AQUIFOLIACEAE Holly Family

A small family of trees and shrubs, related to the Ebenaceae.

Ilex L. Holly

Grains oblately flattened when moist, 26.8 to 33.1 μ in diameter. Furrows three, meridionally arranged, or occasionally four or six, tetrahedrally arranged, in which case the grains may or may not be giants. Furrows broad and long, somewhat tapering to rounded ends, their membranes heavy and conspicuously flecked with coarse granules; germ pores represented by hyaline thickenings, one below the center of each furrow, causing a rounded bulge which may or may not break through the furrow membrane when the grain is moistened. Exine very thick and rigid, presenting a coarsely pebbled appearance in surface view, structurally composed of rounded prisms embedded in a matrix of material of different refractive index.

The genus comprises about 280 species of shrubs, mostly America. The pollen of various species has been recovered from Postglacial silts, and in this connection that of *I. agrifolia* has been described and illustrated by Docturowsky and Kudrjaschow (1923) and Erdtman (1923). The hollys are not regarded as hayfever plants.

Ilex bronxensis Britt. Northern winterberry (Plate IX, Fig. 6) type. Grains uniform, 29.6 to 33.1 μ broad, 28.5 to 31.9 μ deep. Exine exceedingly coarsely granular, presenting a pebbled appearance.

A medium-sized shrub with evergreen leaves and orange-red berries. Flowers in June and July, insect pollinated but sheds rather a large amount of pollen.

Ilex decidua Walt. Swamp, meadow, or deciduous holly. Grains 26.8 to 28.5 μ broad and 22.8 to 23.9 μ deep. Furrows occasionally four or six. Some grains united in tetrahedral tetrads, with the three pores of each grain opposite and adjacent to one of each of its three neighboring grains. Exine heavy and coarsely granular but less so than in the type.

ACERACEAE Maple Family

A family of trees containing, besides the genus *Acer*, only the monotypic genus *Dipteronia* Oliv. of central China.

ACER L. Maple

Grains when moistened oblately spheroidal, ranging in size in the different species from about 28 to 36 μ in diameter, prevailingly tricolpate, but occasionally dicolpate or, less frequently, tetra-, penta-, and hexacolpate.

In normal tricolpate grains the furrows are equally spaced around the equator and directed meridionally (Plate X, Fig. 1), but in the grains with higher numbers of furrows they are not so arranged; instead they tend to conform to the tetrahedral configuration, though they are more often badly deformed, and their furrows unrelated to any system. When unexpanded the grains are ellipsoidal, with the furrows appearing as shallow, longitudinal grooves, but upon expanding they gape widely open, permitting the grain to become decidedly flattened. The furrow membranes are smooth or occasionally slightly flecked. They are not provided with germinal apertures; instead, the germ pore is represented only by a slight swelling in the center of each. The general surface of the exine is always conspicuously granular, and in the grains of all species, except those of *A. Negundo*, the granules are arranged or tend to be arranged in rows, giving the exine a more or less striate appearance. In this respect the grains of the maples resemble those of the roses. The patterns of the granular striae are not exactly duplicated in any two species, giving this character high diagnostic value.

The maples are mostly large or medium-sized trees. All, except *A. Negundo*, are primarily insect pollinated. Nevertheless, they are rather imperfectly adapted to this mode of pollination, and the pollen of several species of maple, besides those of *A. Negundo*, can often be caught on atmospheric pollen plates at considerable distances from the trees. The part that the maples play in the production of hayfever is not yet understood, but it is likely that they should be regarded as a contributory cause of the early spring type. Maple pollen is occasionally found in Postglacial silts; and in this connection are figured grains of *A. saccharum* (Sears, 1930) and unnamed species (Docturowsky and Kudrjaschow, 1923).

Key to the Species

I. Surface granules arranged in rows forming more or less distinct striae.

A. Striae always distinct and unmistakable (less distinct in *A. rubrum*).	A. Pseudo-platanus A. platanoides A. rubrum
B. Striae extremely faint and in some grains not present at all.	A. saccharum
II. Surface granules not arranged in rows, surface not striate.	A. Negundo

Acer Pseudo-platanus L. Sycamore maple (Plate X, Fig. 1) type. Grains mostly uniform, when fully expanded spherical, 35.5 to 36.3 μ in diameter; tricolpate, with furrows meridionally arranged, or rarely dicolpate, with the furrows opposite, fused at the poles and encircling the grain as a single furrow. Furrows normally long and tapering, their membranes smooth. Exine granular-striate.

The surface texture of these grains is very characteristic; at lower magnification it has the appearance of being striate, with the striae forming patterns which resemble those of thumbprints. These striae have a tendency to run parallel to the furrows and are obviously modified by them in their arrangement. Seen with the higher resolving power of the microscope, the texture may be described as coarsely granular, with the granules arranged in rows of various length. The striate pattern, though difficult to describe, is highly specific.

The sycamore maple is a medium-sized tree extensively planted about city streets. It flowers in June, the flowers opening after the leaves have fully expanded. The flowers are insect pollinated but rather imperfectly adapted to this mode of pollination, so that much pollen is scattered in the air and probably should be considered as a contributory factor in hayfever.

Acer platanoides L. Norway maple. Grains similar to the type but slightly smaller and less uniform in size, 32 to 34 μ in diameter, oblately spheroidal, always tricolpate. Surface markings similar to but finer than in the type. Furrow membranes slightly flecked.

A large tree extensively planted about city streets. Flowers in June. Insect pollinated but sheds much pollen which becomes atmospheric and can readily be detected in the air and is probably a contributory cause of hayfever. The pollen is also sometimes found in Postglacial silts and in this connection has been figured by Erdtman (1923).

Acer rubrum L. Red maple, scarlet maple. Grains similar to the type, except that the surface striae are much less distinct, always a large proportion of the grains abnormal; tetracolpate and pentacolpate giants, with the furrows in the tetrahedral position, some double zonate or more often irregular and asymmetrical. Normal grains 30.8 to 35.3 μ in diameter, tricolpate.

A large tree in swamps and low grounds and much planted elsewhere. Nova Scotia to Manitoba, Nebraska, Florida, and Texas. Flowers appearing before the leaves in March or April. Primarily insect pollinated but very imperfectly so. Its pollen is frequently caught on atmospheric pollen plates and is probably a contributory cause of early spring hayfever.

Acer saccharum Marsh. Sugar or rock maple. Grains essentially as in the type, occasionally dicolpate, with the furrows fused at the poles and encircling the grain as a single furrow, ellipsoidal, 36.5 to 40 μ in diameter. Texture extremely finely granular, with the granules tending to be arranged in striae, but less so than in the grains of *A. rubrum*, in this respect intermediate between the latter and those of *A. Negundo.*

Apparently these grains do not expand so much upon being moistened as the type, for they retain their ellipsoidal form, and the furrows do not gape widely open.

Acer Negundo L. (*Negundo aceroides* Moench., *N. fraxinifolia* Nutt.) Box elder, ash-leaved maple. Grains similar to the type, prevailingly tricolpate but frequently dicolpate with furrows opposite and fused, encircling the grain as a single furrow or in the position of the tricolpate furrows, as if one had been omitted; occasionally with more than three furrows, but such grains are usually irregular. Texture granular but not striate, in which character this species appears to be unique in the genus.

A large tree common along streams and much planted elsewhere. Maine and Ontario to Manitoba south to Florida, Texas, and Mexico. Flowers in April, wind pollinated, shedding large quantities of pollen which undoubtedly causes some hayfever in the early spring. Several varieties are recognized which greatly extend its range. Variety *violaceum* Kirch. in the eastern States, variety *texanum* Pax. in eastern Texas and adjoining states, variety *interior* Sarg. in the Rocky Mountain states, variety *arizonicum* Sarg. in southern Arizona and New Mexico, variety *californicum* Sarg. in the Pacific coast states. For a discussion of these different varieties the reader is referred to Sargent (1922).

The pollen of *Acer Negundo* in one or more of its varieties is said to be important in the production of hayfever in Oregon (Chamberlain, 1927), and its pollen has been shown to occur abundantly in the air in the neighborhood of Kansas City while the trees are in bloom (Duke and Durham, 1928).

TILIACEAE Linden Family

A large family of trees, shrubs, or rarely herbs, represented in northern regions by the single genus *Tilia*.

Tilia americana L. Basswood, Linden (Plate X, Fig. 2). Grains uniform in shape and size, oblately flattened and about 36.5 by 28 μ; germ pores three, rarely two or four, deeply sunken, elliptical in shape, and equally spaced on the equator. Exine reticulate pitted.

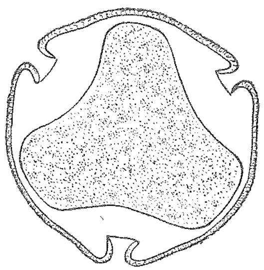

Fig. 105.—Pollen grain of *Tilia americana*, transverse optical section.

Furrows in the ordinary sense of the word are absent, but the pits in which the pores are situated are slightly elongate in a meridional direction and must undoubtedly be regarded as vestigial furrows. Underlying each pore is a relatively large thickening of the intine which forms a very conspicuous feature of the grain in optical section (Fig. 105) and causes the region surrounding the pore to be slightly elevated.

A large tree widely distributed throughout the eastern half of the United States. Flowers in May and June. Insect pollinated but generally shedding much pollen. It is not a factor in hayfever, but its pollen is frequently caught on atmospheric pollen plates and is found abundantly in Postglacial silts. In this connection this and other species of the genus have been described and illustrated by Sears (1930) and by Docturowsky and Kudrjaschow (1923), who describe the rudimentary furrows as false pores, merely pits in the exine.

VIOLACEAE Violet Family

VIOLA L. Violet

Grains when dry ellipsoidal or tending to be cylindrical with rounded ends, the furrows appearing as shallow grooves. When

moistened becoming spheroidal, the furrows gaping widely open. Furrows generally three, occasionally four or six (in *V. tricolor* var. *hortensis* five, six, or four, never three) long and tapering to pointed ends; furrow membranes smooth, easily ruptured; germ pore circular or more or less irregular. Exine nearly or quite smooth.

The furrows when three are equally spaced around the equator, with their long axes meridionally directed, or, when there are four or six, in the tetrahedral configuration, except in the grains of *V. tricolor* var. *hortensis*, in which they are approximately equally spaced on the equator, with their long axes directed almost exactly meridionally, though they may tend somewhat to converge in pairs. Violet pollen grains have a strong tendency to overexpand when moistened, with the complete rupture of the furrow membrane, permitting the cell contents to protrude from the furrows, the grain becoming flattened and angular in outline. In this condition, which is, indeed, the one most generally encountered, unless precautions are taken to prevent its occurrence, they bear a superficial resemblance to the grains of *Quercus* but may easily be distinguished from the latter by the smooth texture of their exine and the absence of hyaline bodies.

A large genus of low shrubs and herbs, flowering in the early part of spring or, by cleistogamous flowers, throughout the summer; insect pollinated, producing only small amounts of pollen; not a cause of hayfever.

Viola lobata Benth. Violet type. Grains as in the generic description, spheroidal, tricolpate, 28.5 to 31.9 μ in diameter. Exine faintly granular.

California and southwestern Oregon.

Viola palmata L. Early blue violet. Grains as in the type, generally tricolpate or occasionally tetracolpate or hexacolpate, with the furrows in the tetrahedral configuration, about 30.8 μ in diameter. April and May. Massachusetts to Minnesota, southwest to Florida.

Viola hirsutula Brainard Southern wood-violet. Grains ellipsoidal when moist unless overexpanded, tricolpate, about 37.6 μ in diameter, otherwise as in the type. Flowers in April and May, southern New York to central Alabama and Georgia.

Viola cucullata Ait. Marsh. Blue violet. Grains spheroidal, tricolpate, 36 to 40 μ in diameter, exine smooth, otherwise as in type. April and June. Quebec to Ontario, southward to Georgia.

Viola odorata L. English or Sweet violet. Grains as in the type, 29.6 to 31.2 μ in diameter. Flowers March to May. Introduced from Europe and frequently planted in America.

Viola conspersa Reichenb. American dog violet. Grains spheroidal, generally tricolpate, occasionally tetra- or hexacolpate, with furrows in the tetragonal configuration, about 30.8 μ in diameter, otherwise as in the type. Flowers April and May. Quebec to Minnesota, southward to Georgia.

Viola tricolor L. var. **hortensis** DC. Pansy, Heartsease. Grains various in size; when dry cylindrical with rounded ends, with the furrows showing as shallow, longitudinal grooves; when expanded decidedly oblately flattened, about 85 by 63 μ, with the furrows more or less equally spaced around the equator and nearly or quite meridionally arranged, except when there are four, in which case they tend to converge in pairs. Furrows long and tapering to pointed ends; furrow membranes flecked, easily ruptured by overexpansion. Germ pore irregular in outline but tending to be circular. Texture finely granular.

Flowers in early summer, cultivated.

HALORAGIDACEAE Water-milfoil Family

Aquatic or marsh plants with inconspicuous flowers in leafy spikes. The family includes about 100 species in eight genera.

MYRIOPHYLLUM L. Water milfoil

Grains similar to those of *Alnus* but lacking the connecting bands between the pores; uniform in size, oblately flattened and angular in outline, with the pores at the angles, 23 to 33 μ in diameter. Pores aspidate, with narrowly elongate or slit-like apertures, four, three, or rarely five, their number bearing no reference to the size of the grain, equally spaced around the equator—when three, meridionally arranged; when four or five, with their axes biconvergent. Texture of the exine slightly rough, especially around the pores.

These grains may be distinguished from those of *Alnus* by their narrower germinal apertures, less sharply defined aspides, and absence of connecting bands between the pores.

The genus is represented by about 10 species in North America and about 10 others elsewhere. All are perennial aquatic herbs, apparently wind pollinated but shedding little pollen. They are not a cause of hayfever, but their pollen is found in Post-glacial silts, and, in this connection, that of four species has been described and illustrated by Meinke (1927, page 384).

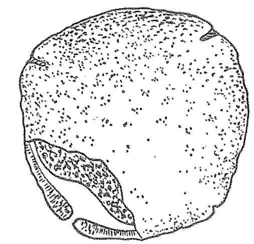

Fig. 106.—Pollen grain of *Myriophyllum spicatum*, polar view, one pore shown in optical section.

Myriophyllum spicatum L. (Fig. 106) type. Grains uniform, 23.1 to 33 μ in diameter, germ pores four, three, or rarely five, their apertures 2.85 by 1.14 μ. About twice as many grains have four pores as have three.

Low, aquatic herb, growing in deep water, with submerged leaves and aerial flowers, widely distributed throughout most of North America, except the southeastern United States and Mexico. Flowers in summer.

Myriophyllum heterophyllum Michx. Grains about 32 μ in diameter, essentially the same as the type, except that they have nearly always four pores, rarely five or three.

Aquatic herb of ponds and slow streams, mostly near the Atlantic and Gulf coasts of the United States.

CORNACEAE Dogwood Family

Grains tricolpate. When moist, oblately flattened, 36 to 37.6 μ in diameter. Exine finely granular. Furrows long and tapering, reaching almost from pole to pole, equally spaced and meridionally arranged. Furrow membranes nearly smooth or slightly flecked, each provided with a well-defined aperture through which the germ pore bulges prominently. When dry the grains are spheroidal or ellipsoidal, the furrows closed tightly, assuming the form of shallow grooves.

Abortive grains and those which have lost their cell contents frequently retain the latter form even when wet, though not invariably so. Consequently, in attempting their identification in fossilized material, it must be borne in mind that shapes of these grains may be decidedly flattened, approximately spheroidal or ellipsoidal. Perhaps the most characteristic feature about them is the slight inwardly projecting subexineous thickening bordering the furrows, more pronounced around the pores. These thickenings are not conspicuous in normal, healthy grains, but in abortive grains and those which have lost their contents, as in fossil material, the thickened rims are conspicuous and serve as the most reliable diagnostic feature. The granular nature of the exine is about the same in the grains of both *Cornus* and *Nyssa* and is sometimes difficult to see, particularly in fossil material, but is of value in identification.

The Cornaceae are trees, shrubs, and perennial herbs, comprising about 10 genera, of which *Cornus* and *Nyssa* are the best known in the United States.

Nyssa sylvatica Marsh. Sour gum, Tupelo, Pepperidge (Plate X, Fig. 5) type. Grains uniform in size, all normal, tricolpate; when moistened oblately flattened, 37.2 by 27.4 μ, triangular in outline; the furrows at the angles long and tapering, expanding principally toward their centers, each provided with a distinct germinal aperture, elliptical in outline and with its long axis crossing that of the furrow. Furrow membrane flecked, pores bulging through with a ragged edge, as if having ruptured the furrow membrane. Exine finely but distinctly granular, with the granules appearing as the ends of fine, vertical rods of one material embedded in a matrix of another material of different refractive index, in optical section appearing radially striate.

Sour gum is a large tree inhabiting moist and swampy ground. Maine and Ontario to Florida, Michigan, Missouri, and Texas. Flowers in June. It is primarily insect pollinated but imperfectly so, some pollen becoming scattered in the air. In some experiments carried out by the author it was found that pollen slides exposed about 500 ft. from a tree caught a few grains of its pollen every day throughout its flowering period.

Sour-gum pollen is not known to cause hayfever but has been found by Lewis and Coke (1930) in great abundance in the Post-glacial peat of the Dismal Swamp in the United States. These authors have also illustrated the pollen in its fossilized form.

Nyssa Ogeche Marsh. Ogeechee plum. Grains exactly as in the type.

A large tree in swamps. South Carolina to Georgia and Florida. Flowers in June.

Cornus florida L. (*Cynoxylon floridum* (L.) Raf.) Flowering dogwood. Grains essentially as in the type, except that they are

a little larger, averaging 37 by 34 μ, and the texture of the exine is less distinctly granular.

A small or medium-sized tree, with large, showy white or pink flowers. Maine and Ontario to Florida, Minnesota, Kentucky, Kansas, and Texas. Flowers in July. Strictly insect pollinated and not a cause of hayfever.

OLEACEAE Olive Family

Grains spheroidal or somewhat oblately flattened, 19.5 to 30 μ in diameter, generally tricolpate or tetracolpate, with furrows conforming in arrangement to the trischistoclasic system. Furrows various in character among the different species. Furrow membranes smooth or variously flecked. Germ pores not sharply defined but represented in the grains of some species by a small swelling. Exine variously but always conspicuously reticulate.

The outstanding character of these grains is their reticulate exine. The pattern consists of a continuous and generally uniform lacework of elevated ridges, dividing the surface into angular lacunae. In the grains of some species the reticulum is simple; in those of others it is complex, the ridges which partition off the larger lacunae themselves bearing smaller lacunae. The smaller the lacunae the less angular they are—those borne in the ridges are almost circular in outline. This type of reticulum is not unique but characterizes the grains of such widely divergent groups as the Salicaceae, Platanaceae, Liliaceae, and others. It is thus typical of a class of phylogenetic characters which recur again and again with slight modifications in entirely different associations. We find it in the grains of *Salix*, with the lacunae smaller toward the furrows, and in those of *Platanus*, with the lacunae a little smaller and less angular throughout and associated with furrows which are more sharply defined. We find it again in the grains of the Liliaceae, associated with a single longitudinal furrow, and in those of *Potamogeton* in the absence of furrows.

In the Oleaceae the pattern is specifically constant but various among the different species. In the grains of *Ligustrum*, *Syringa*, *Forsythia*, and, to a lesser extent, *Olea* it is always rather coarse, consisting of large, hexagonal and pentagonal lacunae of uniform size and with high ridges. In the grains of *Ligustrum* and *Syringa* the ridges are buttressed with rounded thickenings at their bases, while in those of *Forsythia* they are thick and bear within their walls much smaller, roundish lacunae. This form calls to mind the structure of a soap foam consisting of large bubbles of rather uniform size in a matrix containing much smaller bubbles. In the grains of *Olea* there is some trace of the buttressing, but it is much less pronounced than in those of *Ligustrum* and *Syringa*. In the grains of *Fraxinus*, which is wind pollinated, the structure of the reticulum is less rugged, with the ridges lower and the lacunae smaller, roundish, and with no trace of buttressing. The relation of the form of the grains of *Fraxinus* to that of *Ligustrum*, *Syringa*, and *Forsythia* is parallel to that existing between the grains of *Populus* and *Salix*, in which similar differences are definitely correlated with their modes of pollination, the former by wind and the latter by insects. In the present instance *Ligustrum*, *Syringa*, and *Forsythia* are insect pollinated, and associated with this is the high degree of development of the surface reticulum; while *Fraxinus* is wind pollinated, and associated with this is a marked reduction in the reticulum. If the degree of this reduction can be taken as a measure of the adaptation of these trees to anemophily, *Fraxinus* appears to be highly specialized in this respect, while *Olea* exhibits only a tendency toward anemophily.

Associated with the reduction of the reticulum in the former is found a flattening out of the furrow margins. In the grains of *Olea* and other entomophilous members the furrows are sharply defined and harmomegathically functional, opening and closing with the changes in volume of the grain, while in the grains of the anemophilous *Fraxinus* they are poorly defined and with the furrow membranes flecked with what appear to be fragments of the reticulum. Clearly, one of the functions of the furrows is to permit the contraction and expansion of the cell against the resistance of a rigid exine; therefore with the reduction of the reticulum and consequent loss of rigidity of the exine goes the need of a special structure to accomplish harmomegathy. In any case it may be said of the Oleaceae that anemophily is associated with a reduction of the surface reticulum and a lessening in the degree of the development of the furrows.

Key to the Genera

I. Furrows vaguely defined.	
A. Texture finely reticulate, furrows mostly 4.	Fraxinus
B. Texture more coarsely reticulate, the ridges slightly beaded. Furrows mostly 3.	Olea
II. Furrows sharply defined.	
A. Texture very coarsely reticulate, the ridges markedly beaded. Furrows mostly 3.	
i. Furrows short.	Ligustrum
ii. Furrows long and tapering.	Syringa
B. Texture double-reticulate, *i.e.*, with smaller lacunae within the ridges; furrows 3, long.	Forsythia

FRAXINUS (Tourn.) L. Ash

Grains uniform, when fully expanded 20 to 25 μ in diameter, flattened and angular in outline, tetra-, tri-, or pentacolpate. Exine reticulate, the net simple and weakly developed, constant for all the grains of any given species but of various coarseness among the different species.

The reticulate pattern resembles that found on the grains of *Salix* and *Platanus*, but in those of *Fraxinus* it is more uniform throughout, not tending to become finer toward the poles and along the margins of the furrows, as is generally the case in the grains of *Salix*, and always it is much coarser than in the grains of *Platanus*. In the grains of *Fraxinus* the size of the mesh is maintained right up to the edge of the furrows, where it ends with open lacunae, suggesting that the furrows are torn through it with the expansion of the grain. This impression is heightened by the appearance of the furrows themselves. These are rather poorly defined; as seen in the expanded condition they are short and broad, with their membranes stretched and bulging and dotted with small flecks of material which look like fragments of the torn reticulum scattered over the surface. They are without germ pores, the whole surface serving as a place of exit for the pollen tube. They are always equally or approximately equally spaced around the equator. When there are four or five of them they cross the equator obliquely, with their axes converging in pairs alternately above and below the equator, but when there are three they cross the equator at right angles and converge toward the poles along meridional lines; thus, whatever their number they conform to the trischistoclasic system.

The grains of *Fraxinus* differ from those of the other members of the family in their finer reticulum, thinner exine, and more irregular and less sharply defined furrows. These are characteristic morphological modifications resulting from pollination by wind.

All species of *Fraxinus* are excellently adapted to pollination by wind and scatter enormous quantities of pollen in the air. In the author's experience in the vicinity of New York City and in that of Duke and Durham (1928) in the vicinity of Kansas City ash pollen becomes very abundant in the atmosphere during the short flowering period of the trees. Only occasionally, however, have any of the ashes been reported as factors in hayfever. Thus, *F. oregona* is regarded as one of the most important causes of the hayfever occurring in early spring in western Oregon (Chamberlain, 1927), and *F. attenuata* as one of the most important in February and March in Arizona (Phillips, 1922, 1923).

Fossilized grains of ash pollen have occasionally been found in European bog deposits, and in this connection a species of ash pollen has been illustrated by Meinke (1927), who points out its similarity to that of *Adoxa* (page 381), and the grains of *F. excelsior* are illustrated by Docturowsky and Kudrjaschow (1923). In similar studies in America the grains of *F. lanceolata* (*i.e.*, *F. americana* L.) are illustrated by Sears (1930). Hugo Fischer (1890, page 44) describes the grains of *F. excelsior* L. as generally tricolpate—"regelmässig dreifaltig."

The genus includes about 30 or 40 species of trees and shrubs widely distributed in the temperate regions of the Northern hemisphere and in Cuba and Java.

Fraxinus americana L. White ash, Cane ash (Plate X, Fig. 4) type. Grains uniform, when expanded about 24 μ in diameter, flattened and angular in outline. Furrows four, less often three, or rarely five, short and broad, gaping widely open as the grain expands and giving it its angular appearance. Furrow membranes distinctly flecked. Exine more finely reticulate than in the grains of *F. coriacea* and *F. Toumeyi*.

The white ash is a large forest tree in rich woods, almost throughout the United States and Canada. It sheds large quantities of pollen which is borne great distances in the air, in April and May, the flowers opening just before the leaves. It is, however, not known to cause hayfever.

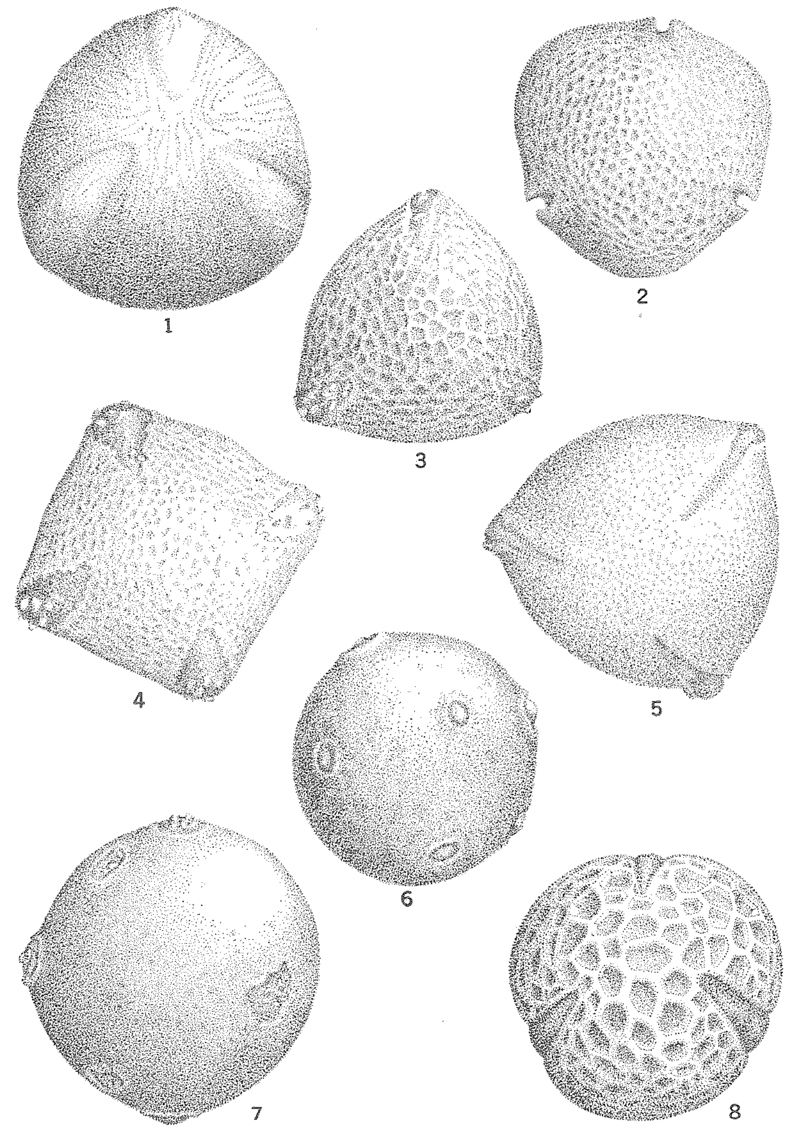

PLATE X.—Pollen grains of Aceraceae, Tiliaceae, Cornaceae, Oleaceae, and Plantaginaceae. 1, *Acer Pseudo-platanus*, polar view, 36 μ in diameter. 2, *Tilia americana*, polar view, 33 μ in diameter. 3, *Olea europaea*, polar view, 22 μ in diameter. 4, *Fraxinus americana*, polar view, 24 μ in diameter. 5, *Nyssa sylvatica*, polar view, 37 μ in diameter. 6, *Plantago lanceolata*, 35 μ in diameter. 7, *Plantago Rugelii*, 23 μ in diameter. 8, *Ligustrum Ibota*, polar view, 30 μ in diameter.

Fraxinus coriacea S. Wats. (*F. velutina* var. *coriacea* Rehd.) Desert ash. Grains as in the type, about 20 μ in diameter, always a few that are abortive, and with some variation in those that are normal, the latter nearly always tetracolpate, rarely tri- or pentacolpate. The reticulum is a little coarser than in the type.

A large tree shedding much pollen in early spring. Probably the cause of some hayfever in regions where abundant. It is one of the commonest ashes in southern Arizona, somewhat less abundant in adjacent parts of New Mexico and Mexico.

Olea europaea L. Olive (Plate X, Fig. 3) type. Grains flattened, about 22 μ in diameter, tricolpate, rarely tetracolpate, and those that are variously irregular and apparently abnormal. Exine reticulate, similar to that of the grains of *Fraxinus*, except that the mesh is much coarser and the ridges buttressed, in this respect resembling the grains of *Ligustrum*. Furrows broad, rather short, and vaguely defined, as in the grains of *Fraxinus*; their membranes flecked, without germinal apertures, the latter represented merely by a bulge which appears in the center of the furrow membrane when fully expanded.

Underlying the center of each furrow, embedded in the cell contents and radially oriented, is a hyaline rod, which expands upon being moistened, causing the bulge in the center of the furrow membrane. These organs are exactly homologous with those found in the grains of *Quercus*, though not quite so highly developed. The difference between the grains of *Fraxinus* and *Olea* lies principally in the better development of the ridges in the former and in the relatively unimportant, though conspicuous, haptotypic character of the number of germinal furrows, which are predominantly three in the grains of *Olea* and four in those of *Fraxinus*.

The olive is primarily insect pollinated, bearing flowers closely resembling those of privet, but sheds large amounts of pollen which becomes atmospheric. Flowers in April and May. It is native of Europe but has been introduced into some parts of California and Arizona where it is said to be a serious cause of hayfever and is stated by Rowe (1928) to be important in California. The genus includes about 40 species of trees and shrubs, native of the tropics and warm parts of the Old World and New Zealand.

LIGUSTRUM L. Privet

Grains similar to those of *Olea europaea* but considerably larger, ranging in the different species from 28 to 30 μ in diameter. Reticulum of the exine much coarser, with lacunae larger and ridges higher and buttressed, presenting a beaded appearance, as in the grains of *Olea* but much more pronounced. Toward the furrows the reticulum is a little finer than elsewhere, and it ends abruptly along the furrow margins with closed lacunae. Furrows generally three, occasionally four, a little shorter and more sharply defined than in the grains of *Olea*, an appearance obviously due to the more rugged character of the reticulum. Furrow membranes smooth, and each provided with a fairly well-defined germ pore.

The genus comprises about 50 species of both deciduous and evergreen shrubs, native of Asia, Australia, and the Mediterranean region. About a dozen species are cultivated as hedges or for their showy white flowers which open early in summer. They are all insect pollinated and are rarely a serious cause of hayfever, though they have occasionally been suspected of being so.

In the superficial appearance of the plants the privets bear little resemblance to the ashes, but their relationship to the latter is abundantly attested by the characters of their pollen grains. Those of the privets differ from those of the ashes only in the greater thickness of their exine and better development of the reticulum, characters which we have already seen are definitely correlated with their mode of pollination by insects.

Ligustrum Ibota Sieb. Privet (Plate X, Fig. 8) type. Grains averaging about 30.5 μ in diameter, ranging from 28 to 32 μ, otherwise as in the generic description.

A garden shrub closely resembling *L. vulgare*. Introduced into America from China and Japan. Flowers in June.

Ligustrum vulgare L. Common privet. Grains uniform, averaging about 28.5 μ in diameter, otherwise as in the generic description.

A garden shrub introduced into America from Europe and Asia, now common in the eastern United States and Canada. Flowers in June, occasionally suspected of causing hayfever.

Ligustrum ovalifolium Hassk. Privet. Grains about 30 μ in diameter, 28.5 to 31 μ, generally with three but occasionally with four furrows which are a little shorter than those of the grains of *L. vulgare*. Otherwise as in the generic description.

A garden shrub existing in several forms with variegated leaves. Native to Japan but extensively cultivated in America.

Syringa vulgaris L. Common lilac. Grains spheroidal, similar to the type (*Ligustrum Ibota*, Plate X, Fig. 8), about 26.3 μ in diameter. Furrows three or occasionally four, in which case either strictly tetrahedral in arrangement or irregular and entirely asymmetrical; normally sharply defined, long, slender, and tapering, reaching almost from pole to pole, their membranes smooth, but each provided with a germ pore appearing as a small, rounded bulge at its center but without a well-defined aperture. Underlying the pores is a small mass of hyaline material, similar to but much smaller than the corresponding structures in the grains of *Olea*. In the great length of their furrows these grains are quite distinct from those of both *Olea* and *Ligustrum* but tend to resemble those of *Forsythia*.

The lilac is a garden shrub introduced into America from Europe and Asia where the genus is represented by about 30 species. Some half dozen of these are cultivated throughout the United States and Canada. All species are entirely insect pollinated and shed but little pollen, but some have been suspected of occasionally causing hayfever.

Forsythia suspensa Vahl. Forsythia, Golden bells. Grains various, 19.4 to 37.6 μ in diameter, normally about 28.5 μ, similar to the type (*Ligustrum Ibota*, Plate X, Fig. 8). Furrows three, long and tapering, their membranes smooth; germ pores not sharply defined, represented by a slight bulge in the middle of each furrow membrane. Exine doubly reticulate.

The reticulum of these grains is remarkable and beautiful, composed, for the most part, of a double system, consisting of rather uniform lacunae separated by ridges which are broader than those of the grains of *Syringa* and *Ligustrum* and bearing within their walls a series of smaller lacunae. As a result of this the surface of these grains presents the appearance of lacework delicately wrought in alabaster and studded with jewels.

Forsythia is a common garden shrub, insect pollinated and flowering very early in spring before the unfolding of its leaves or sometimes late in the autumn; not known to cause hayfever. The genus includes four species, native of Japan, China, and southern Europe. Of these, three have been introduced into cultivation in America.

PLANTAGINACEAE Plantain Family

PLANTAGO L. Plantain

Grains spheroidal, 16 to 40 μ in diameter. Furrows, in the ordinary sense of the word, absent. Pores 4 to 14, not elongate, circular or irregular in outline, scattered. Pore membranes flecked or with a single central thickening. Exine thin and more or less rough-granular. Intine thin and without conspicuous thickenings.

The pores of these grains should probably be regarded as shortened furrows; though they are not elongate, their furrow nature is suggested by their arrangement, which seems to conform to the trischistoclasic system. Harmomegathy is not required, because the exine is thin and flexible enough to accommodate all changes in volume. The thin exine and pore-like furrows suggest that these grains are reduced in form in response to wind pollination.

The genus contains over 200 species of low herbs, of wide distribution.

Plantago lanceolata L. English plantain (Plate X, Fig. 6) type. Grains approximately spheroidal when expanded, exceedingly various in size, 25 to 40 μ in diameter. Germ pores 7 to 14, distributed rather evenly over the surface and for the most part conforming to the trischistoclasic system, 10 to 14.8 μ apart, approximately circular in outline but sometimes with slightly wavy margins, 2.8 to 4.6 μ in diameter.

Each pore is encircled by a slight thickening of the exine which takes the stain a little more deeply than the rest of the surface, and each is crossed by a delicate membrane marked by a conspicuous central thickening. These two characters give the pores an appearance almost identical with the single pore of the grains of the grasses. There is much variation in the size of the pores on different grains, even among those of similar size, but on any single grain they are uniform. The grains of this species of plantain are notable for their great variation in size, a character which has been discussed at some length by Stout (1919). There appears to be no definite correlation between the size of the grain and the size, number, and distance apart of the germ pores. It can, however, be said that the larger grains tend to have larger pores, a greater number of them, and at greater distances apart.

The texture is characteristically mottled, but this is difficult to see unless the grains are well stained. Though this mottling is rather coarse, it is much less so than in the grains of the two following species.

A common weed of gardens and waste places almost throughout North America. Wind pollinated, flowering from April to November, shedding large amounts of pollen which is well known to be a potent cause of hayfever, generally in the early summer when the plants reach their best development. Plantain pollen is caught on pollen slides in large quantity almost throughout the summer.

Plantago Rugelii Dcne. Rugel's plantain (Plate X, Fig. 7). Grains approximately spheroidal, various in size but less so than those of *P. lanceolata*, 22.8 to 24.5 μ in diameter. Germ pores 6 to 10, very irregular in shape and with a jagged margin, various in size and not surrounded by an annular thickening; pore membranes flecked with a number of granules which tend to aggregate toward the centers of the membranes but are not generally fused. Texture similar to that of *P. lanceolata* but with the mottling coarser and sometimes almost warty.

This grain is easily distinguished from that of *P. lanceolata* by the ragged edges of its pores, the flecked character of the pore membranes, and the coarser texture of its exine.

A common weed distributed almost throughout North America. Flowers from June to September. It is wind pollinated but sheds so little pollen that it cannot be regarded as a factor in hayfever. It is occasionally caught on atmospheric pollen slides but in very much smaller quantity than the pollen of *P. lanceolata.*

Plantago major L. Common plantain. Grains somewhat various, approximately spheroidal, 16 to 21 μ in diameter. Germ pores four to six, according to the size of the grain, but generally five, irregular in shape; their membranes flecked with granules. Texture of the exine rough and warty.

In the texture of their exine, which is coarser even than that of the grains of *P. Rugelii*, and in the small number and irregular shape of their germ pores these grains are easily distinguished from those of the two preceding species.

A common weed, remarkably similar to *P. Rugelii;* in fact the plants themselves are more difficult to distinguish from each other than are their pollen grains. Of cosmopolitan distribution. May to September. Wind pollinated but shedding only a small amount of pollen which, though frequently caught on atmospheric pollen slides, is not regarded as a cause of hayfever.

COMPOSITAE Composite Family

CICHORIEAE Chicory Tribe

Grains globular, generally tricolpate, occasionally tetracolpate or, some abnormal grains, with higher numbers of furrows; echinolophate or occasionally simply echinate. Lacunae generally 12 to 20. Ridges high, generally vertically striate, never perforate, though occasionally appearing to be. Spines prominent, sharp and conical. Texture of the ridges and thickened parts of the exine more or less granular.

The pollen grains of the Cichorieae are generally characterized by an elaborate and beautiful system of sculpturing which, taken throughout the tribe, exhibits a wide range of variation but, in the majority of species, does not depart far from a certain form which may be considered basic for the tribe. Owing to the nature of the variations among the different species, and the fact that most of the forms encountered seem to be derivatives, through modification or reduction, from the basic form, a clear understanding of the relationship of the different forms to each other can best be gained by first examining in detail one typical form.

Such a form is that of the normal grains of *Taraxacum* (Plate XI, Fig. 2). These possess a characteristically trimerous pattern, but, if the sculpturing is stripped off, as sometimes happens when the pollen is prepared for microscopic examination, the underlying shape is found to be oblate-spheroidal, with three large germ pores bulging out as broad rounded papillae (Fig. 117). It is the presence of these three pores equally spaced around the equator of the grain which governs its trimerous pattern. The exine is thrown into an elaborate system of high ridges which anastomose enclosing variously shaped lacunae, the floors of which are covered by only the thinnest possible layer of smooth exine. The raised or thickened part of the exine is uniformly fine-granular and provided with long sharp conical spines, a condition designated as *echinolophate.*

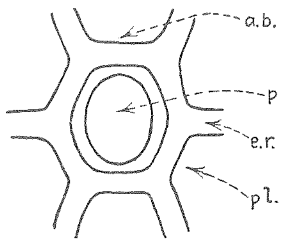

FIG. 107.

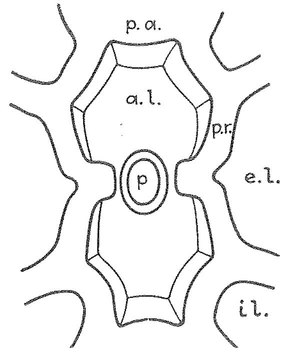

FIG. 108.

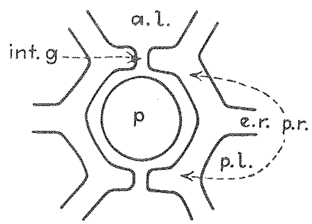

FIG. 109.

FIGS. 107–109.—Germ pores and surrounding ridges of pollen grains of Cichorieae: Fig. 107, *Scolymus hispanicus;* Fig. 108, *Tragopogon pratensis;* Fig. 109, *Taraxacum officinale:*— *a.l.*, abporal lacuna; *p*, germ pore; *p.l.*, paraporal lacuna; *p.a.*, polar area; *p.r.*, paraporal ridge; *e.l.*, equatorial lacunae; *int. g*, interlacunar gap; *e.r.*, equatorial ridge; *il.*, interporal lacuna. *tr*, transequatorial ridge.

The normal pattern in the grains of *Taraxacum* consists of 15 lacunae (Plate XI, Fig. 2), which are of definite shape and arrangement and can be readily identified from whatever direction the grain happens to be viewed. The three lacunae which encompass the three pores are hexagonal in form, but with two gaps in their ridges, and are known as the poral lacunae. If the grains be observed in polar view, *i.e.*, so oriented that the three pores are on the limb or edge of the apparent disk, and consequently one of the poles is uppermost, there will be seen six more

lacunae (Fig. 110). Three of these are adjacent to and in meridional line with the poral lacunae. These are the abporal lacunae. They are pentagonal in form, and each communicates with its adjacent poral lacuna through a narrow gap in the separating ridge (Fig. 109); in the polar view (Fig. 110) the poral lacunae are in side view, so that only one bounding ridge of each is seen, but they are easily recognized by their interlacunar gaps. Alternating with the pores, and between the abporal lacunae, are the three broad paraporal lacunae. These are also pentagonal in form. On the limb of the grain (seen in side view in Plate XI,

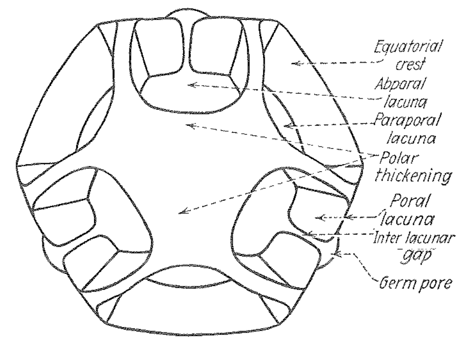

FIG. 110.

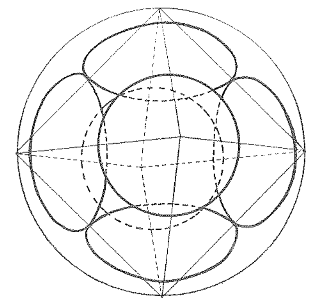

FIG. 111.

FIG. 110.—Diagram of the form elements of a pollen grain of *Taraxacum.* The large polar thickening varies in size and shape in the different grains of this species.

FIG. 111.—Diagram of the octahedral arrangement of six cells, which frequently occurs in the pollen mother-cells of *Taraxacum officinale* and some other species of the Cichorieae. The six cells are represented by heavy lines, the pollen mother-cell by the enclosing circle; and an octahedron is drawn in faint lines over the whole group to suggest the octahedral relation that the cells bear to each other.

Fig. 2) is the equatorial crest traversing the equator from poral lacuna to poral lacuna, separating from each other the adjacent paraporal lacunae of opposite hemispheres. In some cases it gives off a small projection into one or more of the paraporal lacunae. These, however, are omitted from the figures, because they seldom occur in the normal grains of *Taraxacum;* but they occur more frequently in the grains of other species, *e.g.*, those of *Scolymus* (Plate XI, Fig. 1). Over the pole is seen a rather large triangular or hexagonal area of thickened exine of variable extent—the polar thickening (Plate XI, Fig. 2). Since both hemispheres are alike, the whole pattern of the normal *Taraxacum* pollen grain comprises 3 poral, 6 abporal and 6 paraporal lacunae, making a total of 15. These are summarized in Table V. They correspond in arrangement to the faces of a pentakaidecahedron, with 12 pentagonal and 3 hexagonal faces.

The heaping of the material of the exine into vertical ridges serves to stiffen the exine to such an extent as nearly to demobilize the furrows, preventing them from opening and closing freely. Moreover, in the construction of the pattern of the grains of *Taraxacum*, the presence of the equatorial crests exerting a lateral thrust against the paraporal ridges bounding the furrows effectively prevents them from spreading apart to any extent despite the presence of gaps in the transverse ridges of the poral lacunae. As a consequence of this partial or complete demobilization of the furrows and their resultant loss of ability to accommodate changes in volume of the grain, the pores are very large and bulge prominently when the grain is moistened, thus taking over the greater part of the impaired harmomegathic function of the furrows.

We have already seen a similar example of the loss of harmomegathic function as a consequence of the development of high ridges on the exine, in the grains of *Polygonum* and *Persicaria*. In those of *Polygonum chinense* this was compensated by a great enlargement of the three pores, while in the various species of *Persicaria* it was compensated by increasing the number of pores up to 30 and more, all of which could bulge out as the grain increased in volume. In the grains of *Taraxacum* the compensation for the loss of harmomegathy of the furrows is made by an increase in the size of the pores and not by an increase in their number, for normally there are only three germ pores.

The basic form as exemplified by the grains of *Taraxacum* prevails, with little modification, among the majority of the species of the tribe. In the grains of *Hypochaeris*, *Sonchus* and *Nabalus* the pattern of the sculpturing is exactly as described for those of *Taraxacum*. In the grains of *Cichorium* (Plate XI, Fig. 6), *Crepis* and *Hieracium* the pattern differs only in the polar thickenings being less extensive and triradiate in outline owing to the encroachment upon them of the abporal lacunae. In the grains of *Haensèlera*, *Krigia*, *Cynthia*, and *Lactuca* the pattern differs in the polar thickenings being absent, represented only by the unexpanded confluences of three ridges at the poles. This

latter is likewise true of the grains of *Scolymus* (Plate XI, Fig. 1), but these, besides, lack the interlacunar gaps between the poral and abporal lacunae. These grains are of particular interest because, with the closing of the interlacunar gaps, the furrow is completely demobilized, and it necessarily follows that its harmomegathic function devolves entirely upon the pores. As a consequence the latter are large. But it is true that they are no larger in proportion than the pores of the grains of *Taraxacum* and others, in which the interlacunar gaps are present. It, therefore, appears that the interlacunar gaps in such grains as these are only useless vestiges of vanishing furrows, and that the closing of the interlacunar gaps in the grains of *Scolymus* is the final stage in their elimination, and stamps these grains as representing a step further in advance along the evolutionary line which led to the production of the lophate character, with its resultant demobilization of the furrows.

In the grains of *Tragopogon pratensis* (Plate XI, Fig. 4) and *Scorzonera hispanica* (Plate XI, Fig. 5) are found the widest deviations from the basic form of pattern encountered in the tribe. Those of *Tragopogon* have 15 lacunae, and those of *Scorzonera* have 20 (Table V), and in neither case do they correspond at all closely to the 15 lacunae of the grains of *Taraxacum*. In both cases the poral lacunae are lacking (Figs. 108, 116), and each abporal lacuna communicates directly with its corresponding member of the opposite hemisphere through a rather broad gap in which the germ pore is situated, the two communicating abporal lacunae thus forming the germinal furrow. There are no equatorial crests; instead, the regions of the equator between the pores are occupied by large equatorial lacunae. In the grains of *Tragopogon* (Fig. 108) there is a single hexagonal equatorial lacuna in each of these regions, while in those of *Scorzonera hispanica* (Fig. 115) there are two pentagonal lacunae in each. The joining of the abporal lacunae to form a furrow and the absence of equatorial crests in both of these grains, permit lateral movement of the paraporal ridges, which resemble, in action and appearance, a crossbow (Figs. 108, 116). That in both cases the two joined abporal lacunae function as a furrow is obvious from the small size of the germ pore, for in the grains of these two species it is much smaller than in those of any other member of the tribe. Its mode of operation is truly unique and brings into

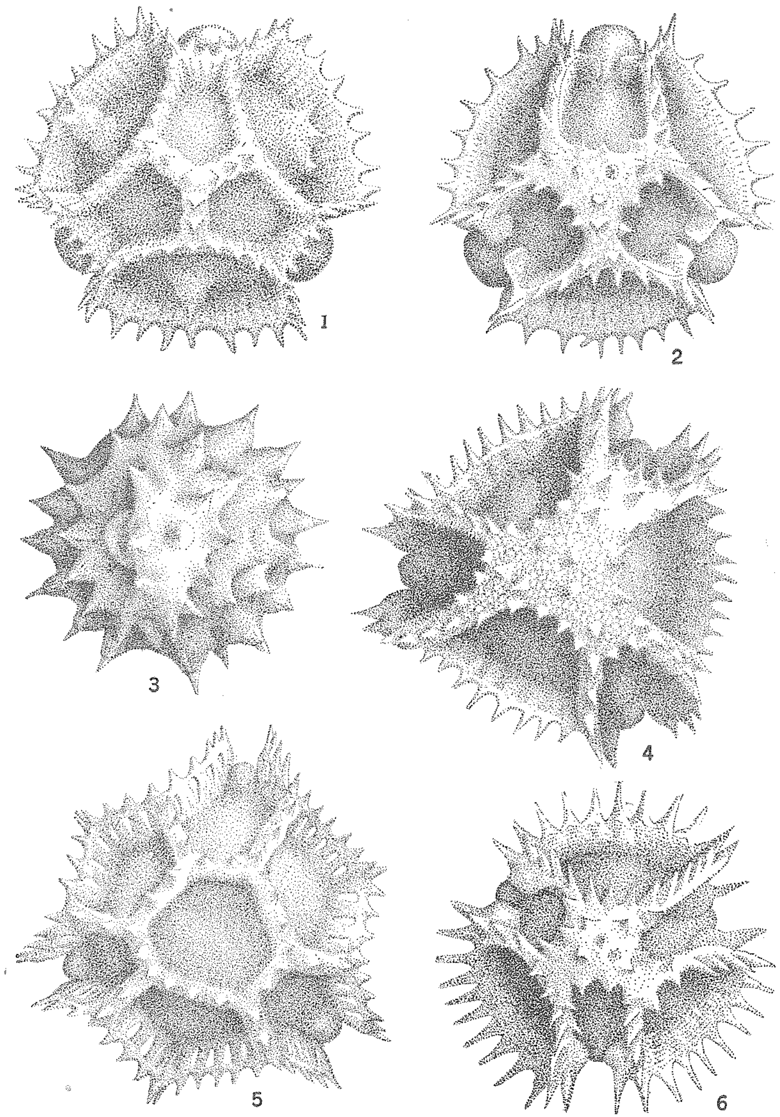

PLATE XI.—Pollen grains of Cichorieae. 1, *Scolymus hispanicus*, polar view, 35 μ in diameter. 2, *Taraxacum officinale*, polar view, 26 μ in diameter. 3, *Catananche caerulea*, side view, 27.4 μ in diameter. 4, *Tragopogon pratensis*, polar view, 32 μ in diameter. 5, *Scorzonera hispanica*, polar view, 37 μ in diameter. 6, *Cichorium Intybus*, polar view, 40 μ in diameter.

play a mechanism which is effective and beautiful in its simplicity. The pore in its interlacunar gap is tightly squeezed, in the one

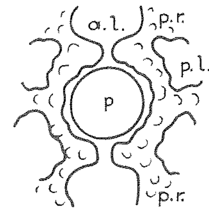

FIG. 112.

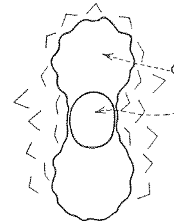

FIG. 113.

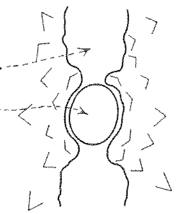

FIG. 114.

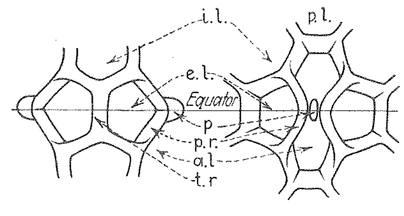

FIG. 115 FIG. 116.

FIGS. 112–116.—Details of pore patterns and surrounding ridges of pollen grains of Cichorieae: Fig. 112, *Dendroseris micrantha;* Fig. 113, *Catananche caerulea;* Fig. 114, *Catananche lutea;* Fig. 115, *Scorzonera hispanica*, with equatorial lacunae uppermost; 116, *Scorzonera hispanica*, with germ pore uppermost. Parts lettered as in figures 107–109.

case, between the projecting bosses of the lateral ridges (Fig. 108) and, in the other, between the ridges themselves (Fig. 116). It contains a plug of callose substance which upon absorbing water expands and in doing so pushes apart the two lateral ridges which are unhindered in their lateral movement owing to the presence of the equatorial lacunae into which they may move. When the grains are unexpanded the paraporal ridges are like bent crossbows with their backs pressing against the pores, but when the grains expand the paraporal ridges straighten like a bow that has been released. Such a movement, so nicely provided for in the grains of *Tragopogon* and *Scorzonera*, is entirely prevented in

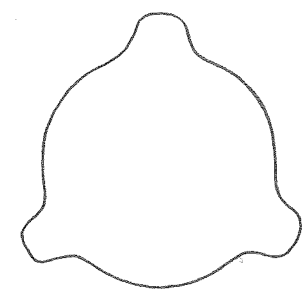

FIG. 117.—Pollen grain of *Taraxacum officinale* stripped of its exine to show the basic form upon which its elaborate pattern is built.

all grains like those of *Taraxacum* (Fig. 109) by the presence in these of equatorial crests which exert a thrust counteracting any lateral movement of the paraporal ridges. The remarkably wide deviation of the forms of the grains of *Tragopogon* and *Scorzonera* from the basic form of the tribe suggests that they are genetically divergent from the rest of the tribe but rather close to each other.

The grains of *Dendroseris micrantha* and *Catananche* (Plate XI, Fig. 3) show the pattern of the Cichorieae reduced to its lowest terms, which suggests that they occupy isolated positions in the tribe. But I think that their resemblance to each other is only superficial and without phylogenetic significance, because the forms of these grains are such as to suggest entirely different origins. In the grains of *Dendroseris* the reduction of the sculpturing appears to be the result of the extension of the polar thickenings toward the equator leaving the lacunae, though reduced in size, fairly sharply defined in the region of the equator (Fig. 112); while in the grains of *Catananche,* though this might likewise be true, the rudimentary pattern appears more likely to be due to a partial development of the ridges throughout, resulting in the formation of unrecognizable vestiges of lacunae over all of the surface. Moreover, the rudimentary lacunae appear to be quite different in the two cases (*cf.* Table V; Figs. 113, 114). Both forms may be derivative, though the possibility of one of them being primitive must not be overlooked. If one of them is primitive, it is most likely that of *Catananche*, in which case we witness here, in the clumping of the spines with irregularly shaped blank spaces between them, the initiation of the echinolophate system which characterizes the grains of almost the whole tribe; and in the grains of *Dendroseris micrantha* we witness the elimination of the echinolophate system by the encroachment upon it of the polar thickenings and the loss of spines.

The lacunar patterns of the Cichorieae resolve themselves into three well-marked types to which all but one of the forms may be referred as subsidiary or derived. The cardinal types of pattern are the *Taraxacum* type (No. 1, Table V, Plate XI, Fig. 2), with 15 lacunae, including 3 poral but no equatorial lacunae; the *Tragopogon* type (No. 3, Table V, Plate XI, Fig. 4), also with 15 lacunae, including 3 equatorial but no poral lacunae; and the *Scorzonera* type (No. 4, Table V, Plate XI, Fig. 5), with 20 lacunae, including 6 equatorial and no poral lacunae.

The *Taraxacum* type of lacunar pattern is represented in by far the greatest number of species. It characterizes, with certain modifications such as the fluctuation in extent of the polar thickenings, the grains of *Cichorium*, *Haenselera Krigia*, *Cynthia*, *Lactuca*, *Hypochaeris*, *Crepis*, *Hieracium*, and *Nabalus*. A four-pored tetraradiate derivative of this form, with 20 lacunae, characterizes about 90 per cent of the grains of *Sonchus oleraceus* (No. 1*a*, Table V) and a fair proportion of those of *Taraxacum*, *Cichorium*, *Hieracium aurantiacum*, and *H. pratense*. This differs from the basic trimerous pattern only in the addition of a fourth set of form elements. The tetraradiate pattern, in spite of its regular symmetry, should probably be regarded as entirely abnormal and will be discussed below. Another slight modification of this type is seen in the *Scolymus* form of pattern (No. 2, Table V), which characterizes both of the species of *Scolymus* here described. It differs from the *Taraxacum* pattern only in its closed poral lacunae (Fig. 107).

The *Tragopogon* type of lacunar pattern (Table V, Plate XI, Fig. 4), distinguished by its possession of three equatorial lacunae and no poral lacunae, is found only in the grains of *Tragopogon* and has no derivatives among the species here considered.

The *Scorzonera hispanica* type of lacunar pattern (No. 4, Table V), distinguished by the possession of six equatorial lacunae, two polar, and no poral lacunae, characterizes, without modification, only the grains of *S. hispanica*, but, with the replacement of the polar lacunae by polar thickenings, it characterizes the grains of *S. purpurea*, *S. graminifolia*, *S. nervosa;* by an enlargement of the polar thickenings, almost or quite obliterating the interporal lacunae, it characterizes the grains of *S. parviflora* and *S. humilis;* and, by a further encroachment of the polar thickenings, obliterating the equatorial lacunae, possibly those of *Catananche caerulea*.

The lacunar pattern of *Dendroseris micrantha* (Table V) is entirely aberrant in its possession of 12 paraporal lacunae. The extensive development of its polar thickenings suggests that it is a derived form but apparently not from one of the three cardinal forms mentioned above.

Tetraradiate Grains.—The pollen of many species in this tribe is characterized by the presence, in varying proportion, of abnormal grains. For the most part these are asymmetrical and malformed, often not identifiable. Notable among these, however, is the occurrence, mentioned above, of tetracolpate grains which are tetramerous and strictly tetraradiate. They constitute a fairly large proportion of the pollen of *Taraxacum*, *Cichorium*, several species of *Crepis*, and about 90 per cent of the pollen of *Sonchus oleraceus*. This condition has also been noted by Fischer (1890), who says, "Abweichungen von dreifaltigen Gestalt sind auch hier nicht häufig; ich fand vier parallele Falten, mit entsprechender Vermehrung der Flächen und Leisten, bei: *Hieracium aurantiacum*, *H. villosum*, *H. boreale*, *H. rigidum*, *Mulgedium Plumieri*, *Sonchus oleraceus*, bei letzterer häufiger als die dreifaltigen." Thus, the condition is apparently widespread in the tribe. This form is just as radially symmetrical as the typical forms, differing from them only in the possession of 4 pores and, as a consequence, 4 abporal and 4 interporal lacunae in each hemisphere, *i.e.*, a total of 20 on the grain, and with four- or eight-sided polar thickenings (No. 1*a*, Table V). Generally, the 4 furrows converge toward the poles at angles of exactly 90 deg. instead of the usual angle of 120 deg. These are the only examples that I have ever seen of truly tetraradiate pollen grains.

Such tetraradiate grains are of the utmost interest because they violate the law of equal triconvergent angles, which seems to be almost universal for furrow arrangements. Nevertheless, the reason for the tetraradiate configuration of the furrows of these grains is quite apparent if we inquire into the early stages of their formation. These I have observed in *Taraxacum*, the pollen mother-cell of which is notorious for its extraordinary and numerous irregularities of division. One of the commonest of these is the division of the mother-cell nucleus into six instead of the usual four daughter-nuclei. When these happen to be all of the same size, as they frequently are, they take up their positions in the mother-cell equidistantly from each other which results in their being octahedral in arrangement (Fig. 111). Then when the subsequent division of the mother-cell, which is simultaneous by furrowing, takes place, the result is that at the final separation each of the daughter-cells is connected with four of its neighbors of the hexad through four pit connections with the result that each daughter-cell comes to have four furrows equatorially arranged. Since each of these furrows originates through a separate impulse, each is independent of the others and receives a meridional orientation in the same way that the three furrows in ordinary tricolpate pollen grains receive meridional orientation through three independent contact impulses.

Among the numerous atypical forms that occur in this tribe, this is the only one that is radiosymmetrical. There are, besides these, four-pored grains bearing patterns which are asymmetrical and variously distorted—frequently so much that it is difficult to interpret them, but they appear to correspond to the ordinary tetracolpate form in which the furrows converge in pairs toward four centers, corresponding in arrangement to four of the six edges of a tetrahedron, the form of grain which we have seen results from daughter-cells' making *two* points of contact with their neighbors of a tetrad.

The numerous irregularities among the pollen grains of this tribe are generally, if indeed not always, to be associated with the widespread occurrence of an irregular distribution of chromosomes in the reduction divisions. Certainly this is true of some of the species of *Hieracium* and *Crepis* (Hollongshead and Babcock, 1930; Babcock and Clausen, 1929) and can generally be associated with hybridity of origin, and such pollen is known to be frequently sterile, the seeds forming apogamously. For example, Osawa (1913) finds that in *Taraxacum platycarpum* Dahlst. pollination is necessary for seed formation, while in *T. albidum* Dahlst. it is unnecessary. In the former the pollen mother-cells divide normally, forming four pollen grains in the usual way, while in the latter there is much irregularity in the meiotic divisions. Frequently the pollen mother-cell nucleus may give rise to fewer or more than the usual four daughter-nuclei, which, according to Osawa, is due either to lagging of the chromosomes in the first division, forming extranuclear chromosomes which later become cells, or to an amitotic division of the nucleus in the second division.

Since the patterns of the grains are largely the result of their relations with their neighbors during their formative period—whether they be formed in diads, tetrads, or hexads or whether they be smaller or larger than their neighbors—and since these relations depend largely upon the complement of chromosomes that each grain receives, it is likely that much can be learned regarding the distribution of chromosomes, in cases where such irregularities occur, by simply inspecting the pollen-grain patterns.

The lophate character, which is the outstanding feature of the Cichorieae, is not confined to this tribe alone. Among the Compositae it is also characteristic of the pollen grains of the tribe of Vernonieae, of *Barnadesia* in the tribe of Mutisieae, and of *Berkheya* in the tribe of Arctotidae. In the grains of the Vernonieae* an enormous range of variation occurs in the different species, but they can generally be distinguished from those of the Cichorieae by the greater number of lacunae which prevails almost throughout the tribe. Thus, there are 27 in that of *Stokesia* (Plate XII, Fig, 2), 30 in the grain of *Vernonia Wrightii* (Plate XII, Fig. 3) and 32 in that of *V. jucunda* (Table V), and in those of *Struchium*, and *Pacourina* (Plate XII, Fig. 1) they are too numerous to count with certainty. In *Barnadesia** patterns numerically similar to those of the Vernonieae are encountered; but the ridges are always without spines (Table V, Plate XII, Figs. 6 to 8).

Among the Arctotidae the grains of *Berkheya heterophylla* have a lophate pattern consisting of 29 lacunae of a quite distinctive form. The crests are without spines, as in *Barnadesia;* but the grains may be distinguished from these and all others by the curious bilateral nature of their pattern, in which there are two paraporal and two interporal lacunae in each hemisphere (Table V). In these grains the pattern is as fully and beautifully expressed as in any of the other groups but so different in the number and arrangement of its elements that it is scarcely comparable with any of the others, particularly those of the Cichorieae. Such a pattern, however, appears to be exceptional among the Arctotidae, for it is entirely absent in the grains of *Arctotis grandis.* The latter are simply echinate and spheroidal.

From a study of the occurrence of the lophate patterns among the Cichorieae and other groups of the Compositae, it thus appears that the presence or absence of this character is no criterion of relationship, any more than is the presence or absence of the ordinary reticulate pattern which we have seen to occur

* For a detailed account of the pollen grains of the Vernonieae see Wodehouse (1928*a*); of *Barnadesia*, Wodehouse (1928*b*).

again and again in unrelated groups, but the nature of the lophate character when present is of the highest phylogenetic value; and the divergences in number and spacial configuration of the pattern elements are also likely to prove of great value in the study of the irregular distribution of chromosomes.

Key to the Species

I. Equatorial ridges present, and equatorial lacunae absent; poral lacunae present; texture fine-granular or smooth.	
A. Lacunar pattern 1.* Interlacunar gaps present between the poral and abporal lacunae.	
1. Polar thickenings large, triangular or hexagonal.	
a. Grains 19 to 25 μ in diameter.	Taraxacum officinale Hypochaeris radicata
b. Grains 26 to 30 μ in diameter.	Sonchus oleraceus
c. Grains 30 to 35 μ in diameter.	Nabalus altissimus
2. Polar thickenings moderately developed, triradiate.	
a. Grains 17 to 32 μ in diameter.	Crepis virens biennis japonica taraxacifolia tectorum Hieracium auricula venosum patens aurantiacum umbellatum
b. Grains 35 to 40 μ in diameter.	Cichorium Intybus
3. Polar thickenings not developed, represented only by the unexpanded confluence of three ridges at the poles.	
a. Grains 22 to 25 μ in diameter.	Krigia virginica Cynthia virginica Lactuca virosa
b. Grains 30 to 40 μ in diameter.	Haenselera granatensis
B. Lacunar pattern 2.* Interlacunar gaps absent, poral lacunae hexagonal. Polar thickenings not developed, represented by the unexpanded confluence of three crests at the poles.	
1. Poral lacunae approximately isodiametric.	Scolymus hispanicus
2. Poral lacunae meridionally elongate.	Scolymus grandiflorus

II. Equatorial lacunae present. Equatorial crests and poral lacunae absent. Texture coarsely granular. The pattern may be elaborate, represented by 15 or 20 lacunae, or may be greatly reduced, in which case the grains resemble those of Sec. III.

A. Equatorial lacunae 3; polar thickenings large and hexagonal; lacunar pattern 3.*

1. Ridges high. — Tragopogon pratensis, minor
2. Ridges low. — porrifolius, orientalis

B. Equatorial lacunae 6.

1. Polar thickenings absent; polar lacunae present, triangular or hexagonal; lacunar pattern 4.* — Scorzonera hispanica
2. Polar thickenings present but not greatly extended; polar lacunae absent. Lacunar pattern 4*a*.* — Scorzonera purpurea, graminifolia, nervosa
3. Polar thickenings greatly extended lacunar pattern nearly obliterated, 4*b*.* — Scorzonera parviflora, humilis

III. Equatorial lacunae absent. Lophate pattern represented only by the poral and a few other more or less rudimentary lacunae or entirely absent. Texture fine-granular.

A. Poral lacunae present.

1. Paraporal lacunáe 6, clearly defined, each separated from its neighbor of the opposite hemisphere by a well-defined equatorial crest; lacunar pattern 7.* Spines sharp conical. — Dendroseris pinnata
2. Paraporal lacunae 12 but vestigial. spines reduced or vestigial. Lacunar pattern 8.* — Dendroseris micrantha

B. Lacunae absent, except a poorly defined vestige of the poral or abporal or both.

1. Furrow constricted once in the middle, suggesting that it represents the union of 2 paraporal lacunae, with lacunar pattern 5.* — Catananche caerulea
2. Furrow constricted twice, on either side of the pore, suggesting that it represents the union of a poral and abporal lacunae, with lacunar pattern of 6.* — Catananche lutea

*See table of lacunar patterns (p. 472).

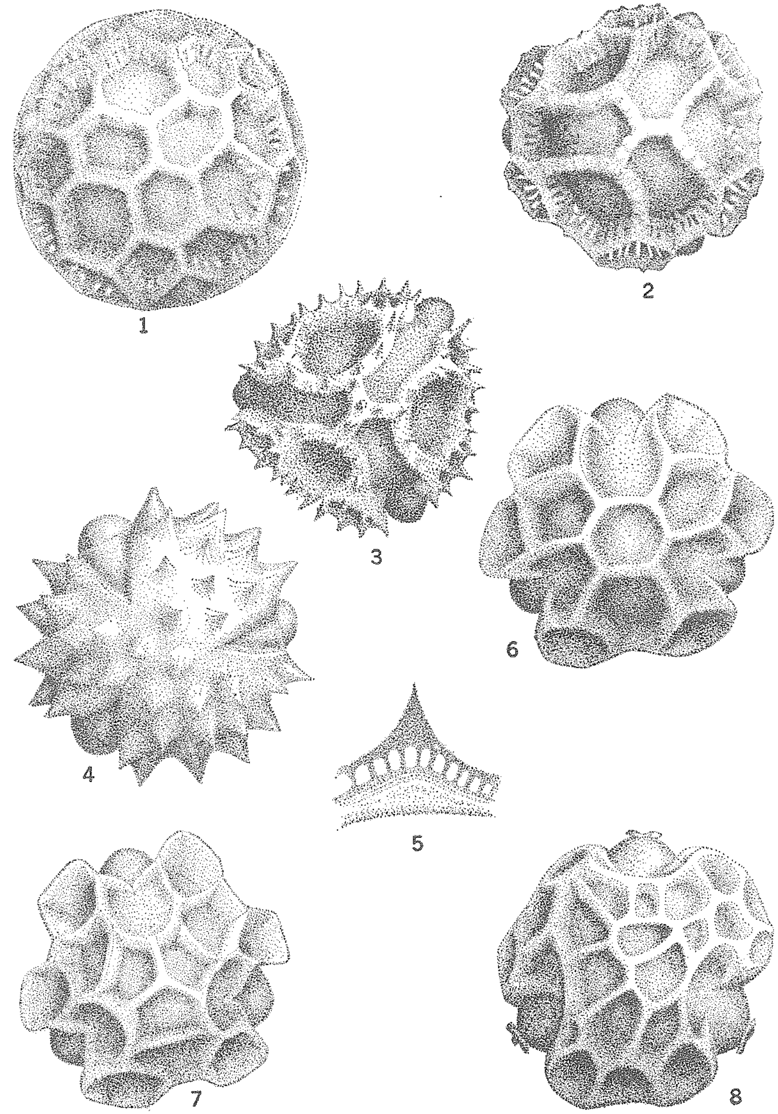

PLATE XII.—Pollen grains of Vernonieae, Astereae, and *Barnadesia*. 1, *Pacourina edulis*, 50 μ in diameter. 2, *Stokesia laevis*, polar view, 55 μ in diameter. 3, *Vernonia Wrightii*, polar view, 39.4 μ in diameter. 4, *Solidago speciosa*, polar view 23 μ in diameter. 5, Enlarged spine of the same as seen in optical section. 6, *Barnadesia trianae*, polar view, 50 μ in diameter. 7, *B. venosa*, polar view, 67.5 μ in diameter. 8, *B. berberoides*, polar view, 52 μ in diameter.

TABLE V.—LACUNAR PATTERNS

Lacunae	1. Taraxacum	1a. Sonchus oleraceus	2. Scolymus hispanicus	3. Tragopogon pratensis	4. Scorzonera hispanica	4a. Scorzonera purpurea	4b. Scorzonera parviflora	5. Catananche caerulea	6. Catananche lutea	7. Dendroseris pinnata	8. Dendroseris micrantha	9. Vernonia jucunda	10. Vernonia Wrightii	11. Barnadesia trianae	12. Barnadesia venosa	13. Berkheya heterophylla
Poral	3	4	3	0	0	0	0	0	3	3	3	3	3	3	3	3
Equatorial	0	0	0	3	6	6	6	0	0	0	0	3	3	3	3	6
Paraporal	6	8	6	0	0	0	0	0	0	6	12	12	12	12	12	4
Abporal*	6o	8o	6c	6o	6o	6o	6o	6o	6o	6o	6o	6c	6o	6o	6o	6o
Interporal	0	0	0	6	6	6	Faint	0	0	0	0	6	6	6	6	4
Polar	0	0	0	0	2	0	0	0	0	0	0	2	0	2	6	6
Total	15	20	15	15	20	18	12	6	9	15	21	32	30	32	36	29

* o, open; c, closed, in reference to the presence or absence of interlacunar gaps opening into the poral lacunae or abporal lacunae of the opposite hemisphere.

Taraxacum officinale Weber (*T. Taraxacum* Karst., *T. Dens-leonis* Desf. *Leontodon Taraxacum* L.) Dandelion (Plate XI, Fig. 2) type (see page 457). Grains extremely various; about one-half of them abnormal, *i.e.*, asymmetrical or deviating in various ways from the basic form of the family. Normal grains 24 to 27.5 μ in diameter, with ridges about 4.6 μ high and spines 2.3 μ long. Polar thickenings various in extent, hexagonal, triangular, or tending to be triradiate. Texture distinctly granular, and crests marked with conspicuous vertical striae.

Among the atypical grains are found many that are tetracolpate and hexacolpate. Most of these are extremely irregular and entirely asymmetrical, though some are strictly tetraradiate. This latter form has already been discussed at some length (see page 466).

The dandelion is a common weed of almost universal distribution. It is said to have lost its sexuality, its embryos developing by apogamy (Strasburger, 1908, pages 93, 518). Indeed, the appearance of most of its pollen grains suggests that they are incapable of effecting fertilization.

The genus consists of 20 or 25 species of low perennial or biennial herbs with radical pinnatifid or runcinate leaves; native of Europe, but some species widely distributed elsewhere.

Hypochaeris radicata L. Cat's-ear. Grains uniform, oblately spheroidal, 19.4 to 20.5 μ in diameter, as in *Taraxacum* type. Polar thickenings large; texture fine-granular, vertical striae of the crests faint; spines short but sharp, irregularly arranged over the greater part of the polar thickenings but serried along their margins.

A low herb with basal leaves and slightly branching scapes bearing a few small heads of yellow flowers. Introduced in fields and waste places in eastern North America. The genus contains about 40 or 50 species, native of Europe, the Mediterranean region, northern Asia, and South America.

Sonchus oleraceus L. Common or Annual sow thistle. Grains oblately spheroidal, 26.2 to 28.5 μ in diameter, ridges about 2.3 μ high, spines 2.3 μ long.

As in the case of dandelion pollen, both triradiate and tetraradiate forms are found, the latter constituting about 90 per cent. Both forms are essentially the same as the corresponding forms of the dandelion pollen, except that in the tetraradiate form of

Sonchus the polar thickenings are more or less broken by small, asymmetrically arranged lacunae. The grains of *Sonchus* appear always to form in tetrahedral tetrads; therefore the explanation of the tetramerous forms is not the same as in the case of *Taraxacum* and deserves investigation.

A common weed with leafy stems, bearing small heads of pale-yellow flowers in summer; widely distributed in waste places. Native of Europe.

The genus includes about 45 species of herbs, native of the Old World.

CREPIS L. Hawk's-beard

Grains essentially as in the *Cichorium* type but generally smaller and with the polar thickenings larger in proportion. The pollen of some species is characterized by great lack of uniformity, often presenting many atypical grains. There is generally much variation in the character of the polar thickenings among the different species or even among the different grains of the same species; sometimes the polar thickening is only a small, triradiate expansion of the three convergent ridges at the poles, and sometimes it is as extensive as in the grains of *Taraxacum*. When large it is generally broken and occupied by one or more rudimentary and asymmetrically placed lacunae. The texture of the ridges is only faintly striate; that of the polar thickenings, faintly granular.

The genus comprises about 170 species of small or occasionally large herbs, with yellow or sometimes red flowers. Mostly of the Northern Hemisphere in the Old World, also in North America, tropical Africa, and one species in the Andes of Bolivia.

Crepis biennis L. (*Hedypnois biennis* Huds.) Rough hawk's-beard. Grains various in size and form, the majority abnormal. Normal grains oblately spheroidal, 20 to 27.5 μ in diameter, with ridges 3.5 μ high and spines 2.3 μ long. Polar thickenings large, as in the *Taraxacum* type, but generally broken, provided with one or more rudimentary lacunae. Otherwise as in the *Cichorium* type.

A large proportion of the grains are tetracolpate, but these are not tetraradiate; they are, instead, variously irregular.

A low biennial herb, native of Europe but introduced into California.

Crepis japonica Benth. Grains somewhat various, a small proportion of them exhibiting irregularities of pattern. Normal grains about 18.2 μ in diameter, with ridges 3.4 μ high and spines 1.7 μ long. Otherwise as in the *Cichorium* type.

Tropical Asia and Australia.

Crepis taraxacifolia Thuill. (*C. praecox* Balb. *Barkhausia taraxacifolia* DC.). Grains uniform, 19.8 to 22 μ in diameter, ridges 2.3 μ high, spines 2.3 μ long. Polar thickenings more extensive than in the *Cichorium* type but less so than in that of *Taraxacum*.

This species is regarded by Hegi (1929) as a subspecies of *C. vesicaria*.

Europe.

Crepis tectorum L. (*Hieracium tectorum* Karsch.) Narrow-leaved or smooth hawk's-beard. Grains uniform in size and pattern, 19.4 to 20.5 μ in diameter; ridges 2.3 μ high; spines 2.3 μ long; paraporal lacunae generally provided with a small group of detached spines; texture scarcely granular, and ridges only faintly striate. Otherwise as in the *Cichorium* type.

A slender herb about 1 ft. high and branching from the base. In fields and waste places, naturalized in America from Europe.

Crepis capillaris (L.) Wallr. (*C. virens* L. *Lampsana capillaris* L.) Smooth hawk's-beard. Grains uniform, 19.4 to 20.5 μ in diameter, ridges 2.3 μ high, spines 1.7 μ long. Pattern of the ridges and lacunae as in the *Cichorium* type, except that the polar thickenings are larger, in some cases even larger than in the grains of *Taraxacum*.

A low herb 1 to 3 ft. high. Almost throughout Europe and in the Canary Islands. Introduced into California. It occurs in many different forms, some of which have received specific names.

HIERACIUM L. Hawkweed

Grains indistinguishable from those of *Crepis*, 17 to 35 μ in diameter; ridges about 2.3 μ high, faintly or not at all striate on their sides or granular on their tops.

The grains of some species exhibit irregularities which are so extreme as to baffle analysis and make it impossible to relate them to any type form. Most of such grains are obviously abortive or otherwise defective.

Hispid or hirsute and often glandular perennial herbs, with single or panicled heads of showy, generally yellow flowers in summer and early autumn.

Hieracium auricula L. Grains uniform, about 17 μ in diameter, ridges 2.3 μ high, and spines 2.3 μ long. As in the *Cichorium* type but with the polar thickenings somewhat more extensive.

Small herbs with slender scapes bearing a few heads of yellow flowers throughout the summer. Native of Europe.

Hieracium venosum L. Rattlesnake weed. Grains uniform, about 22.1 μ in diameter, ridges 2.3 μ high, and spines 2.8 μ long, which is unusually long for grains of this genus. Otherwise as in the *Cichorium* type.

Herbs with stem 1 to 2 ft. high arising from a basal rosette of purple-veined leaves. Dry plains and woods, eastern United States and Canada.

Hieracium pratensis Tausch. Field hawkweed. Grains various, many of them abnormal and obviously abortive. Normal grains 19.4 to 20.5 μ in diameter, essentially as in the *Cichorium* type, except that the polar thickenings are more extensive, and the germ pores elliptical—elongate in the equatorial direction, an unusual condition in the family.

Many grains are tetracolpate, and some of these are strictly tetraradiate, as in the pollen of *Taraxacum*.

A low herb of Europe and northern Asia.

Hieracium aurantiacum L. Orange or Golden mouse-ear, Devil's-paintbrush, Tawny hawkweed. Grains extremely various and irregular, more than half of them tetracolpate but not tetraradiate. Normal grains about 22.5 μ in diameter, ridges 1.7 μ high, and spines 2.8 μ long.

The pattern of these grains is so much distorted that it is impossible to relate it to any type. There is a marked tendency for the lacunae to become obliterated, the grain approaching the form of *Catananche*. Such grains, however, are apparently always defective.

The plant is a low, hispid or hirsute herb, with deep orange- to flame-colored heads of flowers, borne in panicles or singly, on leafy scapes arising from a rosette of basal leaves. A common weed of fields and roadsides.

New England to New York. Naturalized from Europe.

Hieracium umbellatum L. Grains extremely various, apparently all or nearly all defective, exactly as in *H. aurantiacum*.

A low herb with slender, leafy scape, 6 to 12 in. high, with one or a few large, showy heads of yellow flowers.

Throughout Europe, parts of Asia, Japan, and North America.

Nabalus altissimus (L.) Hook. (*Prenanthes altissima* L.) Rattlesnake root. Grains uniform, about 22 μ in diameter, ridges about 3.4 μ high and spines 3.4 μ long. Texture distinctly and rather coarsely granular, and ridges conspicuously striate. Pattern essentially as in the *Taraxacum* type, but ridges a little narrower; polar thickenings of various extent but generally rather large. Germinal lacunae rounded hexagonal, usually isodiametric, or occasionally elongate in the equatorial direction.

Tall, perennial herbs, with a slender, leafy stem rising to a height of 3 or 7 ft. and bearing numerous small heads of greenish or purplish flowers, in late summer.

Rich woods, New England to Minnesota and northward.

The genus comprises about 26 species, mostly of Europe, the Canary Islands, and Japan.

Haenselera granatensis Boiss. Grains uniform, spheroidal or somewhat oblately flattened, 28 to 35 μ in diameter, with ridges about 4 μ high and spines 3.4 μ long; pattern nearly always symmetrical, similar to the *Taraxacum* type, except that the polar thickenings are represented only by the unexpanded confluence of three crests at the poles, as in the grains of the *Scolymus* type (Plate XI, Fig. 1). The poral lacunae are elliptical, lengthened in a meridional direction, and each closely surrounds its bulging germ pore, which is large and has apparently entirely taken over the harmomegathic function. Interlacunar gaps are present but generally small and inconspicuous. The ridges are faintly striate and granular both on their tops and on their sides.

This grain is distinguished from that of *Tragopogon* by the presence of equatorial crests instead of lacunae, from those of *Scolymus* by the presence of interlacunar gaps and its heavier ridges, from those of *Taraxacum* and the species associated with it in the key by the lack of polar areas, and from those of *Krigia* and genera associated with it by its much larger size.

Perennial herb with a smooth, leafy scape, bearing a single head of yellow flowers. Regarded by Boissier as closely related to *Scolymus*.

The only species of the genus rather rare in southern Spain.

Krigia virginica (L.) Willd. Carolina dwarf dandelion. Grains uniform 22.5 to 25.5 μ in diameter, ridges 4.0 μ high, spines 1.7 μ long. Essentially as in *Haenselera*, excepting their smaller size and shorter spines, differing from the *Taraxacum* type in the lack of development of the polar thickenings, in which respect they resemble those of *Scolymus*.

Small herbs with lyrate leaves resembling those of the common dandelion. Flowers yellow in small heads. April to August. New England to Minnesota and southward.

Cynthia virginica (L.) D. Don (*Krigia amplexicaulis* Nutt.) Cynthia, Virginia goatsbeard. Grains uniform, about 25.1 μ in diameter; ridges faintly striate, about 2.8 μ high, spines 1.7 μ long; in pattern indistinguishable from those of *Krigia*, sharing with them the unusually short spines.

Plants similar to *Krigia*, generally growing on moist banks, common. Minnesota and southward, bearing small heads of yellow flowers.

Lactuca virosa L. (*L. scariola* L.) Prickly lettuce. Grains uniform, 24 to 25 μ in diameter, ridges 3.5 μ high, spines 2.3 μ long; in pattern, etc., indistinguishable from those of *Krigia*.

A common weed with prickly leaves, generally vertically oriented, waste grounds and roadsides; flowers purplish in small heads, appearing in summer. Introduced from Europe but now widely distributed throughout North America.

The genus contains about 100 species, mostly native of the Old World, and a few in North America and the West Indies.

Cichorium Intybus L. Chicory, Succory (Plate XI, Fig. 6) type. Grains extremely various, many of them giants, tetra- and hexacolpate and sometimes tetraradiate. These are of the utmost interest in throwing light on the origin of symmetry patterns of the Compositae and other groups (Wodehouse, 1929). Normal grains are three pored and with a triradiate pattern, oblately spheroidal in form, about 40 μ in diameter, provided with vertical ridges about 5.7 μ high, conspicuously striate, and topped with conical, sharp spines about 2.3 μ long. The pattern is similar to that of the *Taraxacum* type, which has been fully described (page 457). The poral lacunae are circular or hexagonal, each closely surrounding its large, bulging germ pore and communicating with the adjacent abporal lacunae through generally narrow interlacunar gaps. The three lacunae so joined form a germinal furrow which possesses partial harmomegathic function. The equatorial crests extend in a straight, unbroken line from poral lacuna to poral lacuna around the equator of the grain, occasionally giving off a short projection into one or more of the large, pentagonal, interporal lacunae. The three ridges which converge toward the poles are expanded at their confluence into a polar thickening which is triradiate and not triangular or hexagonal in shape, as in the *Taraxacum* type.

Chicory is a common weed with heads of delicate blue flowers appearing in summer. Introduced from Europe, it is now widely distributed in fields and along roadsides throughout most of the eastern half of the United States and Canada. Several varieties are cultivated and are of considerable culinary value.

SCOLYMUS L. Golden thistle

Grains uniform, oblate-spheroidal, about 35 μ in diameter, with the pattern well developed, sharply defined, and beautifully symmetrical (Plate XI, Fig. 1). It consists of 15 lacunae separated by high uniform ridges which are conspicuously marked by vertical striae and topped with a row of conical sharp spines. Their pattern conforms, in general, with the basic pattern form of the tribe but is distinctive in its possession of closed poral lacunae (Fig. 107). These are hexagonal, isodiametric, or elongate in a meridional direction but do not communicate with the abporal lacunae through interlacunar gaps, as the poral lacunae do in the grains of most other members of the tribe. The paraporal lacunae are large and pentagonal, and the equatorial ridges which separate those of opposite hemispheres from each other generally give off into each a short projection bearing two or three spines. The abporal lacunae are elongate-pentagonal, their apexes converging toward the poles but separated from each other at the poles by a triradiate crest which is not expanded to form a polar thickening. The closed poral lacunae, together with the absence of polar thickenings, serves to distinguish the grains of *Scolymus* from those of all other members of the tribe so far examined.

The genus comprises three or four species of perennial herbs, native of the Mediterranean region.

Scolymus hispanicus L. Spanish oyster plant, Salsify (Plate XI, Fig. 1) type. Grains about 34.2 μ in diameter. Ridges 4 to 4.6 μ high, topped with spines of varying length, about 3.4 μ long. Germ pores large, about 11 μ in diameter, each tightly filling its hexagonal poral lacuna.

The poral lacunae are nearly isodiametric and are apparently too short to permit harmomegathy, this function being entirely taken over by the large, bulging germ pores. The polar areas are generally occupied by the unexpanded confluences of three convergent ridges, but occasionally the confluence is spread apart to admit a polar lacuna at one or both poles. This condition, however, is generally accompanied by various other irregularities and often asymmetry of pattern.

A biennial herb about 2 ft. high, with spiny, thistle-like leaves and a few heads of golden-yellow flowers. Native of southern Europe, it is cultivated for its edible root which is similar to that of the true salsify (*Tragopogon porrifolius*).

Scolymus grandiflorus Desf. Grains uniform, similar to the type but with ridges a little thinner, 3.4 to 4.6 μ high, topped with spines, 2.3 to 3.4 μ long. The poral lacunae are always elongate in a meridional direction and appear to exercise some harmomegathy, for the pores are considerably smaller than those of the type. The pattern is much less uniform and frequently exhibits a pentagonal or irregularly shaped lacuna at one or both poles, introducing various irregularities.

These grains may always be distinguished from those of the type by the lighter construction of their ridges and their elongate poral lacunae. The grains of this species have been described and illustrated by Fritzsche (1837).

A perennial herb, occasionally cultivated for the beauty of its golden-yellow flowers.

TRAGOPOGON L. Goatsbeard

Grains generally symmetrical and uniform, spheroidal or somewhat oblately flattened, 28 to 38 μ in diameter; ridges rather broad, coarsely granular on top, conspicuously marked with vertical striae and topped with slender, conical, sharp-pointed spines (Plate XI, Fig. 4).

The lacunar pattern of these grains is unique, quite different from that of the grains of any other member of the family. The ridges anastomose in such a way as to form 15 symmetrically arranged lacunae, some of which correspond to those of the grain of *Taraxacum*, and others of which do not. There are always three pores equatorially arranged but smaller than in the *Taraxacum* type and not enclosed in lacunae (Fig. 108); poral lacunae in these grains are entirely absent. The abporal lacunae are hexagonal in shape, and each communicates with its meridionally adjacent neighbor of the opposite hemisphere through a broad gap in which the germ pore is situated. The two lacunae, so connected, obviously serve as a germinal furrow possessing harmomegathy; and this is reflected in the small size of the pore, since it is not called upon to accommodate changes in volume. The equatorial crest is absent, unless two short bosses abutting against each pore on the equator be regarded as vestiges of it. The three areas on the equator between the pores are occupied by as many six-sided equatorial lacunae; and it is obviously the presence of these broad spaces, in place of the usual equatorial ridge, which permits the free expansion of the furrows. Alternating with the abporal lacunae in each hemisphere are three large, four-sided, interporal lacunae.

The lacunar pattern of this grain therefore includes six tetragonal and nine hexagonal faces. Relating this to polyhedrons, we find that no pentakaidecahedron with such a combination of faces can exist (see page 199). If, however, the two polar areas be regarded as filled-in hexagonal lacunae, making 17 lacunae in all, the pattern corresponds to a heptakaidecahedron with 6 tetragonal and 11 hexagonal faces, which appears to be the proper interpretation of this pattern.

These grains may be distinguished from those of all other members of the family so far investigated by their lack of poral lacunae together with their possession of three equatorial lacunae and their much coarser granular texture. These two former characters stamp *Tragopogon* as genetically distinct. Their grains thus represent the culminating development of the lophate character in the tribe, equaled only in the grains of *Scorzonera*.

The grain of a species of *Tragopogon* has been described and illustrated by Fritzsche (1837), but he regards the polar thickenings as lacunae filled with spines and so describes the grain as having 17 instead of 15 lacunae.

The plants are stout, glabrous biennials or perennials with entire grass-like clasping leaves and large, solitary heads of yellow or purplish flowers. The genus contains 30 or 40 species, in the Mediterranean region and central Asia.

Tragopogon pratensis L. Goatsbeard (Plate XI, Fig. 4) type. Grains uniform, about 32 μ in diameter, with ridges about 3.2 μ high and spines 3.4 μ long. Otherwise as in the generic description.

A weed of fields and roadsides. New England to New Jersey and Minnesota. Introduced from Europe. Flowers yellow, summer.

Tragopogon minor Mill. Grains uniform, 28 to 34.5 μ in diameter. Otherwise as in the type.

Regarded by Hegi (1929) as a variety of *T. pratensis*. Native of Europe.

Tragopogon porrifolius L. Salsify, Oyster plant. Grains uniform, about 28.5 μ in diameter, ridges about 5.7 μ high, spines 3.5 μ long. Otherwise as in the type.

Plant similar to *T. pratensis;* cultivated for its edible taproot. Introduced into America from Europe and occasionally escaped. Flowers purple, summer.

Tragopogon orientalis L. Grains uniform, about 32 μ in diameter, ridges about 4 μ high, spines 2.9 μ long. Otherwise as in the type. Regarded by Hegi (1929) as a variety of *T. pratensis*.

Native of Europe and northern Asia.

SCORZONERA L. Viper's-grass

Grains 28 to 42 μ in diameter, extremely various in the different species, from fully echinolophate almost to simply echinate with the pattern represented only by the lacunae of the equatorial region, and then reduced in size. Poral lacunae absent. Abporal lacunae of opposite hemispheres joined to form a single hourglass-shaped lacuna (functionally the germinal furrow with the germ pore at the center of the constriction. Equatorial lacunae 6, arranged in pairs tandem fashion with their apexes impinging on the pores.

The most elaborate form of grain of the genus is that of *S. hispanica* (Plate XI, Fig. 5). In this the ridges are high, of uniform width, topped by short, conical spines, and frequently

they present the appearance of being perforated by a row of small holes between the bases of the spines. The floors of the lacunae are covered with a thin layer of exine which exhibits a fine but distinctly granular texture. The pattern formed by the ridges is quite unique, as far as I am aware, not duplicated elsewhere in the tribe. The ridges anastomose in such a way as to form 20 lacunae instead of the usual 15 (Fig. 116). The poral lacunae are entirely absent. The abporal lacunae are hexagonal in shape, but the sixth side is missing because each communicates with its neighbor of the opposite hemisphere through a gap which replaces the sixth side. In this gap the germ pore is situated, recalling the condition in the grains of *Tragopogon* which they resemble, except that in the grains of *S. hispanica* the gaps are wider and without the projecting bosses. The two lacunae thus joined form an hourglass-shaped germinal furrow which is evidently effective in accommodating changes in volume because the pores are too small to serve this purpose. The polar area is occupied by a large, six-sided polar lacuna of which the three sides facing the pores are short and the three facing between the pores are long. The paraporal lacunae are absent; but between each pair of pores on the equator are two pentagonal equatorial lacunae arranged tandem fashion (Fig. 115), base to base, with their separating ridge crossing the equator in a meridional direction midway between the pores and forming a transequatorial ridge, and with their apexes rounded and impinging upon the pores. In each polar hemisphere are three large, interporal lacunae (Plate XI, Fig. 5), so called because they alternate with the abporal lacunae. Each is pentagonal, with its base on a long side of the polar lacuna, two of its sides against the abporal lacunae, two against the equatorial lacunae, and its vertex impinging upon the end of a transequatorial ridge. The complement of lacunae of these grains therefore consists of 2 polar, 6 abporal, 6 interporal, and 6 equatorial, giving a total of 20 lacunae, corresponding to the 20 faces of an eikosahedron with 12 pentagonal and 8 hexagonal faces. They lack the polar thickenings, paraporal lacunae, and equatorial crests, elements that occur in the patterns of the grains of most Cichorieae.

In the other species of this genus the polar lacunae are absent, their places being occupied by polar thickenings similar to those of the grains of *Taraxacum* (Plate XI, Fig. 2) but enormously variable in extent. In fact, the main differences between the grains of the species of *Scorzonera* are due to the differences in extent of the polar thickenings. In some they are quite small, in which case the rest of the pattern is essentially the same as in the grains of *S. hispanica;* in others the polar areas are so extended that only vague fragments of the lacunae are represented in the region of the equator. But always the pattern about the pores is essentially the same, consisting of an hourglass-shaped furrow with the pore at its constriction and six equatorial lacunae. These serve to distinguish the grains of *Scorzonera* from those of all other genera, though the forms in which the extension of the polar thickening is excessive otherwise bear a strong resemblance to those of *Catananche lutea.*

The genus comprises about 100 species of large or small herbs, native of Europe, the Mediterranean region, and Central Asia.

Scorzonera hispanica L. Black salsify, Viper's-grass (Plate XI, Fig. 5) type. Grains somewhat various in size, 32 to 42 μ in diameter, but uniform in pattern. Ridges narrow, of uniform width, about 5.1 μ high, topped by short, conical spines about 2.8 μ long.

The ridges are conspicuously striate and present the appearance of bearing perforations between the roots of the spines, lacunar pattern 4 (Table V). This form is selected as the type of the genus and fully discussed above.

A branching perennial herb with yellow flowers borne on long peduncles, and a black-skinned edible fleshy root, for which it is cultivated, like that of the true salsify, *Tragopogon porrifolius.* Native of Central and Southern Europe; cultivated in America and occasionally escaped. Said to be closely allied to salsify.

Scorzonera graminifolia L. Grains oblately flattened, about 36 μ in diameter, with ridges about 4.6 μ high and spines 4 μ long. Essentially as in the type, except that the polar lacunae are absent, replaced by large polar thickenings, Lacunar pattern 4*a* (Table V) and not quite so sharply defined as in the type. Native of Siberia.

Scorzonera purpurea L. Grains uniform, oblately spheroidal, about 37 μ in diameter, with ridges about 4 μ high and spines about 3 μ long. Similar to the type, except that the polar areas are occupied by thickenings instead of lacunae. Lacunar pattern 4*a* (Table V).

The plant is a low herb with a leafy scape bearing one or a few large heads of showy purple flowers. Native of Europe and northern Asia.

Scorzonera nervosa. Trev. (*S. latifolia* DC.). Grains uniform, about 28.5 μ in diameter, with ridges about 5.7 μ high and spines 3.5 μ long. Similar to the type but with polar thickenings instead of lacunae, and these are so extensive as to occupy the greater part of the surface of the grain. Nevertheless, all of the lacunae except the polar are represented, though small and poorly defined. The lacunar pattern is expressed by 4*a* (Table V).

Native of Persia.

Scorzonera parviflora Jacq. (*S. caricifolia* Pall.). Grains oblately spheroidal, about 28 to 32 μ in diameter, with ridges about 3.4 μ high and spines 2.3 to 3.2 μ long. The polar thickenings are excessively extended, encroaching upon the rest of the grain to such an extent that almost its whole surface is evenly echinate, except the three furrows. These are hourglass-shaped, clearly representing the two abporal lacunae intercommunicating through a broad gap in which the pore is situated, as in the type. The equatorial lacunae are small and triangular in shape, separated from each other by a broad area of thickened exine which represents the greatly expanded transequatorial crest. The pores are larger than in the type, probably on account of the partial demobilization of this furrow—owing to its shortness and the stiffening effect of its well-developed paraporal ridges. The assemblage of lacunae around the pores, however, clearly indicates the relationship of this form of grain to the type. It is numerically expressed by the lacunar pattern 4*b* (Table V).

Native of Europe and northern and western Asia.

Scorzonera humilis Jacq. Grains uniform, approximately spheroidal, about 36.5 μ in diameter; almost the entire surface covered with sharp, conical spines about 4.6 μ long; texture granular.

These grains have been described by Fischer (1890) as "ringsum stachlig, wie *Catananche.*" In spite of the extreme reduction of their pattern they resemble the type of the genus in the hourglass shape of the furrow and the presence of equatorial lacunae, though the latter are small and poorly defined. Their lacunar pattern is numerically expressed by No. 4*b* (Table V).

The plant is a low herb with heads of yellow flowers borne singly on slender scapes rising from a cluster of basal linear leaves. Native of Europe.

CATANANCHE L.

Grains oblately spheroidal, rather uniform in size, 27 to 31 μ in diameter. The surface is without the pattern characteristic of the family; instead its rather thick exine is covered with short, conical, sharp spines. The only characteristics which hint at any connection of these grains with the rest of the Cichorieae are an irregular and clumped distribution of the spines, with small, irregular, blank spaces between them which suggest rudimentary lacunae and the constrictions of the furrows which suggest that they are composed of two or three fused lacunae.

The genus contains five species of low herbs, native of the Mediterranean region.

Catananche caerulea L. Blue succory (Plate XI, Fig. 3) type. Grains oblate-spheroidal, tricolpate or tetracolpate, 27.4 to 28.4 μ in diameter. Spines about 4.5 μ long. Furrows various but generally short, hourglass-shaped with a single constriction opposite the pore (Fig. 13). Lacunar pattern 5 (Table V).

In the tetracolpate grains the furrows are longer than in the tricolpate grains, equatorially arranged and converging in pairs alternately above and below the equator, in the ordinary hexacolpate configuration. Frequently they are fused at some or all of their points of convergence, and so traverse a broken or continuous zigzag course around the grain.

The plant is a perennial garden herb, cultivated for the beauty of its blue flowers, which it displays throughout most of the summer. Native of the Mediterranean region.

Catananche lutea L. f. Grains similar to the type, uniform and all tricolpate, about 30.8 μ in diameter; texture granular. Furrows longer and narrower than in the type and exhibiting two constrictions which vaguely suggest their derivation from the fusion of three lacunae (Fig. 114). This rudimentary pattern is numerically expressed by 6 (Table V).

DENDROSERIS D. Don

The grains of the two species here described are so far distinct that they are treated separately, under their species headings.

The plants are known only from the island of Juan Fernández. According to Bertero (Decaisne, 1835), who originally described these plants under the name of *Rea*, all of the species are small trees 10 to 20 ft. high, with the trunk or branches terminated with leaf clusters from the center of which arise large panicles of strange and exotic-looking flowers. The bark is smooth and green, and the flowers are snowy white, recalling in shape certain species of *Prenanthes*. Bertero describes the pollen as "pollen globosum, echinulatum," but in spite of its aberrant character, he regards the genus as most closely affiliated with *Sonchus*.

Bentham (1873) regards the genus as divergent from the rest of the tribe but associated with another arborescent genus, *Fitchia*. He says, "Both are truly Cichoriaceous in their corollas, anthers and styles, and *Dendroseris*, at least, in the milky juice of its bark; but their achenes are different from those of the Cichoriaceae generally, as well as their involucre and habit; and *Fitchia* in its receptacular paleae, awned achenes etc., recalls the Helianthoideae." I have examined the pollen grains of *Fitchia* and find that their form virtually excludes the possibility of the plants' belonging to the Cichorieae but conforms rather well to the pollen-grain form of the Heliantheae. I have therefore excluded *Fitchia* from this discussion of the Cichorieae.

Dendroseris micrantha Hook. & Arn. (*Rea micrantha* Bert.) type. Grains oblate-spheroidal, about 25 μ in diameter, generally tricolpate, but a small proportion tetracolpate. Lacunar pattern 5 (Table V), but greatly reduced by the excessive encroachment of the polar thickenings upon it. Poral lacunae present, communicating through interlacunar gaps with the small meridionally adjacent abporal lacunae (Fig. 112), the three lacunae so joined forming a short furrow. Paraporal lacunae small and poorly defined or, occasionally, absent. Spines mostly reduced or vestigial. Texture coarsely granular.

Altogether this form of grain is so far aberrant from the basic form of the tribe that, were it not for the peculiar form of its germinal furrow, consisting of three lacunae joined together, it would be difficult to recognize it as belonging to the Cichorieae.

An excessively branched tree, with leaves large and entire, somewhat alternate, though mostly collected at the ends of the branches. Flowers white, borne in small heads in large panicles. In cool and shady woods in mountains. Flowers in May.

Dendroseris pinnata Hook. & Arn. (*Rea pinnata* Bert.). Grains spheroidal or somewhat oblately flattened, uniform, about 27.5 μ in diameter. Lacunar pattern greatly reduced by the encroachment of the polar thickenings. Polar lacunae present, communicating through broad interlacunar gaps with the adjoining abporal lacunae forming a medium-sized furrow. Paraporal lacunae present, three in each hemisphere, each separated from its corresponding member of the opposite hemisphere by the well-developed equatorial crest which reaches from poral lacuna to poral lacuna around the equator. Spines conical and sharp, about 4.6 μ long. Texture minutely and faintly granular. The grains resemble the type (*D. micrantha*) only in the great extent of the polar thickenings which occupy the greater part of its surface. They differ from the type in the greater length and conical shape of their spines, their 6 instead of 12 paraporal lacunae, and their continuous equatorial crest reaching from pore to pore. These differences are such as to suggest that the two plants may be genetically unrelated.

A tree 10 to 15 ft. or more high, with pinnate leaves 1 ft. or more long, the pinnae unequally bifurcate. Flowers snowy white, borne in small heads in large, branching panicles.

ASTEREAE Aster Tribe

The grains of the Astereae are spheroidal or slightly flattened (Plate XII, Fig. 4). In size they range from about 16.5 to about 32 μ in diameter. They are always provided with well-developed and characteristic spines which are uniform in size and present the appearance of uniformity of distribution over the surface. The spines are short, broad at the base, and nearly conical in shape (Plate XII, Fig. 5). Sometimes they are strictly conical to their apexes, and sometimes they taper slightly into a more or less acuminate tip. Though the shape of the spines is occasionally obviously different in the different species this variation is generally too slight and intangible to lend itself to analysis. The length of the spines and their distance apart are somewhat various in the different species, and there is evidence that measurements of the spine lengths and spine intervals may be used to distinguish some of the genera.

The arrangement of the spines in the grains of most species of Astereae appears to be highly uniform and regular, arranged in the isometric system, patterned after the arrangement assumed by spherical bodies of uniform size when crowded together, as for example, when shot are caused to pack closely together in a single layer on a plane surface. This arrangement may be described by saying that if any one of the shot is regarded as a center, it will be surrounded by six others, all in contact with it and with each other. In other words, the centers of the shots are all equidistant from each other along the sides of an equilateral hexagon and equidistant from that of the shot at the center of the hexagon. In the distribution of the spines over the surface of the grains such an arrangement appears to be followed as faithfully as possible, but, owing to certain mathematical considerations which are discussed elsewhere, a continuous, regular, hexagonal pattern is impossible on the surface of a sphere. Thus we always find interspersed among the hexagonal groupings a few that are pentagonal, and we find upon measuring the angles and intervals between the spines, even in the most regular-appearing hexagonal configurations, that the variations are surprisingly great, so we are forced to the conclusion that the regularity of this arrangement is more apparent than real. Nevertheless, the intervals between the spines and their spacial configurations are almost as uniform as is mathemetically possible over the surface of a sphere.

The texture of the grains of the Astereae is always granular; the roughening is rather faint between the spines, but surrounding their bases it is coarser and somewhat more sharply defined; this granular appearance, however, does not extend far up the shaft of the spine, which throughout most of its upper part is quite smooth and homogeneous in appearance. Viewed in optical section, the structures which appear as granules in surface view are seen as radial striae of darkly staining material in a lightly staining matrix (Plate XII, Fig. 5).

The pollen of many species of Astereae is characterized by excessive abnormalities. Besides the usual number of abortive grains there are frequently found many giants with supernumerary furrows and some dwarfs with fewer or no furrows at all. Such abnormalities are encountered from time to time in nearly all groups of Compositae and many other plant families. Their origin is generally due to an irregular distribution of chromosomes in the maturation divisions (Beer, 1907), as the result of hybridity

(Jeffrey, 1916) or from other causes. The problem of the origin of such forms is a subject deserving further study.

A comparison of the dwarf, normal, and giant grains shows that the length of the spines and their distance apart bear no relation to the size of the grain; the dwarfs do not, as a consequence of their small size, have spines reduced or packed any closer together, and the giants do not have giant spines, nor are they more widely separated. It is as though each grain had at its disposal a quantity of exine of a standardized pattern; and of this it appropriates enough to cover its surface, which is accomplished by a little stretching here and there to fit the curvation or a little compressing to fit awkward corners, but uses it without other modification, whether the grain be a dwarf with only a small surface or a giant with several times the normal surface area. The total number of spines on these grains therefore is a function of their surface area. Hence it is useless to count or estimate the total number of spines per grain. The number of spines per unit area, however, or spine frequency is a definite and useful character. The spine frequency, spine length, and various other characters of the exine are emphytic. The basic morphogenetic principle involved is that the size of the pattern elements and the size of the grains are not positively correlated.

Throughout the entire tribe there is little variation in the emphytic characters, which is in keeping with the close relationship believed to exist between all the species. The interrelationships of these species are so close that their differences do not come to visible expression in basic characters such as those of the structure of the pollen grains.

SOLIDAGO L. Goldenrod

Grains generally uniform in size and shape, 17 to 26 μ in diameter, spheroidal or slightly oblately flattened; prevailingly tricolpate, occasionally some grains tetra- or hexacolpate. Furrows of medium length, their membranes smooth and germinal apertures well defined and circular. Exine rather thick, finely and faintly granular. Spines apparently uniform in size and arrangement, typical of the tribe, short-conical and sharp pointed, 2.5 to 3.4 μ long and 4.6 to 5.7 μ apart.

The pollen grains of the different species are essentially all alike; there are slight differences in the average size of the grains, and in the size and distance apart of their spines; also some species show a greater tendency than others to produce grains with supernumerary furrows. But apart from these relatively minor differences, there is no means of distinguishing the pollen grains of the different species from each other.

The genus comprises over 125 species, almost entirely North American in distribution, except for a few in South America and two or three in Europe. The plants are branching perennial herbs producing showy yellow (occasionally white) flowers during the latter part of summer. The flowers are insect pollinated, though somewhat imperfectly adapted to this mode of pollination. Most species shed only minute quantities of pollen. Nevertheless, there are several species, notable among which are *S. speciosa* and *S. sempervirens*, that produce much pollen, which certainly becomes at times atmospheric.

The question of whether or not goldenrod is a cause of hayfever has received much discussion in the past, and there are still adherents to both the affirmative and negative sides. In the minds of many hayfever sufferers the goldenrods are inseparably associated with their affliction. But this is largely due to a misconception rising out of the fact that goldenrods flower during the latter part of the summer, during a time which very nearly coincides with the third and most serious hayfever season of each summer. It may be said, however, that, in the main, the conception of causal relationship between the two is not well founded, observers having overlooked the various wind-pollinated species such as ragweed, false ragweed, and cocklebur, which are nearly always associated with the goldenrods and escape attention because, they lack attractive coloring. And it may be safely said that nearly all late-summer hayfever, particularly in the eastern United States, is due primarily to the ragweeds and their allies and not to goldenrods.

On the other hand, the goldenrods, in some regions, unquestionably play a contributing part in the production of late-summer hayfever. Practically all hayfever patients who respond to ragweed pollen by means of the skin test respond to goldenrod pollen to the same or only a slightly lesser extent. Hence it follows that, should such patients breathe goldenrod pollen in quantities comparable to that of ragweed, they would get comparable hayfever symptoms. Under certain conditions this is possible, *e.g.*, when the hayfever sufferer gathers goldenrod flowers or otherwise comes in close proximity to one of the several species which produce a sufficient quantity of pollen. Hayfever from close association with goldenrod is well known. For instance, a flower gatherer carelessly whisking a bunch of goldenrod in front of the face of a hayfever victim can easily precipitate a spasm of sneezing. It is such obvious connection as this between cause and effect that has led goldenrod to assume more than its share of the blame for producing hayfever.

Even without coming in actual contact with the goldenrod flowers, hayfever patients may at times breathe a certain amount of goldenrod pollen. In experiments with atmospheric pollen I have found that, in the city of Yonkers, during the ragweed season, among the numerous ragweed-pollen grains caught by the slides there are nearly always a few grains that can be identified with almost positive certainty as belonging to goldenrod. Their number is very variable. For the most part it is quite small, averaging from day to day under normal weather conditions about 1 or 2 per cent of the total pollen caught. But in dry, windy weather their number rises considerably, and toward the end of the season when the ragweed plants are on the wane, which is the time when *Solidago speciosa* is at its height, the number of goldenrod-pollen grains caught on the atmospheric pollen slides may outnumber those of the ragweeds; consequently, there can be no doubt that goldenrod is at times a factor in hayfever, paling, it is true, by comparison with the enormously more abundant and prolific members of the ragweed tribe.*

Solidago speciosa Nutt. Showy or Noble goldenrod (Plate XII, Fig. 4) type. Grains uniform in size except for a very few that are abortive and a small proportion of aberrant forms. About 22.8 μ in diameter. Spines about 2.8 μ long and 5.1 μ apart. Texture finely and rather faintly granular.

Among the aberrant forms of grains are found some micro grains, some dicolpate grains with furrows opposite, a few hexacolpate, and a few giants which, judging from the pentagonal configuration which their furrows assume, are 30-colpate, with their furrows arranged after the fashion of a pentagonal dodecahedron, though it is virtually impossible to count the furrows of such complicated configurations.

* For a further discussion of this matter see p. 143.

The showy goldenrod is a tall, showy plant with straight, columnar inflorescence, one of the most beautiful of the eastern species; abundant in rich soil, Massachusetts to North Carolina to Tennessee to Arkansas to Minnesota. Insect pollinated but shedding much pollen which, under favorable conditions, becomes atmospheric. This species sheds many times more pollen than any of the other species mentioned below, except *S. sempervirens*, which, however, is much scarcer and confined to salt and brackish places. Both species will shed pollen freely when cut and placed in water. August to October.

Solidago sempervirens L. Seaside goldenrod. Grains rather various in size, with a large proportion abortive or in other ways abnormal. Normal grains spheroidal or slightly flattened, 20.5 to 22.8 μ in diameter. Spines about 3.1 μ long and 5.1 to 6.2 μ apart. Otherwise as in the type.

Among the abnormal grains which constitute rather a large proportion of the pollen of this species are a few micro grains, grains with 2, 4, 6, and 12 furrows arranged in the trischistoclasic system, and some grains showing various degrees of reduction of their spines. Besides these there are a large number of grains united in tetrahedral tetrads. These appear to be abortive and are without spines. Among such "tetrads" are a few containing a fifth very small grain. The presence of a fifth grain in some of the tetrads which have brought their development to a successful conclusion suggests that it may be the cause of the aberrant forms, introducing asymmetrical contacts in the tetrad. The presence of the fifth grain is probably traceable to an irregular distribution of chromosomes in the reduction division, a matter which suggests hybridity of origin and invites further cytological study.

The seaside goldenrod is a tall, erect plant with thick, fleshy leaves rather abundant along seashores and in tidal marshes, New Brunswick to Florida and Mexico, also in Bermuda. August to December. It is insect pollinated but sheds large quantities of pollen which can easily be collected by placing the plants in water and allowing them to shed on sheets of paper. In hayfever a minor factor of only local importance.

Solidago rugosa Mill. Tall, Hairy, Wrinkle-leaved or Pyramid goldenrod. Grains uniform, except a few that are abortive, spheroidal or slightly flattened, about 26.2 μ in diameter, with spines 2.3 μ long and 3.4 to 5.7 μ apart. Otherwise as in the type.

A tall, handsome plant, from 1 to 7 ft. high, usually in dry places in fields and roadsides. Newfoundland to Western Ontario to Texas to Florida. July to November. Sheds much less pollen than the two preceding species and is of slight importance in hayfever.

Solidago altissima L. (*S. procera* Ait., *S. canadensis scabra* T. & G.) Tall or high goldenrod. Grains essentially as in the type, uniform except for a small proportion of abortive or aberrant forms, slightly flattened, 17.1 to 20.5 μ in diameter, with spines 2.3 to 2.9 μ long and 4.0 to 5.1 μ apart. Besides the grains of normal form, there are a few dicolpate grains, with furrows opposite and united encircling the grain as a single furrow with two apertures.

A tall, handsome plant, 2 to 8 ft. high, common in dry soil, Maine to Ontario to Texas to Georgia. August to November, shedding relatively little pollen, of secondary importance in hayfever.

Solidago juncea Ait Early or sharp-toothed goldenrod. Grains uniform, only very few abortive and no aberrant grains are seen; spheroidal in shape or slightly flattened, 17 to 19.4 μ in diameter, with spines uniform, about 2.5 μ long and 4 μ apart. Otherwise as in the type.

Plants 1½ to 4 ft. high, common in dry soil in waste places and roadsides. New Brunswick to Hudson Bay to Saskatchewan to Missouri to North Carolina. June to November. Sheds relatively little pollen, but the plants occur in enormous numbers. Of secondary importance in hayfever.

Solidago latifolia L. (*S. flexicaulis* L.) Zigzag or broad-leaved goldenrod.

Grains uniform, except for a few abortive and a few that are tetracolpate; spheroidal or slightly flattened, about 20 μ in diameter, with spines uniformly 3.4 μ long and 4.6 to 6.8 apart. Otherwise as in the type.

A small plant 1 to 3 ft. high, in rich woods. Nova Scotia to Missouri to Tennessee. July to September. Sheds insignificant amounts of pollen. Not a factor in hayfever.

Solidago bicolor L. White or pale goldenrod, Silverrod.

Grains uniform, except a very few that are abortive, slightly flattened, 21.6 to 22.8 μ in diameter, with spines uniformly 3.4 μ long and 4.6 to 5.7 μ apart. Otherwise as in the type. A low plant ½ to 4 ft. high, in dry soil. Prince Edward Island to Ontario to Minnesota to Tennessee to Georgia. July to September. Sheds insignificant amounts of pollen. Not a factor in hayfever.

Callistephus chinensis Ness. China aster. Grains as in *Solidago speciosa* (q.v.). Uniform except for a few abortive and a few tetracolpate grains, slightly flattened oblately, 21.6 to 23.9 μ in diameter, with spines 2.3 to 3.4 μ long and 4.6 to 6.4 μ apart.

China aster is a common garden annual introduced from China and Japan; with ray corollas of almost all colors except yellow. Flowers in late summer and fall. Insect pollinated but shedding rather large amounts of pollen which may cause hayfever if the flowers are handled.

ASTER L. Aster

Grains in no way distinguishable from those of *Solidago* (q.v.). A genus of about 250 species of herbs, mostly of North America.

Aster patens Ait. Late purple aster. Grains rather uniform in size, except for a few that are abortive; spheroidal or slightly flattened, 27.5 μ in diameter, with spines about 2.9 μ long and 4.6 μ apart, texture finely granular, particularly at the base of the spines. New York, Minnesota, Florida, Louisiana, and Texas. August to October.

Aster novae-angliae L. New England aster. Grains essentially as in the type, uniform except for a few that are abortive, about 21.6 μ in diameter, with spines 2.8 μ long and 5.7 μ apart.

Eastern United States, August to October. Not a factor in hayfever.

Erigeron strigosus Muhl. (*E. ramosus* (Walt.) B.S.P.) Daisy fleabane. Grains extremely various, and many abortive. Many giants with furrow numbers ranging up to 12, furrows very irregular, frequently not conforming to any pattern. Normal grains 18.2 μ in diameter, spines about 2 μ long and about 3.2 μ apart. The grains of this species are the most irregular yet encountered in the Astereae.

A common weed of waste places, almost throughout North America. Flowers from May to November. Not an important factor in hayfever but may produce symptoms upon contact.

ANTHEMIDEAE Mayweed Tribe

Grains 17 to 34.2 μ in diameter, normally tricolpate, but some species with varying proportions of their grains with other numbers of furrows arranged according to the trischistoclasic system. Furrows of medium length, broad and tapering to pointed ends, their membranes smooth, each provided with a conspicuous germ pore. Exine moderately to exceedingly thick, coarsely and conspicuously granular; in insect-pollinated members provided with broad, conical spines; in wind-pollinated members, with spines greatly reduced or entirely absent.

The most distinctive and constant character of the grains of the Anthemideae lies in the *coarse-granular nature of their exine*. In the echinate forms, in which the exine is always extremely thick, the granules are most conspicuous, but even in the non-echinate forms, in which the exine is much less thick, they are quite pronounced. In the echinate grains the exine, if observed in optical section, is seen to consist of two layers (Plate XIII, Figs. 1, 2). The inner is the thicker and appears to be built up of large, vertical prisms presenting the appearance of coarse, radial striae. Overlying this is the much thinner layer of more transparent material marked with very fine radial striae. In surface view the inner layer shows plainly through the outer, presenting the coarse-granular appearance consisting of large, irregularly shaped, deeply staining bodies embedded in a less deeply staining matrix. The overlying fine-granular layer can be seen in surface view only with difficulty, even under the most favorable conditions, on account of its transparency and the optically disturbing effect of the underlying layer. In the non-echinate grains, in which the exine is thinner, the same sort of granular texture prevails, but usually it is much finer, and in optical section the outer layer appears as only a thin, structureless line, while in surface view it does not show at all. Nevertheless, there is a certain similarity between the granular nature of the two types of grain, which, though elusive of description, becomes recognizable from experience and is the best diagnostic character of the grains of the tribe.

The furrows are generally long and sharply defined and, owing to the thick and semirigid nature of the exine, are required to function freely as harmomegathi. They are deep and in most cases give the grain a three-lobed appearance. The furrow membranes are always smooth, and the germ pores circular in outline, rather large, and bulging prominently when the grains are expanded.

The *spines*, when present, are broadly conical, sharp pointed, and generally large in proportion to the size of the grain. They range, among the insect-pollinated species, from 1.1 to 4.6 μ in length and from 1.6 to 11.4 μ in distance apart. They are uniform in length on any given grain but somewhat various in their distance apart. Nevertheless, there is a rough correlation between these two dimensions. Thus, in a general way, it may be said that the shorter the spines the more closely together they are placed. For example, in the grains of *Leucanthemum Leucanthemum*, in which the spines are 4.6 μ long, they are 8 to 10.2 μ apart; while in those of *Tanacetum gracile*, in which they are only about 1.1 μ long, they are 4.5 to 5.7 μ apart; in the grains of the wind-pollinated *Crossostephium insulare*, in which the spines are only vestigial—too small to be measured—they are only a little over 1 μ apart. These differences are quite apparent to the eye, even unaided by measurements. For example, if the grains are observed in optical section and polar view, in those of *Leucanthemum* only 3 or 4 spines are seen on each of the three lobes at its limb; in those of *T. gracile* about 6 are seen on each lobe; while in those of *Crossostephium* 15 or more tiny protuberances are seen on each lobe. This relation between the length of the spines and their distance apart is not a peculiar property of the grains of the Anthemideae but likewise exists in the grains of the Ambrosieae and the Cynarieae and appears to be universal among the Compositae. But owing to the wide normal variation in the distance apart of the spines, the numerical relation between this distance and their size could be expressed only after making many measurements and striking averages for many different species. Until this is done, all that can be said on this point is that the smaller the spines the closer together and more numerous they are.

The cause of the wide difference in the number and size encountered among the grains of the members of this genetically rather compact group is most certainly due to their different modes of pollination. We have seen in other plant families that anemophily tends to induce a thinning of the exine and a loss of its external decorations. So it is in this group. The different species of *Anthemis*, *Leucanthemum*, and *Chrysanthemum*, which are insect pollinated, have grains in which the spines are well developed and the exine thick; while those of *Artemisia*, *Crossostephium*, and *Picrothamnus*, which are wind pollinated, have grains in which the spines are vestigial or absent and the exine much less thick. On this basis the members of this tribe may be divided rather sharply into two groups—those which are echinate grained and insect pollinated and those which are nearly or quite smooth grained and wind pollinated.

The genetic gap between the two groups is wide. I have not been able to find any really intermediate forms; and there appear to be now in existence no nicely intergrading series of forms, like those in the Ambrosieae, between the fully echinate-grained and the nearly smooth-grained forms. Nevertheless, there is considerable variation both in the size of the spines among the grains of the echinate group and in the prominence of the spine vestiges in the nonechinate group. Perhaps the most extremely echinate form is typified by the grains of *Leucanthemum* and *Chrysanthemum*, in which the spines are about 4 μ long; and the least echinate by those of *Artemisia* and *Chamartemisia*, in which the spines are vestigial and generally too small to be seen with certainty or are even entirely absent.

Though there are no truly intermediate forms, it is interesting to note that among the echinate-grained group the grains with the smallest spines are found in the genus *Tanacetum*, *e.g.*, *T. gracile* and *T. camphoratum;* and among the nonechinate-grained group those with the most prominent spine vestiges are found in the genera *Crossostephium*, *Sphaeromeria*, *Vesicarpa*, and *Chamartemisia*. In a way this is in keeping with the classification of Rydberg (1916), who places these four genera between *Tanacetum* and *Artemisia*. At the same time, however, the characters of these pollen grains suggest that these four genera are much closer to *Artemisia* than to *Tanacetum*.

That the echinate character is closely associated with the mode of pollination is attested by the fact that the echinate pollen is always produced in relatively small amounts and is heavily

impregnated with lipoid substances which cause the grains to adhere together, effectively preventing them from being carried by air currents. A corollary to this is that they cannot be counted among the serious causes of hayfever, but there is no doubt that several of the species may, upon close contact, cause hayfever symptoms with some people. Though I have on several occasions found on atmospheric pollen slides echinate grains of Anthemideae, which were probably those of *Leucanthemum*, it seems unlikely that these never occur in sufficient abundance to cause hayfever. When they are caught on the slides they generally occur adhering in groups of three or four. On the other hand, the nonechinate-grained species produce large amounts of pollen which is light and borne long distances by the wind; and among these are counted some of the most important hayfever plants of the western United States, *e.g.*, the sagebrushes and mugworts. The pollen of these possesses relatively little surface oil—not enough to cause them to adhere to each other—and when they are caught on atmospheric pollen plates they occur separately and in large numbers.

Grains with supernumerary furrows and aberrant furrow patterns are strikingly abundant in the pollen of most of the species of this group. It cannot always be assumed, however, that the irregularities of furrow pattern which are here recorded are universal for the species, because these records are based on too few observations. Sometimes such irregularities may be only individual peculiarities. Nevertheless, in the one instance in which this question was put to the test, *viz.*, that of *Picrothamnus desertorum*, it was found that plants collected in widely separated localities yielded grains with exactly the same aberrant furrow arrangements, just as numerous and in the same proportions. As we have seen (page 182), such aberrant forms arise from differences in size of the daughter-cells of a pollen mother-cell, an irregularity which, in turn, is generally due to an irregular distribution of chromosomes at the reduction divisions; these aberrant furrow patterns therefore point to a lack of genetic stability among the species which exhibit them. That such a lack of stability exists among the Anthemideae in general is abundantly attested by the large number of forms, varieties, and minor variations recorded in the literature (*cf.* Hall and Clements, 1923). Particularly is this true of the genus *Artemisia*.

The measurements of the grains here recorded were all made with them fully expanded. In each case they are the maximum and minimum of some half-dozen or dozen normal grains taken at random, avoiding only the aberrant forms. Consequently, they do not generally represent the entire range of size of even the normal grains and make no attempt to include that of the aberrant forms. The measurements of the grains do not include the spines but do include the thickness of the exine to the base of the spines. When only one dimension is given it is always the equatorial diameter.

The classification followed is essentially that of Rydberg (1916). The distribution of the pollen-grain characters throughout the tribe is, for the most part, quite consistent with it, but there are a few instances where they are found to be decidedly at variance. Unfortunately, in such cases the pollen-grain characters are of more negative than positive value; though they occasionally point rather definitely to a lack of consistency in the classification, they seldom suggest a better arrangement. Consequently, I have had to content myself with pointing out the instances of disagreement between the pollen-grain characters and Rydberg's classification, retaining his arrangement virtually unmodified. It is to be hoped, however, that other investigators will be stimulated by the suggestions of the pollen-grain characters to reopen the question of the classification of the Anthemideae.

Key to the Species

I. Echinate, with spines conspicuous, broadly conical, but sharply pointed. Exine very thick and coarsely granular, heavily impregnated with oil.
- *A.* Grains 22.5 to 34.2 μ in diameter; spines 2.3 to 4.6 μ long and 4.6 to 1.4 μ apart. — Achillea, Cota, Anthemis, Maruta, Leucanthemum, Chrysanthemum, Tanacetum (in part)
- *B.* Grains 19 to 26.2 μ in diameter; spines 1.1 to 2.3 μ long and 4.6 to 9.1 μ apart. — Chamomilla, Tanacetum gracile, Tanacetum artemisioides

II. Nonechinate; spines vestigial or entirely absent. Exine not excessively thick. Grains 17.5 to 29.6 μ in diameter. Exine generally sharply and coarsely granular but less so than in I.
- *A.* Spine vestiges distinctly visible, approaching in some cases the condition described as subechinate. — Crossostephium artemisioides, Artemisia norvegica
- *B.* Spine vestiges minute but large enough to be seen with certainty. — Sphaeromeria, Crossostephium insulare, Crossostephium foliosum, Crossostephium californicum, Vesicarpa potentilloides, Picrothamnus desertorum, Artemisia frigida, Artemisia camporum, Artemisia canadensis, Artemisia pycnocephala
- *C.* Spine vestiges represented by only a vanishing trace or, in some grains, apparently absent. — Artemisia Bigelovii, Artemisia gnaphalodes, Artemisia Absinthium, Artemisia dracunculoides
- *D.* Spine vestiges generally entirely absent, though a trace of them may occasionally be seen in some grains. — Artemisia heterophylla, Artemisia filifolia, Artemisia tridentata, Chamartemisia compacta, Artemisiastrum Palmeri.

Anthemis nobilis L. (*Chamomilla nobilis* Gord., *Matricaria nobilis* Baill.) White or low camomile. Grains essentially as in the *Tanacetum* type (page 504), uniform, 24 to 25 μ in diameter, spines about 3.4 μ long and 8 μ apart. Exine thick and coarsely granular.

A low herb with daisy-like flowers. Native of Europe but extensively cultivated elsewhere and occasionally escaped. Flowers June to August.

Maruta Cotula (L.) DC. (*Anthemis Cotula* L.) Mayweed, dog fennel, fetid or wild camomile. Grains essentially as in the type, indistinguishable from those of *Anthemis nobilis*. 22.5 to 25.5 μ in diameter, spines about 2.8 μ long and about 8 μ apart.

A common weed with strongly aromatic odor, similar to the preceding species but less showy. Native of Europe, now naturalized throughout North America. Flowers June to November.

CHAMOMILLA (Hall) Gilib. CAMOMILE

Grains similar to the *Tanacetum* type (page 504), 19.4 to 22.8 μ in diameter. Spines 1.7 to 2.3 μ long and 4.6 to 6.8 μ apart. These are the smallest grains yet found among the echinate-grained Anthemideae, except those of *Tanacetum gracile*.

The genus includes about 20 species of daisy-like perennial herbs, of wide distribution.

Chamomilla Chamomilla (L.) Rydb. (*Matricaria Chamomilla* L.) Wild camomile. Grains as in the generic description, except that a large proportion of them are giants with 4, 6, or 12 furrows, always arranged in the trischistoclasic system. Normal grains 19.4 to 20.5 μ in diameter, with spines 2.3 μ long.

Native of Europe. Sometimes cultivated and in America extensively naturalized. Flowers in Summer.

Chamomilla occidentalis (Greene) Rydb. (*Matricaria occidentalis* Greene). As in the generic description, 19.5 to 22.8 μ in diameter, spines 1.7 μ long and 4.6 to 8 μ apart.

Middle California to southern Oregon.

Chamomilla suaveolens (Pursh.) Rydb. (*C discoidea* J. Gay, *Matricaria discoidea* DC., *M. matricarioides* (Less.) Porter) Rayless camomile or wild marigold. Grains uniform, as in the generic description, about 20.5 μ in diameter, with spines 2.3 μ long and 5.7 to 6.8 μ apart.

Pacific coast and eastward to Arizona. Also occasionally naturalized in the eastern United States and in Europe. May to August.

Leucanthemum Leucanthemum (L.) Rydb. (*Chrysanthemum Leucanthemum* L.) Oxeye daisy. Grains as in the type, uniform, about 24 to 28.5 μ in diameter, spines 4.6 μ long and 8 to 10.2 μ apart.

A common weed, native of Europe but naturalized almost throughout North America and elsewhere. May to November. The daisy is entirely insect pollinated, but its pollen is recognized as an occasional cause of hayfever symptoms upon direct contact. It is also occasionally caught on atmospheric-pollen slides.

Leucanthemum arcticum (L.) DC. (*Chrysanthemum arcticum* L.) Arctic daisy. Grains indistinguishable from those of *L. Leucanthemum*.

Similar to the preceding species but somewhat smaller. Coast of Hudson Bay to Alaska, also in arctic Europe.

CHRYSANTHEMUM L.

Grains essentially as in the type, *Tanacetum*. In most of the species here recorded, however, they are somewhat various, and many of them abnormal. Normal grains 24.2 to 34.2 μ in diameter, spines 2.3 to 4.6 μ long and 5.7 to 11.4 μ apart.

The inner layer of the exine is extremely thick and very coarsely granular, but the outer layer is thinner than in the type yet sharply and distinctly granular and generally easily discernible. The furrows are long and pointed and, on account of the great thickness of the exine, are deeply depressed.

The genus comprises about 100 species of wide distribution in the Northern Hemisphere. All are entirely insect pollinated and, as a general rule, do not cause hayfever, though some of those which are cultivated are known to produce hayfever symptoms upon the patient's coming into direct contact with the plants. Also the leaves of some species are said occasionally to cause dermatitis (Goldstein, 1931).

Chrysanthemum coccineum Willd. (*Pyrethrum roseum* Sieb.) Common Pyrethrum. Grains rather various, many of them tetra- and hexacolpate, and many giants. Normal grains as in the generic description, 24.2 to 28.5 μ in diameter, spines 4.6 μ long and 5.7 to 8 μ apart.

The plant is a bushy herb, resembling the oxeye daisy and bearing white, pink, lilac, or crimson flowers. Native of Asia but extensively cultivated both as a source of insect powder and, in some of its varieties, as a garden perennial.

Chrysanthemum morifolium Ram. (*C. sinense* Sabine) Florists' chrysanthemum. Grains rather various; many tetra- and hexacolpate, and many variously irregular. Normal grains 31 to 34.2 μ in diameter, with spines 2.3 μ long and 8 to 11.4 μ apart.

The plant is a cultigen of unknown origin but believed to be a hybrid with an admixture of *C. indicum* L. The defective and variously irregular condition of its pollen points to hybridity of origin.

Chrysanthemum carinatum L. (*C. tricolor* Andr.) Tricolor chrysanthemum. Grains as in the generic description, uniform and all normal, except for a few abortives and dwarfs. Normal grains 28 to 30 μ in diameter, spines 3.4 μ long and 6.8 to 8 μ apart.

Annual, 2 to 3 ft. high. Disk flowers purple and rays banded with two other colors. Native of Morocco. Several garden races with different-colored ray flowers are in cultivation.

TANACETUM (Tourn.) L. Tansy

Grains approximately spheroidal but deeply three lobed by their furrows, 25 to 32 μ in diameter. Exine excessively thick and composed of two layers (Plate XIII, Figs. 1, 2), the inner coarsely granular and much the thicker of the two, the outer finely but distinctly granular and thicker than usual in this tribe.

There is considerable variation in the size of the spines among the different species; they are generally broadly conical and so large in proportion to the size of the grain that only four show on each lobe at the limb. The furrows are long and tapering to pointed ends, with their membranes perfectly smooth, but each provided with a round germinal aperture through which the germ pore may bulge prominently. Owing to the extreme thickness of the exine, the deep furrows impart to the grain a deeply three-lobed form, even when fully expanded.

The genus comprises about 30 species of coarse, aromatic, leafy perennial herbs, of wide distribution in the northern hemisphere. All species appear to be primarily insect pollinated, and none is known to cause hayfever. But they suggest a tendency toward anemophily in the reduction or suppression of the ligulate corollas of the marginal flowers, and there can be no doubt of their rather close relationship to *Artemisia* which is entirely anemophilous.

Tanacetum vulgare L. Tansy type. Fully one-half of the grains abortive, many of them dicolpate, fewer tetra- and hexacolpate. Normal grains uniform, as in the generic description, 25 to 26.5 μ in diameter, with spines 2.8 μ long and 4.6 to 6.8 μ apart.

Among the abnormal grains those that are dicolpate are as large as those that are normal; their two furrows are opposite and united at the poles, thus encircling the grain as a single furrow with two germ pores. The tetra- and hexacolpate grains are apparently always giants, and the furrows are arranged in the trischistoclasic system.

Native of Europe and Asia but naturalized as a roadside weed throughout North America. Flowers July to September.

Tanacetum Camphoratum Less. (Plate XIII, Figs. 1, 2). Grains as in *T. vulgare*, except that they are a little larger—29.7 to 32 μ in diameter—with spines 2.2 μ long and about 9 μ apart. Di-, tetra-, and hexacolpate grains also present.

Beaches, California and Oregon.

Tanacetum bipinnatum (L.) Sch.-Bip. Grains essentially as in the type. A few tetracolpate grains are found.

Alaska, Yukon, and Mackenzie, also eastern Siberia.

Tanacetum Falconeri Hook. Grains essentially as in the type, all normal, 27.5 to 32 μ in diameter, with spines 3 to 4 μ long and 8 to 10.8 μ apart.

The Himalayas.

Tanacetum huronense Nutt. As in the type, 27.4 to 28.5 μ in diameter, spines 3 to 4 μ long and 8 to 10.3 μ apart. New Brunswick and Maine to Michigan and Hudson Bay.

Tanacetum longifolium Wall. As in the type, 27.5 to 28.5 μ in diameter. Spines 2.4 μ long and 6.5 to 8.0 μ apart.

The western Himalayas.

Tanacetum Douglasii DC. (*T. huronense* Gray). As in the type, 28.5 to 30 μ in diameter, with spines 2.8 μ long and 8 to 10.3 μ apart.

British Columbia to Oregon.

Tanacetum artemisioides Sch.-Bip. As in the type, a large proportion of the grains abortive. Normal grains 22.8 to 26.2 μ in diameter; spines about 2.2 μ long, 6.8 to 8.0 μ apart.

Western Tibet.

Tancetum gracile (Hook.) F. Thomas. Similar to the type, except that the spines are much smaller. 19.4 to 20 μ in diameter. Spines 1.1 μ long, and 4.6 to 5.7 μ apart. The grains of this species approach in character most closely to those of the non-echinate group.

Closely related to the preceding species. Native of western Tibet.

SPHAEROMERIA Nutt.

Grains similar to the *Crossostephium* type (Plate XIII, Figs. 3, 4) but with their spine vestiges smaller, standing in this respect intermediate between the *Crossostephium* and *Artemisia* types. The exine is rather thick and rigid but much less so than that of such echinate forms as *Tanacetum* and appearing to lack the overlying layer of fine, granular material characteristic of the latter. The furrows are long and rounded at their ends, but, on account of the much thinner exine, they do not impart a three-lobed outline to the grains, as do the furrows of those of *Tanacetum*. Nevertheless the furrows function freely in accommodating the exine to the changes in volume of the grain. When the grains are fully expanded they are approximately spheroidal or slightly flattened oblately, but when they are dry the furrows close, and the grains tend to become ellipsoidal. The furrow membranes are smooth, and each is provided with a rather small germ pore. The thinness of the exine and smallness of the spines are clearly correlated with their mode of pollination by wind and, at the same time, point to a closer relationship to the smooth-grained Artemisias than to the echinate-grained Tanacetums, unless, of course, anemophily was developed in this genus independently of *Artemisia*, which is unlikely.

The genus consists of about five species of low, cespitose perennials with woody base or small shrubs. In many ways these are intermediate in appearance between *Tanacetum* and *Artemisia* but resemble the latter more closely. Nevertheless, they are regarded by Hall and Clements (1923) as representing a section of the genus *Tanacetum*, associated with the plants which are treated here as *Chamartemisia*. Their pollen-grain characters confirm their relationships with *Chamartemisia* but suggest that both are more closely related to *Artemisia* than to *Tanacetum*. Furthermore, the marginal flowers are not ligulate, the heads lacking entirely the radiate character which marked all of the echinate-grained species. This, together with the smooth character of the pollen grains, seems ample justification for removing these plants from the genus *Tanacetum*.

Sphaeromeria argentea Nutt. (*Tanacetum Nuttalii* T. & G.). Grains uniform, similar to the *Crossostephium* type, 24 to 25.5 μ in diameter. Spine vestiges clearly visible though extremely minute—slightly smaller than in the type but more prominent than in the three succeeding species.

Arid hills, Wyoming and Montana.

Sphaeromeria cana (D. C. Eat.) Heller (*Tanacetum canum* D. C. Eat.). Grains uniform in size, 20 to 22.8 μ in diameter, essentially as in the *Crossostephium* type, except that the spine vestiges are slightly less prominent.

Nevada, eastern California, and Oregon.

Sphaeromeria capitata Nutt. (*Tanacetum capitatum* T. & G.). Grains uniform, 25.1 to 29.6 μ in diameter, essentially as in the *Crossostephium* type, except that the spine vestiges are slightly less conspicuous.

Wyoming and southern Montana.

Sphaeromeria simplex (A. Nels.) Heller (*Tanacetum simplex* A. Nels.). Grains similar to the *Crossostephium* type, except that the spine vestiges are much less conspicuous. They can be seen only with difficulty under the most favorable conditions and are distinctly smaller than in the preceding species.

Wyoming.

CROSSOSTEPHIUM Less.

The grains of three of the four species of this genus are practically indistinguishable from those of *Artemisia*, while those of the fourth, *C. artemisioides* (Plate XIII, Figs. 3, 4), differ in their spine vestiges, which are more prominent than those of any of the species of *Artemisia*. The grains of all four species are approximately spheroidal when expanded. The exine is rather thick and coarsely granular but much less so than that of the grains of *Tanacetum*. The furrows are only moderately long and not sharply pointed. They function freely as harmomegathi but do not impart a three-lobed outline to the normal grains, as do the furrows of the grains of *Tanacetum*. Abortive and empty grains, however, are deeply lobed, with the furrows tightly closed at the bases of the grooves.

According to the classification of Rydberg (1916, page 243), which is followed in this discussion, the genus includes the four species mentioned below, but Hall and Clements (1923, page 32) retain in it only *C. artemisioides*, which grows in Japan, the Philippines, and China, and they refer the other three species, which are American, to *Artemisia*. Apparently the latter treatment more correctly interprets the phylogeny of these plants, for in view of the striking difference in their pollen-grain characters it seems decidedly inappropriate to place the Asiatic *C. artemisioides* in the same genus with the three American species.

The plants are small or large shrubs of arid and semiarid regions, with the habit and appearance of the sagebrushes. All are wind pollinated, and one at least is the cause of much hayfever.

Crossostephium artemisioides Less. (*C. chinense* (L.) Merr., *Tanacetum chinenses* Gray, *Artemisia chinensis* Val.) (Plate XIII, Figs. 3, 4) type. Grains as in the generic description, 20 to 22.8 μ in diameter. Spine vestiges quite distinct, the largest found in the nonechinate group and occasionally almost reaching the proportions described as subechinate. In this respect this species seems to occupy a somewhat intermediate position between *Tanacetum* and *Artemisia*, though closer to the latter.

Much cultivated in Japan, China, the Philippines, and Indo-China, a native of China, currently known in Manila, where it is cultivated in pots, as *ajenjo*, which is a Spanish name for *Artemisia*.

Crossostephium insulare Rydb. (*Artemisia californica* Less.). Grains extremely various. Many of them abortive, giants or dwarfs, and some with two furrows. Normal grains differing from the *Crossostephium* type in their much smaller spine vestiges and thinner exine, resembling more closely the *Artemisia* type (Plate XIII, Fig. 5), 21.6 to 22.8 μ in diameter.

According to Hall (1923, page 54), this species should be regarded as a minor variation of *A. californica* Less. (*C. californicum* Rydb.). The presence in its pollen of a large proportion of abnormal and defective grains suggests that the plant is a hybrid, and the thinner exine and extremely vestigial nature of its spines suggest that it is more closely related to *Artemisia* than to the type of the present genus.

Crossostephium foliosum (Nutt.) Rydb. (*Artemisia foliosa* Nutt.). Grains uniform, as in the *Artemisia* type and indistinguishable from those of the preceding species.

A woody shrub regarded by Hall (1923, page 53) as a minor variation of the next species.

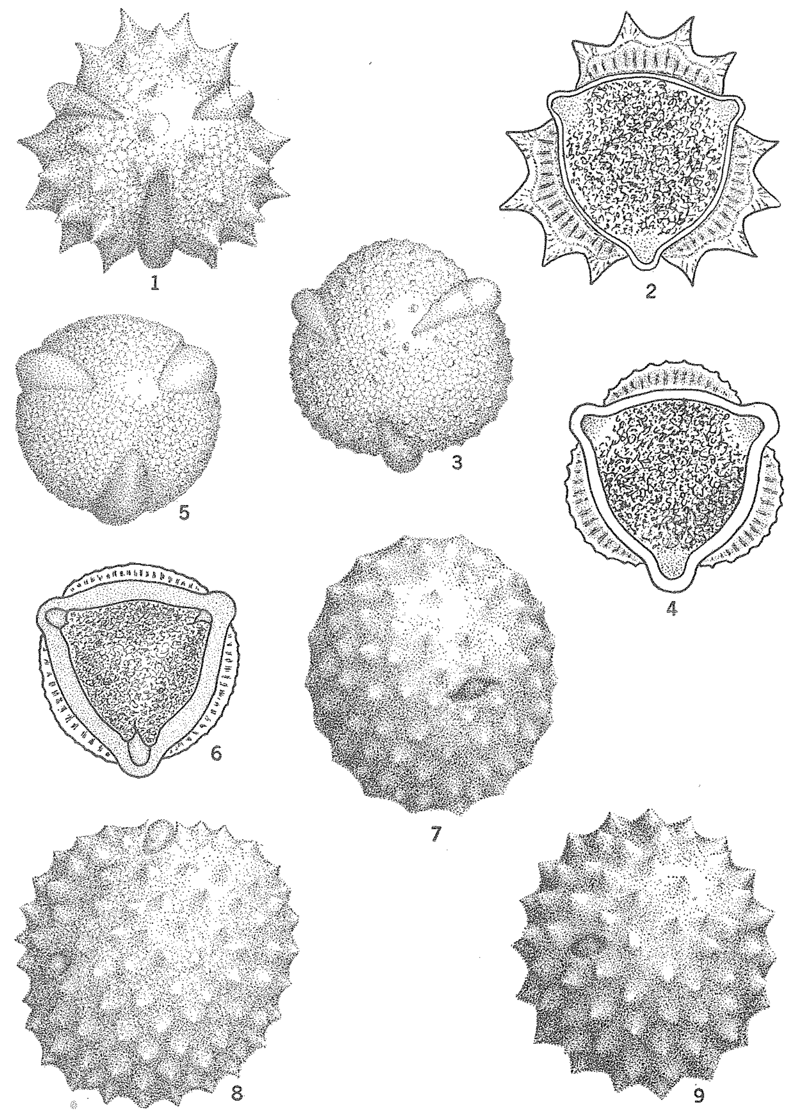

PLATE XIII.—Pollen grains of the Anthemideae and Ambrosieae. 1, *Tanacetum camphoratum*, polar view, 29.7 μ in diameter. 2, The same in optical section. 3, *Crossostephium artemisioides*, polar view, 20.9 μ in diameter. 4, The same in optical section. 5, *Artemisia tridentata*, polar view, 28.5 μ in diameter. 6, The same in optical section. 7, *Ambrosia elatior*, 18.3 μ in diameter. 8, *Ambrosia psilostachya*, 25 μ in diameter. 9, *Ambrosia trifida*, 17.7 μ in diameter.

Crossostephium californicum (Less.) Rydb. (*Artemisia californica* Less.) Coast sagebrush. Grains mostly uniform but accompanied by a small proportion of giants, and some with supernumerary furrows. Normal grains as in the *Artemisia* type, with spine vestiges extremely minute, oblately flattened, 22 to 26.2 μ in diameter.

A shrub 3 to 9 ft. high, extremely abundant along the hills of the coast ranges from central California southward. Wind pollinated, shedding large amounts of pollen, which is the cause of much hayfever during the latter part of summer (Rowe, 1928; Selfridge, 1920; Hall 1917, 1923).

Vesicarpa potentilloides (Gray.) Rydb. (*Artemisia potentilloides* Gray, *Tanacetum potentilloides* Gray, *Sphaeromeria potentilloides* A. Heller). Grains as in the *Artemisia* type, 22.8 to 25.1 μ in diameter, with rather long, pointed furrows, fine but distinctly granular texture.

A perennial herb with woody root. The genus is regarded by Hall (1923) as most closely related to *Tanacetum.* The form of its pollen grain, however, in the absence of spines and its thin exine, points to a much closer relationship with *Artemisia.* The plant itself presents an appearance intermediate between *Tanacetum* and *Artemisia.*

Chamartemisia compacta (Hall.) Rydb. (*Tanacetum compactum* Hall). Grains uniform, as in the *Artemisia* type, with spines represented only by doubtful traces, apparently entirely absent in most grains, 20.5 to 22.8 μ in diameter.

A small, cespitose perennial, with woody root, resembling in appearance *Sphaeromeria.* Known only to occur at the head of Lee Canyon, Charleston Mountains, Nevada. The genus is most closely related to *Sphaeromeria.* Hall (1923) treats the two genera together as a section of *Tanacetum.* Their pollen grains, however, while in every way similar to each other, differ from those of *Tanacetum* in their lack of spines and in their much thinner exine and suggest that both *Chamartemisia* and *Sphaeromeria* are more closely related to *Artemisia* than to *Tanacetum.*

Picrothamnus desertorum Nutt. (*Artemisia spinescens* Eat.). Bud sagebrush. Grains extremely irregular, only a small proportion of them normal. Many are obviously abortive and empty, while others are dwarfs or giants. A large proportion of the latter are provided with supernumerary furrows, generally arranged in the trischistoclasic system. The furrow arrangements which are most in evidence are the tetracolpate, hexacolpate, octocolpate, nonacolpate, and dodecacolpate. Besides these there are a number of grains of the zonate type, and still others which are variously irregular.

The normal grains are exactly like the *Artemisia* type, with spine vestiges recognizable but extremely small, 21.6 to 27.4 μ in diameter. In the giants the diameter may reach as much as 43 μ.

Low, spiny shrubs of desert areas, somewhat similar to sagebrush when growing in similar habitats. Wyoming to New Mexico, Oregon, and California. Flowers from March to June, producing large quantities of pollen which is the cause of much hayfever (Scheppegrell, 1917; Hall, 1923).

This plant is regarded by Hall (1923) as a member of the genus *Artemisia* in the section DRACUNCULUS, in which he finds it in agreement in all important technical characters with *A. dracunculus* and *A. campestris.* The characters of the normal pollen grains certainly show no reason for separating it from *Artemisia.* The large proportion of abnormal and defective grains suggests that it may be a hybrid. Contrary to such a view, however, is the fact that the species exhibits a remarkable lack of variability, which has been noted by Hall (1923, page 133), who says, "Perhaps it is because of its fixed characters and incapacity for adaptation to new environments that the species has produced no forms that have received taxonomic recognition." It is difficult to see how a plant with such extreme variability of its pollen should exhibit such great somatic stability, unless, perchance, the pollen is not required for fertilization, the plant producing its seeds apogamously, as do the common dandelion and some species of *Hieracium*, a problem which deserves further study.

ARTEMISIA L. Sagebrush, Mugwort, Wormwood

Grains when expanded spheroidal or oblately flattened, 17.6 to 28.5 μ in diameter, normally tricolpate. Furrows long and tapering, fully functional, their membranes smooth, provided with a germinal aperture. Exine thick and coarsely granular, though much less so than in the *Tanacetum* type, the outer layer thin, occasionally slightly overlapping the furrow membranes along their margins. Spine vestiges small or absent (Plate XIII, Figs. 5, 6).

In optical section the grains generally appear rounded-triangular in shape, with the pores bulging out on the three sides; the exine is seen to be thickest in the middle of the lunes, tapering in thickness gradually, in sweeping curves, to the edges of the furrows. The coarsely granular nature of the exine appears coarsely striate in the optical section.

Perhaps the most noteworthy feature of the *Artemisia* pollen grains is the minuteness of their spines. Nevertheless, in the pollen of nearly all species some vestige of them can be seen in at least some of the grains. Moreover, there is considerable variation in this character among the grains of the different species, and this is of such a nature that it is of some diagnostic value. Thus, on the basis of the size of the spine vestiges, it is possible to group the species which are considered here into four different classes as follows: (1) spine vestiges conspicuous, only slightly smaller than in the *Crossostephium* type (Plate XIII, Fig. 3), *Artemisia norvegica;* (2) spine vestiges minute but still quite large enough to be seen with certainty under favorable conditions, *A. frigida, A. camporum, A. Pycnocephala, A. canadensis;* (3) spine vestiges represented only by a vanishing trace or even entirely absent in some grains, *A. gnaphalodes, A. Bigelovii, A. Absinthium, A. dracunculoides;* (4) spine vestiges generally entirely absent, though a trace of them may occasionally be seen on some grains, *A. heterophylla, A. filifolia, A. tridentata.* The distinction among these groups is generally vague. There is, however, no trouble in distinguishing the grains of group 1 from those of group 2 or those of group 2 from those of group 4; but the distinction between those of groups 2 and 3 and between those of 3 and 4 is somewhat uncertain.

The artemisias are all wind pollinated, and most of them shed large amounts of light pollen which may be borne long distances in the air. Virtually all species that occur in sufficient abundance are generous contributors to the production of hayfever.

The taxonomy of the group is extremely complicated and difficult. The number of species recognized by different authors varies from 17 to 72. Many of them are unstable, occurring in a great array of forms, varieties, and minor variations. It is largely owing to a lack of agreement among the different authors

regarding the status of these that such disagreement originates in the numbers of species recognized by them. Nevertheless, the interrelationships between most of these is now exceedingly well understood, owing to the extraordinary and beautiful researches of Hall and Clements (1923). In the present treatment I am following the classification and terminology of Rydberg (1916), owing to its simpler nature and to the fact that this is not primarily a taxonomic work in which ultrataxonomic refinements are required.

Artemisia norvegica Fries. (*A. arctica* Less. *A. hyperborea* Macoun) Boreal sage. Grains somewhat various, some of them giants, abortive, or variously irregular. Normal grains 23.9 to 27.4 μ in diameter. Exine conspicuously but rather finely granular, provided with spine rudiments only slightly less conspicuous than those of *Crossostephium* (Plate XIII, Fig. 3).

A cespitose perennial herb, widely distributed in America and Europe in northern and mountainous regions. It occurs in many forms and varieties, some of which have been given specific names. Flowers from July to October and may cause some hayfever.

Artemisia Suksdorfii Piper (*A. heterophylla* Nutt., *A. vulgaris californica* Gray, *A. vulgaris litoralis* (Suksd.) Hall) California mugwort. Grains essentially as in the *A. tridentata* type, uniform, oblately flattened, 25.1 to 28.5 μ broad and about 23.9 μ deep. Exine distinctly and rather coarsely granular. Spine vestiges generally entirely absent.

Large, bushy perennial herb, 3 to 6 ft. high; common along stream banks and elsewhere. California to British Columbia. Flowers during the latter part of summer, shedding enormous quantities of pollen which is known to be an important cause of hayfever, particularly in the coastal regions of California (Hall in Scheppegrell (1917), Selfridge, 1920).

Artemisia gnaphalodes Nutt. (*A. vulgaris gnaphalodes* (Nutt.) Hall) Prairie or Western sage, Cudweed mugwort, Sagewort. Grains somewhat various, a small proportion of them giants, with four or six furrows or otherwise abnormal. Normal grains rather uniform, slightly flattened, 24 to 25.3 μ in diameter.

A low, cespitose perennial, attaining scarcely 3 ft. in height. Extremely abundant in prairie regions. Ontario and Michigan to Missouri, Texas, Coahuila, California, British Columbia, and

Saskatchewan and sparingly introduced in the eastern United States. Flowers during the latter part of summer and, in regions where abundant, is the cause of much hayfever.

Artemisia Bigelovii Gray. Flat or dwarf sagebrush. Grains extremely various, many of them dwarfs or giants with supernumerary furrows. Normal grains 24 to 25.6 μ in diameter. Texture conspicuously and rather coarsely granular; spine vestiges extremely minute, but generally visible.

Among the aberrant forms are dicolpate grains with furrows opposite, and hexa- and dodecacolpate grains, any of which may or may not be giants. In all, except the dicolpate forms, the furrow arrangements correspond rather closely to the trischistoclasic system, though one or more of the furrows may be missing from any of the configurations without otherwise deforming their arrangement.

A low perennial shrub, 6 to 18 in. high, silvery canescent throughout. Western Texas to southern Colorado, Utah, and Arizona. Flowers August to October. Known to be a contributing factor in hayfever.

Artemisia Absinthium L. Common wormwood, Sagewort, Absinth. Grains uniform, as in the *Artemisia* type. Texture coarsely granular, spine vestiges scarcely visible or entirely absent.

A perennial herb with woody base and fragrant leaves; about 3 to 6 ft. high. Native of Europe, where it is much cultivated for the aromatic oil that may be obtained from its roots. Widely introduced into North America, particularly in the eastern states. July to October. At present it is only an unimportant factor in hayfever but is spreading rapidly.

Artemisia frigida Willd. Carpet, Pasture, or Prairie sage. Grains mostly uniform, essentially as in the type, spheroidal or slightly flattened when expanded, 21.6 to 25.1 μ in diameter. Spine vestiges extremely minute but visible. Besides the normal grains there are a few that are tetracolpate and larger (27.5 μ in diameter).

A low perennial 10 to 20 in. high, with woody base, silky canescent throughout. On dry plains and in rocky soil. Minnesota to Saskatchewan, Yukon, Idaho, Nebraska, Texas, and Arizona. July to October. An important cause of hayfever.

Artemisia dracunculoides Pursh. (*A. dracunculus glauca* (Pallas) Hall, *A. Dracunculus* Pursh.) Indian wormwood, Linear-leaved wormwood. Grains extremely various, many of them abortive, and many giants with three or higher numbers of furrows. Normal grains 20.5 to 27.9 μ in diameter. Spine vestiges extremely small but visible in most of the grains.

A glabrous perennial, 2 to 4 ft. high. Abundant on dry plains and prairies. Manitoba to British Columbia, Illinois, Missouri, Nebraska, Texas, Chihuahua, New Mexico, and California. July to November. Next to *A. tridentata* this is the most plentiful species in North America and is known to be an important cause of hayfever throughout a large part of its range (Rowe, 1928; Selfridge, 1920; Hall, 1917).

Artemisia canadensis Michx. (*A. campestris borealis* (Pallas) Hall, *A. peucedanifolia* Juss.) Field sagewort, Canada sage. Grains extremely various; many of them giants, abortive, and with supernumerary furrows (*e.g.*, 6, 9, and 12). Normal grains essentially as in the *A. tridentata* type, 19.4 to 21 μ broad and 17 to 18.5 μ deep. Spine vestiges extremely small but generally visible.

Stout herb 1 to 2 ft. high from a perennial creeping rootstock; in rocky soil. Newfoundland to Hudson Bay, Maine, Vermont, westward along the Great Lakes and to the Pacific Coast. July to August.

Artemisia camporum Rydb. (*A. campestris pacifica* (Nutt.) Hall, *A. pacifica* Nutt.) Field sagewort. Normal grains uniform, essentially as in the type, 17.6 to 19.8 μ in diameter but accompanied by many giant grains ranging in size from 24 to 33.6 μ in diameter and usually with supernumerary furrows (*i.e.*, tetra-, hexa-, and dodecacolpate) generally in the trischistoclasic system, though there are some in which they are entirely irregular. Texture coarse and conspicuously granular; spine vestiges minute but conspicuous enough to always be seen with certainty.

Ontario to Saskatchewan, Yukon, Arizona, and Nebraska.

Artemisia pycnocephala (Less.) DC. (*A. campestris pycnocephala* (Less.) Hall). Grains essentially as in the type, uniform, 19.4 to 21.6 μ in diameter and with furrows a little shorter than in the type. Texture finely granular; spine vestiges minute but always large enough to be seen with certainty.

A perennial with cespitose, woody base from which emerge stalks bearing the inflorescences. Common on sea beaches, central Oregon to Monterey, California. Said to be an important cause of hayfever in regions where abundant (Rowe, 1928).

Artemisia filifolia Torr. (*A. plattensis* Nutt.) Silvery wormwood, Sand sagebrush. Grains as in the type, uniform, except for a few that are abnormal, 22.8 to 24.5 μ in diameter. Among the abnormal grains are bicolpate grains with furrows opposite and hexacolpate grains with furrows in the trischistoclasic system. Spine vestiges generally not visible, though occasionally a trace of them may be seen.

A coarse, bushy shrub 1 to 3 ft. high, shedding large quantities of pollen during the latter part of summer. Known to be the cause of much hayfever in regions where abundant. Nebraska and Wyoming to Nevada, Chihuahua, and Texas.

Artemisia tridentata Nutt. Common sagebrush (Plate XIII, Figs. 5, 6) type. Grains as in the generic description. When expanded oblately flattened, 25.1 to 28.5 μ in diameter and about 23.4 μ deep. Texture coarsely and distinctly granular. Spine vestiges generally entirely absent—in only a few grains can traces of them be seen.

A coarse, bushy shrub or small tree, extremely abundant in arid and semiarid regions: South Dakota and Montana to British Columbia, Lower California, and New Mexico. July to September. An important cause of hayfever. In some parts of Arizona outranking the ragweeds (Phillips, 1923). In regions of the Rocky Mountains, where the plant reaches its greatest size, it causes a type of hayfever known locally as "mountain fever."

Artemisiastrum Palmeri (Gray) Rydb. (*Artemisia Palmeri* Gray) Tall sagebrush. Grains uniform as in the *Artemisia* type, 18.8 to 21.1 μ in diameter. Spine vestiges entirely absent or represented by doubtful traces.

A tall shrub with herbaceous branches, rather rare and of local distribution in southern California and northern Lower California.

AMBROSIEAE Ragweed Tribe

Grains spheroidal or oblately flattened, 16.5 to 30 μ in diameter, generally tricolpate; but in the pollen of some species tetracolpate grains are frequent, and hexacolpate occasional. Furrows various, long and tapering, of medium length or merely rounded pits only slightly meridionally elongate, almost coinciding in extent with their enclosed germ pores. Exine rather thick but generally less so than in the grains of entomophilous Compositae, more or less distinctly granular; generally provided with spines which are short-conical or rounded, or vestigial, less frequently with spines well developed and sharp pointed.

In the following discussion the ragweeds and their allies will be treated as a tribe of the Compositae. In recent years Britton and Brown and other authors of floras have chosen to give the group the status of a family, making of the Compositae three families, Ambrosiaceae, Cichoriaceae, and Carduaceae. Bentham (1873) has truly stated that "the Compositae are at once the largest, the most distinct, and the most uniform, and therefore the most natural, of all orders of phenogamous plants"; and Bentham's statement still remains unchallenged. Since the business of taxonomy is to show relationships and suggest the trend of evolution, the breaking up of the most natural of all orders of flowering plants is not in the best interests of taxonomy.

The relationship of the Ambrosieae to the other tribes of the Compositae has been very definitely established as closest to the Heliantheae, though some investigators have regarded it as closer to the Anthemideae. Cassini (1834), the greatest of all the earlier synantherologists, regarded the Ambrosieae as related to the Heliantheae, also to the Anthemideae. Delpino (1871) believed that they were related to the Anthemideae through the Artemisias. Bentham (1873) stated, "They are, without doubt, connected with *Artemisia* as well as with the Melampodineae,* having much of the habit of the former and passing into the latter through *Parthenice;* but geographically as well as structurally, the relationship to the Melampodineae appears to me to be the closest." Small (1917) says, "The affinity between *Iva* and *Parthenice* is so close that there can be no doubt of the systematic position of the Ambrosiinae in the Heliantheae and . . . the origin of the subtribe . . . via *Parthenium* and *Parthenice.*" Moreover, the closeness of the relationship of the Ambrosieae to the Heliantheae is abundantly attested by the morphology of their pollen grains; consequently, the taxonomy might be even better expressed by treating the Ambrosieae as a subtribe of the Heliantheae, thus retaining the classification of Bentham and Hooker (1873).

* The Melampodineae are a subtribe of the Heliantheae, including *Parthenium* and *Parthenice*.

There is wide variation of form in the pollen grains of the Ambrosieac, and all the pollen characters which the members of the tribe possess in common are likewise found in the other tribes of the family, yet it is nearly always easy to recognize the pollen grains of the Ambrosieae by the characters which they possess individually. In spite of their wide variation the different forms are clearly related to each other; they appear to represent stages in a progressive evolution of the pollen grains of this group away from the basic thick-walled, echinate form, which characterizes the family, and toward the smooth, thin-walled, highly specialized form of the Euxanthium section of *Xanthium*.

The pollen-grain characters of the different species of the Ambrosieae which appear to have distinctive or phylogenetic value are listed in Table, VI and some of them illustrated in Plate XIV.* The important points brought out here are the marked differences in the size of the spines and length of the furrows in the grains of the different genera. The spines show a more or less progressive reduction through the different groups, from the completely echinate form of the grain of *Oxytenia* (Plate XIV, Fig. 1) to the nearly smooth form of the grain of Euxanthium (Plate XIV, Fig. 7). The furrow likewise shows a progressive reduction throughout the series. It is long in the grains of most of the subtribe Iveneae but slightly reduced in those of *Euphrosyne* and greatly reduced in those of *Iva* (Plate XIV, Fig. 5). It is short in those of all the subtribe Ambrosineae (Plate XIV, Figs. 6 to 8; Plate XIII, Figs. 7 to 9). Correlated with the reduction of the spines and the length of the furrow is a noticeable reduction in thickness of the exine. This is not shown in the table, but it may be stated here that all the long-furrowed grains, *e.g.*, those of *Oxytenia* (Fig. 118), *Chorisiva* (Fig. 119), and *Cyclachaena* (Fig. 120), *i.e.*, those of all of the Iveneae except *Iva*, have a noticeably thicker exine than those of *Iva* and those of the Ambrosineae, which have reduced spines and short furrows, *e.g.*, *Xanthium* (Fig. 122) and *Ambrosia* (Fig. 121).

Another point which is brought out by Table VI is that in genera which are represented by more than a single species the pollen

* The classification and nomenclature relating to the Ambrosieae (exclusive of *Xanthium*) are used here as expressed by Rydberg (1916, 1922); and that pertaining to *Xanthium*, by Millspaugh and Sherff (1916, 1922).

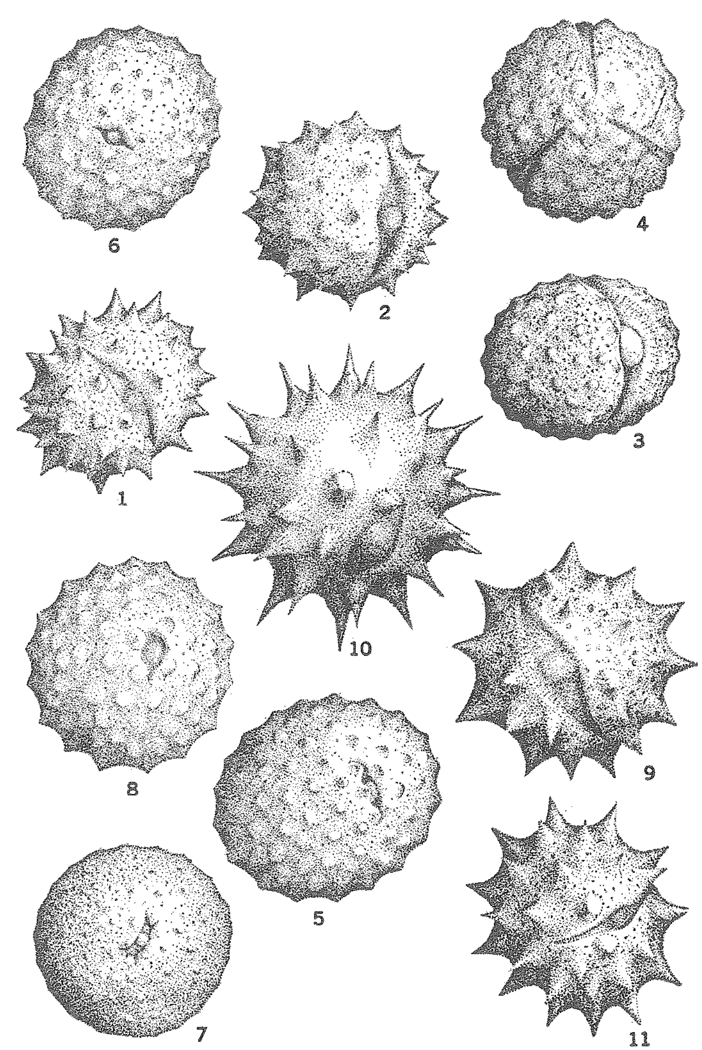

PLATE XIV.—Pollen grains of the Ambrosieae and allied genera. 1, *Oxytenia acerosa*, side view, 18.1 μ in diameter. 2, *Chorisiva nevadensis*, side view, 16.5 μ in diameter. 3, *Cyclachaena ambrosiaefolia*, side view, 19 μ in diameter. 4, The same in polar view. 5, *Iva axillaris*, side view, 20.9 μ in diameter. 6, *Ambrosia psilostachya*, side view, 23 μ in diameter. 7, *Xanthium pennsylvanicum*, side view, 23.4 μ in diameter. 8, *Xanthium catharticum*, side view, 20.9 μ in diameter. 9, *Anthemis nobilis*, side view, 23.1 μ in diameter. 10, *Helianthus annuus*, side view, 27.7 μ in diameter. 11, *Parthenice mollis*, side view, 15.8 μ in diameter.

grains exhibit marked uniformity throughout the genus, and the grains of most genera, except those which are admittedly very closely related, present some distinguishing character. Thus it is seen that in the grains of all four species of *Cyclachaena* (Plate XIV, Figs. 3, 4) the furrows are long and constricted, the grains are subechinate and flattened, and in size they vary only from 17.8 to 19 μ in diameter. In *Dicoria* the grains of the two

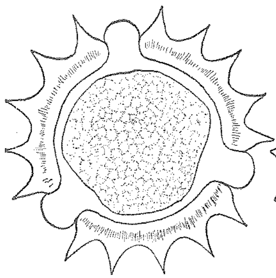

FIG. 118.

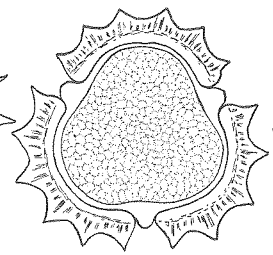

FIG. 119.

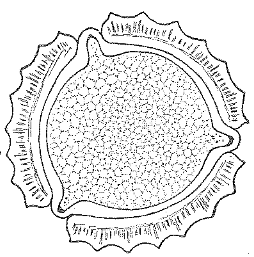

FIG. 120.

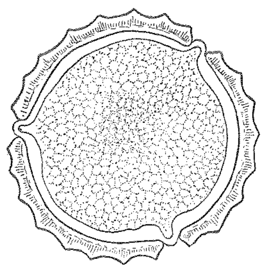

FIG. 121.

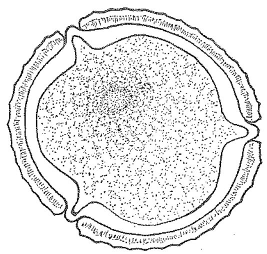

FIG. 122.

FIGS. 118–122.—Pollen grains of Ambrosieae, diagrammatic equatorial sections, showing progressive thinning of the exine and reduction in the size of the spines through the ascending phyletic scale. Figure 118, *Oxytenia acerosa;* Fig. 119, *Chorisiva nevadensis;* Fig. 120, *Cyclachaena xanthifolia;* Fig. 121, *Ambrosia elatior;* Fig. 122, *Xanthium speciosum.*

species recorded in the table are subechinate, with furrows long and constricted, and are practically identical with each other in all other observable respects. In *Iva* the grains of all species are subechinate, with the spines still further reduced, and in size they range only from 19.1 to 21 μ in diameter. Their most striking character is their uniformly short furrows, a character which separates them distinctly from the rest of the Iveneae and stands in sharp contrast with the long-furrowed grains of *Cyclachaena*, despite the fact that both *C. xanthifolia* and *C.*

ambrosiaefolia are regarded by many botanists as belonging to the genus *Iva.*

In the grains of *Ambrosia* (Plate XIV, Fig. 6), and *Acanthambrosia*, which is admittedly very closely related to it, the furrows are short in the grains of all species; the grains are subechinate, showing in this respect slightly less reduction in the spines than do those of *Hymenoclea* or even most of the Ivas. In size somewhat greater variation is found in the grains of these two genera than in the others; still it is not extreme, ranging only from 17.3 to 23 μ in diameter.

In *Franseria*, which is regarded as a transition genus between *Ambrosia* and *Xanthium*, the grains show a corresponding variation. In *Franseria tenuifolia* they are subechinate, with the spines quite as prominent as in those of *Ambrosia.* From this condition the spines range downward in size through the various species to those of the grains of *F. ilicifolia* and *F. deltoidea* in which they are represented by the merest traces. In fact the grains of *F. deltoidea* are scarcely distinguishable from those of the various species of Euxanthium (Plate XIV, Fig. 7) in which the spines are vestigial. It so happens that those species of *Franseria* which are most like *Ambrosia* in their grosser morphological characters have subechinate grains like those of *Ambrosia*, while those that are most like *Xanthium* have nearly smooth grains like those of Euxanthium.

In the grains of the genus *Xanthium* the most conspicuous thing is the wide difference in form existing between those of the two sections. In Acanthoxanthium the grains are small, with spines rather well developed, fully as prominent as in those of *Ambrosia*, while in Euxanthium the grains are larger, and invariably the spines are only vestigial. In view of the extreme uniformity of pollen-grain form found in most of the other genera of this tribe, this seems to be strong evidence that the two sections of *Xanthium* represent widely different genetic lines and should not be retained within the same genus. Indeed, the morphology of the plants themselves shows considerably more difference between these two sections of *Xanthium* than exists between the genera *Ambrosia*, *Franseria*, and *Acanthambrosia*, so on this ground alone, if these three genera are to be admitted, the classification would be much more consistent if the two sections of *Xanthium* were likewise given generic rank. The curious objection is offered to this procedure by American systematists that there is but a single American species belonging to the section Acanthoxanthium.

The grains of all species of the Ambrosieae are rather small, the average of the species listed in the table ranging from 14.8 to 26.4 μ in diameter. At first sight this might be regarded as an adaptation to wind pollination, but that this is not so is seen from the fact that the most highly specialized group, *Xanthium*, have the largest pollen grains, while the less highly specialized genera, *Oxytenia* and *Chorisiva*, have the smallest; in other words the development within the tribe has been toward an increase in pollen-grain size. Strange as it may seem, this increase in size in the development of the pollen grains of the Ambrosieae may actually be a response to wind pollination, for, from a study of wind-pollinated plants of other families, we find that neither those with very small nor those with very large pollen grains are ever wind pollinated but only those of intermediate size, ranging generally between 17 and 40 μ in diameter. The size of *Xanthium* pollen grains thus appears to be the optimum.

The reduction in the size of the spines and the thinning of the exine which are encountered among the Ambrosieae are almost certainly the result of their anemophilous habit. We have already seen that in groups where wind pollination is the rule the pollen grains are without spines or conspicuous adornments of any kind and with thin exines. This is true of such anemophilous families as the Gramineae, Cyperaceae, Juglandaceae, Betulaceae, and Chenopodiaceae and of *Populus* among the Salicaceae, of *Rumex* among the Polygonaceae, and of *Artemisia* and its allies among the Compositae. Here, again, among the Ambrosieae is further evidence of the law that anemophily leads to a thinning of the exine and a reduction of external adornments.

A graphical expression of the probable sequence of the characters discussed above is displayed in Fig. 123. The grain of *Oxytenia* is placed at the beginning of the sequence, representing the form least removed from the basic echinate form of the Compositae, *i.e.*, least affected by anemophily. Its spines are sharp and prominent, and its furrows are long and constricted at their ends. By a simple reduction of its spines this form could have given rise to that of *Chorisiva*, by a further reduction to those of *Cyclachaena* and *Dicoria*, and by a still further reduction to that of *Leuciva*. The derivation of these four forms from that of *Oxytenia* is accomplished solely by a reduction of their spines, together with a slight increase in size, the other characters remaining constant.

From such a form as that which characterizes the grains of *Cyclachaena* and *Dicoria*, by a reduction in the length of the furrows, could have arisen that of *Euphrosyne;* and by a still further reduction in the length of the furrows and of the size of the spines, together with a slight increase in the size of the grains, could have arisen that of the grains of *Iva*.

These seven genera constitute the subtribe Iveneae, which are characterized by monoecism with the staminate and pistillate flowers in the same heads, resembling in this respect section Dracunculus of the genus *Artemisia*, where the condition is associated with and probably induced by anemophily. In *Artemisia* it is associated with the most highly specialized forms and is as far as the separation of the sexes is carried in that genus. But in the Ambrosieae it is associated with the less highly specialized forms, characterizing the Iveneae and serving to distinguish them from the the more highly specialized Ambrosineae in which the staminate and pistillate flowers are always borne in separate heads.

The separation of the sexes into staminate and pistillate heads in the Ambrosieae is not accompanied by any abrupt change in the forms of their pollen grains. Those of *Ambrosia*, *Acanthambrosia*, *Hymenoclea*, and the *Ambrosia*-like *Franserias*, in all of which the sexes are separate, are almost the same as those of *Iva*, in which the sexes are united. Higher up the scale though, in the grains of the *Xanthium*-like Franserias and of Euxanthium, the reduction in size of the spine is resumed, and in the latter group the spines are almost obliterated. In this respect Euxanthium may be regarded as the climax development of the Ambrosieae.

Since the trend of development within the Ambrosieae is toward a reduction in the thickness of the exine and the size of the spines, a reduction of the length of the furrows, and an increase in size of the grain, by reversing this we are able to say that the ancestral form of grain must have been small, with thick exine and well-developed, sharp spines and with long, tapering furrows. Furthermore, the texture of the exine must have been finely but distinctly granular, for this character is fairly constant throughout the group.

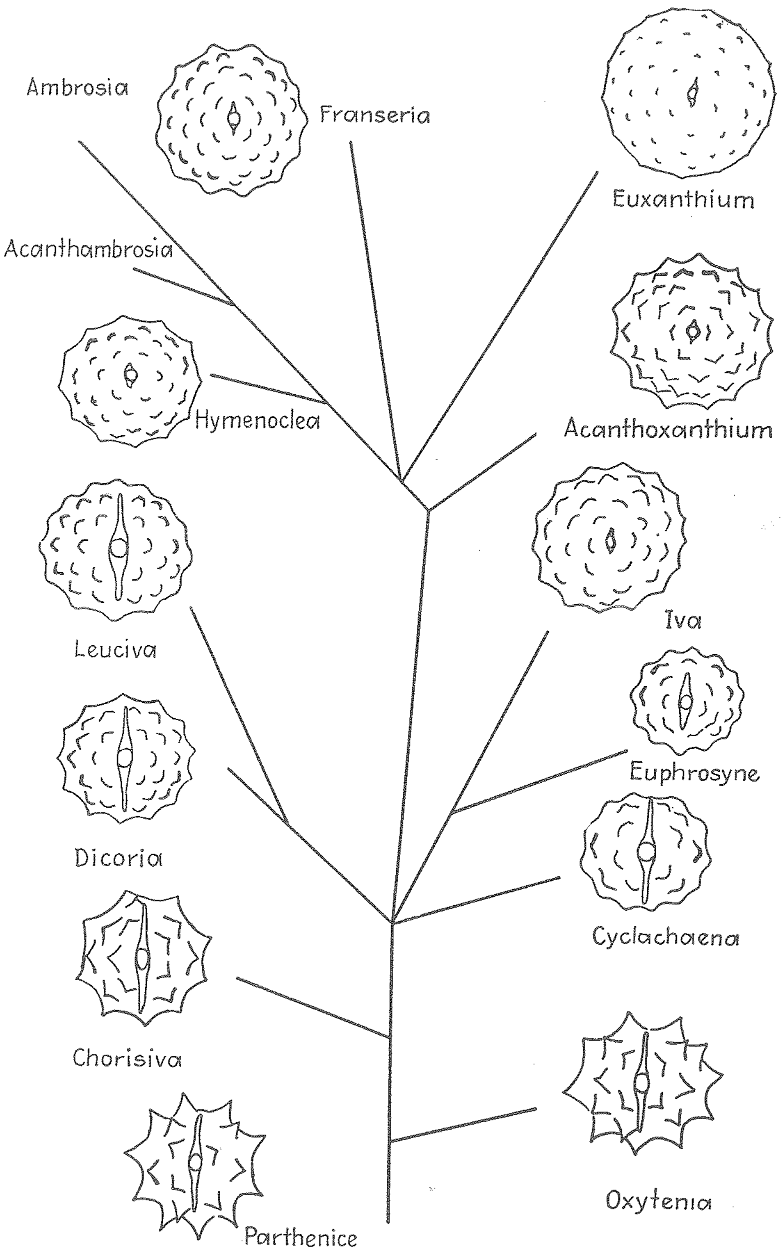

FIG. 123.—Phylogenetic arrangement of the genera of the Ambrosieae, as interpreted from the morphology of their pollen grains.

Which species among living forms comes nearest to satisfying these requirements? As we have already seen, it is claimed by Delpino and others that the relationship of the Ambrosieae is primarily with the Anthemideae and by Bentham and by Small that it is primarily with the Heliantheae through *Parthenium* and *Parthenice*. Let us see how near the grains of the Anthemideae come to fulfilling the requirements of the ancestral form. For example, the grain of *Anthemis nobilis* (Plate XIV, Fig. 9), which is characteristic of that tribe, has short, heavy spines; its furrows are rather long but are also very broad and not at all constricted at their ends; the texture of the exine is much more coarsely granular than that of any species of the Ambrosieae, and, in size, the grain of *Anthemis nobilis* is about 23.1 μ in diameter—much larger than demanded by the prototype. Clearly, this form of grain is quite remote and not at all in line with the trends within the Ambrosieae. Now let us see how near the grains of *Parthenice*, among the Heliantheae, come to satisfying the requirements of the prototype. For example, that of *P. mollis* (Plate XIV, Fig. 11) is small (15.4 μ in diameter)—smaller than those of either *Oxytenia* or *Choriseva*, as would be demanded by the upward trend in size within the group. The grain of *Parthenice mollis* is also echinate, provided with spines essentially the same as those of *Oxytenia*. It is tricolpate, with long furrows reaching almost from pole to pole and strongly constricted toward their ends, and with the surface texture only finely granular. In all of these characters it fulfills the requirements of the prototype almost perfectly—certainly much better than the grains of any of the Anthemideae. The grains of *Parthenium* are essentially the same as those of *Parthenice*, except for their size, which is somewhat larger (15.4 to 22.7 μ in diameter), in this respect, less in line with trend in size within the group. *Parthenice mollis* is regarded by Bentham as still closer to the Ambrosieae than *Parthenium;* in keeping with this it has a grain serving better as our hypothetical prototype. The evidence of the pollen grain therefore indicates that the Ambrosieae are connected with the Heliantheae through *Oxytenia* among the former and *Parthenice* among the latter.

KEY TO THE GENERA

I. Furrows more or less elongate, functioning as harmomegathi.

A. Furrows long and tapering, reaching almost from pole to pole.	
1. Echinate, provided with well-developed, sharp spines; 16.5 to 19.1 μ in diameter.	
a. Spines about 2.5 μ long and 4.6 μ apart.	Oxytenia
b. Spines about 1.1 μ long and 3.4 μ apart.	Chorisiva
2. Subechinate, with spines greatly reduced, and somewhat rounded; 16.5 to 19.0 μ in diameter.	Cyclachaena
3. Not echinate, spines represented only by vestiges; about 20.9 μ in diameter; spines 2.3 to 2.8 μ apart.	Leuciva
B. Furrows short to medium length but clearly functioning as harmomegathi. Grains about 16.2 μ in diameter; spines greatly reduced, almost vestigial, about 2.3 μ apart.	Euphrosyne
II. Furrows greatly reduced, without harmomegathic function, generally represented only by pits in the exine and scarcely extending beyond their enclosed germ pores.	
A. Subechinate, with spines reduced but presenting a conspicuous feature of the exine, 17 to 26.2 μ in diameter.	Hymenoclea Iva Ambrosia Acanthambrosia ACANTHOXANTHIUM Franseria (in part)
B. Spines vestigial, usually represented only by inconspicuous papillae.	
1. Grains about 20.3 μ in diameter.	Franseria deltoidea
2. Grains 22 to 30 μ in diameter.	EUXANTHIUM

Oxytenia acerosa Nutt. (Fig. 118; Plate XIV, Fig. 1). Grains uniform, oblate-spheroidal, about 19.1 by 17.2 μ. Furrows long and tapering, almost meeting at the poles; germ pores rather large and generally somewhat bulging. Exine thick, finely but distinctly granular. Spines conical and sharp, about 2.5 μ long and 4.6 μ apart.

Monoecious shrubs 3 to 6 ft. high, with canescent, pinnatifid leaves. In dry and sandy places; southern Colorado, southern Utah, Arizona, and southeastern California. Flowers in August. Not known to cause hayfever.

Chorisiva nevadensis (Jones) Rydb. (*Iva nevadensis* Jones) (Fig. 119; Plate XIV, Fig. 2). Grains similar to those of *Oxytenia*, uniform in size, less flattened, about 16.5 μ in diameter. Spines about 1.1 μ long and about 3.4 μ apart. Exine finely granular.

A low, diffusely branched annual 4 to 8 ft. high, with canescent, pinnately cleft leaves. Deserts, Nevada.

CYCLACHAENA Fresn.

Grains oblate-spheroidal, 16.7 to 19 μ in diameter, subechinate, with spines more or less conspicuous, 2.3 to 4 μ apart. The grains are generally tricolpate, but in the pollen of some species a small proportion are tetracolpate. The furrows are always long and tapering, almost meeting at the poles and obviously functioning as harmomegathi. Exine rather thick and finely but distinctly granular. These grains differ from those of *Oxytenia* and *Chorisiva* only in their smaller spines. Those of the four species of the genus are virtually indistinguishable from each other; the only observable differences between them are that the spines of *Cyclachaena xanthifolia* and *C. pedicellata* are slightly larger and farther apart than those of *C. ambrosiaefolia* and *C. lobata*, and in the pollen of *C. xanthifolia* are found a few grains with four instead of the usual three furrows. But these distinctions are too slight to be relied upon as criteria.

The genus includes four species of coarse annuals, mostly of arid and semiarid regions of the southwestern United States and Mexico. They are quite distinct from *Iva*, though frequently treated as a section of that genus. Though all possess the characters of hayfever plants, only *C. xanthifolia* is known to be a cause of hayfever.

Cyclachaena xanthifolia (Nutt.) Fresn. (*Iva xanthifolia* Nutt., *Euphrosyne xanthifolia* Gray) Prairie ragweed, Burweed, Horse-weed, Careless weed (Fig. 120; Plate XIV, Figs. 3, 4). Grains as in the generic description, 17.6 to 19.8 μ in diameter, spines 2.3 to 3.4 μ apart.

A tall, coarse annual, 2 to 6 ft. high, in waste places, Illinois to Saskatchewan, Idaho, New Mexico, Texas, and Missouri. Flowers July and August, shedding large quantities of pollen which is the cause of much hayfever in regions where the plant is abundant. Mullin (1922) states that in Colorado 27 per cent of the hayfever patients react to this pollen; Hall (Scheppegrell, 1917) states that in the Rocky Mountain and Pacific coast states prairie ragweed ranks as a hayfever plant next in importance to *Artemisia*.

This plant is perhaps more frequently known by its synonym *Iva xanthifolia*, which is a misnomer. And, because of its mistaken association with the genus *Iva*, it is frequently called marsh elder. In hayfever studies it is generally known as "burweed marsh elder."

Cyclachaena pedicellata Rydb. Grains as in the generic description, 17.6 to 18.7 μ in diameter, about 15.4 μ measured through their polar axes. Spines 2.8 to 4 μ apart.

A tall annual herb, similar to the preceding but less common. New Mexico and western Texas.

Cyclachaena ambrosiaefolia (Gray) B. & H. (*Euphrosyne ambrosiaefolia* Gray, *Iva ambrosiaefolia* Gray) (Plate XIV, Figs. 3, 4). As in the generic description, 18.7 to 20 μ in diameter. Spines 2.3 to 2.8 μ apart.

A low annual herb, about 1½ ft. high. Texas to Arizona, Zacatecas, and San Luis Potosi.

Cyclachaena lobata Rydb. Grains as in the generic description, 16.5 to 18.7 μ in diameter. Spines 2.3 to 3.4 μ apart.

A little-known annual, California.

DICORIA T. & G. Dicoria

Grains similar to those of *Cyclachaena*, uniform, oblate-spheroidal, 16.5 to 18.7 μ in diameter; subechinate, spines 2.3 to 3.4 μ apart; tricolpate, furrows long and tapering but less extended than in the grains of *Cyclachaena*. Exine distinctly but finely granular. The grains of the two species here described are identical in appearance.

The genus contains about seven species of annual or biennial herbs, sometimes with a woody base; inhabiting the arid regions of southwestern United States and Mexico. Known to be capable of causing hayfever but unimportant in this respect owing to their restriction to desert regions.

Dicoria canescens Gray (*D. calliptera* Rose & Standl.). Annual herb 2 to 4 ft. high. Desert wastes. Arizona, southern California, and Utah. Flowers June to November.

Dicoria Brandegei Gray. A diffusely branching cinereous herb 1 to 3 ft. high. Sandy bottoms. Southern Colorado to southern Utah to Arizona. Flowers in August.

Leuciva dealbata (Gray) Rydb. (*Iva dealbata* Gray). Grains somewhat various, nearly one-half of them tetracolpate, with furrows arranged in the trischistoclasic system. Normal tricolpate grains similar to those of *Cyclachaena*, oblately flattened, about 22 by 19.4 μ, subechinate, with spines very small, almost vestigial and only slightly more prominent than those of the grains of *Cyclachaena*. Texture rather coarsely and distinctly granular.

Low tomentose annual, about 1½ ft. high. Of desert regions. Texas, New Mexico, Coahuila, and Chihuahua. This species was formerly included in the genus *Iva* but appears to be more closely related to *Cyclachaena*.

Euphrosyne parthenifolia DC. (*Gymnostyles parthenifolia* Moc.). Grains uniform, oblately flattened, subechinate, with spines almost vestigial. Furrows short and tapering but obviously functioning as harmomegathi, though less effectively than those of *Cyclachaena*. Germ pores slightly larger than in the preceding species.

Perennial herb about 2½ ft. high. Mexico.

HYMENOCLEA T. & G. Greasebush

Grains mostly uniform, oblately flattened, 18 to 19.6 μ in diameter, subechinate, with spines greatly reduced, almost vestigial. Furrows short but meridionally extended beyond the pore as pointed projections. Pores small, elliptical, about 2.7 μ long, with their long axes directed meridionally. Obviously, neither the pores nor the furrows of these grains are sufficiently developed to accommodate changes in volume. The exine, however, is thin, and when the grain contracts it is drawn inward, forming three deep meridional depressions with the pores at their bottoms. Exine finely but distinctly granular.

The grains of the three species here recorded are practically identical, except that a large proportion of those of *H. monogyra* are tetracolpate.

Dioecious shrubs with unisexual flower heads, the pistillate one-flowered and with the involucre dilated to form a number of transverse wings. In distribution confined to desert regions of southwestern United States and Mexico. The pollen of several species is known to be an active cause of hayfever, but, owing to their restriction to deserts, the shrubs are not often important in this respect.

Hymenoclea Salsola T & G. (*H. polygyra* Delpino). A large shrub 3 to 6 ft. high. Southern Utah and Arizona to California and Lower California.

Hymenoclea fasciculata A. Nels. A low shrub, 1 to 3 ft. high. Nevada.

Hymenoclea monogyra T. & G. A large shrub 3 to 12 ft. high. Western Texas and Coahuila to southern California and Sinaloa.

IVA L. Marsh elder, Poverty weed, Bozzleweed, Salt sage

Grains oblate-spheroidal, 19 to 21 μ in diameter, subechinate, with spines relatively small, less prominent than those of *Ambrosia elatior*. Furrows very short, merely pits slightly elongate meridionally and without harmomegathic function. Exine finely but distinctly granular. In general these grains are similar to those of *Hymenoclea* but somewhat larger. Those of the four species recorded here are practically identical, except for slight differences in the size and distance apart of their spines. Their size is always too small to measure, but they vary in distance apart from 2.3 to 4.9 μ.

The marsh elders are perennial or annual herbs or shrubs resembling the ragweeds but generally growing in swampy or moist places. The genus contains about 15 species, native of North America. They all shed large quantities of pollen which produces hayfever symptoms similar to those caused by ragweed.

Iva oraria Bart. (*I. frutescens* Bigel.) Marsh elder, High-water shrub. Grains as in the generic description, 21 to 22 μ in diameter. Spines 4 to 4.9 μ apart. July, August.

A common shrub on banks of tidal streams and in salt marshes, along the Atlantic coast from Massachusetts to Virginia. Its pollen produces skin reactions with ragweed-hayfever patients but, owing to the localized distribution of the plants, is not a serious cause of hayfever.

Iva frutescens L. Marsh elder, High-water shrub. Grains identical in every respect with those of the preceding species.

The plants themselves differ from the preceding species only in their geographical distribution which extends, in similar habitat, from Virginia to Florida and Texas, and in the slightly smaller size of their involucres and achenes, characters of doubtful value in specific distinctions.

Iva ciliata Willd. (*I. annua* Michx.) Rough marsh elder. Grains about 21 μ in diameter, similar to those of *I. oraria* but with their texture more coarsely granular and spines slightly larger, 3.4 to 4.6 μ apart.

A coarse annual 1 to 6 ft. high, resembling *Ambrosia*, generally in moist soil. Illinois to Nebraska, New Mexico, and Louisiana. Flowers August to September, shedding large quantities of pollen which is the cause of much hayfever.

Iva axillaris Pursh. (*I. foliosa* Nutt.) (Plate XIV, Fig. 5.) Small-flowered marsh elder, Poverty weed. Normal grains 19.8 to 22 μ in diameter, similar to those of *I. oraria*. Spines very small, about 2.8 μ apart. A large proportion of the grains tetracolpate or variously irregular.

Low, perennial weed with leafy, herbaceous stems rising 1 to 2 ft. high from a woody base; common in alkaline or saline meadows. Manitoba to Oklahoma to New Mexico to California to British Columbia. Flowers from May to September, shedding much pollen which certainly causes some hayfever in regions where abundant. It is regarded by Rowe (1928) as unimportant in this respect in California but is stated by Hall (Scheppegrell, 1917) to be next in importance to sagebrush.

Iva Hayesiana Gray. Normal grains rather uniform in size, 21 to 22 μ in diameter. Spines small, almost vestigial as in *Xanthium*, 2.8 to 3.4 μ apart. Many grains tetracolpate or variously irregular.

A bushy perennial about 3 ft. high; southern California, Lower California, and adjacent islands. Its pollen probably causes some hayfever in regions where abundant.

Iva angustifolia Nutt. Grains uniform, about 19.2 μ in diameter. Spines similar to those of *I. oraria*, about 3.4 μ apart.

A slender annual 1 to 3 ft. high. Gravelly banks and ponds. Arkansas, Oklahoma, Louisiana, and Texas.

Iva cheiranthifolia H. B. K. Grains uniform, about 20 μ in diameter; subechinate, with spines rather prominent, 2.8 to 3.4 μ apart.

Bushy perennial. Banks of streams and coastal plains. Cuba and the Bahamas.

AMBROSIA L. Ragweed

Grains oblate-spheroidal, 17 to 24 μ in diameter, subechinate, with spines too short to be conveniently measured but various in size and various in their distance apart among the different species from 2.3 to 4.3 μ. Furrows short, not at all or only slightly elongate in a meridional direction, virtually coinciding in extent with the germ pores. Exine rather thin, always conspicuously granular. The pollen of the different species can occasionally be distinguished from each other by the diameter of the grains, the size and distance apart of their spines, and the presence or absence of tetracolpate grains. But these distinctions are generally rather slight and of difficult application.

The ragweeds are monoecious, branching herbs, notorious for the enormous quantities of pollen that they produce, and among them are counted the worst known causes of hayfever. The genus consists of about 15 species of wide distribution in North America.

Key to the Species

I. Grains 17 to 20 μ in diameter.	
A. Spines comparatively large, 3.4 to 4.3 μ apart.	A. bidentata
	A. trifida
B. Spines comparatively small, 2.3 to 3.4 μ apart.	A. elatior
	A. aptera
	A. cumanensis
	A. tenuifolia
	A. peruviana
II. Grains 22 to 30 μ in diameter.	A. psilostachya
	A. coronopifolia
	A. hispida

Ambrosia elatior L. (*A. artemisiaefolia* T. & G.). Common or Short ragweed (Plate XIII, Fig. 7) type. Grains spheroidal or slightly oblate, uniform, nearly always tricolpate, rarely tetracolpate, 17.6 to 19.2 μ in diameter (average 18.3 μ), subechinate. Spines flat-conical, scarcely pointed at their tips, about 2.8 μ apart. Exine rather thin and flexible, distinctly, and comparatively coarsely, granular. Furrows short, merely small pits, almost coinciding with their enclosed germ pore.

These grains may be distinguished from those of *A. trifida* by their *larger* average diameter, and by the smaller size, less pointed character, and closer arrangement of their spines. They may be distinguished from those of *A. psilostachya* and *A. coronopifolia* by their *smaller* average size, smaller and more closely arranged spines, and the almost total absence of tetracolpate grains which characterize the pollen of the two latter species.

A coarse, branching annual with fibrous roots, a pernicious weed of cultivated fields throughout the northern part of the United States and adjacent Canada, though less abundant westward. It is known to consist of several slightly differing races, and, though all are probably equally active in producing hayfever, there is evidence that some of them possess slight immunological distinctions. August to October.

Ambrosia psilostachya DC. (Plate XIII, Fig. 8; Plate XIV, Fig. 6) Western ragweed. Grains spheroidal or oblately flattened, somewhat various in size, 22 to 24.7 μ in diameter, tricolpate or tetracolpate with about equal frequency. Spines larger than those of the grains of *A. elatior*, resembling those of *trifida*, 2.8 to 3.4 μ apart.

Bushy herbs from perennial, creeping rootstocks; similar in outward appearance to *A. elatior* but distinguished by their perennial habit. Louisiana to New Mexico and Tamaulipas. August to October. A frequent cause of hayfever.

Ambrosia coronopifolia T. & G. (*A. psilostachya* Gray) Western ragweed. Grains identical with those of the preceding species—a similar proportion of them tetracolpate.

The plants of this species are distinguished from those of *A. psilostachya* only by the relatively unimportant technical characters of the presence on their fruit of fewer and less pointed tubercles and the absence of pustulate bases to the hairs of their leaves. In view of the identity in form of their pollen grains and the presence of the same proportion of tetracolpate grains among both, it seems likely that these two species should be merged.

The present species (generally spoken of as *A. psilostachya*) is extremely abundant in lowland and waste places. Illinois to Saskatchewan, Texas, Mexico, and California. Throughout much of its range it is the cause of a large proportion of all the hayfever occurring during its flowering period, from July to October.

Ambrosia hispida Pursh. (*A. maritima* Ferrero). Grains oblate, rather various, 22.8 to 28.5 μ in diameter, many tetracolpate which may or may not be giants. Spines similar in appearance to those of *A. elatior*, 2.9 to 4 μ apart.

Sea beaches, southern Florida and West Indies. Flowers almost throughout the year but is not regarded as a serious cause of hayfever.

Ambrosia trifida L. Tall or Giant ragweed (Plate XIII, Fig. 9). Grains uniform, spheroidal or somewhat oblately flattened, 16.5 to 19.2 μ in diameter (average 17.7 μ), with spines relatively large and distinctly sharp pointed, about 3.4 μ apart. Texture distinctly granular.

These grains can be distinguished from those of *A. elatior* by their smaller average size and by their spines which are slightly larger, more sharply pointed, and farther apart. They can be distinguished from those of *A. psilostachya* and *A. coronopifolia* by their smaller size and the almost total absence of tetracolpate grains which characterize the pollen of the two latter species.

A coarse, annual weed, characteristically branching at the base, reaching a height of 13 ft.; with leaves undivided, three parted or five parted, and their petioles marginate. Exceedingly common throughout the northern part of the United States and adjacent Canada, less abundant westward. It sheds enormous quantities of pollen from early August until killed by frost. Its pollen and that of *A. elatior*, with which it is frequently associated, are the cause of most of the late summer hayfever in the northeastern United States.

Ambrosia aptera DC. (*A. trifida texana* Scheele). Grains oblate-spheroidal, about 18.2 μ in diameter, excepting a few giants which are about 22 μ in diameter; apparently always tricolpate. Spines distinctly sharp, resembling those of the grains of *A. trifida*, 2.6 to 3.1 μ apart.

A tall annual, 3 to 15 ft. high, closely resembling *A. trifida* but may be distinguished from it by the lack of lateral wings on its petioles and its habit of branching high up instead of at or near the ground. Louisiana to Arizona and adjoining Mexico. The cause of much hayfever in regions where abundant but not generally distinguished from *A. trifida* in hayfever studies.

Ambrosia cumanensis H. B. K. Grains oblate-spheroidal, uniform, 17.3 μ in diameter, with spines greatly reduced, similar to those of *A. elatior*, 2.8 to 3.4 μ apart.

A bushy perennial, 2½ to 6 ft. high. Mexico to Colombia, Brazil, and Cuba. Not known to cause hayfever.

Ambrosia bidentata Michx. Grains uniform, oblate-spheroidal, 19.8 to 21 μ in diameter. Spines sharp and rather prominent, similar to those of *A. trifida*, about 4.3 μ apart.

A low, hirsute annual, usually much branched, 1 to 3 ft. high. Prairies, Illinois, Kansas, Louisiana, and Texas. July to September. Known to be the cause of some hayfever within its somewhat restricted range, though in hayfever studies it is not generally distinguished from the other species of *Ambrosia* with which it is usually associated.

Ambrosia tenuifolia Spreng. Grains uniform, oblately flattened, 19.8 to 25 μ in diameter, with spines rather prominent; similar to those of *A. trifida*, 2.8 to 3.4 μ apart.

A low annual 1 to 2 ft. high. Native of Argentina and Uruguay but naturalized in Louisiana and Puerto Rico.

Ambrosia peruviana Willd. (*A. artemisiaefolia* Benth.). Grains uniform, oblately flattened, 17.6 to 19.8 μ in diameter. Spines greatly reduced, similar to those of *A. elatior*, 2.6 to 3.4 μ apart.

An annual or perennial herb 2 to 6 ft. high. Jamaica, Puerto Rico, Mexico to Chile and Paraguay.

Acanthambrosia Bryantii (Curran) Rydb. (*Franseria Bryantii* Curran). Grains somewhat various, about one-quarter of them having four instead of the usual three furrows. Normal grains spheroidal or slightly oblate, 22 to 23.1 μ in diameter. Spines small, similar to those of *A. elatior*, 3.7 to 4.6 μ apart.

A low shrub. Lower California.

FRANSERIA Cav. (*Gaertneria* Medic.) False ragweed

Grains similar to those of *Ambrosia*, oblate-spheroidal in shape, 18 to 23.5 μ in diameter, subechinate, the spines various in size, in some species vestigial.

The false ragweeds are annual or perennial herbs or shrubs, to be distinguished from the true ragweeds only on minor technical details. They likewise shed large amounts of pollen which causes much hayfever, mostly during the latter part of summer.

Franseria tenuifolia Harv. & Gray (*Gaertneria tenuifolia* Ktze., *Xanthium tenuifolium* Delpino). Slender ragweed. Grains various; many of them tetra- and hexacolpate, and these may or may not be giants. Normal grains 19.8 to 22 μ in diameter. Spines slightly more prominent than those of *Ambrosia trifida*, the most prominent observed in the genus, about 1.5 μ long and 3.3 to 3.4 μ apart.

A perennial herb, in general appearance resembling western ragweed and frequently confused with *Ambrosia tenuifolia*, which it resembles even more closely. "It grows in warm dry districts from the westerly part of the Mississippi valley to Colorado, Nevada and southern California and ranges southward to Texas." (Hall in Scheppegrell, 1917.) Flowers May to November and is the cause of much hayfever in Arizona (Phillips, 1923) and in California (Selfridge, 1920).

Franseria dumosa Gray (*Gaertneria dumosa* Ktze.) Sandbur. Grains uniform, 19.8 to 24.2 μ in diameter. Spines small, less prominent than those of *Ambrosia elatior*, 2.8 to 3.4 μ apart.

"A low spreading, white-stemmed shrub, with brittle, woody branches. It grows in great abundance on the hot dry deserts from southern Utah to southeastern California and southern Arizona." (Hall in Scheppegrell, 1917.) Flowers March to June and is known to cause much hayfever.

Franseria acanthicarpa (Hook.) Coville (*F. Hookeriana* Nutt., *Gaertneria acanthicarpa* Britt., *Ambrosia acanthicarpa* Hook.) Bur ragweed. Grains uniform, 18.7 to 20.3 μ in diameter. Spines less prominent than those of *Ambrosia elatior*, 2.8 to 3.7 μ apart.

A spreading, bushy annual or biennial weed with ashy-gray leaves, somewhat resembling western ragweed. It inhabits sandy plains and is common in arid sections from the Rocky Mountains nearly to the Pacific coast. In California, Oregon, and Washington it is restricted to the eastern or drier parts of the states. Flowers from August to December and is the cause of much hayfever throughout a large part of its range (Phillips, 1922, 1923; Selfridge, 1920).

Franseria ilicifolia Gray (*Gaertneria ilicifolia* Ktze.). Grains various, but apparently none has supernumerary furrows, 20.9 to 22 μ in diameter. Spines vestigial, only slightly more prominent than those of the grains of Euxanthium, 2.8 to 2.9 μ apart.

A shrubby perennial about 3 ft. high. Arizona, southern California, and Lower California. Not known to cause hayfever.

Franseria albicaulis Torr. Grains uniform, rarely tetracolpate, about 18.7 μ in diameter. Spines small, less prominent than in the grains of *Ambrosia elatior*.

A low, branching shrub, finely tomentose when young. Southern California to southern Utah, Sonora, and Lower California. Not known to cause hayfever.

Franseria bipinnatifida Nutt. (*Gaertneria bipinnatifida* Ktze., *Ambrosia bipinnatifolia* Greene). Beach sandbur. Grains rather uniform, 22.5 to 25.3 μ in diameter; a few tetracolpate. Spines almost vestigial only slightly more prominent than in the grains of Euxanthium.

A low, spreading herb of sea beaches and sand dunes, occasionally elsewhere in waste places. Flowers from April to December and is believed to be an important cause of hayfever in California (Rowe, 1928).

Franseria deltoidea Torr. (*Gaertneria deltoidea* Ktze.) Canyon ragweed, Rabbit bush. Grains uniform, 20.3 to 22 μ in diameter. Spines vestigial as in the grains of Euxanthium.

A shrubby perennial with finely tomentose branches. Southern Arizona. Flowers in spring and early summer and is an important cause of hayfever (Watson and Kibler, 1922; Phillips, 1923).

XANTHIUM L. Cocklebur

Section 1. Acanthoxanthium. Grains subechinate, with the spines prominent and sharp pointed, larger than those of the grains of *Ambrosia trifida*, 3.4 to 5.1 μ apart. Furrows extremely short, only slightly extended beyond the small germ pore which each encloses. Texture finely but conspicuously granular. The grains of the three species here included are virtually alike but are entirely dissimilar from those of all the species of the second section of the genus, Euxanthium, in their smaller size and much larger spines (Plate XIV, Fig. 8).

Xanthium spinosum L. (*Acanthoxanthium spinosum* Fourr.) Spiny clothbur, Clotweed, Burweed. A large, coarse annual herb with dark-green leaves, smooth and shining on the upper surface and armed with conspicuous three-pronged axillary spines.

Sporadically introduced almost throughout the United States, particularly abundant in California where it is regarded as an important cause of hayfever (Rowe, 1928). June to November. Native of the Mediterranean region and Australia.

Xanthium ambrosioides B. & H. Grains uniform, as in the sectional description.

Xanthium catharticum Kth. (Plate XIV, Fig. 8). Grains as in the sectional description.

Section 2. Euxanthium. Grains spheroidal, mostly larger than those of section Acanthoxanthium, 22.1 to 29.1 μ in diam-

TABLE VI.—POLLEN GRAINS OF THE AMBROSIEAE

Species	Furrows	Sculpturing	Shape	Size μ	Spine length, μ	Spine distance apart, μ
Iveneae:						
Oxytenia acerosa	Long	Echinate	Flattened	18.1	2.5	4.6
Chorisiva nevadensis	Long	Echinate	Spheroidal	16.5	1.1	3.4
Cyclachaena xanthifolia	Long	Subechinate	Flattened	18.7	....	2.6–3.4
C. pedicellata	Long	Subechinate	Flattened	16.7	....	2.8–4.0
C. ambrosiaefolia	Long	Subechinate	Flattened	19.0	....	2.3–2.8
C. lobata	Long	Subechinate	Flattened	17.8	....	2.3–3.4
Euphrosyne parthenifolia	Medium	Subechinate	Flattened	14.8	....	2.3
Dicoria Brandegei	Long	Subechinate	Slightly flattened	17.6	....	2.3–3.4
D. canescens	Long	Subechinate	Slightly flattened	17.8	....	2.3–3.4
Leuciva dealbata	Long	Subechinate reduced	Flattened	20.3	....	2.3–2.8
Iva ciliata	Short	Subechinate reduced	Spheroidal	20.9	....	3.4–4.6
I. oraria	Short	Subechinate reduced	Spheroidal	20.9	....	4.0–4.9
I. frutescens	Short	Subechinate reduced	Spheroidal	19.1	....	2.3–4.0
I. angustifolia	Short	Subechinate reduced	Spheroidal	19.4	....	3.4
I. cheiranthifolia	Short	Subechinate reduced	Slightly flattened	20.0	....	2.8–3.4
I. Hayesiana	Short	Subechinate reduced	Slightly flattened	21.0	....	2.8–3.4
I. axillaris	Short	Subechinate reduced	Spheroidal	20.9	....	2.8
Ambrosineae:						
Hymenoclea fasciculata	Short	Subechinate much reduced	Flattened	18.1	....	2.3–3.4
H. Salsola	Short	Subechinate much reduced	Flattened	19.6	....	2.3–3.4
H. monogyra	Short	Subechinate much reduced	Flattened	18.8	....	2.3–3.4
Ambrosia elatior	Short	Subechinate	Spheroidal	18.3	....	2.3–3.4
A. trifida	Short	Subechinate	Spheroidal	17.7	....	3.4
A. aptera	Short	Subechinate	Spheroidal	18.5	....	2.6–3.1
A. cumanensis	Short	Subechinate	Slightly flattened	17.3	....	2.8–3.4
A. psilostachya	Short	Subechinate	Spheroidal	23.4	....	2.8–3.4
A. coronopifolia	Short	Subechinate	Spheroidal	24.5	....	3.4–4.0
A. hispida	Short	Subechinate	Flattened	25.0	....	2.9–4.0
A. bidentata	Short	Subechinate	Slightly flattened	19.5	....	4.3
A. tenuifolia	Short	Subechinate	Spheroidal	22.0	....	2.8–3.4
A. peruviana	Short	Subechinate	Slightly flattened	17.3	....	2.8–3.4
Acanthambrosia Bryantii	Short	Subechinate	Slightly flattened	22.8	....	3.7–4.6
Franseria tenuifolia	Short	Subechinate	Slightly flattened	20.7	....	3.3–3.4
F. bipinnatifida	Short	Subechinate much reduced	Spheroidal	23.3	....	2.3–2.8
F. acanthicarpa	Short	Subechinate reduced	Slightly flattened	19.8	....	2.8–3.7
F. dumosa	Short	Subechinate much reduced	Slightly flattened	20.6	....	2.8–3.4
F. albicaulis	Short	Subechinate much reduced	Slightly flattened	18.1	....	2.3
F. ilicifolia	Short	Subechinate much reduced	Slightly flattened	21.3	....	2.8–2.9
F. deltoidea	Short	Spines vestigial	Slightly flattened	20.3	....	2.3
Xanthium spinosum	Short	Subechinate prominent	Spheroidal	22.0	....	4.6
X. catharticum	Short	Subechinate prominent	Spheroidal	20.9	....	3.4–5.2
X. ambrosioides	Short	Subechinate prominent	Spheroidal	21.0	....	4.6
X. speciosum	Short	Spines vestigial	Spheroidal	26.4	....	2.3–2.8
X. strumarium	Short	Spines vestigial	Spheroidal	22.1	....	2.3–2.6
X. globosum	Short	Spines vestigial	Spheroidal	22.1	....	2.3–2.4
X. pennsylvanicum	Short	Spines vestigial	Spheroidal	25.0	....	2.6–2.8
X. chinense	Short	Spines vestigial	Spheroidal	23.4	....	2.6

eter, with spines vestigial, generally scarcely apparent, 2 to 2.8 μ apart. Furrows short, scarcely extending beyond their enclosed germ pore. Exine thin, collapsing easily as the grain shrinks, rather coarsely and conspicuously granular. There is scarcely any difference between the grains of the following species, except possibly in their size and in the distance apart of their spine vestiges.

Coarse, branching, rough, annual herbs. About 15 species of wide geographical distribution. Most of them produce large amounts of pollen which is known to give reactions by skin test with hayfever patients but generally less than the ragweeds, and several of them are important causes of hayfever.

Xanthium speciosum Kearney. Great clotbur (Fig. 122). Grains as in the sectional description.

A coarse and very stout weed 3 to 4½ ft. high. North Dakota to Wisconsin, Tennessee, Montana, Nebraska, and Texas. August to September. An important cause of hayfever, producing more pollen than most of the other species.

Xanthium strumarium L. (*X. brevirostre* Wallr.). Grains as in the sectional description.

Coarse, branching, pubescent herb about 3 ft. high. Native of Europe, introduced into California and Massachusetts.

Xanthium globosum Schull. Grains as in the sectional description.

Low, spreading herb with reddish, purple, or straw-colored stems. Missouri and Kansas.

Xanthium pennsylvanicum Wallr. (Plate XIV, Fig. 7). Grains as in the sectional description.

Coarse, scabrous herbs, about 2½ ft. high. Throughout the United States and adjoining Mexico and in the Hawaiian islands.

Xanthium chinense Mill. (*X. longirostre* Wallr., *X. canadense* Rowlee.). Grains as in the sectional description.

Coarse, robust herbs, reaching a height of 6 ft. Ontario to Massachusetts, Florida, Texas, and rarely California, Mexico, and throughout the West Indies.

GLOSSARY

Abporal lacuna, a lacuna meridionally opposite a germ pore. It may be closed as in the grain of *Scolymus* (Plate XI, Fig. 1), communicate with its adjoining poral lacuna as in that of *Taraxacum* (Plate XI, Fig. 2), or, if the poral lacuna is absent, it may communicate with its meridionally opposite abporal lacuna.

Acolpate, without furrows or pores. See Colpate.

Aspidate, bearing aspides.

Aspis, pl. **aspides,** a shield-shaped, subexineous thickening surrounding a germ pore.

Bladder, see Wing.

Cap or disk, the thickened dorsal surface of the winged grains of the Abietineae and Podocarpineae.

Circumpolar lacunae, those lacunae, generally six in each hemisphere, surrounding the polar lacuna or polar thickening in lophate grains.

Colpate, possessing germinal furrows or harmomegathi, generally used with numerical prefixes as mono-, di-, and tri-, signifying the number of furrows (Gr. κόλπος, a fold).

Cribellate, possessing a number of rounded germinal apertures more or less equally spaced. Example: *Salsola pestifer* (Plate VIII, Fig. 4) (Lat. *cribellum*, a little sieve.)

Disk, see Cap.

Dorsal, the side of the grain turned inward in the tetrad and opposite the furrow in monocolpate grains; opposed to ventral (q.v.).

Echinate, provided with long or conspicuous and generally sharp, pointed spines, *e.g.*, the grains of *Solidago* (Plate XII, Fig. 4) and *Oxytenia* (Plate XIV, Fig. 1) (Gr. ἐχῖνος, a hedgehog).

Echinolophate, lophate, with the ridges bearing spines on their crests.

Emphytic characters, those that are the result of a specifically inherited cell form (Gr. ἔμφυτος, innate).

Equator, the great circle midway between the two poles and dividing the grain into two polar hemispheres.

Equatorial lacuna, a lacuna situated on the equator between two germ pores and as much in one polar hemisphere as the other. It may be remote from contact with the pores or poral lacunae, as in the grains of *Vernonia jucunda*, or in contact with one of them, as in those of *Scorzonera* (Plate XI, Fig. 5), or with two of them, as in those of *Tragopogon* (Plate XI, Fig. 4).

Equatorial ridge, an interlacunar ridge extending from pore to pore along the equator in lophate grains. It may be continuous, as in the grains of *Taraxacum* (Plate XI, Fig. 2), or interrupted to admit the equatorial lacunae when these are present, as in the grains of *Scorzonera hispanica* (Plate XI, Fig. 5) and *Tragopogon pratensis* (Plate XI, Fig. 4).

Furrow, see Germinal furrow and Harmomegathus.

Furrow membrane, the area of the exine enclosed by the germinal furrow, generally a delicate elastic membrane which stretches as the furrow opens, *e.g.*, in the grains of *Solidago speciosa* (Plate XII, Fig. 4).

Furrow rim, the lip of the furrow, the edge or fold of exine bounding the furrow, sometimes thickened and in the winged grains of the Podocarpineae, bearing the ventral roots of the bladders.

Germinal aperture, a hole in the furrow membrane through which the germ pore protrudes. The term is also used to designate the rounded apertures which frequently occur in the general surface of the exine in the absence of germinal furrows, *e.g.*, in the grains of *Salsola pestifer*, though these should probably be regarded as germinal furrows which are rounded in form and coinciding in extent with their enclosed germ pores.

Germinal furrow, a longitudinal groove or opening in the exine, either enclosing a germ pore or serving directly as the place of emission of the pollen tube, also generally serving as a harmomegathus (q. v.).

Germ pore, a pollen-tube anlage or the place of emergence of the pollen tube, generally denoted by a rounded papilla, *e.g.*, in the grains of *Eriogonum gracile* (Plate VIII, Fig. 6). Germ pores are generally enclosed in a germinal furrow as in the above example, but they may penetrate the exine directly, *e.g.*, in the grains of *Salsola pestifer* (Plate VIII, Fig. 4). *Cf.* Germinal aperture.

Haptotypic characters, those which are due to internal or prenatal environment, such as the stimuli received by a developing pollen grain from contacts with its neighbors (Gr. ἅπτειν, touch, and τυπόω, make an impression).

Harmomegathus, an organ or mechanism which accommodates a semirigid exine to changes in volume, *e.g.*, the three germinal furrows of the grains of *Solidago speciosa* (Plate XII, Fig. 4).

Harmomegathy, volume-change accommodation (Gr. ἁρμόζω, accommodate or adapt, and μέγαθος, size).

Heterotasithynic, due to unequal lateral stresses, *i.e.*, bilateral stresses, the forces which produce vertical cracking in a wall. This is due to a lateral shrinking at right angles to the vertical thrust of gravity. Such an effect is encountered in the oblong pollen grains of *Impatiens*, with four furrows, one at each corner of the grain and not arranged in the trischistioclasic system (Gr. ἕτερος, other, τάσις, a straining, and ἰθύνετο, in a straight line).

Intercolpar, between the furrows.

Intercolpar thickening, thickened areas in the exine, *e.g.*, in the grains of *Chorizanthe pungens* (Plate VIII, Fig. 3).

Interlacunar ridge, one separating lacunae from each other in lophate grains, *e.g.*, those of *Taraxacum officinale* (Plate XI, Fig. 2).

Interporal lacuna, a lacuna situated between, and bounded on one or two sides by abporal lacunae and wholly within one polar hemisphere in lophate grains, *e.g.*, those of *Scorzonera hispanica* (Plate XI, Fig. 5).

Isometric, equal space appropriation, used here in a sense slightly modified from the usual meaning, characterized by equal measure, to describe the arrangement of spines and, occasionally, of pores which tend to be arranged at equal distances in all directions from each other.

Isotasithynic, due to equal lateral stresses, the forces which produce trischistoclasis, tending to form hexagons on a plane surface or hexagons, pentagons, squares, and triangles on a spherical surface, *e.g.*, cracks in a plaster wall, caused by the shrinking of the plaster equally in all directions. Stands in contrast to heterotasithynic (Gr. ἴσος equal, τάσις, a straining, and ἰθύνετο, in a straight line).

Lacuna, a large pit or depressed space in the exine of lophate or reticulate grains. Lacunae are never germ pores or furrows but may be occupied by one or the other of them.

Limb, the visual boundary or edge of the apparent disk of a sphere. In pollen grains it is the same as the equator only when the grain is viewed with one of the poles exactly uppermost.

Lophate, with the outer surface thrown into ridges, anastomosing or free, as for example in the grains of *Pacourina edulis* (Plate XII, Fig. 1) or *Taraxacum officinale* (Gr. λόφος, a crest).

Lune, an area on the surface of a sphere bounded by arcs of two great circles passing through the poles.

Marginal ridge, the slightly projecting rim of the cap or disk, *e.g.*, in the grains of *Pinus* (Fig. 78).

Monocolpate, having a single germinal furrow or harmomegathus on one side of the grain. Example: *Ginkgo biloba* (Plate II, Fig. 6). If the grain is encircled by a single furrow, it is regarded as dicolpate or zonate.

Operculum, a thickening, of measurable bulk and clearly defined, of the pore membrane. Example: grass pollen (Plate V, Figs. 2, 3), *Castalia* (Plate VI, Fig. 1).

Paraporal lacuna, a lacuna adjoining on one side a poral lacuna and wholly within one hemisphere, *e.g.*, in the grains of *Taraxacum officinale* (Plate XI, Fig. 2).

Paraporal ridges, the ridges bounding the germinal furrows and extended in a meridional direction, *e.g.*, in the grains of *Tragopogon pratensis* (Plate XI, Fig. 4).

Polar hemisphere. See Equator and Pole.

Polar lacuna, the one or more lacunae at the pole or center of symmetry in lophate grains in which the pattern is radiosymmetrical or nearly so. When there are more than one at each pole they are polar lacunae, unless, by definition, they are interporal or abporal lacunae. Example: the grain of *Barnadesia trianae* (Plate XII, Fig. 6) and *Barnadesia venosa* (Plate XII, Fig. 7).

Pole, one of the extremities of the axis of symmetry of radiosymmetrical pollen grains. If there is more than one such axis of symmetry, the word applies only to the extremities of the axis which is directed toward the center of the tetrad or was so directed during the grain's formation. From these tetrad relations the two poles and two hemispheres may be designated as inner and outer or proximal and distal, though in mature pollen grains that are not shed in tetrads the two hemispheres are rarely distinguishable.

Poral lacuna, a lacuna enclosing a germ pore. It may be open through a cleft, as in the grain of *Taraxacum* (Plate XI, Fig. 2), or closed, as in those of *Scolymus* (Plate XI, Fig. 1).

Pore, see germ pore.

Pore membrane, a delicate membrane covering a germ pore. It may be flecked or bear an operculum.

Psilate, unadorned—without spines ridges or projections of any kind, other than germ pores (Gr. ψιλός, smooth). Examples: *Phleum pratense* (Plate V, Fig. 2) and *Rumex Acetosella* (Plate VIII, Fig. 1).

Psilolophate, lophate, with the ridges smooth on their crests.

Reticulate, with the surface thrown into anastomosing ridges enclosing lacunae, generally smaller than in lophate grains, *e.g.*, in the grains of *Ligustrum* (Plate X, Fig. 8).

Ridge, see Interlacunar ridge.

Subechinate, provided with short and sometimes rounded spines, *e.g.*, the grains of *Ambrosia elatior* (Plate XIII, Fig. 7).

Subechinolophate, lophate, with the crests bearing reduced spines, *e.g.*, the grains of *Stokesia laevis* (Plate XII, Fig. 2).

Sublophate, with the surface thrown into ridges which are imperfectly defined, *e.g.*, in the grains of *Catananche caerulea* (Plate XI, Fig. 3).

Tasicolpate, bearing furrows in some systematic arrangement, apparently resulting from stresses acting over the surface of the grain; distinct from the furrow of a monocolpate grain which arises from the collapse of the grain on its unsupported side (Gr. τάσις, straining).

Tasithynic, due to lateral stresses, the stresses that arise from shrinking, as in plaster, mud, or pollen-grain surfaces (Gr. τάσις, a straining, and ἰθύνετο, in a straight line).

Transverse furrow, a short, elliptical or elongate opening in the intine underlying the true furrow and with its long axis crossing that of the latter at right angles.

Tricolpate, possessing three meridionally arranged germinal furrows.

Trischistoclasic, triradiate cracking, the system in which the furrows of the pollen grains of the higher dicotyledons tend to form, a system similar to the cracking of drying mud or shrinking plaster, as if produced by equilateral stresses (τρίς, three; σκιστός, branching or parted; κλάσις, -εως, a breaking).

Ventral. The side of a grain turned outward in its tetrad. In monopored or monocolpate grains it is the side upon which the pore or furrow is borne. In other grains the dorsal and ventral sides are generally not distinguishable from each other after the grains have separated from their tetrads.

Vestigial spines, those of less prominence than of subechinate grains. Example: *Xanthium* (Plate XIV, Fig. 7).

Wing, the bladdery projection flanking or surrounding, frill-like, the germinal furrow of the grains of some Abietineae and Podocarpineae. It is generally greatly distended and attached by its ventral roots along the furrow rim and by its dorsal roots just ventrad of the marginal ridge.

Zonate, provided with one or more furrows, each encircling the grain as a lesser circle, wholly in one hemisphere and usually parallel to the equator.

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