation of the embryo sac, no walls being formed between them. The four nuclei are arranged in a cross-like manner, with a large vacuole between them; two successive nuclear divisions follow, the resulting 16 free nuclei being arranged in various ways, depending on the species. The egg apparatus consists of the egg and a single synergid. In *Peperomia pellucida* eight nuclei form the fusion nucleus and six degenerate, while in *Peperomia hispidula* 14 nuclei form the fusion nucleus.

Various modifications of the *Peperomia* type are seen in certain other families. Thus, in *Gunnera*, three nuclei form the egg apparatus, seven unite to form the fusion nucleus, and six degenerate. In the Penaeaceae and certain species of *Euphorbia* the 16 free nuclei are arranged in four groups of four each. One member of each group becomes a polar nucleus, the four polar nuclei fuse, while the three remaining nuclei in each group become organized as cells. The three cells at the upper end of the embryo sac constitute the egg apparatus, the other cells finally degenerating.

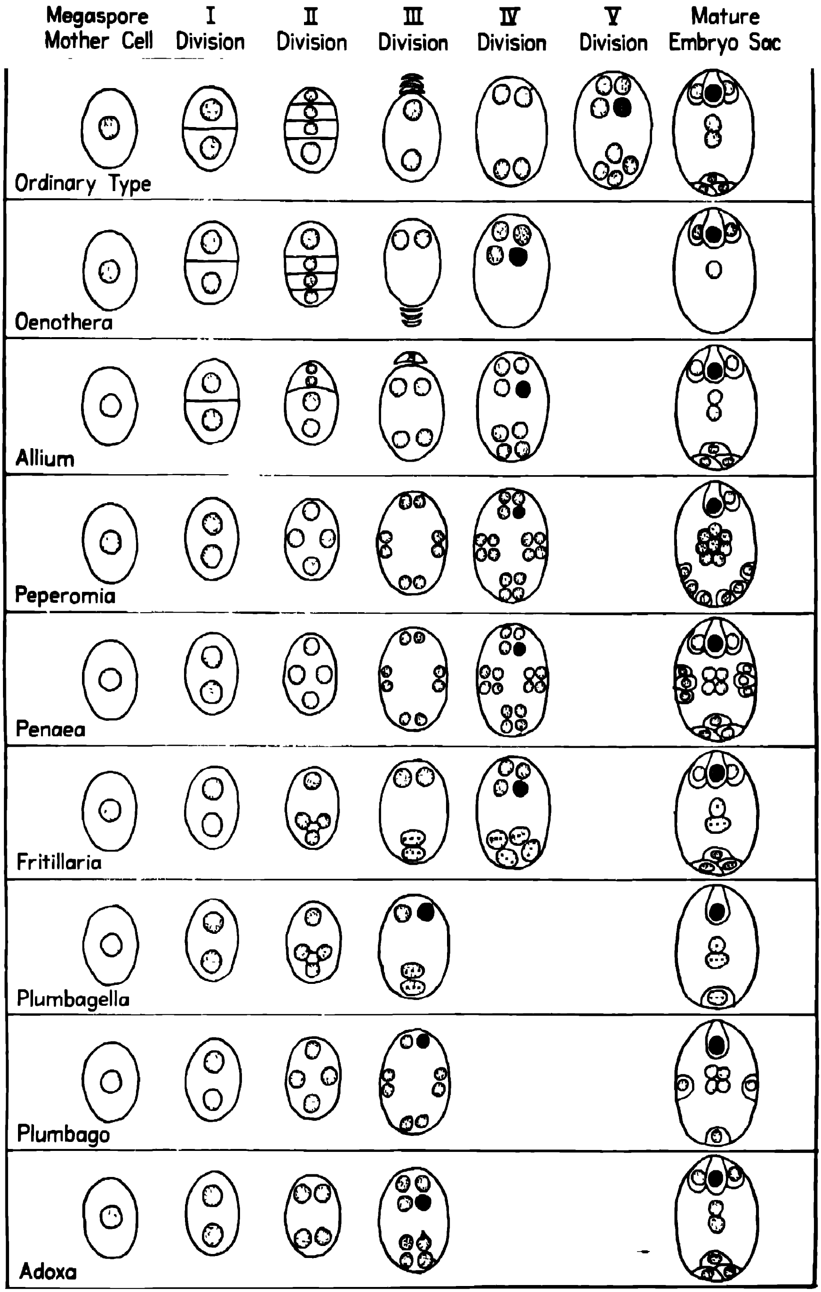

FIG. 332. Principal types of embryo-sac development in angiosperms.

Fritillaria. In *Fritillaria*, *Tulipa*, *Lilium*, and certain other Liliaceae, as well as members of other families, a characteristic development occurs (Fig. 333). The four megaspore nuclei, arranged in a linear row, are not separated by walls. As the embryo sac enlarges, the three lower megaspore nuclei migrate to the chalazal end. All four nuclei now begin to divide, but before the division is complete, the three lower nuclei fuse. As a result, a second four-nucleate stage appears, the two micropylar nuclei being separated from the two chalazal ones by a large vacuole. The micropylar nuclei are haploid, the chalazal ones triploid. After another free-nuclear division occurs, the upper group of four nuclei give rise to the egg, two synergids, and a haploid polar nucleus, the lower group to three antipodals and a triploid polar nucleus. Sometimes only two antipodals are formed.

Plumbagella. The embryo sac of *Plumbagella,* one of the Plumbaginaceae, closely resembles that of *Fritillaria.* Four megaspore nuclei arise without any wall formation. The three lower nuclei pass to the chalazal end of the embryo sac, a large vacuole appearing between them and the micropylar nucleus. The three chalazal nuclei fuse. Both nuclei now divide and the embryo sac usually remains four-nucleate. The egg is organized from one of the two haploid nuclei, an antipodal cell from one of the two triploid nuclei. The fusion nucleus is formed by the union of the two remaining nuclei, one of which is haploid and the other triploid.

Plumbago. In *Plumbago* and several other genera of the Plumbaginaceae, a unique type of embryo sac is seen. The four megaspore nuclei, formed without the appearance of walls and arranged in a cross-like manner, undergo one more division. One of each pair of nuclei becomes a polar nucleus, the second member of the micropylar pair is organized into the egg, while the three other nuclei degenerate. The mature embryo sac has only two nuclei—that of the egg and a fusion nucleus formed by the union of the four polar nuclei.

Adoxa. The type of development seen in this genus and in *Sambucus*, both members of the Caprifoliaceae, has been reported in members of many other families, but some of these (*e.g.*, *Lilium*) have been shown to belong to other types, while many others are doubtful. In *Adoxa* no cell-wall formation accompanies the two divisions of the megaspore mother cell, the four nuclei dividing again to form an eight-nucleate gametophyte. Thus the egg is separated from the megaspore mother cell by only three free-nuclear divisions and all four megaspore nuclei participate in the formation of the embryo sac. This has the ordinary type of mature organization.

Male Gametophyte. In angiosperms the male gametophyte is reduced even more than in gymnosperms. No prothallial cells are produced. Before the anther dehisces, the microspore nucleus divides to form the

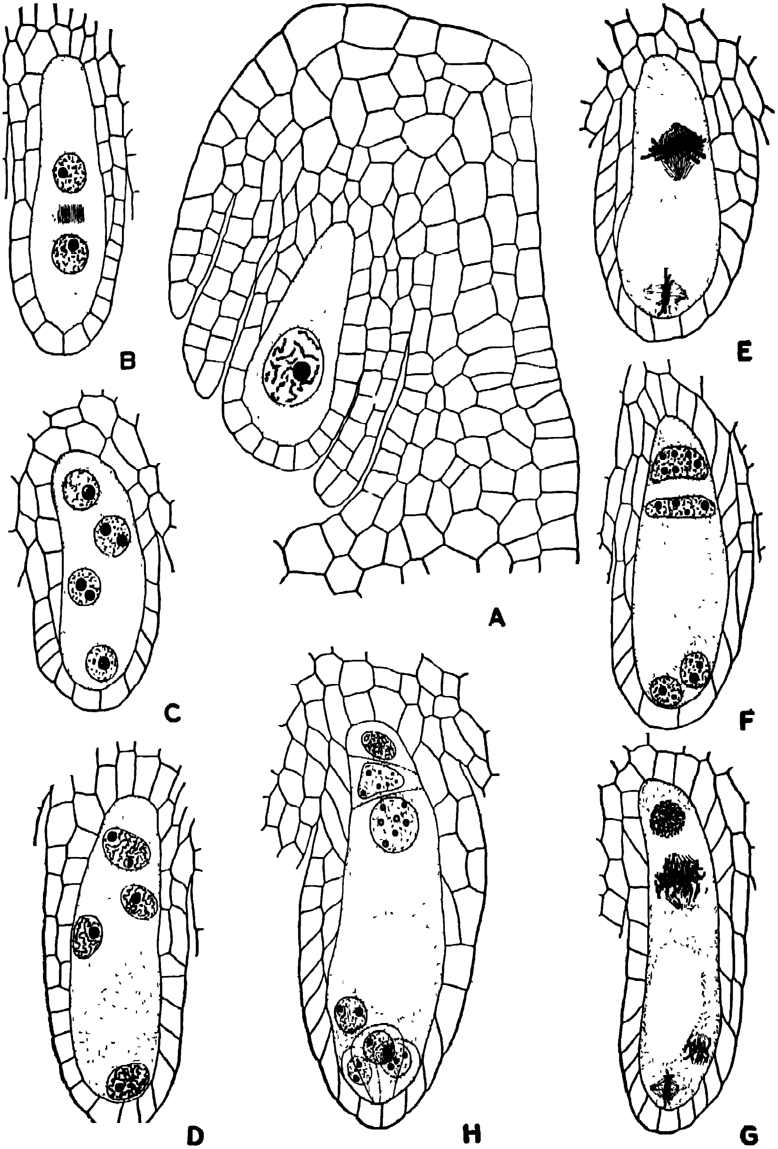

FIG. 333. Development of the embryo sac of *Fritillaria biflora* ×200. *A*, entire ovule with megaspore mother cell; *B*, 2-nucleate stage; *C*, first 4-nucleate stage; *D*, the four megaspore nuclei beginning to divide; *E*, third division, the three chalazal nuclei having fused to form a single large mitotic figure; *F*, completion of division, resulting in second 4-nucleate stage, the two micropylar nuclei being haploid and the two chalazal ones triploid; *G*, the two micropylar nuclei and one of the chalazal nuclei dividing again; *H*, mature embryo sac with egg, two synergids, and haploid polar nucleus at micropylar end and triploid polar nucleus and two antipodal cells at chalazal end.

generative nucleus and tube nucleus, the former becoming organized as a small, naked generative cell lying within the larger tube cell (Fig. 334). The generative cell is usually elliptical, lenticular, or spindle-shaped. The tube nucleus is generally large, with a large nucleolus and little chromatin. The generative nucleus is usually smaller, with a small nucleolus or none, and with considerable chromatin. The generative cell gives rise directly to two male cells, dividing either within the pollen grain or, somewhat more frequently, in the pollen tube. The male cells show considerable variation in form but are never ciliated. In most angiosperms the male cells remain intact, while in some the membrane around each seems to disappear, leaving their nuclei free. The male nuclei often become vermiform, especially after entering the embryo sac.

Fertilization. As in gymnosperms, pollination must precede fertilization but, because the ovules of angiosperms are enclosed in an ovary, the pollen grains cannot come in contact with them. Pollen is transferred by various agencies from the anther to the receptive surface of the style (the stigma), where it germinates, putting forth a long pollen tube that grows down the inside of the style and into the cavity of the ovary. Branching pollen tubes, characteristic of gymnosperms, are found in only a few angiosperms, notably among members of the amentiferous orders.

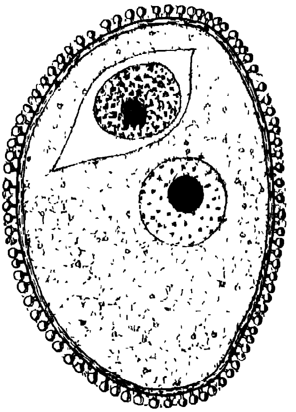

FIG. 334 Section of a pollen grain of lily (*Lilium auratum*) in the shedding condition, ×750. The smaller, naked generative cell lies within the larger tube cell, each having its own nucleus.

Where there is a stylar canal, the pollen tube usually grows down through it, but where the style is solid, as is more commonly the case, the tube secretes enzymes that digest a passageway to the ovary. The nucleus and cytoplasm of the tube cell, as well as the generative cell, pass down the pollen tube as it develops. The tube nucleus usually lies at the tip of the advancing pollen tube and apparently is concerned with its development. While the tube is developing, or frequently before the pollen grain is shed, the generative cell gives rise to two male cells.

Upon reaching the cavity of the ovary, the pollen tube grows along the ovary wall until it reaches one of the ovules, which it then enters, ordinarily through the micropyle. After penetrating the intervening nucellar tissue, the tip of the pollen tube ruptures and its contents are discharged into the embryo sac. The tube nucleus soon disintegrates, but both male cells (or male nuclei, as the case may be) enter the embryo sac. One of the male nuclei penetrates the egg and unites with the female nucleus, thus effecting fertilization (Fig. 335). Although distinct male cells may be present in the pollen tube, or even in the embryo sac, there is evidence indicating that, in most angiosperms, only a male nucleus enters the cytoplasm of the egg. Immediately after fertilization, the egg becomes surrounded by a cell wall.

The second male nucleus entering the embryo sac now unites with the nucleus resulting from the fusion of the two polar nuclei, thus forming the *primary endosperm nucleus.* This unique behavior, which has been called "double fertilization," has been observed in so many angiosperms that it must be regarded as characteristic of the group as a whole. Usually one of the synergids is destroyed by the entrance of the pollen tube, while the other synergid, as well as the antipodal cells, generally disappear soon after fertilization has taken place.

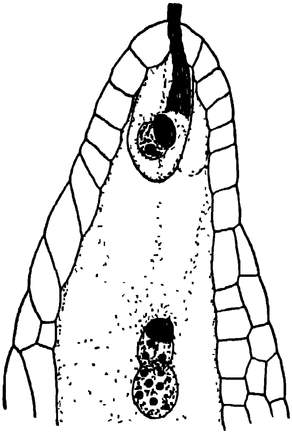

FIG. 335. Fertilization in *Fritillaria biflora*, ×250. One male nucleus is in contact with the egg nucleus, while the other has joined the two polar nuclei.

Although ordinarily the pollen tube enters the ovule through the micropyle (*porogamy*), in some of the more primitive Archichlamydeae it may penetrate the lower end of the ovule. This behavior, known as *chalazogamy*, has been observed in the Casuarinaceae, Juglandaceae, Corylaceae, Urticaceae, and Euphorbiaceae. In certain other angiosperms the pollen tube may follow an intermediate route, entering the ovule through the integument (*mesogamy*).

The behavior of the polar nuclei is variable, depending on the species. Generally they unite before the pollen tube enters the embryo sac, forming the fusion nucleus (Fig. 331). To this the male nucleus later is added. Sometimes, as in *Fritillaria* and *Lilium*, the fusion of the polar nuclei is delayed until the male nucleus has joined them, all three then fusing simultaneously (Fig. 335). Sometimes the polar nuclei remain at opposite ends of the embryo sac until the pollen tube has entered. Then the male nucleus fuses with the micropylar polar nucleus, the other one joining them later.

Because typically a male nucleus unites with two haploid polar nuclei, the primary endosperm nucleus, of course, is triploid. In some forms, however, as in the Onagraceae, it is diploid, being formed by a union between the male nucleus and one polar nucleus; while in such genera as *Peperomia*, *Fritillaria*, *Lilium*, *Plumbago*, and *Penaea* various degrees of polyploidy are attained, the primary endosperm nucleus arising from the fusion of four or more nuclei of the embryo sac, with the addition of the male nucleus.

Following fertilization, the petals and stamens wither and drop off, and often the sepals do likewise. As the ovules are transformed into seeds, the ovary enlarges to form a fruit. Thus normally fertilization provides a stimulus that has far-reaching effects.

Endosperm. Typically endosperm arises from a triple-fusion nucleus, division of which usually precedes that of the fertilized egg. Sometimes each of the nuclear divisions is accompanied by the formation of a wall, so that a tissue is formed at once (Fig. 336*A*). More commonly, however, the formation of endosperm is initiated by free-nuclear division (Fig. 336*B*). These free nuclei are usually parietally placed but sometimes fill the embryo sac. Unless the endosperm is absorbed by the embryo while still in the free-nuclear stage, wall formation then takes place, often simultaneously throughout the endosperm, resulting in a compact tissue without intercellular spaces. Reserve food becomes stored in its cells, generally in large quantities. This may be deposited as hemicellulose on the cell walls, which often become very thick, as in the date and many other palms. In some angiosperms, as in many of the Podostemaceae and Orchidaceae, the endosperm is absent or greatly reduced, often being represented by only a few free nuclei. The endosperm may persist in the seed as a food-storage tissue or may be entirely absorbed by the developing embryo.

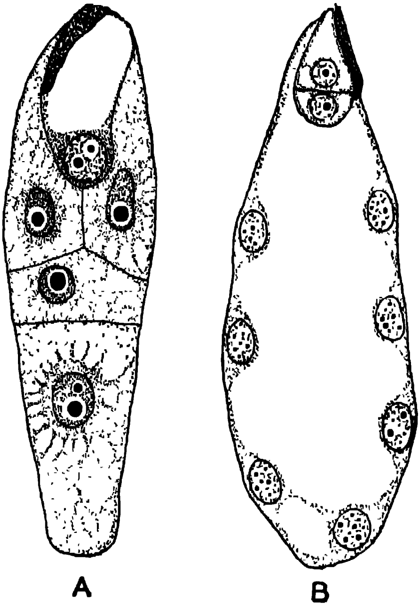

FIG. 336. vo methods of endosperm formation. , *Silphium laciniatum*, nuclear division followed immediately by wall formation, ×300; *B*, *Fritillaria biflora*, endosperm arising by free-nuclear division, ×150. In *A*, the fertilized egg (above) has not yet divided; in *B*, it has divided once.

The integument or integuments of the ovule are transformed into the testa of the seed. The nucellus is almost or entirely destroyed during the development of the seed, but in such forms as the Centrospermales it persists and gives rise to a tissue, called *perisperm*, which becomes the chief food-storage region. In the Nymphaeaceae the seed contains both endosperm and perisperm.

The nature of the endosperm in angiosperms is very confusing. In gymnosperms it is obviously vegetative tissue of the female gametophyte, and thus necessarily arises before fertilization. In angiosperms it arises after fertilization, ordinarily from a triple fusion of nuclei, one of which is male, another female (since it is sister to the egg nucleus), and a third vegetative. Some have regarded endosperm as gametophyte tissue stimulated to develop by nuclear fusions. Others have considered it to be sporophyte tissue, the twin of the embryo. Since it is ordinarily triploid, however, it cannot be either gametophyte or sporophyte in the strict sense of the terms. It might better be regarded as undifferentiated tissue continuing the growth of the female gametophyte and stimulated to develop by nuclear fusions. The union of the male nucleus with the polar nuclei cannot be regarded as an act of fertilization because (1) the effec of the fusion is merely to furnish a growth stimulus; (2) more than a single male and female nucleus is involved; and (3) the product of the triple fusion is not a new individual.

Embryo. The development of the embryo from the fertilized egg does not, as in nearly all gymnosperms, begin with free-nuclear division, but each division is accompanied by the formation of a cell wall. Since embryogeny differs in dicotyledons and monocotyledons, except in the earliest stages, a representative example of each will be described.

Capsella. The sequence of embryonic stages can be followed easily in the common shepherd's-purse (*Capsella*), a dicotyledon belonging to the Cruciferae. Here the zygote, by a series of transverse divisions, gives rise to a proembryo of varying length (Fig. 337*A*, *B*). The terminal cell (the one farthest from the micropyle) forms practically all the embryo, while the other cells give rise to the suspensor. The basal cell of the suspensor is much larger than the others. The terminal cell undergoes three successive divisions, each at right angles to the preceding one, thus resulting in the formation of octants (Fig. 337*C*, *D*). The first division is always vertical but the second vertical and the horizontal divisions may occur in either order. Of the eight cells now constituting the embryo, the upper tier of four cells eventually gives rise to the cotyledons and stem tip, the basal tier to all the hypocotyl except its tip.

The suspensor elongates, becoming 8 to 10 cells in length and pushing the embryo downward. A peripheral layer of primary epidermal cells, the *dermatogen*, is now cut off by periclinal walls appearing in all 8 cells of the embryo (Fig. 337*E*). Additional longitudinal and transverse divisions occur in the inner cells and soon the *periblem*, comprising the cells eventually to produce the cortex, is differentiated from the *plerome*, which gives rise to the stele (Fig. 337*F*). The plerome is complete at the tip of the hypocotyl but the periblem and dermatogen are not. They are completed at the expense of the adjacent cell of the suspensor. This divides

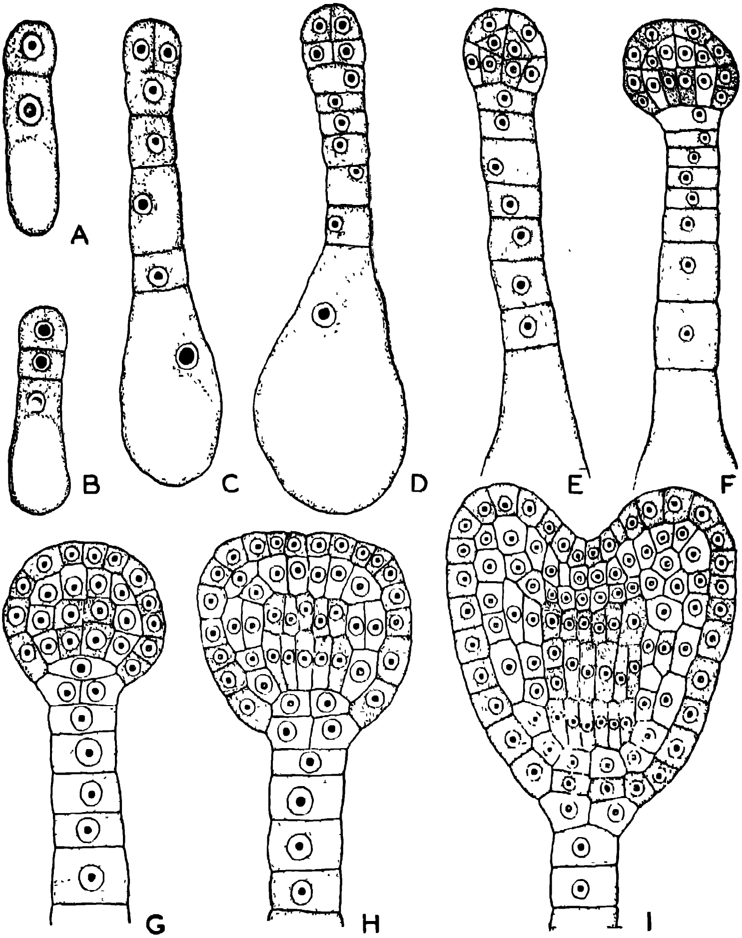

FIG. 337. Successive stages in early development of the embryo of *Capsella bursa-pastoris*, a dicotyledon, ×500. *A*, two-celled proembryo; *B*, three-celled proembryo, *C*, proembryo with longitudinally divided terminal cell and enlarged basal cell, *D*, terminal cell divided to produce octants, four cells lying beneath the four shown, *E*, cutting off of dermatogen by periclinal walls; *F*, differentiation of periblem and plerome, the former indicated by lighter shading; the cell at the upper end of the suspensor is the hypophysis, *G*, completion of periblem by cell cut off the hypophysis; *H*, later stage, showing cell divisions throughout the embryo; *I*, completion of dermatogen from middle tier of cells derived from the hypophysis.

transversely into two cells. The upper cell, called the *hypophysis*, contributes to the embryo, while the lower one is added to the suspensor.

The hypophysis divides transversely, the cell next to the embryo completing the periblem and the other cell undergoing two longitudinal divisions at right angles to each other to form a plate of four cells (Fig. 337*G, H*). In a later stage, each of these four cells divides transversely, the upper tier completing the dermatogen and the lower tier forming the first layer of the rootcap (Fig. 337*I*). This stage is further marked by the appearance of the two cotyledons, one on each side of the stem tip, which lies at the upper end of the hypocotyl. Thus the stem tip is terminal and the cotyledons are lateral.

Many dicotyledons follow the general course of embryogeny as seen in *Capsella*, but there are a number of departures from it. In the Nymphaeaceae, for example, a globular proembryo is developed and generally no suspensor is formed. In the Myrtaceae a massive proembryo fills the micropylar end of the embryo sac and several embryos may be differentiated from it. In the Rubiaceae and Leguminosae the suspensor is enormously elongated.

Sagittaria. The development of the embryo of *Sagittaria*, one of the Alismaceae, is representative of the more primitive families of monocotyledons. Here the proembryo is a filament of three cells—a large basal cell, a middle cell, and a terminal cell (Fig. 338*A*, *B*). The basal cell enlarges considerably but does not divide, constituting the greater part of the suspensor. The middle cell, by a series of transverse and vertical divisions, forms the stem tip, hypocotyl, root tip, and the rest of the suspensor (Fig. 338*C–F*). The terminal cell gives rise to the cotyledon. It divides first by a vertical wall and then by walls in the two other planes, thus forming octants (Fig. 338*D*, *E*). The dermatogen arises in the cotyledon by the formation of periclinal walls and proceeds toward the root end of the embryo (Fig. 338*G*). Later the periblem and plerome are differentiated. The stem tip arises as a depression in the side of the embryo, thus being lateral in position rather than terminal as in the dicotyledons (Fig. 338*H*, *I*).

A number of modifications of the *Sagittaria* type of embryogeny have been noted. For example, the Araceae have a massive proembryo and lack a suspensor. The Liliaceae have a filamentous proembryo that soon becomes massive. In the Orchidaceae the body regions are not differentiated and, in many forms, a large suspensor becomes a haustorial organ.

In *Agapanthus*, a member of the Liliaceae, dicotyledonous embryos are occasionally produced. The proembryo is more or less massive. Its tip broadens and a peripheral cotyledonary zone gives rise to two growing points. The entire zone then grows upward, resulting in the formation of a cotyledonary ring surrounding a depression from which the stem tip develops. If both growing points continue to develop equally, a dicotyledonous embryo results, but if only one continues, a monocotyledonous embryo is formed. This indicates that dicotyledony is more primitive than monocotyledony. It also suggests that the stem tip is really terminal and the cotyledons lateral, even though only one cotyledon is produced.

Apomixis. Irregularities in the normal process of sexual reproduction occur occasionally in some angiosperms, constantly in others. *Apomixis* is a condition in which sexual reproduction in the flower is replaced by some form of asexual reproduction. It may take the form of *parthenogenesis*, which is the development of an embryo from an unfertilized egg. This has been observed in a number of angiosperms, such as *Thalictrum*, *Antennaria*, *Alchemilla*, *Erigeron*, and *Taraxacum*. In all these and similar cases the reduction of chromosomes fails to take place in connection

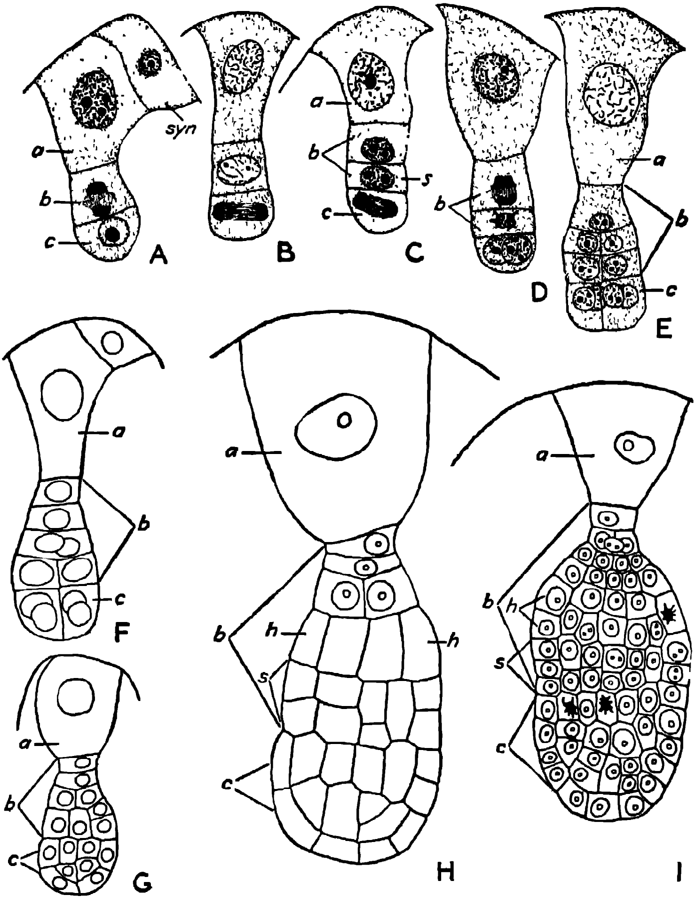

FIG. 338. Successive stages in early development of the embryo of *Sagittaria variabilis*, a monocotyledon. *A* and *B*, three-celled proembryos, showing synergid (*syn*), basal cell (*a*), middle cell (*b*), and terminal cell (*c*) from which the cotyledon is derived; *C*, division of middle cell into two cells, one of which (*s*) gives rise to the stem tip; *D*, slightly older stage; *E*, formation of four cells from the terminal cell; *F*, further development of the middle region; *G*, differentiation of dermatogen in the terminal region; *H*, further development of dermatogen and differentiation of middle region into hypocotyl (*h*) and stem tip (*s*); *I*, later stage. (*After Schaffner.*)

with megaspore formation. Consequently the egg is a diploid cell and fertilization is unnecessary. Haploid parthenogenesis is very rare, having been reported in only a few plants.

The development of an embryo from other cells of the embryo sac than the egg, called *apogamy*, has been observed in *Antennaria, Alchemilla, Allium, Iris*, and other forms, but is not known to occur constantly in nature. Here a synergid or an antipodal gives rise to an embryo, which may be diploid or haploid, depending on whether or not meiosis occurred in the division of the megaspore mother cell. *Sporophytic budding* occurs when cells of the nucellus or integument project into the embryo sac and give rise to embryos. It has been reported in *Citrus, Coelebogyne, Funkia*, and other angiosperms, where it frequently accompanies apogamy.

The Fruit. The fruit develops as the seeds ripen and always encloses them. Like the flower, it has no morphological individuality. A *true fruit* consists merely of a ripened ovary, while an *accessory fruit* includes in addition one or more associated parts of the flower, such as the calyx or receptacle. The ripened ovary wall is the *pericarp*. When a fruit develops from an inferior ovary, its wall consists of the pericarp united with the receptacle. At maturity, fruits may be dry or fleshy; when dry, they may be dehiscent or indehiscent. Sometimes the pericarp becomes fleshy on the outside and stony within. Some fruits develop from simple pistils, others from compound pistils. An *aggregate fruit* arises from a group of separate ovaries, belonging to a single flower, that become more or less consolidated. A *multiple fruit* is similar, except that it is derived from the ovaries of a number of flowers. The development of a fruit without fertilization is called *parthenocarpy*. Parthenocarpic fruits are nearly always seedless.

The Seedling. In practically all angiosperms the embryo goes into a state of dormancy as the seed matures, this being accomplished by the withdrawal of most of the water present and by important chemical changes. In the presence of favorable external conditions, germination occurs by the resumption of growth of the embryo and of other processes within the seed.

In many seeds, particularly those of dicotyledons, the endosperm is completely absorbed by the embryo while the seed is ripening, the reserve food being thus transferred to the embryo itself, principally to the cotyledons. In seeds containing endosperm, this is absorbed by the embryo in germination.

When germination begins, the root tip pushes through the testa and grows downward into the ground, giving rise to the primary root. The hypocotyl may remain short or may elongate considerably, depending on the kind of germination. Where it remains short, the cotyledon or cotyledons remain inside the testa, the plumule soon giving rise to a shoot that pushes upward. Where the development of the primary root is accompanied by elongation of the hypocotyl, the cotyledon or cotyledons are pulled out of the testa and are carried above the ground, where they often expand and function as foliage leaves. In such seedlings the development of the plumule into the shoot is usually considerably delayed.

Chief Orders of Angiosperms

It would be beyond the scope of the present work to include an extensive account of the classification of angiosperms, a subject of concern mainly to the taxonomist. A general survey of the chief orders, however, will demonstrate the complexity of the group and illustrate its principal evolutionary trends, many of which have already been mentioned. The orders in each of the three series do not represent a phylogenetic sequence but merely different levels of progress. The interrelationships of many groups is obscure, so that the tracing of lines of descent is difficult and will not be attempted here.

1. ARCHICHLAMYDEAE

The Dicotyledoneae include the Archichlamydeae and Metachlamydeae. The Archichlamydeae are the primitive stock of angiosperms from which both the Metachlamydeae and Monocotyledoneae have been derived. Their flowers are naked, apetalous, or choripetalous, the parts being usually cyclic but frequently more or less spiral.

Piperales. The Piperales comprise 4 families and about 1,200 species of mostly tropical herbs and shrubs, nearly all belonging to the Piperaceae. The peppers (*Piper*) and peperomias are the best-known examples. The flowers, borne in spikes, are perfect or imperfect, mostly naked, typically trimerous but usually reduced, hypogynous, and mostly apocarpous.

Salicales, Juglandales, and Fagales. These orders, with several others of minor importance, were once grouped together as the Amentiferae, because their flowers are borne in aments or catkins. The Salicales include a single family, the Salicaceae, to which belong the willows (*Salix*) and poplars (*Populus*). The Juglandales also comprise a single family, the Juglandaceae, including the walnuts (*Juglans*) and hickories (*Carya*). The Fagales contain two families, the Corylaceae and Fagaceae. To the Corylaceae belong the birches (*Betula*), alders (*Alnus*), etc., and to the Fagaceae the beeches (*Fagus*), chestnuts (*Castanea*), and oaks (*Quercus*). The Amentiferae are woody plants with imperfect flowers. In the Salicaceae and Corylaceae both kinds of flowers are in aments, but in the Juglandaceae and Fagaceae only the staminate flowers are. In all families except the Salicaceae, the flowers of some members have a simple bract-like perianth. The pistillate flowers are hypogynous in the Salicaceae and epigynous in the other families; they are syncarpous in all.

Urticales. This is an order of about 1,500 species distributed among 4 families: the Ulmaceae and Moraceae, which are mostly woody, and the Cannabinaceae and Urticaceae, which are mostly herbaceous. Representative members of the Ulmaceae are the elms (*Ulmus*); of the Moraceae, the mulberries (*Morus*) and figs (*Ficus*); of the Cannabinaceae, hemp (*Cannabis*) and hop (*Humulus*); of the Urticaceae, the nettles (*Urtica*). The flowers are mostly imperfect, apetalous, hypogynous, and syncarpous. The stamens equal the perianth segments in number. The ovary is unilocular, usually having a single ovule.

Santalales. These are parasitic herbs and woody plants, numbering about 1,200 species, mostly tropical. The Loranthaceae and Santalaceae are the largest of 8 families. The mistletoes belong to the Loranthaceae. The flowers are perfect or imperfect and epigynous, mostly with a petaloid perianth consisting of a single whorl but sometimes differentiated into a calyx and corolla. The stamens equal the sepals in number. There are generally three united carpels, mostly forming a unilocular ovary.

Aristolochiales. This is a small order of herbs and woody plants, the principal family, the Aristolochiaceae, numbering about 200 species. The chief genus is *Aristolochia*. The flowers are perfect and epigynous, with a highly developed petaloid perianth consisting of a single whorl of united parts. The ovary is multilocular and has an indefinite number of ovules.

Polygonales. This is a small order of 800 species of herbs and woody plants, all belonging to the Polygonaceae. Representative genera are smartweed (*Polygonum*), dock (*Rumex*), rhubarb (*Rheum*), and buckwheat (*Fagopyrum*). The small flowers, mostly borne in spikes, are perfect or sometimes imperfect, regular, hypogynous, and syncarpous. The perianth, consisting of a single whorl, is bract-like. The unilocular ovary contains a single ovule.

The preceding orders, with some others of less importance, constitute the apetalous series of the Archichlamydeae. They are characterized by flowers that, with few exceptions, have a simple perianth which is not differentiated into a distinct calyx and corolla but consists of a single whorl of parts. Some members have naked flowers. Most of these orders are of uncertain relationships. Some may be primitive, while others are doubtless reduced.

The following orders, constituting the choripetalous series of the Archichlamydeae, typically have a perianth consisting of two distinct whorls—calyx and corolla—the members of which are separate and distinct.

Centrospermales. This assemblage is often broken up into two orders, the Chenopodiales and Caryophyllales. It includes about 3,500 species of herbs grouped into 10 families, of which 4 are of greatest interest, *viz.*, the Chenopodiaceae, to which belong the goosefoots (*Chenopodium*), beet (*Beta*), spinach (*Spinacia*), etc.; the Amaranthaceae, including pigweed (*Amaranthus*) and coxcomb (*Celosia*); the Portulacaceae, represented by *Portulaca;* and the Caryophyllaceae, containing the carnation and pinks (*Dianthus*), catchfly (*Silene*), chickweed (*Stellaria*), etc.

The flowers are mostly perfect, regular, mostly hypogynous, syncarpous, and usually pentamerous. The perianth may consist of either one or two whorls. The ovary is mostly unilocular. The Centrospermales represent a transition between the apetalous and choripetalous dicotyledons, as the lower families have a bract-like undifferentiated perianth, while the higher families have a distinct calyx and corolla, the latter being very showy. A characteristic feature is the presence of abundant perisperm in the seed. This takes the place of endosperm as a food-storage region. The Centrospermales show some resemblances to the Polygonales, and the two orders may be related.

Ranales. The Ranales are a great genetic order, comprising 16 families and about 5,000 species of herbs, shrubs, and trees. The largest family, the Ranunculaceae, has 1,200 species, and includes such common forms as buttercup (*Ranunculus*), *Hepatica*, *Anemone*, *Clematis*, columbine (*Aquilegia*), larkspur (*Delphinium*), and peony (*Paeonia*). Other important familes are the Nymphaeaceae, Berberidaceae, Magnoliaceae, and Lauraceae.

This order is ill defined. The flowers are perfect and mostly regular, but some are irregular. The perianth, usually consisting of a distinct calyx and corolla, is often undifferentiated and petaloid. Although the floral parts are often indefinitely numerous and wholly or partly spiral, there is a strong tendency toward the establishment of a cyclic condition with definite numbers, especially in the perianth. Hypogyny and apocarpy are features of the order, perigyny and syncarpy being infrequent. In the Berberidaceae and Lauraceae the carpels are reduced to one. The Ranales are generally regarded as a primitive order that has given rise both to the more specialized orders of dicotyledons and to the monocotyledons.

Papaverales. This order represents a specialized offshoot from the Ranales. There are 6 families and about 3,600 species, the principal families being the Papaveraceae, Fumariaceae, and Cruciferae. The Cruciferae, with 3,000 species, includes such well-known forms as the mustards (*Brassica*), radish (*Raphanus*), *Alyssum*, stocks (*Matthiola*), shepherd's-purse (*Capsella*), etc. The flowers of the Papaverales are mostly regular, hypogynous or sometimes perigynous, and syncarpous. The flowers are cyclic except that the stamens are spiral in some members. The pistil usually consists of two united carpels, syncarpy being the chief point of difference between this order and the Ranales. The Cruciferae are a distinct family whose members can be recognized by the floral formula 4-4-6-2.

Sarraceniales. This is a small order of insectivorous plants, comprising 3 families, and represented by the pitcher plants (*Sarracenia* and others) and the sundews (*Drosera*). As in the Papaverales, the flowers are regular, hypogynous, and syncarpous. The two orders seem to have undergone a parallel development, the chief difference between them being the placentation.

Rosales. The Rosales constitute the great central order of Archichlamydeae. They include 16 families and 15,000 species of herbs, shrubs, and trees distributed throughout the world. The three chief families are the Saxifragaceae, Rosaceae, and Leguminosae. The Leguminosae, with 12,000 species, is the second largest family of dicotyledons. The Saxifragaceae are represented by the saxifrages (*Saxifraga*), gooseberries and currants (*Ribes*), and *Hydrangea*. The Rosaceae include the roses (*Rosa*), strawberries (*Fragaria*), raspberries and blackberries (*Rubus*), cherries and plums (*Prunus*), hawthorns (*Crataegus*), pear and apple (*Pyrus*), etc. The Leguminosae include the acacias, locust (*Robinia*), lupines (*Lupinus*), clovers (*Trifolium*), beans (*Phaseolus*), peas (*Pisum*), etc.

The Rosales overlap the Ranales, on the one hand, with regularity, hypogyny, apocarpy, and indefinite numbers of stamens and carpels, but advance far beyond them, on the other hand, with irregularity, epigyny, syncarpy, and definite numbers. The perianth is typically pentamerous. The Rosaceae have regular flowers that are perigynous or epigynous and usually have several carpels. The Leguminosae have mostly irregular flowers that are hypogynous or somewhat perigynous and have a single carpel.

Geraniales. This large order of herbs and woody plants, containing about 9,000 species, is broken up into 20 families. Half of the species belong to the Euphorbiaceae, of which the largest genus is *Euphorbia*. Some familiar genera belonging to other families are *Geranium*, *Pelargonium*, *Oxalis*, *Linum*, and *Citrus*. The flowers are regular or irregular, hypogynous, syncarpous, and pentamerous throughout or often reduced. In the Euphorbiaceae the flowers are imperfect and apetalous, while in some members they are naked. The stamens of the Geraniales are rarely more than twice as many as the petals and usually equal to them in number. This is the first definitely cyclic and isocarpic order in the Archichlamydeae, but it shows a tendency to reduce the number of carpels.

Sapindales. The Sapindales, with about 3,000 species, most of which are woody, are separated into 21 families. Here belong the sumacs (*Rhus*), hollies (*Ilex*), maples (*Acer*), buckeyes (*Aesculus*), balsams

(*Impatiens*), etc. The flowers are regular or irregular, mostly hypogynous, and syncarpous. The perianth is mostly pentamerous but the stamens are usually reduced to eight. Most members are isocarpic. This order has developed parallel with the Geraniales, being distinguished from it chiefly by certain obscure ovule characters.

Rhamnales. This order includes about 1,100 species of woody plants belonging to 2 families, the Rhamnaceae, represented by the buckthorns (*Rhamnus*) and *Ceanothus*, and the Vitaceae, including the grapes (*Vitis*) and Virginia creeper (*Parthenocissus*). The flowers are regular, mostly hypogynous, syncarpous, and tetracyclic. The perianth is trimerous or tetramerous. The Rhamnales have developed parallel with the Geraniales and Sapindales, differing from them chiefly in having the stamens opposite the petals instead of alternate with them.

Malvales. This is an order of 8 familes and about 2,300 species of herbs and woody plants. The best-known families are the Tiliaceae, represented by the basswood (*Tilia*), and the Malvaceae, to which belong the mallows (*Malva*), hollyhock (*Althaea*), cotton (*Gossypium*), etc. The flowers are regular, hypogynous, syncarpous, and have a pentamerous perianth. The stamens are usually indefinitely numerous (rarely five) and more or less united. The placentation is axial.

Parietales. The Parietales, containing 30 families and about 5,000 species of herbs and woody plants, is an order representing an extremely confused classification. The most familiar forms are the violets (*Viola*). The order is characterized by parietal placentation, its other characters being rather inconstant. The flowers are regular or irregular; hypogynous, perigynous, or epigynous; and mostly syncarpous. They are typically pentamerous, but the stamens may be 3, 5, 10 or indefinitely numerous.

Opuntiales. Here belongs a single family, the Cactaceae, with about 1,100 species indigenous to America. The flowers are regular, epigynous, and syncarpous; they are peculiar in being spiral and polymerous. Thus the group represents a combination of primitive and advanced features.

Myrtales. This is a large tropical order of herbs and woody plants. It contains about 7,500 species grouped into 19 families, of which the Myrtaceae and Onagraceae are well known. The myrtles (*Myrtus*), *Eugenia*, and *Eucalyptus* belong to the Myrtaceae, while the fireweeds (*Epilobium*), evening primroses (*Oenothera*), and *Fuchsia* are familiar members of the Onagraceae. The flowers are mostly regular, perigynous or epigynous, and syncarpous. The perianth is mostly pentamerous and the stamens often indefinitely numerous. The carpels vary from two to many. This order resembles the Rosales in many ways, but here the carpels are never free.

Umbellales. The Umbellales constitute the highest order of the Archichlamydeae. They include 3 families and about 3,000 species, nearly all herbaceous. Of these, 2,500 species belong to the Umbelliferae, where are found such familiar forms as carrot (*Daucus*), celery (*Apium*), parsnip (*Pastinaca*), and dill (*Anethum*). The order is characterized by regular, epigynous flowers having a tetramerous or pentamerous perianth, a reduced calyx, a single whorl of stamens, and usually a bicarpellary, bilocular ovary with a single ovule in each locule. The floral formula of the Umbelliferae, 5-5-5-2, is an advanced one.

2. METACHLAMYDEAE

The Metachlamydeae are characterized chiefly by their sympetalous corollas, and so are often called the Sympetalae. The entire group has reached a condition of definite numbers for all the floral sets, and therefore is constantly cyclic. The stamens are generally attached to the corolla.

Ericales. The Ericales comprise about 2,000 species of woody plants, mostly shrubs. Of its 6 families, the Ericaceae, with about 1,500 species, is by far the largest. It includes such well-known genera as azalea (*Rhododendron*), wintergreen (*Gaultheria*), heather (*Calluna*), heath (*Erica*), and blueberry (*Vaccinium*). The flowers of the Ericales are regular or nearly so, tetramerous or pentamerous, pentacyclic or sometimes tetracyclic, mostly isocarpic, hypogynous or often epigynous, and syncarpous. In tetracyclic flowers the stamens are opposite the petals. The ovary is multilocular. Some of the Ericaceae are choripetalous and in nearly all the stamens are free from the corolla. Thus this order serves to connect the Archichlamydeae and Metachlamydeae.

Primulales. The Primulales constitute an order of about 1,100 species of herbs grouped into 4 families, of which the Primulaceae is of chief interest. The representative genus is primrose (*Primula*). The flowers are regular, pentamerous, tetracyclic, isocarpic, mostly hypogynous, and syncarpous. The single whorl of stamens stands opposite the petals and not, as in the higher tetracyclic orders, alternate with them. The outer whorl of stamens is often vestigial. The ovary is unilocular and has free-central placentation. In some respects this order resembles the Centrospermales.

Ebenales. This is an order of about 1,000 species of tropical trees and shrubs. There are 4 small families, the characteristic one being the Ebenaceae, of which the ebony and persimmon (*Diospyros*) are examples. The flowers are regular, tetramerous or pentamerous, pentacyclic, isocarpic, mostly hypogynous, and syncarpous. The ovary is multilocular. The floral parts show some variation in number, with an occasional increase in stamens and carpels.

The preceding orders constitute the pentacyclic isocarpic series of

Metachlamydeae, in which the floral formula is typically 5-5-10-5. They are more primitive than the other sympetalous orders and more closely related to the Archichlamydeae. They are, with few exceptions, regular and hypogynous.

The following orders comprise the tetracyclic anisocarpic series of Metachlamydeae, in which the floral formula is generally 5-5-5-2. Here belong three hypogynous and two epigynous orders.

Gentianales. This is a genetic order. It comprises about 5,000 species of herbs and woody plants separated into 5 families, the principal ones being the Oleaceae, Gentianaceae, and Asclepiadaceae. The Oleaceae is represented by the olive (*Olea*), ashes (*Fraxinus*), lilacs (*Syringa*), and privets (*Ligustrum*); the Gentianaceae by the gentians (*Gentiana*); and the Asclepiadaceae by the milkweeds (*Asclepias*). The flowers are regular, tetramerous or pentamerous, tetracyclic, anisocarpic, hypogynous, and apocarpous or syncarpous. They have two carpels. The Oleaceae have the peculiar floral formula of 4-4-2-2.

Tubiflorales. This great central order of Metachlamydeae is closely related to the Gentianales and difficult to separate from it. It includes 20 families and about 16,000 species, most of which are herbs. The eight principal families, with several representative genera, are as follows: Convolvulaceae—bindweed (*Convolvulus*), morning-glory (*Ipomoea*), and dodder (*Cuscuta*); Polemoniaceae—*Polemonium*, *Phlox*, and *Gilia*; Hydrophyllaceae—*Hydrophyllum*, *Nemophila*, and *Phacelia*; Boraginaceae—forget-me-not (*Myosotis*), bluebells (*Mertensia*), and *Heliotropium*; Verbenaceae—*Verbena* and *Lantana*; Labiatae—sage (*Salvia*) and mint (*Mentha*); Solanaceae—nightshade (*Solanum*), tobacco (*Nicotiana*), and *Petunia*; Scrophulariaceae—mullein (*Verbascum*), foxglove (*Digitalis*), and snapdragon (*Antirrhinum*).

The flowers of the Tubiflorales are regular or irregular, mostly pentamerous, tetracyclic, anisocarpic, hypogynous, and syncarpous. They have two carpels (three in Polemoniaceae). The corolla is mostly regular in all families except the Verbenaceae, Labiatae, and Scrophulariaceae, where it is almost always irregular. These three families have only four stamens, or sometimes only two, while the others have five. The ovary is unilocular or bilocular in the Hydrophyllaceae; mostly bilocular in the Convolvulaceae, Solanaceae, and Scrophulariaceae; mostly trilocular in the Polemoniaceae; and mostly tetralocular in the Boraginaceae, Verbenaceae, and Labiatae.

Plantaginales. These are the plantains, comprising one family of about 200 species of herbs. The principal genus is *Plantago*. The flowers are regular, tetramerous, tetracyclic, anisocarpic, hypogynous, and syncarpous. They have two carpels. The corolla is dry and membranaceous. This order is related to the Tubiflorales.

Rubiales. This order consists of over 5,000 species of herbs and woody plants distributed among 5 families, by far the largest being the Rubiaceae, to which belong coffee (*Coffea*) and *Cinchona*. The Caprifoliaceae, another family, is represented by the honeysuckles (*Lonicera*), *Viburnum*, and the elders (*Sambucus*). The flowers are regular or irregular, tetramerous or pentamerous, tetracyclic, anisocarpic, epigynous, and syncarpous. They have usually two or three carpels. The calyx is reduced. This order shows a resemblance to the Umbellales.

Campanulales. This is the culminating order of Metachlamydeae. It includes 8 families and 16,000 species, about 13,000 of which belong to the Compositae, the largest family of dicotyledons. A few well-known genera are goldenrod (*Solidago*), *Aster*, sunflower (*Helianthus*), *Chrysanthemum*, thistle (*Cirsium*), dandelion (*Taraxacum*), lettuce (*Lactuca*), etc. Other familiar families are the Cucurbitaceae, Campanulaceae, and Lobeliaceae. The flowers are regular or irregular, pentamerous, tetracyclic, anisocarpic, epigynous, and syncarpous. They have two or three carpels. The calyx is reduced. A special feature is the tendency of the five stamens to be united in various ways. The flowers of the Compositae are organized to form a compact head surrounded by an involucre of many bracts. The head is usually composed of peripheral ray flowers and central disk flowers.

3. MONOCOTYLEDONEAE

The monocotyledons are generally regarded as having been derived from the Ranales region of the Archichlamydeae. In the lower orders the floral parts fluctuate in number and are more or less spiral in arrangement, while in the higher orders they are constant and cyclic.

Pandanales. This is a very primitive order of about 450 species grouped into 3 families. Many are hydrophytes. The screw pine (*Pandanus*) of the tropics is the representative form, but the most familiar member in temperate regions is the cattail (*Typha*). The flower clusters are usually surrounded, when young, by a conspicuous sheathing bract. The flowers are imperfect and mostly naked, but sometimes a simple bract-like perianth is present. The stamens and carpels show great variation in number and are mostly spiral. Both hypogyny and apocarpy are features of the order.

Helobiales. Here belong about 300 species of primitive aquatic and marsh plants comprising 6 families. Familiar genera are *Potamogeton*, *Sagittaria*, *Elodea*, and *Alisma*. The Helobiales are a genetic group, showing several lines of descent. A sheathing bract surrounds the inflorescence, as in the Pandanales, but the flowers are usually perfect. The flowers may be naked, apetalous, or choripetalous, are usually hypogynous but, in one family, are epigynous. The stamens range from indefinite to definite in number, the pistils from apocarpy to syncarpy. The numerous stamens and apocarpous pistils suggest a relationship to the Ranales.

Glumales. The Glumales include the Cyperaceae, or sedges, and the Gramineae, or grasses, together numbering about 8,000 species. The flowers are surrounded by scale-like bracts, called glumes, the perianth being either wanting or represented by minute scales. The flowers, which are mainly perfect, have six stamens or less (mostly three), and a unilocular ovary with a single ovule. The pistil, commonly said to consist of a single carpel, really is formed of three completely united carpels. All members are hypogynous. There is much evidence indicating that the Glumales are not primitive but reduced from lily-like ancestors.

Palmales. This order includes only the Palmaceae, with about 1,200 species, mostly of tropical and subtropical trees. The flowers are small, mostly imperfect, and borne in a massive inflorescence at first surrounded by a large sheathing bract. The presence of a perianth is a constant feature of the group; it is inconspicuous and composed of two similar whorls of three members each. The flowers are mostly trimerous, hypogynous, and mostly syncarpous. They commonly have six stamens (often more) and three carpels.

Arales. This order, of about 1,500 species, comprises 2 families of herbs, the principal one being the Araceae. Most of its members are tropical, some familiar ones being jack-in-the-pulpit (*Arisaema*), calla lily (*Zantedeschia*), and elephant's-ear (*Colocasia*). The flowers, which are small and inconspicuous, are borne on a fleshy axis, the *spadix*, surrounded by a conspicuous bract, the *spathe*. They are perfect or imperfect, hypogynous, and syncarpous. A simple scale-like perianth is sometimes present, its absence in most forms being a result of reduction. The number of stamens and carpels, although variable, is small.

The preceding orders constitute the spiral series of Monocotyledoneae. They are characterized, for the most part, by fluctuating numbers of floral parts, a simple perianth or none, apocarpy, and the development of sheathing bracts. In the Glumales the bracts appear in connection with the individual flowers, in the other orders, in connection with the inflorescence.

The following orders constitute the cyclic series of Monocotyledoneae. Here the flowers are typically trimerous, pentacyclic, and syncarpous. The perianth consists of a distinct calyx and corolla. In a relatively few members the perianth parts are more or less united; otherwise they are separate.

Farinales. The Farinales comprise an order of about 2,500 species of mostly grass-like herbs distributed into 13 families. The most familiar member is the spiderwort (*Tradescantia*), but the pineapple (*Ananas*) belongs here and also the "long moss" (*Tillandsia*) of the Southern United States. The flowers are regular or nearly so, mostly trimerous and pentacyclic, hypogynous or sometimes epigynous, and syncarpous. The perianth may or may not be differentiated into a calyx and corolla and the latter may be bract-like or petaloid. A special feature is the presence of mealy (farinose) endosperm.

Liliales. The Liliales are the great central order of monocotyledons. They number about 5,000 species, most of which are herbs. They are grouped into 9 families, the principal ones being the Juncaceae, Liliaceae, Amaryllidaceae, and Iridaceae. The Juncaceae include the rushes (*Juncus*). The Liliaceae contain such well-known genera as *Trillium*, *Erythronium*, lily (*Lilium*), tulip (*Tulipa*), hyacinth (*Hyacinthus*), onion (*Allium*), and *Yucca*. The Amaryllidaceae are represented by the tuberose (*Polianthes*), *Agave*, and *Narcissus*. The Iridaceae comprise the flags (*Iris*), *Crocus*, *Gladiolus*, etc.

The flowers are mostly regular and have a perianth consisting of two trimerous whorls that are nearly always alike, being bract-like in the Juncaceae and petaloid in the other families. They have mostly six stamens (three in the Iridaceae) and a tricarpellary pistil. The flowers are either hypogynous (Juncaceae and Liliaceae) or epigynous (Amaryllidaceae and Iridaceae).

Scitaminales. Here belong 4 families and about 1,000 species of mostly tropical herbs, including *Canna*, banana (*Musa*), and ginger (*Zingiber*). The perianth, displaying a special type of irregularity, is composed of two whorls that are often entirely petaloid. All members are epigynous. Generally only one fertile stamen is present. The pistil is tricarpellary and the ovary trilocular.

Orchidales. This is the highest order of monocotyledons as well as the largest. It comprises 2 families and about 15,000 species of herbs, nearly all of which belong to the Orchidaceae. The orchids reach their greatest display in the tropics, where most of them are epiphytes. The flowers of the Orchidaceae are irregular, epigynous, and syncarpous. The irregularity is of a special type. The perianth consists of two trimerous whorls, one petal being strikingly different from the others. The stamens are reduced to three, but these do not belong to the same whorl; usually only one stamen is fertile. The pistil is tricarpellary and the ovary unilocular. The seeds are without endosperm.

COMPARISON OF GYMNOSPERMS AND ANGIOSPERMS

The most important distinguishing characters of the Gymnospermae and Angiospermae are as follows:

Gymnospermae	Angiospermae
Plants woody	Plants woody or herbaceous
Wood without vessels (except in Gnetales)	Wood almost always with vessels
Sporophylls borne in strobili (except in Cycadofilicales); perianth absent	Sporophylls borne in flowers; perianth generally present
Ovules freely exposed, not in a closed ovary	Ovules in a closed ovary formed by one or more megasporophylls
Female gametophyte with abundant vegetative tissue and with archegonia (except in *Welwitschia* and *Gnetum*)	Female gametophyte with little or no vegetative tissue, consisting typically of an eight-nucleate embryo sac; archegonia absent
Pollen coming in direct contact with ovules	Pollen not coming in direct contact with ovules
Male gametophyte usually with one or more prothallial cells; generative cell producing a stalk cell and a body cell, the latter giving rise to two male cells that may or may not be organized as ciliated sperms	Male gametophyte without prothallial cells; generative cell directly producing two male cells that are never ciliated
Endosperm formed from vegetative tissue of female gametophyte	Endosperm arising after fertilization, generally from a triple fusion of nuclei
Development of embryo initiated by free-nuclear division (except in *Welwitschia* and *Gnetum*)	Development of embryo without a free-nuclear stage
Cotyledons two to many	Cotyledons one or two

GENERAL CONCLUSIONS

The two most outstanding features of the spermatophytes are the presence of seeds and the development of the flower. They excel the pteridophytes in the complexity of their vegetative organs, while the gametophyte is subordinated to the sporophyte to such an extent that it is always dependent upon it. The microsporangia and megasporangia are borne by sporophylls that, with few exceptions, are considerably less leaflike than the sporophylls of most pteridophytes. Almost invariably the megasporangium (nucellus of the ovule) produces only one functional megaspore, which always gives rise to the female gametophyte without being shed. In all spermatophytes the development of the sporangia is eusporangiate, as among the lower pteridophytes, but the initials are hypodermal rather than epidermal in origin.

In gymnosperms the archegonia are more reduced than in pteridophytes, while in angiosperms they are eliminated. The male gametophyte produces only two sperms, or male cells, and true antheridia are not present. Among existing groups, ciliated sperms occur only in the Cycadales and *Ginkgo*. Fertilization, accomplished with the aid of a pollen tube, results in an embryo that develops inside the ovule.

The Seed. The adaptation to life on land is more nearly perfect in the spermatophytes than in any other group of plants. This has come about partly through the greater complexity of their vegetative organs, but chiefly by the development of the seed. The development of the seed is a result of three conditions—heterospory, retention of the megaspore within the megasporangium, and formation by the zygote of a dormant embryo.

Both the bryophytes and pteridophytes are handicapped in their adjustment to the land habit by two basic requirements: (1) In order to reach the egg and effect fertilization, the sperm must swim through water, a handicap persisting from aquatic ancestors. (2) After fertilization has taken place, the embryo must continue its development whether external conditions are favorable or not.

The seed overcomes both these handicaps. The necessity for external water as a means by which the sperm may reach the egg is obviated by the transportation, through air, of the male gametophyte, inside a pollen grain, to the vicinity of the female gametophyte and the development of a pollen tube through which the male gamete can pass. In this way fertilization is made more certain. Following fertilization, the passing of the embryo into a state of dormancy, as well as the formation of a protective seed coat, enables the embryo to live until conditions become favorable for its continued growth.

The Flower. The flower is difficult to define because every possible transition exists between a typical strobilus and a typical flower. It is apparent, therefore, that the strobilus is the forerunner of the flower and that the changes involved in passing from the one to the other represent an important evolutionary advance. The perianth probably arose as a protective envelope for the sporophylls, but later came to have additional functions, such as the attraction of insects. In gymnosperms the transfer of pollen is precarious, depending upon the vagaries of the wind. To increase the chances of success, an enormous excess of pollen must be produced, thus involving a tremendous waste. The transfer of pollen by insects, to which the flowers of most angiosperms are highly adapted, is more certain and consequently much less wasteful than wind-pollination. Probably the most important factor responsible for the evolutionary progress made by the angiosperms has been the development of the flower in adaptation to insect pollination.

Associated with the development of the flower and its specialization for insect pollination has been the enclosure of the ovules. Originally the carpels of seed plants must have been leaf-like structures bearing marginal ovules, a condition preserved in such existing gymnosperms as *Cycas revoluta*. The change from the open carpel with its ovules freely exposed to the closed carpel with its ovules inside a cavity marks another great advance which the angiosperms have made over the gymnosperms. This change led to the development of the fruit.

Interrelationships. The fossil record gives no evidence as to which of the two great Paleozoic groups of gymnosperms—the Cycadofilicales and the Cordaitales—is the older. Except for the presence of seeds, however, the Cycadofilicales are so fern-like as to leave little doubt that they have been derived from some ancient fern stock. The Cordaitales, less fern-like, may have branched off from the Cycadofilicales early in the Paleozoic, although it seems more likely that both groups have had a common origin. The Cycadofilicales very probably gave rise to two divergent lines of descent, one represented by the Bennettitales of the Mesozoic, a specialized offshoot that became extinct, the other leading to the Cycadales, a group that still survives.

There is strong evidence that the Cordaitales were ancestral to both the Ginkgoales and the Coniferales, orders that reached a climax in the Mesozoic. Except for *Ginkgo biloba*, the Ginkgoales are extinct, while the Coniferales are still so abundant as to constitute the largest order of living gymnosperms. The Gnetales are a group of obscure origin. They may represent a specialized offshoot from the Coniferales, but any relationship to the angiosperms is very doubtful.

The oldest undoubted angiosperms appear in the deposits of the Lower Cretaceous. Their characters are so distinct that they must have originated at a much earlier time, but it is not known when or from what older group they arose. There is a possibility that the angiosperms originated independently from the pteridophytes, but this is remote in view of the many common features existing between gymnosperms and angiosperms. There is no convincing evidence, however, indicating from what group of gymnosperms the angiosperms may have sprung.

One theory holds that the angiosperms have been derived from the Gnetales. Their compound strobili resemble the inflorescences of certain angiosperms with monosporangiate (imperfect) flowers and a simple undifferentiated perianth. The presence of vessels in the secondary wood is a character shared by both groups. If the resemblances between the Gnetales and angiosperms are a result of parallel evolution, there can be no direct relationship between them, although they may have come from a common ancestry.

Another theory claims the derivation of the angiosperms from the Bennettitales. Their strobilus, which is bisporangiate, somewhat resembles the flower of a magnolia, but the stamens, and particularly the carpels, are very different in the two groups. On the whole, the cycadeoid strobilus is so specialized that it is very unlikely that an angiosperm flower could have evolved from it. It seems more reasonable to suppose that the resemblance between them is a result of parallel development and does not denote any direct relationship. The fossil record has not produced transitional forms connecting the gymnosperms and angiosperms. In their absence, speculation concerning the ancestry of the angiosperms seems futile.

CHAPTER X

EVOLUTION OF THE PLANT KINGDOM

The doctrine of evolution states that all forms of life, living and extinct, have been derived from preexisting forms by a process of gradual change. This principle of "descent with modification," supported by an overwhelming mass of evidence, has been fully established as a fundamental axiom of biology. The method by which evolution has taken place, however, is imperfectly understood and considerable uncertainty exists as to the relative importance of the various factors involved.

These factors are of two kinds: primary or causative and secondary or directive. Causative factors give rise to heritable variations, which are the raw materials of evolution. These are built up into new species under the influence of directive factors, which determine the course of evolution. Heritable variations arise both from new combinations of genes in fertilization and by mutation, a process involving changes in the chromosomes of reproductive cells, the causes of which are largely unknown. The addition or loss of one or more chromosomes by irregularities in meiosis may cause changes affecting several or many characters simultaneously. Much more common and of greater importance are changes involving individual genes, these giving rise to innumerable small variations that supply most of the raw material upon which the directive factors of evolution operate. Thus evolution is mainly dependent upon the appearance of mutations, especially gene mutations.

The general trend of evolution is toward greater fitness to the conditions of existence. Some of the variations arising by recombination of genes or by mutation are adaptive, while others are not. By natural selection, favorable variations having survival value are preserved and accumulated through successive generations, thus bringing about greater adaptation to the environment. Natural selection determines which individuals among a diversified population shall survive in the "struggle for existence." It is generally regarded as the most important directive factor yet discovered.

Theories dealing with the causes of evolution are concerned chiefly with the origin of species. One of the great problems of morphology is the determination of the origin and phylogenetic development of the larger plant groups. The fossil record demonstrates that groups once dominant on the earth have been replaced by others more advanced, but it seldom indicates from which older group a younger one has been derived. Interrelationships among the larger groups must be inferred principally from evidence based on studies in comparative morphology. The "lower" groups of plants are merely those which have undergone relatively little modification, the "higher" groups, a vastly greater amount. Existing groups are usually represented as twigs on a phylogenetic tree The larger branches denote divergent lines of descent. These are often obscure and difficult to trace, but become clear as knowledge advances.

Specialization. The general trend of evolution toward greater adaptation to the environment has resulted in the development of specialized forms from generalized forms. Structural complexity is always a result of evolution from a simpler condition of organization, but simplicity does not always represent a primitive state. Often it denotes reduction from a more highly developed ancestry. Sometimes there is structural evidence of such reduction, especially in ontogeny, but usually this evidence is obscure or wanting. Consequently it is often difficult to ascertain whether structural simplicity is a primary or a derived condition.

Higher types have arisen from generalized members of lower groups, not from specialized members. Highly specialized groups, like the red algae and the mosses, represent blindly ending lines of descent. They may change in the direction of greater specialization, but cannot revert to a generalized condition and then become specialized in another direction.

In many groups evolutionary advance has not affected all parts of the plant to the same extent and, as a consequence, advanced features are often combined with primitive ones. For example, although the cycads are seed plants, they have retained swimming sperms, an extremely ancient character, the phylogenetic continuity of which can be traced back to the algae. Sometimes the development of one character is associated with the suppression of another. Thus, in the Compositae, the formation of an involucre has resulted in a reduction of the calyces of the individual flowers in the head. Similarly the strong development of mechanical tissues in the stems of many large herbaceous angiosperms is related to the weak development of xylem and might be regarded as a compensation for it. Such instances of compensation are common throughout the plant kingdom.

Parallel Development. The same evolutionary tendency, acting independently in different groups of plants, may bring about similar changes, thus resulting in parallel development or homoplasy. For example, heterogamy has arisen independently in a number of widely separated algal groups and heterospory in various groups of vascular plants. Epigyny has developed independently in many different families of angiosperms. Structural similarity resulting from parallel development is no indication of phylogenetic relationship. It merely signifies that evolution in two or more different groups has occurred in the same general direction and often in response to the same influence. Instances of parallel development are numerous. Unless they are recognized, false conclusions regarding relationships may be drawn.

Real relationships among different kinds of plants are shown by the presence of similar characters derived from a common ancestry. The members of every natural group, despite superficial differences, are built according to the same basic pattern. This is expressed by the characters that distinguish it from other groups. Related plants display many structural resemblances because of a common origin, while their differences are a result of divergent evolutionary tendencies. The greater the degree of basic resemblance between any two kinds of plants, the closer is their relationship and the less remote their common ancestry.

Homologous Structures. In any natural group the various members possess certain structures that are considered as homologous, or morphologically equivalent. Such structures may display considerable diversity in form or function, but have a similar ontogeny and so bear the same relation to the plant as a whole. In liverworts, for example, spores and elaters are homologous, since they develop from the same mass of undifferentiated sporogenous tissue. In angiosperms stamens and carpels are homologous with leaves, as well as with the sporophylls of other vascular plants. Tendrils and thorns may be homologous either with stems or leaves, depending on their place of origin on the plant. Cladophylls are homologous with stems, while bracts and scales are homologous with leaves.

Recapitulation. Developmental stages not only reveal homology between different kinds of structures, but frequently furnish other evidence of evolutionary changes. In the early development of many plants, stages appear that correspond to adult stages in less highly specialized plants. This suggests that such developmental stages may represent ancestral conditions. The theory that "ontogeny recapitulates phylogeny" cannot be regarded as a principle of broad application, however, for in many plants embryonic or juvenile stages have no apparent evolutionary significance. On the other hand, the theory receives support from many sources. For example, among kelps *Laminaria* is a generalized type, the simplest species consisting of a holdfast, stipe, and an undivided blade. Most of the other kelps are more highly differentiated when mature, but in early development pass through a *Laminaria*-like stage. This indicates that *Laminaria* represents the ancestral condition.

The occurrence of a protonemal stage in the life history of a moss recalls an algal stage in the ancestry. The presence of needle-like leaves on the seedlings of certain conifers and of scale-like leaves on older plants suggests that the juvenile foliage represents the ancestral type. The seedlings of some species of *Acacia* have bipinnate leaves that are soon replaced by phyllodia, the adult form of foliage. In such species transitional stages are common. In the development of the common bracken fern (*Pteridium aquilinum*), the young plant passes through a protostelic and then a siphonostelic stage before the dictyostelic or permanent condition is reached. These stages represent a phylogenetic series. In the seedlings of most monocotyledons the stem is at first a siphonostele, gradually becoming a dictyostele with scattered vascular bundles. This indicates that the siphonostelic condition is the more primitive one.

PROMINENT EVOLUTIONARY TENDENCIES

Comparative morphology furnishes abundant evidence of evolution along determinate lines. Changes that have taken place in definite directions are apparent throughout the plant kingdom. Because some members are more advanced than others, it is possible, within a group, to construct a series of forms showing various degrees of modification. Such a series may indicate either an advance or a decline, depending on whether evolution has been progressive or retrogressive. The species of *Lycopodium* display various stages in the organization of a strobilus, while the genera of Fucales show a reduction series with respect to the number of eggs produced in an oogonium. Often an advance in one direction has been accompanied by a decline in another. The development of an irregular corolla in certain families of angiosperms, such as the Labiatae and Scrophulariaceae, has resulted in a reduction in the number of stamens from five to four or two. Evolutionary tendencies, whether progressive or retrogressive, usually continue as long as the group displaying them persists. Some of the more conspicuous evolutionary tendencies seen in the major groups of green plants will be briefly summarized.

Algae. Among the algae vegetative advance has been marked by the organization of single cells into colonies and the development of multicellular bodies into filamentous, plate-like, and massive types. Progress is also shown by the beginning of cellular differentiation, resulting in specialization of different parts of the body for particular functions.

From a condition where reproduction is wholly asexual, an advance is seen in the establishment of sexual reproduction and in its change from isogamy to heterogamy. The tendency to interpose a vegetative growth phase between gametic union and meiosis has resulted in the establishment of an alternation of haploid and diploid generations. Some algae show a tendency to develop the sporophyte at the expense of the gametophyte. The algae are a polyphyletic group representing a number of parallel evolutionary lines whose connections are very uncertain. Most groups seem to have arisen independently from a flagellate ancestry.

Bryophytes. The contributions of the bryophytes to the evolution of the plant kingdom include the establishment of the land habit, the appearance of archegonia and multicellular antheridia, and the development of a distinct alternation of unlike generations as a constant feature of the group. Prominent evolutionary trends include a differentiation of the gametophyte in internal structure, the development of a leafy gametophyte from a thallus, and a tendency of the sporophyte to become partially independent of the gametophyte. From a sporophyte almost wholly sporogenous, progress has been made by ever-increasing sterilization of tissue and its diversion to other functions. This is seen in the development of a foot and seta, elaters, and a dehiscence mechanism, in the formation of a columella, and in the development of green tissue.

Relationships between the bryophytes and green algae are mainly conjectural, there being no direct fossil connection between the two groups. However, the bryophytes seem clearly to have been derived from aquatic ancestors, their structural advances being correlated with the establishment of the land habit. These include a compact plant body, absorptive rhizoids, jacketed sex organs, heavy-walled aerial spores, etc.

Pteridophytes. The advance of the pteridophytes over the lower groups is shown by the establishment of an independent sporophyte, evolution of a vascular system, organization of a strobilus, and appearance of heterospory. With few exceptions, the sporophyte consists of roots, stem, and leaves. In one line of descent the leaves have remained small, undivided, and single-veined; in the other line they have become large, divided, and many-veined. In the evolution of the vascular system the trend has been from exarch to mesarch xylem and then to endarch, also from a protostelic to a siphonostelic condition and then to a dictyostelic one. The presence of leaf gaps in the ferns is regarded as an advanced feature, their absence in other pteridophytes being primitive.

Lycopods show an advance from those with every leaf a sporophyll to those with a compact strobilus. Both lycopods and ferns show a trend from homospory to heterospory. Heterospory has accelerated the reduction of the gametophyte generation and sex organs. Among homosporous forms, subterranean gametophytes have been derived from aerial ones. Ferns show evolutionary tendencies affecting the sporangia, such as a change from the eusporangiate to the leptosporangiate type, reduction in the thickness of the wall and in the output of spores, development of an annulus, etc.

The origin of pteridophytes is uncertain, a direct connection with either the algae or the bryophytes being hypothetical. Some paleontological evidence indicates that the major groups have been derived independently from the Psilophytales.

Spermatophytes. The spermatophytes reach the culmination of evolution in the development of the seed, development of pollen tubes, ultimate enclosure of the seed by the carpel (angiospermy), ultimate elimination of swimming sperms and later of archegonia, a great reduction in the gametophyte generation, and the evolution of the flower.

The abandonment of ciliated sperms by the conifers resulted in a change in the pollen tube from a branched haustorial organ to a carrier of the male cells. The male gametophyte has undergone a reduction in the number of male cells to two and of prothallial cells to two or one and finally to none. Throughout gymnosperms the female gametophyte exhibits various stages in reduction that reach an extreme in angiosperms. The tendency for eggs to mature earlier and earlier in the development of the gametophyte has finally resulted in the elimination of archegonia.

A marked feature of evolution in the seed plants has been the development of the strobilus into a flower. Among angiosperms floral evolution has been marked by a number of evolutionary tendencies, among which are the following: floral parts numerous and spiral to few and cyclic, pentacyclic to tetracyclic, free to united; perianth undifferentiated to differentiated into a distinct calyx and corolla; corolla regular to irregular; flowers hypogynous to perigynous and epigynous; ovules with two integuments to only one; embryo dicotyledonous to monocotyledonous; endosperm abundant to little or none; fruit simple to aggregate and multiple. Angiosperms also show trends from a woody to an herbaceous habit, from erect types to vines, from perennials to annuals, from a spiral to a cyclic arrangement of leaves, from simple to divided leaves, and from net-veined to parallel-veined leaves.

It is clearly evident that the gymnosperms have been derived from the pteridophytes and are a much older group than the angiosperms, whose origin is obscure. If the angiosperms have not come from the gymnosperms, the presence of seeds, pollen tubes, and many other common features are a result of parallel development.

EVOLUTION OF SEX

There are two primary types of reproduction in the plant kingdom, sexual and asexual. The distinctive feature of sexual reproduction is the fusion of two cells to form a zygote. In asexual or vegetative reproduction no such fusion occurs.

Asexual Reproduction. Cell division is the simplest and oldest method of reproduction and in many unicellular plants it is the only method. In multicellular plants cell division does not result in reproduction but in growth. To make reproduction possible, a cell or group of cells must become detached from the parent plant. A spore shares with ordinary vegetative cells its ability to divide, but does so only after being liberated. It differs from other cells not in power but in opportunity. Asexual reproduction by means of spores is a feature of nearly all the green algae and of most fungi, occurring even in some of the unicellular forms.

It should be understood that the formation of vegetative spores never involves a reduction of chromosomes. In fact, with few exceptions, they are borne on a haploid plant body. Vegetative spores always give rise to the same kind of plant body as the one that produced them. Spores formed by meiosis from a diploid cell, like tetraspores in the red algae, ascospores and basidiospores in the fungi, and all spores in the higher plants, are not vegetative spores but meiospores and belong to the sexual life cycle.

In plants above the thallophyte level, asexual or vegetative reproduction is carried on by various means, such as gemmae, bulbils, bulbs, tubers, runners, isolated branches, etc. Each of these consists of a group or mass of vegetative cells isolated from the parent and capable of reproducing it.

Origin of Sex. Most algae producing vegetative zoospores, whether unicellular or multicellular, also bear gametes on the same kind of vegetative body. Gametes not only resemble zoospores structurally but, in isogamous forms, commonly intergrade with them. This indicates that gametes have been derived from zoospores. It is not known what induced reproductive cells to first unite in pairs, but the tendency soon became a fixed habit.

The fact that the zygote becomes a thick-walled resting cell in most green algae suggests that the original function of sexual reproduction was protection over a period of unfavorable conditions. In fact, experiments have shown that the advent of such conditions induces gamete formation. When conditions for vegetative growth are at their best, reproduction does not occur. When they become somewhat less favorable, vegetative activity begins to wane and spores are formed. As conditions become more severe and the plant approaches the end of its growing season, gametes appear. The conditions favoring gamete production in the green algae are those that inhibit germination of the zygote and result in its dormancy. When it germinates at the beginning of the next season, conditions are usually not conducive to maximum vegetative activity. It is possible that the formation of spores by the zygote, a feature of so many green algae, is merely a response to these conditions.

Differentiation of Gametes. In isogamy all the gametes are alike in appearance and behavior. The fact that they pair, however, implies a mutual attraction and indicates that a difference exists between them. Each of the pairing gametes must represent an opposite sex. In heterogamy the differences between the two kinds of gametes merely become apparent, so that they are recognizably male and female.

Isogamy represents the original condition of gametic union. It has been retained by many green and brown algae. These groups display various degrees of heterogamy, however, indicating that this condition has been derived from isogamy by a differentiation of gametes into sperms and eggs. In isogamy, as a rule, both kinds of gametes are motile and equally small, neither containing much food. In heterogamy there is a division of labor, the sperm providing motility and remaining small, the egg providing food and becoming large. Its advantage lies in the greater supply of food available for the zygote and the young plant that develops from it. In the red algae, where heterogamy is universal, the sperm is nonmotile but much smaller than the egg. Heterogamy is established in all the higher plants, with swimming sperms occurring in all bryophytes, all pteridophytes, and a few gymnosperms.

Evolution of Sex Organs. The production of gametes in ordinary vegetative cells is characteristic of most of the green algae. In isogamous forms these cells remain unchanged, while in nearly all heterogamous forms they become modified in size and shape. Thus there are not only two kinds of gametes but two kinds of gametangia, the sperms arising in antheridia and the eggs in oogonia. A differentiation of gametes has been accompanied by a differentiation of sex organs, but the gametes develop from the protoplasts of vegetative cells.

In a few green algae, such as *Vaucheria*, in the Charophyceae, and in nearly all the brown and red algae a more advanced condition has been reached. Here the gametes are borne in sex organs that have never been a part of the vegetative body, but arise as special reproductive branches. A differentiation has taken place between cells that remain entirely vegetative in function and those that are strictly reproductive. Although this condition is found mainly among heterogamous algae, it occurs in a few isogamous members of the Phaeophyceae, such as *Ectocarpus*, where gametangia are developed on special branches.

Thus among the algae three stages may be recognized in the evolution of sex organs, depending upon whether gametes are produced in (1) an unmodified vegetative cell, (2) a transformed vegetative cell, or (3) a special reproductive cell distinct from the rest of the body. The first stage is characteristic of isogamous forms, the second and third of heterogamous forms.

The sex organs of the bryophytes and pteridophytes are more highly developed than those of the algae in that both kinds are multicellular and have an outer jacket of sterile cells usually forming a single layer. The sterile jacket, which protects the gametes from drying out, was probably developed as a response to air exposure. Although the bryophytes are thought to have arisen from chlorophycean ancestors, existing green algae have unicellular sex organs. Therefore it is necessary to assume that the ancestral forms had multicellular gametangia of the *Ectocarpus* type. The bryophyte antheridium could readily have been derived from such a gametangium by sterilization of the outer layer of cells. The archegonium, having diverged more widely from its original condition, went through several stages in its evolution. At first it may have resembled the antheridium, consisting of a group of fertile cells enclosed by a sterile jacket. Further progress may have been marked by reduction of the fertile cells to a single row and then by sterilization of all of these except the lowest one, the other cells in the row becoming canal cells. Evidence for this theory comes from the occasional appearance, in both liverworts and mosses, of reversionary archegonia with multiple eggs, with two rows of canal cells, or with some of the canal cells replaced by spermatogenous cells.

The sex organs of bryophytes and pteridophytes perform accessory functions related to gametic union and embryo development. The sterile jacket of the antheridium not only protects the developing sperms but facilitates their dispersal. Frequently dehiscence occurs suddenly and the sperms are discharged with considerable force. The neck of the archegonium serves as a passageway for the entrance of sperms, the canal cells breaking down to form mucilage through which the sperms swim. The venter of the archegonium enlarges after fertilization, protecting the embryo and aiding in the transfer of food to it.

Antheridia with a large number of spermatogenous cells and archegonia with many neck canal cells are generally regarded as primitive. Throughout the bryophytes and pteridophytes the tendency to reduce the number of these cells reaches an extreme in the heterosporous pteridophytes, where the antheridium may produce only four sperms, as in *Isoetes*, and the archegonium has only one neck canal cell. These trends are continued into the spermatophytes, where antheridia are not organized and only two sperms or their equivalent are formed and where archegonia, without any neck canal cells, are present only in the gymnosperms.

The embryo sac of angiosperms may have evolved from the typical female gametophyte of gymnosperms, but, except for the formation of free eggs in the Gnetales, intermediate stages are lacking. Although most angiosperms possess an eight-nucleate embryo sac that develops in a characteristic way, many deviations from the typical pattern occur. These reveal several trends, such as the participation of more than a single megaspore nucleus in the formation of the embryo sac and a reduction in the number of nuclear divisions that intervene between the formation of the megaspore nuclei and the egg nucleus.

Further Expressions of Sexuality. In the evolution of sex the differentiation of gametes was soon followed by a differentiation of sex organs. A further stage was the differentiation of structures bearing the sex organs, while a final stage was a sexual differentiation of entire individuals.

In most liverworts belonging to the Marchantiales the antheridia are borne on male receptacles and the archegonia on female receptacles. These show a marked structural differentiation. In some members, such as *Marchantia,* there is also a differentiation of individuals, the male plants bearing antheridial receptacles and the female plants archegonial receptacles. In *Sphaerocarpus,* belonging to another group of liverworts, the male plants are much smaller than the female. Certain species of *Oedogonium* have dwarf male filaments consisting of only a few cells.

Although *Spirogyra* has not reached the level of heterogamy, some species show a differentiation of sexual individuals. This expresses itself only in the behavior of the gametes, those of one member of a pair of conjugating filaments being active, while those of the other are passive. The occurrence of distinct male and female individuals is a feature of many heterogamous algae, such as *Cutleria, Dictyota, Polysiphonia,* and many others.

In plants with an alternation of generations the gametophyte is commonly called the sexual generation and the sporophyte the asexual one. This misconception arises from failure to regard fertilization and meiosis as complementary processes, both of which are integral parts of a complete sexual life cycle. Vegetative spores are asexual but meiospores are not. Where the zygote directly gives rise to four meiospores, as in *Oedogonium,* it is easy to associate their formation with fertilization. Where meiospores are borne on a sporophyte, the time interval between fertilization and meiosis is longer, but the relation between them is the same.

In the bryophytes and homosporous pteridophytes the sporophyte does not express any sexual characters. But, with the establishment of heterospory, sexual differentiation becomes extended from the gametophyte to the sporophyte. The significance of heterospory lies in the production of a male gametophyte by the microspore and a female gametophyte by the megaspore. The occurrence of two kinds of gametophytes is reflected in a visible differentiation of the spores. This differentiation may be extended to the sporangia, sporophylls, strobili, and even to the entire sporophyte. In *Selaginella* the visible consequences of heterospory are not as far-reaching as in seed plants, where the organs associated with the production of microspores (stamens and pollen sacs) and of megaspores (carpels and ovules) are as highly differentiated as the sex organs of bryophytes and pteridophytes. Stamens and carpels are not sex organs, but their differences are associated with a sexual differentiation that has been extended to them from the gametes.

Among the gymnosperms a separation of microspore-bearing and megaspore-bearing structures to two kinds of cones is another expression of sexual differentiation. In the cycads, *Ginkgo*, and some conifers this is extended to the entire sporophyte, so that there are male and female plants as well as male and female cones. Most angiosperms bear flowers having both stamens and carpels, but some have two kinds of flowers, one with stamens and the other with carpels. The two kinds may occur on the same plant or on separate plants, depending on the species.

Significance of Sex. The most important feature of sexual reproduction is the union of the two gametic nuclei. This brings together two haploid sets of chromosomes to form a diploid zygote nucleus. Each set consists of innumerable genes that determine hereditary characters and each ordinarily represents a somewhat different assortment of genes. Meiosis, sooner or later following gametic union, provides a means of reshuffling the paternal and maternal chromosomes brought together in the previous act of fertilization, thus resulting in many new gene combinations.

It is evident that sexual reproduction, through fertilization and meiosis, creates great variation among individuals related by descent and so furnishes raw material for evolutionary processes to work upon. Asexual reproduction results in organic similarity; sexual reproduction results in diversity. The significance of sexual reproduction is not primarily the multiplication of individuals, but the production of heritable variations that accelerate the process of evolution. It is in this feature that its great advantage lies. In plants first reaching the level of sexuality, this advantage would tend to be perpetuated through natural selection and to become established as a permanent part of the life history.

ALTERNATION OF GENERATIONS

Many algae and fungi, as well as all plants above the thallophyte level, are characterized by an alternation of generations, in which the life cycle consists of two kinds of individuals that follow each other in alternate sequence. One of these, the gametophyte, is haploid and produces gametes, while the other, the sporophyte, is diploid and produces spores. The diploid condition arises in the zygote, produced by gametic union. The zygote develops into a sporophyte, meiosis taking place when spores are formed. The spore gives rise to the gametophyte. The zygote is the first cell of the sporophyte generation, and the spore is the first cell of the gametophyte generation.

Types of Life Cycles. Fertilization and meiosis are the two cardinal events in every life cycle involving sexual reproduction and each is a necessary consequence of the other. Thus every plant with sexual reproduction displays both a haploid and a diploid phase, but in many thallophytes the life cycle includes only one kind of individual. In most green algae the vegetative body is haploid and meiosis occurs in connection with the germination of the zygote. Here a prolonged haploid growth phase alternates with a single diploid cell, the zygote. Although the zygote usually gives rise to four spores, it could hardly be regarded as a sporophyte, and so there is no true alternation of generations.

In many diatoms, Siphonocladiales, Siphonales, and in all the Fucales the vegetative body is diploid, meiosis occurring when gametes are formed, as in animals. Here a prolonged diploid growth phase alternates with a few haploid cells, the gametes, and again there is no true alternation of generations. Thus, where the life cycle includes only one vegetative phase, this may be either haploid, meiosis directly following fertilization, or diploid, meiosis immediately preceding fertilization.

An alternation of generations occurs wherever a diploid growth phase intervenes between fertilization and meiosis, and a haploid growth phase between meiosis and fertilization. Such a condition is displayed by *Ulva* and a few other green algae, by most brown and red algae, and by all bryophytes and pteridophytes. It is also characteristic of the spermatophytes, although in angiosperms the haploid phase (gametophyte) consists of only a very few cells or nuclei. Obviously this is a result of reduction, while in *Fucus*, for example, where a somewhat similar condition prevails, reduction may have taken place but evidence is lacking.

In *Fucus*, where spores are absent from the life cycle, a diploid plant body produces gametes. In *Ulothrix* and *Oedogonium*, on the other hand, a haploid body may produce either gametes or spores. Such spores are vegetative spores and are not homologous with the four spores derived from the zygote or with the spores borne by the sporophyte of the higher plants, both of which are meiospores and belong to the sexual life cycle. Either a haploid or a diploid plant body may be propagated vegetatively by various means without fertilization and meiosis being involved. Vegetative reproduction is always asexual.

Origin of Alternation of Generations. Regarding the origin of alternations, two different theories have been advanced, the homologous theory and the antithetic theory. The homologous theory was based originally on conditions in those algae in which a single plant can produce either spores or gametes. It assumes that these functions later became separated into two distinct individuals, sporophyte and gametophyte, alternating regularly in the life cycle. The theory furnishes a more adequate explanation of alternation where the two generations are alike vegetatively than where they are unlike. Against it may be urged the fact that vegetative spores produced by a haploid plant body and meiospores produced by a zygote or a sporophyte are not morphologically equivalent. Also, the homologous theory fails to account for the difference in chromosome numbers that exists between the gametophyte and sporophyte. The phenomena of apogamy and apospory have been cited as evidence in favor of this theory, but they are merely digressions from the normal life cycle.

The antithetic theory seems to be more in accord with actual conditions in the plant kingdom. It contends that the gametophyte is the original generation and the sporophyte a later one interpolated in the life history between fertilization and meiosis. It holds that the sporophyte has evolved from the zygote, an initial stage occurring in such algae as *Oedogonium,* where the zygote gives rise to four meiospores. A second stage might be represented by *Coleochaete,* where the zygote, after undergoing meiosis, forms a small group of spore-producing cells (up to 32). In a third stage, as seen in *Riccia,* the zygote develops into a very simple sporophyte in which meiosis is delayed until spores are formed. In the evolution of the plant kingdom, such a delay may have taken place in a single step by mutation.

Where the zygote becomes a thick-walled resting cell, its nucleus divides reductionally upon germination. This is a feature only of fresh-water green algae. Where the zygote germinates at once, it gives rise to a diploid vegetative body. This occurs in the marine green algae, in the brown algae, and in most of the red algae.[1] In most algae with a diploid vegetative phase, there is a distinct alternation of generations, exceptions being such forms as *Acetabularia, Codium, Bryopsis,* and the Fucales.

It is apparent that the behavior of the zygote is related to environmental conditions. Seasonal variations are more pronounced in bodies of fresh water than in the ocean. A resting zygote, usually formed near the close of the growing season, carries the plant over a period of unfavorable conditions. Algae with a resting zygote display no diploid vegetative phase. Thus the origin of alternation of generations may be sought in a determination of the factors that induce prompt germination of the zygote with an accompanying postponement of meiosis. Perhaps these factors have been responsible for a mutation that has resulted in the establishment of a diploid generation.

Alternation of generations, once established in a group of plants, conferred such advantages that it would tend to be retained as a permanent feature. These advantages are: (1) An increase in the number of individuals produced as a result of a single gametic union, thereby conferring on them any beneficial results of such a union which, in many of the lower plants, sometimes occurs with a great deal of rarity. Instead of produc-

---

[1] In the red algae the zygote always germinates promptly, but subsequent stages are variable and complicated by the formation of carpospores. These are haploid in the two lowest orders, where the zygote is the only diploid cell in the life cycle, and diploid in the other orders, where they give rise to sporophytes.

ing only one new plant, the zygote now indirectly produces, through the development of the sporophyte, a large number of new plants. (2) An increase in the possible range of variation. Where the zygote undergoes meiosis only two genetically different lines of descent are possible, since the segregation of genes takes place during the first reduction division. The development of a sporophyte results in meiosis in many spore mother cells, all descended from the same zygote, and so makes possible a great many new chromosome combinations. The advantages of alternation of generations are proportional to the size and length of life attained by the sporophyte and account, at least in part, for its dominance over the gametophyte in vascular plants.

The evolution of the sporophyte in the higher plants has been marked by a prolongation, through vegetative growth, of the interval between fertilization and meiosis. The sporophyte of *Riccia* represents a primitive condition in that its growth period is short and nearly all its cells produce spores. Throughout bryophytes and pteridophytes progressive sterilization of potentially sporogenous tissue has resulted in an elaboration of vegetative structures. At the same time, not only is relatively less and less tissue devoted to spore production, but it appears later and later in the life history.

As the sporophyte has achieved independence and become the dominant generation in all vascular plants, the gametophyte has undergone a progressive decline. This has been accentuated by the development of heterospory, first seen in the pteridophytes. In spermatophytes the gametophyte has become not only greatly reduced structurally, but actually is parasitic on the sporophyte, thus reversing conditions in the bryophytes, where the sporophyte is parasitic on the gametophyte throughout its entire existence.