CHAPTER VI

HAYFEVER

It is almost a tradition among hayfever sufferers that their malady is caused by roses, when it comes in the early summer, or by goldenrod, when it comes in the late summer. Usually such traditional bits of misinformation can be traced back to some half truth; in this case it is that both roses and goldenrod play minor parts in the production of hayfever. Nevertheless the hayfever that afflicts people in the early summer months when the roses are blooming is never caused primarily by roses; likewise that which afflicts people during the closing summer months when the goldenrod is blooming is never primarily due to goldenrod. Roses and goldenrod contribute so little that they need scarcely be considered as hayfever plants. The principal factor in the production of hayfever is not the beautiful or conspicuous flower, which is pollinated by insects, but the one that sheds most pollen, always drab and inconspicuous, and pollinated by wind. In a way, the amount of pollen that a plant can disseminate in the air is a measure of its ability to produce hayfever.

Though the flowers that cause hayfever are not objects of admiration and usually pass unnoticed, they are frequently associated with more conspicuous kinds, in both their habitat and time of flowering, with the result that the latter are sometimes blamed for the misdeeds of their less conspicuous cousins. Thus it is that when roses delight the eye and fill the air with their fragrance, the careful observer will always find near by species of grass with flowers neither beautiful nor fragrant but which cast to the winds enormously more pollen than is produced by the roses. In the same way when at the close of summer the many species of goldenrod garnish the fields and hills with their beautiful golden sprays there will always be found in the ditches along the roadside and in abandoned or poorly cultivated fields great masses of one or more species of ragweeds, filling the atmosphere from inconspicuous greenish flowers with infinitely more pollen than is produced from their more showy neighbors.

Besides the grasses and ragweeds many other plants contribute to the production of hayfever. An analysis of these has shown that each climatic area has its own particular group of hayfever plants. These flower in most localities in three distinct seasons. The hayfever of the first season or *early spring* type is generally mild and of short duration, coinciding with the flowering of such trees as elm, oak, poplar, birch, maple, walnut, and willow, which, taking advantage of the leafless condition of the trees in the early spring, scatter enormous amounts of pollen to the winds. The duration of their flowering is relatively short; consequently this type of hayfever is less important than that of the two following seasons. The second or *early summer* hayfever season coincides with the flowering of the commoner grasses, which are its primary cause. The grasses begin to shed their pollen just when or even a little before the trees are completing their flowering, and continue until about haying time. The flowering period of most grasses, though generally short, is longer than that of most trees, and so many species with slightly different flowering periods are found associated that the season is considerably longer. And the irritation caused by their pollen much more intense than that caused by the tree pollen.

The third period corresponds with the flowering of the ragweeds, cockleburs, and goldenrods in the East and with the ragweeds, false ragweeds, cockleburs, sagebrushes, and many others in the West.

Early Spring Hayfever.—The trees which contribute their pollen to the cause of hayfever in the early spring are all wind pollinated, except the maples and willows. The *maples* undoubtedly employ insects to effect pollination. The flowers of the red maple, for example, are colored, sweet scented, and provided with nectar, offering every inducement to insects to visit them. Nevertheless, in most species of maple, adaptation to pollination by insects is rather imperfect; the anthers protrude beyond the floral envelopes so that when the insects clamber over the flower clusters in search of nectar a large amount of pollen is knocked loose and drifts away in the breeze. And some species of maple as, for example, the ash-leaved maple or box elder are entirely wind pollinated.

The *willows*, like the maples, are both wind and insect pollinated. Unlike most trees they have a long flowering period, and many species and varieties are found growing together and flowering at different times. As a consequence the blooming of all the willows together often covers a period extending from the time of the disappearance of the last snows when the first shrubby pussy willows flower while their branches are still leafless, to well into June when some of the larger tree forms complete their flowering after the leaves are fully developed. It is not known which of the numerous species and varieties of willow are the heaviest contributors to hayfever; probably they are not distinguishable in hayfever studies and, too, cases of willow hayfever are rather rare.

The *birches*, like the willows are generally represented by several species in the same locality. Thus in the northeastern United States the gray or poplar birch is generally found associated with the black and yellow birches, and, though each has a flowering period of scarcely over a week, that of the three together often extends over three or four weeks. Many more cases of birch hayfever than of willow have been recorded. This is in keeping with the fact that a larger amount of pollen is produced by the birches, and that wind is the sole agency employed in pollen transference.

The *elms* constitute a potential cause of hayfever, and severe cases of elm hayfever have been recorded. Though there are several species of elm in the United States, they are not commonly associated. Their flowering periods are usually less than a week, and the few cases of elm hayfever that have been reported, though frequently severe, are generally of short duration. The pollen of most elms is shed long before the leaves unfold, and the flowers are so small and inconspicuous that it is not surprising that they are seldom suspected of causing hayfever. When the flowers are shedding really prodigious quantities of pollen they look from the ground like rather large, dark reddish buds, swollen and about to burst.

The *poplars* or *cottonwoods*, like the birches, flower before the first unfolding of the leaves. They are frequently represented by several species in the same locality, but the one that is most commonly planted about city dwellings is *Populus Eugenei*, a hybrid produced in Germany by crossing the necklace poplar with the balsam poplar. It is always propagated by cuttings and exists only in the male or pollen producing sex. However, as with most hybrids, the pollen is largely abortive, represented in the anthers by empty skins, and most of the catkins fall prematurely from the trees. Few, if any authentic cases of poplar hayfever have been attributed to this or the various other species of poplar in the eastern states. In the western states, however, Arizona cottonwood, which is extensively planted in southern Arizona and California, is regarded by investigators as a frequent cause of hayfever; so also are the California cottonwood, western cottonwood, and the narrow-leaved cottonwood in regions of the West and Southwest, where they are abundant.

Of the many species of conifers, such as pines, spruces, and cedars, which are notorious for their large quantities of pollen and, consequently would be expected to cause hayfever, only the mountain cedar has definitely been shown to be a factor of importance. In the United States this species is confined to the limestone hills of southern Texas and to a lesser extent New Mexico. Flowering in December and January, it is said to be the cause of winter hayfever in these regions.

The *walnuts* of the East (black walnut and butternut), though they shed large quantities of light air-borne pollen, do not constitute a serious factor in hayfever. On the other hand, the California black walnut, which is much planted as a shade tree in the Sacramento, Napa, and Russian river valleys of California, is regarded as the most frequent cause of spring hayfever in those regions. It is interesting to note that the English walnut, also much grown in California and elsewhere and frequently associated with the California black walnut, is stated by eminent authorities to be of no consequence in hayfever.

The *oaks* which are among the last trees to come into leaf in the spring shed from their slender pendent green catkins an abundance of pollen just when the delicate bluish-green leaves are unfolding. Many cases of oak hayfever have been recorded, some of them very severe, but they are fewer than would be expected from the enormous quantities of pollen that these trees shed. In some regions where oak trees are abundant their pollen greatly outranks that of all other plants for a period of several weeks in May. In the eastern United States a large number of species are involved, including the white, black, red, chestnut, and swamp-white oaks. In the western and southwestern parts of the United States other species are regarded as of considerable local importance. Thus the black oak of California and Oregon, and the live oak of California have been suspected of causing hayfever, and the black oak of western Texas, New Mexico, and Arizona and the white oaks of similar distribution are regarded as important in these regions.

Among the *sycamores* or *plane-trees* apparently our native species are quite harmless. In California, however, where an exotic species has been introduced and is extensively planted as a shade tree under the name of California sycamore, it is said to be a serious cause of early-spring hayfever.

The *hackberries* or *nettle-trees* have quite frequently been blamed for hayfever. They bloom early in spring when the leaves are beginning to unfold and shed large quantities of light, air-borne pollen, thus appearing to qualify for the production of hayfever. In the northeastern states, however, no cases of hayfever have been recorded for the species that grows there; but in the southern states, particularly in the Mississippi valley where a large form, *Celtis mississippiensis*, is abundant, it is probably the cause of some hayfever.

In general it may be said that trees with blossoms that are showy, sweet scented, or otherwise attractive to insects shed so little pollen that they need not seriously be considered as factors in hayfever. On the other hand, those that constitute the primary cause of early-spring hayfever have inconspicuous flowers, frequently pendent catkins, are without scent, and are rarely of any interest to insects. It is not safe, however, to say that only wind-pollinated trees can cause hayfever. Insect-pollinated trees that are not perfectly adapted to this mode of pollination may become a potential menace to hayfever sufferers, and this is a measure of the imperfection of their adaptation to insect pollination.

Early Summer Hayfever.—Following closely on the heels of the tree hayfever comes the early summer hayfever. In most places it begins before the close of the early spring hayfever season, but reaches its height in June when the roses are in bloom. On this account the malady is even sometimes called rose cold, an unfortunate name because roses rarely have anything to do with it. Possibly the name was not originally intended to imply causal relationship, though in the past such a belief has been entertained by many. *Roses* are poorly equipped to cause hayfever; they produce but little pollen, and this is not buoyant, instead it is adapted to insect transmission. Besides this, most of the double roses in cultivation are of hybrid origin and produce little or no viable pollen, so that it is only from the wild species and some single-flowered cultivated varieties that any appreciable quantity of pollen may be obtained. The hayfever of this period is caused almost entirely by the less conspicuous plants such as the grasses and plantain, which are associated with the roses in their habitat and time of flowering.

The *flowers of grasses* are small and inconspicuous and are not regarded as objects of beauty. They are mostly green or greenish and so much less attractive then their more showy neighbors the roses and many other beautiful flowers of the summer garden, that they are nearly always overlooked. The florets of grass lack entirely the conspicuously colored corolla and calyx familiar in the better known flowers, the place of these being taken by small green bracts. The stamens, however, are well developed; each floret generally possesses three, appearing as double sacs. A number of florets open each day, sometimes with clock-like regularity. The bracts spread apart; the anthers emerge, open, shed their pollen, wither, and die; and the green bracts close protectingly about the young seed. The process is repeated each day, in many species always at precisely the same time, a fresh set of flowers coming into play at each opening until all the florets in the spike have opened, shed their pollen, and closed.

In the eastern United States the first species to flower is the *low spear grass* generally starting in April but continuing to flower throughout the greater part of the summer. Low spear grass can generally be distinguished by its slender leaves of a yellowish green and its whitish flowering spikes. The plants generally sprawl flat on the ground and show no tendency to stand erect unless crowded by each other or by other species. The species is abundant in lawns, and, owing to frequent cutting, its flowering period is generally prolonged until late in summer.

Apparently low spear grass contributes only little to hayfever because of its small size, low form, and the small amount of pollen produced. At any rate, it usually starts to flower several weeks in advance of the appearance of early summer hayfever symptoms.

A more important species is the *sweet vernal grass*, which follows soon after the first flowering of low spear grass. The flowers are borne in compact, pointed spikes at the tops of erect stems. This species may usually be distinguished by its fragrant odor of cumarin, which can be detected upon drying or bruising the leaves. Sweet vernal grass was introduced from Europe as a meadow grass and has since become abundant throughout most of the northern part of North America. It dies soon after flowering, and its place in the meadows is taken by some of the late flowering grasses.

June grass and orchard grass follow closely on the heels of sweet vernal grass. Both flower at about the same time in May and June, and both are extremely abundant throughout the United States and most of Canada, except in very arid regions.

June grass is perhaps the commonest lawn grass. Though it is seldom permitted to flower in lawns, it has escaped from cultivation and is found everywhere. It flowers excessively in nearly all roadside ditches and waste places. When properly developed the plants stand about 2 ft. high and are distinguished by their soft, spreading, bluish panicles. This species is the favorite pasture grass throughout the more humid regions and is generally cultivated under the name of blue- or Kentucky bluegrass and is one of the most valuable and universally distributed grasses of the United States.

Orchard grass is about twice as tall as June grass and is coarse and stiff. It cannot be grown in lawns because it has a tendency to form tussocks. As a consequence of this habit it is sometimes called bunch grass. The flowering panicle stands erect, and when mature its branches stand almost straight out from the central axis; the lower branch is generally much larger than the others and, standing off abruptly from the central axis, causes the inflorescence to bear a remote resemblance to the foot of a cock, the enlarged lower side branch representing the spur; hence the name cocksfoot grass, by which it is frequently known, particularly in England.

Both June grass and orchard grass start to flower toward the end of May and continue through most of June, shedding large quantities of light, air-borne pollen.

Closely following these come redtop and timothy, which begin to flower late in June and continue through most of July. Both are cultivated in humid regions. Redtop is a valuable meadow and pasture grass frequently succeeding sweet vernal grass in its pollination in moist meadows. It is low, with soft, spreading panicles, somewhat resembling June grass, from which it can easily be distinguished by its later flowering period and the purple-reddish color developed by its panicles as they approach maturity. Though redtop resembles June grass in outward appearance, the two are seldom found together, because June grass does not thrive in acid soil which is favorable to the best development of redtop.

Timothy is the standard hay grass throughout the more humid parts of the United States. When made into hay it is cut at the height of its flowering season, while shedding an abundance of light, air-borne pollen. In many regions in which timothy is cultivated it covers large tracts of land and in these regions causes much of the hayfever occurring during the latter part of June and the early part of July. However, it is much less abundant in waste places, vacant lots, neglected fields, and along roadsides than are the other species and therefore is less productive of hayfever among suburban and city dwellers.

Though there are undoubtedly many other species of grass that contribute to the production of early summer hayfever, there is no doubt that the five species—sweet vernal, June grass, orchard grass, timothy, and redtop—are responsible for the greater part of the early summer hayfever. It is significant that hayfever of this type in the northeastern United States stops with the cessation of flowering of timothy and redtop; consequently, there is little need to consider such grasses as barnyard grass, crab grass, squirrel-tail grass, the witch grasses, and innumerable others that flower subsequently to this time.

There are, however, several others that should be mentioned; though a good deal less general in distribution and less abundant than the five species mentioned above, they should be regarded as contributory factors and sometimes as primary causes of hayfever.

For example, *meadow fescue* is frequently found associated with June grass; it flowers at about the same time. *Red fescue*, flowering a little later, is distinguished by its dark bluish-green, wiry leaves, forming basal rosettes in dry, sandy, or impoverished soils. *Velvet grass,* with its soft, velvety leaves and stems and purplish flower panicles, flowers in moist meadows and roadside ditches. *Tall oat grass,* with its graceful plumes, forms a conspicuous element of our roadside vegetation in July. *Meadow foxtail,* an old-fashioned grass formerly cultivated widely, now occurs only in isolated patches where it has been able to hold its own against its more hardy competitors. It is similar and closely related to timothy but can be distinguished from it by its early period of flowering.

In the warmer and more arid regions of the United States the hayfever sufferer has other species to contend with. Possibly the worst of these are *Bermuda grass* and *Johnson grass.* The former has a range extending from coast to coast in the southern part of the country, and the latter a range but little less extensive. Both were introduced from the Mediterranean region as forage grasses. Both are drought resistant and, once established, can scarcely be eradicated.

Of the two, *Bermuda grass* is the more important, because its pollen is the lighter and more easily dispersed by wind currents, and it has the longest flowering period of all the grasses, flowering from April to September and in some places practically throughout the year. When there is insufficient moisture it withers and dies to the ground but springs up again as soon as there is rain and bursts into flower.

Johnson grass is very different; the plants are tall and stout, usually reaching a height of 4 or 5 ft. or sometimes much more. The flowers are borne in large, open panicles but shed a disproportionately small amount of pollen of large and heavy grains. But what the pollen lacks in buoyancy and amount is largely compensated for by the height and abundance of the plants. In some parts of the Southwest it is a pernicious weed and has become so abundant that it has rendered farming unprofitable. In such localities it is said to be the worst hayfever weed that the sufferer encounters.

Farther west are other kinds of grass. Hall, (1922) in his catalogue of California plants, lists about 25 species that are to be regarded as at least contributory causes of hayfever. Besides these of the Pacific coast, there are many species in the Great Plains region deserving attention; but altogether they are so numerous that any adequate treatment of them is beyond the

scope of this discussion. The reader who wishes to go more deeply into the subject is referred to Hall's list and other bulletins of the U. S. Department of Agriculture and bulletins issued by the various state departments.

Though the grasses are responsible for by far the greater part of early summer hayfever, there are several weeds that occasionally play an important part. For example, *English plantain,* a common weed of dooryards, vacant lots, and meadows, is frequently found associated with sweet vernal grass. It starts to flower at about the same time and continues, shedding large quantities of light, air-borne pollen well into July.

Of somewhat less importance are the several species of dock, as the yellow or curly dock and sheep sorrel. Besides these there are a number of plants characteristic of the Great Plains and of semiarid regions as, for example, Russian thistle, several kinds of salt bush, pigweeds, and various others which begin to flower in the early summer but reach their maximum development during the latter part of the summer and, therefore, more properly belong to the late summer group.

Late Summer Hayfever.—The expression, late summer hayfever, will call to the minds of many the goldenrods, sunflowers, and other gorgeous components of the waning summer's landscape, for the impression that these flowers must be the cause of their malady has become deeply fixed with many whose sufferings are ushered in with the appearance of such flowers. The term "goldenrod fever" has been popularly suggested to describe the form of hayfever occurring when the goldenrods bloom but with only the justification of coincidence in time.

Ragweeds are offenders in the East. Most of the hayfever occurring in the eastern part of the United States in the late summer is due to the ragweeds and their allies. All of them produce large quantities of pollen capable of being carried long distances by light winds. There are nearly 60 species in the ragweed family. The majority of these flower toward the end of summer, and, though there is considerable range in size and form of pollen grain in the different species, all possess in a high degree the characteristics of hayfever pollen. All are light and buoyant, they are shed in large quantities over long periods of time, and, as far as tests have been made, they are nearly all more or less toxic to hayfever patients. Thus the relative importance of the different species is largely a matter of their abundance and local distribution.

In the eastern states the common or dwarf ragweed and its near relative the giant ragweed are found growing in great profusion in roadside ditches and waste places. The *dwarf ragweed* can be distinguished by its finely divided leaf; each leaf is cut into many segments and each segment is again divided, giving it a fern-like appearance. The plants branch extensively and, when allowed to grow unhampered, assume a pyramidal form 4 or more ft. high, spreading at the base to 3 or 4 ft. They are so prolific that they are usually found growing in masses of hundreds or thousands together, often forming solid banks of vegetation. Toward the middle of August they become covered with the greenish-yellow flower spikes from which they shed their pollen.

The *giant ragweed* can easily be distinguished by its broad leaf, which is three-lobed or five-lobed or not divided at all; the blade of the leaf is carried down the leaf stalk as a narrow wing on each side. It also has the habit of branching extensively just above the ground, forming a more or less columnar bush frequently attaining a height of 12 or 13 ft.

Both species flower at almost the same time, the giant preceding the dwarf by only a few days. Many have observed the precision of the annual recurrence of their flowering period. Unlike the early spring flowers, which are frequently delayed in their appearance for several weeks by cold, rainy weather, the ragweeds are not influenced by weather conditions. It is now known that the principal factor governing their time of flowering is length of day, and thus it is that their reappearance can be predicted almost to a day in any given latitude.

The pollen-bearing flowers of the ragweed are extremely small and are borne in immense numbers in small heads, which are arranged in long spikes at the top of the plant and at the ends of the side branches, usually standing conspicuously out from the general mass of the bushes. These spiked flowers bear no seeds. Their entire effort is given to the production of pollen, which is shed in such enormous quantities that it rises up like clouds of smoke if the plant is shaken on a still day.

These two species are the only ragweeds found in northeastern United States. They have each about the same range reaching almost across the continent in the northern states and Canada. They are much less abundant in the western part of their range and do not quite reach the Pacific coast. But these two species have their counterparts in the western ragweed and western giant ragweed.

The *western ragweed* is scarcely to be distinguished in outward appearance from the common or dwarf ragweed; they are about the same in size and habit, but the leaf of the western is not so consistently twice divided, and the plants spring anew each year from the same roots, while the eastern form must come afresh each year from seed. In southern California and throughout the Southwest the western ragweed is almost as abundant as the common ragweed is in the East and flowers at about the same time.

The *western giant ragweed* is likewise remarkably similar to the eastern giant ragweed; both have the same general habit and much the same shaped leaf. The western form differs, however, in showing a tendency to branch well above the ground—generally rising from the root on a central stalk—and the leaf blade is not carried down the sides of the leaf stalk, which is thus wingless. The western giant ragweed has a much more restricted range than have the other species mentioned; it is almost entirely confined to the southwestern states, from Louisiana to Arizona.

There are 11 other species of true ragweed in the United States, but of these possibly only the *southern* or *lance-leaved ragweed* is of importance in hayfever. This species is much smaller than the others and is distinguished by its slender lance-shaped leaves, with generally one or more large teeth near the base. It has a still less extensive range, being confined mainly to the central states, where it is known to cause some trouble to hayfever patients.

Scarcely less important than the ragweeds are the so-called *false ragweeds,* of which there are probably 25 species in the United States. They are similar in general appearance to the true ragweeds and are distinguished from them only on technical details such as their more spiny seed pods. Of these, the slender ragweed and bur ragweed are common in the Southwest and in Colorado; the latter also ranges northward into Alberta and Saskatchewan, where it is abundant in most arid regions, shedding large quantities of pollen during the latter part of the summer.

The *marsh elders* belong to the same family as the ragweeds and false ragweeds but are different from them, having the pollen-bearing and seed-bearing flowers in the same heads; they lack the long spikes of pollen-bearing flowers typical of other members of the family. Consequently they do not possess so efficient a pollen-dispersing apparatus. The high-water shrub or bushy marsh elder is common in tidal marshes along the Atlantic coast. It sheds large quantities of light, air-borne pollen in late summer, and clinical tests have shown that it is frequently active with hayfever cases but less so than the ragweed.

Other species of marsh elder, *e.g.*, poverty weed, prairie ragweed, and rough marsh elder—are found in moist, saline, or alkaline soils throughout most of the western part of the United States. They contribute to a certain extent to the production of hayfever.

The *cockleburs* constitute another group of plants related to the ragweeds. Fifteen species frequent waste places and impoverished ground. They are coarse, ill-smelling herbs with broad, bristly leaves. The staminate flowers are borne in comparatively large spheroidal heads, which are in turn arranged in elongate spikes standing conspicuously above the burs of the seed-bearing flowers. The pollen of the cockleburs has been shown to react with late summer hayfever patients, and in some regions they are troublesome hayfever plants.

The *sagebrushes* and *mugworts* constitute another important group of hayfever plants. There are about 200 species, of which nearly one-third are North American. Generally speaking, they are commonest in the arid and semiarid regions, reaching their greatest abundance in the Rocky Mountain states. The best known and commonest of these is the ordinary sagebrush. It is extremely abundant on the western slope of the Rocky Mountains and in the Great Basin. In some places the dusty, gray-green sagebrush plants are the only living things the eye can see for miles across the deserts.

Ordinarily, sagebrush reaches a height of only 3 or 4 ft., but under favorable conditions it may attain to 12 or 15 ft., assuming the form of a small tree with a fair-sized trunk distinctive for its shredding, reddish bark. The tree form is most commonly found in mountainous regions, where it sheds enormous quantities of light, air-borne pollen, which produces a type of hayfever known locally as mountain fever.

Of equal importance is the common mugwort, a herbaceous species which in its many varieties is found almost throughout the North American continent. One form of this species, known more especially as prairie sage, is common in the prairies of British Columbia, Washington, and southward; another slightly different form is common in the foothills of the mountains. Of the many other species perhaps the most important are the California mugwort and hill sage, both common in the Pacific coast states and in these regions serious causes of hayfever, and the silvery wormwood, which is widespread throughout the arid regions. In the Mesilla valley in southern New Mexico the silvery wormwood is a troublesome cause of hayfever. There are so many species and varieties involved, however, that any adequate consideration of them would be beyond the scope of this discussion. For a detailed account of the group and their relative importance in hayfever the reader is referred to the work of Hall and Clements (1923).

Among the Compositae are many other species which, like the goldenrods, sunflowers, and dahlias, may at times produce some hayfever symptoms but are frequently credited with much more than is their share. The pollen of all these is covered with long, sharp spines and is waxy, so that when shed the grains nearly all remain clumped together and can get into the atmosphere in only limited amounts. They can scarcely be counted as factors in hayfever unless brought in close proximity or actual contact with the sufferer. The pollen of such species frequently gives some reaction by the cutaneous test with ragweed patients, but this is probably solely on account of their biologic kinship with the ragweeds.

The groups of the *chenopods* and *amaranths* also contain many hayfever plants. One of the worst of these is Russian thistle or tumbleweed. It is of wide and ever increasing distribution, already covering nearly the whole of the United States. It is mainly in the western part of its range that it reaches its best development and becomes a hayfever menace.

Russian thistle must not be confused with the true thistles with which it has no kinship but to which it bears a certain resemblance in the sharp, spiny tips of its leaves. The plants branch excessively with long, slender branches, formed in such profusion that they fairly mat together. When fully developed they form compact, dome-shaped, and prickly bushes, which give off large quantities of pollen from July to September. After September they begin to dry up, and finally, breaking off at the root, they are rolled about the plains by the winds, distributing their seeds as they go, until they become entangled in a fence or some other obstruction, where they frequently accumulate in great masses. In eastern Washington and in Oregon, Idaho, Montana, and Wyoming Russian thistle is regarded as the worst of all hayfever plants. In the eastern part of its range it is comparatively harmless.

Also belonging to the chenopod family is the group of *salt bushes*, of which the desert holly, much used for Christmas decorations, is a well-known but harmless example. Many other species are important contributors to the production of hayfever. For example, the annual saltbush is said to be one of the worst causes of hayfever in southern Arizona. Also important through much of the Southwest are red orach, silver scale, all scale, and shad scale. These and the many other species inhabit mostly desert and semidesert regions in which the human population is sparse and scattered. Were it not for this fact it is likely that these plants would cause much hayfever, for the pollen of many species has been shown to be toxic to hayfever patients.

A close relative of the western salt bushes is greasewood. It is particularly abundant in saline situations in the Great Basin region, where it is often associated with sagebrush. It is generally a large, spiny, sprawling shrub, 4 or 5 ft. high or occasionally much higher, with small, narrow, fleshy leaves. The pollen-bearing flowers are borne in small, cone-like inflorescences standing upright at the ends of the spiny twigs. They shed large quantities of pollen from May to September. Greasewood is not regarded as a serious cause of hayfever, though its pollen has been shown to give cutaneous reactions with hayfever patients. There are other plants of the chenopod family, such as lamb's-quarters, winged pigweed, and poverty weed, which in some localities are of importance.

Among the *amaranths* the western water hemp is regarded as one of the worst hayfever plants when it is abundant. It is a tall, branching, coarse weed frequenting swampy or moist soils. The pollen-bearing flowers are borne in long, slender, or slightly drooping spikes, shedding large quantities of pollen from July to September. Fortunately its range is restricted, being confined for the most part to the states of the Great Plains region. Similar to western water hemp and closely related to it are the various species of amaranth. These are mostly coarse weeds of gardens and ditches, as redroot pigweed and careless weed, and are frequent causes of hayfever in the Southwest.

Just how finely specific it is necessary to be in the diagnosis and treatment of hayfever is still an open question. Hall and Clements (1923), in speaking of the common mugwort, which, as regarded by them, includes 15 subspecies, almost all of which are considered as separate species by other authors, say: "Preliminary studies indicate that the pollens of the different subspecies all react alike. Therefore in testing and treating hayfever cases, the specialist need pay no attention to the complicated series of subspecies and minor variations."

Diagnosis.—The exact species of pollen, whether it be one or several which affect the hayfever sufferer, can be discovered by the hayfever specialist by means of the skin reaction at any time, because the abnormal sensitivity which hayfever sufferers possess to certain species of pollen exists as much in the skin of all parts of the body, and throughout the year regardless of season, as it does in the mucous membranes of the eyes and upper respiratory tract at the time when the pollen is in the air. Consequently, at any time of the year, whether the patient happens to exhibit hayfever symptoms or not, his sensitization may be determined by the appropriate application of the pollen to the skin.

The hayfever specialist provides himself with extracts of the pollen of all the different species of plants which are likely to cause hayfever in his vicinity. In making his collection of these, unless he has, as his guide, the results of a botanical survey of the region, the pollen of every wind-pollinated species and of the most abundant and copious pollen shedders among those that are insect pollinated should be included. From these he selects the extracts of the species which flower during the time that the patient has hayfever.

In making the skin test the application of the pollen is generally done by means of the scratch method. The flexor surface of the forearm is cleaned with 70 per cent alcohol, and the points at which the tests are to be made are marked by means of a skin pencil. These should be about ¾ in. apart, and since the average arm is just broad enough to accommodate three such tests in a row, they are generally arranged in transverse rows of three each, starting with the first row at the proximal end of the forearm. Done in this way the ordinary arm accommodates 8 to 10 rows, *i.e.*, 24 to 30 tests, which is generally quite sufficient. Abrasions are then made by lightly nicking the outer surface of the skin with a medium-sized needle mounted in a handle or with the tip of a fine, sharp scalpel. The scarifier should penetrate only the outer impervious layer of the skin and should not draw blood. When properly made, these abrasions do so little injury to the skin that they can scarcely be detected; hence the necessity of previously marking their positions. To each is added a drop of the pollen solution to be tested, reserving the first and last for control tests. The most convenient way of applying the solutions is with a capillary tube about 3 in. long. This, when dipped in the solution in a slanting position, will draw it up by capillary force and, when removed and turned in a vertical position, can be made to release a drop on the abrasion. Upon each of the controls is similarly placed a drop of the solvent used to make the pollen extracts. Occasionally it is necessary to add a second drop to each of the tests if the solution on them dries before the reactions are obtained. In any event each should be kept moist with the pollen extract for about 15 min. or until the reactions appear, after which the test material should be removed with cotton, and the forearm wiped again with alcohol.

Typical skin reactions to pollen extracts are essentially the same as the reactions of the same skin to mosquito bites. There generally appears a central whitish or yellowish edematous area surrounded by a reddish areola (Fig. 12). The edema may be round in outline, or it may extend outward in irregularly shaped pseudopodia of varying length, coming to resemble the form of an *Amoeba proteus*. These visual manifestations of the reaction are generally accompanied by the same sort of itching as that of mosquito bites. There is much variation among different people in their response to the test; occasionally, in highly sensitized cases, the reactions may be very violent and, if obtained with many of the tests at the same time, nearly the whole of the tested surface may become edematous, with long pseudopodia coursing upward on to the upper arm toward the axillary fossa. On the other hand, the reactions may be manifested only by a slight reddening about the scratches, occasionally even so small that it is necessary to compare them closely with the control tests to determine whether they are positive or not. Whether the reactions are large or small, both their visual manifestations and itching reach a maximum in about 20 min. and subside in an hour's time.

After the exact kind or kinds of pollen which cause the patient's hayfever have been determined by the skin test, the physician may institute a course of treatment. This consists of introducing subcutaneously minute but gradually increasing amounts of a specially prepared extract of the one or more species of pollen which cause the patient's hayfever. By so doing, a resistance to the toxicity of the pollen may be built up before the hayfever season opens, enabling the patient to resist the effect of the pollen when it is encountered in the atmosphere. Pollen extracts for this purpose can be prepared only by those thoroughly familiar both with the general sterility procedures observed in the preparation of vaccines and with the very special methods of handling pollen materials. There are many adequate pollen extracts on the market, and since the manufacturers of these always prescribe in great detail how their products must be used, a further discussion of them will not be entered into here.

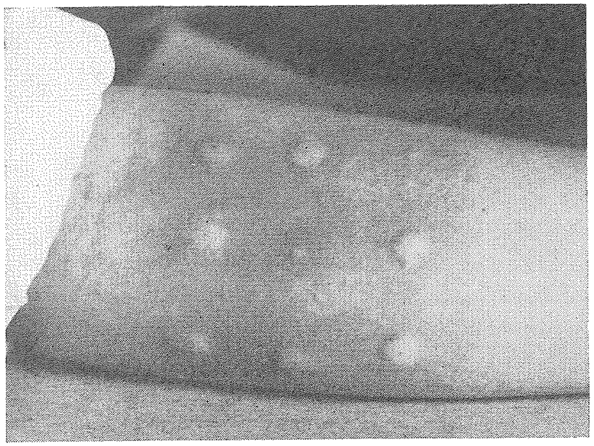

FIG. 12.—Arm of a hayfever patient, showing cutaneous reactions to pollen extracts, scratch test by pick method.

A word of caution is, perhaps, necessary. In spite of the apparent simplicity of both the diagnosis and treatment of hayfever, and their complete harmlessness in the hands of trained specialists, both these procedures in the hands of the inexperienced are attended with very grave dangers and may even result in serious injury or death to the patient. Accordingly, neither should be attempted except by a qualified physician and with properly prepared materials.

CHAPTER VII

POLLEN-GRAIN CHARACTERS

I. GENERAL

The forces that shape pollen grains, as with other organisms, are hereditary and environmental. But, because pollen grains are generated generally in groups of four and set free generally as individuals to wander at great distances in the fulfillment of their destinies, their environmental influences come under two distinct categories—first, those of the prenatal or internal environment and, second, those of the postnatal or external environment. To the circumstance that pollen grains during their development are acted upon by their neighbors of the tetrad they owe such fundamental and conspicuous characters as the number and arrangement of their germinal furrows or the number of their germ pores, and the numerical type of symmetry of their sculptured patterns. And, when they reach maturity, they must be adapted to whatever means of transportation are available. Pollen grains are, therefore, unique in that the influences which determine their form are threefold—heredity, internal environment, and external environment. The effects of these three factors are inseparable but not indistinguishable.

Hereditary Characters.—As far as their hereditary characters are manifest, pollen grains of the same species and of closely related species tend to be alike, and, if the environmental factors are uniform, the degree of their similarity is a measure of their closeness of relationship. For example, the grains of tansy (Plate XIII, Figs. 1, 2), chrysanthemum, camomile, and daisy, which all belong to the same tribe of the Compositae, are so much alike that they can scarcely be distinguished from each other. They all have a thick, coarsely granular exine, bearing sharp conical spines, and their surface is covered with a copious layer of oil. They also have three characteristic germinal furrows, each enclosing a round germ pore. The similarity of the pollen grains of these three species is clearly a manifestation of the closeness of their relationship, and such characters as the above are purely hereditary or phylogenetic.

Internal Environmental Characters.—On the other hand, if the internal environment is not uniform, striking differences may result in the forms of the pollen grains, though they be closely related or even of the same species. For example, the grains of sunflower (Fig. 13) are provided with long, sharp spines and three broad short germinal furrows in conformity with their phylogenetic position in the tribe Heliantheae. But those of *Dahlia* (Fig. 14), which belongs to the same tribe, have the same sort of long, sharp spines and short germinal furrows, but instead of three of these they always have six. This is because the grains of *Dahlia* do not form from the pollen mother-cell in the way that is usual for the tribe (Wodehouse, 1931) but are formed in a way distinctly aberrant and, thus, engendered under different conditions, the grains possess different internal environmental characters.

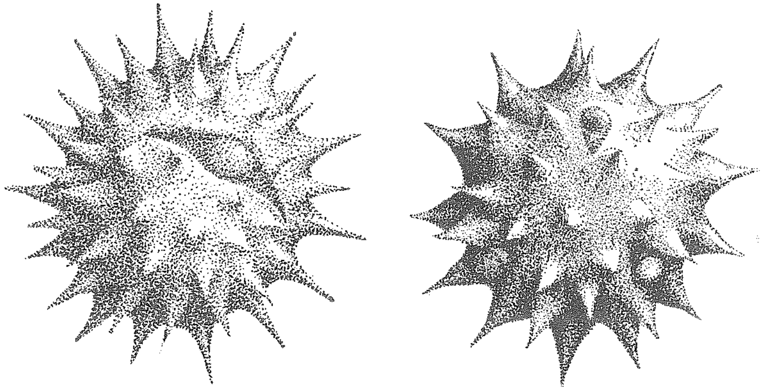

Fig. 13. Fig. 14.

Figs. 13, 14.—Pollen grains of the sunflower tribe. Fig. 13, *Helianthus annuus*, side view showing one of its three furrows; Fig. 14, *Dahlia excelsa*, showing three of its six furrows, their major axes converging toward a point on the upper hemisphere.

External Environmental Characters.—In the same way, if the external environmental factors are not uniform, pollen grains may be extremely diverse in spite of a closeness in their relationship. The tendency of related species to resemble each other may be suppressed by the development of characters induced by outside influences to such an extent that little similarity is recognizable. Thus it is that the pollen grain of tansy, which is insect pollinated, bears little resemblance to that of sagebrush (Plate XIII, Figs. 5, 6), which is wind pollinated. The grains of the latter have a thinner exine without spines, or with only minute vestiges of them, and are provided with only a trace of oil. Yet tansy is probably just as closely related to sagebrush as it is to the daisy with which its pollen-grain form is identical. The differences between the pollen grains of tansy and sagebrush are due to external environmental factors—tansy is pollinated by insects, while sagebrush is pollinated by wind.

From the above examples the conclusion may be drawn that, while heredity or phylogeny tends to dominate the basic form of pollen grains, the internal environment tends to control the number and arrangement of their germinal furrows and pores, and the external environment tends to modify their sculpturing. Accordingly, the characters of pollen grains may be classified as phyletic, internal environmental, and external environmental. The lines of demarcation between these classes of characters are often vague; the same character may even occur as much through one of the influences as through the other. For example, the smooth form of a grain may be either a family character inherent in the group, as with the pollen grains of rose (Plate IX, Fig. 4), mesquite (Plate IX, Fig. 1), and acacia (Plate IX, Fig. 3), which are smooth because smoothness is a character of the pollen grains of the Rosales, the order to which they belong. Or the same character might be induced by wind pollination, as we have seen was the case with the grains of sagebrush (Plate XIII, Fig. 5), which are almost perfectly smooth even though sagebrush belongs to a tribe of predominantly echinate-grained plants. Moreover, inherited characters may be expressed either as inherent per se or as the characteristic way in which the grains respond to their environmental stimuli. Though the results of these three influences are intimately bound together, they may generally be recognized and are frequently so marked that they form a natural basis for the classification of pollen-grain characters.

Characters of the Exine.—The morphological characters of pollen grains have to do principally with the exine and, to a lesser extent, with the intine. The function of the exine, like that of the skin of animals, is the protection of the organism from injury by external agencies, such as excessive desiccation, destruction by light, and mechanical injury. It is also called upon to perform two other functions which are the special properties of pollen grains. These are to provide for the emergence of the pollen tube at the time of fertilization and to accommodate changes in volume as the grain takes up and gives off moisture, which it readily does in response to the ever changing humidity of the atmosphere that it encounters as a free living organism. For the former function are provided germ pores; for the latter are provided furrows or harmomegathi.*

Germinal Furrows.—The form and character of the germinal furrows are generally rather strictly phyletic, tending to be constant throughout families and other large groups; but their number and arrangement are controlled to a large extent by their internal environment, which, in turn, is determined by the number and arrangement of the grains as they are formed from the pollen mother-cell, and may, therefore, be various even in grains from the same anther. Moreover, since the furrows are organs of the exine, which is subject to enormous external environmental modifications, they are indirectly subject to the same modifications. For example, the exine of the pollen grain of willow, which is primarily insect pollinated, is thick and provided with well-developed functional furrows, while that of the grain of the closely related poplar, which is wind pollinated, is thin and fragmentary and totally lacks furrows because the exine is so far reduced that it is incapable of supporting furrows. Thus it is that indirectly, through its effects on the exine, an external environmental influence, *viz.*, wind pollination, may completely banish the germinal furrows.

Germ Pores.—The furrows, besides accommodating changes in volume of the grain, always enclose the germ pores when the latter are present or, in the event of their absence, function directly as germ pores. A good example of the former condition is seen in the grains of goldenrod (Plate XII, Fig. 4). When such a grain is moistened and expands, the furrows gape widely open, and the germ pores bulge through the apertures which are situated in the middle of each furrow membrane; and when the grains dry, the furrows close tightly, hiding the germ pores from view. In such a form as that of maple (Plate X, Fig. 1), in which furrows are present but without pores in their membranes, the furrows take over the function of the pores, serving both as *harmomegathi* and as places of exit for the pollen tube. This latter is suggested by the slight bulge that is generally seen in the center of the furrow membrane of such grains.

---

* See Glossary.

Many grains, such as those of the Chenopodiaceae and some Polygonaceae, entirely lack germinal furrows in the ordinary sense of the word but are provided, instead, with a number of rounded apertures in the exine. Functionally these are germ pores, since they permit the emergence of the pollen tube. They also permit a bulging out or a sucking in of the intine in accommodating volume changes. Though their shape, and their function of serving as places of exit for the pollen tube, prompt us to call them germ pores, there is much evidence to show that such apertures are morphologically furrows which have become so shortened that they coincide in extent with their enclosed germ pores. Their arrangement on the surface of the grain is that of furrows; and grains with furrows representing some of the various stages in the shortening process are found among the Polygonaceae. It may therefore be said that germ pores, when present, are always enclosed by germinal furrows and that the rounded apertures, such as those of the pollen of the Chenopodiaceae, are, in reality, shortened furrows.

Character of the Furrows.—The characters of furrows, whether they be long and tapering, as in the grains of goldenrod, or broad and short, as in the grains of sunflower, or circular and coinciding in extent with their contained germ pore, as in the grains of the Chenopodiaceae, are mainly hereditary and phyletic in their distribution, and are of the greatest value in the identification and classification of plants. Likewise, whether there be but a single furrow or a larger number of them is a character of the deepest phylogenetic significance. The presence of a single furrow is the sign of the monocotyledons, the primitive gymnosperms, or the primitive dicotyledons; while the presence of a larger number of furrows, whether it be 3 (only very rarely 2) on up to 30 or more, is a sign of the higher dicotyledons. On the other hand, *the number and arrangement of the furrows*, when more than one, are almost entirely internal environmental because they are the result of the number and arrangement of the pollen grains during their formation in the pollen mother-cell.

ORIGIN OF POLLEN CHARACTERS

For our first clear understanding and concise statement of the origin of these classes of characters we are indebted to Harper (1918), who states that at least two sets of factors are involved in determining the form of cells, their internally determined or specifically inherited cell form—including their capacity to respond to stimuli—and their contact and other relations with their neighbors during growth. This latter involves especially the conflict between the laws of cell bipartition with rectangular intersection of the successive planes of division, on the one hand, and, on the other, the tendency of single cells and groups of cells to assume least-surface configurations.

The problem as to which of the great variety of characters found among pollen grains are specifically inherited and which are the result of interrelations with their neighbors is thus sharply defined; and since there appear to be no words to designate adequately these two classes of cell characters I propose to call those which are the result of specifically inherited cell form *emphytic;** and those which are due to contact and other relations with their neighbors during growth, *haptotypic.** Emphytic cell characters are usually strictly phylogenetic in distribution and consequently of high diagnostic value, while haptotypic cell characters are almost fortuitous in their phyletic distribution and of much less diagnostic value but are of the greatest histogenetic interest.

Though three is the characteristic number of germinal furrows among the higher dicotyledons, it is a significant fact that in the pollen of many plants are also found a varying number of grains with four, six, or two. Most frequently grains with aberrant numbers of furrows constitute only a small proportion of the total, but in some species, *e.g.*, the sorrel dock and white ash, almost one-half of the grains have four germinal furrows. In the grains of *Dahlia*, as already pointed out, the number of furrows is always six, despite the fact that three is almost the universal number throughout the Compositae; and in one specimen of tarweed (*Stenotus lanuginosus*) approximately one-half the grains have two germinal furrows.

---

* See Glossary.

Number of Furrows Due to Arrangement in Tetrad.—Why should three be the characteristic number of furrows among dicotyledonous pollen grains; and how do the other numbers originate? In the formation of pollen grains the pollen mother-cell nucleus always goes through two successive divisions and nearly always gives rise to four daughter-cells, producing in due course four mature pollen grains. In the dicotyledons these four cells are formed after two nuclear divisions which take place in rapid succession, at right angles to each other, without the dividing cell walls' forming until after the four daughter nuclei have separated and reorganized. Regardless of the relative orientation of the spindles by which they were formed, the daughter nuclei generally tend to take up positions as far from each other as possible within the confines of the pollen mother-cell, which results in their being tetrahedrally arranged. Other arrangements sometimes occur; in fact, all possible arrangements of four cells in contact are found; but in the tetrads of dicotyledons the arrangement is prevailingly tetrahedral, and it is in this position that the phragmoplasts are formed, and the cells rounded off and separated.

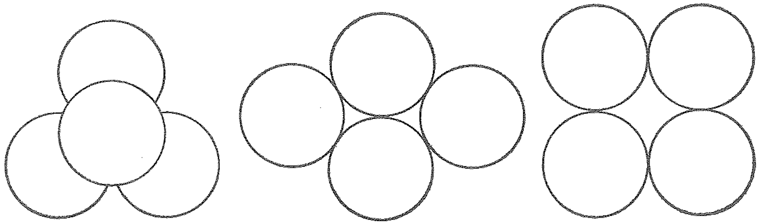

FIG. 15. FIG. 16. FIG. 17.

FIGS. 15–17.—Diagrams of typical arrangements of four spheres in contact: Fig. 15, tetrahedral; Fig. 16, rhomboidal; Fig. 17, square.

If four spheres are placed together in the tetrahedral arrangement, it will be seen that each must make contact at one point with each of its three neighbors, giving each sphere three equally spaced contact points (Fig. 15). This suggests an explanation of the prevailingly tricolpate character of the dicotyledonous pollen grains.

For purposes of discussing the symmetry relations of these spheres it is convenient to speak of their polar axes as lines extending through the centers of the spheres and directed toward the center of the tetrad, where they would all four meet, if so extended, as stated by Fischer (1890). Thus each sphere comes to have an inner and an outer pole, a proximal and distal polar hemisphere, and the equator is the boundary between the two polar hemispheres. In the case of the four spheres, the three points of contact on each occupy the positions of the angles of an equilateral triangle, and all lie in the proximal polar hemisphere; whereas the three furrows in dicotyledonous pollen grains generally lie on the equator—midway between the poles.

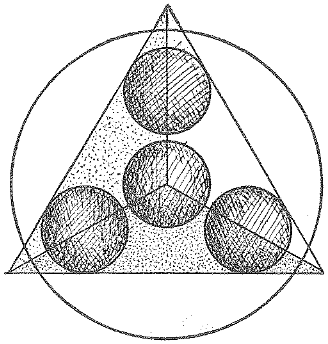

Fig. 18.—Diagram of four daughter nuclei in the tetrahedral arrangement showing their spacial relation to a tetrahedron, the mother-cell wall represented by the large circle.

Furrows Form at Points of Contact in the Tetrad.—Now let us see what the situation is when the four cells of the pollen tetrad remain united at maturity. Such is the case among most of the Ericaceae; for example, in the pollen of *Azalea* the four cells of the tetrad remain firmly united in the tetrahedral position, forming a four-celled compound pollen grain at maturity (Fig. 19). Each of the cells is much flattened against its three neighbors of the tetrad so that, instead of their contacts' being points, as in the case of spheres in this arrangement, they are broad, flat surfaces, the flattening extending very near, or even quite to, the equators of the grains. Each of the four cells has three germinal furrows contiguous and continuous with those of its three neighbors directly across the edges of their contact faces. Each furrow encloses a single germinal aperture at its point of contact with the furrow of the neighboring grain. Obviously, in this case the position of the furrows and apertures is determined by the tetrahedral arrangement of the grains in the tetrad group and is, therefore, a haptotypic character.

Another example of tetrad pollen grains is that of *Salpiglossis sinuata* (Fig. 20). The cells are in the tetrahedral position, but their union is looser than that of the grains of *Azalea*, as if formed under less pressure, and the contact faces are correspondingly less extended so that their edges do not nearly reach

the equator. The furrows are spindle-shaped, broadening out in the middle to contain the germinal aperture and tapering toward their ends. Though they exactly meet each other on the line of contact between the flattened faces of the adjacent cells, their apertures are not at the edges of contact, as in those of *Azalea*, but are on the equators of the individual cells. This shows that in these grains the longitudinal positions of the furrows are controlled by the contacts between adjacent grains but that their latitudinal positions are independent of contacts with neighboring grains; *i.e.*, they take symmetrical positions midway between the poles.

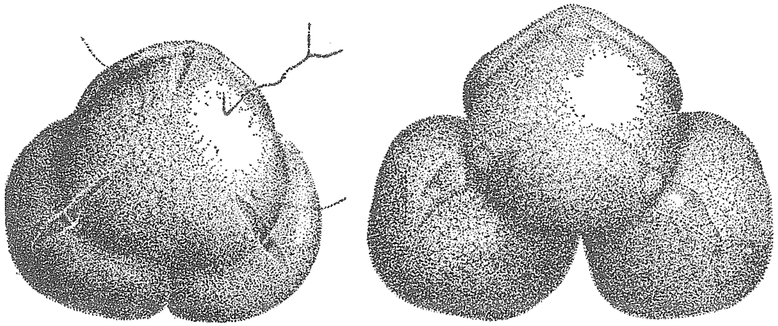

Fig. 19. Fig. 20.

Figs. 19, 20.—Mature pollen grains in tetrahedral tetrads: Fig. 19, *Azalea*, in which the four grains are closely packed; Fig. 20, *Salpiglossis sinuata*, in which the four grains are loosely attached.

Tetrahedral Arrangement Due to Quadripartitioning by Furrowing.—When the grains remain united at maturity, as in *Azalea* and *Salpiglossis*, the relationship of the furrows to the arrangement of the grains in their tetrad is obvious. But when the grains are separate, as they much more often are, information of the same sort may be obtained by examining the pollen grains in the early stages of their development. After the two divisions of the pollen mother-cell nucleus are complete and the four nuclei have taken up positions as far apart as possible—consequently, in the tetrahedral arrangement—thickenings are formed on the inside of the pollen mother-cell wall in the regions of least pressure. This can perhaps be visualized if we think of the four nuclei contained within the spherical wall of the pollen mother-cell as being situated at the four angles of an imaginary tetrahedron (Fig. 18). Such a figure is bounded by four plane surfaces—each an equilateral triangle—six edges, and the four solid angles toward which the four nuclei have migrated. Now, when the soft, gelatinous inner layers of the mother-cell wall begin to swell, the viscous material is molded inwardly in the zones of least pressure which lie between each group of three nuclei. There are four such regions, each triangular and centering outside the centers of each of the triangular faces of such an imaginary tetrahedron. These four interior ridges of the mother-cell wall continue to develop inwardly until they meet in the center of the tetrahedron. At this stage each of the four daughter-cells is still connected with its neighbors through three broad channels, six in all. As the thickening of the mother-cell wall proceeds, the six, broad connecting channels are progressively narrowed until, at the last stage before complete separation, the cells remain united by pit connections which lie in the same planes as the six edges of the assumed tetrahedron and thus become the middle points of the contact faces of the four pollen cells. These pit connections are finally severed as the cells round up and become completely separated by the continued thickening of the pollen mother-cell wall. According to Farr (1916), Gates (1925), and others, this method of quadripartition by furrowing is prevalent among the dicotyledons.

Development of Sculpturing.—It is soon after the grains have separated that their sculpturing begins to appear. Its formation consists in the deposition in organized form of the material from outside and is not secreted by the grain. As a general rule, in normal grains little or no suggestion of the pattern or hint of the position of the germinal apertures is discernible until after the separation and rounding up of the daughter-cells are complete. Consequently, from an examination of normal material, the relation of the germ pores to the points of mutual contact is not generally apparent, except in grains which remain united.

In pollen grains which exhibit a complicated system of sculpturing this nearly always presents a radiosymmetrical pattern which is definitely related to the germinal apertures. For example, in the normal grains of chicory there are three apertures, and the pattern of the sculpturing is triradiate (Plate XI, Fig. 6); it is characterized by six prominent paraporal crests, so called because they are arranged one on each side of the germinal pores and their adjoining abporal lucanae. In aberrant grains in which there are more than three apertures the triradiate pattern is never found, which shows that the numerical type of the pattern is dependent upon the number of germinal apertures.

Fortunately, in the development of the pollen grains of some varieties of chicory there are encountered many irregular formations which show the nature of this relationship. In these the pollen mother-cells either fail entirely to divide, or their divisions are arrested before completion. For example, in the variety known as "red-leaved treviso"* a large proportion of the pollen mother-cells do not divide; in these the material of the special mother-cell walls is deposited in a granular concretion on the surface, but such cells appear to be deficient in power properly to organize it and become formless giants without germinal apertures, and with no suggestion of the symmetrical pattern characteristic of the normal grains. Yet, at least in some cases, spines are weakly developed, and they and the texture of the exine bear an unmistakable resemblance to those of the normal grains. The numerical symmetry of the triradiate pattern of chicory pollen is a haptotypic character and, in this case, lacking the contact stimuli, fails to develop; but the spines and texture are emphytic and develop, at least in part, independently of contact stimuli.

Abortive Tetrads.—In other anthers of the same chicory flowers the pollen mother-cells divide normally, but the four daughter-cells die without further growth and become quite empty; nevertheless, the pattern develops as typically on these small dead cells as on the normal grains. A similar condition has been described by Tischler (1908) and others among the grains of sterile hybrids; they state that, if a pollen cell dies after only the first rudiments of the sculpturing are laid down, the pattern continues to form and develops to completion even though the cell be dead and empty.

Symmetry Patterns Are Determined by Contact Points in the Tetrad.—Between these two extreme types of behavior are found

---

* I am indebted to Dr. A. B. Stout of the New York Botanical Garden for the use of the slides upon which these observations of the developing chicory pollen grains were made. The plants were grown from seed obtained from Dippe Brothers, Quedlinburg, Germany. It is interesting to note that they are characterized by excessive fasciation. See A. B. Stout, Duplication and cohesion in the main axis of *Cichorium Intybus*, *Mem. Brooklyn Bot. Gardens*, **1**: 480–485, 1918.

a few pollen mother-cells which appear to abort during the process of separation of the four daughter-cells. Occasionally this takes place when the furrowing has all but completed the separation of the cells; with the death of the protoplast they become "frozen," so to speak, in the final act of separation when each of the daughter-cells is still connected with its three neighbors by the pit connections which now become extended as six narrow tubes (Fig. 21). Though the process of division is arrested with the death of the cell, other processes continue; the special mother-cell walls thicken, and the pattern of the newly formed cells is carried nearly to completion, resulting in the phenomenon of four daughter-cells still united in the tetrad but with the pattern of the finished cells clearly defined. And in such cells the pattern exhibits triradiate symmetry, bearing the same relation to the three connecting tubes as in the normal grains it bears to the three germ pores.

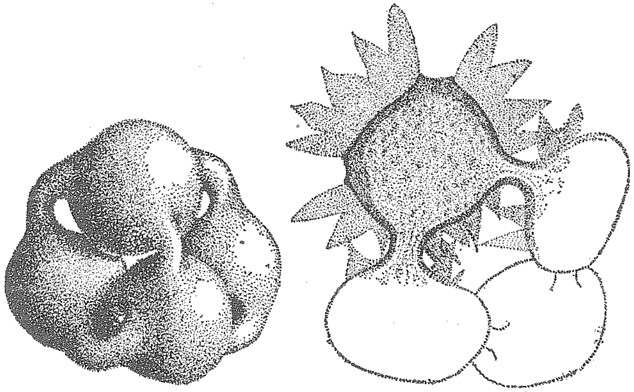

FIG. 21. FIG. 22.

FIGS. 21, 22.—Abnormal pollen grains of chicory, arrested in their development just before the final separation of the daughter-cells: Fig. 21, in the tetrahedral arrangement, with the external sculpturing omitted from the drawing; Fig. 22, in the square arrangement with the external sculpturing partly represented, in optical section.

Thus it is that in the grains of chicory the triradiate type of symmetry is determined by the number and position of the germinal apertures, and these, in turn, are formed at the last points of communication between the adjoining cells, the former sites of the three phragmoplasts which joined each cell to its three neighbors of the tetard. Since tetrad formation is prevailingly tetrahedral among the dicotyledons, we have the explanation of the fact that the patterns on the pollen grains of dicotyledons are prevailingly triradiate. This fact is the more remarkable since among floral and other symmetrical structures the pentagonal is the prevailing type of symmetry among the dicotyledons (see, for example, the many beautiful photographs by Blossfeldt, 1928), while the triradiate or triangular and the hexagonal symmetries are much less frequently encountered. We are evidently dealing in this case with phenomena which are to be classed in fundamentally different categories.

It has already been pointed out that in the pollen of many species of dicotyledons varying proportions of the grains may exhibit certain symmetries other than the triradiate. Among the grains of species which are typically tricolpate are frequently found a few which are tetracolpate, hexacolpate, and occasionally dicolpate. How can these be related to tetrad formations?

Tetrad Arrangements.—It was well known to Nägeli (1842) that, when pollen tetrads are formed, frequently there are a few in which the cells fail to get into the tetrahedral position. Two other arrangements which they may assume are the square and rhomboidal. In the square (Fig. 17) all cells are in the same plane; it is the arrangement which would result from bipartition with rectangular intersection with no readjustment toward a least-surface configuration. In this grouping each cell makes only two points of contact with its neighbors. It is known to occur sometimes among dicotyledons and is normal for many monocotyledons. In the rhomboidal arrangement (Fig. 16) all four cells are in approximately the same plane, but two cells have two points of contact, and two have three. Such an arrangement would result from bipartition with rectangular intersection followed by a partially expressed tendency to assume the least-surface configuration. This arrangement was called by Nägeli the half tetrahedral. These two types of divergence from the tetrahedral arrangement cause either all four cells to have two points of contact or two cells to have two and two to have three. But, experience shows that grains with two germinal furrows are the most rarely encountered of those with aberrant numbers. The commonest aberrant number of furrows is four—a number which, if each furrow formed only at a contact point, would require at least five cells in a group, which almost never occurs.

Four Furrows.—An explanation of the origin of four germinal furrows is found in the developing chicory pollen referred to above; among the irregular grains are occasionally found some "frozen" tetrads arrested in their development in the *square* arrangement with pit connections at only two points in each grain. In some few such cases the development of the external features of the grains has proceeded far enough to show quite definitely that two germ pores were forming at the two points of contact, as would be expected, but there were also two more, developing opposite these points (Fig. 22), thus giving each of these grains four germinal apertures and four furrows.

Thus we see that apertures and furrows are not confined exclusively to the points of contact or pit connections, but, when these are in such a position as to cause the cell to be asymmetrical, a degree of symmetry may be achieved by the development of supplementary furrows symmetrically placed.

Six Furrows.—The next most common aberrant number of furrows is six; this number is frequently found in grains of which the normal number of furrows is three. It is, as we have seen, characteristic of the grains of *Dahlia* (Fig. 14). The arrangement of these six furrows is always tetrahedral (Figs. 27, 28) in the sense that they occupy the same relative positions as those of the edges of a tetrahedron. It will readily be seen that in this arrangement each furrow is subtended on the other side of the grain by another which is exactly opposite and with its long axis at right angles to the first. In the grains of *Dahlia* the achievement of symmetry is carried a step farther than in those of chicory. Four furrows are formed from two points of contact in the same position and orientation as those of the grains of chicory, but two more furrows are developed in such positions and orientations as to complete the tetrahedral configuration. Consequently, the grain of *Dahlia* is more completely symmetrical than the four-furrowed grain of chicory.

In these two cases the two contact points, which induced the formation of four furrows in the one case and six in the other, were about one-quarter of the periphery or equator of the grain apart. When such is the case the addition of two supplementary furrows achieved symmetry partly, but it required the addition

of four to achieve it completely. If the contact points are less than one-quarter of the equator apart, various other numbers of furrows would have to be supplied to complete the symmetry. As we shall see, this basic principle leads to the formation of a wide range of furrow patterns.

These observations lead us to the conclusion that the number and arrangement of the germinal furrows in the grains of most dicotyledons are determined by the tetrahedral or other arrangement incident to their formation in tetrad. And, inasmuch as the numerical type of symmetry of the pattern is determined by the position and number of the germinal apertures, it may be stated that the number and arrangement of the elements in the symmetry patterns of pollen grains are haptotypic characters, that is to say, are the result of their cellular interrelations and directly due to the conflict of the law of bipartition with rectangular intersection, in opposition to the tendency to assume the least-surface configuration.

FURROW PATTERNS

In the pollen of perhaps the majority of species of plants the haptotypic characters are constant, showing relatively minor deviations in the number and arrangement of the furrows in only a few exceptional grains. But in certain groups of plants it seems to be a prerogative for the pollen to exhibit an enormous range of variation in haptotypic characters, sometimes within a single or a few closely related species, running almost the entire gamut of possibilities. Such a group is the genus *Haplopappus*,* a large genus of Composites in the tribe Astereae. And, on account of the light which these grains throw on the general tendencies of furrow arrangement, they will repay our careful examination.

Tricolpate Grains.—The basic or typical form of the pollen grains of *Haplopappus* (Plate I, Fig. 10) is similar to that of the grains of most other Compositae. They are spherical or oblate spheroidal. The walls are thick and inflexible and are provided with germinal furrows. These are generally three, equally spaced around the equator, which they cross at right angles, converging along meridional lines toward two centers which, it follows, are triradiate and at opposite poles of the sphere. The axes of the furrows, if extended, would thus intersect at angles of

---

* The genus *Haplopappus* is used here as defined by Hall (1928).

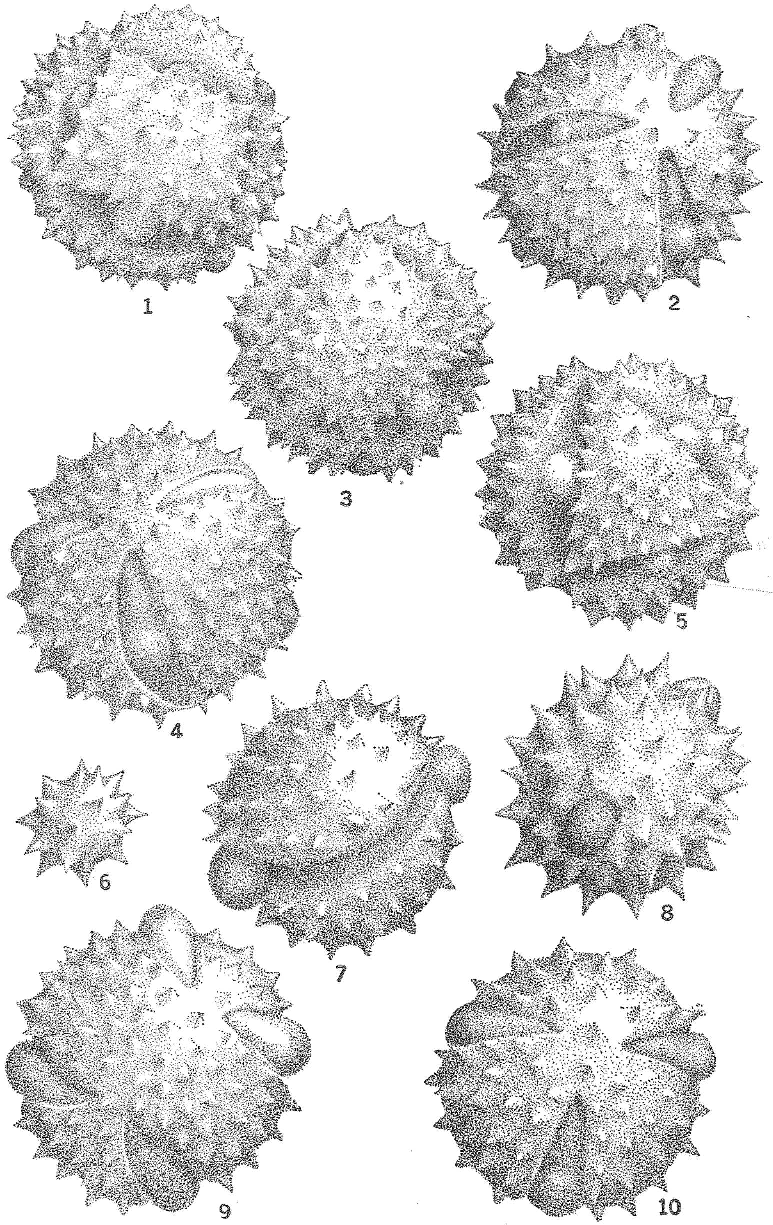

Plate I.—Pollen grains of *Haplopappus* and allied species, illustrating furrow configurations. 1, *H. MacLeanii*, dodecacolpate; 2, *H. MacLeanii*, nonacolpate; 3, *Erigeron strigosus*; octocolpate; 4, *H. acaulis*, hexacolpate; 5, *H. stenophyllus*, nonacolpate; 6, *H. MacLeanii*, dwarf; 7, *H. lanuginosus*, dicolpate; 8, *H. acaulis*, acolpate; 9, *H. MacLeanii*, tetracolpate; 10, *H. chrysanthemifolius*, tricolpate.

one-third of a circle or 120 deg. at each of the poles and thus divide the surface of the spheroid into three equal lunes. Though there is some variation in the lengths of the furrows, among the grains of different species, they never quite meet, always ending some distance short of the centers of convergence. Such a form of grain is called tricolpate.

The furrows appear as deep gashes cut into the exine. When the grain is moist they spread widely open and are seen to be crossed by a thin layer of the exine—the furrow membrane—which lacks the granular texture and characteristic sculpturing of the general exine. In the center of each is a rounded aperture or pore through which the pollen tube may grow at the time of germination and through which the germinal papilla always bulges when the grain is moist and expanded. The exine of the furrow membrane is elastic and permits the opening and closing of the furrow, thus accommodating changes in volume of the grain with the absorption and liberation of moisture.

In the pollen of many species of *Haplopappus* are found a varying proportion of grains with more or fewer than three furrows. Sometimes these present great irregularity and asymmetry in arrangement and form, but more often they are symmetrical, the various numbers of furrows forming characteristic patterns. These configurations are well defined, and, with some study, it is generally possible to assign patterns of any of the grains with supernumerary furrows to one or another of a rather small number of different type arrangements. The distribution of these aberrant configurations among the different species is quite fortuitous, the various forms occurring abundantly in the pollen of some specimens and being entirely absent from that of others of the same species. The most usual atypical numbers of furrows are 6 and 4. Other numbers of furrows encountered less frequently are 12, 9, and very rarely 2 and 8, and in one specimen none at all.

On account of the geometrical relations which the configurations of the atypical numbers of furrows bear to each other, it will be best to discuss them in the ascending order of their complexity.

Acolpate Grains.—Grains which apparently have no furrows have instead three germinal apertures (Plate I, Fig. 8). These apertures should probably be regarded as furrows which are so short that they coincide with the pores; nevertheless, they are quite round and without hint of meridional orientation. Only in the pollen of one specimen of *Haplopappus* was the acolpate form observed. In this all the grains are alike and differ from those of other species only in the notably larger size of their germ pores, which is obviously an adaptive response compensating for the loss of harmomegathy due to the absence of the furrows. In several other specimens of this species of which the pollen was examined it was found to be normal. The condition must, therefore, be regarded as exceptional.

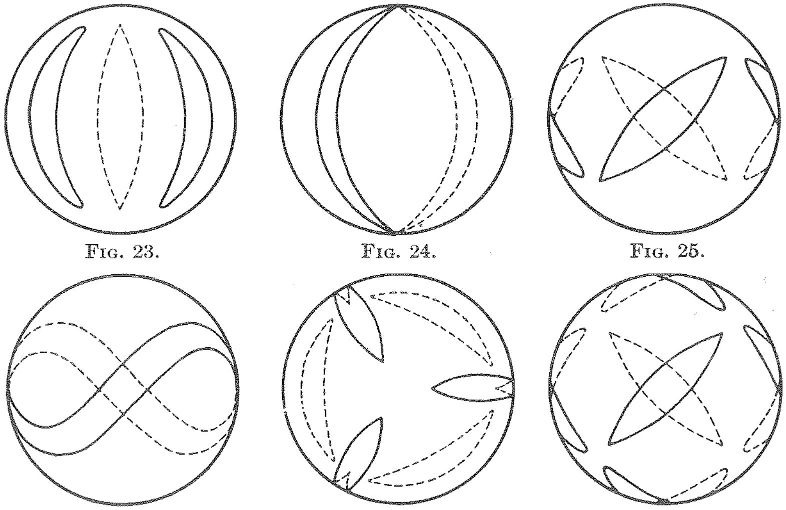

FIG. 23. FIG. 24. FIG. 25.

FIG. 26. FIG. 27. FIG. 28.

FIGS. 23–28.—Diagrams of furrow arrangements: Fig. 23, tricolpate; Fig. 24, dicolpate with the two furrows opposite and united; Fig. 25, tetracolpate, the same as hexacolpate but lacking two furrows; Fig. 26, zigzag form, a tetracolpate derivative; Fig. 27, hexacolpate, one of the four centers of convergence uppermost; Fig. 28, hexacolpate, one of the six furrows uppermost.

Dicolpate Grains.—When the grains have only two furrows they are generally in the position of those of normal tricolpate grains, with their axes converging toward the poles at angles of 120 deg., as if one of the normal three had been dropped without otherwise disturbing the organization of the grain. When in this arrangement, the furrows have a tendency to be extended and become fused at one or both poles as if the absence of the third furrow led to the lengthening and fusion of the remaining two. This type of grain corresponds to Fig. 23, if we omit the furrow shown in dotted line on the underside of the grain. Occasionally a careful inspection of dicolpate grains with furrows in this position reveals a trace of the third furrow represented by a slight rift in the exine, suggesting that this form of dicolpate grain arises from the partial or complete suppression of one of the furrows. The furrows in dicolpate grains may also be exactly opposite each other. When so arranged they nearly always join together at both ends and completely encircle the grain as a single furrow (Fig. 24) but with two germinal pores opposite each other (Plate I, Fig. 7). Dicolpate grains of either form are rare but are found in the pollen of several species of *Haplopappus*.

Tetracolpate Grains.—When the grains have four furrows they are equally spaced on the equator (Fig. 25), but the axes of such furrows are never meridionally arranged; instead, they cross the equator obliquely and converge in pairs, at angles of 120 deg., toward four centers Plate I, Fig. 9). If such a grain is oriented under the microscope so that the center of one furrow with its germinal pore is uppermost, focusing down on the lower side of the grain will always reveal another furrow exactly opposite but with its long axis crossing that of the upper at right angles. The germinal pores of the other two furrows will be seen bulging out on opposite sides of the limb or the apparent boundary of the sphere. As the focus is changed (better seen with a binocular microscope giving stereoscopic vision) these two furrows will be seen to curve around the horizon and inward, with their axes approaching those of the upper and lower furrows, thus converging in pairs toward four centers, with angles of convergence of 120 deg. or one-third of a circle. This configuration suggests that from each center is missing a third furrow, which if restored would complete the hexacolpate configuration (Figs. 27, 28) to be discussed under the description of that type, and from which this may be regarded as a derived form.

In tetracolpate grains the furrows are often long and coalescent at their ends, thus traversing, as a single furrow, a zigzag course around the grain, crossing its equator four times. From such furrows any one or more of the germ pores may be absent, and the angles of convergence may be lost in broad, sweeping curves, causing the furrow to assume much the form of the curved seam in the fabric covering of a tennis ball (Fig. 26). The tetracolpate form, with furrows converging toward four centers, is quite common in this genus and is encountered in many different families.

Hexacolpate Grains.—When grains have six furrows, their usual configuration is such that they are equally distributed over the surface, with their long axes converging toward four centers, which are triradiate and equally spaced (Plate I, Fig. 4). This arrangement is perhaps best visualized by comparing the six furrow axes to the six edges of a tetrahedron and the points of convergence to the four solid angles of such a figure (Fig. 27). This configuration of furrows was observed by von Mohl (1835, page 225) in the pollen of several species of *Corydalis* and described by him as tetrahedral: "Toute la surface des grains se trouve ainsi partagée par six fissures en quatre triangles, ou en d'autres termes, les bandes de ce grain forment les arêtes d'un tétrahèdre." It was also described and illustrated by Fritzsche (1837, Plate VI, Fig. 5) in the grains of several species of *Corydalis* and of *Basella* and likewise regarded by him as the tetrahedral arrangement: "Mit sechs den Kanten des Tetraëders entsprechenden Spalten" (page 724).

When a hexacolpate grain is oriented so that one furrow is exactly uppermost, focusing down will reveal another furrow on the lower side, with its long axis directed at right angles to that of the upper; the four other furrows will be barely visible bending over the limb—the boundary of the median optical plane (Fig. 28)—but their four germinal pores can generally be seen bulging at four points equally spaced on the limb. If, on the other hand, the grain is so oriented that one of the centers of convergence is uppermost (Fig. 27), the three converging furrows will be almost wholly in view directed radially. And if now the microscope be focused on the lower surface, the three other furrows will be seen with their long axes directed tangentially, forming an equilateral triangle, and with their three apertures alternating with the three above. This form of hexacolpate pollen grain is exceedingly common. It constitutes a fair proportion of the pollen of most species of *Haplopappus*. It is likewise found here and there among all groups of Compositae and, as we have seen, is the characteristic form of the grains of *Dahlia* pollen. Outside the Compositae it is found regularly, and occasionally in the pollen of many different groups, including *Salpiglossis sinuata*. This latter is of peculiar interest because, as we have seen, its grains are shed united in their tetrads and so show the relation between this type of furrow configuration and the tetrad arrangement, a relation which will later be discussed at greater length (page 182).

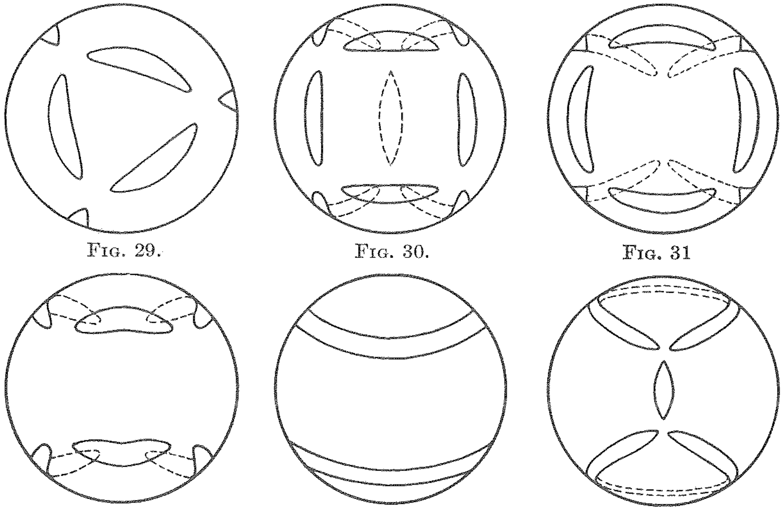
FIG. 29. FIG. 30. FIG. 31
FIG. 32. FIG. 33. FIG. 34.

FIGS. 29–34.—Diagrams of furrow arrangements: Fig. 29, Nonacolpate, viewed with one of its spherical triangles uppermost; Fig. 30, nonacolpate, viewed with one of its spherical squares uppermost; Fig. 31, octacolpate, similar to the nonacolpate, except that one furrow is missing; Fig. 32, hexacolpate, derived form; Fig. 33, zonate; Fig. 34, half-zonate. The three latter are nonacolpate derivatives.

Grains are occasionally found with six furrows in an entirely different configuration which is not related to the tetrahedral. In this arrangement the furrows converge in pairs toward six centers, which are bilateral, instead of triradiate (Fig. 32), but with angles of convergence at least approximating 120 deg. This suggests that this form may be regarded as a derivative from the nonacolpate configuration to be described next, which likewise has six centers of convergence, and bears the same relation to the nonacolpate form that the tetracolpate configuration bears to the ordinary hexacolpate type. But this form is rare and is usually accompanied by ugly distortions of the grains, rendering them extremely difficult of analysis; usually some of the furrows lack apertures and are fused at one or more of their centers of convergence, thus traversing a more or less discontinuous course around the grain in each hemisphere between the equator and poles. Quite frequently grains are found with just two furrows completely encircling them in the position of the tropics on the terrestrial globe, and I believe that such zonate furrows represent the complete fusion and flattening out of the convergent angles of the six furrows of this form of hexacolpate configuration (Fig. 33).

This type of hexacolpate grain, which is perhaps best regarded as a nonacolpate derivative, is found occasionally in the pollen of *H. MacLeanii;* and its zonate derivative, which is much more easily recognized on account of its striking appearance, is found in the pollen of *H. stenophyllus* and outside the genus in the pollen of *Artemisia spinescens* in the Anthemideae and of *Limnia spathulata* in the Portulacaceae.

Nonacolpate Grains.—When grains have nine furrows they are as equally spaced as possible over the surface and are so arranged that their axes converge toward six centers which are triradiate (Plate I, Figs. 2, 5). This form bears the same relation to a form of pentahedron that the hexacolpate bears to the tetrahedron. This pentahedron is a right-triangular prism of which three sides are equal squares, and two, which are opposite, are similar equilateral triangles (Fig. 44). In the nonacolpate grain there are three viewpoints which show the four uppermost furrows with their axes forming the sides of a square (Fig. 30). Focusing down from any one of such reveals four more furrows curving around the limb of the sphere and converging toward the two ends of the ninth furrow, which subtends the upper square and is parallel to two of its sides. There are two views which show the axes of three furrows forming a triangle (Fig. 29; Plate I, Fig. 5). Focusing down from one of these brings into view three other furrows forming a triangle on the lower surface and exactly subtending that above; the three remaining furrows are seen curving over the limb from the angles of one triangle toward the corresponding angles of the subtending triangle. This type of grain is not common, having been found, in the present group, in the pollen of only two species, *Haplopappus stenophyllus* and *Erigeron strigosus*, but is fairly abundant in the latter. Outside this group it is occasionally found in the pollen of *Artemisia gnaphaloides* and *Rivina humilis* and is frequent among the grains of *Talinum multiflorum.* This type of furrow arrangement is stated by von Mohl (1835, page 225) to characterize some of the grains of the pollen of *Corydalis lutea,* of which he says, "Le grain représente un prisme triangulaire dont les faces latérales sont bombées, aussi bien que les terminales."

The nonacolpate type, besides giving rise to a certain form of hexacolpate and through this to the zonate type as noted above, apparently also gives rise to a curious half-zonate form (Fig. 34) by the dropping out of two furrows and the fusion of those remaining at their resulting bilateral centers of convergence. Grains of this form are of frequent occurrence among the pollen of *Limnia spathulata,* and it is likely that a further search will bring them to light in other species.

Octacolpate Grains.—When grains have eight furrows they present a very unusual symmetry; the axes of the furrows converge toward six centers, of which four are triradiate, and two bilateral (Fig. 31). If such a grain is oriented under the microscope with the four triradiate centers visible in the upper hemisphere, four furrows will be seen in the position of the sides of a square. Focusing downward will bring into view four other furrows appearing to start on the limb at the four angles of the square and converge in pairs toward two close but discrete centers in the lower hemisphere.

This form may be regarded as a derivative of the nonacolpate through the omission of one furrow and the moving together of the others partially to occupy its space. Occasionally the two bilateral centers approach very closely or actually coincide, producing a single tetraradiate center, but more often they are separated, presenting an appearance similar to that shown in Plate I, Fig. 9, of a tetracolpate grain.

The octacolpate form is rather rare; it has been found only in a few grains of *Fresenia fasciculata* and *Erigeron strigosus.* Outside the Astereae, it is common in pollen of *Artemisia spinescens* and *Talinum multiflorum.*

Dodecacolpate Grains.—When grains have 12 furrows they are equally spaced and so arranged that their axes converge toward eight triradiate centers, the furrows dividing the surface of the grain into six squares (Figs. 35, 36, Plate I, Fig. 1). This form bears the same relation to a cube that the hexacolpate form bears to the tetrahedron, and the nonacolpate form to the right-triangular prism. The form has been admirably described by Fritzsche (1837) for the pollen of *Talinum patens* in which it is clearly and beautifully seen on account of the absence of spines and the transparency and regularity of the grains. As Fritzsche says (page 725), "Die Anordnung der Spalten ist auch hier höchst regelmässig, indem sie den zwölf Kanten eines Würfels entsprechen; sie sind von ziemlich grosser Ausdehung und theilen die Exine in sechs viereckige, mit den Ecken zusammenhängende Stücken."

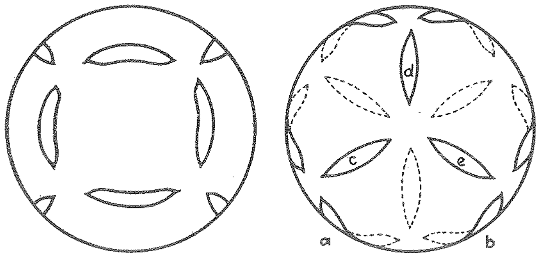

FIG. 35. FIG. 36.

FIGS. 35, 36.—Dodecacolpate furrow configuration: Fig. 35, viewed with one of its four spherical squares uppermost; Fig. 36, viewed with one of its eight centers of convergence uppermost. (For further explanation see text.)

If such a grain is examined with any one of the centers of convergence exactly uppermost (Fig. 36), focusing downward will bring into view another center exactly below but with its radii alternating with those of the center above. Or, if the grain is oriented so that the axes of the furrows on the upper surface form a square (Fig. 35), focusing down will bring into view another square exactly subtending the one above, and four other furrows will be seen bending over the limb from the angles of one square toward the corresponding angles of the other square. In grains of this form the 12 furrows are never all occupied by pores; usually only four pores may be counted.

The dodecacolpate furrow configuration occurs among the grains of *Erigeron strigosus* and in those of *Haplopappus MacLeanii*. Outside the Astereae, besides being found in the pollen of some species of *Talinum* as noted above, it is occasionally found in the pollen of *Artemisia spinescens* and, in its various derivatives, in that of *Limnia spathulata*. It is said by Franz (1908) to characterize the pollen of some species of Portulacaceae and is said by von Mohl (1835, page 225) to be found among the pollen of *Corydalis lutea* and *Clerodendron paniculatum*. It is also the characteristic form of the pollen of some species of Malpighiaceae.

SIGNIFICANCE OF FURROW CONFIGURATIONS

Recapitulation.—The study of the arrangement of the furrows of various numbers reveals controlling their configurations certain underlying laws, which may be deduced as follows: When a pollen grain forms in the tetrahedral arrangement, it makes three points of contact—one with each of its three neighbors of the tetrad—and consequently acquires three furrows equally spaced around the equator, and this explains the tricolpate form and triradiate patterns which characterize the majority of dicotyledonous pollen grains. But pollen grains do not always have three furrows, nor do they always form in the tetrahedral arrangement. When they form in some other arrangement with two unsymmetrical points of contact, two furrows are formed with orientation on the two points, but the cell maintains its symmetry in spite of this by the formation of symmetrically balancing furrows. Asymmetry in space relations among pollen grains, and perhaps among all cells, is avoided as far as possible. This is probably partly a matter of physical equilibrium, for, as Thompson (1917, page 209) notes, "in every symmetrical system any deformation that tends to destroy the symmetry is complemented by an equal and opposite deformation that tends to restore it."

Among the grains of the Astereae are many with four furrows which undoubtedly arose in this fashion; but there are even more grains with six and other numbers of furrows in which the symmetry is more complete than in those with four.

The Law of Equal Triconvergent Angles.—We have noticed that, in all the various configurations assumed by the furrows they tend to converge toward each other in threes with equal angles of convergence, which consequently tend to be 120 deg. This may be stated as the law of equal triconvergent angles. Occasionally, it is true, one of the furrows may be absent, leaving only two furrows converging toward a center, but in such cases one of the two convergent angles tends to be 120 deg. This law appears to be almost universal for grains which are spheroidal, as are those of the Astereae, but does not apply to grains which are much flattened or greatly elongated. Furthermore, when a furrow is missing from a center of convergence, the two remaining furrows have a strong tendency to coalesce at their ends, or sometimes such a condition may even lead to the total collapse of such defective configurations, resulting in sadly distorted and misshapen grains and suggesting an unstable condition at such biradiate centers. From this it becomes evident that, unless a grain have three furrows, or some multiple of three, it must have some biradiate centers of convergence, with their resulting lack of stability. "Die ganzen Zahl hat Gott gemacht; alles anders ist Menschenwerk."

Furrow Configurations and Polyhedrons.—The interesting relation between the various furrow configurations and certain polyhedrons will become clear if we consider the characters of polyhedrons in relation to the sphere as follows. The tetrahedron (Fig. 43), for example, which is the simplest polyhedron, is bounded by four equal faces, each of which is an equilateral triangle with angles of 60 deg. If a sphere be circumscribed about a tetrahedron, and the four vertices joined by the shortest possible lines in the surface of the sphere subtending the edges of the tetrahedron, these lines will be arcs of great circles and will intersect at the four vertices in such a way as to make three equal convergent angles at each, and, incidentally, they divide the surface of the sphere into four equal spherical triangles whose angles are not 60 but 120 deg. The arrangement of such lines corresponds precisely to the furrows of a hexacolpate grain. In the same way if a sphere be circumscribed about a cube, and arcs of great circles passed through the vertices of the cube so as to correspond to its edges, these arcs will correspond in position to the 12 furrows of a dodecacolpate grain and will divide the surface of the sphere into six spherical squares, whose angles, since there are three, equal and convergent at each of the vertices, are 120 deg. These are the kind of square pieces that Fritzsche meant when he said, in speaking of the furrows of the grains of *Talinum patens*, "Sie . . . theilen die Exine in sechs viereckige . . . Stücken." In this connection the interesting geometrical observation comes to light that polygons, whether they be triangles, squares, or pentagons, when drawn over the surface of a sphere so as to divide the whole surface into equal parts, must always have their angles equal to 120 deg.

TABLE II.—COMMON FURROW CONFIGURATIONS

No. of faces	No. of edges or furrows	Furrow configuration	Corresponding polyhedron	Description of polyhedron	Example
	0	Acolpate	None	None	Haplopappus (Pl. I, Fig. 8)
3	3	Tricolpate	None	Three lunes	Rosa, Haplopappus (Pl. I, Fig. 10)
4	6	Hexacolpate	Tetrahedron	4 equilateral triangles	Dahlia; Haplopappus (Pl. I, Fig. 4)
5	9	Nonacolpate	Triangular prism	2 triangles and 3 squares	Haplopappus (Pl. I, Figs. 2, 5)
6	12	Dodecacolpate	Cube	6 squares	Haplopappus (Pl. I, Fig. 1)
7	15	Pentadecacolpate	Pentagonal prism or heptahedron	5 squares, 2 pentagons	Talinum patens
12	30	Triacontacolpate	Pentagonal dodecahedron	12 equal pentagons	Persicaria amphibium (Fig. 100) Fumaria spicata

If we write out the series of symmetrical furrow configurations commonly occurring in pollen grains, it is seen that to each of these corresponds a polyhedron; also, some other interesting facts become evident (Table II).

As the number of furrows increases by steps of three, the number of faces of the corresponding polyhedrons increases by steps of one, a relation which may be expressed by $E = 3F - 6$, where E is the number of edges or furrows, and F is the number of faces, an equation which expresses the series however far extended.

Obviously, there can be no polyhedron corresponding to grains with no furrows. Grains with three furrows, according to this equation, would require a polyhedron with three edges and three faces. No such polyhedron exists, because three planes cannot enclose space; but three curved faces can enclose a space, as they do in the simplest and commonest form the tricolpate, in which three arcs of great circles divide the surface of the grain into three equal lunes.

The largest number of furrows counted with any degree of certainty in the pollen grains of *Haplopappus* and the Astereae is 12. The higher numbers of furrows are difficult to count because of the nature of the grains; so whether or not numbers higher in the series than 12 exist among them is still uncertain. Outside the Astereae, however, 15 *furrows* are reported by Fischer (1890, page 56) for the grains of *Talinum patens* and *Montia fontana*, in which he says that their arrangement corresponds to the edges of a five-sided prism; also, in the pollen of *Platycapnos spicatus* (= *Fumaria spicata* L.) (page 37). The next number that, so far as I am aware, is recorded in the literature is 30 *furrows*, described by von Mohl for the grains of *Rivina brasiliensis*, *R. humilis*, and *Fumaria spicata*. In the last he states that the great transparency of the granular exine permits the distinction of areas marked off by the furrows and distributed in such a way that the whole surface of the grain is divided into pentagons which form a pentagonal dodecahedron (page 225). A similar configuration is described for the grains of *Polygonum amphibium* and *Alsine media* by Fritzsche (1837, page 725), who lays special emphasis upon the regularity of the pentagons and their arrangement. A similar figure is likewise described by Fischer 1890, (page 56) for the grains of *Portulaca oleracea* L. and *P. grandiflora*. Furthermore, in the Portulacaceae the dodecahedron is said by Franz (1908, page 33) to be the usual configuration for a large section of the family: "Die Grundform des Pollens ist in der ersten grossen Gruppe, bei den Portulacoideae, das Pentagondodekaeder."

The *pentagonal dodecahedron* with 12 faces and 30 edges fits into our series, fulfilling the requirements of $E = 3F - 6$, so it is not surprising that grains should be found with furrows conforming to this configuration. It is something more than a coincidence, however, that so many kinds of pollen grain exhibit the dodecahedron as the ground plan of their furrow arrangement, while apparently few exhibit the numbers of furrows intervening between 15 and 30. Why should the pentagonal dodecahedron be so favored among mathematical configurations, to the neglect of several simpler configurations involving fewer furrows? In the first place, the pentagonal dodecahedron is a striking and unique figure. It differs from the prisms and other polyhedrons which would accommodate the furrow numbers of our series between 12 and 30 *in being perfectly regular*. It is one of the five possible regular polyhedrons. All its faces are regular pentagons, with all their sides equal, all their angles 108 deg., and all their interfacial angles equal. The other regular polyhedrons are the tetrahedron, octahedron, icosahedron, and cube. Of these only the tetrahedron, which is bounded by four triangles, and the cube, which is bounded by six squares, share with the pentagonal dodecahedron the convergence of three and only three edges and angles at their vertices. The regular octahedron and icosahedron present four and five convergent angles at their vertices, a condition quite incompatible with the triconvergent angular pattern of pollen-grain-furrow configurations; consequently they may be dropped from further consideration.

When a sphere is circumscribed about a pentagonal dodecahedron and its vertices joined along the arcs of great circles, that is to say, when a pentagonal dodecahedron is constructed with its faces of spherical pentagons instead of plane pentagons, the convergent angles will be equal and exactly 120 deg. It thus becomes clear that perfect symmetry of configuration can be attained only when the furrows correspond in number and arrangement to the edges of regular polyhedrons having three equal convergent angles. It is such symmetry relations as these that account for the tetrahedron, cube, and pentagonal dodecahedron's being favored members of the numerical series of furrow configurations.

If, on the other hand, we draw a right-triangular prism, in its spherical form, equality of the three convergent angles at each of the centers of convergence cannot be attained, because in the plane-triangular prism the angles of the equilateral triangles are 60 deg., while those of the associated squares are 90 deg. When such a figure is adapted to the spherical curvature, and the edges take up the positions of arcs of great circles, the disproportion of these angles is further increased, though their total is now equal to four right angles. Thus we have a conflict between the law of equal triconvergent angles and the difference between the spherical values of a right angle and a 60-deg. angle. When the angles of the polyhedron are small, as 60 and 90 deg., an adjustment takes place. This is accomplished in various ways; sometimes a compromise is struck by a shift of the furrows which bound the triangle a little out of the paths of great circles, tending to equalize the angles. If this is carried far, the grain sometimes shows a tendency to alter its shape, adapting the surface curvature to that of the furrows in such a way as to cause them to follow geodetic curves; the result is a slight bulge through the triangular faces. Such an adjustment, though common in the grains of some plants, appears not to be found in the grains of the Astereae; in these the adjustment is apparently made mostly at the expense of the equality of the triconvergent angles, with perhaps a little shifting of some of the furrows out of the paths of great circles. Seldom does the grain change its shape.

The scarcity of the 15-furrowed grains and the still greater scarcity of grains with furrows numbering between 15 and 30 is apparently due to the difficulty or impossibility of making such an adjustment. All four of the polyhedrons missing from our list (Table II) would have more than one kind of face; and, since their internal angles are therefore different, this at once precludes the possibility of equal triconvergent angles. Such grains, with furrow configurations corresponding to these missing numbers, must be less symmetrical and consequently less stable than those with the more perfect symmetry corresponding to the regular polyhedrons, which have equal triconvergent angles and in which there is no conflict between the angles of different types of polygon. There are only three such regular polyhedrons—the tetrahedron, cube, and pentagonal dodecahedron.

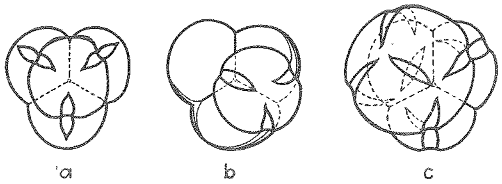

FIG. 37.—Arrangements of the four cells in *Salpiglossis* pollen, diagrammatic: *a*, tetrahedral; *b*, half-tetrahedral, the upper cell with only two points of contact; *c*, one cell a giant with only two points of contact which are about ¼ circumference apart.

The Configuration Developed Depends upon the Contact Points of the Grain in Its Tetrad.—The question now arises: What determines which one of these configurations shall be adopted by the grain? When a grain has three points of contact in the normal tetrad, these points are equidistant, and such a grain will acquire three furrows; but if it has only two points of contact, it may acquire a larger number. We have seen (page 166) that, in the dividing chicory pollen grain, two points of contact can result in four furrows. In the particular instance cited, the four cells of the tetrad were all of the same size but in the square instead of the tetrahedral arrangement. Further light is thrown on this point by a condition sometimes found in the grains of *Salpiglossis*. Its pollen, as we have already seen, is shed united in tetrads which are generally tetrahedral, and each grain tricolpate (Fig. 20). Occasionally, however, one finds tetrads in which one of the cells did not quite achieve the tetrahedral position, though approaching very closely to it but making only two points of contact (Fig. 37). Such cells may acquire three furrows in the ordinary tricolpate configuration (Fig. 37*b*), four furrows with their axes converging in pairs at 120 deg.; or more frequently two other furrows, generally without germ pores, are thrown in between the two biradiate centers (Fig. 37*c*). These bear a striking resemblance to the polar furrow or *Brechungslinie*, which is nearly always developed in segmenting eggs when four cells are formed in contact and which would otherwise all meet at a point (Fig. 38*a*, *b*). In the same way that the "breaking line" in the segmenting egg breaks the unstable tetraradiate center into two stable triradiate centers, thereby restoring the stability of the segmenting egg, these two connecting furrows in the pollen grain of *Salpiglossis* each join together two unstable biradiate centers and in so doing complete the tetrahedral hexacolpate configuration and thereby restore the symmetry and stability of the grain.

If two contact points can induce the formation of 3, 4, or 6 furrows, there seems no reason why two contact points could not likewise induce the formation of 9, 12, or more furrows, the choice depending upon the distance apart of such points in relation to the size of the grain. For example, if the formation of two furrows should be induced by contacts in such positions on the limb, as *a* and *b* (Fig. 36), so as to require four more to balance them symmetrically on the limb, these six furrows would converge in pairs and thus establish six unstable biradiate centers of convergence. From such an arrangement symmetry could be completed by the formation of three connecting furrows, as *c*, *d*, *e*, in each hemisphere. Our grounds for assuming that three connecting furrows would form under these conditions to join the six furrow ends in each hemisphere are again based upon observations in developing embryos; for here when six cells are formed in contact so that they would otherwise meet at a point (Fig. 38*c*) they are always separated by the formation of three intermediate walls or breaking lines, which are themselves frequently triradiate in arrangement and form with the walls of the six cells three more triradiate centers with all the angles 120 deg. (Fig. 38*d*).

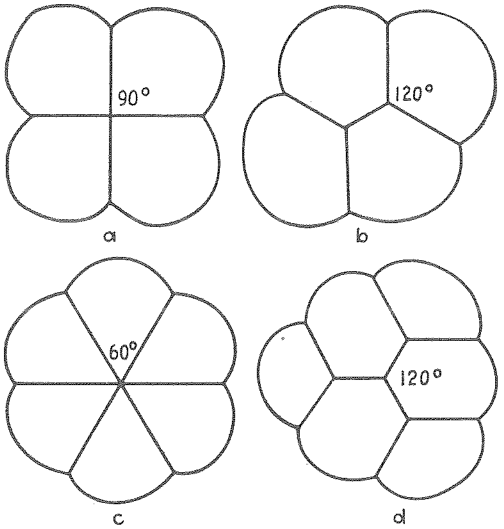

FIG. 38.—Arrangements of cells in one plane: *a*, four cells, unstable; *b*, four cells stable; *c*, six cells, unstable; *d*, six cells, stable.

The distance apart of the initiating points must depend partly upon the position of the grain in its tetrad but to a larger extent upon its size in relation to that of its neighbors. It is obvious that a shifting in the tetrad may change the distance apart of the contact points, but much larger relative differences are brought about by an increase in the size of one of the grains. Thus it happens that grains of normal size may occasionally bear four or six furrows, while the giants nearly always bear four, six, or larger numbers of furrows; and likewise grains with supernumerary furrows are most frequently giants.

It is interesting and perhaps not without profit to speculate further as to the origin of the furrows. The unequivocal insistence upon the 120-deg. angle and the almost equal insistence upon the triradiate centers of convergence of the furrow axes suggest that the furrows are the expression of stresses—whether they be pressure or tension, the orientation would be the same. In a plane surface, pressure between objects of similar size and offering similar resistance to the pressure results in a hexagonal configuration with internal angles of 120 deg. So familiar is this configuration that it is always recognized at once as the result of pressure. In soap films the configuration likewise tends to be hexagonal and with the same insistence upon the 120-deg. angle, and we recognize it at once as the result of tension.

On the sphere, hexagons of finite size are incompatible with equal convergent angles between furrows, for reasons which we have already seen. In the case of the segmenting embryo it is well known that the arrangement of the cells is brought about by the tendency to assume least-surface configurations, which in turn is the result of surface tension and, as Plateau has shown, is equally the property of oil drops and soap films. Consequently, it is reasonable to suppose that the furrow configurations are brought about by similar forces. But if we recognize the hexagonal system with its internal angle of 120 deg. as denoting relations of stress in a plane surface, by the same token we can recognize triangles, squares, and pentagons with angles of 120 deg. on a spherical surface as likewise denoting relations of stress. This being so, it follows that supernumerary furrows and their configuration on the surface of pollen grains are due to stresses set up in the grain by contact stimuli received at two points in the tetrad. And the particular type of configuration is determined by the distance apart of the two points relative to the size of the sphere. A critical study of the various furrow configurations viewed in this light shows that they are subject to the same laws as ordinary mud cracks or plaster cracks, and the many varied and complicated patterns which they describe are the result of their adaptation to a spherical surface.

II. THE TRISCHISTOCLASIC SYSTEM

When a layer of mud dries and shrinks, the shrinkage is manifest by the development of a system of small cracks (Fig. 39). Under favorable conditions such a system of cracks tends to divide the mud continuously into a number of hexagonal pieces.

It is true that such hexagonal cracking in mud is never exactly uniform. This is because the system is made up of a number of triradiate cracks of small extent which originate in random positions independently of each other and therefore must make rather violent adjustments as they merge together. Nevertheless, the system tends to approach an ideal, *i.e.*, the breaking of the surface into uniform hexagonal pieces. Such an ideal would be attained if, instead of a large number of independent triradiate cracks originating separately, there should start but a single one, and it should branch dichotomously with equal triconvergent angles and cracks of equal lengths until the whole sheet of mud was cracked. Such an ideal may easily be imitated if, from a point a (Fig. 40) in a plane surface, three equal lines be drawn at equal angles (*i.e.*, 120 deg. each) ab_1, ab_2, ab_3; and from the ends of each of these be drawn in the same way two more lines equal to the first, b_1c_1, b_1c_2, b_2c_3, b_2c_4, etc.; then from the ends of each of these lines be drawn in the same way two more equal lines c_1d_1, c_1d_2, etc. Three equal hexagons will be completed, with six free lines and six apices in positions to form nine more hexagons surrounding the initial group of three, if the branching be repeated once more. Such a system of triradiate branching on a plane surface is open, and it may be continued indefinitely or until the entire available surface has been divided into equal hexagons.

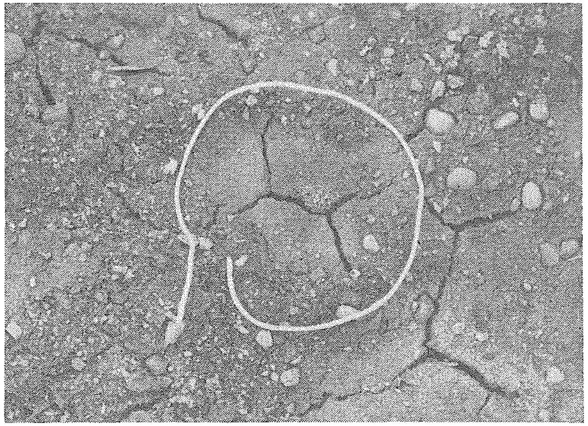

FIG. 39.—Mud cracks approximating the trischistoclasic system in their arrangement. Compare the part surrounded by a piece of string with Figs. 37*c* and 41.

Since the outstanding character of this system is its triradiate nature, I have designated it as the system of triradiate cracking or to use a single word, *trischistoclasic* (see Glossary). The system is extremely common. It may be stated as a law that the trischistoclasic system divides a plane surface continuously into equal hexagons, however far it may be extended. In its ideal form it is closely approached in the arrangement of the hexagonal cells of a honeycomb. In a cruder form, with imperfect adjustments between the different triradiate centers, it may be seen in mud cracking along the roadside and in plastered walls.

Due to Equilateral Stresses.—The conditions which bring it about are stresses equal in all directions. An interesting corollary to this is that if cracks appear in this system on a plastered wall, one may be reasonably sure that they penetrate only the plaster and not the body of the wall. The reason for this is that the plaster, being relatively light, is not influenced by gravity, so only the stress of its shrinkage, which is equal in all directions, is brought to bear on the formation of the cracks. If, on the other hand, the cracks in the wall tend to be vertical or parallel, one may be equally sure that they penetrate the body of the wall and are due to the lateral pull of the shrinking wall acting at right angles to the vertical thrust of gravity, two stresses which are unequal and, in this case, opposite in sign.

Since lateral stresses acting equally in all directions are the basic cause of the trischistoclasic system, another name for the system is naturally suggested, *viz.*, the system of equilateral stresses or, to use a single word, *isotasithynic* (see Glossary). This system stands in contrast to the system of vertical or parallel cracks which is due to unequal lateral stresses, and which therefore may be called *heterotasithynic* (see Glossary).

Furrow Patterns Isotasithynic.—In pollen grains of spheroidal form, in which all surface stresses naturally tend to be equal, the arrangement of the furrows always follows the trischistoclasic or isotasithynic system, unless there is some good reason why it should not do so, *e.g.*, in the tetracolpate grains of *Taraxacum*, q. v., and in the squarish grains of *Impatiens*, where it appears to follow the heterotasithynic system. Though on a plane surface the trischistoclasic system must be uniformly hexagonal if the individual lines composing it are of uniform length and angular deviation, when applied to the surface of a sphere of finite size and itself composed of lines of finite length, it can never be uniformly hexagonal. The numerous furrow patterns, which we have seen consist of triangles, squares, and pentagons, are various expressions of the trischistoclasic system in terms of the sphere. The explanation of this can readily be found if we try the experiment of drawing lines in the trischistoclasic system over the surface of a sphere in the same fashion as we drew them on a plane surface. When done on a sphere the system is closed. It does not stop with free lines and angles with the possibility of being extended indefinitely, as on a plane surface. Instead, the number of its lines and, within certain limits, the character of the polygons which they will describe are fixed as soon as any single dimension of the system in relation to the size of the sphere is chosen, such as the length of the lines or the distance apart of their centers. On this account simplicity in the experiment is served if we start with the lines of the system instead of a triradiate center. But in doing so we must not lose sight of the fact that the system is still one of progressive branching.

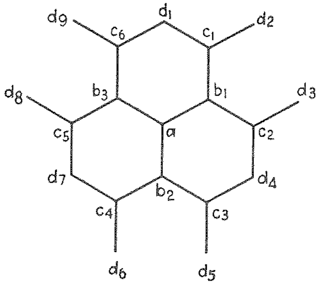

Fig. 40.

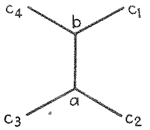

Fig. 41.

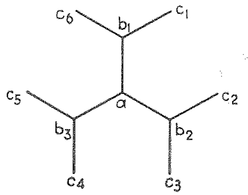

Fig. 42.

Figs. 40–42.—The trischistoclasic system on a plane surface. Fig. 40 shows that it may be extended indefinitely; Fig. 41 represents the tricolpate furrow configuration; Fig. 42 the hexacolpate furrow configuration.

The simplest expression of the trischistoclasic system in spherical terms is obtained if we select two points on a sphere spaced 120 deg. apart or one-third of the great circle upon which they happen to lie. The circle we shall call, for convenience, the equator; and the distance between the points, the interval of the system. Through these points draw two arcs of great circles in such a way that they meet at an angle of 120 deg. The point at

which they meet will be found to be a pole of the sphere. Extended in the opposite direction these two lines will meet at the opposite pole of the sphere. Now, if each pole is made a triradiate center by drawing a third line at 120 deg. to the other two, they will coincide with each other, so that, in all, there will be only three lines. If lines were drawn in this way on a plane surface, they would appear as in Fig. 41; but since they are drawn on a sphere with their interval so chosen as to cause them to meet at the poles, they divide the sphere into three equal lunes. Such a system of lines is the lowest possible expression of the trischistoclasic system in spherical terms. It corresponds to the ordinary tricolpate furrow configuration, which is the commonest among pollen grains of the dicotyledons. Here, as we have seen, it is usually initiated by three contact points equally spaced on the equator, but it may also be initiated by two contact points one-third of the equator or 120 deg. apart.

In order to discover the next higher expression of the system in spherical terms, select two positions on the equator of the sphere one-quarter of the circle or 90 deg. apart, and draw lines through them converging toward each other at angles of 120 deg. as before. This time they will not meet at the poles but will meet at four points, two in the upper and two in the lower hemisphere. Such an arrangement corresponds to the ordinary tetracolpate furrow configuration. Now, make each of these points triradiate by joining together the two of the upper and the two of the lower hemisphere. The result will be six lines converging at four triradiate centers and marking the surface off into four equal equilateral triangles. This corresponds to the hexacolpate furrow configuration (Figs. 27, 28). The corresponding pattern on a plane surface is shown in Fig. 42. On a spherical surface, however, the number of lines is reduced, because b_1c_1 coincides with b_2c_2; b_2c_3, with b_3c_4; and b_3c_5, with b_1c_6.

The Series of Perfect Polyhedrons.—It will readily be seen that we may repeat the experiment of drawing lines in the trischistoclasic system over the sphere in as many different ways as we wish, selecting each time a shorter interval for the system; but only when we select an interval which permits the lines to assume a configuration corresponding to the edges of one of the perfect polyhedrons, the tetrahedron, cube, and pentagonal dodecahedron will it divide the surface of the sphere into polygons all of the same kind. The four equal equilateral triangles produced in the present instance, with an interval of 90 deg., correspond to the four faces of a tetrahedron (Fig. 43). If drawn with an interval of 60 deg. or one-sixth of the great circle, it would divide the surface of the sphere into six equal squares corresponding to the six faces of a cube. Drawn with an interval of 36 deg. or one-tenth of the great circle, it would divide the surface of the sphere into 12 equal pentagons, corresponding to the faces of a pentagonal dodecahedron. We thus see that the intervals of the system that can produce perfectly symmetrical configurations on the surface of a sphere are mathematically determined, as:

120 deg. or ⅓ circle..........	3 lunes corresponding to a 3-colpate grain
90 deg. or ¼ circle.........	4 triangles corresponding to a tetrahedron or 6-colpate grain
60 deg. or ⅙ circle.......	6 squares corresponding to a cube or 12-colpate grain
36 deg. or ⅒ circle.......	12 pentagons corresponding to a pentagonal dodecahedron or a 30-colpate grain

This series is mathematically fixed and cannot be extended in either direction. These four patterns are unique in that, with each, the triconvergent angles are exactly equal, the lines are all equal, and all are arcs of great circles. All the patterns drawn with other than these four cardinal intervals will be more or less irregular and necessitate compensating adjustments of the lengths of the lines, of their angular deviations, even of the intervals themselves and compromises between the paths of the lines with the arcs of great circles. For example, if the interval of the system lies between 90 and 60 deg., since the 90-deg. interval gives a pattern of four triangles and the 60-deg. interval gives a pattern of six squares, an interval between 90 and 60 deg. will necessarily give a pattern composed of triangles and squares. The ordinary nonacolpate configuration presents such a pattern, obtained from an interval of about 72 deg. As we have seen, it consists of three squares and two triangles corresponding to a right-triangular prism (Fig. 44). It is rare among furrow patterns of pollen grains. If the interval of the system lies between 60 and 36 deg., since the former gives a configuration consisting of squares, and the latter of pentagons, a pattern drawn with an interval between these two must be composed of pentagons and squares. Such a pattern is represented by the ordinary 15-colpate furrow configuration, which is also rare among pollen grains. As we have seen, it consists of two pentagonal and five square faces and corresponds to the right-pentagonal prism (Fig. 47).

If we continue to draw trischistoclasic patterns over our sphere, choosing each time a smaller interval, after we pass the interval of 36 deg., which gives 30 furrows corresponding in arrangement to the edges of a pentagonal dodecahedron, an adjustment has to be made using tetragons (which may or may not be exactly square), pentagons, and hexagons; and, as the interval continues to decrease, *i.e.*, as the faces become more numerous, more and more hexagons are required in proportion to the tetragons and pentagons. And this greater proportion of hexagons over the other polygons will continue to increase as we approach a 0-deg. interval or an infinite number of polygons.

Possible Furrow Configurations.—It is interesting to examine in the light of the trischistoclasic system some of the polyhedrons which correspond to the rarer furrow configurations of this series up to and beyond the 30-colpate and to discover the possible extent of their variation within the trischistoclasic system (Table IV). For example, corresponding in number of edges and faces to the dodecacolpate configuration or *hexahedron* can be constructed another polyhedron quite different in form from the cube, yet possessing 6 faces and 12 edges as does the cube (Fig. 46). This figure is bounded by two triangles, two tetragons, and two pentagons. It is, of course, irregular and probably for this reason is less favored than the cube among pollen-grain furrow configurations.

The next figure in the series (Table IV) is the *heptahedron*, with seven faces and 15 edges. Three different forms of heptahedron can be constructed. The most obvious of these is the pentagonal prism (Fig. 47), which we have already seen is bounded by two pentagonal and five square or tetragonal faces. Another heptahedron is bounded by one triangular, three tetragonal, and three pentagonal faces (Fig. 48); and another by two triangular faces, two tetragonal, two pentagonal, and one hexagonal (Fig. 49).

The next numerical group of polyhedrons in the series is that of the *octahedrons*, with eight faces and 18 edges (Table IV). Several such figures can easily be constructed. The most obvious is the hexagonal prism (Fig. 50), possessing six tetragonal

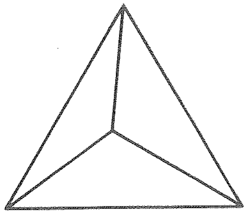

FIG. 43.

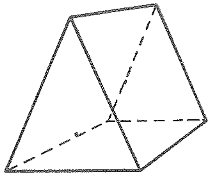

FIG. 44.

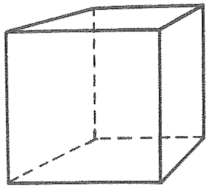

FIG. 45.

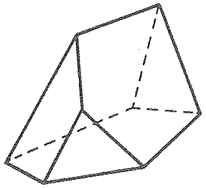

FIG. 46.

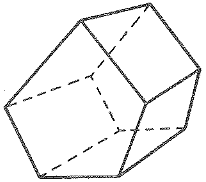

FIG. 47.

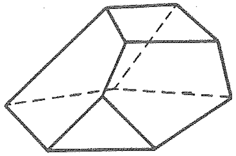

FIG. 48.

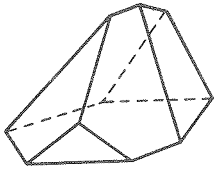

FIG. 49.

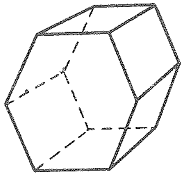

FIG. 50.

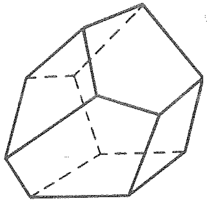

FIG. 51.

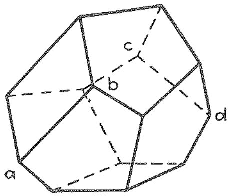

FIG. 52.

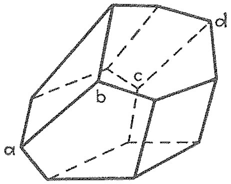

FIG. 53.

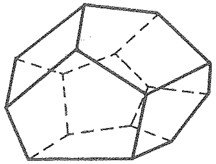

FIG. 54.

FIGS. 43–54.—Polyhedra which correspond to some pollen-grain furrow configurations: Fig. 43, tetrahedron, corresponding to the normal hexacolpate configuration; Fig. 44, pentahedron or right-triangular prism, corresponding to the nonacolpate furrow configuration; Fig. 45, hexahedron, in this case a cube, corresponding to the dodecacolpate furrow configuration; Fig. 46, hexahedron, in this case not a cube, but with the same number of edges and faces as a cube; Fig. 47, heptahedron or right-pentagonal prism, *cf.* Figs. 48 and 49; Fig. 48, heptahedron; Fig. 49, heptahedron; Fig. 50, octahedron or right-hexagonal prism, *cf.* Fig. 51; Fig. 51, octahedron; Fig. 52, nonahedron; Fig. 53, nonahedron; Fig. 54, decahedron.

and two hexagonal faces. Another octahedron can easily be constructed by simply dividing one of the two pentagonal faces of the pentagonal prism (Fig. 51) among the foregoing heptahedrons. A way in which this may be done is shown in Fig. 55, which represents a pentagonal prism opened up and laid on a flat surface. If the pentagon is divided by the line *ab*, there will be formed from the divided pentagon a tetragon and a pentagon. But as soon as this is done, if the medium in which we are working is as plastic as the exine of a developing pollen grain, a readjustment will take place, causing the new angles about the points *a* and *b* to approach as closely as possible to 120 deg., as indicated by the dotted lines. Thus the bisection of a pentagon flanked by two tetragons converts the flanking tetragons into pentagons. Accordingly, the new polyhedron now has eight faces, four of which are pentagons and four tetragons. Figure 51 represents such an octahedron. It was constructed from the pentagonal prism (Fig. 47), a heptahedron, by dividing its front pentagonal face into a tetragon and pentagon and thereby, through the action of the law of equal triconvergent angles in plastic material, converting the two adjacent tetragonal faces into pentagons. This figure has eight faces and 18 edges, and, therefore, it satisfies the equation $E = 3F - 6$, as required by the series.

In the same way a *nonahedron* may be derived from the preceding octahedron (Fig. 51) by dividing its back pentagonal face. In doing this there are obviously two choices. If the dividing line be drawn so that its ends impinge on two of the three tetragonal faces which surround this pentagonal face, these two tetragons will be converted, as before, into pentagons, and at the same time the divided pentagon will yield a pentagon and a tetragon. The total number of tetragons is, therefore, reduced by one, and the number of pentagons increased by two. Such a nonahedron is shown in Fig. 52. It has three tetragonal and six pentagonal faces. It also has 21 edges and therefore satisfies our equation as required by the series. This figure may be identified in Table IV by its designation three tetragons, six pentagons.

Quite a different kind of nonahedron is produced if, in dividing the back pentagonal face of the octahedron (Fig. 51), the dividing line is passed in such a direction that its ends impinge upon the edges of two pentagonal faces, instead of upon those of two tetragonal faces, converting the pentagons into hexagons. This will become clear from Fig. 56, which shows the octahedron (Fig. 51) laid open on a plane surface with the back pentagonal face centrally placed. If this face is now divided by the line *cd*, the divided pentagon yields a tetragon and a pentagon, thus increasing the total number of faces by one, and the adjoining pentagons are converted into hexagons, as indicated by the dotted lines. Such a nonahedron has been constructed (Fig. 53). Two of its faces are hexagons, five are tetragons, and two are pentagons, *i.e.*, a total of nine, and it has 21 edges, thus satisfying the equation for the series.

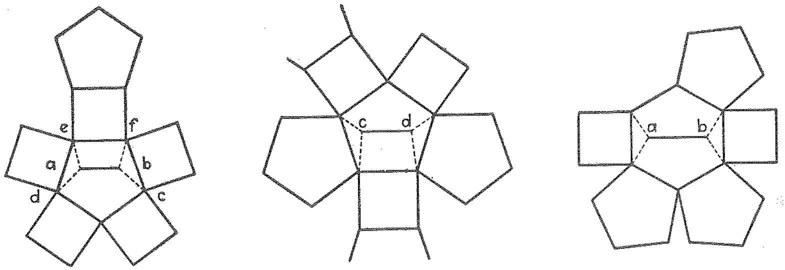

Fig. 55. Fig. 56. Fig. 57.

Figs. 55–57.—Dissections of polyhedrons to show the effect of the division of their faces: Fig. 55, the division of a pentagonal face flanked by tetragonal faces; Fig. 56, the division of a pentagonal face flanked by two other pentagonal faces; Fig. 57, the division of a hexagonal face flanked by two tetragonal faces.

The conversion of an octahedron into a nonahedron could be made equally well in a third way by dividing one of the pentagonal faces of the octahedron in such a way that the dividing line impinges upon a pentagonal face at one end and a tetragonal one at the other. If this is done, the divided pentagonal face is made into a tetragon and pentagon as before, increasing the total number of faces by one, and at the same time the adjoining pentagon is converted into a hexagon, and the tetragon into a pentagon. As a consequence, if the original octahedron had four pentagonal and four tetragonal faces, the resulting nonahedron would have four pentagonal, four tetragonal, and one hexagonal face.

Modes of Changing One Polyhedron into Another.—From these experiments the following generalization may be drawn for the *division of a pentagonal face* of a polyhedron surrounded by tetragonal and pentagonal faces, assuming that the three convergent angles at the points of impingement of the dividing line become adjusted to approach equality: According to the pentagon chosen for division and the orientation of the dividing line, the total number of faces of a polyhedron will be increased by one through the addition of hexagons, and the addition and subtraction of tetragons and pentagons, in the following three ways:

If the line dividing the pentagon impinge upon

a. Two tetragons, by	− 1 tetragon + 2 pentagons	
b. Two pentagons, by	+ 1 tetragon − 2 pentagons	+ 2 hexagons
c. A tetragon and pentagon, by		+ 1 hexagon

Another possibility is the *division of a tetragonal face.* In this case it is itself converted into two tetragonal faces, but at the same time, through the adjustment of the angles of impingement of the dividing line, it alters the flanking faces with the three following results:

If the line dividing the tetragon impinge upon

d. Two tetragons, by	− 1 tetragon + 2 pentagons	
e. Two pentagons, by	+ 1 tetragon − 2 pentagons	+ 2 hexagons
f. A tetragon and pentagon		+ 1 hexagon

The *decahedrons,* which are the next group of polyhedrons in our series, are of five different forms (Table IV), but all are related to the nonahedrons in the same way that the latter are related to the octahedrons. Some of the decahedrons may be derived from the octahedrons by the division of a pentagonal face as before. But other forms of the decahedron can be derived from nonahedrons only by the division of a hexagonal face. When this happens the divided hexagon yields two pentagons, and at the same time one more side is added to each of the flanking faces. This will become clear from Fig. 57, which shows such a hexagonal face of a nonahedron surrounded by some of its flanking faces opened up along their edges and laid on a flat surface. If the centrally placed hexagon be divided by the line *ab* and the angles of impingement at *a* and *b* be equalized, the two flanking tetragons will be thereby converted into pentagons. In the same way if *ab* impinge on pentagons, the latter will be converted into hexagons. Consequently, it may be stated that the effect of the *division of a hexagonal face* upon the sum total of the faces of a polyhedron will be as follows:

If the line dividing the hexagon impinge upon

g. Two tetragons,	− 2 tetragons + 4 pentagons − 1 hexagon
h. Two pentagons,	+ 1 hexagon
i. A tetragon and pentagon	− 1 tetragon + 2 pentagons

We thus have nine ways of increasing the number of faces of a polyhedron by one, but it will be noted that the results of *a*, *d*, and *i* are alike, also of *b* and *e*, and of *c*, *f*, and *h*. Therefore, only four different results are obtained.

TABLE III.—FOUR POSSIBLE RESULTS OF INCREASING THE NUMBER OF FACES OF A POLYHEDRON BY ONE

Formula	Tetragons	Pentagons	Hexagons	Done by
(1)	−1	+2	0	Dividing a pentagon with a line impinging upon 2 tetragons or dividing a hexagon with a line impinging upon a tetragon and a pentagon or dividing a tetragon with a line impinging upon two tetragons
(2)	+1	−2	+2	Dividing a pentagon with a line impinging upon two pentagons or dividing a tetragon with a line impinging upon two pentagons
(3)	0	0	+1	Dividing a pentagon with a line impinging upon a tetragon and pentagon or dividing a hexagon with a line impinging upon two pentagons or dividing a tetragon with a line impinging upon a tetragon and pentagon
(4)	−2	+4	−1	Dividing a hexagon with a line impinging upon two tetragons

Applying these formulas to the nonahedrons of the table, we shall readily see that three of them may be applied to the first four of the nonahedrons there described, and all four to each of the succeeding nonahedrons, but this does not result in a total of 15 different decahedrons, for some of them are duplicates of the others. Of the 15 different ways in which decahedrons may be derived from nonahedrons only five give different results.

Figure 54 shows one of the possible decahedrons. This one was obtained from a nonahedron having three tetragonal and six pentagonal faces by dividing one of its pentagonal faces with the dividing line impinging upon two tetragonal faces [formula (2)]. The same figure could likewise be obtained from a nonahedron with four tetragonal faces, four pentagonal, and one hexagonal face, by dividing the hexagonal face and letting the dividing line impinge upon two tetragonal faces [formula (4)].

By applying our four formulas to the five different decahedrons we find that we are able to derive six different endecahedrons. And by applying the four formulas to these in turn we are able to obtain seven dodecahedrons. It is interesting here to note, in passing, that the pentagonal dodecahedron, one of the regular polyhedrons, is derived from an endecahedron having two tetragons, eight pentagons, and one hexagon, by dividing the hexagon so that the dividing line impinges upon the two flanking tetragons [formula (4)]. A glance at our four formulas and the five endecahedrons which have hexagonal faces will show that no other division of any of the faces of any other endecahedrons can produce it.

From the various dodecahedrons may be derived seven triskaidecahedrons, and from these in turn may be derived seven tetrakaidecahedrons. One of these, that having six tetragonal and eight hexagonal faces, is known as the orthic tetrakaidecahedron. It has recently acquired the reputation of being the only polyhedron which can uniformly partition space. For this reason it is worth while to note that it may be derived only from a triskaidecahedron having five tetragonal, two pentagonal, and six hexagonal faces, by dividing a tetragonal face with the dividing line impinging upon a tetragonal and a pentagonal face.

By continuing to divide the pentagons, tetragons, and hexagons in their various relations to the other faces we may extend this list of polyhedrons indefinitely. But it is without profit to extend it farther, for we are already in a position to predict what all the others will be. An inspection of Table IV shows that each addition of a face offers seven possibilities of combining tetragons, pentagons, and hexagons. In each numerical class of polyhedrons so obtained the tetragons range continuously from 0 to 6, while co-ordinately with them the pentagons range from 12 to 0, by steps of two, and the hexagons range from n to $n + 6$, where n is the smallest number of hexagons in the numerical class of polyhedrons in question. Inspection of Table IV shows that $n = F - 12$ (where F is the total number of faces), since the smallest number of hexagonal faces in each numerical class of polyhedrons is 12 less than the total number of their faces. Hence the seven possible polyhedrons in any numerical class are characterized as follows: They must have 0 to 6 tetragonal faces and co-ordinately 12 to 0 (by steps of two) pentagonal faces and co-ordinately $F - 12$ to $F - 6$ hexagonal faces. This gives us a complete picture of all the possible polyhedrons. For example, if we wish to discover what the seven possible polyhedrons with 30 faces are like, by applying the above formula the first of these will have as faces 0 tetragons, 12 pentagons, and 18 (*i.e.*, 30 − 12) hexagons. The second will have 1 tetragon, 10 pentagons, and 19 hexagons; and so on to the seventh and last, which will have 6 tetragons, 0 pentagons, and 24 hexagons.

It will be noticed in the table that the number of hexagons in the successive numerical classes increases with the number of faces, while the numbers of tetragons and pentagons remain within their respective ranges, with no increase as we progress in the series. Consequently, when the number of faces reaches infinity the hexagons will be infinitely more numerous than the tetragons and pentagons, which is the same thing as saying that if the faces of an infinitely large polyhedron are of a finite size, they must be hexagonal. Since an infinitely large polyhedron with finite faces is a plane surface, we are brought to the conclusion that the only polygon that can divide a plane surface continuously is the hexagon, which, of course, is a recognized fact and the basic principle of the trischistoclasic system.

In this series I have purposely omitted, for the sake of simplicity, the polyhedrons with triangular faces in the higher numerical classes. Undoubtedly furrow configurations corresponding to these do occur. In fact they may occasionally be found among the pollen grains of *Portulaca oleracea*, which have as many as 30 furrows, but with grains of higher numerical furrow configuration the triangular arrangement is extremely rare, if indeed it ever occurs. The reason for this appears to be that in a series of this kind triangles cannot be propagated, for

TABLE IV.—THEORETICALLY POSSIBLE FURROW CONFIGURATIONS

Faces	Furrows or edges	Polyhedron or numerical class of polyhedrons	Description of polyhedrons			
0	0	None	None, corresponds to acolpate grains			
3†	3	None	None, corresponds to three lunes in 3-colpate grains			
4	6	Tetrahedron*	4 triangles*	0 tetragons	0 pentagons	0 hexagons
5	9	Pentahedron or triangular prism	2	3	0	0
6	12	Hexahedron, (*cube*)*	0 2	6 2	0 2	0 0
7	15	Heptahedron or pentagonal prism	0 1 2	5 3 2	2 3 2	0 0 1
8	18	Octahedron	0	4 5 6	4 2 0	0 1 2
9	21	Nonahedron		3 4 5 6	6 4 2 0	0 1 2 3
10	24	Decahedron		2 3 4 5 6	8 6 4 2 0	0 1 2 3 4
11	27	Endecahedron		1 2 3 4 5 6	10 8 6 4 2 0	0 1 2 3 4 5
12	30	Dodecahedron (*pentagonal dodecahedron*)*		0 1 2 3 4 5 6	12 10 8 6 4 2 0	0 1 2 3 4 5 6
13	33	Triskaidecahedron		0 1 2 3 4 5 6	12 10 8 6 4 2 0	1 2 3 4 5 6 7
14	36	Tetrakaidecahedron Orthic tetrakaidecahedron‡		0 1 2 3 4 5 6	12 10 8 6 4 2 0	2 3 4 5 6 7 8
15	39	Pentakaidecahedron		0 1 2 3 4 5 6	12 10 8 6 4 2 0	3 4 5 6 7 8 9

* Regular polyhedron.

† Appears to belong to the series, though it has no corresponding polyhedron.

‡ Orthic tetrakaidecahedron is supposed to be the only polyhedron that can partition space.

they are not formed from the divisions of the other polyhedrons; and when a triangle itself divides, the result is a triangle and a tetragon. Moreover, the equalization of the angles of impingement, which must always take place, would in this case tend to obliterate the remaining triangle, reducing it to a line. And if such a triangular face should escape obliteration by this means, it must inevitably sooner or later become converted into a tetragon through the impingement upon one of its sides of a dividing line of an adjacent polygon. So the chances of a triangular face's surviving to one of the higher numerical classes of polyhedrons are extremely remote.

I have also omitted to give consideration to the division of a polygonal face with the dividing line impinging upon one or two hexagons. If this should happen, it would convert the flanking hexagons into heptagons requiring internal angles greater than 120 deg., which is mathematically impossible in our series. Whether or not this is a valid reason for the nonoccurrence of heptagons I am unable to say. At any rate it seems certain that the inherent tendency of the three convergent angles to be equal, and therefore not greater than 120 deg., would militate strongly against such an occurrence and probably force an impending division to some other region or delay it until the neighboring faces were ready to divide, resulting in simultaneous divisions in the one or more threatened hexagons, thus allowing the dividing lines to impinge upon the products of their division which are pentagons. It is conceivable that in a region where the majority of faces are hexagonal the difficulty that each would experience in dividing in defiance of the law of equal triconvergent angles would delay their division until all were ready to divide, with the result that the divisions would be simultaneous throughout the region. Since laws similar to these apply to the division of tissue cells, herein may lie the explanation of the simultaneous divisions which are occasionally encountered in tissue cells.

PART II

CLASSIFICATION