AGROPYRON Gaertn.

Grains spheroidal or ovoidal, with the pore at the large end, 47 to 52 μ in diameter. Germinal aperture circular, 5.7 to 6.4 μ in diameter; operculum irregular, 2.8 to 4.6 μ in diameter.

The genus comprises about 60 species in temperate regions of both hemispheres; about 25 species in the United States.

Agropyron Smithii Rydb. Western wheat grass, Bluejoint, or Bluestem grass. Grains as in the generic description.

Manitoba and Minnesota to British Columbia, south to Missouri and Texas. Flowers in early summer, causing some hayfever. Said to be important in this respect in Wyoming (Scheppegrell, 1917).

Agropyron repens (L.) Beauv. Quick, Quitch, or Quack grass. Grains as in the generic description.

A common weed introduced from Europe in fields and waste places almost throughout North America. Flowers in June and July but sheds relatively little pollen, of only secondary importance in hayfever.

Lolium perenne L. Ray grass, Rye grass. Grains somewhat various, tending to be spheroidal or ovoidal, 28.5 to 33.1 μ in diameter. Germinal aperture circular, 2.8 to 4.0 μ in diameter; operculum irregular, 1.1 to 1.7 μ in diameter. Texture faintly granular.

A common weed in cultivated ground and waste places almost throughout the United States and Canada. Flowers in June and July, shedding much pollen, which is admirably adapted to wind pollination and is always an important factor in hayfever in regions where abundant. It is stated to be "the most important hayfever producer of all the grass family on the Pacific coast" (Selfridge, 1920).

Secale cereale L. Rye. Grains ellipsoidal, with the germ pore on the side near one end. This character is rather unique among the grasses and serves to distinguish this species from all others that I have examined. The grains are also rather large, 62 by 40 μ. Germinal aperture approximately circular but with wavy margin, 5.1 to 5.7 μ in diameter; operculum irregular in outline, about 2.3 μ in diameter. Texture distinctly granular.

Cultivated. Flowers in spring or early summer. Known to be a cause of hayfever but has a short effective range owing to the large size of its pollen grains.

Triticum aestivum L. (*T. sativum* Lam., *T. vulgare* Vill.) Wheat (Fig. 87). Grains rather irregular in shape but tending to be ovoid, 48 to 57 μ in diameter. Germinal aperture irregular in shape, 6.3 to 9 μ in diameter; operculum irregular, 4.5 to 6.3 μ in diameter. Texture finely but distinctly granular.

Cultivated throughout North America. Flowers in early summer shedding little pollen and on this account of little or no importance in hayfever.

Phalaris minor Retz. Mediterranean canary grass. Grains somewhat various in shape but tending to be spheroidal, 40 to 45.6 μ in diameter. Germinal aperture circular but with slightly wavy margin, 3.7 to 5.7 μ in diameter; operculum irregular in outline, 2 to 2.3 μ in diameter. Texture faintly granular.

Introduced from Europe and cultivated in California, Oregon, and elsewhere. Not regarded as a cause of hayfever.

Anthoxanthum odoratum L. Sweet vernal grass. Grains always spheroidal or nearly so, 37.6 to 45.6 μ in diameter. Germinal aperture generally circular but with wavy margin, 4 to 6.3 μ in diameter; operculum irregular, 1.7 to 2.3 μ in diameter. Texture nearly smooth, presenting only the faintest possible granular appearance.

A common grass of fields and meadows nearly throughout North America. Flowers in April and May, shedding enormous quantities of pollen which is admirably adapted to wind dispersal and is extremely toxic to hayfever patients. In the northeastern United States and Canada sweet vernal grass is the first of the hayfever grasses to flower and is the undisputed cause of much hayfever, generally serving to start the season.

Zea Mays L. Indian corn, Maize. Grains spheroidal or nearly so, 90 to 100 μ in diameter. Germinal aperture generally almost exactly circular, 6.8 to 9.1 μ in diameter; operculum very irregular, 2.3 to 3.4 μ in diameter, frequently represented by an aggregation of more or less distinct fragments on the pore membrane, and the latter itself is frequently visibly streaked. Texture finely but distinctly granular. This grain may be distinguished with certainty from those of all other grasses by its large size and large germinal aperture, in which characters it greatly exceeds those of all other species that I have observed in these studies.

Native of America but known only in cultivation. Flowers throughout most of the summer, shedding large quantities of pollen which is extremely toxic to some types of hayfever cases, but owing to its short range which is restricted by the large size of its grains, it is rarely an important cause of hayfever.

CYPERACEAE Sedge Family
CAREX L. SEDGE

Grains when moist and expanded ovoid or pear-shaped, with a single irregularly shaped germ pore (Plate V, Fig. 6). Exine thin and more or less rough-granular in appearance. Over the area of the germ pore, which is symmetrically placed at the large end of the grain, the exine is fragmented; the germ pore is thus poorly defined. Intine thick, especially on the sides of the grain, where it dips deeply into the protoplast. When the grain dries and shrinks, it generally does so with the formation of three or four large concavities on its sides and a smaller one at the large end, causing it to become polyhedral, sometimes more or less tetrahedral—though there is much variation in this. In the expanded condition, while the grain as a whole assumes a symmetrically ovoid form, the contained protoplast does not expand much, retaining its angular form. This curious and distinctive appearance has been variously misinterpreted, and the grain described as having four or five furrows, which indeed it appears to have when observed in its collapsed or partially collapsed condition.

The thin, almost fragmentary condition of the exine and the thick intine and poorly defined germinal furrow without harmomegathic function are characters encountered again and again among wind-pollinated plants that were derived from insect-pollinated ancestors, *e.g.*, those of *Populus* and *Fraxinus*, and suggest that the grains of *Carex* are likewise so modified in response to wind pollination and that *Carex* is probably derived from some ancestral form which was insect-pollinated.

Carex is a genus of about 1,000 species of grass-like herbs, widely distributed throughout the temperate regions of the world. All are entirely wind-pollinated and *Carex* pollen is frequently caught on pollen slides but it is not known to cause hayfever.

Carex stricta Lam. Tussock sedge (Plate V, Fig. 6) type. Grains when fully expanded 38.8 to 46.7 μ long and 32 to 38 μ broad. Texture sharply granular and fragmented, suggesting the appearance of the exine of the grain of *Populus*.

A tall, slender herb in swamps; of wide distribution throughout most of North America. Flowers in April and May, shedding rather large amounts of pollen.

Carex pennsylvanica Lam. Pennsylvania sedge. Grains as in the type, about 37.4 μ long.

A low, grass-like herb in dry fields and woods. New Brunswick to North Dakota to Tennessee to North Carolina. Flowers in May and June.

Eleocharis spi. Spear rush. Grains similar to those of *Carex* but with no vestige of a germ pore and a more coarsely granular texture. Various in shape and size but tending to be long pear-shaped and about 34 by 48 μ.

Rush-like herbs in wet meadows and marshes.

JUNCACEAE Rush Family

Juncoides campestre (L.) Ktze. (*Juncus campestris* L., *Luzula campestris* DC., *L. comosa* Meyer) Common wood rush (Plate V, Fig. 7). Grains uniform in shape and size, always united in tetrahedral tetrads, the four grains so closely appressed that the tetrad is almost spherical. Individual cells 25.1 to 29.6 μ in diameter. Exine thin, flecked with small granules, continuous from grain to grain over the whole tetrad, but the sutures between the adjoining grains plainly visible through the exine. Intine thick and hyaline, thicker on the walls of the dissepiments than on the outside walls (Fig. 88).

The germinal furrow is not sharply defined but is represented by a thin area of the exine on the outer face of each grain. This area is further distinguished from the rest of the grain by the elastic nature of its exine and the more open distribution of its granular flecks. Underlying each are a number of large, globular bodies of hyaline material which swell upon being moistened, causing the overlying areas of the exine to bulge outward and contract upon drying so that it becomes invaginated. Though these thin elastic areas are generally overlooked, they are undoubtedly true furrows, as proclaimed by their position on the outer face of each grain and by their harmomegathic function. Moreover, it is through them that the pollen tube emerges at time of germination. At best, however, the germinal furrow of these grains is vestigial. Its reduction is obviously correlated with the extreme thinness of their exine which, in turn, is correlated with their mode of pollination by wind.

The grains of *Juncoides* are so far reduced that they suggest little of their relationships with those of other plant families. It is not possible in the present state of our knowledge to say even whether or not they are derived from some insect-pollinated ancestor—though the floral structure of the Juncaceae is generally believed to indicate that such is the case. Nevertheless, the thinness of the exine, almost complete loss of the furrow, and persistent and complete union of the grains in tetrahedral tetrads stamp them as actually advanced.

The common wood rush is a grass-like perennial, of almost universal distribution throughout the United States, Canada, and the cooler parts of the rest of the world. It flowers very early in spring, shedding much pollen which is often caught in abundance on atmospheric-pollen slides, but it is not known to cause hayfever.

The genus includes about 65 species of low, grass-like herbs, widely distributed, flowering in spring. The family Juncaceae includes about eight genera and 300 species, mostly aquatic or semiaquatic. Their pollen grains have not been much investigated, but Fischer (1890) describes the grains of six species of *Juncus* and six of *Luzula*, "alle mit glatter Exine und zu vier nach den Ecken einer Teträders verwachsen." It therefore seems probable that the grains of the great majority, if not all, of the Juncaceae will be found to be united in tetrahedral tetrads.

DICOTYLEDONS

MAGNOLIACEAE Magnolia Family

The grains of the Magnoliaceae are so different in the three tribes of the family that it is more satisfactory to describe them by their tribes than to attempt a family description. The classification here employed is that of Prantl (1891).

Magnolieae
  Magnolia
  Svenhedinia
  Michelia
  Liriodendron
Illicieae
  Drimys

  Illicium
  Zygogynum
Schizandreae
  Schizandra
  Kadsura

In more recent treatments the tribes Illicieae and Schizandreae are separated entirely from the Magnoliaceae and constitute the related family Schizandraceae. The evidence of the pollen-grain forms of these plants is decidedly in favor of such a separation. Nevertheless, there is an obvious connection between the different forms. And because this is highly illuminating and suggestive of phylogenetic trends, I have chosen to retain the older classification.

Magnolieae. Grains elongate, boat-shaped. 41 to 63 μ in length and about one-third to one-half as broad, with a single furrow. Exine smooth, granular, or warty but not reticulate.

Trees and shrubs of widespread distribution. Insect pollinated and frequently with showy flowers.

Illicieae. Grains not elongate, 18 to 34.3 μ in diameter; either with a single furrow and united in tetrads (*Drimys*) or with three furrows and not united in tetrads (*Illicium*). Exine always reticulate.

Shrubs or small trees, native of Asia, Australia, and adjoining islands.

Schizandreae. Grains oblate spheroidal, 22 to 28 μ in diameter, not united in tetrads, with six furrows meridionally arranged, three long and meeting at one pole and three short and not meeting at either pole.

Woody climbers, native of tropical Asia and Himalaya.

"The Magnoliaceae must be among if not the most primitive of all the angiosperms" (Wieland, 1909). The author of this statement regards them as most closely allied to the Mesozoic Bennettitales. Indeed, as he points out, their likeness to *Williamsonia* and to *Wielandiella* of that group leaves little doubt of their common genetic origin with them. This conclusion is abundantly sustained by the forms of the pollen grains of at least the tribe Magnolieae, for the grains of the four genera of that tribe are virtually indistinguishable in outward appearance from those of the Bennettitales and are of the most primitive type found among the dicotyledons. In these grains, however, we do not find any trace of the prothallial tissue which appears to have characterized the grains of the Bennettitales; but this is in line with the progressive reduction of prothallial tissue which was initiated among the pteridosperms.

The grains of the two remaining tribes of the family, Illicieae and Schizandreae, are very different, and they are of the utmost interest, because we can learn from them much regarding the organization of the grains not only of this group but of the dicotyledons in general. The grains of these two tribes, like those of the Magnolieae, are primitive, but, besides pointing backward toward the ancestral gymnosperms, those of some species show characters pointing unmistakably forward toward the higher angiosperms.

The grains of *Drimys* are of particular interest, because in them we see demonstrated two of the most important laws of pollen morphology. The grains happen to occur united in tetrads, a condition which is exceedingly rare among the lower angiosperms and gymnosperms. They are of the monocolpate or single-furrowed type, as would be expected in the Magnoliaceae, and, still more important, their furrows always face outward; that is to say, the furrow of each grain is on the distal side, the side remote from contact with its neighbors of the tetrad, as we have seen was the case among the gymnosperms. The grains of *Glyptostrobus*, for example, which are sometimes united in tetrads, are joined together by their dorsal surfaces, each with its pore facing outward; this is according to Fischer's law which appears to be universal for monocolpate grains. Thus Fischer (1890) says, "Wo jedes Körn eine Austrittsstelle besitzt, liegt diese stets nach aussen, dem Berührungspunkt der vier Körner gegenüber." Also Fritzsche points out (1837, page 711) that the four grains of the tetrads of *Philydrum lanuginosum* are grown together back to back with their furrows facing outward. It is therefore reasonable to assume that the same relation holds with other monocolpate grains, even though they are separated from each other before they reach maturity, and, conversely, the side upon which the pore or furrow occurs in all monocolpate grains is the distal side, and the opposite the proximal, in relation to its former position in its tetrad. This gives us points of orientation which are essential in making comparisons between the pollen grains of different species, families, and orders.

The most important difference between the grains of *Drimys* and those of the Magnolieae, apart from the union of the former in tetrads, is their shape, which tends to be isodiametric instead of elongate. The reason for this is probably entirely due to the fact that the tetrads are tetrahedral, with which arrangement an elongate shape is obviously incompatible. On the other hand, when grains are arranged in tetrads which are in a single plane they may become elongate in a direction at right angles to the plane of their union. For example, Fritzsche (1837) has pointed out that the pollen grains of *Annona tripetala* are united in one plane, and his figure (Plate IV, Fig. 7) shows that they are distinctly elongate transversely to the plane of the tetrad. A similar example is found in the grains of *Philydrum lanuginosum*, which in many ways are similar to those of *Drimys*. They have a single broad furrow and are joined back to back in the tetrad, but this special arrangement is not always the same; it may be square, rhomboidal, or tetrahedral, with the result that those grains which are associated in a single plane tend to be ellipsoidal and have an elliptical furrow, while those that are associated in the tetrahedral arrangement tend to be more nearly isodiametric, with the furrow circular or somewhat triangular in outline. It can therefore be stated as our second law that the association of pollen grains in tetrahedral tetrads tends to impose upon them an isodiametric form, while association in flat tetrads permits an elongate form.

According to the position at the beginning of the dicotyledonous series assigned by taxonomists to the Magnoliaceae, their pollen grains would be expected to be of a form standing somewhere between that of a pteridophyte spore and that of a higher angiosperm pollen grain. In most ways this is true. Particularly is this brought out when we compare the mechanisms whereby these pollen grains discharge their principal functions with those of the Pteridophyte spores, which come before, and those of the higher Angiosperms, which come after in the evolutionary scale. Two important functions which both spores and pollen grains have to perform are to provide a place of exit for the growing prothallus or for the emerging pollen tube, as the case may be, and, if the spore walls are thick and rigid, to provide an expanding mechanism to accommodate changes in volume due to changes in moisture. The means whereby these two functions are performed is clearly reflected in the morphology of the grain and, in a way, is a sign of the stage to which the pollen grain has attained in its advance up the evolutionary scale.

Among the pteridophyte spores there frequently occurs a triradiate crest with the radii reaching almost halfway round the grain (Fig. 89). Such spores originate in tetrahedral tetrads, and the radii of the triradiate crest mark the boundaries of the three faces of contact that each spore made with its three neighbors of the tetrad during its formative period; therefore the triradiate crest marks the proximal side of the grain. Germination of such spores commonly takes place by the dehiscence of the spore wall

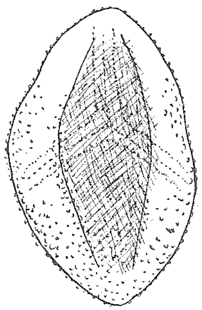
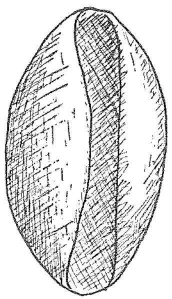
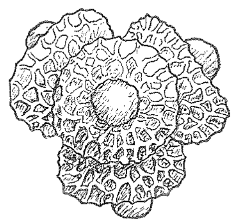

FIG. 89. FIG. 90. FIG. 91.

FIG. 89.—Spore of *Osmunda regalis*, 80 μ long, ventral view, drawn as if transparent in order to show the triradiate crest on the dorsal side.
FIG. 90.—Pollen grain of *Magnolia Soulangeana*, 35 by 40 μ, ventral view, partly expanded.
FIG. 91.—Tetrad of *Drimys Winteri*.

along the three ridges, forming a triradiate cleft through which the developing prothallus emerges. The pteridophyte spores appear to have no well-defined mechanism for accommodating changes in volume. In some, particularly those in which the surface is rendered inflexible by the presence of prominent reticulate thickenings, the spores shrink by a cupping in of the three flattened areas alternating with the three radii, probably because in these areas the reticulate thickenings are much less developed or absent, *e.g.*, in the spores of *Lycopodium*. In others of which the distal surface is not stiffened by reticulate thickenings, *e.g.*, the spores of *Osmunda* (Fig. 89), a cup-like depression forms on the distal side, opposite to the triradiate crest. This type of spore is the more interesting to us because the concavity resulting from this method of contraction often

closely simulates the furrow of the monocolpate pollen grain, usually slightly distorted, it is true, by the presence of the triradiate crest on the opposite side of the grain. Nevertheless, its appearance suggests that, were it not for the asymmetrical stiffening effect of the triradiate crest, this false furrow of the pteridophyte spore would be essentially the same as the single furrow of the monocolpate pollen grain.

In the monocolpate grains of the Magnolieae and primitive gymnosperms the three lines of dehiscence are ordinarily absent, and both the function of volume-change accommodation and pollen-tube emergence are fulfilled by the single furrow which, in these grains, is a permanent organ. It is long, deep, and much more sharply defined than is the false furrow of the pteridophyte spores. The pollen-grain furrow also tapers similarly at both ends because of the absence of the disturbing effect of the triradiate crest, and it tends to give the grain the shape of a boat, unless, like the grain of *Drimys*, it happens to be formed and remain at maturity in a tetrahedral tetrad which mechanically prevents it from becoming elongate. This furrow is probably strictly homologous with the false furrow of the spores of pteridophytes but has here become a permanent organ. It has become hereditarily fixed in its position on the distal side of the grain, forced into that position by the presence of the triradiate crest on the proximal side. There it remains, though in pollen grains the triradiate crest has since become lost. The origin of this structure is in the same category as the origin of the four-lobed shape of the cells of a *Pediastrum* colony, as described by Harper (1919). The four-lobed shape of these cells was called forth by contact stimuli that each cell sustained from its neighbors of the colony; nevertheless, these cells are now

> . . . able to attain their characteristic forms—, when almost entirely free from their normal environmental relations with the other cells of the colony. . . . We have here evidence that a cell form which may well have arisen first simply as a response to environmental stimuli has become fixed in heredity until now the series of growth processes by which it develops can go on quite independently of the stimulative conditions which originally called it forth.

That is to say, both in the cells of *Pediastrum* and in monocolpate pollen grains their basic form is an acquired character—acquired from contact stimuli, but permanently inherited even in the absence of the stimuli.

Among the higher dicotyledons the basic form of grain has three or more furrows arranged in the trischistoclasic system or system of equal linear stresses, as already described, and we know that these furrows occur at the points of contact that the grain made with its neighbors during its formation in the tetrad or elsewhere on its surface through stresses set up by these points of contact. These furrows are entirely different in origin and in form from the single furrow of the monocolpate grain, but their functions are the same, serving to allow both pollen-tube emergence and volume-change accommodation. In some respects, therefore, the trischistoclasic dicotyledonous type of grain is the direct antithesis of the monocolpate form of grain, for in the former the several furrows are initiated either at, or as a consequence of, its points of contact in the tetrad during its formative period, while in the latter the single furrow is initiated at the point on the grain most remote from contacts, originally so placed on account of the absence in this part of the grain of stiffening structures tending to prevent its formation.

The gap between these two types of grain is really very great, truly an expression of the enormous genetic difference that in general exists between the gymnosperms and the higher dicotyledons, and, were it not for the remarkable condition found among the grains of *Schizandra* (Plate V, Fig. 10) and *Kadsura*—the next genera of the Magnoliaceae that we have to consider—a connection between the two types of pollen grain might never be explained. But in the grains of these two genera, we find, existing side by side, the principal features of the triradiate pteridophyte spore, the monocolpate gymnosperm pollen grain, and the trischistoclasic dicotyledonous pollen grain. The grains of *Schizandra* are always shed singly, but the orientation of their parts in relation to their tetrad is clear from what we have learned from the grains of *Drimys* and *Glyptostrobus*, which are shed in tetrads, and from the Pteridophyte spore. The grains of *Schizandra* and *Kadsura* possess a triradiate crest which must have been proximal in the tetrad, marking the boundaries of the contact faces. Opposite the triradiate crest is a flexible area which cups in as the grain dries and bulges outward when it is moistened, homologous with the single furrow in the grains of

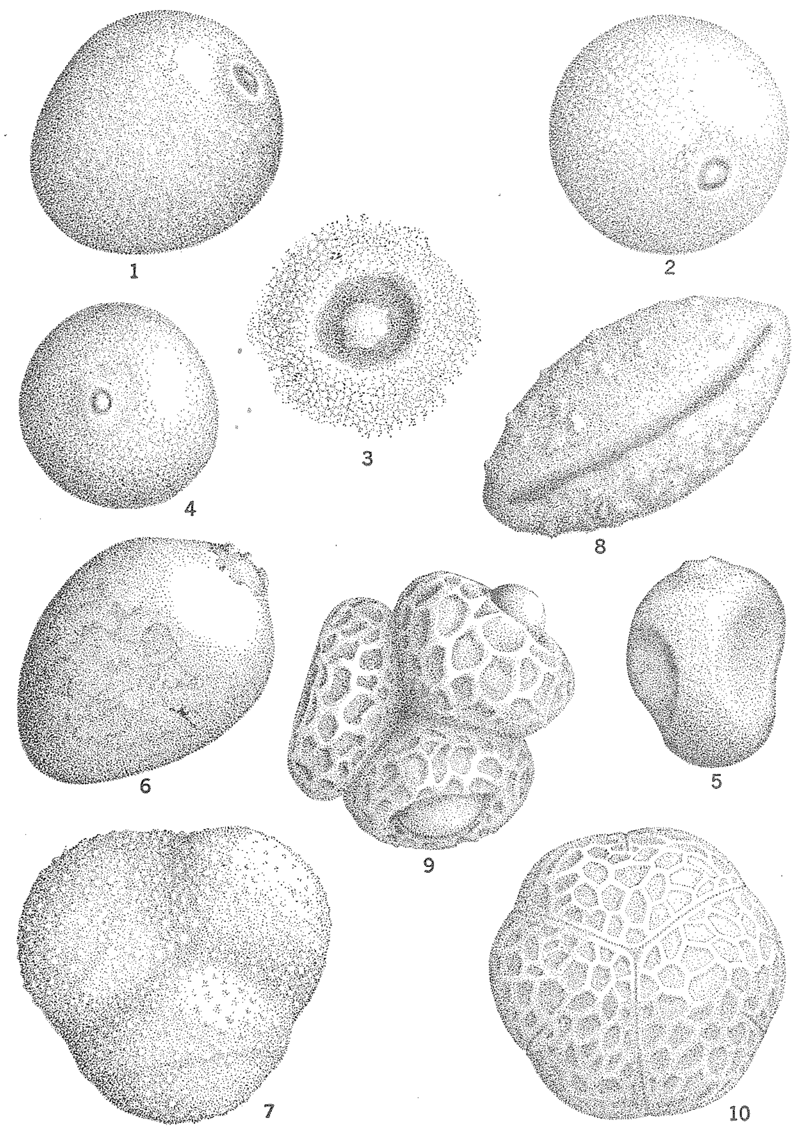

Plate V.—Pollen grains of Gramineae, Cyperaceae, Juncaceae, and Magnoliaceae. 1, *Festuca elatior*, side view, 32 μ in diameter. 2, *Phleum pratense*, ventral view, 35 μ in diameter. 3, Germ pore and surrounding exine of a pollen grain of *Avena fatua*, diameter of the aperture 7.5 μ. 4, *Agrostis palustris*, ventral view, expanded, 28 μ in diameter. 5, The same contracted. 6, *Carex stricta*, side view, 44 μ long. 7, *Juncoides campestris*, whole tetrad, 38 μ in diameter. 8, *Liriodendron Tulipifera*, ventral view, 40 by 62 μ. 9, *Drimys Winteri*, each grain of the tetrad 34.2 μ in diameter, *cf.* Fig. 91. 10, *Schizandra chinensis*, dorsal view, 21.6 μ in diameter, *cf.* Fig. 93.

Drimys, and must have been distal in the tetrad. Alternating with the radii of the triradiate crest and on the equator of the grain, there are three short furrows which must have traversed in a meridional direction the three contact faces in the tetrad and are therefore homologous with the three furrows which commonly characterize the trischistoclasic grains of the dicotyledons. Thus in many ways this form of grain marks the bridging of the gap between the form of the gymnosperm grain and that of the higher dicotyledons (Fig. 93).

It is interesting to note that the three short furrows of the grains of *Schizandra* and *Kadsura* accommodate neither the pollen-tube emergence nor volume changes, as their homologues do in the pollen grains of the higher dicotyledons. In the grains of *Schizandra* and *Kadsura* the three long furrows which are homologous with the radii of the triradiate crest of fern spores perform the former function, and the flexible area on the distal side of the grain performs the latter. Nevertheless, the structure of the short furrows is exactly the same as that of the long furrows, so it seems reasonable to suppose that, with the loss of the triradiate crest, which appears to be entirely absent from the grains of all the higher dicotyledons, these three short furrows could easily take over their function, by simply splitting longitudinally, just as do the long furrows of this grain and the radii of the triradiate crest of the pteridophyte spores; and, having once acquired a longitudinal split, they could likewise take over the function of volume-change accommodation. Such, I believe, is the origin of the three furrows which characterize the basic form of pollen grains of the higher dicotyledons. In the grains of *Schizandra* and *Kadsura* they appear to function only as structural stiffenings of the walls of the grain, serving with the three long furrows to limit the invaginating area to the ventral side. In the grains of the higher dicotyledons they represent the taking over of two additional functions coincidently with the elimination of the organs that formerly performed them.

The development of these furrows was the great achievement of the dicotyledonous pollen grain. With it the grain was released from the limitations imposed upon it by the single long, deep furrow of the monocolpate form of grain which had been its heritage from the pteridosperms of the remotest antiquity. With this release came the most surprising diversity of form,

through the relatively short succeeding span in the evolutionary scale, standing in remarkable contrast to the continuous monotony of the preceding development of the one-furrowed grain which we have traced step by step from the pteridosperms to the Magnoliaceae. In such a form as this of *Schizandra* and *Kadsura* the grain was freed through the acquisition of a new set of organs allowing it a new way of doing things. And in the following pages will be shown some of the multifarious forms of pollen grain which arose from its liberation.

Key to the Species

I. Furrow one	
A. Grains not in tetrads, boat-shaped; exine not reticulate; 41 to 63 μ long.	
1. Exine smooth.	
About 41 μ long.	Svenhedinia minor
About 51 μ long.	Michelia champaca
2. Exine granular, not warty.	
About 60 by 31 μ.	Magnolia acuminata
About 54 by 22 μ.	Magnolia Soulangeana
3. Exine granular and covered with conspicuous warts, 62 by 40 μ.	Liriodendron Tulipifera
B. Grains in tetrads, exine reticulate.	
1. About 34.2 μ in diameter, tetrads rather loose.	Drimys Winteri
2. About 18 to 19.5 μ in diameter, tetrads compact.	Drimys piperita
II. Furrows more than one, meridional; exine reticulate.	
A. Furrows three, meeting at both poles, grains 27.5 to 28.5 μ in diameter.	Illicium floridanum Illicium religiosum
B. Furrows three, not meeting at either pole, 28.5 to 31 μ in diameter.	Illicium yunnanense Illicium sp. Maire 3327
C. Furrows six, meridional, three of them long and meeting at one pole but free at the other; and three of them short, not meeting at either pole. Grains oblate-spheroidal. 22 to 28 μ in diameter. Area of the exine around the blank pole flexible and dipping in as the grain dries.	Schizandra spp. Kadsura spp.

MAGNOLIA L. Magnolia

Grains boat-shaped, with a single deep, longitudinal furrow, essentially like that of the grains of *Cycas* and *Ginkgo*, capable of gaping widely open (expanded) or becoming completely evaginated (over expanded); 50 to 60 μ long and about one-third as broad when moist but with the furrow still invaginated.

They are a little more elongate than those of the cycads and taper more toward their ends than those of *Ginkgo*. The furrow is slightly pointed and appears to effect a rather complete closure when the grains dry, differing in this respect from those of gymnosperms with the same type of furrow. Exine rough-granular on the outside but less so than in the grains of *Liriodendron* (Plate V, Fig. 8), which they otherwise resemble closely; inside the furrow, however, the exine is nearly or quite smooth. When the grains are moistened they may, but do not always, swell enormously, the floor of the furrow bulging out and causing the grain to assume a spherical form. In this condition the part that was inside the furrow can always be recognized by its smoother texture and thinner exine, showing that the furrow is a permanent organ.

About 30 species of trees and tall shrubs in Asia, eastern North America, and southern Mexico. Commonly with large, showy white, rose, purple, or yellow flowers, appearing in spring with or before the leaves. Many species are cultivated. Insect pollinated and not a cause of hayfever.

Magnolia acuminata L. Cucumber-tree type. Grains as in the generic description, 60 to 65 μ long; texture minutely and uniformly rough-granular, by which character they can easily be distinguished from those of the next species.

A large forest tree, reaching nearly 100 ft. in height. Flowers appearing with the leaves, not showy, Ontario to Alberta and southward. Often planted.

Magnolia Soulangeana Soul. Magnolia (Fig. 90). Grains as in the generic description; texture conspicuously granular and blotchy in appearance, suggesting to a certain extent that of the grains of *Liriodendron* (Plate V, Fig. 8); 49 by 35 μ when moist but not overexpanded, 54 by 23 μ when dry, showing that expansion in width is accompanied by a shortening in length.

A common garden shrub or small tree of hybrid origin, with large white flowers tinged with purple, appearing before the leaves. Insect pollinated and not a cause of hayfever.

Svenhedinia minor Urb. (*Talauma minor* Urb.). Grains essentially as in *Magnolia* but a little narrower in shape and a little more tapering at their ends, 51 by 27.4 μ. Exine smooth inside and out. When the furrow evaginates the grain becomes ellipsoidal or nearly spheroidal, the exine appearing to be uniform throughout in texture and thickness.

A small tree, native of Cuba.

Michelia champaca L. Champaca. Grains essentially the same as those of *Magnolia*, uniform in size, about 41 μ long and 24 μ broad when moist but not overexpanded; texture smooth throughout. Apparently these grains expand easily, the floor of the furrow bulging so far out that the grain becomes more convex on its ventral than on its dorsal side. The part which was inside the furrow can be distinguished by its much thinner exine. In the expanded condition the grain is the same length as when unexpanded but increases in width to about 28.5 μ.

A medium-sized tree, similar in most respects to *Magnolia*, native of tropical Asia and cultivated elsewhere in tropical countries. The genus includes about 13 species of shrubs and small trees in tropical Asia, Himalaya, and China.

Liriodendron Tulipifera L. Tulip tree (Plate V, Fig. 8). Grains boat-shaped, and, in general form, essentially the same as those of *Magnolia*, about 62 μ long and 40 μ broad when moist but not overexpanded. Texture of the outside is extremely finely pitted, with large, wart-like nodules superimposed in irregular fashion. The rugged, coarse appearance that these grains present is unique and serves to distinguish them from all other monocolpate grains that I have seen.

A tall and beautiful forest tree, attaining a height of over 100 ft., with large, showy flowers which bear a superficial resemblance to yellow tulips. Throughout most of the eastern United States. Flowers in May and June after the leaves are fully developed. Insect pollinated and not a cause of hayfever.

Liriodendron was widely distributed in North America and Europe during the Cretaceous period but is now represented only by the present species and *L. chinensis* Sarg. in central China.

DRIMYS Forst.

Grains always in tetrads, which are nearly always tetrahedral, though occasionally, in *D. Winteri*, groups in other arrangements are found. Individual grains circular or somewhat triangular in outline, about 18 to 34.2 μ in diameter, each with a single furrow occurring as a large, roundish or irregularly shaped depression in the center of its distal (outer) side, with three flattened faces on its proximal (inner) side where pressed against its three neighbors of the tetrad. All of the exposed surface of the grain, except the furrow, is covered by a reticulate system of high ridges enclosing angular lacunae, similar to but much coarser than those of the grains of *Illicium* and *Schizandra*. The pattern of the reticulum is not continuous from grain to grain throughout the tetrad. In each grain its mesh becomes finer toward the junctures with the other grains; at the angles where the surfaces of three grains come together it may even be quite smoothed out; along the edge of the furrow it ends abruptly with closed lacunae. The floor of the furrow is deeply depressed and smooth and when the grain is moistened bulges out like a bubble, accommodating its expansion.

This tetrad is similar to that of *Glyptostrobus*, except that here the grains are constantly and firmly united. The four grains function as individuals, each expanding and contracting, through a distention and retraction of its furrow floor, quite independently of its neighbors to which it is joined. The only effect that the union of the four grains appears to have had upon them is to give them a roundish shape, and even this is due not so much to the fact that the grains remain united in a tetrad as to the fact that the tetrad is tetrahedral. It is interesting to compare the effect of the grouping of this pollen tetrad with that of the Droseraceae or with the 16-celled compound grain of the Mimosaceae (q.v.), in both of which the whole group functions, in part at least, as a unit, the individual grains becoming profoundly modified as a consequence of their union, with a great reduction or total loss of both the pores and furrows which are conspicuous features of the grains of their nearest relatives. Certainly the tetrads of *Drimys* and *Glyptostrobus*, in which the union has produced virtually no modification of the grains, must be regarded as the more primitive type.

The genus includes about 10 species of shrubs and small trees with pellucid-dotted leaves and white or whitish flowers, distributed in America from Mexico to the Straits of Magellan and in Australia, the Philippines, New Zealand, and adjoining islands. Included in it are such interesting plants as the aromatic pepper tree *D. aromatica*, of Tasmania; the pepper tree *D. axillaris*, of New Zealand; and the pepper shrub *D. dipetala*, of New South Wales, Australia; besides the two following species:

Drimys Winteri Forst. Winter's bark or Cinnamon tree (Fig. 91; Plate V, Fig. 9) type. Tetrads generally tetrahedral, though occasionally they are found in other arrangements. Grains not closely pressed together, 34.2 μ in diameter; reticulum rather coarse but less so than in the grains of *D. piperita*.

A small tree, about 50 ft. high. Straits of Magellan in South America; with milk-white, jasmine-scented flowers. Occasionally cultivated.

Drimys piperita Hook. f. Grains similar to the type but always tetrahedral and more closely pressed together so that the tetrad is almost completely spherical. Reticulum more open, and its ridges conspicuously buttressed. The individual grains measure about 18.2 μ to 19.4 μ in diameter. These grains can easily be distinguished from those of *D. Winteri* by their more spherical tetrads, more open reticulum, and smaller size.

A bushy shrub with large, leathery leaves which are aromatic and peppery and small axillary white flowers. Native of the high mountains of Borneo, the Philippines, and New Guinea.

ILLICIUM L. Chinese anise Star anise

The pollen grains of the various species of *Illicium* exhibit two distinct types between which no obvious relationships are apparent. These are described under their specific headings.

The genus includes about 20 species of aromatic shrubs or small trees with thick evergreen leaves and small yellowish or purple flowers. In distribution they are mostly oriental (India, China, and the Philippines), with two species in the southern United States. The star anise used in flavoring is obtained from the Chinese species, *I. verum* Hook.

Illicium floridanum Ellis Anise tree, "Star anise," Poison bay (Fig. 92). Grains uniform, spheroidal, about 28.5 μ in diameter; tricolpate, occasionally dicolpate. Furrows long and slender, meeting at both poles, without germ pores. Exine completely covered by a system of anastomosing ridges bounding angular lacunae and ending with closed and somewhat smaller lacunae along the furrows, the ridges coalescing to form a sort of rim; mesh of the reticulum somewhat finer than in the grains of *Drimys Winteri*, otherwise similar.

When the grains expand the furrows broaden throughout their entire length, appearing as channels of uniform width, and display on each furrow membrane a central thickening extending its full length. In their confluence at the poles and in their linear shape these furrows differ from those of other dicotyledons and may not even be homologous with them. Instead, they suggest by their appearance and the fact that the grains readily split open along them, with the split starting at the poles, that they are lines of dehiscence, homologous with the triradiate crests of Pteridophyte spores. To settle this point, however, it would be necessary to observe the orientation of these grains in their tetrads.

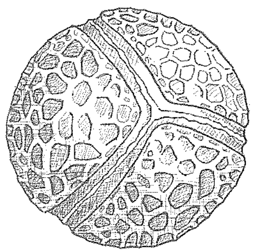

FIG. 92.—Pollen grain of *Illicium floridanum*, 28.5 μ in diameter, fully expanded, polar view. The opposite pole is exactly the same.

The anise tree is a shrub 6 to 10 ft. high, in swamps. Florida to Louisiana. It flowers early in spring, producing large, purple, nodding flowers.

Illicium religiosum (*I. anisatum* (L.) Sieb. & Zucc.) Shikimi, Japanese sacred anise tree. Grains indistinguishable from those of the preceding species, about 28 μ in diameter.

Shikimi is a small tree, native of Japan, occasionally cultivated in the southern part of the United States.

Illicium yunnanense Franchet. Grains uniform, oblately flattened and more or less three-lobed in outline, about 30.8 μ in diameter, tricolpate, with furrows long and tapering but not quite meeting at either pole, deeply sunken, imparting to the grain its three-lobed appearance. Furrow membranes marked with median linear thickenings throughout their length but with no indication of germ pores. Exine of the general surface uniformly reticulate, similar to that of the grains of *Schizandra* (Plate V, Fig. 10) but of heavier ridges and smaller and less angular lacunae.

I am unable to say whether or not the furrows of this grain are homologous with the long furrows of the two preceding species. The fact that they taper and do not meet at the poles suggests that they belong to the ordinary trischistoclasic system of the higher dicotyledons; but if this is so, the possession of such furrows by the grains of this species certainly denotes a very great

genetic difference between it and the preceding species. This matter deserves further investigation and could be determined by finding out the orientation of the grains in their tetrads—whether the furrows are so arranged that they bound the faces of contact or pass through their centers.

A shrub or small tree about 10 ft. high, with yellowish, fragrant flowers, native of China; it has been collected in and about Yunnan, Tsangshan range, between Tatzang and Hsiakuan.

SCHIZANDRA Michx. BAY STAR VINE

Grains generally uniform, oblately spheroidal, 22.8 to 28.5 μ broad and about 18 to 19 μ deep. Provided with *six* meridionally

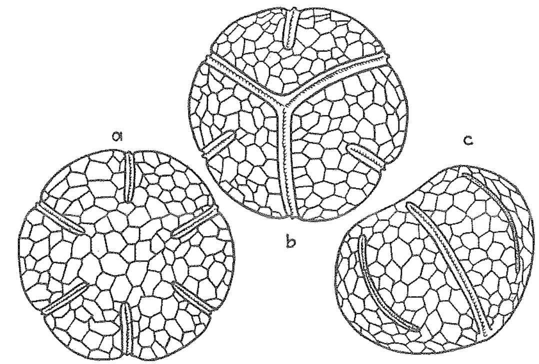

FIG. 93.—Pollen grain of *Schizandra chinensis* (*cf.* Plate V, Fig. 10); *a*, ventral; *b*, dorsal; *c*, side views.

arranged furrows; the whole surface adorned with a reticulate system of lacunae bounded by low, delicate ridges similar to those of the grains of *Illicium* but finer than in those of *Drimys*. The furrows are also the same as those of the grains of *Illicium floridanum* in their structure, their linear form, and the central thickening of the furrow membrane. They are sunken in the surface of the grain and, being perfectly symmetrical in arrangement, impart to it a six-lobed outline when seen in polar view.

The furrows are of two kinds: Three of them are long, fused at one pole and reaching in a meridional direction about two-thirds of the way toward the opposite pole; while the other three are short, ranged around the equator alternately with the three long furrows and also directed meridionally (Fig. 93). The short furrows are various in length in the different species but never meet at either pole, though they may approach as far as the long furrows toward the blank pole. Both kinds of furrow are exactly alike, in structure, differing only in their length. The long furrows appear to serve as lines of dehiscence, for the grains are frequently found breaking open along them, starting at the convergent pole, recalling the condition found in Pteridophyte spores.

When these grains expand and contract the furrows play no part in the volume-change accommodation; instead, the area about the blank pole dips in cup fashion when they dry and rounds out when they are moistened. The rims of the furrows are thickened, and the intine underlying them is also slightly thickened, rendering the furrows inflexible so that they act like the ribs of an umbrella, serving to prevent the bending in of the walls of the grain except in the region beyond their ends. The area that is permitted to invaginate is thus delimited by the ends of the furrows surrounding the blank pole. The surface of this flexible area is reticulate, as is the rest of the grain, but it is clearly defined and obviously functions as an expansion mechanism for the accommodation of changes in volume. It therefore seems justifiable to assume that it is homologous with the single furrow of the grains of *Drimys*. If this is so it then follows that the blank pole must have been distal and the convergent pole proximal in the tetrad, as is the case in fern spores, lending strength to the belief that the three long furrows are homologous with the triradiate crest of fern spores and therefore represent the boundaries of the three contact faces that the grain made with its neighbors of the tetrad; this being so, the three short furrows pass through the centers of the three contact faces and are therefore homologous, in position at least, with the three furrows of ordinarily tricolpate pollen grains and others of the trischistoclasic system among the dicotyledons. They do not function as furrows, either as expansion mechanisms or as places of emergence for the pollen tubes, the former function being retained by the area about the distal or blank pole, and the latter accomplished by dehiscence along the three long furrows at the proximal or convergent pole. In this respect this grain is anomalous but is of the utmost interest because it shows the spatial relation between the furrows of the trischistoclasic or linear stress system, the single furrow of the monocolpate grain of the lower gymnosperms, and the three lines of dehiscence or triradiate crest of the pteridophyte spore.

Schizandra is a genus of about six or seven twining woody vines, in China and Japan, one in the United States, others in tropical Asia and Himalaya. Several species are cultivated for their bright-green leaves and cup-shaped white or crimson flowers which are followed by scarlet, berry-like fruits in autumn.

The genus is said to be an "anomalous member of the family" (Bailey 1924), but it is very closely related to *Kadsura* with which its pollen grains are identical. The similarity of its pollen grain, to that of *Illicium* and possibly to a certain extent of *Drimys* is also evidence of its genetic relationship with them.

Schizandra chinensis K. Koch. (Plate V, Fig. 10) type. Grains as in the generic description, uniform, 21.6 μ in diameter, short furrows not extending noticeably farther toward the blank pole than toward the convergent pole, thus approximately bisected by the equator.

A twining shrub, China and Japan. Flowers in May and June.

Schizandra coccinea Michx. Bay star vine. Grains uniform, 25 to 28 μ in diameter. The short furrows do not extend quite so far toward the convergent pole as toward the blank pole, thus are not bisected by the equator. The thickened rim of both the long and short furrows is a little broader than in the previous species.

A slender, high-climbing woody vine with monoecious crimson-purplish flowers and scarlet berries; in woods; South Carolina to Florida to Louisiana. Flowers in spring and summer.

Schizandra Hanceana Baill. (*Kadsura chinensis* Hance, *K. japonica* Benth.). Grains as in the type, uniform oblately spheroidal, about 24 μ in diameter. All six furrows end evenly around the area at the blank pole. The short furrows do not extend quite so far toward the convergent as toward the blank pole so are not bisected by the equator.

A woody climber, native of China and occasionally cultivated in the warmer parts of Europe.

KADSURA Juss.

Grains as in the *Schizandra* type, except for minor specific differences, showing less deviation from the type than is found within the genus *Schizandra* itself.

Woody climbers with mostly leathery leaves and axillary, rather inconspicuous, whitish or rose-colored flowers. Native of tropical Asia. Though the flowers are not showy, some species are cultivated for the beauty of their dark-green lustrous leaves and clusters of scarlet fruit in autumn.

Kadsura peltigera Rehder & Wilson. Grains as in *Schizandra* type, uniform, 25.1 to 26.2 μ broad and 18 μ deep. All six furrows end evenly around the area at the blank pole. The short furrows extend about as far toward the convergent pole as toward the blank pole, so that they are approximately bisected by the equator.

Climbing shrub 8 to 12 ft. high with solitary, axillary yellow flowers, about 2.5 cm. broad.

In forests in Kiangsi and Yunnan, China.

Kadsura scandens Blume. Grains uniform, oblate spheroidal, 22.8 to 24 μ broad. Essentially as in the *Schizandra* type, except that the blank area about the distal pole is, on the average, a little larger in proportion to the size of the grain.

A climbing shrub reaching a height of 75 ft. in Java, Sumatra, and Borneo.

Kadsura paucidenticulata Merr. Grains uniform, oblate spheroidal, 23.9 to 25.1 μ broad, essentially as in the *Schizandra* type. Polar area rather larger, and short furrows shorter, extending farther toward the blank pole than toward the convergent pole.

A climbing shrub, native of the Philippines, similar to *K. philippinensis* Merr. and *K. Macgregorii* Merr., also inhabiting the same region.

Kadsura japonica Juss. Grains as in the *Schizandra* type, uniform, 22.1 to 22.8 μ in diameter; short furrows rather long and bisected by the equator.

Japan and eastern China.

NYMPHAEACEAE Water-lily Family

Grains of various size and shape, provided with a single large furrow which is nearly closed by an operculum of similar character to the exine of the general surface but separated from the latter by a narrow strip of thin, flexible exine which generally completely surrounds the operculum and functions as the furrow. Exine thin, of warty-granular texture, and generally provided with conspicuous spines or nodules of widely various character (Fig. 94; Plate VI, Figs. 1, 6).

Morphologically the ring-shaped band of thin exine together with the islet of thicker exine that it surrounds seems to be homologous with the furrow. That this is the proper interpretation is borne out by the fact that the detached piece of exine is usually slightly different in texture, sculpturing, and thickness from the general exine of the grain, recalling the difference in texture and thickness encountered between the furrow floor and the general exine of the grains of the Cycadales. Consequently I shall regard it in this light and, for the convenience of the present discussion, shall call the ring-shaped strip of thin exine the furrow ring; and the enclosed islet of thicker exine, which is homologous with the furrow floor of the grains of the primitive gymnosperms, the operculum (Fig. 94).

In the grains of *Castalia* (Plate VI, Fig. 1) the operculum is broadly elliptical or circular in outline and so large that it occupies most of the ventral half of the grain. In the grains of *Nymphaea* it is elongate and extremely narrow (Plate VI, Fig. 6). Though these two types of furrow are strictly homologous, mechanically they act quite differently, so that at first sight the two forms appear to bear no relation to each other. When the grain of *Castalia* dries the furrow ring permits the operculum to be drawn into the dorsal hemisphere, causing the grain to assume the shape of a round-topped bun. When that of *Nymphaea* dries, the long elliptical furrow, together with its operculum, is invaginated as if it were a simple elongate furrow, causing the grain to simulate the familiar boat-shaped form of the primitive gymnosperms, Magnoliaceae, monocotyledons etc. Nevertheless, the only truly morphological difference between the grains of *Castalia* and those of *Nymphaea* is in the shape of the furrow; in one it is short and broad, and in the other long and narrow. Functionally in both, the operculum insures complete closure of the furrow; it finds its functional analogy in the strip-like thickenings on the furrow membranes of the grains of some of the Nassauvineae (Wodehouse, 1929). Its morphological homology, however, is with the floor of the furrow of the grains of the primitive gymnosperms.

The pollen grains of the Nymphaeaceae have been described by many authors. Thus Fischer (1890) regards the grains of

Castalia as provided with a single lid, but those of *Nymphaea* he regards as provided merely with a single furrow. Bauer has shown "*Nuphar advena*" (*i.e.*, *Nymphaea advena*) as spherical and without any furrow. Heintze (1927), from evidence based partly on their pollen grains, associated the Nymphaeaceae with the Piperaceae and Magnoliaceae in his class Pseudo-dicotyledoneae, a group which seems to include most of the primitive dicotyledons.

The Nymphaeaceae are a family of aquatic plants with submerged or floating leaves and aerial flowers. Included in the family, besides the two genera treated here, are *Victoria* Lindl. *Euryale* Salisb. and *Barclaya* Wall., of which I have not been able to examine the pollen. According to Fischer (1890, page 62), however, the pollen of *Victoria regia* is similar to that of *Castalia*, except that its grains remain at maturity united in tetrahedral tetrads. They are smooth, and each has a single furrow occupying almost a half of its ventral side. From his description this form recalls in striking fashion the grains of *Drimys* among the Magnoliaceae.

Regarding the relationships of the Nymphaeaceae that are suggested by their pollen-grain forms, we have already seen that the Magnoliaceae, the several tribes of the Coniferae, and the monocotyledons (*e.g.*, the Palmaceae) inherited the broad, open, cycadean type of furrow, and each devised its own way of modifying, protecting, or eliminating it. Now, in the grains of the Nymphaeaceae, we see still another way of accomplishing the same end. Thus, as far as their pollen morphology is concerned, the Nymphaeaceae may represent a genetic line coordinate with the tribes of the Coniferales, the monocotyledons, and the lower dicotyledons.

Key to the Species

I. Furrow elongate, provided with a narrow operculum; exine finely warty-granular and covered with long, conical spines. Grains about 57 μ long. — Nymphaea advena

II. Furrow circular or broadly elliptical, occupying the major portion of the ventral side of the grain, almost completely closed by its operculum. Exine various.

- *A.* Exine bristly or nodular. Grains 30 by 28 μ. — Castalia odorata
- *B.* Exine nodular, not bristly.
  - 40 to 42 μ long. — Castalia flava
  - 34 to 38 to long. — Castalia mexicana
- *C.* Exine smooth. Grain 30 to 34 μ long. — Castalia amazonum, Castalia gracilis

Nymphaea advena Soland. (*Nuphar advena* Ait.) Yellow pond lily (Plate VI, Fig. 6) type. Grains rather uniform, about 51.3 μ long, provided with a single, longitudinal furrow closed by a narrow, linear operculum. Exine heavy, slightly granular, with long, sturdy, and obtusely pointed spines which are longer on the dorsal than on the ventral side, varying from 5 to 8.5 μ in length, irregularly arranged.

When dry the grains are more or less boat-shaped, with the furrow tightly closed and somewhat invaginated. When moistened the furrow becomes evaginated, causing the grain to assume an oblate spheroidal form, with the furrow extending a little less than half around it on the ventral side. In this condition the furrow can be seen to be provided with a narrow strip of exine, which is the operculum, of a texture similar to that of the rest of the grain but bearing spines a little shorter.

Nymphaea advena is an aquatic herb with floating leaves, submersed leaves seldom present, and large, showy yellow flowers appearing in June and July. Nova Scotia to the Rocky Mountains and southward to Florida, Texas, and Utah.

The flowers are insect pollinated but shed large amounts of pollen, which, when found in Postglacial silts, can easily be identified and is valuable in showing the local conditions under which such deposits were laid down, since its mode of pollination precludes the likelihood of its being transported far from its place of origin in effective quantities.

In his studies of the pollen grains of ancient sediments, Meinke (1926) has depicted this grain and states that the spicules are fairly far apart and that the surface between them is reticulate. Such a reticulate appearance of the exine I find tends to develop upon drying after being soaked in water; therefore it cannot be regarded as a morphological character. Von Mohl (1835) illustrates the grain of *Nymphaea* and draws attention to the fact that it has a single furrow.

The genus comprises about eight species, of rather wide distribution in the North Temperate Zone, all rather similar in habit and appearance. Of these I have examined the pollen of

N. hybridus and *N. bombacini* but was unfortunately not able to procure material in condition suitable for detailed studies. However, their grains appear to be the same as those of *N. advena* described on page 343.

CASTALIA Salisb. WATER LILY

Grains dome-shaped, 30 to 46 μ in diameter, monocolpate, with a large, circular or broadly elliptical furrow occupying the greater part of the ventral surface and almost completely closed by an operculum. Exine warty-granular and provided with rounded nodules and conspicuous spines extremely irregular in their size, shape, and arrangement, or smooth.

When moist and fully expanded the grains are approximately globular but slightly flattened on the ventral side and slightly elongate, with the furrow ring broad and encircling the grain

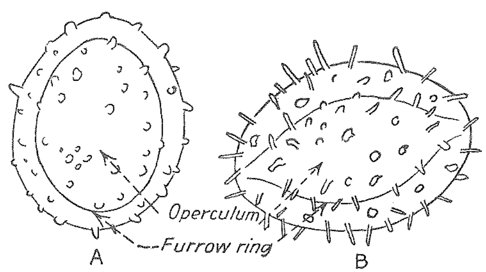

FIG. 94.—Pollen grain of white water lily, *Castalia odorata*, ventral view: *A*, a grain with its operculum completely surrounded by a furrow ring; *B*, with its operculum joined at the two ends to the general surface of the exine.

just below the equator. In this condition the large operculum occupies the major portion of the ventral side. When dry and contracted the operculum is drawn tightly inward and more or less flattened, but the dorsal part of the grain retains its spherical curvature. The grain in this condition suggests the appearance of a turtle with its appendages withdrawn. Underlying the margins of the furrow is a subexineous thickening which calls to mind the thickened furrow rim of the grains of *Podocarpus*, with which it appears to be homologous. In the grain of *Nymphaea* this rim furnishes a sort of seat for the operculum in its valve-like action in closing the orifice of the furrow.

When observed from the ventral side in the contracted condition (Fig. 94*a*) the grains may present a more or less circular outline, the invaginated furrow appearing as a smaller and complete circle, concentric with the periphery of the grain; but more often the grains in this condition are broadly elliptical in outline, in which case the furrow ring may be discontinuous, leaving the exine of the operculum connected with that of the general surface of the grain through two isthmuses (Fig. 94*b*). Such a furrow recalls that of the grains of the cycads and Bennettitales, and is further evidence that the operculum of the grain of *Castalia* is homologous with the furrow floor of the ancient cycadean type of pollen grain.

The pollen grains of *Castalia*, on account of their large size and characteristic appearance, are easy to recognize and yield valuable data in paleoclimatic studies. They have been studied by many investigators and variously interpreted. Meincke (1927) describes them as spiculed on one side and bulging and smooth on the other, one-half seeming without spicules. A grain stated to be that of *Castalia* in the fossilized form is illustrated by Lewis and Coke (1929), but their figure, which shows a grain with regular conical spines evenly distributed in serried ranks over its surface and with a single longitudinal furrow, precludes the possibility of its being that of *Castalia*. If the spines of their figure were a little less uniform in their arrangement, it would suit, however, the grains of *Nymphaea*. Grains of *Castalia Lotus* are illustrated in both the wet and dry condition by von Mohl (1835) and show admirably the mechanism whereby harmomegathy takes place. Hugo Fischer (1890) includes the grains of *Castalia* in his group of "grains with a single lid."

Castalia odorata (Soland.) Woodv. & Wood (*Nymphaea odorata* Soland.) White water lily, Water nymph (Plate VI, Fig. 1) type. Grains about 30 by 38 μ.

The entire surface is generally covered with long, conspicuous spines or with rounded, wart-like protuberances or both. The spines are unique: they have a resinous appearance and, when they reach their best development, are long, straight, cylindrical rods, not tapering but maintaining their full diameter almost or quite to their tips, which are generally rounded but may be truncated squarely or obliquely or bluntly pointed. They are set on the surface of the grain at all possible angles and are often extremely oblique. They are never uniform, in spacing, shape, or length, differing in these respects markedly from the spines encountered in the grains of most other plants. Sometimes they are well developed throughout the grain, imparting to the whole surface, except for the furrow ring which is always smooth, a bristly appearance, but nearly always they are better developed on the dorsal surface than on the ventral, and frequently on the operculum they are represented only by little wart-like nodules. When examined with high magnification the nodules have an appearance suggestive of spines that have been melted down and spread out into resinous-like lumps. But within the same flower may be found grains that are entirely spine covered and others that are entirely nodular.

Castalia odorata is an aquatic herb with submerged and floating leaves and aerial flowers, in ponds and slow streams. Newfoundland to Manitoba, southward to Florida, Louisiana, and Kansas. Flowers June to September. The flowers are entirely insect pollinated but shed large amounts of pollen.

Castalia flava (Leitner) Greene. Grains as in the type, except that they are provided with only poorly developed spines or are entirely nodular, 46.7 to 52 μ in diameter. The dorsal surface is generally covered with closely packed tubercles, but the operculum has only a few along its margin and is otherwise smooth.

An aquatic herb in lakes, lagoons, and slow streams. Florida. Flowers all summer.

Castalia zanzibarensis Casp. (*Nymphaea zanzibarensis* Casp.) Grains various in size, many empty and abortive, about 40 by 37.5 μ. Exine nodular, without spines.

Tropical Africa.

Castalia mexicana Zucc. Yellow water lily. Grains in general shape as in the type but without spines, 37.5 by 41 μ. Exine warty, with irregularly shaped nodules on the dorsal surface, resembling droplets of varnish that form when applied to a glassy surface, but nearly or quite smooth on the ventral.

Mexico.

Castalia amazonum (Mart. & Zucc.) Britt. & Wilson. Grains as in the type, except that they lack all trace of spines, the texture of the exine being quite smooth throughout; uniform in size, about 33.5 by 29.6 μ.

Haiti, Puerto Rico, Trinidad, Cuba, Santo Domingo.

Castalia gracilis Rose. Grains as in the type, except that the texture of the exine is quite smooth throughout; uniform in size, about 30.8 by 27.5 μ.

Mexico.

SALICACEAE Willow Family

The family Salicaceae consists of the two genera, *Salix* and *Populus*, which are unquestionably closely related but differ from each other in their modes of pollination. All species of *Populus* are completely limited to wind pollination, while those of *Salix* are primarily insect pollinated. In keeping with this are found great differences between the pollen grains of the two genera, despite their close relationship. Those of *Salix* are tricolpate and heavily reticulate (Plate VI, Fig. 2), characters which we have seen are associated with insect pollination, and they show no considerable deviation from the basic dicotyledonous form, while those of *Populus* are nearly smooth and entirely without furrows (Plate VI, Fig. 4), characters which we have seen are distinctly anemophilous.

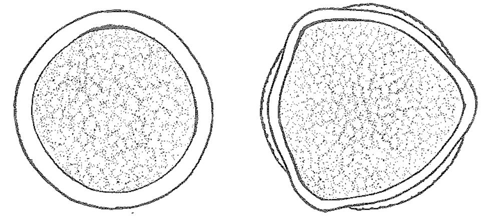

Fig. 95. Fig. 96.

Fig. 95.—Pollen grain of *Populus nigra*, optical section.
Fig. 96.—Pollen grain of *Salix fragilis*, optical section in the plane of the equator.

The exine of the grains of *Salix* is thick, and this together with its heavily reticulate surface imparts to their walls considerable rigidity (Fig. 96). Associated with this are well-developed furrows which function as harmomegathi, opening and closing freely in response to the volume changes of the grain. The pattern of the reticulum is of a type found in the grains of many other species in widely separated groups. Its lacunae are rather large and angular, and their ridges high. The character of the mesh has a tendency to vary in different parts of the grain. Generally it is most open in the middle of the lunes, and closer toward the poles and toward the margins of the furrows along which it ends abruptly with closed lacunae, showing that the furrow is not torn through the reticulum but is developed simultaneously with it as a co-ordinate structure.

In the pollen grains of the poplars, in association with their mode of pollination by wind, the reticulum of the exine is either completely lacking or only barely recognizable, but there is some variation in this among the different species. Accompanying the reduction in thickness of the exine has gone the disappearance of furrows, which are entirely lacking in all species of *Populus*. The exine, however, is marked all over by small rifts, as if it were inelastic and too small to cover the grain as it attained its full size, an appearance which suggests that the exine of *Populus* is a vanishing structure.

There are grounds, other than the evidence of their pollen grains, for believing that the willows are in the transition stage in their mode of pollination, developing in the direction of anemophily. This is suggested by the arrangement of their flowers in catkins with both the anthers and styles exserted and by the separation of sexes and the abundance of their pollen which is blown freely about in the air. The opposite interpretation has been placed on these facts by Arber and Parkin (1907), who regard "*Populus* as the older genus and *Salix* as derived from a poplar-like ancestor at a more remote period," believing that "entomophily in *Salix* is but a recently acquired character." If Arber and Parkin's interpretation is correct and the tendency is toward entomophily, the pollen grains of *Salix* must have greatly outstripped the other characters of the plants in their evolutionary processes, becoming completely entomophilous even before the flowers themselves, a supposition which is highly improbable because, in evolutionary processes, the pollen grains are notoriously inert, generally lagging far behind the other organs of the plant. It seems to me much more likely that both *Salix* and *Populus* are derived from some willow-like ancestor which was entomophilous and that, while the poplars have become entirely wind pollinated, the willows have not yet proceeded far enough toward anemophily to effect any characteristic modification in their pollen grains.

Key to the Species

I. Grains spheroidal or oblate, about 17 to 18 μ in diameter, generally with three furrows or occasionally other numbers in the trischistoclasic system. Exine heavily reticulate. — Salix fragilis; Salis discolor

II. Grains spheroidal or somewhat irregular, 24 to 37 μ in diameter, exine thin, scarcely reticulate, acolpate.
- *A*. Exine fragmentary or broken by rifts. — Populus Sargentii; Populus Fremontii; Populus balsamifera; Populus Eugenei; Populus nigra
- *B*. Exine continuous, not broken by rifts. — Populus grandidentata; Populus MacDougalii; Populus angustifolia

SALIX (Tourn.) L. Willow, Osier

Grains spheroidal, flattened, three-lobed, or, when dry, ellipsoidal; about 17.8 μ in diameter; prevailingly tricolpate. Exine reticulate, with sharply angular lacunae and vertical ridges which are thin and blade-like on their crests but thickened toward their bases (Plate VI, Fig. 2).

The mesh of the reticulum is generally coarser toward the centers of the lunes, finer toward the poles, and sharply bounded along the margins of the furrows with much smaller lacunae. The furrows are long and tapering, their membranes flecked as if covered with detached fragments of the reticulum, without a true germ pore but generally with a central bulge representing the point of emergence of the pollen tube.

The genus comprises about 150 species of trees and shrubs in nearly all moist temperate regions and well up into the Arctic Circle. Some of the species flower very early in spring, long before the first appearance of the leaves, while others flower at the same time as the unfolding of the leaves, and still others after the leaves are fully developed. Thus in many localities the different species of willow flower throughout a period extending over several months. They are obviously primarily insect pollinated, since the flowers are provided with nectar and sweet scent, and they succeed in attracting many bees and other insects. Nevertheless, the pollen of willows can be caught on atmospheric pollen slides in considerable quantities during the flowering period, and sometimes it becomes an important factor in hayfever; the pollen of *S. lasiolepis* is said by Chamberlain (1927) to be a common cause of hayfever in Oregon. On the whole, however, experience indicates that the willows can be regarded as only relatively unimportant in hayfever.

Willow pollen is frequently found in Postglacial silts. In this connection the pollen of *Salix repens* has been described and illustrated by Erdtman (1923), and that of *S. serecia* by Sears (1930). Pollen grains of unnamed species are illustrated by Docturowsky and Kudrjaschow (1923) and by Meinke (1927), the latter author drawing attention to their resemblance to the grains of *Fraxinus* and *Adoxa*. Fossilized pollen of willow is described and illustrated by Lewis and Coke (1930), who found it in the Dismal Swamp peat of Virginia and North Carolina at all levels, though the trees are nearly absent from the region at the present time. In his studies of the pollen carried by bees, Høeg (1924) was able to recover willow pollen occasionally from bees collected in Novaya Zemlya, and he also found that it was the pollen most frequently occurring on bees from Ellesmere Land (1929).

Salix fragilis L. Crackle willow (Plate VI, Fig. 2) type. Grains slightly oblate or spheroidal; tricolpate; uniform; about 17.8 μ in diameter; otherwise as in the generic description.

A large tree introduced from Europe but now widely distributed throughout much of the eastern part of the United States, generally along the borders of streams. Flowers in May at the time when the leaves are unfolding.

Salix discolor Muhl. Pussy willow. Normal grains spheroidal or slightly oblate; about 17.6 μ in diameter. There are always some giant grains with six or four furrows and others that are entirely irregular.

A shrub or occasionally a small tree of moist places, consisting of several races. Flowering very early in spring—March to May—before the first appearance of the leaves. Nova Scotia to Saskatchewan, Delaware, and Missouri.

POPULUS (Tourn.) L. Poplar, Cottonwood, Aspen

Grains spheroidal or somewhat irregular in shape, 24 to 37 μ in diameter, acolpate, *i.e.*, without germinal furrows in the ordinary sense. Exine extremely thin, sometimes even fragmentary, minutely reticulate, or granular in appearance. Intine thick.

The only resemblance that these grains bear to those of *Salix* is in the vaguely reticulate character of their exine. The latter is apparently a vanishing structure; in the pollen of some species it is not even a continuous coat, but is marked by a number of

rifts irregular in size, shape and arrangement, and which give the impression of having been torn through the exine with the expansion of the grain, yet they are found as readily when the grains are dry and unexpanded as when moist and expanded. The absence of true furrows is a necessary corollary to the thinness of the exine; we have already seen that the formation of furrows is the result of stresses, and such an exine as this is too weak to transmit stresses. Moreover furrows are not needed to permit either pollen-tube emergence or volume-change accommodation in the presence of such a flexible and easily ruptured exine. The extreme thinness of the exine appears to be compensated by a corresponding increase in thickness of the intine which is uniformly much thicker than that of the grains of *Salix*.

The condition encountered here is an example of a principle of broad application. That is that pollination by wind tends to bring about a reduction of the exine with an attendant loss or reduction of its structures such as furrows, pores and sculpturing, and this tends to be compensated by an increase in thickness of the intine. A similar condition is found in the grains of *Fraxinus*, for example. *Fraxinus* is wind pollinated while belonging to a family of otherwise insect-pollinated plants, and its pollen grains have exines greatly reduced in thickness and intines greatly thickened as compared with those of other members of the family. We have already seen that pollination on or under water also tends to bring about a reduction of the exine, but in this case it is not attended with a corresponding increase in thickness of the intine. Many of the Gymnosperms, which are all wind pollinated, have developed this type of pollen grain. For example the pollen grains of the Taxodineae and Cupressineae have deviated far from the basic primitive form of the gymnosperms and developed a form of grain not unlike that of the poplars.

The poplars are mostly large trees, highly specialized in their adaptation to wind pollination, shedding huge quantities of light, air-borne pollen early in spring before the leaves unfold. In many regions where the trees are abundant they cause much hayfever. Thus *P. deltoides* is said to cause hayfever in Oklahoma (Balyeat, 1926) and in Colorado is credited with about 19 per cent of the hayfever cases (Mullen, 1922), while other species are important in Oregon (Chamberlain, 1927) and Colorado (Waring, 1926). Still other species will be mentioned under their descriptions.

It is stated by Waring and Pope (1927) that the "cotton"—the copious tomentum borne by the seeds—of the cottonwood trees is a factor in hayfever. This assertion is based upon experimental results obtained with seven hayfever patients in the neighborhood of Denver, Colorado, who gave positive skin tests to the cotton. The species employed are not definitely stated, but *P. balsamifera*, *P. angustifolia*, *P. deltoides*, *P. nigra* var. *italica*, and *P. Sargentii* are mentioned as the species probably producing the cotton in the air at the time when the symptoms of hayfever were manifest. On the other hand, it is emphatically denied by Phillips in Arizona (1923, p. 274) that the cotton of cottonwood trees can cause hayfever. He likewise does not state which species, but it appears that he had reference, at least in part, to *P. Macdougalii.*

The fragile and unresistant nature of the exine of poplar pollen grains renders it doubtful if they can be recognized with any degree of certainty in peat deposits, but in this connection *P. deltoides* is described and figured by Sears (1930) and *P. tremula* by Docturowsky and Kudriaschow (1923).

Populus Sargentii Dode. Western cottonwood (Plate VI, Fig. 4) type. Grains all normal, uniform in size and shape, spheroidal, averaging about 27 μ in diameter. The surface texture would be described as scurfy, but upon minute examination it is found to be derived from a broken or fragmentary reticulum, though this is less apparent in this species than in some of the others. Otherwise as in the generic description.

A large tree in semiarid regions, shedding much pollen very early in spring. It has been found to give marked reactions with hayfever patients and causes some hayfever in regions where abundant, more so than *P. angustifolia* (Hall in Scheppegrell, 1917). Flowers in March and April. Saskatchewan to North Dakota, Nebraska, Kansas, and New Mexico.

Populus Fremontii S. Wats. Fremont's cottonwood. Grains all normal and nearly uniform, averaging about 25.3 μ in diameter. The reticulum of the exine is exceedingly fine but is more easily seen than in the type and, though much broken by irregular rifts, does not present a scurfy appearance. Otherwise as in the type.

A large tree. Flowers very early in spring; throughout western California and Lower California. Exists in several varieties, some of which are planted as shade trees in California, where they are known to produce hayfever (Selfridge, 1920).

Populus MacDougalii Rose California cottonwood. Grains variously irregular in size and shape, many abortive, suggesting hybridity of origin; normal grains averaging about 36.4 μ in diameter. Surface reticulum slightly more marked than in the other species and without rifts. Otherwise as in the type.

A large tree in semiarid regions. Sheds much pollen very early in spring, causing some hayfever starting about Feb. 1 (Phillips, 1923). Abundant on the Colorado River delta, parts of California, Nevada, and Arizona. It is doubtful if this species is distinct from *P. Fremontii* S. Wats. It should probably be regarded as a variety of the latter.

Populus grandidentata Michx. Large-toothed aspen. Grains uniform in size and apparently nearly all normal, but irregular in shape, about 28.9 μ in diameter. They differ from the type in the extremely fine reticulate pitting of their exine which also lacks the rifts that are characteristic of the type.

A large tree flowering in April. Nova Scotia to Ontario and Minnesota. South to Delaware, North Carolina, and Tennessee.

Populus nigra L. Black poplar. Grains nearly all perfect. Spheroidal, averaging 24.4 μ in diameter. Exine covered by an extremely fine reticulum, more apparent than in the type and more suggestive of the pattern of *Salix*, broken by irregular rifts. Figured by Meinke (1927).

This species consists of several varieties and is perhaps better known in the variety *italica* Du Roi, Lombardy poplar, naturalized from Europe and much planted. Flowers in April and May.

Populus angustifolia James Narrow-leaved cottonwood. Grains mostly normal and uniform but generally accompanied by some that are abortive. Spheroidal, averaging about 25.7 μ in diameter. Surface reticulum coarser and not broken by rifts. Otherwise as in the type.

A large tree in moist soil, especially along streams. Flowers in April and May, before the opening of the leaves. Assiniboia to South Dakota, Nebraska, New Mexico, and Chihuahua. Is said to cause some hayfever in California, though less than *P. Sargentii* (Hall in Scheppegrell, 1917).

Populus balsamifera var. **virginiana** Sarg. (*P. deltoides Marsh.*) Necklace poplar. Grains irregular in size, many abortive. The normal grains average about 34.5 μ in diameter. Exine clearly reticulate. Otherwise as in the type.

A common tree, frequently planted about cities and probably responsible for some hayfever. Quebec to Manitoba, south to Connecticut, Florida, and Tennessee. Flowers April and May.

Populus Eugenei Simon Louis Carolina poplar. The pollen of this species is conspicuous for its large proportion of abortive grains constituting more than half of it. Normal and apparently healthy grains range in size from about 34.7 to over 40 μ in diameter, averaging about 36 μ. The texture of the exine is extremely fine, and reticulate markings cannot be discerned with certainty, but it is marked with rather conspicuous rifts. Otherwise as in the type.

A large tree, originated as a hybrid in cultivation and exists only in the male form; much planted about streets in cities. It sheds large amounts of pollen very early in spring but is not known to cause hayfever.

JUGLANDACEAE Walnut Family

The pollen grains of the Juglandaceae are characterized by extreme simplicity. The exine is always thin and entirely lacking in sculpturing but is more or less granular in texture. In keeping with this they lack germinal furrows but have, instead, a varying number of pores which are always surrounded by subexineous thickenings. In form the grains are more or less oblately flattened and with a circular or angular outline, depending upon the number, arrangement, and character of the pores.

In the grains of *Juglans* and *Carya* the pores tend to be crowded into one hemisphere, leaving the opposite quite void of pores. For convenience I shall call the former the dorsal and the latter the ventral hemispheres. In these grains the subexineous thickenings are rather thin but of large extent. In those of *Juglans* they are generally discrete, though they may touch each other, but in those of *Carya* the subexineous thickenings are completely fused except *C. Pecan*, over the whole of the dorsal hemisphere and encroach part way on to the ventral but always leaving a large area of the latter free of thickenings. When the grains dry and shrink they become invaginated on the ventral side,

the unthickened area dipping inward and causing the grain to assume a cup shape. When they expand they become oblate-spheroidal or almost quite spherical through the bulging out of the ventral concavity. Immediately underlying this area is a large, globular, hyaline mass (Fig. 98), and it is principally to the contraction and expansion of this that the cupping in and bulging out of the ventral surface are due.

The grains of *Pterocarya*, *Platycarya*, and *Engelhardtia* have the pores equatorially arranged and show no distinction between the dorsal and ventral hemispheres. The subexineous thickenings surrounding the pores in the grains of these three latter genera are less extensive but more abruptly thickened and cause the pores to protrude, giving the grain an angular outline. These grains closely resemble those of the Betulaceae and, to a lesser extent, those of some species of the Urticaceae, such as *Momisia*. Indeed, it is often difficult to distinguish the species of these three families.

The Juglandaceae are represented in North America only by *Juglans* and *Carya*, the others being tropical and subtropical, but the remains of all five genera are found in North American Tertiary deposits. All are wind pollinated and shed enormous quantities of pollen, and several species of *Juglans* and *Carya* are known to cause some hayfever.

Key to the Species

I. Pores more or less confined to one hemisphere.	
A. Pores more than 3, their subexineous thickenings not fused. Grains conspicuously flattened dorsiventrally. 34 by 29.5 μ to 41.6 by 38.2 μ.	*Juglans*
1. Pores 11 to 15 (most grains with 12), elliptical. Texture granular.	
Pores 12 or rarely 13; texture fine.	J. nigra J. major
Pores 11 to 15 (most grains with 12). Texture coarse.	J. californica
2. Pores various in number, only occasionally 12; apertures nearly or quite circular. Texture fine-granular or smooth.	
Pores 6 to 16, grains about 41.6 by 38.2 μ, fine granular.	J. regia
Pores 5 to 9, grain about 35.3 by 33.3 μ, smooth.	J. cinerea.

B. Pores generally 3, occasionally some grains with 4 or 6. Grains nearly or quite spherical, 40 to 52 μ in diameter.	*Carya*
1. Subexineous thickenings separate, texture coarse-granular.	C. Pecan
2. Subexineous thickenings united, covering more than half the surface of the grain.	
About one-half of the grains with 4 germ pores.	C. glabra
Nearly all grains with 3 germ pores.	
Grains 52 by 45 μ.	C. minima
Grains 40 by 46 μ.	C. ovate, C. alba, C. myristicaeformis
II. Pores equatorially arranged. Grains angular in outline, with the pores at the angles.	
A. Pores 3 to 7, generally more than 3. Subexineous thickenings of small extent. 26 to 35 μ in diameter.	Pterocarya hupehensis, fraxinifolia, Paliurus, stenoptera
B. Pores always three. 14 to 22 μ in diameter.	
1. Pores slit-shaped; exine conspicuously warty-granular. About 14 μ in diameter.	Platycarya strobilacea
2. Pores elliptical to circular. Exine faintly granular. 19 to 22 μ in diameter.	Engelhardtia spicata

JUGLANS J. WALNUT

Grains, when expanded, decidedly flattened, oblate-spheroidal, 34 to 42 μ in diameter. Pores elliptical to circular, 2.3 to 3.3 μ in length, always surrounded by subexineous thickenings which are generally discrete, though they sometimes touch and are occasionally even partly fused with each other. There are always more than 3 pores (about 6 to 15) confined mostly to the dorsal hemisphere (Fig. 97) and, though encroaching somewhat upon the ventral, always leaving the greater part of it free. The orientation of the pores is not fortuitous but depends upon their number and relative positions and is so ordered that the long axes of their apertures tend to converge in twos or threes at angles of 120 deg., suggesting that their arrangement is according to the trischistoclasic system. The surface texture of the exine is more or less granular.

The pollen of the walnuts is frequently caught on atmospheric pollen slides and is known occasionally to cause hayfever (Hall, 1922). In its fossil form it has been recorded from the Green River oil shales (Wodehouse, 1933*a*) and from Postglacial silts and has been illustrated in this connection by Erdtman (1927).

Juglans nigra L. Black walnut (Fig. 97; Plate VI, Fig. 9) type. Grains 34.2 to 30.8 μ in diameter. Germ pores elliptical, 12 or occasionally 13, about 2.85 μ in length, confined to an area covering a little more than the dorsal hemisphere, generally more or less regularly arranged; in the typical arrangement three of the pores are found around the dorsal pole with their long axes directed tangentially, *i.e.*, according to the sides of an equilateral triangle, and the remaining pores spaced at slightly unequal intervals on a circle slightly above the equator and so oriented that their long axes converge in pairs (Fig. 97). The exact relation of these with the three pores below them is virtually impossible to determine, because the apertures are too nearly circular to enable the direction of their axes to be discerned unless observed in nearly full view. Nevertheless, they appear to be arranged in the trischistoclasic system. Texture finely granular.

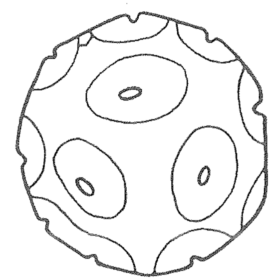

FIG. 97.

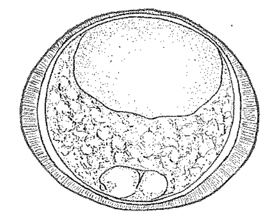

FIG. 98.

FIG. 97.—Pollen grain of *Juglans nigra*, diagram of dorsal surface (*cf.* Plate VI, Fig. 9).

FIG. 98.—Pollen grain of *Carya Pecan*, optical section passing through the ventral and dorsal poles, at the top and bottom respectively.

A large tree flowering in May. Ontario to Florida and westward to Minnesota, Nebraska, and Kansas. It sheds large quantities of pollen which in my own experience and that of Duke and Durham (1928) is frequently caught on pollen slides but is not known to cause hayfever.

Juglans major (Torr.) Hell. Arizona walnut, Nogal. Grains as in the type, apparently offering no distinguishing features.

Southern New Mexico, Arizona, and Colorado. Not known to cause hayfever.

Juglans californica S. Wats. California black walnut. Germ pores 11 to 15 but generally 12, more or less regularly arranged, texture coarsely granular, almost papillate. Otherwise as in the type.

A large tree, flowering in March and April, in southern California coastal region where it is known to be an important cause of hayfever (Hall, 1918) and is said to be the most important tree in this respect within its restricted range (Selfridge, 1920).

Juglans cinerea L. Butternut. Grains spheroidal, uniform in size, averaging 35.3 by 33.5 μ. Germ pores 5 to 9, their apertures more or less circular, averaging 3.9 μ in diameter, irregularly arranged around the equator and in the dorsal hemisphere. Texture smooth.

May. New Brunswick to Georgia and westward to Minnesota and Arkansas. Sometimes regarded as a contributory cause of hayfever.

Juglans regia L. English walnut. Grains uniform, oblate-spheroidal, 41.6 by 48.2 μ. Germ pores 6 to 16, with their apertures more or less circular, irregularly arranged, 3.3 μ in diameter, crowded more or less into one hemisphere. Texture nearly or quite smooth.

A large tree extensively cultivated in California but not believed to cause hayfever.

CARYA Nutt. Hickory

Grains spheroidal or oblate, less flattened and larger than those of *Juglans*, 40 to 52 μ in diameter. Germ pores generally three (occasionally some grains with four or six), apertures short, elliptical, or nearly circular, 3.4 to 5.7 μ in diameter, equally spaced on a circle a little dorsad of the equator and with their axes directed meridionally or, when there are four or six pores, converging at angles of approximately 120 deg. Subexineous thickenings greatly extended and completely fused, except in *C. Pecan*. Texture fine-granular or smooth.

These grains are easily distinguished from those of *Juglans* by their fewer germ pores and their larger size. The trees are dioecious and shed large amounts of pollen in late spring, of doubtful importance in hayfever. The pollen has been shown to occur in abundance in the Dismal Swamp peat (Lewis and Coke, 1930). In the fossilized condition it can readily be distinguished by the three large germ pores in one hemisphere.

Carya cordiformis (Wang.) K. Koch (*Hicroia minima* Britt.) Bitternut (Plate VI, Fig. 8) type. Grains various in size, and some abortive. Normal grains oblate-spheroidal to nearly or quite spheroidal, averaging 52.4 by 45.6 μ. Pores three or, in some grains which may or may not be considerably larger than normal, four, equally spaced just dorsad of the equator, apertures circular or broadly elliptical, averaging 5.24 μ in diameter; the subexineous thickenings completely fused and extending over the whole surface of the grain, except a small area at the ventral pole. Texture slightly granular.

May. Eastern and central United States and Canada. Of doubtful importance in hayfever.

Carya glabra (Mill.) Spach Sweet pignut. Essentially as in the type, except that the grains are somewhat smaller—44.8 by 38.7 μ—a large proportion have four pores, and a few, which are always giants, have six. Apertures slightly elongate, 4.56 μ in length. When three they are meridionally arranged with their long axes converging toward the poles; but when four, converging in pairs.

May. Eastern and central United States and Canada. Of doubtful importance in hayfever.

Carya alba (L.) K. Koch Mockernut. Grains nearly spheroidal, 40.3 μ in diameter. Pores always three, with their apertures more or less elliptical, 4.5 μ in length. Texture slightly granular. Otherwise as in the type. Massachusetts, Florida, eastern Texas, Ohio, southwestern Ontario.

The most abundant hickory of the southern states. Of doubtful importance in hayfever.

Carya ovata (Mill.) K. Koch Shagbark hickory. Grains uniform spheroidal, 42 μ in diameter. Germ pores three (occasionally four, and such grains are not giants); apertures elliptical, 4.5 μ in diameter. Texture slightly granular. Otherwise as in the type. May. Northeastern United States and Canada. Of doubtful importance in hayfever.

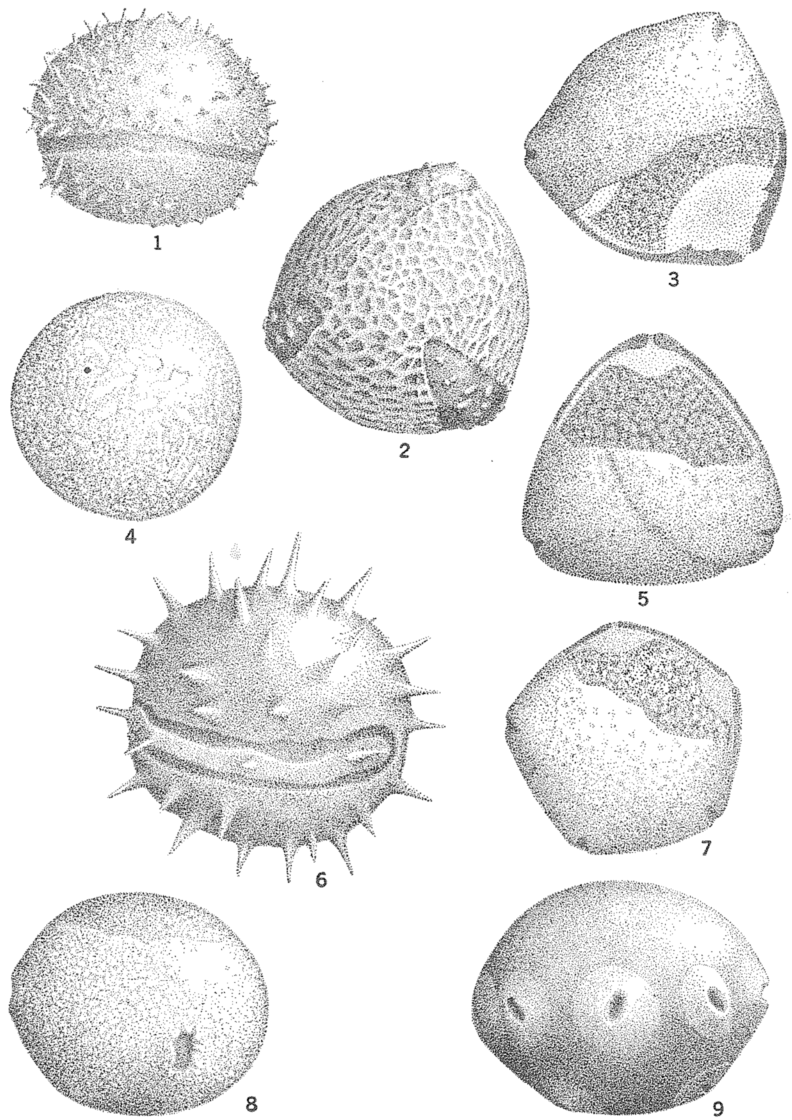

PLATE VI.—Pollen grains of Nymphaeaceae, Salicaceae, and Juglandaceae. 1, *Castalia odorata*, side view, expanded, 30 μ in diameter. 2, *Salix fragilis*, polar view, expanded, 27 μ in diameter. 3, *Engelhardtia spicata*, polar view, 20 μ in diameter. 4, *Populus Sargentii*, 27 μ in diameter. 5, *Platycarya strobilacea*, 14 μ in diameter, upper portion shown in optical section. 6, *Nymphaea advena*, ventral view, expanded, 51 μ in diameter. 7, *Pterocarya hupehensis*, polar view, 30 μ in diameter, upper part shown in optical section. 8, *Carya cordiformis*, side view, 52 μ in diameter. 9, *Juglans nigra*, side view dorsal side uppermost, 34 μ in diameter.

Carya myristicaeformis (Michx.) Nutt. Nutmeg hickory. Grains uniform, slightly flattened, 45.6 by 41 μ. Germ pores circular or broadly elliptical, 5.7 μ in diameter. Texture slightly granular. Otherwise as in the type.

Southern Arkansas and adjoining states, where it is believed to be a minor cause of hayfever.

Carya Pecan Asch. & Graeb. Pecan (Fig. 98). Grains uniform, spheroidal, 44.4 μ in diameter. Germ pores three, their apertures elliptical, 3.4 μ in diameter; subexineous thickenings not fused but sometimes touching. Texture decidedly granular, more noticeably so than in the other species of the genus. These two characters—the separate subexineous thickenings and granular texture—serve to distinguish the grains of this species from others of the genus and suggest a somewhat closer relationship of this species with *Juglans*.

Flowers April and May. Indiana to Iowa and Kansas, southward to Alabama and Texas. Known to cause some hayfever.

Engelhardtia spicata Blume (Plate VI, Fig. 3). Grains much flattened, uniform, 19.4 to 21.6 μ in diameter, triangular in outline. Pores three, one at each angle, aspidate, their apertures elliptical to circular, 2.6 to 3.4 μ long, their membranes smooth or slightly flecked; pore diagram similar to that of *Myrica* (Fig. 99*b*). Subexineous thickenings extending deeply into the cell below the pores. Exine faintly granular.

A large tree, native of Asia from the Himalayas to Java and the Philippines. The genus is now represented in America by *Oreomunnea* in the mountains of Central America, but during the Tertiary period it was widespread in both Europe and America. All species are wind pollinated and shed large amounts of pollen but are not known to cause hayfever.

Platycarya strobilacea Sieb. & Zucc. (Plate VI, Fig. 5). Grains much flattened, uniform, 14 μ in diameter, triangular in outline. Pores three, one at each angle, aspidate, their apertures slit-shaped, 2.3 μ long. Pore diagram as in *Corylus* (Fig. 99*c*). Subexineous thickenings beneath the pores shallow and not laterally extensive. Exine coarsely but faintly granular; always crossed by two grooves, one on each side at right angles to each other.

A small tree, native of Japan and northern China.

PTEROCARYA Kunth.

Grains much flattened, 27 to 34 μ in diameter, occasional grains much smaller. Pores 3 to 7, never constant in number, one at each angle, aspidate, their apertures elliptical, 3 to 4.6 μ long, arranged around the equator and meridionally oriented or converging in pairs alternately above and below the equator, occasionally variously irregular in arrangement. Pore diagram as in *Carpinus* (Fig. 99*d*). Subexineous thickenings beneath the pores shallow. Exine faintly granular.

The genus consists of a few species of trees in Transcaucasian Federation, China, and Japan but is abundantly represented in Tertiary floras of both Europe and North America.

Pterocarya hupehensis Skan. (Plate VI, Fig. 7) type. Grains 29 to 30.5 μ in diameter, generally five pored, occasionally four or six. Otherwise as in the generic description.

Tree about 30 ft. high, native of China in the province of Hupeh.

Pterocarya Paliurus Bat. Grains about 33.1 μ in diameter. Pores six, seven, or five; in grains with the higher numbers not generally strictly equatorially arranged. Otherwise as in the type.

Tree native of China in the mountains of Ning-po.

Pterocarya caucasica C. A. Mey (*P. fraxinifolia* Spach.). Grains 33 to 35.3 μ in diameter. Pores six or five or occasionally four. Otherwise as in the type.

A beautiful tree along the rivers and mountains of Caucasia.

Pterocarya stenoptera C. DC. Grains 26.2 to 30.4 μ in diameter. Pores six or five, occasionally three or four. Otherwise as in the type.

Tree, native of China.

BETULACEAE Birch Family

Grains smooth or only faintly granular, spheroidal or more or less oblately flattened, 20 to 40 μ in diameter, provided with three to seven germ pores which tend to be equally spaced around the equator. In shape the germinal apertures differ in the different species, being circular, elliptical, or slit-shaped. When elongate they are meridionally oriented—when there are three—or with their major axes converging in pairs when more

than three. The most distinctive character of these grains, however, is that their germ pores always protrude as rounded domes and give the grains an angular outline when seen in polar view. This character I have called "aspidate" owing to the resemblance of such a protruding pore to a small circular shield or *aspis*. The dome-shaped protrusions are due to a thickening of the intine underlying the region of the pore and frequently also to a lesser annular thickening of the exine.

All of these characters the grains of the Betulaceae share with those of the Myricaceae; *Myriophyllum* among the Haloragidaceae; *Platycarya*, *Engelhardtia*, and *Pterocarya* among the Juglandaceae; *Momisia* among the Urticaceae; and *Casuarina;* and they are also closely approached in the grains of *Broussonetia*, *Morus*, *Humulus*, and *Cannabis* among the Urticaceae. In fact the grains of the Betulaceae represent a form toward which those of many wind-pollinated species of diverse origins tend to approach. This together with a close intrafamily resemblance of the various genera makes the recognition of the pollen grains of the Betulaceae always difficult and occasionally uncertain. They can generally be distinguished, however, by certain minor characters which they possess individually.

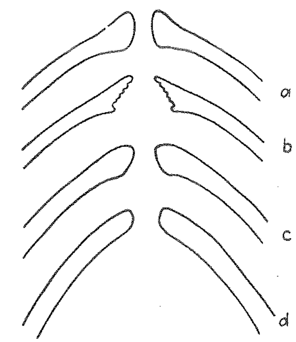

Fig. 99.—Pore patterns: *a*, broad-knob or *Betula* pattern; *b*, tarsus or *Myrica* pattern; *c*, club-shaped or *Corylus* pattern; *d*, unexpanded or *Carpinus* pattern.

One such character is found in the annular thickening of the exine surrounding the pore. When seen in optical section the germinal aperture appears as a gap at which the walls on either side end with knob-like thickenings. In fossil material the underlying layers are absent, leaving little or no trace of their former position; consequently in such material we need be concerned only with the structure of the outer layers.

Passing in review the grains of the various members of the Betulaceae and those of the families with which it is possible to confuse them, four fairly well-marked types of pore pattern may be distinguished. These are (1) the broad-knob or *Betula* pore pattern (Fig. 99*a*) in which the exine appears to end at the pore in a broad and abrupt expansion, and in grains with this type of pore pattern the pores are raised sharply above the surface of the grain. This pore pattern is characteristic of all species of *Betula*, *Myriophyllum*, and, with a slight modification toward the next type, of *Alnus;* (2) the tarsus or *Myrica* pore pattern in which the wall thickening suggests in appearance the terminal joint or tarsus of the hind legs of some insects (Fig. 99*b*). This pore pattern in its fullest development characterizes the grains of *Myrica* and *Comptonia* and is somewhat approached in those of *Engelhardtia* and *Alnus;* (3) the club-shaped or *Corylus* pore pattern (Fig. 99*c*) in which the exine is only slightly and gradually expanded at the pores. As a consequence the pores are only slightly raised above the surface. This characterizes the grains of *Corylus*, *Pterocarya*, *Platycarya*, *Momisia*, and, with a certain tendency toward the tarsus pattern, those of *Ostrya;* (4) the unexpanded or *Carpinus* pore pattern (Fig. 99*d*). In this the walls of the exine are not at all or only very slightly expanded at the pores. It must be admitted that the distinction between this and the previous pore pattern is often vague. This pore pattern characterizes the grains of *Carpinus* and, with a modification toward the tarsus type, those of *Engelhardtia*. Fortunately we are aided in the distinction of these two grains by the fact that that of *Carpinus* is the largest, while that of *Engelhardtia* is the smallest of all the grains possessing this pore pattern.

Jentys-Szafer (1928), after making extensive studies of the pollen of *Corylus*, *Myrica*, and *Betula*, describes the thickenings beneath the pores in all these genera as follows: "Sous l'exine, on voit s'étendre l'intine, mate et incolore, étroitmente accolée à la première; elle entoure le contenu du grain, à la surface duquel on distingue trois petites cuvettes caractéristiques qui se trouve au-dessous des pores." She finds that the grains of these three genera, though at first sight much alike, present certain differences which enable them to be distinguished, when they are caused to swell or disintegrate by treatment with sulphuric acid, dilute chromic, or potassium hydrate. By such means it can be shown that the exine of the grains of *Corylus* consists of five layers, two of which are rather thick and three very thin; while in the grain of *Myrica* one can recognize only three layers—one thick and two thin—yet the exine of the grain of *Myrica* is, in general, a little thicker than that of *Corylus*. She finds that these characters may be used in distinguishing the species in their fossil condition.

The *Betula* pollen grain may be recognized by the double nature of the exine around the pores, according to Dokturowsky and Kudrjaschow (1923). When seen in optical section, if the focus of the microscope is just right, they present the appearance of two serpents face to face with their mouths open ("deux gueules de serpent, ouvertes l'une en face de l'autre"). It is true that a similar appearance is produced in the grains of *Corylus* by appropriate focusing, but it is much less marked, and the lower jaws of the serpents are somewhat undershot.

Madame Szafer also shows that the pollen grains of the different species of *Betula* differ from each other in such minor characters as the thickness of the exine around the germinal apertures and in their sizes. The differences in size between the different species are slight, but if hundreds of grains are accurately measured and size-frequency curves plotted, each is found to have its characteristic shape. Such curves may be used to detect mixtures of different species of pollen in fossil material and give a fair estimate of the relative amounts of each.

The pollen grains of the Betulaceae are of frequent occurrence and well preserved in Postglacial silts, and in this connection the European species have been studied and described by many investigators. Docturowsky and Kudrjaschow (1923) give figures of *B. humilis* Schr., *B. verrucosa* Ehr., and *B. nana* L., which they point out may be distinguished from each other by their sizes. They find that there are minute but tangible differences between the species within the genera *Corylus*, *Betula*, and *Alnus* and give diagrams which bring out the differences. Erdtman (1923, 1927) illustrates a species of *Betula*. Von Mohl (1835) likewise illustrates a grain of *Betula*, describing the pores as "on the angles of the grain with large halos." Lewis and Coke (1929) illustrate fossil grains of *Betula*, *Alnus*, and *Myrica* and state, "The pollens of *Betula* and *Myrica* are much alike, though they may be distinguished with certainty in well-preserved specimens." Their figures of the fossilized remains of these grains show well-marked differences in outline which are by no means apparent in fresh material.

The Betulaceae are mostly dioecious trees or shrubs. They shed large quantities of light, air-borne pollen which is the cause of some hayfever in early spring. The pollen is found in large quantities in both recent and ancient bog deposits, and it is caught in great abundance on pollen slides exposed several miles from any trees.

KEY TO THE GENERA OF BETULACEAE AND MYRICACEAE

I. Germ pores mostly 3; a small proportion of the grains may have 4 or rarely more.
  A. Germinal apertures always more or less elliptical, equatorially arranged and equally spaced; some grains, which are generally giants, with 4 to 7 pores. Betula, Carpinus
  B. Germinal apertures generally not elliptical, though they may occasionally be so, mostly approximately circular or somewhat irregular.
    1. Germ pores mostly 3, equally spaced on the equator.
      Pores circular or slightly elliptic. Corylus
      Pores irregular in outline, tending to be circular. Myrica
    2. Germ pores 3 or 4 or, occasionally, 5, not equally spaced. Comptonia
II. Germ pores various in number, always a large proportion of the grains with 4, 5, or 6, elliptic.
  A. Grains without thickened bands connecting the pores; pores 3 or 4 (generally four in *Carpinus Betulus*); pore membranes marked by a central elongate thickening. Ostrya, Carpinus
  B. Grains with thickened bands connecting the pores; pores 4 or 5, rarely 6, their apertures narrowly elongate, their membranes without central thickening. Alnus

BETULA L. BIRCH

Grains flattened, angular, 20 to 40 μ in diameter (generally less than 27 μ); pores three, occasionally, in some grains, four and higher numbers up to seven, strongly aspidate and somewhat protruding, imparting to the grain its angular appearance. Exine slightly granular or nearly smooth. Pore pattern as in Fig. 99a.

Mostly large trees flowering in early spring a little in advance of the unfolding of the leaves. They shed enormous quantities of light, wind-borne pollen which is one of the most prevalent causes of hayfever of the early spring type, in the production of which the different species are apparently not distinguishable. In the author's experience in New York State where the three species *B. populifolia*, *B. lutea*, and *B. lenta* are frequently associated and flower successively in the sequence named, those

patients afflicted with birch hayfever exhibit their symptoms throughout the flowering periods of all three species.

Betula populifolia Marsh. Gray, White, or Poplar-leaved birch (Plate VII, Fig. 1) type. Grains uniform in size and appearance, except for an occasional four-pored giant. Normal grains about 20 by 28.2 μ. Germinal apertures elliptical, about 2.3 μ in length, with a somewhat wavy margin, their long axes directed meridionally, except when there are four pores, in which case they coverge in pairs.

A small tree shedding much pollen in May. Nova Scotia to southern Ontario, Pennsylvania, and Delaware.

Betula lutea Michx. f. Yellow or Gray birch. Essentially as in the type, except that more of the grains have four and occasionally more pores up to seven. Grains about 29.6 by 25.1 μ, length of aperture 3.14 μ.

A large tree shedding much pollen, beginning to flower at just about the time when *B. populifolia* ceases. The grains of this species are figured by Sears (1930), who does not find that they bear any characters that distinguish them from those of other species. Newfoundland to Manitoba, southward to Delaware, Illinois, and Minnesota, also in Tennessee and North Carolina.

Betula lenta L. Black or cherry birch. Grains as in the type, about 25.9 by 21.6 μ; pores about 2.3 μ long.

A large tree shedding an enormous amount of pollen in May, a little later than *B. populifolia*. Newfoundland to Ontario, southward to Delaware, Indiana, and Iowa, also along the mountains to Florida and Tennessee.

Betula alba L. European white birch. Grains various in size but always three-pored, 20.5 to 30.4 μ in diameter. Exine finely and faintly granular, slightly more so around the pores.

A small or large tree, native of Europe but extensively cultivated in the United States, occurring in many varieties. Flowers in May. An important cause of hayfever.

Betula alnoides Buch.-Ham. Grains uniform, as in the generic description, 22 to 26.5 μ in diameter.

A medium-sized tree. Temperate and subtropical Himalaya, in moist ravines. Flowers in April.

Betula utilis D. Don. Grains uniform, large, 36 to 40 μ in diameter, always three-pored. Exine faintly granular. Exceptional in the genus in their large size.

A shrub or small tree, northwestern Himalaya and western Tibet. Flowers with the young leaves in May.

CARPINUS L. Hornbeam, Ironwood

Grains similar to those of *Betula* but more nearly spherical, various in size, 25.6 to 41 μ in diameter. Pores generally three, sometimes four, rarely five or six. Pore pattern similar to that of the grains of *Betula*, but exine surrounding the pore less thickened.

The genus comprises about 15 species of trees, widely distributed in the Northern Hemisphere. All are wind pollinated and in the early spring shed large quantities of pollen, which probably causes some hayfever.

Carpinus caroliniana Walt. Hop hornbeam. Grains various, 26.8 to 33.1 μ in diameter; pores three or four, occasionally five or six, their apertures circular, about 4 μ in diameter, often operculate. Exine smooth or faintly granular.

A small tree, shedding large quantities of pollen in the early spring. Nova Scotia to western Ontario and southward. The grains of this species have been figured by Sears (1930) showing three germ pores.

Carpinus Betula L. Hornbeam. Grains various, 36.4 to 41 μ in diameter. Pores generally four, occasionally three or five, their apertures circular or broadly elliptical, generally operculate. Exine smooth or faintly granular.

These grains may be distinguished from those of *Alnus*, which also have generally four pores, by their larger size and lack of connecting bands and from those of *Betula* and *Alnus* by their less protruding pores.

A small tree, native of Europe and western Asia, frequently planted in America. The grains of this species have been figured by Docturowsky and Kudrjaschow (1923), who state that the pores are four, rarely five; also by Erdtman (1923, 1927) and Meinke (1927), both stating that they have four or five pores.

Carpinus viminea Wall. Grains uniform, virtually as in *C. caroliniana*, about 25.6 μ in diameter. Pores three or rarely four, small and circular, generally operculate.

A small tree. Temperate Himalaya, from Chamba eastwards. Flowers March to April.

Ostrya virginiana (Mill.) K. Koch Blue beech. Pollen with a large proportion (about one-third) of its grains four-pored; 28 by 25 μ in diameter; apertures of the pores decidedly elliptical, often more than twice as long as broad, 4.5 μ long, pore membranes marked with a slight fleck. Otherwise as in the *Betula* type.

This species is figured by Sears (1930) showing three germ pores with apertures circular. The European *Ostrya carpinifolia* pollen is figured by Erdtman (1923).

A small tree, similar in habit to *Carpinus*. Flowers early in spring before the leaves unfold. Cape Breton, Indiana to Manitoba, Newfoundland, Florida, and Texas.

CORYLUS L. Hazel

Grains essentially as in the *Betula* type, about 22 to 26.5 μ in diameter. Pores always three, their apertures slightly elliptical or quite circular, 3.4 to 3.7 μ in diameter.

Medium-sized shrubs shedding large amounts of air-borne pollen very early in spring—March to April—long before the leaves unfold. Suspected of being a minor cause of hayfever. The pollen of the various species is extremely abundant in Postglacial silts. Of it Erdtman (1929, page 114) says, "A peat deposit in the vicinity of Lake Constance holds the European record for pollen of hazel, which was laid down during the first half of the Boreal period. It is therefore a pioneer shrub." It is figured by Docturowsky and Kudrjaschow (1923), Meinke (1927), and Erdtman (1923), the latter stating that it "ist Morphologische nicht ganz sicher von der *Myrica* zu unterscheiden." Luersen (1869) has endeavored to show the structure of these grains.

Corylus americana Walt. Hazelnut. Grains uniform in size, 22.8 μ in diameter. Apertures of pores 3.42 μ in diameter.

Manitoba and Ontario to Saskatchewan, Florida, and Kansas.

Corylus Avellana L. Filbert, hazelnut. Grains somewhat various in size, averaging about 26.5 by 22 μ. Apertures of pores 3.7 μ in diameter.

Habit as in *C. americana*, native of Europe and north Africa but widely cultivated in North America.

ALNUS (Tourn.) Hill Alder

Grains flattened, 19 to 27 μ in diameter, with four or five or rarely three or six germinal apertures which are narrowly elliptical or slit-shaped, 2.5 to 4.5 μ long, aspidate, *i.e.*, surrounded by subexineous thickenings. These cause the pores to protrude and give the grains an angular outline. Texture smooth or slightly granular (Plate VII, Figs. 2, 3).

The most distinctive characteristic of these grains is the presence of band-like thickenings beneath the exine, apparently of the same material as the thickenings of the exine surrounding the pores and extending out from them in geodetic curves from pore to pore on each side of the equator. These can generally be seen only with difficulty in unstained material, but when appropriately stained they become quite conspicuous. Similar band-like thickenings are not found elsewhere among the Betulaceae, as far as these studies have gone, and serve to distinguish the grains of all species of alder from all others of the Betulaceae.

Alder pollen is occasionally an important factor in hayfever. Thus *A. oregona* is stated by Chamberlain (1927) to be an important hayfever plant in Oregon and Washington. The pollen of various species of alder have been recorded in Postglacial silts and have been recorded and illustrated by Lewis and Coke (1929) from the Dismal Swamp in the United States. *Alnus* pollen is recorded from most European bogs that have been studied. It was figured by Erdtman (1923) showing the curved linear thickenings. He regards it as almost a pioneer, in the Boreal period, following closely *Corylus* and *Pinus*. It is also figured by Meinke (1927), omitting the curved linear thickenings because, he states, they do not show except in fossilized material.

Alnus rugosa (Du Roi) K. Koch (Plate VII, Figs. 2, 3) Smooth alder type. Grains flattened, about 21.5 by 17.8 μ. Germ pores four or five, rarely three or six, their apertures generally extremely narrow, often slit-shaped.

A shrub or small tree, along the shores of ponds and river banks. Maine to Florida and westward to Texas and Minnesota. Flowers very early in spring, long before the unfolding of the leaves.

Alnus sinuata (Regel) Rydb. Mountain alder. Grains as in the type, except that they are slightly larger—about 27 by 24 μ—and somewhat various; pores four or five, occasionally three, their apertures elliptical, about 4.5 μ long, converging in pairs.

A large shrub. May to July. Oregon, Wyoming, and Alberta.

Alnus incana (L.) Moench Speckled or Hoary alder. Grains about 24 μ in diameter. Pores four or five, occasionally three, apertures long-elliptic, 3.4 μ in length. Frequently the pores are not equatorially arranged, but the apertures tend to converge in pairs. Otherwise as in the type. The grains of this species have been figured by Sears (1930), Docturowsky, and Kudrjaschow (1923) without band-like thickenings. They have also been figured by Erdtman (1923), drawing attention to the connecting bands extending from pore to pore.

Flowers in April and May. Alaska to California to New Mexico to the Yukon.

Alnus nepalensis D. Don. Grains as in the generic description, uniform, 19.4 to 20.5 μ in diameter. Pores four, occasionally three; connecting bands rather faint.

A large tree, China, Burma, and Himalaya, in valleys and along streams. Flowers October and November.

MYRICACEAE Sweet-gale Family

Grains similar to those of the Betulaceae and discussed with them (p. 362 *et seq.*).

MYRICA L.

Grains similar to those of *Betula*, 25 to 27 μ in diameter, their apertures irregular, approximately circular, not generally elliptical, about 3.5 μ long, in optical section presenting a pore pattern as in Fig. 99*b*.

Myrica pollen is known to occur abundantly in Postglacial silts. Lewis and Coke (1930) state, "The pollen of *Betula* and *Myrica* are much alike, though they may be distinguished with certainty in well-preserved specimens (Figs. 20, 22)." These figures, which are of fossilized material, show differences in outline which are not apparent in fresh material. Jentys-Szafer (1928) gives several very interesting figures and states that the grains of *Myrica Gale* are most likely to be confused with those of *Corylus*. They may be distinguished, however, because the exine of those of *Myrica* is a little thicker than of *Corylus*, especially near the pores, and when treated with concentrated sulphuric acid, followed by dilute chromic acid, it is seen in the grains of *Myrica* to consist of three layers, two of which are thin, with one much thicker in between. The grains of *Myrica* are also a little smaller than those of *Corylus*, measuring in glycerin 21 to 27.5 μ in diameter, but the difference in size is too slight to be relied upon in distinguishing them when found together in peats. In the fossil form, however, Jentys-Szafer states, these two species may be distinguished from each other by the difference in the thickness of their walls and by the presence in the grains of *Myrica* of three arcuate thickenings, one underlying each of the pores but entirely absent from the grains of *Corylus*.

It has frequently been stated that, though the grains of *Corylus* are abundant in peat deposits, those of *Myrica* are not preserved in such deposits, but Jentys-Szafer believes that, on account of the similarity of the structure and the behavior of the grains toward such destructive reagents as sulphuric acid and potassium hydroxide, there is no reason to suppose that one could be preserved while the other is destroyed under identical conditions. In fact, upon examining certain European peats, she found as many grains presenting the characters of *Myrica* as of *Corylus*. Nevertheless, she admits, the differences are slight and can be discerned only in typical grains. Docturowsky and Kudrjaschow (1923) give figures of *Myrica* pollen, but these do not show that it can be distinguished from that of *Corylus*.

Myrica Gale L. Sweet gale. Grains as in the generic description, about 27 by 23.5 μ. Pores three. Exine slightly roughened, especially around the pores.

A low shrub in swamps and along ponds and streams, throughout most of the northern part of the United States and Canada, also Europe and Asia. Flowers in April and May.

Myrica cerifera L. Wax myrtle. Grains as in the generic description, uniform, 24 to 26.2 μ in diameter. Pores always three, broadly elliptical. Exine faintly granular, especially around the pores.

A shrub or small tree, reaching a height of about 40 ft. In sandy swamps or wet woods, southern New Jersey to Florida and Texas. March to April.

Myrica Nagi Thunb. Grains as in the generic description, about 22.8 μ in diameter.

A small tree. Subtropical Himalaya. Flowers August to September.

Comptonia perigrina (L.) Coulter (*Myrica asplenifolia* L.) Sweet fern, Ferngale. Grains generally more or less flattened but various in this respect, about 27.1 μ in diameter. Germ pores three, four, or rarely six, their apertures circular, 3.5 μ in diameter, and slightly more protruding than in the grains of *Corylus* and *Betula*.

The pores may be equally spaced around the equator of the grain as in those of *Myrica*, but they are more often irregularly arranged, particularly when there are three when they are generally gathered into one hemisphere. They may be easily distinguished from those of *Betula* by the frequent occurrence of four pores and their frequently asymmetrical placement and from those of *Alnus* by the absence of linear thickenings which characterize the grains of that genus.

A small shrub. Flowers in April and May. Nova Scotia to Saskatchewan, North Carolina, Indiana, Michigan.

FAGACEAE Beech Family

The pollen grains of the Fagaceae are of two entirely different types. Those of *Quercus* and *Fagus* are similar, so also are those of *Castanea* and *Castanopsis*, but there is no obvious relationship between the two former and the two latter. Accordingly detailed descriptions are given of these under their generic headings.

Key to the Genera

Grains when moist flattened and angular. Furrows three or occasionally four or six, broadly expanded, one at each angle of the grain. Exine thin, warty-granular. Hyaline bodies underlying the furrows conspicuous.	Quercus
Grains when moist spheroidal. Furrows long, narrow, and tapering, their margins slightly raised, normally three, but some grains with two or a single furrow encircling the grain. Exine heavy and coarsely granular. Hyaline wedges underlying the furrows spherical and not conspicuous.	Fagus
Grains when moist ellipsoidal. Furrows three, slender and tapering, with a germ pore bulging through a well-marked transverse furrow. Exine smooth. Hyaline wedges none.	Castanea Castanopsis

QUERCUS L. Oak

Grains spheroidal, or oblately flattened and angular in outline, according to the extent of their expansion; tricolpate or occasionally some grains with more than three furrows; beneath the center of each furrow an internal hyaline body. Furrows meridional in arrangement or, if 4 or 6, tetrahedral; long and tapering to pointed ends, their membranes smooth but generally ruptured and not observable in grains that have been prepared for microscopic examination in the ordinary way. Exine rather thin, more or less warty-granular. Intine thick (Plate VII, Fig. 6).

The most conspicuous and distinctive feature of the grains of *Quercus* is their possession of hyaline wedge-shaped plugs embedded in the cell contents, underlying the furrows, one beneath each, and radiating toward them from the center of the cell (Plate VII, Fig. 7). Their function appears to be to rupture the furrow membrane and spread open the furrows when the grain is moistened. When the grain is dry it is ellipsoidal in shape, with the furrows tightly closed, visible from the surface only as shallow grooves, and the hyaline plugs are small and inconspicuous, but as soon as the grain begins to take up moisture it assumes a spherical form, and the furrows gape slightly open. Immediately underlying the center of each furrow the end of the hyaline wedge may be seen apparently penetrating the furrow membrane. One cannot be certain, however, whether the opening in the membrane, which appears as an irregular break extending longitudinally, is a rupture caused by the protrusion of the hyaline wedge or a true germinal aperture. At any rate the furrow membrane is narrow and does not permit of much stretching. As the grain expands further the wedge underlying each furrow elongates and tears the furrow membrane wide open almost from end to end. Through these slits protrudes the expanding gelatinous cell content covered by its elastic intine. The grain in this condition is flattened and triangular in shape, with the three furrows appearing as more or less irregular slits torn through the exine. In the partly expanded condition when the grain is spherical it bears some resemblance to that of *Fagus;* the furrows are narrow and of medium length, with their margins slightly above the general level of the exine.

The grains of the different species are much alike, and there appear to be no reliable criteria for distinguishing them from each other. They vary somewhat in the texture of their exine and in their size range from 30 by 25 to 36 by 26 μ, measured in the expanded condition.

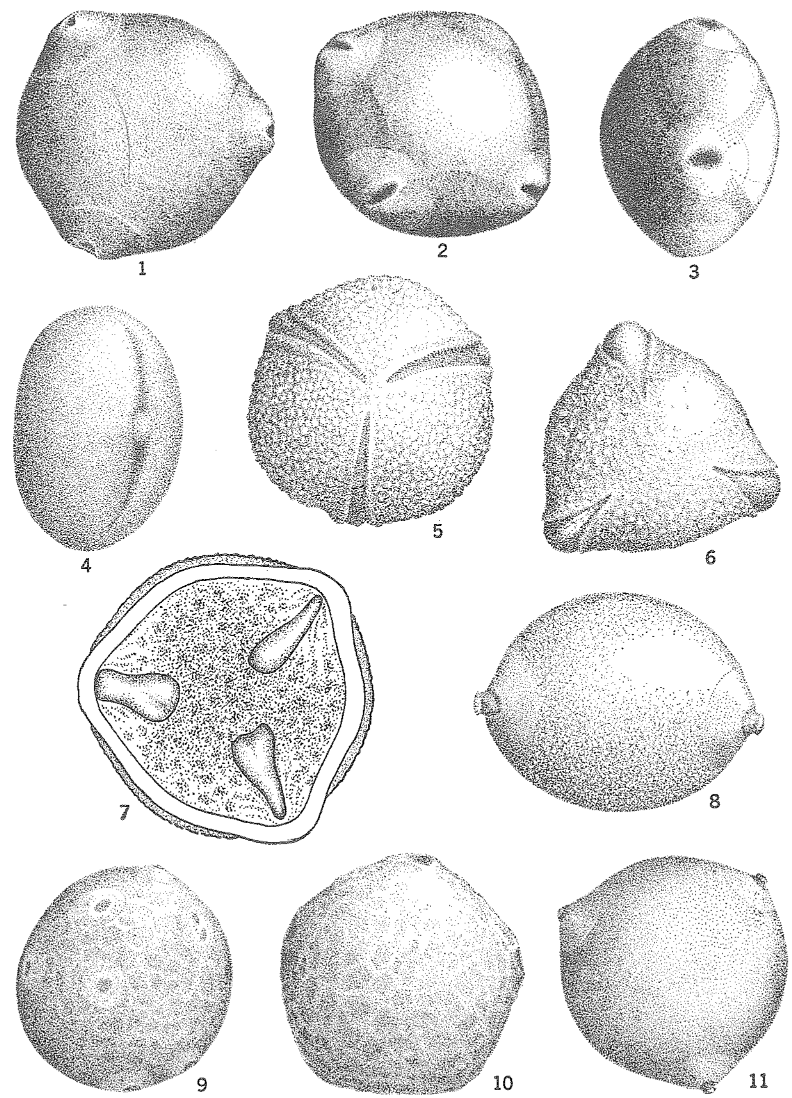

PLATE VII.—Pollen grains of Betulaceae, Fagaceae, and Urticaceae; 1, *Betula populifolia*, polar view, 20 μ in diameter. 2, *Alnus rugosa*, 21.5 μ in diameter, partly side view. 3, *Alnus rugosa*, side view. 4, *Castanea dentata*, 14.7 by 11 μ, side view, fully expanded. 5, *Fagus grandifolia*, polar view, fully expanded, 40 μ in diameter. 6, *Quercus alba*, 34 μ in diameter, polar view, fully expanded and furrow membranes ruptured. 7, *Quercus venustula*, optical section. 8, *Morus alba*, side view, 20 μ long. 9, *Celtis occidentalis*, 40 μ in diameter. 10, *Ulmus americana*, polar view, 37.2 μ in diameter. 11, *Maclura pomifera*, polar view, 22 μ in diameter.

It has frequently been stated that the pollen grains of oak are indistinguishable from those of violet, and this is cited as a remarkable example of morphological convergence. Beyond the fact that the grains of violet have a tendency to overexpand when moistened, causing the furrows to tear wide open, there is no resemblance. The exine of the violet grain is nearly smooth, lacking entirely the warty-granular texture characteristic of the oak grains; and the violet grain has no hyaline wedges. Its germinal apertures are well defined and quite conspicuous, unless the furrow membranes are ruptured. Furthermore, some species of violet have some or all of their grains provided with four, six, or even five furrows. In such cases the furrows are arranged around the equator and directed meridionally, unless there are four, in which case they converge in pairs. Some species of oak likewise have supernumerary furrows, but, unlike those of the violet, these are always arranged according to the trischistoclasic system. The supposed convergence of form between the oak and violet pollen grains is entirely superficial, based only on an accidental resemblance which results from the fact that both have a tendency to overexpand, accompanied by the rupture of the furrow membranes.

Oak pollen has been described and figured by several authors. For example, Meinke (1927) gives figures of *Q. robor* and *Q. sessilis* and states that the pollen of oak may be distinguished from that of violet by its more coarsely granular exine. Docturowsky and Kudrjaschow (1923) show a figure of the pollen grain of a species of oak, pointing out that it resembles that of maple but may be distinguished by its exine's being thinly papillate and not cleft as in the pollen of maple. Pollen of *Q. sessiliflora* is shown by Erdtman (1923, 1927). Fossilized oak pollen is figured by Lewis and Coke (1930), who regard it as similar to that of willow, but state that it may be distinguished by its lack of a reticulate surface, and its larger size.

Oak pollen is found at nearly all levels in Postglacial silts. For example, the work of Stark (1925), Budde (1930), Lewis and Coke (1930), and many others shows that the oaks have been prevalent in both Europe and America continuously since the last recession of the continental ice sheet. Erdtman (1929), in speaking of the Postglacial history of the British forests, states "Oak forests have generally played a prominent rôle since the immigrations of the oak in the Boreal period."

The oaks shed enormous quantities of pollen. In the vicinity of New York City it was found that for several weeks each spring the pollen grains of the various species of oak greatly outnumber all others (see Chart I). Similar observations have been recorded by other investigators; for example Duke and Durham (1928) have shown that the atmospheric pollen count of oak in Kansas City when at its maximum, about Apr. 27, outnumbered all others except elm. Oak pollen undoubtedly causes some hayfever, but much less than would be expected from the enormous quantities that are found in the air. The relative importance in this respect of the many different species is not understood, but, in view of the close interrelationship existing among them, it is hardly to be expected that the specificity of their biological reaction would be very marked. *Q. marilandica* is said to cause some hayfever in the neighborhood of Oklahoma City (Balyeat, 1926); *Q. Garryana*, in western Oregon (Chamberlain, 1927). Several species are mentioned by Hall (1922) as of little or no importance in California, though shedding much pollen. This point will be discussed in connection with the several species as they are considered.

Quercus alba L. White oak (Plate VII, Fig. 6) type. Grains in the overexpanded condition, flattened, triangular in outline, about 34.2 by 26.2 μ in size, tricolpate, with the furrows appearing as rather short slits in the exine and gaping widely open, with the cell contents protruding as if forced out by pressure within; hyaline wedges conspicuous; texture warty-granular.

The grain of this species is figured by Sears (1930), who states that it is probably not possible to distinguish it from those of other species of oak.

A large tree, abundant in the northeastern United States and Canada. The flowers are borne in pendant racemes which emerge with the leaves in May, shedding large amounts of pollen which, with that of other species of oak, is one of the most frequent causes of the early spring or tree hayfever in the northeastern United States.

Quercus borealis Michx. (*Q. rubra* Du Roi) Red oak. Grains indistinguishable from the type, 36.5 by 25.6 μ. Figured by Sears (1930).

A large tree, abundant in the northeastern United States and Canada. Frequently planted. Flowers in May.

Quercus velutina Lam. Black oak. Normal grains essentially as in the type, except that the hyaline wedges are rudimentary, and the surface texture slightly finer. The pollen upon which these observations were made exhibited many irregularities in form, such as generally denote hybridity of origin; many of the grains were obviously abortive; others were giants possessing supernumerary furrows and variously misshapen; and some were united in tetrads. The furrows of these irregular grains when more than three (four or six) were found to be arranged in the trischistoclasic system. I am not prepared to say whether such irregularities are inherent into the species or characterize only certain individuals.

A large tree, native of the eastern half of the United States. Flowers in May, shedding much pollen which causes some hayfever.

Quercus venustula Greene Scrub oak. Grains uniform, about 35 by 27.5 μ, as in the type, except that the hyaline wedges are more prominent, cigar-shaped with the large end outward.

A small shrub, 3 to 6 ft. high, abundant in Colorado and New Mexico, where it is known to cause some hayfever.

Quercus Engelmanii Greene Evergreen oak, Mesa oak. Grains uniform, as in the type, about 31 by 24 μ.

A tree 50 to 60 ft. high, of limited distribution in California, "occupying with *Q. agrifolia* a belt about fifty miles wide and extending to within fifteen or twenty miles of the coast, from the neighborhood of Sierra Madre and San Gabriel, Los Angeles County, to the mesa east of San Diego; in northern Lower California" (Sargent, 1922). Within this restricted area it is regarded as an important factor in hayfever (Selfridge, 1920).

Quercus bicolor Willd. Swamp white oak. Normal grains essentially as in the type, about 27.5 μ in diameter. A small proportion of the grains have four or six furrows, which are always in the tetrahedral arrangement.

A large tree, often 100 ft. high, shedding enormous quantities of pollen in May, common in moist places throughout almost the eastern half of the United States.

Quercus Prinus L. Chestnut oak. Normal grains essentially as in the type, 31 by 25 μ. Furrows rather long and sharply defined, regular in outline; hyaline wedges rather conspicuous. A large proportion of the grains are tetracolpate and hexacolpate, with the furrows in the tetrahedral arrangement.

A large tree with thick and deeply furrowed bark. It sheds enormous quantities of pollen in May. Of general distribution in the Atlantic coast states.

Quercus agrifolia Neé. California live oak, Encina. Grains all normal, except a few that are abortive, essentially as in the type, about 31 by 25 μ; furrows rather long and sharply defined.

A tree 80 to 90 ft. high, with evergreen leaves. In distribution confined to California and Lower California, where it is the largest and most generally distributed oak tree between the mountains and the sea, covering the lower hills and ascending to altitudes of 4,500 ft. (Sargent, 1922). It flowers through most of March and April, shedding rather large quantities of pollen which has been shown to give positive skin tests with hayfever patients (Hall, 1922) and is apparently an important factor in hayfever. It is stated by Selfridge (1920) to be the most important hayfever tree in California. But by Rowe (1928) it is regarded as unimportant in the San Francisco Bay region.

FAGUS L. Beech

The grains of *Fagus* in their general construction and their appearance in the unexpanded condition, are similar to those of *Quercus*, but their exine is thicker, the internal hyaline bodies are more spherical, and when the grains are moistened there is much less distortion of their form—they remain almost spherical—and, though the furrows gape somewhat open, their membranes do not rupture.

The genus comprises but a single American species, though the European *Fagus sylvatica* L. "is frequently planted for ornament in the eastern states, in several of its forms, especially those with purple leaves and pendulous branches" (Sargent, 1922). Beech pollen is commonly recorded from European Postglacial bog deposits. For example, it is recorded by Keller (1929), Stark (1925), and Budde (1930), and grains of *F. sylvatica* are figured by Erdtman (1923, 1927) in connection with his pollen-analysis studies. But it has apparently not yet been recorded from similar deposits in America.

Fagus grandifolia Ehrh. (*F. americana* Sweet, *F. ferruginea* Ait.) American Beech type (Plate VII, Fig. 5). Normal grains spheroidal, uniform, averaging 40 μ in diameter; exine heavy and decidedly roughened; furrows long, narrow, and tapering, equally spaced around the equator and meridionally arranged, their margins raised slightly above the general surface of the exine, each enclosing a germ pore which is rather small and elliptical. Underlying each is a hyaline body which is similar to those of the grains of *Quercus*, yet these grains do not tend to overexpand and rupture their furrow membranes as do those of *Quercus*, probably on account of the greater thickness of their exine.

In the pollen of some trees are found a large number of grains with only two furrows. Such furrows may either be in the normal tricolpate position, as if one of the usual three had failed to develop, or they may be exactly opposite, in which case they are confluent at the poles and encircle the grain as a single furrow which may or may not be provided with two germ pores. Such grains may or may not be smaller than normal.

The grains of this species have been figured by Sears (1930), who points out that they may be distinguished from those of oak by the thickened margins of the germinal furrows. To this I should add the further distinction that the general surface of the exine is more constantly and more coarsely roughened, the exine is heavier, and the hyaline wedges are much less conspicuous than in the grains of oak.

The American beech is a large tree, conspicuous for its grayish-white bark. It is of rather general distribution in the eastern United States and Canada, from New Brunswick and Ontario southward to Virginia and, in its variety *caroliniana*, southward to Florida.

The flowers open in May at about the same time as the unfolding of the leaves. They are obviously wind pollinated, though they appear to shed less pollen than most anemophilous trees. The pollen of beech appears to be a minor cause of hayfever, and it is caught on pollen slides at considerable distances from the trees.

CASTANEA Hill CHESTNUT, CHINQUAPIN

The grains of both *Castanea* and the next genus, *Castanopsis*, are characterized by their small size—about 14 by 10 μ. They bear no resemblance to those of *Fagus* or *Quercus;* they lack entirely the granular texture of these two, and they possess a well-developed germ pore emerging through a transverse furrow.

The chestnuts and chinquapins are unquestionably wind pollinated but shed much less pollen than most anemophilous trees. Their pollen is not known to cause hayfever, though that of *Castanea sativa* is listed by Hall (1922) as a probable cause. The grains of various species are occasionally reported from Postglacial silts. In this connection the fossil pollen of *C. sativa* is described and illustrated by Erdtman (1923).

Castanea is a small genus of large trees widely distributed throughout North America, and the European species *C. sativa* has recently been introduced into some parts of North America.

Castanea dentata Borkh. Chestnut (Plate VII, Fig. 4) type. Grains uniform, tricolpate; when fully expanded ellipsoidal in shape, 14.7 by 11.2 μ. Furrows long and tapering, almost meeting at the poles, each enclosing a well-marked germinal aperture and a distinct transverse furrow with a thickened rim. The latter is conspicuous in optical section, and serves as a useful means of identification in fossil material. In fresh material, when the grains are expanded, the pore membrane is always seen to bulge through its aperture. Exine perfectly smooth. When these grains dry the furrows close up tightly and appear as narrow grooves and hide the germ pore from view, the grains themselves becoming columnar in shape.

A large tree, occasionally 100 ft. high. Flowers in June and July. Formerly abundantly and widely distributed in the eastern part of the United States but now almost extinct throughout most of its range owing to the ravages of a parasitic fungus, *Endothia parasitica* Anders.

Castanea pumila Mill. Chinquapin. Grains as in the type, 14.5 by 18.9 μ.

A small tree or shrub, sometimes forming thickets. New Jersey to Indiana and southward to Florida, most abundant in southern Arkansas and eastern Texas. Flowers May and June.

Castanea floridana (Gray) Ashe Chinquapin. Grains as in the type, 13.5 by 10.5 μ.

A small tree sparingly distributed in the Gulf Coast states.

Castanea nana Muhl. Chinquapin. Grains uniform and exactly as in the type, 11.7 by 11.2 μ.

A low shrub forming thickets on sand hills and in barrens, Georgia and Florida to Louisiana. Flowers in early spring.

CASTANOPSIS Spach

A genus with two species in California and the Pacific coast states but a larger number of species in southern Asia. Similar in most respects to *Castanea* to which it is closely allied.

Castanopsis chrysophylla DC. Golden chinquapin. Grains exactly as in *Castanea dentata*, 13.7 by 11.9 μ.

A large tree, Washington to California.

URTICACEAE Nettle Family

The family is here considered in its broadest sense, including the groups Ulmaceae, Moraceae, and Cannabinaceae, which are frequently regarded as separate families. Their pollen grains may be described as spheroidal or oblately flattened, entirely lacking germinal furrows but provided with two to seven germ pores equatorially arranged.

In all species the grains are extremely simple, lacking any but the most rudimentary sculpturing, such as a granular or warty texture, and even this is present in only a few. This is in keeping with their habit of wind pollination.

The grains are extremely various in size in the different species, ranging in diameter from about 13 μ, in *Broussonetia* and *Urtica*, to over 40 μ, in some species of *Celtis*. The germ pores are likewise various in character and size. In most species they are decidedly aspidate, often approaching very closely to the form of the grains of the Betulaceae, but in the grains of *Ulmus*, *Planera*, *Holoptelea*, and *Zelkova* the grains are not aspidate or possess only rudimentary subexineous thickenings around the germ pores. These four genera which lack the aspidate character all belong to the group of Ulmaceae and are apparently rather closely related. Other members of the same group, however, differ in this respect. For example, the grains of *Celtis*, *Pteroceltis*, and *Gironniera*, which likewise belong to the group of Ulmaceae, are decidedly aspidate, which shows that the character, in this family at least, is not of real phylogenetic value. The aspidate character is one that frequently appears in wind-pollinated groups of diverse origins; therefore it seems most likely that the degree to which it is expressed is a measure of the response of the species to that mode of pollination rather than an indication of relationship. Besides being characteristic of most of the Urticaceae, the aspidate form of pores is found in the grains of the Betulaceae, Myricaceae, Haloragidaceae, Casuarinaceae, and Juglandaceae, families which are for the most part widely separated; but all are wind pollinated.

The following Asiatic genera omitted from this discussion have grain similar to those of *Urtica*: *Pouzolzia*, 9.4 to 11 μ, pores two or three; *Debregeasia*, 14 to 16.5 μ, pores three; *Maotia*, 14.8 to 17 μ, pores two.

Key to the Genera

I. Germ pores 3 to 7, mostly 5; not aspidate, or surrounded by only inconspicuous subexineous thickenings, apertures elliptic, pore membranes not capped but occasionally slightly flecked.
- *A*. Exine marked by internal reticulate thickenings or with connecting bands between the pores. Texture smooth.
  - 1. Exine not marked by internal reticulate thickenings but with conspicuous band-like thickenings extending from pore to pore. — Planera aquatica
  - 2. Exine marked by internal reticulate thickenings, connecting bands between the pores absent or only faintly expressed (*Ulmus crassifolia*). — Ulmus
- *B*. Exine not marked by internal reticulate thickenings or by connecting bands between the pores. Texture more or less granular.
  - 1. Texture finely granular, 16 to 18.2 μ in diameter. — Gironniera
  - 2. Texture coarsely warty-granular, 25 to 32 μ in diameter. — Holoptelea, Zelkova

II. Germ pores two to six, mostly three or two, more or less aspidate, *i.e.*, surrounded by quite conspicuous subexineous thickenings; their apertures circular, irregular, or broadly elliptic in outline. Pore membranes capped, flecked, or smooth.
- *A*. Germ pores mostly two, only occasionally three.
  - 1. Grains large, 20 to 25 μ in diameter, ellipsoidal, with the pores near the ends but not diametrically opposite.
    - *a*. Texture warty-granular, pore membrane smooth. — Trema
    - *b*. Texture smooth, pore membrane flecked. — Morus
  - 2. Grains small, less than 14 μ in diameter, spherical or irregular in form. — Broussonetia

B. Germ pores mostly three or four, only occasionally two.

1. Grains small, mostly less than 14 μ in diameter. Urtica
2. Grains larger, 20 to 31 μ in diameter (frequently some giants with supernumerary pores in *Celtis* and *Momisia*).

Pore membrane capped.	Maclura
Pore membrane not capped.	Humulus
	Cannabis
	Celtis
	Pteroceltis
	Momisia

ULMUS L. Elm

Grains oblate, 23 to 38 μ in diameter. Germ pores three to seven, generally five or four, rarely three, elliptical in shape, their apertures 3.5 to 6 μ in length, equatorially arranged, with their long axes converging in pairs. Subexineous thickenings absent or only faintly represented. Pore membranes smooth or slightly flecked but never capped. Texture of the exine smooth but marked by slight undulations which are due to internal thickenings and which present the appearance of being the result of impressions made on the inner surface of the exine by the pressure of the starch grains with which these grains are always packed. The impressions, however, are permanent and persist after the starch is dissolved away by sulphuric acid.

The grains of *Ulmus* are very similar to those of *Holoptelea, Zelkova,* and *Planera* but may be distinguished from those of *Planera* by the absence of curved linear thickenings reaching from pore to pore.

Large trees shedding prodigious quantities of pollen, in most species, generally very early in spring, preceding the leaves by several weeks. It is well known that elm pollen is the cause of much hayfever, but the relative importance of the different species is not yet fully understood.

In the experience of the author, also in that of Duke and Durham (1928), elm pollen is found greatly to outrank all others in abundance in the air during a short period in March. The pollen of several species of elm has been found in Postglacial silts (*e.g.*, Erdtman, 1922; Budde, 1930; Rudolph and Firbas, 1924), and that of *U. foliacea* has been illustrated by Erdtman (1923) and by Docturowsky and Kudrjaschow (1923).

Ulmus americana L. White elm (Plate VII, Fig. 10) type. Grains distinctly flattened, averaging about 37.2 by 29.6 μ. Germ pores three to seven, most commonly five, arranged around the equator; apertures short-elliptical, with their long axes converging in pairs alternately above and below the equator, pore membranes flecked. When there are five pores the interval between the unpaired pore and its neighbor on one side is generally visibly greater than between the others. Thus if such grains are observed in polar view, their outline suggests a pentagon with one side longer than the others. The heavy reticulate thickenings underlying the exine suggest the surface markings of a peanut shell. These are difficult to see when the grain is full of starch but become clearly discernible when treated with sulphuric acid which dissolves out the cell contents. The surface texture is otherwise quite smooth.

A large tree flowering very early in spring before the leaves, shedding an abundance of light, air-borne pollen which is the undisputed cause of some early spring hayfever. Widely distributed throughout most of the United States and Canada east of the Rocky Mountains.

Ulmus campestris L. English elm. Grains essentially as in the type. Germinal apertures generally five, occasionally four or six.

A large tree flowering in early spring. Native of England and Europe, extensively introduced into America.

Ulmus fulva Michx. Slippery elm. Grains essentially as in the type, except that they are slightly smaller, 29.1 by 23.4 μ in diameter, germ pores generally four, less commonly five, with their apertures converging in pairs.

A large tree flowering early in spring. Widely distributed in the northeastern United States and Canada.

Ulmus alata Michx. Winged elm. Grains essentially as in the type, 27.8 by 22.8 μ in diameter. Germ pores generally five, less commonly four, 4.3 μ in length. As the pore membranes bulge through the apertures they may be seen to be slightly flecked as in the type but not capped as in the grains of *Maclura* and *Morus*.

A large tree shedding much pollen which is known to be the cause of some hayfever in early spring. Widely distributed throughout the southeastern United States.

Ulmus floridana Chapm. Florida elm. Essentially as in the type. Germinal apertures generally five.

A small tree flowering in late winter and early spring. North Carolina to Florida.

Ulmus crassifolia Nutt. Cedar elm. Grains as in the type except that the subexineous thickenings around the pores are slightly more pronounced, and there is a suggestion of linear thickenings reaching from pore to pore, though much less pronounced than in the grains of *Planera*. The grains are also somewhat smaller than in the type, averaging 23.5 μ in diameter, and germinal apertures 3.5 μ in diameter.

Flowers August to October and is known to cause some hayfever. The common elm tree of eastern Texas and adjoining states.

Planera aquatica Gmel. Water elm. Grains as in *Ulmus*, flattened, averaging 35.3 by 30.8 μ in diameter: germ pores generally four, only occasionally five, their apertures ellipsoidal, with their long axes converging in pairs, averaging 5.9 μ in length, the pore membranes slightly bulging when moist and quite noticeably flecked. The pores are surrounded by slight subexineous thickenings. From these extend out band-like thickenings reaching from pore to pore, apparently following geodetic curves, after the fashion of those of the grains of *Alnus* but less pronounced. The presence of these thickenings and the fact that the grains are generally provided with only four germ pores offer the only distinguishing features between these grains and those of *Ulmus americana*.

A small tree in river swamps. Indiana and Missouri to North Carolina, Florida, and Texas. Flowers in early spring.

Gironniera rhamnifolia Blume. Grains uniform, 16 to 18.5 μ in diameter, approximately spherical or somewhat triangular in polar view. Pores three, not surrounded by subexineous thickenings, apertures nearly circular; pore membranes smooth. Exine thin, slightly thickened around the pores, faintly warty-granular.

A small tree native of New Guinea. The genus comprises about eight species of trees and shrubs in Malaya and East India.

Holoptelea integrifolia Planch. Grains 25 to 28.5 μ in diameter; pores generally five, occasionally four. Exine coarsely warty-granular. Otherwise as in the *Ulmus* type.

A small tree native of the East Indies and Ceylon.

Zelkova acuminata Planch. Grains 29 to 32 μ in diameter. Otherwise indistinguishable from those of *Holoptelea*.

A small tree native of Japan.

Trema amboinensis Blume (*Sponia amboinensis* Dcne.). Grains uniform, 21.5 to 24 μ in diameter, broadly ellipsoidal. Germ pores two, one at each end, as in the grains of *Morus* but not directly opposite; apertures not elongate, circular or more or less irregular in outline; pore membranes smooth. Subexineous thickenings very deep, the two together occupying nearly half the cell. Exine rather thick, coarsely warty-granular, greatly thickened around the pores.

Morus alba L. Mulberry (Plate VII, Fig. 8) type. Grains ellipsoidal or spheroidal, about 20.6 by 17.1 μ in diameter. Germ pores two, occasionally three, not diametrically opposite each other. Apertures circular, 3.5 μ in diameter; pore membranes generally noticeably bulging and capped with a thickening of material, with the same staining properties as the general exine. Texture smooth or slightly granular. This grain bears a close resemblance to those of *Broussonetia* and *Urtica* but is distinguished from them by its larger size. It is likewise similar to those of *Trema* but is distinguished by its smooth texture and capped pores.

A small tree shedding in early June much pollen which may be detected in large quantities in the air. It has been shown to be the cause of hayfever (Bernton, 1928). Naturalized from the Old World in fields and waste places. Maine to Minnesota, Georgia, and Texas.

Broussonetia papyrifera Vent. Paper mulberry. Grains irregular in shape but tending to be spherical, thin-walled, usually somewhat collapsed, 13.4 μ in diameter. Germ pores two, usually not exactly opposite, aspidate and slightly protruding, and the subexineous thickenings extending deeply inward. Pore membranes not generally bulging through the apertures and not capped or flecked. Apertures circular or approximately so, 2.3 μ in diameter. Texture smooth.

These grains are characterized by their small size and two aspidate germ pores, characters which, however, they share with those of *Urtica*. In shape and structure they also closely resemble the grains of *Morus alba* (Plate VII, Fig. 8), but the latter may be distinguished by their much larger size.

A small tree, in June shedding much pollen, which it does by an explosive action in response to light (Balyeat, 1932). It has been shown (Bernton, 1928) to be a potent cause of hayfever. Introduced from Asia. New York, Missouri, and Florida.

Urtica dioica L. Stinging nettle. Grains spheroidal or irregular, thin walled and collapsing easily, 10.5 μ in diameter. Germ pores two or three, aspidate, with subexineous thickenings extending deeply into the cell; apertures circular, 1.7 μ in diameter; pore membranes slightly protruding and capped. Texture smooth.

These grains are scarcely distinguishable from those of *Broussonetia* but differ from those of *Morus alba* in their smaller size.

A low perennial herb, wind pollinated, flowering in summer and fall. Nova Scotia to Minnesota, South Carolina, and Missouri. Naturalized from Europe and Asia. Not known to cause hayfever.

Urtica vividis Rydb. Nettle. Grains essentially as in *Urtica dioica,* differing only in their possession of three or four pores and their slightly larger size—13.7 μ in diameter. Not known to cause hayfever.

Maclura pomifera Schneider, (*Toxylon pomiferum* Raf.). Osage orange (Plate VII, Fig. 11) type. Grains slightly flattened, those with the same number of germ pores of uniform size averaging 22 by 19.6 μ. Germ pores generally three, though a considerable proportion of the grains have four or occasionally two. Four-pored grains generally larger than the three-pored, averaging 22.9 μ in diameter. Pores circular or nearly so, about 1.7 μ in diameter, aspidate, the subexineous thickenings very thick. Pore membranes bulging when moistened, always thickened in the center, presenting the appearance of a little cap. Texture smooth.

A large tree with inconspicuous greenish flowers, shedding in early June much pollen which may be readily caught on pollen slides. It has been shown (Bernton, 1928) to cause some hayfever. Virginia to Arkansas, Georgia, and Texas.

Humulus Lupulus L. Hop. Grains similar to those of *Maclura* (Plate VII, Fig. 11). Spherical or slightly flattened oblately, about 24.5 μ in diameter. Germ pores three or four, occasionally six or two, aspidate, with the pore membranes protruding and the subexineous thickenings extending deeply into the cell. Apertures broadly elliptic or nearly circular, 3.1 μ in diameter; pore membranes only slightly flecked or smooth, not capped. Texture faintly granular or smooth. These grains differ from the type of *Maclura pomifera* only in the much weaker development or entire absence of pore caps and the more elliptic shape of their germinal apertures.

A climbing vine, dioecious, bearing greenish staminate flowers, shedding large amounts of light, air-borne pollen throughout most of the summer. Hop pollen is not known to cause hayfever but, on account of its kinship with such undoubted hayfever plants as *Broussonetia* and *Morus,* deserves further investigation. Native of Europe and Asia. Escaped from cultivation. Nova Scotia, Manitoba, Florida, Arizona, and elsewhere in America.

Cannabis sativa L. Hemp. Grains similar to those of *Maclura,* oblate, averaging about 25 μ in diameter. Germ pores generally three but often four and, occasionally, two, aspidate, with the subexineous thickenings extending deeply into the cell. Apertures circular or nearly so, 2.3 μ in diameter; pore membranes not capped and only occasionally slightly flecked. Texture smooth. The character which distinguishes this grain from that of *Maclura* is the much weaker development or entire absence of pore caps in the former.

CELTIS L. Hackberry, Nettle tree

Grains spheroidal, not appreciably flattened. Texture noticeably granular. Germinal apertures nearly circular; pores aspidate, not raised perceptibly above the surface of the grain. Subexineous thickenings less pronounced than in the grains of *Maclura;* pore membranes flecked. Internal reticulate thickenings of the exine faintly represented but not persisting when the cell contents are dissolved away by sulphuric acid.

Celtis laevigata K. Koch (*C. mississippiensis* Spach) Hackberry. Grains nearly or quite spherical, averaging 40 μ in diameter. Germ pores three equally spaced around the equator, aspidate but not protruding above the surface of the grain. Pore membranes marked by a single fleck but less so than those of the grains of *Maclura.* Texture slightly granular and appearing almost warty in the regions of the pores. This grain differs from the type (*M. pomifera*) principally in its thinner subexineous thickenings.

Celtis occidentalis L. Hackberry (Plate VII, Fig. 9). Grains spherical, packed with starch grains, texture slightly granular. Germ pores aspidate; apertures circular or more or less irregular but not elliptical; pore membranes sometimes marked by a single fleck. These grains show an enormous variation. In size they range from 25 to 55 μ in diameter; the germ pores range in number from 3, a number that is rare, upward to 10 or more. The pores exhibit no regularity of arrangement or size, and sometimes two or three appear to coalesce, but generally the larger grains have the larger numbers of pores. This great irregularity, together with a large number of abortive grains that are always found, suggests hybridity of origin.

A small tree, generally of gnarled appearance. The flowers open in early spring with the unfolding of the leaves. They shed large amounts of wind-borne pollen which probably causes some hayfever. This species is apparently not distinguished from *C. laevigata* in hayfever literature. The grains are described and illustrated by Sears (1930), showing only three germ pores, as in those of *C. laevigata*.

Pteroceltis Tatarinowii Maxim. Grains uniform, spheroidal or slightly triangular in outline, 23.5 to 27 μ in diameter. Pores three, their apertures circular or slightly elliptical. Otherwise as in *Celtis*.

Small tree, native of Mongolia and north China.

Momisia Iguanaea Rose & Standl. Cockspur. Grains somewhat various, 20 to 27.5 μ in diameter, spheroidal or oblately flattened and somewhat triangular in outline. Pores three, occasionally two, aspidate, equatorially arranged, their apertures broadly elliptic with their long axes directed meridionally. Exine thin, finely granular, especially around the pores.

These grains are scarcely distinguishable from those of *Celtis* and *Pteroceltis*, excepting in the slightly more elliptical shape of their germinal apertures.

A woody vine, Florida, West Indies, and tropical America.

Momisia aculeata (Lw.) Klotz. (*Celtis aculeata* Klotz.). Normal grains as in *M. iguanaea* but extremely various and irregular, with many of them giants or dwarfs and others obviously abortive and with various numbers of germ pores, in this respect similar to the pollen of *C. occidentalis*.

A small tree native of the West Indies and tropical America.

POLYGONACEAE Knotweed Family

The pollen grains of the Polygonaceae are extremely various, apparently without any general underlying similarities, so that it is useless to attempt to frame a definition for them. A study of the different forms, however, is of peculiar interest because it shows that they are related to each other and reveals several developmental tendencies which are remarkable and of far-reaching importance. In this family we see a suggestive illustration of how the ordinary tricolpate or three-furrowed type of grain with heavy walls and broad, deep furrows might have given rise to the thin-walled type with furrows reduced to thread-like grooves or entirely absent. Also, we discover how the same tricolpate form of grain could have given rise to the many-pored or cribellate form of grain which reaches perhaps its highest development in the Chenopodiaceae and Amaranthaceae. As regards the morphology of their pollen grains, the Polygonaceae are a transitional family.

The basic form of the grains of this family can be typified by that of *Eriogonum* (Plate VIII, Fig. 6). It is ellipsoidal, heavy-walled with a thick exine of granular structure but perfectly smooth on its surface, and gashed almost from pole to pole by three long, tapering furrows which function freely as harmomegathi, closing up tightly when the grain dries and gaping open widely when it is moistened, with a sort of hinge action at their pointed ends. In the middle of each furrow is a single roundish or elliptical germ pore, which is freely exposed when the furrow is open but more or less hidden when it is closed. This form of grain is always associated with insect pollination and can be regarded as the basic form not only of the Polygonaceae but also of most of the higher dicotyledons. In this family it characterizes, with relatively little modification, the pollen of such entomophilous species as *Eriogonum*, *Triplaris*, *Antigonum*, *Fagopyrum*, and some species of *Polygonum*. Generally there are just three furrows, but in the pollen of some species there are always to be found, besides the ordinary tricolpate grains, some with larger numbers. Among the pollen of the species that we have before us, that of *P. allocarpum* exhibits grains with 3, 4, 5, 6, 9, and 12 furrows, nearly always beautifully arranged in the trischistoclasic system. The occasional possession of more furrows than the usual three must be regarded as a tendency inherent in the family, a vagary which, after all, is only an extension within the system of equal stress arrangements and characterizes the pollen of many unrelated dicotyledons which have tricolpate grains as the basic form.

An environmental modification of this form of grain is found in the pollen of the anemophilous members *Rumex*, *Rheum*, and *Muehlenbeckia*. The inevitable result of this mode of pollination is that their grains are thin walled, and its corollary that the furrows are much reduced, their harmomegathic function being unnecessary in association with a thin and flexible wall. In all of these the furrows are just linear grooves of negligible width even when expanded. When such grains dry, their surface dips in along the furrows, and they become deeply lobed, the furrows acting throughout their entire length as hinges for the bending of the thin exine. When the grains are moistened they become spheroidal, disclosing a small and weakly developed germ pore in the middle of each furrow. Owing to the hinge action of the furrows they are necessarily long, reaching almost from pole to pole when the grains are tricolpate or almost meeting each other at the centers of convergence when polycolpate. If the reduction in the thickness of the exine had been carried a little farther, it is quite conceivable that it would have resulted in the total disappearance of both pores and furrows, for they are organs of the exine. Indeed, so near the vanishing point have they approached in the grains of some species of *Rumex* that it seems likely that such is the origin of the furrowless and poreless forms of grain that are encountered here and there among the pollen of wind-pollinated plants of other families; but in this family I have not found grains of this type entirely devoid of furrows.

A directly opposite line of development is found among the pollen grains of some of the members of this family which have retained insect pollination, *e.g.*, those of *Persicaria*, *Tracaulon*, and some species of *Polygonum*. In these not only has the exine remained thick, but it has become built up into an elaborate system of high, vertical ridges which, anastomosing freely throughout, impart a stiffness to the exine, causing the grain to be encased in a shell of rigid inflexibility, which results in a loss of furrows and a great increase in the number of pores. The character of these grains has departed so far from the basic form that it would be difficult to see any relation between them, were it not for a few intermediate forms which clearly establish the connection. In the grains of *Polygonum californicum* (Plate VIII, Fig. 7), for example, part of the surface is alveolate, and part of it is unmodified. Though only a part of the surface is involved, it includes the areas over both poles—the regions which must take up most of the bending when the furrows open and close—and consequently their harmomegathy is necessarily greatly impeded. Associated with this—probably as a consequence of it—these grains have very short and ineffective furrows. Moreover, there is no compensating device to offset the reduction of the furrows; and I think that the reason for this is to be found in the size and shape of the grains, for they are very small, measuring, exclusive of the alveolate thickenings at the poles, 19.4 by 12.5 μ, the smallest in the family. Owing to the fact that in solid bodies volume is a function of the cube of the linear dimensions while surface area is a function of the square of the same dimensions, the small size of these grains results in a relatively small ratio between their volume and their surface area, and this ratio is still further reduced by their elongate shape; consequently, there is sufficient elasticity in their walls to accommodate whatever slight changes in volume there are, without any help from the furrows. In some ways this grain may be regarded as intermediate between the basic smooth type and the fully alveolate and suggests the mode of origin of the latter from the former, though itself—in its small size—divergent from both.

A more complete development of the alveolate structure is found in the grains of *Polygonum chinense* (Plate VIII, Fig. 8). Here the entire surface is covered with anastomosing upstanding ridges of such a character as to impart the utmost rigidity to the whole exine, which, it may readily be seen, would effectively prevent the opening and closing of any type of furrow, particularly the long, tapering one which characterizes the basic form of grain of this family. The furrows of the grains of *P. chinense* are three and moderately long, and it is obvious that their operation as expansion mechanisms is greatly impeded by the alveolate structure of the exine, for when the grains are fully expanded the furrows do not open wide throughout their full length but merely bulge out in the middle, pushed apart by the protrusion of the large germ pore, remaining pinched off toward their ends. These grains are large—43.2 μ in diameter—which means that their volume is about twenty times as great as that of the grains of *P. californicum*, while their surface area is only about nine times as great. As a consequence, in this case some compensating device is necessary to make up for the lack of harmomegathy of the furrows. This is apparently accomplished by an increase in the size of the pores, which are remarkable in this respect, measuring about 10.3 by 13.8 μ and bulging prominently when the grain is moistened. They appear to be quite large enough to accommodate changes in volume, thus taking over, to a large extent, the impaired harmomegathic function of the furrows.

In the grains of *Persicaria* (Plate VIII, Fig. 5) a still further advance in the same direction is found. Here the demobilization of the exine is complete, no trace of the furrows remains, and the pores are each completely enclosed in a single lacuna; but in this case the loss of the furrows is abundantly compensated by the large number of the pores. These cannot actually be counted, but their distance apart, taken in consideration with their arrangement, permits one to estimate their number at about 30. Their arrangement is plainly that which they would occupy if they were at the centers of furrows arranged in the trischistoclasic system.

Briefly, then, it may be said that, in the evolution of these pollen-grain forms the tendency to develop an alveolate structure, with its resultant stiffening of the exine and demobilization of the furrows, stimulated a compensating increase in the number of the pores, a tendency manifestly already inherent in the family, and this resulted in the development of the extraordinarily beautiful form of grain of *Persicaria* and allied genera, decorated with a continuous reticulum of high ridges and provided with about 30 pores. This form is the culmination of this line of development in the family.

It is interesting to look ahead and see what the next step in such a line of development might be. There seems to be a widespread tendency among the angiosperms to abandon insect

pollination and adopt wind pollination, a step which tends to induce a reduction of pollen-grain sculpturing. Anemophily has originated among the angiosperms many times quite independently. This is reflected in the classification of living species of wind-pollinated plants, for they are generally found in families which also include others which are insect pollinated, *e.g.*, the poplars in the willow family, the ragweeds and sagebrushes in the composite family, and the ashes in the olive family. In all such instances the change from insect to wind pollination was accompanied by a reduction of, or entire loss of, surface decorations of the pollen grains.

There are no wind-pollinated members of the Polygonaceae derived from ancestors with many-pored alveolate grains. (We have already seen that the forms of the grains of the wind-pollinated *Rumex*, *Rheum*, and *Muehlenbeckia* were derived from the ordinary tricolpate form of grain.) But the neighboring families, Chenopodiaceae and Amaranthaceae, are entirely wind pollinated, and consequently their grains are devoid of decorations. These two families may not have been derived from the Polygonaceae, but a consideration of their grains in association with those of the Polygonaceae is suggestive of the form to which an extension of the evolutionary sequence of forms established in the Polygonaceae might lead, under the influence of wind pollination. The grains of the Chenopodiaceae and Amaranthaceae are cribellate, *i.e.*, characterized by a large number of pores, giving the exine a sieve-like appearance. They are thin walled, and the exine is devoid of decorations other than the numerous round germ pores. It is likely that the many-pored character of the grains of these two families was called forth in some ancestral species by some form of sculpturing which brought about the demobilization of the exine but which has since been lost as the result of their adoption of wind pollination.

Key to the Species

I. Furrows present.
   A. Furrows long and extremely narrow linear channels; exine thin.
      1. Furrows always 3; germ pores circular; texture fine-granular. — Rheum officinale
      2. Furrows 3 or 4, generally both tri- and tetracolpate grains present; germ pores elliptical.

a. 26.5 to 32 μ in diameter, pores 4.6 μ long.
- (1) Texture granular. — Muehlenbeckia vulcanica
- (2) Texture finely pitted.
  - (*a*) Furrows generally 3, rarely 4 or 5. — Rumex crispus
  - (*b*) Furrows prevailingly 4, less frequently 3, and rarely 5 or 6. — Rumex obtusifolius

b. Grains 18.2 to 23.9 μ in diameter.
- (1) Furrows prevailingly 4, less frequently 3. — Rumex Acetosella
- (2) Furrows prevailingly 3, less frequently 4. — Rumex Acetosa
- (3) Furrows always 3. — Rumex scutatus

B. Furrows not linear, broader toward the middle, tapering toward their ends; exine thick.

1. With the entire surface conspicuously granular or pitted or both. Germ pores circular or somewhat elliptical.

a. Grains over 40 μ in length; texture very coarsely granular and pitted throughout.
- (1) Grains long-ellipsoidal, furrow membranes heavily flecked; germ pore decidedly elliptical. — Fagopyrum esculentum
- (2) Grains nearly spherical; furrow membrane lightly flecked, germ pore somewhat elliptical or circular. — Antigonum guatemalense

b. Grains less than 40 μ in length.
- (1) Bulging between the furrows, therefore tending to be triangular in cross section. Furrow margins raised; pore circular; Texture granular throughout. — Chorizanthe pungens, Chorizanthe Parryi
- (2) Not bulging between the furrows; furrow margins not raised.
  - (*a*) Grains 32 to 39.5 μ long; germ pore nearly or quite circular; texture fine-pitted. — Triplaris americana, Triplaris caracasana, Triplaris felipensis

- (*b*) Grains 27.5 to 31 μ long.
  - (1) Germ pores circular
    - Furrow membranes flecked. — Eriogonum gracile
    - Furrow membranes smooth. — Erigonum galioides
  - (2) Germ pore elliptical; furrow membranes smooth. — Polygonum buxiforme, Polygonum allocarpum

2. Chimerical, with part of the surface granular and part alveolate. — Polygonum californicum

3. With entire surface alveolate; furrows always 3, short, not extending much beyond the pores; grains about 43 μ in diameter. — Polygonum chinense

II. Furrows absent; entire surface alveolate; pores about 30, disposed over the surface in the trischistoclasic system; grains 45 to 70 μ in diameter. — Persicaria Muhlenbergii, Persicaria pennsylvanica, Persicaria hydropiperoides, Persicaria Persicaria, Persicaria acuminata, Tracaulon arifolium, Tracaulon sagittatum

RUMEX L. Dock

Grains when moist spheroidal or tending to be somewhat ellipsoidal, slightly bulging between the furrows; somewhat various in size in the different species; those of *R. crispus* and *R. obtusifolius* 18 to 32 μ in diameter. Furrows long, very slender, and pointed at their ends, varying in number from three to six but generally three or four, arranged according to the trischistoclasic system. Furrow membranes smooth. Germ pores elliptical in shape, with their long axes directed in the same sense as those of the furrows, small, 3.4 to 4.6 μ long, sharply defined. Texture of the exine always distinctly pitted, though of somewhat various coarseness in the different species. Normal grains always tightly packed with starch, which shows plainly through the thin, transparent walls of the grain.

Rumex is a genus of about 140 species of mostly homely herbs, of wide distribution. Taxonomically they are grouped in the two sections, Acetosa and Lapathium. To the former belong the sorrels, *R. Acetosella*, *R. Acetosa*, and *R. scutatus*, and to the latter the docks proper, *R. crispus* and *R. obtusifolius*. The slight genetic difference between these two groups is reflected to a certain extent in the dimensions of their pollen grains, those of the ACETOSA group ranging, in the species here examined, from 18.2 to 23.9 μ in diameter, with their germ pores uniformly 3.4 μ in diameter, while those of the LAPATHIUM series range from 26.5 to 32 μ in diameter, with their germ pores 4.6 μ in diameter. The pollen of other species of these two groups should be examined to see if this difference holds for all and is really a character of sectional value.

All are wind pollinated, and some are counted as minor factors in hayfever. *R. hymenosepalus* Torr., Canaigre, is cultivated in California and is said to be an important cause of hayfever in San Fernandez valley (Selfridge, 1920). *R. conglomeratus* Murr. is stated by Hall (Scheppegrell, 1917) to be of only minor importance in California, though abundant and producing much pollen. The pollen of the various species possesses all the physical characters of hayfever pollen and, in my experience, is caught on the pollen slides in fairly large quantities almost throughout the summer. The reason why it should be so much less toxic to hayfever patients than the pollen of the grasses or even of plantain is probably bound up with its chemical make-up and deserves further inquiry.

The grains of six species are described and illustrated by Meinke (1927) in connection with his studies on Postglacial silts, but, as far as I am aware, they are seldom recorded from bog deposits; this is probably owing to the fragile nature of their exine which, in all the species of this genus, is very thin and tends to collapse beyond recognition when empty.

Rumex Acetosella L. Sour dock (Plate VIII, Fig. 1) type. Grains rather uniform in size, 22 to 24 μ in diameter. Furrows three, more frequently four or occasionally six. Germ pores 3.4 μ long. Exine coarsely pitted, more so than in the grains of *R. crispus* and *R. obtusifolius*, about the same as in those of *R. Acetosa* and *R. scutatus*. These grains may be distinguished from the two latter, which they resemble most closely, in being prevailingly tetracolpate.

Low herbs in dry fields and waste places. Wind pollinated, shedding large amounts of light, air-borne pollen, June and July; throughout North America, except in the extreme north; introduced from Europe. Generally speaking, rather an unimportant factor in hayfever. Said to be important in California (Rowe, 1928; Selfridge, 1920) and in Oregon (Chamberlain, 1927).

Rumex Acetosa L. Green sorrel. Sour or Sheep dock. Grains essentially as in the type, rather uniform in size, 18.2 to 21.6 μ in diameter. Furrows three, or less frequently four. Germ pores 3.4 μ long.

A low herb, similar to though much larger than the preceding. Introduced from Europe or Asia, now widely distributed in the United States and Canada, wind pollinated, shedding rather large amounts of pollen in early summer. Not known to be a factor in hayfever but probably not distinguished from the preceding species.

Rumex scutatus L. Roman sorrel. Grains spheroidal, uniform, 23.9 μ to 25.1 μ in diameter, furrows nearly always three, texture more finely pitted than in the two preceding species. Otherwise as in the type. A low weed widely distributed in Europe; wind pollinated but not known to cause hayfever.

Rumex crispus L. Curled or Yellow dock. Grains spheroidal, rather uniform in size, 28.5 to 32.0 μ in diameter. Furrows three or rarely four or five; germ pore 4.6 μ in length. Otherwise as in the type. These grains may be distinguished from those of the three preceding species by their larger size and from those of *R. obtusifolius*, which they resemble more closely, by being prevailingly tricolpate and with a somewhat finer texture to their exine.

Tall rank herbs, roadsides and waste places almost throughout North America; wind pollinated but shedding relatively little pollen and constituting, outside a few restricted localities, only a minor cause of hayfever. It is, however, regarded as important in Oregon (Chamberlain, 1927). In California it is regarded as unimportant by Hall (Scheppegrell, 1917) but as important by Selfridge (1920). In my experience in the vicinity of New York City it sheds too little pollen ever to become a serious factor in hayfever.

Rumex obtusifolius L. Broad-leaved or Bitter dock. Grains spheroidal in shape, somewhat various in size, 26.4 to 31 μ in diameter. Furrows prevailingly four, less frequently three or six, rarely five. When more than three they are somewhat variously united or irregular in arrangement. Germ pores 4.6 μ long. Otherwise as in the type. This grain may be distinguished from that of *R. crispus*, which it resembles most closely, by being prevailingly tetracolpate and of a slightly more coarsely pitted texture.

A rank weed of roadsides and waste places. Similar in habit and appearance to the preceding. Regarded as a minor cause of hayfever in California (Hall in Scheppegrell, 1917).

Rheum officinale Baillon Tibetan rhubarb. Grains similar to those of *Rumex Acetosella*, spheroidal or ellipsoidal, rather uniform, about 30 μ in diameter; tricolpate, with furrows long and very slender, sunken in the surface of the grain to such an extent as to give it a three-lobed shape; each is provided with a single small, round or nearly round pore. Exine somewhat heavier, and pitting finer than in the type.

Native of Tibet and western China. Occasionally cultivated as a foliage plant and the source of at least part of officinal rhubarb. The genus *Rheum* L. includes about 20 species, native of Asia, from Siberia to Himalaya and Palestine. The best known species is the common garden rhubarb or wine plant, *R. Rhaponticum* L.

Muehlenbeckia vulcanica (Benth.) Endl. Grains resembling those of *Rumex Acetosella*, spheroidal or oblately flattened, 26 to 27.5 μ in diameter; texture granular, with the granules fused so as to form a more or less continuous reticulum. Otherwise as in the type.

The genus *Muehlenbeckia* comprises about 15 species of small shrubs and woody climbers, native of Australia, New Zealand, South America, and the Solomon Islands. The flowers are not showy and are unisexual, monoecious, or dioecious; they therefore appear to be wind pollinated, though I have not been able to determine this point with certainty. Among them are such well-known cultivated plants as the wire plant, *M. complexa* Meissn., a creeper from New Zealand, much cultivated in California and elsewhere; and the curious centipede plant, *M. platyclados* Meissn., a curiosity of the greenhouse, from the Solomon Islands.

ERIOGONUM Michx. Eriogonum, Umbrella Plant

Grains uniform in shape and size, ellipsoidal, about 32 by 25 μ; tricolpate, with long, tapering furrows which gape open

when the grain is moist, disclosing the circular germinal aperture through which the pore bulges prominently. The furrow membrane is for the most part smooth, though occasionally it may be lightly flecked with a few granules which tend to occupy a strip along its center. Exine thick, slightly thicker along the margins of the furrows and along three meridional strips between the furrows, recalling the thickenings in the grain of *Chorizanthe;* texture distinctly and rather coarsely granular, with the granules in the vicinity of the germ pores tending to be arranged in rows resembling thumb-print markings but unorganized in other parts of the grain.

These grains differ from those of the foregoing genera in their heavier exine and consequently better development of their furrows. The plants are insect pollinated, while those of *Rumex* and *Rheum* and probably *Muehlenbeckia* are wind pollinated. Thus we see, in the comparison of the grains of these two groups, an expression of an almost universal law—that when pollen becomes dispersed by wind the exine becomes thinner. This form of grain may be regarded as the least specialized in the family, the form from which the others were probably derived.

The genus comprises over 200 species of low herbs, native of America, mostly of the western states. All are insect pollinated, and none is regarded as a cause of hayfever.

Eriogonum gracile Benth. (Plate VIII, Fig. 6). type. Grains as in generic description, furrow membrane occasionally slightly flecked. Dry plains, valleys, and low hills: Great Salt valley and Coast Ranges to southern California and Lower California.

Eriogonum galioides I. M. Johnston. Grains as in generic description, furrow membrane smooth. Low, prostrate, perennial herb, common on San Luis Island, Gulf of California.

CHORIZANTHE R. Br.

Grains similar to those of *Eriogonum*, somewhat ellipsoidal, about 30 by 25 μ, tricolpate, with rather short, tapering furrows with their margins conspicuously raised, forming prominent ridges. Germ pore clearly defined, circular; furrow membrane smooth. The grain bulges quite conspicuously between the furrows, thus giving it something of a triangular shape in optical section (Plate VIII, Fig. 3). Exine thick and very coarsely granular, but granules without lineal arrangement. These grains differ from those of *Eriogonum* in the greater extent of their intercolpar thickenings, their more coarsely granular texture, and their shorter furrows.

About 30 species in western North America and Chile. Low, dichotomously branching desert herbs.

Chorizanthe pungens Benth. (Plate VIII, Fig. 3). As in generic description, indistinguishable from the preceding species. Low, prostrate herb, common in San Francisco Bay region of California and southward.

Chorizanthe Parryi Wats. As in the generic description. Low, flat-topped plants 3 to 15 in. broad, southern California, common on gravelly mesas near Crofton, San Bernardino County.

TRIPLARIS Löfl.

Grains ellipsoidal or nearly or quite spheroidal when fully expanded, tricolpate, with furrows long and tapering but narrower than in *Eriogonum*. Germ pores circular or slightly elliptical. Furrow membranes smooth. Exine rather thick but various in the different species, more or less granular and distinctly but finely pitted. These grains differ from those of *Eriogonum* in their more nearly spheroidal shape, thinner exine without thickenings between the furrows or along their margins, and fine pitting of the exine. In all of these characters they tend to resemble *Rumex*.

A genus of about 10 species of small trees, tropical South America.

Triplaris americana L. Grains uniform, spheroidal or short-ellipsoidal, about 35.3 by 33.1 μ, always tricolpate. Otherwise as in the generic description.

Native of South America, occasionally cultivated under glass or out of doors in the southern states.

Triplaris felipensis Wedd. Grains uniform, spheroidal when expanded, 35.3 to 36.5 μ in diameter. Otherwise as in generic description. Colombia, South America.

Triplaris caracasana Cham. Grains uniform, spheroidal, 31.4 to 34.2 μ in diameter. Pitting of the exine finer than in *T. americana*. Otherwise as in the generic description. Venezuela. Flowers in May.

Fagopyrum esculentum Moench. Buckwheat. Grains long-ellipsoidal in shape, extremely various in size, but the majority of them measuring about 57 by 47 μ; tricolpate, with furrows long and tapering; germ pores not sharply defined but decidedly elliptical; furrow membranes conspicuously flecked with large, coarse granules. Texture conspicuously pitted and with a coarse, underlying granular structure.

A low annual herb, native of Europe and northern Asia, much cultivated elsewhere and frequently escaped. June to September. Insect pollinated.

Antigonum guatemalense Meissn. Grains short-ellipsoidal to spheroidal, 57 to 62 μ long, tricolpate, with rather long, tapering furrows. Germ pores sharply defined, circular or slightly elliptical. Furrow membranes lightly flecked with a few loose, scattered granules. Exine thick and rugged with a coarse-granular and pitted texture. This grain may be distinguished from that of *Fagopyrum* by its more nearly spherical shape, coarse texture, and less conspicuously flecked furrow membranes. Woody climbers in Guatemala.

The genus *Antigonum* comprises three or four species of tendril-climbing vines, in Mexico and Central America. One species, the coral vine or corallita, is cultivated in the southern states for the beauty of its bright-pink flowers.

POLYGONUM (Tourn.) L. Knotweed, Jointweed

Several very different forms of grain are found among the species of this genus, and these exhibit characters both of the preceding genera and of the very different grains of the succeeding genera. The basic form of grain of *Polygonum* is tricolpate, with long tapering furrows, heavy granular exine, and decidedly ellipsoidal shape, essentially the same as that of *Eriogonum* (Plate VIII, Fig. 6) except that it lacks the intercolpar thickenings of the exine and the thickenings along the margins of the furrows of the latter. This form of grain is exhibited, among those members of this genus which we have before us, only by *P. buxiforme*. I have not been able to examine the pollen of more than a very few species and therefore cannot say from personal observation whether or not this form really does characterize the grains of the majority of them. Nevertheless, Fischer (1890) finds that all 10 of the species that he examined "haben drei parallele Falten mit je einer kreisrunden Keimpore; die Exine ist doppelt die Zwischenstäbchen an den Polen feiner und dichter, an den Seiten dicker und weitlänfiger gestellt; Oberfläche fast glatt." It therefore seems safe to assume that such is the basic form of the pollen grains of *Polygonum*.

This simple form undergoes, in some of the species, two highly suggestive modifications. The first is the rather remarkable multiplication of furrows, recalling the condition in *Rumex* and others, *e.g.*, in the grains of *P. allocarpum*. In the grains of this species the furrows are beautifully symmetrical and occur in most of the theoretically possible arrangements of the trischistoclasic series of configurations up to that requiring 12 furrows, and it is likely that an examination of the pollen of other species or possibly a more extended examination of the pollen of this species would discover some grains with higher numbers of furrows in the same system.

The other modification that the simple basic tricolpate grain undergoes in this genus is the development of an alveolate structure of its exine. This is partly expressed in the grains of *Polygonum californicum* in which the alveolate and simple granular characters are combined in chimerical fashion. It reaches its fullest expression, however, in the grains of *P. chinense*, in which the entire surface is alveolate, in this respect resembling the grains of *Persicaria*.

Polygonum buxiforme Small Shore knotweed. Grains uniform ellipsoidal, averaging about 28 by 23 μ. Furrows three, occasionally six, long and tapering, deeply depressed, giving the grains a lobed appearance. Furrow membrane smooth, germ pore elliptical, with its long axis directed in the same sense as that of the furrow. Exine thick, with texture distinctly but finely granular. These grains are similar to those of *Chorizanthe* and *Eriogonum* but do not bulge between the furrows as in the former, and their germ pores are distinctly elongate instead of circular, as in the latter.

A prostrate, bushy weed, on shores and in waste places, almost throughout the United States and Canada. August and September.

Polygonum allocarpum Blake. Grains essentially as in *P. buxiforme*, except that the majority have 6 furrows, relatively

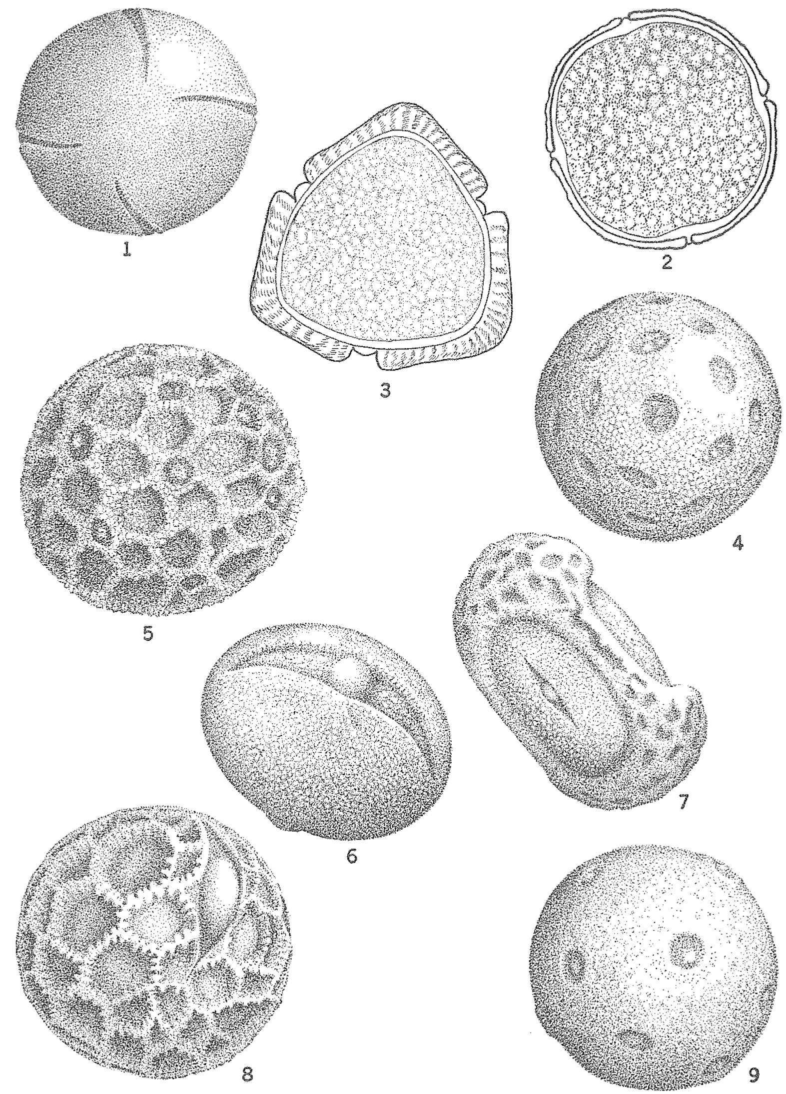

PLATE VIII.—Pollen grains of Polygonaceae and Chenopodiaceae. 1, *Rumex Acetosella*, polar view, 23 μ in diameter. 2, *Rumex Acetosella*, transverse optical section. 3, *Chorizanthe pungens*, optical section, 25 μ in diameter. 4, *Salsola Pestifer*, 27.5 μ in diameter. 5, *Persicaria Muhlenbergii*, 57 μ in diameter. 6, *Eriogonum gracile*, side view, 32 × 25 μ. 7, *Polygonum californicum*, side view, 19 by 12.5 μ. 8, *Polygonum chinense*, 43 μ in diameter. 9, *Sarcobatus vermiculatus*, 28 μ in diameter.

few have 3, and occasionally grains with 4, 5, 9, and 12 furrows are found. In nearly all of these the furrow configurations are beautifully regular, conforming almost exactly with the trischistoclasic system. The grains are uniform in size, 28.5 to 29.6 μ in diameter.

Branching annual herb, seacoasts and adjacent islands, Maine and New Brunswick.

Polygonum californicum Meissner (Plate VIII, Fig. 7). Grains uniform in size and shape, ellipsoidal, 19.0 by 12.5 μ. The exine of the two ends and three longitudinal strips, alveolate, almost as in *Persicaria*, but over three large elliptical areas surrounding the three furrows the exine is granular, as in the grains of *Polygonum buxiforme* and *P. allocarpum*. Furrows short and tapering, furrow membranes smooth, germ pore elliptical. This grain combines the characters of those of *Persicaria* and *Polygonum* in such a way that it may truly be spoken of as chimerical and suggests the mode whereby one form could have been derived from the other.

A slender, wiry annual, diffusely branching, 3 to 7 in. high. Dry foothills, Sierra Nevada and north Coast Ranges; north to Washington. July.

Polygonum chinense L. (Plate VIII, Fig. 8). Grains uniform, spheroidal, about 43.3 μ in diameter, tricolpate, with furrows short and sharply tapering, furrow membrane smooth, germ pore large, elliptical, occupying nearly the whole furrow. The entire surface of the grain is marked off into angular lacunae by a reticulate system of high ridges. In this respect the grain is almost exactly like the grains of *Persicaria*. The ridges have the appearance of being composed of vertical prisms partially fused together, making irregular, jagged, palisade-like partitions between the lacunae. The floors of the lacunae are studded here and there with a few little bead-like thickenings. The alveolar system abuts upon the furrows with mostly closed lacunae, showing that the furrows are not torn through the reticulum but are developed simultaneously with it as co-ordinate structures.

This form of grain is curiously intermediate between the basic form of the genus and the furrowless, alveolate form of *Persicaria* but tends more toward the latter. In its large size, spheroidal form, and alveolate surface it is persicarioid, but in its possession of three furrows with three germ pores it is polygonoid.

A shrubby perennial about 5 ft. high, with white, pink, or purplish flowers in small, panicled heads. Native of the Himalaya region and Ceylon to China and Japan and of the Philippines. Occasionally cultivated.

PERSICARIA (Tourn.) Mill.

Grains spheroidal, rather large, ranging from about 51 to about 70 μ in diameter; alveolate, with the whole or part of the surface marked off into angular lacunae by a reticulate system of well-defined ridges (Plate VIII, Fig. 5). The texture of the floor of the lacunae is more or less pebbled, always coarse but various in the different species. The pebbled structure also involves the ridges, which are extremely rough and jagged as a consequence, presenting the appearance of a breakwater built of closely packed but crookedly driven piles. Elements similar to those which go to make up this remarkable structure are encountered in a lesser degree of development in the granular and pitted texture of the grains of *Fagopyrum* and *Antigonum* and, to a lesser extent, of *Rumex;* so this structure, remarkable as is its appearance, cannot be said to have arisen *de novo* in this genus or in *Polygonum* but is in reality the culmination of a tendency variously expressed in the grains of most of the other species of the family.

Furrows are entirely absent in all species here considered; the germ pores are set here and there in the ordinary lacunae of the reticulum, and the lacunae occupied by them are frequently difficult to distinguish from those that are unoccupied but may generally be recognized by their smaller size and their smooth and slightly bulging floor. The system governing the arrangement of the pores is not readily apparent, because in all the species which we have before us the pores are round and consequently do not divulge their spacial orientation in the way that furrows do. It can readily be seen, however, that their arrangement is not isometric, as would be suggested by their rounded form; for if one pore is regarded as a center of a group, it is found not to be surrounded by five or six others at equal distances, as would be the case if their arrangement were isometric. Instead, they are arranged according to the trichistoclasic system, as in most furrow configurations. In these grains if one pore is regarded as a center, it is found to be flanked by two pairs of pores which are equidistant and on opposite sides (Fig. 100). The pattern of the arrangement of the group of five pores thus obtained resolves itself into two equilateral triangles in which the initial or central pore of the group serves as the apex of both; and we find that each of the three pores of each triangular group is likewise the member of a neighboring triangular group, thus forming a continuous system throughout. The characteristic whereby

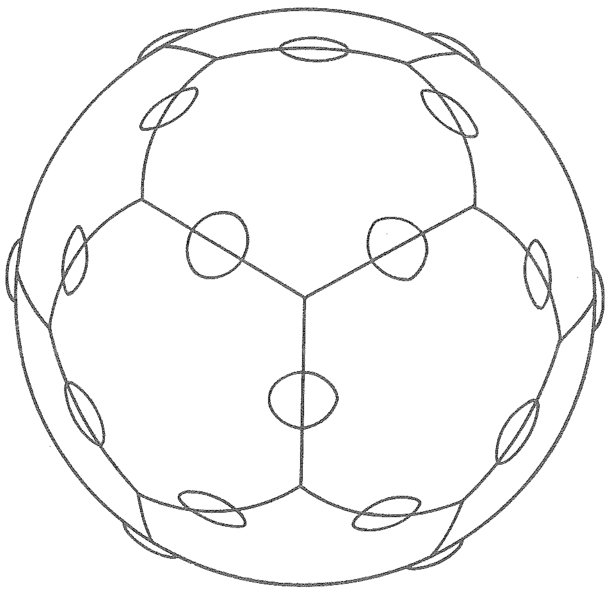

FIG. 100.—Diagram of the pore arrangement of a *Persicaria* pollen grain with 30 pores arranged in the trischistoclasic system. The lines drawn through the pores represent the hypothetical furrow axes and correspond in arrangement to the edges of a pentagonal dodecahedron.

this system may be recognized is the repetition of the triangular group.

The circular form of the pores of the species of *Persicaria*, which we have before us, makes it surprising that their arrangement should be according to that of the trischistoclasic system, one which is generally associated with elongate furrows rather than circular pores. Much light, however, is thrown on their origin by a consideration of the grains of *P. amphibium*, which, according to the description of Fritzsche (1837) and his beautiful figure,

are provided with 30 furrows, marking off the surface of the grain into 12 pentagonal areas corresponding exactly to the 12 faces of a pentagonal dodecahedron. If, in such a grain as this, the 30 elongate furrows were to be replaced by as many round germ pores, their arrangement would be exactly like that of the various species of *Persicaria* which we have before us (except that the number of pores is not always 30), and I have no doubt that such is the explanation of the peculiar arrangement of these pores. They should be regarded as shortened furrows, derived from a many-furrowed grain in which the arrangement of the furrows followed the ordinary trischistoclasic system. The cause of the shortening was probably due to the extraordinary development of the reticulate pattern, with its resultant demobilization. The large number of pores possessed by these grains (about 30) abundantly compensates for the loss of the harmomegathic action of the furrow, for changes in volume are readily accommodated by the bulging or invaginating of so many pores.

A large genus of about 125 species of annual or perennial herbs. Prince's-feather, *P. orientalis* (L.) Spach, is a familiar example in cultivation.

Persicaria Muhlenbergii (S. Wats) Small Swamp persicaria (Plate VIII, Fig. 5) type. Grains rather uniform in size, about 57 μ in diameter, ridges of the reticulum heavy, apparently composed of more or less vertical prisms. The floors of the lacunae quickly and coarsely pebbled. Otherwise as in the generic description. In swamps and moist soil almost throughout North America. July to September.

Persicaria pennsylvanica (L.) Small Pennsylvania persicaria. Grains uniform, 68 to 74 μ in diameter, essentially as in the type, except that the ridges are a little heavier. Nova Scotia to Ontario, Minnesota, Florida, and Texas. July to September.

Persicaria hydropiperoides (Michx.) Small Wild water pepper. Grains rather uniform, essentially as in the type, about 45.6 μ in diameter.

In swamps and wet soil. Almost throughout the United States and adjoining parts of Canada.

Persicaria Persicaria (L.) Small Lady's-thumb, Heartweed. Grains uniform, 43 to 51 μ in diameter, essentially as in the type.

In waste places throughout North America, except the extreme north. Naturalized from Europe. June to October.

Persicaria acuminata (H. B. K.) Grains uniform, about 51.3 μ in diameter. Essentially as in the type. In moist, shady places almost throughout South America.

Tracaulon arifolium (L.) Rap. Halberd-leaved tearthumb. Grains essentially as in *P. Muhlenbergii*, uniform, 51.3 μ in diameter. A slender, reclining, perennial herb with prickly stem, in moist places. New Brunswick and Ontario to Minnesota and south to Georgia. July to September.

Tracaulon sagittatum (L.) Small Arrow-leaved tearthumb. Grains as in *P. Muhlenbergii*, uniform, about 57 μ in diameter. Plants similar to the preceding except for the arrow shape of the leaf.

CHENOPODIACEAE Goosefoot Family

Grains when moist and expanded spheroidal, 19 to 33 μ in diameter. Exine thin and granular, psilate, cribellate. Furrows absent but represented by round pores varying in number from 14 to α (Plate VIII, Figs. 4, 9).

The grains of the Chenopodiaceae are rather uniform throughout the family and are indistinguishable from those of the related family Amaranthaceae. They are similar to those of the Nyctaginaceae but may easily be distinguished from the latter by their smaller size and thinner exine.

The pores are generally nearly circular in outline, though they may be somewhat irregular, but they are never elongate and never resemble furrows in the ordinary sense of the word. Their structure is simple; they are always crossed by a delicate membrane flecked with a number of granules which may be aggregated toward the center and even fused to form a central mass resembling an operculum, as in the grains of the Gramineae. The distribution of the pores over the surface of the grain is not isometric, though at first sight it often appears to be so, and, indeed, in those grains in which the pores are numerous, they closely approximate such an arrangement. On the other hand, in grains in which there are fewer, measurements of the intervals between them reveal great variation in this distance, and, under favorable conditions it can be seen that the pores tend to be grouped in threes in the trischistoclasic system. Consequently, we feel safe in drawing the same conclusion here that we did in the grains of *Persicaria*, that is, that these pores are morphologically furrows which are so shortened that they exactly coincide with their enclosed germ pore.

We have already seen that the multiple-pored condition arose among the grains of the Polygonaceae in response to the necessity of accommodating changes in volume in the face of an impaired harmomegathic function of the furrows. Yet among the Chenopodiaceae the pores play only a negligible part in this function. The pore membranes may be drawn in or pushed out in response to slight changes in volume, but when the grain dries to any extent it always becomes deeply concave on one side. The thin and flexible nature of the exine thus does away with any necessity for special organs of harmomegathy. Why, then, are the pores of these grains so numerous? The answer is probably to be found in the fact that the Chenopodiaceae are derived from some entomophilous ancestor the exine of whose pollen grains was heavily sculptured and demobilized, as in the grains of *Persicaria*, compelling a great increase in the number of the reduced furrows to accomplish harmomegathy. Then, with the subsequent reduction of the sculpturing in response to wind pollination, the large number of pores has remained because it is not in the nature of evolution to go backward. The many-pored condition of these grains must, therefore, be looked upon as a relic character of very ancient origin, whereas their psilate character is a much more recent response to anemophily.

It is interesting, and perhaps not without profit, to speculate further on this doctrine. If the evolution of these grains should continue further in the same direction, the exine would become progressively thinner, and the pore membranes, no longer requiring flexibility, might, with profit to the grain, become thicker and give greater protection, until a stage was reached where there could be no distinction between the exine and the pore membranes. Indeed, some of the many-pored grains of the Chenopodiaceae and Amaranthaceae have very nearly reached this condition. Or if, on the other hand, the plants should return to entomophily, and the grains, released from the necessity of retaining their buoyancy, should greatly increase in size, the pores would likewise increase in size and require some protection for their membranes. Such a condition is realized among the grains of the Nyctaginaceae, a family of plants which are closely allied to the Chenopodiaceae but highly specialized in insect pollination. The grains of many of these are exceedingly large; those of *Mirabilis Wrightii*, for example, are 187 μ in diameter and have a thick and rigid exine provided with spines and various other adornments. But they are cribellate like the grains of the Chenopodiaceae. As a consequence of the rigidity of the exine of these grains, harmomegathy is entirely taken over by the pores which are very large; they bulge prominently when the grain is moistened and sink deeply inward when it is dried. But on account of their large size the pores require protection. They are almost completely covered over by a conspicuous operculum which resembles a spiked helmet and suggests from its appearance that it could have been derived from the aggregation and coalescence of flecks similar to those that characterize the pore membranes of the grains of the Chenopodiaceae. The result is an armored pore possessing great flexibility and clearly excellently adapted to accommodating changes in volume.

The implication of this doctrine is that the Chenopodiaceae and the Nyctaginaceae represent two divergent lines originating from some ancestral form with many-pored grains like those of *Persicaria*, the Chenopodiaceae developing under the influence of anemophily and the Nyctaginaceae under the influence of entomophily.

The Chenopodiaceae include about 550 species in about 75 genera of annual and perennial herbs and shrubs, of wide geographical distribution. Of the American representatives all are wind pollinated, and many of them very serious causes of hayfever. Their pollen has rarely been identified from Postglacial silts, but Lewis and Coke (1930), without attempting to identify the grains, state that "a very considerable number [of pollen grains] of other herbs may be distinguished as belonging mostly to the Chenopodiaceae and related families."

For a discussion of the importance of these plants in hayfever the reader is referred to Lamson and Watry (1933*a*, *b*).

Salsola Pestifer A. Nels. (*S. Tragus* Reichnb.) Russian thistle, Saltwort (Plate VIII, Fig. 4) type. Grains nearly or quite spherical, rather uniform in size, averaging 27.6 μ in diameter. Pores large, the largest observed in the family, 3.7 μ in diameter and about 6.6 μ apart, measured from center to center.

The pore membranes are flecked with six or eight loosely distributed granules and are nearly circular but with slightly wavy margins. The texture of the exine is decidedly granular, more distinctly so than that of the grains of *Chenopodium* and *Amaranthus*, and this, together with the wavy margins of the germ pores, imparts to the grains a more rugged appearance.

Russian thistle is a common weed, particularly of the Great Plains region of the United States. It flowers during the latter part of summer and causes much hayfever; it has been reported among the worst hayfever weeds in Oklahoma (Balyeat, 1926), in Colorado (Mullen, 1922), in Oregon (Chamberlain, 1927), and in Arizona (Phillips, 1923).

Sarcobatus vermiculatus (Hook.) Torr. (*S. Maximiliani* Ness.) Greasewood, Chico (Plate VIII, Fig. 9) type. Grains spheroidal, 23.9 to 29.6 μ in diameter; germ pores rather small, averaging 2.9 μ in diameter, widely spaced, about 10.8 μ apart measured from center to center. In appearance the pores are somewhat irregular in outline and with their membranes marked by a single large fleck with a jagged outline, suggesting that it is composed of a number of smaller flecks fused together. The texture of the general surface is smooth, thus presenting a much less rugged appearance than that of *Salsola Pestifer*. The most distinguishing character of these grains is the wide distance apart of their pores and, consequently, their small number, which is generally about 14 or 16, varying with the size of the grain. The distance between the pores is also extremely various, a necessary corollary to their arrangement in the trischisticlasic system.

Greasewood is a common plant in saline and arid regions; Saskatchewan to Texas to California to Washington; flowering throughout the latter part of summer. The flowers are wind pollinated and shed rather large amounts of pollen which is probably an important cause of hayfever in some regions. It has not been reported from Postglacial silts, but growing in or near salt marshes, as it frequently does, it is likely that it will eventually be found.

Chenopodium album L. Goosefoot, Lamb's-quarters. Grains various in size, many obviously abortive. Normal grains about 28.4 μ in diameter. Germ pores uniform, 2.5 μ in diameter and regularly arranged over the surface, about 5.4 μ apart. Margins of the pores slightly wavy; pore membranes marked by several loosely distributed flecks. Texture of the general surface of the exine sharply but finely granular.

A common weed of gardens and roadsides throughout most of the United States, flowering in late summer. In the eastern part of its range goosefoot is of little or no importance in hayfever, but in the western part it is believed to cause much hayfever. Thus it is said to be important in Colorado (Mullin, 1922), California (Rowe, 1928; Selfridge, 1920), Oregon (Chamberlain, 1927), and southern Arizona (Phillips, 1922) but is stated by Balyeat (1926) to be of little consequence owing to the lack of toxicity of its pollen. In the author's experience, though its pollen occasionally gives slight reactions with hayfever patients, it has proved of no consequence in the northeastern United States.

Chenopodium ambrosioides L. Mexican tea. Grains somewhat various, averaging 22.8 μ in diameter; pores 1.2 μ in diameter, evenly distributed, about 3.8 μ apart, nearly or quite circular and with even margins, membranes marked by a single central fleck which appears to be composed of four or five flecks fused. Texture of the general surface of the exine slightly coarser than that of the grains of *C. album*. These grains also differ from the latter in their slightly smaller and more numerous pores, the tendency toward fusion of the granules of the pore membranes, and the slightly coarser texture of their exine.

A common weed of farms and gardens, flowering in late summer, shedding a large amount of pollen which is probably a minor cause of hayfever throughout most of its range. It is said by Selfridge (1920) to be an important cause of hayfever in California, but Hall (Scheppegrell, 1917) states that it is of minor importance in this region.

Kochia scoparia Schrad. Burning bush, Summer cypress. Grains various, 29 to 34 μ in diameter. Germ pores various about 2.9 μ in diameter and about 5.9 μ apart, approximately circular and with their membranes marked by a central group of small flecks which may be more or less fused. Exine coarsely and distinctly granular.

An ornamental garden plant, introduced from Europe and Asia and extensively cultivated in the United States. In some regions, particularly in parts of Colorado, it has escaped from

cultivation and become a troublesome weed. It flowers in late summer, shedding much pollen which is known to be a frequent cause of hayfever (Mullin, 1922; Waring, 1926).

Eurotia lanata (Pursh) Moq. Winter fat, White sage, Winter sage. Grains various, 22 to 26 μ in diameter; germ pores 2.5 to 3.1 μ in diameter and 3.4 to 6.8 μ apart. Pore membranes marked by flecks tending to clump toward the center. General surface of the exine granular.

A whitish, tomentose undershrub, common in semiarid regions; Saskatchewan to Texas to California to Washington. Flowers in late summer, shedding relatively little pollen, but is occasionally considered to be a cause of hayfever (Waring, 1926).

DONDIA Adans. Sea blite

Grains rather various in size, 18 to 25 μ in diameter. Pores uniform in size and arrangement, their membranes marked with a single central fleck. Texture of the exine distinctly granular but less so than in the type (*Salsola Pestifer*) or most other members of the family.

The sea blites are common weeds, particularly in the warmer parts of the United States. They shed large amounts of pollen throughout most of the summer but are not generally regarded as hayfever weeds, though Hall (1922) regards *D. fruticosa* as important in this respect in California. In this connection, however, they are deserving of further study because, in their enormous abundance in many places in the southwestern United States, the huge quantities and buoyant character of their pollen, and their close relationship to such a toxic hayfever plant as Russian thistle they possess qualities which are strongly suggestive of hayfever plants.

Dondia suffrutescens Heller (*Suaeda suffrutescens* S. Wats.) Sea blite, Alkali blite. Grains various, 18 to 25 μ in diameter, pores about 2 μ in diameter and about 4.27 μ apart.

A common weed in alkaline valleys from southern California to the Rio Grande.

Dondia nigra (Raf.) Standl. (*Suaeda diffusa* S. Wats.). Grains uniform, 22.8 to 23 μ in diameter; pores about 2.28 μ in diameter and about 5.2 μ apart. Otherwise indistinguishable from the preceding species.

A common weed similar to the preceding species, in sagebrush plains and alkaline soils. Wyoming to New Mexico to Arizona to Oregon to northern Mexico.

Spinacia oleracea L. Spinach, Spinage. Grains uniform, except a few that are abortive and a few that are dwarf, 30 to 35 μ in diameter, dwarfs 12 to 16 μ. Pores uniform, 6.48 μ in diameter and 2.28 μ apart; pore membranes marked with a few fine flecks which tend to be aggregated toward their centers. Texture of the exine finely granular and marked with black specks which are clearly defined and widely spaced.

A common garden herb introduced from China. Though it sheds much pollen during the summer it is not known to cause hayfever.

Allenrolfia occidentalis (S. Wats.) Ktze. (*Spirostachys occidentalis* S. Wats.) Burro weed. Grains remarkably uniform, 20.4 μ in diameter. Pores uniform in size and arrangement, 5.13 μ in diameter and 2.85 μ apart, flecked with a few small granules which are sometimes centrally placed. Exine diffusely granular.

A common plant of salt marshes. Utah to Arizona to California to Nevada. Flowers in July and September, but, though it sheds enormous quantities of pollen, it is not known to cause hayfever. On account of its characteristics and associations, however, it deserves therapeutical study.

ATRIPLEX L. Orach, Saltbush, Shad scale

Grains spheroidal, rather various in size, 20.5 to 27 μ in diameter; germ pores uniform in size and distribution, 2 to 3.2 μ in diameter and 4 to 5.7 μ apart in the different species. Pore membranes always flecked with several small granules aggregated toward their centers and, in some species, tending to be fused. Texture of the exine slightly granular.

The grains of the different species are virtually indistinguishable from each other by inspection. Measurements of their diameters and of the diameters and distance apart of the pores show that, in many cases, those of a single species vary enormously, often covering the entire range of the genus. Nevertheless, it appears likely that if biometrical methods were applied to these measurements, as has been done for the birches by Jentys-Szafer (1928) and others, it would be found possible to distinguish the different species of *Atriplex* by their pollen, with a fair degree of accuracy.

The genus comprises about 130 species of general distribution. About 60 species are native of North America, occupying saline, arid, and semiarid soils throughout the continent. They are annual or perennial shrubs or herbs. Many of them shed enormous quantities of pollen which frequently causes much hayfever, particularly in the southwestern United States, where the larger shrubby members of the genus are prevalent. Besides the native American species, the Australian saltbush, *A. semibaccata*, has been extensively cultivated for fodder in America and is regarded as an important cause of hayfever in California (Selfridge, 1920).

Some of the species exist in several forms or races, and, though these present no reliable criteria of distinction, they are frequently regarded as separate species. The large number of species, together with their various forms and a lack of agreement among the different authors upon their specific limits, has led to much confusion in the classification of the species of *Atriplex*. The most recent and successful treatment of this large and difficult genus is that of Hall and Clements (1923). Their treatment recommends itself particularly to hayfever students because their broad species concept corresponds closely to the specificity of allergic reactions.

Atriplex patula L. Spear scale, Spear orach. Grains various, ranging in size from 22.8 to 27.5 μ in diameter. Pores 2 to 2.8 μ in diameter and 4 to 5.4 μ apart; pore membranes flecked. Texture granular.

A low, annual herb, abundant in saline soil and salt marshes almost throughout North America. It sheds relatively much less pollen than most species of the genus and, throughout the greater part of its range, cannot be considered a factor in hayfever, though it is said to be important in Oregon (Chamberlain, 1927). Its grains may occasionally be found in Postglacial silts and have been figured in this connection by Erdtman (1923). The plants are extremely various in form; Hall and Clements (1930) recognize eight subspecies and many minor variations, most of which are treated as separate species by other authors.

Atriplex Wrightii S. Wats. Orach, Annual saltbush. Grains uniform in size, excepting a few that are abortive, about 22 μ in diameter. Pores uniform in size and spacing, 2.28 μ in diameter and 4.56 μ apart, membranes slightly flecked. Texture granular right up to the edges of the pores.

A robust, erect or ascending, annual herb, abundant in saline soil in southwestern New Mexico, Arizona, and adjoining Mexico. Shedding much pollen which is a serious cause of hayfever in central Arizona (Phillips, 1923).

Atriplex bracteosa (Durand & Hillgard) S. Wats. Bractscale. Grains mostly uniform, except a few that are abortive and a few that are giants. Normal grains averaging 22.8 μ in diameter, giants 31.5 μ. Pores rather uniform in size and arrangement, 2.28 μ in diameter, 4.56 μ apart in normal grains and in the giants, showing that there is no correlation between the size of the grains and the size of the pores and their distance apart.

A robust annual herb, abundant in alkaline valleys, California, Lower California, and west-central Nevada. Flowers from April to October and sheds much pollen which is probably an important factor in hayfever, though in this connection it is not distinguished from other species of the genus.

Atriplex canescens (Pursh) Nutt. (*A. Nuttalii* S. Wats.) Wing scale, "shad scale." Grains uniform, excepting a few that are abortive. 23 to 25.5 μ in diameter. Pores 2.2 to 2.6 μ in diameter and 4.5 to 5.2 μ apart. Pore membranes flecked with a group of small granules aggregated toward the center. Texture granular.

A large, erect, woody shrub, exceedingly various, the most widely distributed of the shrubby species of the genus. It has a wide range of adaptability but is usually found in saline soils and alkaline flats. Alberta to Kansas, western Texas and adjacent Mexico, Washington, and Montana. It flowers throughout the summer, shedding enormous quantities of pollen. Owing to its wide range, great abundance, and large quantities of pollen, it is a very serious cause of hayfever in many regions, particularly in the southwestern states (Phillips, 1922, 1923; Watson and Kibler, 1922). This species is generally known in hayfever literature as "shad scale," but the name is not applicable and should be reserved for *Atriplex confertifolia*.

Beta vulgaris L. Beet, Sugar beet, Mangle. Grains rather uniform, except for a few that are abortive, about 19.4 μ in diameter. Pores uniform in size and arrangement, about 2.73 μ in diameter and 5.58 μ apart, their membranes flecked with small granules aggregated toward the center and sometimes fused. Texture of the exine distinctly granular.

A common garden herb, producing much pollen in summer. Not known to cause hayfever.

AMARANTHACEAE Amaranth Family

The grains of the Amaranthaceae, as a family, are not distinguishable from those of the Chenopodiaceae. This is entirely in keeping with the close relationship known to exist between the two families.

The Amaranthaceae are mostly weedy herbs, a few grown for ornament. The family comprises about 40 genera and 500 species, of wide distribution. All are wind pollinated, and many shed enormous quantities of pollen; as a consequence this family contains some of the worst hayfever weeds.

AMARANTHUS L. Amaranth

Grains as in the Chenopodiaceae, spheroidal, 23 to 35 μ in diameter, psilate, cribellate. Germ pores rather numerous, approximately equal in size, rather large, ranging, among the different species, from 2 to 4.5 μ in diameter, arranged in the trischistoclasic system, 5 to 9.1 μ apart. In shape they are generally circular, but sometimes their margins are wavy. The pore membranes are variously flecked with granules which are distributed at random over their surface, showing little tendency to be aggregated toward the centers. Though the size of the grains and the diameters of the pores and their distance apart show much variation within the species, such measurements afford attractive matérial for the application of the biometrical method and would probably reveal valuable interspecific differences.

The texture of the surface is always granular. In this there are some slight differences between the grains of the different species, but these are too slight and difficult of analysis to lend themselves readily to description.

The amaranths are mostly garden weeds, though some, for example, love-lies-bleeding (*A. caudatus* L.) and prince's-feather

(*A. hybridus hypochondriacus* Bailey), are well-known garden plants. All are wind pollinated, and several are troublesome hayfever weeds.

Amaranthus Palmeri S. Wats. Palmer's amaranth. Grains various, 22.8 to 25.3 μ in diameter; pores somewhat various in size and distance apart independently of the size of the grain, 2.28 to 4.56 μ in diameter and 5.1 to 8.0 μ apart. Apertures circular, with slightly wavy margins; pore membranes irregularly flecked.

A common weed in moist grounds. Kansas to Texas to Colorado to California and adjacent Mexico. Flowers from June to September, shedding much pollen which is a serious cause of hayfever in regions where abundant, *e.g.*, Oklahoma (Balyeat, 1926), California (Rowe, 1928), and Arizona (Phillips, 1922, 1923).

Amaranthus retroflexus L. Redroot pigweed, green amaranth, rough pigweed. Grains uniform, apparently all normal and healthy, 23 to 25 μ in diameter, pores uniform in size and evenly distributed, 2.28 to 3.7 μ in diameter and 5.4 to 8 μ apart, their membranes flecked with separate granules. Surface texture finely but distinctly granular, slightly finer than in the grains of *A. Palmeri.*

A common weed throughout North America. Flowers from August to October. It does not shed much pollen; consequently, it only occasionally becomes a factor in hayfever, though it is said to be important in this respect in Arizona (Phillips, 1922), Oklahoma (Balyeat, 1926), California (Rowe, 1928), and Oregon (Chamberlain, 1928). Its grains are not known to occur in Postglacial silts but are figured in this connection by Sears (1930).

Amaranthus spinosus L. Spiny amaranth. Grains as in *A. retroflexus*, 23 to 30.2 μ in diameter. Texture granular. Pores uniform, 2.84 μ in diameter and 7.1 μ apart. Pore membranes flecked with discrete granules.

A common weed throughout the United States and adjacent Canada and Mexico. From June to September it sheds much pollen which is a serious cause of hayfever in regions where the plant is abundant, *e.g.*, Oklahoma (Balyeat, 1926) and California (Hall in Selfridge, 1927).

Amaranthus hybridus L. Spleen amaranth. Grains somewhat various, 26.8 to 28.5 μ in diameter. Germ pores 2 to 3.4 μ in diameter, approximately circular but with wavy margins, their membranes variously flecked with discrete granules. Exine finely granular.

A weed in waste ground almost throughout the North American continent. Flowers August to October. Probably an important cause of hayfever, though in this connection not generally distinguished from *A. retroflexus* with which it is often associated.

Amaranthus graecizans L. (*A. sylvestris* Desf.) Tumbleweed. Grains various, 24.2 μ in diameter. Pores various in size and arrangement, 2.2 to 3.4 μ in diameter and 5.7 to 7.4 μ apart. Pore membranes flecked with discrete granules.

A common weed throughout North America. It sheds much less pollen than most other members of the genus and is, therefore, not generally important in hayfever, but it is said to be a minor factor in this respect in the Rocky Mountain and Pacific coast states (Hall in Scheppegrell, 1917) and an important factor in California (Selfridge, 1920).

Acnida tamariscina (Nutt.) Wood Western water hemp. Grains various, some abortive. Normal grains 21 to 28.5 μ in diameter; pores 2 to 2.8 μ in diameter and 3.4 to 4.6 μ apart, averaging about 4 μ, which is less than the interporal distance of any of the Amaranths. Pore membranes flecked with granules which tend to aggregate toward the center and fuse together.

A common weed of moist places. Illinois to South Dakota to Colorado to New Mexico to Louisiana. Flowers July to September shedding large amounts of pollen which causes much hayfever in regions where abundant. For example, in Oklahoma it is regarded as the worst hayfever weed (Balyeat, 1926). A drawing and photograph of this pollen grain are shown by Balyeat and Steaman (1927).

The genus includes about eight species of amaranth-like herbs, of wide distribution in moist places in the United States. They have not received sufficient study from the hayfever standpoint for us to be able to say to what extent they are responsible for this malady.

DROSERACEAE Sundew Family

Grains always united in tetrads which are generally tetrahedral. Component grains 31 to 67 μ in diameter. Pores 12 to 18, more or less concealed in the grooves between the grains, four or six on each of the contact faces. Exine of exposed surface thick, coarsely granular, and provided with characteristic spines, that of the contact surfaces thin and membranous.

The four cells are fastened together only at the center of the group, the greater part of their adjacent faces merely touching. Each grain is adapted to, and highly modified by, its union with its neighbors of the tetrad. Its three inner faces which are in contact with its neighbors are thin-walled and entirely lack the sculpturing which its fourth or outer face bears. Moreover, they are functionally interdependent, for the germ pores are so arranged that they open into the interstices between the grains, which mechanically serve the purpose of harmomegathi. The expansion and contraction of the grains with changes in moisture content cause the grooves to open and close in the same fashion in which furrows generally do.

Dionaea muscipula Ell. Venus's-flytrap (Plate IX, Fig. 7). Grains always arranged in tetrahedral tetrads; individual grains about 67 μ in diameter, each flattened on the three of its faces that are in contact with its three neighbors but broadly rounded on its outer face, possessing a curvature of shorter radius than that of the group as a whole, resulting in deep grooves between the adjacent faces of the grains. Texture of the exposed face of each cell, including that between the pores in the grooves, coarsely and sharply granular and adorned with short, rounded, peg-like spines of uniform size and shape but irregular arrangement. Germ pores about 12 to each grain, arranged along the outer margin of the flattened faces (four to each) in such a way that they open into the grooves between the cells.

The pores consist of circular holes cut sharply through the exine and each set in a small depression of its own, giving the margin of the cell a scalloped appearance when viewed from above. When the tetrads are moistened each cell expands and tends to become rounded, causing the grooves between them to open widely and expose the pores; but when the grains dry and contract they tend to flatten against each other, closing up the grooves and protecting the pores. Thus the mechanical action of the grooves between the adjacent faces of the grains of the tetrad, in opening and exposing the pores when moistened and closing and protecting them when dried, is the same as the action of the ordinary germinal furrows of the individual grains of other species.

A low bog herb, remarkable for its habit of capturing insects, to which purpose its leaves are admirably adapted. North and South Carolina. Flowers in Spring.

DROSERA L. Sundew

Grains uniform, always united in tetrads, generally tetrahedral in arrangement, rarely rhomboidal or square, of various sizes in the different species, individual grains 31.5 to 43 μ in diameter. Exine of outer surface of each cell thick, rigid, and of a granular texture, provided with close-standing sharp spines of characteristic shape, that of the proximal face of each grain soft and flexible and thrown into plaits which converge toward the innermost point of the grain where it joins with its three neighbors at the center of the tetrad (Fig. 101).

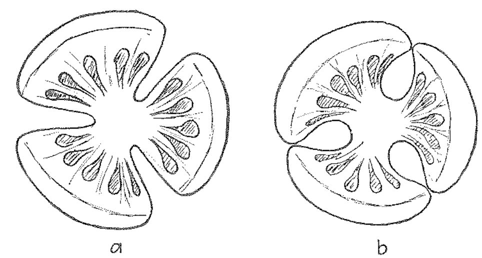

Fig. 101.—Tetrad pollen grains of *Drosera*, diagrammatic, with the upper cell of each removed to show the relative positions of the grains when the tetrad is *a*, moist, and *b*, dry.

Each grain of the tetrad has something the form of certain mushrooms, like *Lactarius* for example, in which the cap is the shape of an inverted pyramid with its gills decurrent a short way down the stalk. The arrangement of the four pollen cells can be visualized if we imagine four such mushrooms cut off their stalks at the point of termination of their decurrent gills and all four joined together by their cut ends. The outer surfaces of the four caps would then be in the relative positions of the four faces of a tetrahedron and correspond to the exposed faces of the four grains, while the decurrent gills on the mushrooms reaching toward the center of the group would correspond to the plaits on the proximal faces of the pollen grains.

When these grains are moistened the inner or soft part expands, causing the four cells to stand apart from each other and leaving a considerable gap between their rims; but when the grains are dry the flexible inner part of each becomes contracted and invaginated into the cap, thus drawing the four cells tightly together and closing the gaps between them. The germ pores, which are arch-like openings between the plaits on the inner surfaces of the grains, are thus shut off from the outside when the grains are dry but freely exposed when moist. In their function of harmomegathy, therefore, these four grains behave as a single unit.

The spines which cover the outer surface of the grains are sharp and generally short—about 1.1 μ long or occasionally as much as 2.3 μ in length. The spine is conical, of two parts, as if truncated at about two-thirds of its height and the top third replaced by a smaller cone of more obtuse angle. They are of uniform height but irregular in arrangement.

The genus includes about 85 species of wide distribution but best represented in Australia. Seven are native of North America. They are insect pollinated and flower during spring and summer. Though they shed but little pollen, this is occasionally found in bog deposits.

Drosera capillaris Poir. Sundew. Grains as in the generic description, individual cells measuring 30.8 to 34.2 μ in diameter, spines short and closely packed, about 1 μ in length.

In and about ponds, South Carolina to Florida. Spring.

Drosera intermedia Hayne Spatulate-leaved sundew. Grains as in generic description. Some tetrads are found in which the grains are in the tetragonal arrangement, and occasionally "tetrads" are found which are composed of four normal grains and a fifth dwarf. Normal cells measure 32 to 37.6 μ in diameter. Spines short, about 1.1 μ in length.

In sandy swamps or ponds, Anticosti to Manitoba, south to Florida and Louisiana, also in West Indies and Europe. Summer.

Drosera filiformis Raf. Thread-leaved sundew. Grains as in the generic description, each cell about 43.3 μ in width. Spines about 2.3 μ long and clearly composed of two sections. These grains may easily be distinguished from those of the preceding species by their larger spines.

In wet sand near the coast. Summer, Massachusetts to Florida and Mississippi.

HAMAMELIDACEAE Witch-hazel Family

Liquidambar Styraciflua L. Sweet gum, Red gum, Star-leaved gum, Bilsted, Alligator tree (Plate IX, Fig. 2). Grains spheroidal, about 38 μ in diameter; provided with 12 to 20 approximately circular pores; pore membranes generally bulging and conspicuously flecked; exine deeply pitted with minute round pits.

The germ pores are variously irregular in outline, though generally nearly circular; in size they are not uniform even on the same grain, 6.8 to 10.2 μ in diameter; in arrangement they appear to be as nearly isometric as possible. Clearly, the pores accommodate changes in volume by bulging out and dipping in, and it is likely that they should be regarded as reduced furrows.

A large tree shedding great quantities of anemophilous pollen in May. Connecticut to Texas, also Mexico and Central America. It is not known to cause hayfever, though it has often been suspected of doing so. Its pollen has the characteristics of hayfever pollens and is always caught on atmospheric pollen slides when exposed near the flowering trees.

Sweet gum is the only member of its genus, and its association with the witch-hazel family is of doubtful propriety. Indeed, its pollen grain suggests that it may not be correct. But the most conspicuous characters of the pollen grain are mainly those of reduction in response to wind pollination and cannot be applied without more extensive study.

PLATANACEAE Plane-tree Family

PLATANUS L. Plane tree, Sycamore

Normal grains, when fully expanded oblately flattened, various in size, 18 by 14 to 21 by 17 μ, tricolpate, with the furrows meridionally arranged, rarely tetracolpate, with the furrows converging in pairs, grains of the latter form sometimes giants; furrows extremely broad and of medium length, with their membranes copiously and uniformly flecked with granules with the same staining properties as the exine, without well-defined germ pores. Exine thin, easily collapsing as the grains dry, finely pitted throughout with angular pits of various size, and sometimes coarse enough to give the surface a reticulate appearance. Intine thick and hyaline, uniform throughout.

When these grains dry the furrows are drawn deeply inward, causing the grain to assume a deeply three-furrowed ellipsoidal form, nearly twice as long as broad. A fair proportion of the grains are abnormal—giants, dwarfs, abortive, and otherwise variously irregular.

The genus contains four or five species in eastern and western North America, Mexico, Central America, and southwestern Asia, all large, handsome trees resembling each other closely and apparently closely related. In North America are found two other species, besides the two mentioned below. One of these, the introduced species *P. acerifolia* Willd. (better known as *P. orientalis*), is believed to cause some hayfever in California (Hall, 1922).

Platanus occidentalis L. Sycamore, Buttonwood, Plane-tree (Plate IX, Fig. 5) type. Grains as in the generic description.

Flowers in May, shedding large amounts of anemophilous pollen. It has occasionally been suspected of causing hayfever and should probably be regarded as a minor contributing factor.

A large and handsome tree easily recognized by its outer bark's flaking off and leaving large, light-colored patches. Abundant throughout most of its range, Maine to Ontario and Minnesota, Florida, Kansas, and Texas, also extensively planted in cities in the Pacific coast states.

Platanus racemosa Nutt. Western sycamore. Grains indistinguishable from the type.

A large, beautiful tree, exceedingly common in all of the valleys of the California Coast Ranges, from Monterey to the southern border of the state, also to a lesser extent in the valleys and foothills elsewhere in California. Flowers from February to April, shedding much light, anemophilous pollen, which is stated (Selfridge, 1920) to cause some hayfever.

ROSACEAE Rose Family

Grains ellipsoidal when dry but readily taking up moisture and expanding, when they become oblately flattened and angular in outline (Plate IX, Fig. 4). This is the condition in which they are generally observed when mounted in glycerin jelly for microscopic examination. In size they range from 25 to 52 μ

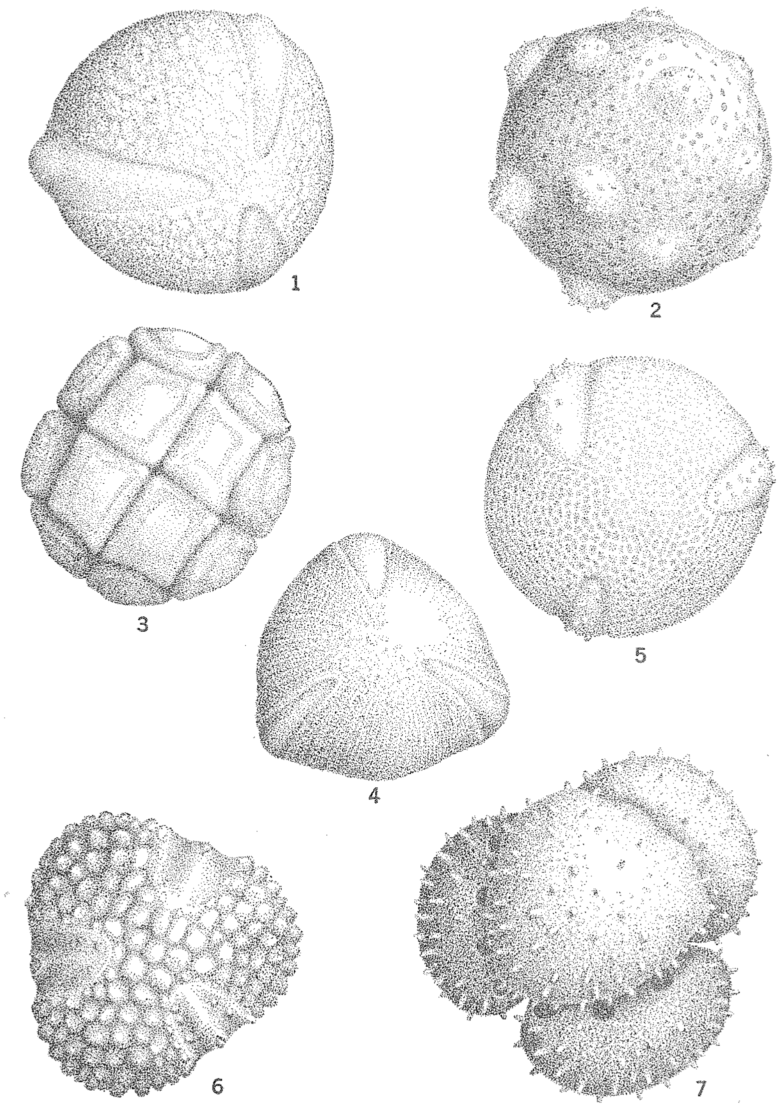

Plate IX.—Pollen grains of Droseraceae, Hamamelidaceae, Rosaceae, Platanaceae, Mimosaceae, and Aquifoliaceae: 1, *Prosopis glandulosa*, 27 μ in diameter. 2, *Liquidambar Styraciflua*, 35 μ in diameter. 3, *Acacia longifolia* 16-celled, viewed from one of its flattened sides, 50 μ over all. 4, *Rosa rugosa*, polar view, 26 μ in diameter. 5, *Platanus occidentalis*, polar view, 20 μ in diameter. 6, *Ilex bronxensis*, polar view, 30 μ in diameter. 7, *Dionaea muscipula*, tetrad expanded, each grain about 67 μ in diameter.

in diameter. Normal grains are tricolpate, with rather long furrows tapering to pointed ends. In the unexpanded condition the furrow is crossed by a delicate, smooth membrane from which the germ pore bulges more or less prominently through a circular aperture, but in the moistened condition the furrow membrane is completely ruptured, and the boundary of the pore obliterated, the cell contents bulging prominently through the furrow. The texture of the exine is always more or less distinctly granular, with the granules generally arranged in rows, giving the surface a characteristically striate appearance, which is various in the different species and can sometimes be used as an aid in telling them apart.

The general form of this grain is almost exactly duplicated in those of the Leguminosae and Platanaceae and in other families of the Rosales. Thus it seems to be basic for the order.

Rosa rugosa Thunb. (Plate IX, Fig. 4) type. Grains somewhat various with a small proportion abortive. In the expanded condition flattened and more or less angular, with the cell contents bulging prominently through the furrows, 25.2 to 28.6 μ in diameter. Tricolpate, occasionally bicolpate; texture of the exine striate, vaguely suggesting the markings of a fingerprint.

The pollen of the different species of rose that I have examined is essentially all alike in the main morphological features. In that of some species the grains are uniform, in both size and shape, while in others there is considerable variation in size, with various irregularities in shape and a large proportion of the grains abortive—conditions that suggest hybridity of origin.* There are, however, slight differences in the texture of the different species. For example, the grains of *R. bracteata, R. centifolia,* and *R. rubiginosa* are like the type in their texture, exhibiting fingerprint markings, while the grains of *R. setigera, R. multiflora,* and *R. noisettiana,* though variously granular, show no trace of such markings.

Most roses shed only small amounts of pollen. Particularly is this true of the cultivated varieties, and a large proportion, even sometimes all of it, is abortive, consisting of empty skins. Of the different species that I have examined *R. rugosa* greatly outstrips all the others in both the quantity and the perfection

* For a discussion of this phase of the subject see Erlanson (1929) and Jeffrey (1916).

of its pollen. Since the roses are entirely insect pollinated, they are not an important factor in hayfever. Only by coming into actual contact with the flowers is it possible for a person to inhale enough pollen from them to produce an attack of hayfever; consequently cases of bona fide rose hayfever are very rare—in my own experience of over 2,000 cases I have encountered only two. It is therefore unfortunate that the name "rose cold" has been adopted for that type of hayfever which comes in the early summer when roses are blooming. Hayfever at that time of the year, as we have already seen, is practically always due to the pollen of the grasses which flower at the same time and, to a lesser extent, to that of plantain.

Pyrus Malus L. (*Malus sylvestris* Mill.) Apple. Grains when moist 27.5 to 28.5 μ in diameter. Texture without fingerprint markings. A large proportion of the grains are generally abortive and exhibit many irregularities. Similar to the type.

Pyrus japonica Thunb. (*Chaenomeles japonica* Lindl.) Dwarf Japanese quince. Grains rather uniform, except for a large proportion that are abortive, 34.2 to 36.5 μ in diameter. Texture granular-striate, with fingerprint markings more pronounced than in the type; otherwise similar to it.

A common garden shrub. Flowers in May, insect pollinated, not a factor in hayfever.

Prunus Persica Sieb. & Zucc. (*Amygdalus Persica* L., *Persica vulgaris* Mill.) Peach. Grains various in size and shape, with many abortive; normal grains 50 to 57 μ in diameter. Surface texture conspicuously marked with fingerprint striae. Otherwise as in the type.

A familiar tree of cultivation, existing in many varieties. Flowers in May, insect pollinated, and not a factor in hayfever, though the dust from the skin of the fruit appears occasionally to cause hayfever and asthmatic symptoms.

MIMOSACEAE Mimosa Family

The most outstanding character of the pollen grains of the Mimosaceae is their tendency to form in compound grains. The number of individuals that are fused together is not fixed but is generally some multiple of four. The grains of *Mimosa pudica* are always in closely knit groups of four. In most species of *Acacia* (Plate IX, Fig. 3), *Inga*, and *Vachellia* 16 is the characteristic number, though in the pollen of the three latter are found groupings of 4, 8, and 32 individuals, and in some species of *Inga* 8 is the characteristic number. Always the union of the cells is very close, and the individuals so interdependent that the group actually functions as an individual in all ways, except in fertilization. Morphologically each grain of the group is profoundly modified by its associations.

But this conglobate character is not universal in the family. There are a few genera, quite properly included in the Mimosaceae, in which the grains are always simple, and these appear to represent the primitive form of the family. The grains of *Prosopis* (Plate IX, Fig. 1), for example, probably furnish us with a fairly accurate conception of what those of all the Mimosaceae might look like if they had never been fused together to form compound grains. They are spheroidal, covered throughout with a heavy exine, and provided with three long, tapering furrows in the ordinary tricolpate configuration. In its appearance and general organization such a form or grain resembles those of the Leguminosae, to which the Mimosaceae are closely related, whereas in the grains of *Acacia*, *Inga*, and others in which compounding is the rule the units are so modified that they exhibit scarcely any characters that would suggest relationship to the Leguminosae or even to *Prosopis*.

Perhaps of even greater interest is the fact that this union has somewhat different effects upon the grains of the different genera. For example, in those of *Acacia* it has induced the formation of a few sketchy and nonfunctional furrows in the dodecacolpate configuration (Plate IX, Fig. 3) while in those of *Vachellia* it has induced the formation of three or four well-marked but still nonfunctional furrows in the hexacolpate configuration (Fig. 103). There are many questions that remain to be answered before our knowledge of these extraordinary pollen grains can be regarded as measurably complete. How is it that identical contact relations can produce furrows in one configuration in the grains of *Acacia* and in a different configuration in those of *Vachellia?* What arrangements do the phragmoplasts take during the formation of these compound grains? And what bearing do they have upon the presence of pore vestiges at some of the angles of the cells and their absence from others? Why should *Acacia*, *Inga*, and *Vachellia* have adopted the formation of compound grains while *Prosopis*, which is closely related and of similar habit, has not? In the answer to these questions and to the many others that cannot fail to occur to the investigator who undertakes the study of this fascinating group will be revealed much that is now obscure of cell organization and interrelationships.

The Mimosaceae include about 40 genera and 1,500 species of mostly shrubby plants or small trees, of wide distribution in the tropics but with a few species in temperate regions. They show a close affinity to the Leguminosae of which they are often treated as a tribe or subfamily. They form, however, a well-marked group, generally easily distinguished from true Leguminosae by their small, actinomorphic flowers with exserted stamens. They are probably mostly insect pollinated, though the structure of their flowers suggests that wind might also sometimes play a part in their pollination. Only *Acacia* and *Prosopis* have ever been suspected of causing hayfever, and it is doubtful if even these should be seriously so regarded. Rowe (1928, page 15) says, "*Acacia* pollen, though usually carried by insects, has been found on our plates, and it causes definite hayfever and asthma in some cases."

Prosopis glandulosa Torr. (*P. juliflora* DC.) Mesquite (Plate IX, Fig. 1). Grains spheroidal or somewhat triangular in outline when expanded but rather various in both shape and size, about 22.5 to 32 μ in diameter. Furrows generally three, broad and tapering to rounded ends, their boundaries not sharply defined. Germ pore represented by an elliptical bulge in the center of each furrow, surrounded by a vaguely defined annular thickening. Furrow membranes smooth. Texture of the general surface of the exine various, from nearly smooth to conspicuously warty but generally fine-granular.

Shrubs or small trees generally armed with sharp spines; common in plains and prairies, Kansas to Texas, Arizona, and Mexico. Not known to cause hayfever but occasionally suspected of doing so.

Besides the grains of *Prosopis*, those of *Leucaena glauca* Benth., *Entada scandens* Benth., and *Desmanthus virgatus* Willd. of this family also occur singly and are of this type (von Mohl, 1835).

ACACIA Willd. ACACIA

Grains compound (Plate IX, Fig. 3), consisting of a number of individuals firmly joined together. Generally there are 16, though groups of both larger and smaller numbers and even grains entirely dissociated are found to constitute various proportions of the pollen of the different species. In the normal 16-celled grains 8 cells are centrally placed, forming a sort of cubical block in which the individuals tend to be arranged in rectangular fashion. The central group is surrounded by eight peripheral cells, all in a plane at right angles to and bisecting the central group. The peripheral cells are so placed that their eight contacts with each other are alternately opposite and midway between the four contacts of the central group. As a consequence of the peripheral arrangement of the outer cells the group, as a whole, is flattened, lens- or biscuit-shaped, with a squarish or more or less rounded outline and with the intersecting lines between the individual grains crossing each other at right angles.

The individual grains of such a group are polyhedral, sometimes short wedge-shaped, each presenting a flat, angular, usually square or oblong face to the outside, with the body of the cell tapering abruptly inward toward the center of the group or truncated, depending upon its position in the group. The exine of the exposed surface is thick and rigid. Its corners are always rounded, leaving conspicuous interstices at the centers of convergence of the angles of adjacent cells. The exine of the inner part of the grain is thin and flexible, allowing it to be shaped by pressing against its neighbors and to fit snugly with them. Those individual grains which occur in abnormal groups of other numbers than 16 cells may differ slightly in shape in response to their different contact relations but, in the main, preserve their form.

In normal grains at the corner of each cell is nearly always found a slight thickening in the intine which causes a corresponding protrusion of the exine at that point (Plate IX, Fig. 3). These protrusions suggest by their appearance the former positions of connecting phragmoplasts between the adjacent cells and are probably to be regarded as germ pores. The furrows are represented by a linear depression in the exine of the cap,

traversing a course parallel to its margin and generally giving off a short branch at each angle, corresponding in arrangement to one of the spherical squares in the dodecacolpate configuration of furrows in the trischistoclasic system. These furrows are vestigial and entirely functionless.

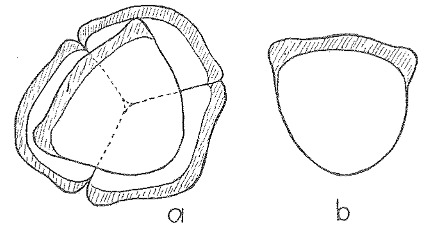

FIG. 102.

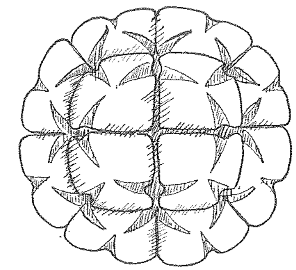

FIG. 103.

FIG. 102.—Abnormal *Acacia* pollen grains, diagrammatic: *a*, four cells united; *b*, a single cell.

FIG. 103.—Compound grain of *Vachellia Farnesiana*, diagram of the arrangement of the individual cells.

Pollen tubes are produced from the inner or protected sides of the grains and emerge from within the group through the interstices between the individual grains, forcing them apart in doing so. When these grains dry they draw a little closer together, the crevices between them becoming a little shallower, and the whole group becoming flatter and smoother. The mechanical accomplishment of these two important functions, *viz.*, pollen-tube emergence and harmomegathy, are both done by the grains' acting in concert and not as individuals. Truly this may be regarded as a colonial type of grain, in which the interstices at the angles of the cells function as germ pores and the intercellular grooves as harmomegathi.

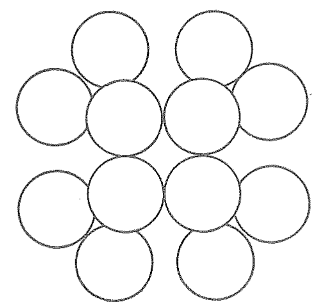

FIG. 104.—Diagram of the most compact arrangement of sixteen globular cells of the same size. The central group contains eight though only four are in view.

The rectangular arrangement of 16 cells encountered in *Acacia* pollen grains is surprising because at first sight it seems to be without regard for the law of least-surface configuration which is the guiding principle of cell arrangements. An analysis, however, shows that the arrangement really consists of four groups of four, each of which is tetrahedral.

If the form of an *Acacia* pollen grain be modeled in clay, the model will be found to break apart readily along two median lines which intersect each other at right angles, into four tetrads, each of which is approximately tetrahedral in arrangement. Each of the four groups is, therefore, within itself, a least-surface configuration. Or, if we reverse the procedure and construct four tetrahedral tetrads of uniform round balls and bring them together, we soon find that the most compact form that they can be made to assume is the same as the arrangement of the units of a 16-celled *Acacia* pollen grain (Fig. 104). There will always remain, however, spaces between the balls of the outer ring. It thus becomes evident that the spherical shape is not the best for units that are to fit together in such a configuration. Even if the balls are pressed together so as to flatten out their contact faces, gaps still remain between those of the outer ring, and large square holes between those of the central group. But if the units are block-shaped instead of spherical, the fitting is much more perfect. This is apparently what has happened in the compound grain of *Acacia*. The fact that there are 16 cells that must be grouped together, and the fact that 16 is an impossible number to group compactly, if the cells are spherical, has produced an environment for each in which isodiametric cells do not fit, and the effect of this environment is such as to induce a change in the form of the cells to one that does fit—hence the strange squared form of the components of this compound grain. The squared cells are like pegs that have been made square to fit into square holes.

So impressed upon the cell has its squared form become that it is retained even when not required to fit into a square hole. Occasionally, abnormal groups of four cells are found in which one cell is misplaced, applied by its side to its three neighbors, yet its form remains almost unchanged (Fig. 102*a*); it has its thick, stiff cap, and its body is covered by only a thin, flexible membrane, a form totally unadapted to its association in such a group. Even entirely dissociated individuals, which are occasionally found, present a thick, rigid, angular cap which tends to be squarish and a flaccid body which is rounded and bag-

shaped (Fig. 102*b*). The form of these grains is clearly the result of environmental stimuli; yet it has become hereditary and is expressed even in the absence of the stimuli which called it forth. An exactly parallel case is found in the colonies of *Pediastrum*. Harper (1918) has shown that individuals of such a colony have acquired a part of their form from the necessity of being able to fit snugly together with a certain predetermined number of others and that this form has become fixed and hereditary and is expressed even when, as sometimes happens, the cell is dissociated or is associated with the other cells of the colony in some abnormal way to which its shape is not at all adapted.

The development of the pollen grains of *Acacia* has been studied by Rosanoff (1866) and Engler (1876), and they have shown that there take place in the pollen mother-cell two successive divisions resulting in the formation of four cells separated by clearly defined walls, and these four cells tend to be all in the same plane and rectangular in arrangement. Each of these daughter-cells appears to divide twice more, producing four cells which assume the tetrahedral arrangement.

The peculiar shape of the component units of the *Acacia* compound pollen grain is the result of the conflict between the law of bipartition and the law of least-surface configuration. The law of bipartition produces 16 cells, a number which, when of isodiametric units, cannot be made to pack together without leaving gaps; the law of least-surface configuration brings these 16 cells into the most compact form possible and fills in the interstices by shaping the cells to fit.

Acacia is a genus of about 450 species, not always clearly defined, of small trees or shrubs, widely dispersed throughout the tropics, especially in Australia. A large number of species are grown in cultivation in California and the warmer parts of the United States of America, and several species are grown elsewhere under glass. The flowers are insect pollinated, appearing very early in spring, and the pollen is said occasionally to cause a mild type of hayfever in California.

Acacia longifolia Willd. (Plate IX, Fig. 3) type. Sydney golden wattles. Grains nearly always 16-celled and grouped in the squared arrangement as in the generic description, though deviations from this are occasionally found. The individual grains measure about 17 μ in diameter, and the whole compound grain 48.5 to 54.7 μ.

A tall shrub or small tree producing bright-yellow flowers in early spring. It occurs in several varieties of which the grains of variety *floribunda* F. Muell. have been examined and are indistinguishable from those of the type.

Besides these the pollen of several unidentified species was examined and found to be likewise identical, except that in some a large proportion of the grains were composed of numbers of individuals other than 16.

Inga myriantha Poepp. & Endl. Grains compound as in *Acacia*, but the components not so closely united, the exposed part of each more rounded, and the exine thicker. The furrow vestiges tend to be formed on the sides of the bulging outer part of the grains. Diameter of the compound grain as a whole about 59 μ, and of its component individuals about 18 μ.

A tree about 30 ft. high, with white flowers. Native of Brazil, Peru, and Guiana.

The genus includes about 150 species of trees resembling the acacias but spineless, with pentamerous flowers having numerous exserted stamens which are generally red. Native of the West Indies and tropical South America. *Inga Feuillei* DC. is cultivated in California for its edible pods.

The grains of *Inga tergemina* Willd. are described by Rosanoff (1865) as eight-celled; those of *Inga anomala* Kunth. are described and figured by von Mohl (1835) as composed of eight functional cells, and the group provided with a stalk and sticky disk whereby it may become attached to insects. This is, perhaps, the highest development attained among the compound grains of dicotyledons, other than the milkweeds, and is quite comparable with that of the pollinia of the orchids.

Vachellia Farnesiana (L.) Wright & Arn. [*Acacia Farnesiana* (L.) Willd.] Frangipanni, Huisache, Casse, Yellow opopanax (Fig. 103). Grains compound and similar to those of *Acacia*, generally 16-celled, occasionally 4- or 8-celled. Individual grains 11.4 to 12.5 μ, and the group as a whole 41.5 to 52.5 μ in diameter. Exine thick and faintly granular, forming a sort of cap over the exposed surface of each grain. Furrows three or five, deep and conspicuous but nonfunctional and without pores, converging from the corners of the exposed surface of each cell toward one or two centers.

In the 16-celled grains, each of the eight central cells of the group presents to the outside a convex face which is square in outline. Underlying the exine can be seen three small thickenings in the intine, one at each distal corner (those remote from the center of the group). These are the germ pores, and from them extend three furrows converging toward a point near the center of the cap. But there is no furrow extending from the proximal or central corner of each cell, which lacks a germ pore. The eight peripheral cells are also four-sided in outline, either square or elongate in the direction of the circumference of the group, and the outer convex face of each is provided with either five or three furrows. Those cells which have three furrows are essentially the same as those of the central group, but those which have five furrows have pore vestiges at each of their four corners, and from these converge four furrows in pairs toward two centers which are joined together by a fifth furrow. In both the three-furrowed and five-furrowed cells the picture presented by their furrow system is that of part of the ordinarily hexacolpate configuration; the former presents one triconvergent center to the outside, while the latter presents two triconvergent centers.

A small proportion of the grains are irregular, presenting other arrangements than the squared one described for the grains of *Acacia*. Occasionally the peripheral row of cells exhibits a conspicuous gap. This is to be expected from purely mechanical reasons which will become clear from reference to the diagram (Fig. 104). It is interesting to note, however, that the gap may occur between any two cells of the peripheral row and is as likely to occur between those at the corners of the group as elsewhere, thus breaking up the tetrads. This is strong evidence that the 16-celled group should not be regarded as a loose assemblage of four better organized tetrads. Rather, the whole group should be regarded as complete within itself, and every cell interdependent with every other cell. A further study of these interesting relations would reveal much regarding the organization of the cell group and, incidentally, of the morphogenesis of pollen grains in general.

Huisache is a shrub or small tree with spreading, spiny branches. Plains and prairies, southern Texas and Mexico. Flowers in early spring, not known to cause hayfever.