

The Phylogenetic Value of Pollen-grain Characters.

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With Plates XX and XXI and two Figures in the Text.

INTRODUCTION.

THE extent to which pollen-grain characters are indicative of relationships among plants is of importance, since pollen-grains are single cells and spores. Spore characters in the lower groups of plants have been found to have high diagnostic value.

The characters of pollen-grains consist, for the most part, in the size and shape of the grain, the number and arrangement of the germinal apertures, and the sculpturings of the exine, such as spines and other protuberances, and ridges or crests, which in some groups are extremely well developed, assuming complicated patterns of diagnostic value and sometimes even specific in occurrence.

DISCUSSION OF THE LITERATURE.

Many investigations have been made of the structure of the walls of pollen-grains, and many species have been exhaustively studied. Notable among such studies are the works of Strasburger (37, 38, 39), Mangin (25), Biourge (4), Woycicki (45), and others. Only a few of these will be touched upon for the bearing that they have on the understanding of the sculpturing and various other characters of pollen-grains that are useful in showing phylogenetic relationships.

Mangin (25) shows that in the pollen-grain of *Spartium juncium* the exine consists of two layers. The inner is cutinized throughout its whole extent; it is thick and uniform except over the germinal apertures, of which there are three, where it is broken into platelets or granules. The outer layer of the exine overlies this as a thin membrane, yellowish in colour and of high refractive index, but difficult to see except in transverse or optical section. This membrane is continuous over the whole extent of the surface of the grain, and over the pores it is cutinized.

The intine is thick and in the region of the pores is much thicker than over the rest of the surface. It does not consist entirely of cellulose as formerly supposed. When stained for cellulose, only that portion occupying the inner surface takes the stain at all deeply, and the colour fades rapidly towards the exterior and is entirely absent in the part of the intine immediately adjacent to the exine. This space is occupied by pectic substance which can easily be distinguished from cellulose by staining with phenosafranin or methylene blue, dyes that do not stain cellulose. This pectic layer is thin over the greater part of the grain, and shades gradually into the cellulose layer below. In the regions of the pores, however, it is greatly thickened. When moistened this substance, unlike cellulose, has the faculty of taking up water, becoming gelatinous and swelling enormously, thus involving the destruction of the exine above and causing a bulging of the intine at the germinal aperture.

Mangin says that the pectic layer is regularly present and stains with great intensity; he has observed it in the grains of *Valeriana*, *Sedum*, *Geranium*, and many others. It is difficult to see in the grasses, but he maintains that its presence in their grains cannot be doubted. Referring to Strasburger's work (37), he says that it is astonishing that an anatomist of the ability of Strasburger has never succeeded in distinguishing a membrane 'the presence of which is constant in all the species which I have examined'.

The intine is not formed, Strasburger (37) says of the pollen grains of *Allium fistulosum*; instead the exine is cutinized throughout, except along the concave side of the grain, where it is greatly thickened. According to Mangin both intine and exine extend all round the grain; the exine is thick on the convex side and thin on the concave side, while with the intine the reverse is the case. Not only is it generally thickened on the concave side, but, being rich in pectic substance, it swells enormously upon being moistened and ruptures the overlying exine.

In the pollen of *Juniperus*, as Mangin points out, the grain is provided with a very thick intine surrounded by a very thin exine. When moistened the intine, consisting almost entirely of pectic substance, swells and completely throws off the exine.

Biourge (4) confirms and extends the work of Mangin, pointing out still further errors in the work of Strasburger. He states that the intine is always present and consists of two layers or sometimes three, the third being callose, but this latter substance is more often formed only around the pores.

According to the work of these investigators there seems little doubt that the function of the pectic substance, concentrated as it is at the pores, or, as in the grains of most Monocotyledons, along the fold, is to expand upon being moistened and rupture the exine, so preparing for the growth of

the pollen-tube. It is apparently the expansion and contraction of this material in the region of the pores that causes the opening and closing of the expansion folds so well described by Vesque (42). He assumes that the closing of the expansion folds over the germinal aperture is an adaptation for the prevention of the loss of water. In speaking of the pollen-grains that have well-developed pores he says: 'La structure du grain de pollen est telle que sa forme reste géométrique, quelle que soit la perte d'eau qu'il subit. Ce résultat est obtenu . . . par des fuseaux méridiens en nombre variable, sur lesquels la membrane reste molle et s'infléchit; le grain, d'abord sphérique, devient ellipsoïde, et au moment où les parties cutinisées se touchent par leurs bords la transpiration est considérablement réduite.' He believes that the number of pores or folds depends upon the size of the grain apart from its phylogenetic associations. He says, 'Lorsque le grain de pollen est plus volumineux, le nombre des plis ou des pores augmente. On conçoit que ce nombre, dépendant en partie du volume du grain, ne puisse pas être considéré comme un caractère d'une valeur taxonomique bien grande, ainsi j'ai trouvé des Hieraciums dont le pollen a trois pores, d'autres à quatre pores.' I believe that the following pages contain abundant evidence that Vesque's conclusions regarding the lack of taxonomic value attributable to these characters are not correct, and that in by far the majority of cases the number of pores or furrows of pollen grains is of the most profound phylogenetic significance. Thus in the Grass family the grains have only one¹ pore, regardless of their size, which varies enormously. In the pollen grains of the Carduales, the three folds, each enclosing a germinal aperture, constitute a character which is persistent throughout the entire order. It is true, however, that in many species of this order, as Vesque points out, some grains are found possessing four folds. Deviations from type of this kind are found in pollen-grains from practically all groups, and their explanation is of great interest and worthy of further study. Nevertheless they need not be considered here, belonging rather in the category of facts, such as the well-known occasional occurrence in *Trillium grandiflorum* of individuals with four petals despite the fact that this species is regularly trimerous—a family character.

There have been many attempts to make use of characters of pollen-grains in the classification of plants. Most of the earlier of these are only of historical interest and will not be discussed here. Possibly the first serious attempt to use pollen-grain characters that is worthy of note is that of Purkinje (31), who pictured the grains of many species and made some attempt to classify the forms observed. Most of his figures are lacking in detail and clearly indicate the inadequacy of the microscope of his day.

¹ Knowlton (23) states that in corn pollen 'when the microscope is properly focused, circular germ pores, one to three in number, can be seen'. My attempts to repeat these observations have always revealed only a single germ pore in corn pollen.

Nevertheless some of his observations are of interest. He noticed the many-pored character of *Mirabilis*, but did not observe the single germinal aperture of the grains of the grasses, though he figured seven different species. He noticed that 'grains of pollen united into a ball are common among the heaths', and he further remarks that in *Acacia* we find six, seven, eight, or even sixteen grains united into a spherical ball. Perhaps the most surprising of his observations, however, is the fact that he noticed the fundamental character of the pollen of the Cichoriaceae, for he says of *Leontodon Taraxacum*: 'Granum pollinis hirtum figura sua dodecaedron pentagonale referens'—a description which was not greatly improved for many years.

The next work of note is perhaps that of Fritzsche (13), who attempted a classification of plants solely on the morphology of their pollen-grains. He divides them into '(1) Pollen of a single grain, (2) pollen of more than one grain'. The former he divides into '(a) pollen with folds, (b) pollen without folds'. The former of these is further divided on the basis of the number of folds, thus building up an entirely artificial classification for purposes of identification. Possibly more important than this is his later work (14), in which he shows figures of the pollen-grains of many different species, generally lacking in detail it is true, but still showing considerable advance in this respect over the work of Purkinje.

The most noteworthy of the earlier workers, however, is von Mohl (28). He gives in accurate detail descriptions of many different kinds of pollen, frequently involving the examination and interpretation of facts that have eluded subsequent investigators. He clearly understood the importance of observing the grains in the moist condition, and states that many have folds extending from pole to pole; he says that when the grain is made wet it expands and the part which was inside the fold becomes the outside, 'mais la portion qui était cachée dans le pli offre toujours une structure différente du reste de la membrane, quoiqu'elle en soit une continuation immédiate'. He also worked out a very elaborate artificial classification of pollen-grains based on their structural characters. Though not entirely successful as a means of identification of pollen, it must be regarded as a valuable contribution to the understanding of relationships as exhibited by pollen-grains.

The work of Schacht (34) goes at great length into the development of pollen-grains and illustrates many different kinds, showing an appreciation of the value of their characters in distinguishing species.

Bennett (3), in his studies in pollination, examined a large number of different kinds of pollen, but his figures are mostly lacking in detail because his observations were confined to dry material. Grass pollen is shown without germinal apertures, and that of the dandelion is depicted without any hint of the strikingly beautiful pattern, which is distinctive not only for

this species but for nearly all the other species of Cichoriaceae, and which had already been noted by Purkinje and again by Fritzsche. Apparently he was entirely unfamiliar with the works of these authors and that of von Mohl, for he insists that the pollen must be examined 'dry and without any cover-glass'.

Smith (36) also makes the mistake of supposing that 'the true form of pollen can only be seen when it is perfectly fresh and dry at the time when it is naturally shed'. He further criticizes Bauer's drawings of pollen-grains which are stored in the British Museum, because 'they have been taken from grains which have been immersed in fluid and so cannot be implicitly depended upon'. Despite the fact that his observations were made on dry material, Smith figured the pollen-grains of some thirty species showing their characters tolerably well.

Pope (30), studying the plants of Colorado, gives a classification of the species found locally, similar to that used by von Mohl and other investigators of his time. Pope also insists that pollen should be observed in the dry form.

Well-preserved pollen-grains are of common occurrence in silts of interglacial and post-glacial origin. In order to facilitate their use in the identification and study of such silts Meinke (27) has illustrated the pollen-grains of 313 species of European bog plants and furnished an artificial, though rather comprehensive key to their identification.

The works of the above authors show very plainly that a classification of plants based on pollen-grain characters alone must be very artificial. The characters that are easily observable frequently have a tendency to bring together plants which are entirely unrelated, and to separate others that are rather closely related. This, of course, is to be expected, as it is true of any other such restricted group of plant characters. But it does not make these same characters any the less valuable when used within groups of reasonably close genetic relationship. Thus Gagnepain (15) shows that in the Geraniaceae certain characters of the pollen-grain are persistent throughout the family, while others are common only to certain genera; such characters as the number of folds and germinal apertures, and the character and arrangement of the papillae on the surface, are valuable in showing phylogenetic relationships.

Another piece of work that shows the indisputable value of pollen-grain characters when used within the proper phylogenetic limits is that of Köhler (24), who shows that in the Gentianaceae the distribution of pollen characters corresponds closely with the classification of Gilg in Engler and Prantl (17). The characters used by Köhler are the numbers of folds and germinal apertures, size and form of the grain, and the character of the raised reticulations on the exine. With these he is able to confirm Gilg's division of the family into tribes.

Urban (41) showed that in the Bignoniaceae the pollen affords valuable information regarding classification, so that he was able to construct a key for their identification based on pollen characters. He draws attention to the fact that in three genera the pollen-cells do not separate, but remain united in tetrads at maturity. The species in which the grains separate are classed according to the arrangement of the furrows, which vary in number from none to twelve. The very fine plate illustrating eighteen species makes his work all the more convincing.

METHODS.

In the preparation of pollen for these studies, the following technique was developed to display to the best advantage the superficial characters, taking no account of those of the underlying layers. The technique for distinguishing the latter has been described at great length by Strasburger, Mangin, and Biourge.

It is first necessary to secure a medium of refractive index resulting in the proper degree of differentiation and into which the pollen can be passed easily, quickly, and without distortion. The medium satisfying these requirements perhaps best was found to be the well-known alcohol-water-glycerine combination, but owing to the difficulty of rendering preparations made with it at all permanent, it was only used in cases where there was no necessity for preserving the specimens.

The next best medium for observing pollen-grains was Brandt's glycerine jelly. This medium is scarcely less useful than plain glycerine and there is no necessity for cementing the covers of specimens made with glycerine jelly. Accordingly it was used for most of this work.

Since the characters used in these studies are almost entirely concerned with the exine it was necessary to select a dye that stains only the exine, leaving the intine and cell contents as transparent as possible. The one that seemed best to satisfy these requirements was aqueous methyl blue. When properly used it gives brilliant and beautifully transparent preparations. It has one unfortunate objection, and that is lack of permanency. In most cases the stain entirely fades out in eight or nine months. No more permanent stain has been found, however, which at the same time possesses the selective qualities of methyl blue.

The procedure employed in the preparation of material is as follows. When naturally shed pollen is available, a small amount is taken on the tip of a scalpel, placed on a slide, moistened with a drop of 95 per cent. alcohol and stirred with a needle to make a paste, which rapidly dries, leaving the pollen lightly stuck to the slide. This is then washed by flowing alcohol slowly over it from one side and drawing it off with cotton from the other. When nearly dry a drop of weak solution of methyl blue is added and the

slide warmed to hasten staining. The amount of stain used should be so adjusted that when the correct intensity is obtained a little colour will still be left in the drop of solution. Further staining may then be prevented by drawing the excess liquid off with filter-paper or cotton.

An appropriate amount of glycerine jelly is melted on the tip of a scalpel and dropped on the pollen. The slide is then warmed in the flame and the pollen properly distributed with a needle under the dissecting microscope and covered with a very thin cover-glass. The gelatin is then allowed to set with the slide inverted in order that the grains may be close to the cover.

In this work nearly all the pollen was obtained from herbarium specimens, necessitating some modification of the method outlined above. As far as possible unopened anthers from mature or nearly mature flowers were used. They were removed with forceps with the aid of a hand-lens. With Composites it is usually sufficient to pull out with the forceps a few unopened florets from a head in which the first flowers have already opened, or, where the heads are small, it is sometimes necessary to remove one or two heads. As a rule, however, sufficient material can be secured without causing any appreciable damage to the specimen.

The anthers or florets are placed on the slide and moistened with 95 per cent. alcohol, followed by a large drop of distilled water. The slide is then heated until the water boils, when the anthers may be opened under a dissecting microscope and the pollen pressed out with needles. If the right amount of water has been added the floral fragments may be removed from the slide with the forceps, leaving most of the released pollen undisturbed. It may then be stained and passed into glycerine or glycerine jelly as desired.

It will readily be seen that the method outlined above presents the pollen in a moist and consequently expanded condition. It is frequently necessary, however, to compare it with dry or shrunken material for the purpose of determining the nature and behaviour of the expansion folds.

The best medium found for this purpose is aniline oil; it gives excellent differentiation on account of its refractive index of 1.58, which is even higher than that of glycerine jelly. Moreover it has the additional advantage of serving as a very good vehicle for several useful dyes. Of those tried the best was gentian violet.

In staining pollen unexpanded the perfectly dry grains are placed on a slide in a drop of aniline oil tinted moderately with gentian violet. The slide is then heated over a flame until the oil steams. Frequently it is necessary to continue heating it for several minutes to secure staining of sufficient intensity. If the mount is required to be permanent it is only necessary to dry off part of the oil and add a drop of balsam.

Preparations made in this fashion sometimes show some expansion;

the amount of this, if any, can generally be determined from comparisons with dry unstained pollen observed in air. In making observations in air only low powers of magnification can be used and but a few of the details seen. Enough, however, is revealed to permit a determination of the nature and extent of the changes induced by the aniline oil.

DESCRIPTION OF POLLEN-GRAINS FROM VARIOUS FAMILIES.

The characters of pollen-grains are as useful as the grosser anatomical characters in determining relationships and are distributed in much the same way. In the Gramineae this is well illustrated by the shape, size, and other characters of the pollen-grains. That of *Phleum pratense* (Pl. XX, Fig. 1) is spherical in shape, about 31.0μ in diameter, thin-walled, smooth, and free from adornments of any kind except the single germinal aperture. This consists of a small pit in the top of a slight elevation caused by an annular thickening in the intine surrounding it. The opening of the pit is always surmounted by a small operculum, suspended across it by a delicate membrane and so arranged that when the grain is moist the operculum bulges out beyond the opening, but when the grain is dry it is drawn tightly in, closing the opening. This type of germinal aperture is extremely characteristic of the Gramineae.

When pollen-grains dry they generally shrink. In *Phleum* this is clearly shown by the collapsed appearance of the grains, which contract without the formation of any well-defined folds (Pl. XX, Fig. 2), somewhat after the fashion of a partly deflated football. This mode of shrinking by simple collapse is constant throughout the grass family, but in other groups shrinking is often favoured by a highly specialized mechanism of contraction.

In my studies it has become necessary to provide a system of descriptive terms for pollen characters. Accordingly this type of grain, which is smooth, without spines, ridges, or adornments of any kind except the single germinal aperture, I have designated as *monopored psilate* (Gr. ψιλός, smooth).

This type of grain persists throughout the entire grass family; species from all of the tribes have been examined and no exceptions found. The only modifications that are encountered are in size and shape. In size the greatest range for different species thus far found is from about 20μ to about 80μ in diameter; while in shape some are ellipsoid and some are ovoid, but most are nearly or quite spherical, so that there really is very little variation throughout the entire family. This, together with the fact that this type of grain is not found outside of the Gramineae, makes it a very good family character.

A similar condition is found in the Chenopodiaceae; the pollen-grain

of *Sarcobatus vermiculatus* (Pl. XX, Fig. 3) is spherical, about $25\ \mu$ in diameter, thick-walled and nearly smooth, possessing only a slightly granular appearance, and without sculpturing or adornments other than the germinal apertures; in this species there are generally fourteen, though grains with sixteen are frequently found. They appear as small round pits sunken more or less deeply into the exine and each crossed at the bottom by a delicate membrane flecked with minute granules. These germinal apertures are equally spaced almost with mathematical precision over the surface of the grain. The appearance presented by grains of this type I have called *cribellate* (Lat. *cribellum*, a little sieve). It is characteristic of the family. For example, the grain of *Salsola pestifer* (Pl. XX, Fig. 4) is perfectly spherical and about the same size, viz. $25\ \mu$, but with the wall slightly more granular; the germinal apertures are much larger and about twice as numerous, and the membrane spanning them bears distinct granules at their centres. An examination of the different members of this family shows that the pollen-grains of all are *cribellate* and essentially the same. The size of the grain ranges in the different genera studied from $15\ \mu$ to $32\ \mu$, the surface texture from nearly smooth to distinctly granular, and the membranes crossing the germinal apertures may be nearly plain, slightly granular, or distinctly tuberculate. The number of germinal apertures in the different species varies from fourteen to about a hundred. The higher numbers are extremely difficult to count, and with material as prepared for these studies the counts of only the lower numbers could be at all relied upon. Nevertheless the counts of many different individuals covering a large number of species seem to indicate that the number of germinal apertures has a strong tendency to fall on some multiple of seven. There is no doubt that in some families the number and arrangement of the germinal apertures is definitely related to the contacts of the pollen-grains with each other during their development within the anther sac, which makes it seem possible that there is some relationship between these numbers and the orthic tetrakaidecahedron which, as shown by Kelvin and others, is the figure which divides space into equal volumes with minimal surface of contact, and, as shown by Lewis,¹ is actually approached in certain animal and plant tissues, for example, in adipose tissues and pith.

The underlying causes of this difference in the numbers of germinal apertures is a matter for further investigation. All that can be said about it at present is that the numbers are more or less constant for each species and, differing widely in the different species, may frequently be used as an aid in specific determinations.

If we now turn to the allied families we find that the *psilate cribellate* form of pollen-grain prevails in the Amaranthaceae without further modifi-

¹ See also Matzke (26) and Gross (20).

cations than those mentioned above. This is entirely in keeping with the close relationship existing between these two families.

This type of grain, with some modifications, is also found in some of the other families of the order. For example, in the Nyctaginaceae, the pollen of *Mirabilis Wrightiana* is cribellate but not psilate; instead, the surface is covered with very small bristle-like spines and is deeply corrugated, giving it a pebbled appearance. But the most striking feature of these grains is their relatively enormous size, 187 μ . The germinal apertures are also large and conspicuous and the membranes crossing them bulge prominently when moistened, and each, bearing at the top one or more pointed tubercles, presents the appearance of a spiked helmet.

The enormous size of the pollen-grain of *Mirabilis Wrightiana* is in itself a phylogenetic character, for it persists throughout the genus as far as observed, and characterizes, to a somewhat less extent, the rest of the family, but apparently does not extend beyond the limits of the Nyctaginaceae. Thus, *Hormidium alipes*, of the Nyctaginaceae, has a grain 147 μ in diameter, and from this size they range downwards to 80 μ in *Galinocarpus diffusus*, which is still well above the size of the average pollen-grain; so that it seems quite possible that the degree to which this character is developed is as fair an index of existing relationships as any single character could be. It is true that this size character, besides being common to all the Nyctaginaceae, is also found in other unrelated groups, viz. the Malvaceae, but here associated with a type of grain very different in other respects.

The Carduales or Compositae afford a great wealth of material for studies such as these, on account of the great diversity of form found in their pollen-grains. The grains may be covered with long sharp spines one-half the radius in length, or with short-rounded protuberances scarcely resembling spines, or even perfectly smooth. The surface may be thrown into an elaborate system of ridges, which may in turn be covered with long sharp spines, merely toothed or perfectly smooth. In spite of this diversity of form there are certain underlying characters that are nearly constant throughout the order.

It is not yet possible to select any one species or group of species of the Carduales as primitive. The various synantherologists have not come to any agreement and widely different opinions are expressed. Thus, Small (35) believes that the Senecioneae most nearly represent the starting-point in the evolution of the group, while perhaps the majority of authors agree with Bentham that the most primitive Compositae are to be found among the Heliantheae. A complete revision of the literature bearing on the origin and development of the Compositae is to be found in Small's papers ((5) also later years). Whatever the primitive Composite may be, the Heliantheae may be regarded as fairly generalized or central in position.

As an example of a generalized Composite pollen-grain, that of *Silphium perfoliatum* (Pl. XX, Fig. 5) will serve. It is spherical, about $27\ \mu$ in diameter, heavy-walled, showing a granular texture, and covered with long sharp spines evenly distributed. This form of grain I have called *echinale* (Gr. ἐχίνος, hedgehog). In keeping with the thickness and rigidity of their walls these grains have well-defined expansion folds.¹ In this case there are three, equally spaced and with their axes parallel. Encompassed by each is a germinal aperture which is bounded by a slight annular thickening in the intine through which a rounded elevation bulges when the grain is moistened. This character, viz. the possession of three longitudinal expansion folds, I have described as *tricolpate* (Gr. τρεῖς, τρις-, three, and κόλπος, fold), and this tricolpate character, with each furrow enclosing a germinal aperture, is perhaps the most persistent and characteristic feature of the pollen-grains of the Carduales.

In the Ambrosiaceae the *Silphium* type is easily recognized. For example, the pollen-grain of *Ambrosia elatior* (Pl. XX, Fig. 6) is tricolpate. In this species the three furrows are short and the germinal pores enclosed by them are small. The most striking difference, however, is in the spines, which here exist merely as rounded protuberances, a condition best described by the term *subechinate*.

This type of grain, tricolpate subechinate, is common to all the Ambrosiaceae except *Oxytenia* and *Chorisiva*. Nevertheless, it undergoes certain modifications. For example, in the grains of *Ambrosia* and *Franseria* the expansion folds are always short, as in those of *Ambrosia elatior*, while in the grains of *Cyclachaena* they are so long that they reach nearly from pole to pole. The spines, while generally very much less prominent than in the grains of most of the Carduaceae, show considerable variation. Thus in *Oxytenia*, though the spines are short, they are sharp and prominent, so that the grain is unquestionably echinate rather than subechinate. In *Chorisiva* the spines, though greatly reduced, are still sharp, so that it is questionable if this form can be considered subechinate. In the other genera of this family they grade down through *Iva*, *Franseria*, *Ambrosia*, and *Xanthium* (Pl. XX, Fig. 7). In some species of the latter only vestiges of them remain.

The reduction of spines in the Ambrosiaceae is perhaps to be regarded as an adaptation to the anemophilous habit of the group, for this type of grain is excellently adapted to wind dispersal. It is interesting, however, to note that the subechinate type of grain is not entirely confined to anemophilous groups. This type of grain is approached in many species of the Inuleae which are entomophilous. Here, however, the reduction of spines

¹ The expression 'expansion fold' in this order, carries the same significance as the recognized expression 'germinal furrow', and is here used synonymously with it. This is not always the case, for in some groups—for example, the Malpighiaceae—not all of the expansion folds enclose germinal pores, and therefore they cannot all be called germinal furrows.

is much less than in the Ambrosiaceae. In *Inula Helenium* (Pl. XX, Fig. 8), for example, though the spines are decidedly rounded on top they are still quite prominent. The Inuleae are strictly insect-pollinated, and the loss of spines has been arrested before it reached a stage so far advanced as that found in the Ambrosiaceae which are wind-pollinated.

In this connexion the Anthemideae are of interest, for the pollen in this tribe appears to possess a tendency towards the loss of spines. The majority of the species conform to the *Silphium* type, except that the spines are very much shorter, as, for example, in the pollen-grain of *Tanacetum* (Pl. XX, Fig. 9). I have already shown that in *Artemisia* (Pl. XX, Fig. 10) and its allies, which are wind-pollinated, the grains are entirely free from spines (44). All of these, except *Crossostephium* (Pl. XX, Fig. 11), have grains which are quite smooth and show no trace of spines. The pollen-grains of *Crossostephium*, however, show distributed over their surface a large number of small tubercles which suggest by their arrangement that they may be vestiges of spines. It seems highly probable that the loss of spines in the Anthemideae is in some way correlated with the anemophilous habit, though the exact connexion is obscure. It is a fairly general rule that anemophilous plants have pollen-grains either entirely without, or with a greatly reduced degree of sculpturing. The reciprocal of this statement, however, is not true; for example, many of the Mutisieae are without spines, yet are distinctly entomophilous.

In the Mutisieae all species that have been examined have pollen nearly or quite free from spines. Most of them—for example, *Chuquiragua* (Pl. XX, Fig. 12)—are tricolpate psilate as in *Artemisia*, from which they can only be distinguished by the character of the three folds, which are longer, and by a slight difference in the texture of the surface. Though the Mutisieae are without spines, the pollen-grains of one genus, viz. *Barnadesia* (Pl. XX, Fig. 13), is conspicuous by the possession of very prominent ridges involving the outer layer of the exine. These ridges anastomose, forming an elaborate pattern which differs in different species, but is constant for the individuals of any given species. This type of grain I have called *lophate* (Gr. λόφος, a crest or ridge), and since the ridges are without spines it is called *psilolophate*. In this case the pattern formed by these ridges is nearly perfectly radio-symmetrical about the poles of the grain. The three germinal apertures are evident on the equator, but their furrows are involved with the ridges. Breaks in the pattern on the two sides of the germinal apertures in line with the axis of the grain clearly indicate the presence of the expansion folds.

The psilolophate grain is characteristic of the genus *Barnadesia*, but has not been found elsewhere in the Mutisieae. Nineteen species covering ten genera were examined, but no hint of it was found elsewhere. In this tribe all that have been examined are tricolpate psilate, as in *Chuquiragua*, except *Barnadesia*.

Nevertheless, as is well known, most phylogenetic characters occur more than once independently, and to this rule the lophate character is no exception, for it occurs in two other groups of the Carduales, viz. the Cichoriaceae and Vernoniaeae. In the Cichoriaceae the pollen-grain of *Cichorium Intybus* (Pl. XX, Fig. 14) may be described as spherical, about $45\ \mu$ in diameter, three-pored, with the outer surface thrown into prominent ridges or crests which are heavily armed with conspicuous spines. According to my system of terms this type of grain is called *echinolophate*, and may be regarded as intermediate between the dahlia or echinate type, and the psilolophate type of *Barnadesia*, from which it differs principally in the possession of spines, the areas of confluence of the ridges also remaining essentially unmodified from the *Silphium* type. In these respects this form of grain may be regarded as somewhat more primitive than that of *Barnadesia*, and may give some hint of the path along which the psilolophate grains of *Barnadesia* evolved.

As Osborne (29) and others have pointed out, such characters, through ancestral affinity, are likely to arise again within the phylum. If they should arise at a much later date in the phylogenetic history of the group we may expect to find them in a comparatively less developed form; also their development may be arrested at any stage.

In our search for possible intermediate forms in the Cichoriaceae, the pollen-grains of twenty-six species, covering fifteen genera, were examined, but all were found to conform to this general plan—except that of *Catananche caerulea* (Pl. XX, Fig. 15). Of *Catananche caerulea* Decaisne (8) says: 'Although it is generally true that the pollen of the Cichoriaceae is polyhedral, this is not a fixed rule; as shown by M. Lessing after the figures of Schkuhr and the remarks of Robert Brown, the pollen is globular in several genera of the Cichoriaceae, e. g. *Catananche caerulea*.'¹ One can scarcely agree with Decaisne in calling the pollen-grains of any of the Cichoriaceae polyhedral, nor yet that of *Catananche* globular, but it is interesting to see that a difference between *Catananche* and the rest of its family had been noted at so early a date, and I am indebted to the above statement for directing my attention to this anomalous form.

In the grain of *Catananche* the three expansion folds flanked by their ridges are almost identical with those of the echinolophate grains of the Cichoriaceae, and, though the grain is nearly covered with spines, these are clumped into groups connected by poorly developed ridges forming only a weakly expressed pattern as compared with that of the fully developed echinolophate grain characteristic of most of the other Cichoriaceae. In these respects the grain of *Catananche* appears to be primitive, and can be regarded as between the echinate type of the Carduaceae and the echinolo-

¹ The other genera referred to by Decaisne, viz. *Robinsonia* and *Balbesia*, have since been shown to belong to the Carduaceae and not to the Cichoriaceae.

phate type of the Cichoriaceae. For this reason I call this form of grain *subechinolophate*. The importance of this type of grain is paramount because it so strongly suggests a possible step in the sequence of forms leading to the origin of the psilolophate grain found in *Barnadesia*.

The sequence of forms suggested, therefore, is as follows: simple echinate type of *Silphium*, subechinolophate type of *Catananche*, echinolophate type of *Cichorium*, and finally the psilolophate type seen in *Barnadesia*.

Like most phylogenetic characters these types occur independently in several other families and tribes of the Carduales. For example, in the Vernonieae all four forms are found, together with many intermediate. Furthermore, all except the psilolophate are found within the genus *Vernonia*. The grain of *Vernonia patens* (Pl. XXI, Fig. 28) is subechinolophate and strongly suggestive of that of *Catananche*, as described above. This form of grain is also observed in three other small genera of the Vernonieae, some of these tending somewhat more towards the simple echinate type, with the ridges less developed and the spines more evenly distributed over the surface. A further development of this form is found in the grain of *Vernonia noveboracensis* (Pl. XXI, Fig. 34), which has grains of the subechinolophate type with the surface more decidedly broken into ridges, but without any very definite pattern formation. This condition is found in *Lychnophora* and others, shading almost imperceptibly through a large number of forms and culminating in the full echinolophate type in *V. remotiflora* (Pl. XX, Fig. 20). In the grain of this species the pattern bears a strong general resemblance to that of *Cichorium Intybus* of the Cichoriaceae. It is nearly perfectly radiosymmetrical, and with the ridges long-spined and strikingly beautiful. With minor modifications this type is characteristic of about one-half of the North American species of *Vernonia* and of several other genera of the tribe.

In the genus *Struchium* (Pl. XX, Fig. 16) the pattern is essentially the same, but the spines are greatly reduced, and appear merely as teeth on the tops of the ridges. In *Stokesia* (Pl. XX, Fig. 17) the pattern is the same again, but the spines are still further reduced so that they are hardly visible. In *Pacourina* (Pl. XX, Fig. 18) they are entirely absent, leaving us with a psilolophate grain similar in this respect to that of *Barnadesia*.

The grain of *Pacourina* is similar to that of *Barnadesia* in this respect, but differs from it in others. In *Pacourina* the ridges mark off the surface of the grain into a large number of approximately equal hexagonal and pentagonal areas, while in *Barnadesia* the ridges, though similar in form, mark off the surface of the grain into a smaller number of areas of varying sizes and shapes. In size the grain of *Pacourina* is about $49\ \mu$ in diameter, while in *Barnadesia* it is about $70\ \mu$ in diameter. In fact, though the grains of *Pacourina* possess psilate ridges, as in *Barnadesia*, they bear a stronger general resemblance to those of their closer, though echinolophate, relatives

Stokesia and *Struchium*, differing from them mainly in the absence of spines from the ridges.

Various interpretations may be put upon these facts, but the one that seems most nearly correct is that *Barnadesia*, among the Mutisieae, acquired the psilolophate condition at a much earlier period than did *Pacourina* among the Vernonieae. In general, however, it may be said that in most families the pollen-grains bear a general similarity throughout, proportional in amount to the closeness of interrelationship within the group.

THE POLLEN-GRAIN OF *VERNONIA*.

Owing to their simplicity of character, it is generally only between the broader groups that differences in pollen-grain character are sufficiently marked to be practically usable. But simplicity of form is not a universal rule among pollen-grains. In some groups the pollen-grain pattern is sufficiently complex to permit so wide a play of expression that closely related species can easily be distinguished from each other. Such a group is the genus *Vernonia*.

This genus is admirably adapted to illustrate the range of characters possible in unicellular structures, because the pollen possesses an elaborate system of ridges complicated enough to permit a wide range of variation without transgressing the bounds of functional requirement, thus being of little or no selective significance; and because the genus contains a large number of species covering a wide and more or less continuous range of habitat. Fortunately the interrelationships of this large and difficult genus are exceptionally well understood through Gleason's painstaking and admirable researches. The genus comprises over five hundred species, ranging through the western hemisphere from Argentina to Manitoba (Gleason (18)). In his monograph of the North American Vernonieae Gleason recognizes one hundred and twenty-three species of *Vernonia*, and he says: 'Within this number a few stand conspicuously isolated from all the others, while many are so closely related in form and structure and so similar in distribution that they must be closely akin genetically. Over thirty species groups have been distinguished in this way.' The interrelationships of most of these groups, as characterized by Gleason, are shown in Table I, p. 924. The vertical line in the table represents the division between North and South America—a line drawn from Columbia to Trinidad—and south of which it is at present impossible to trace back the development of the different genetic lines towards their common origin, which is believed to be in South America.

The species that have reached North America are divided into four sections. The first three, *Stengelia*, *Tephrodes*, and *Stenocephalum*, are represented by but a single species each, while the balance of the hundred and twenty-three species are sufficiently closely related to be regarded as

a single section and are included in the fourth, *Lepidaploa*. The members of this section are, in turn, segregated into species groups, as indicated in the chart (Table I).

Besides these four sections there are several others which are exclusively South American; and still two others, *Leiboldea* and *Eremosis*, are recognized by some authors, but are given generic rank by Gleason and are not considered in this discussion of the genus *Vernonia*.

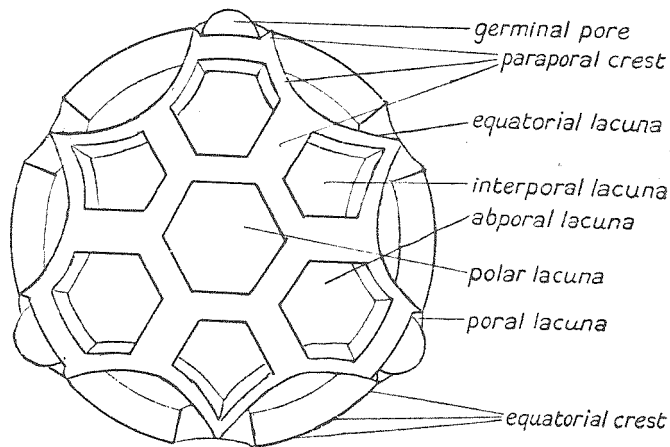
A study of the different forms of pattern exhibited by the grains of the North American sections, and of the species groups of *Lepidaploa*, shows that, in spite of the wide range of pollen-grain form, there is a certain fundamental similarity throughout—a type plan upon which the different forms are constructed. It is as if there were a certain set of form elements which are used in many different combinations, but with no very great modification of the elements themselves, some species showing all and others much fewer. Certain of these elements, or combinations of them, occur again and again, while others are found only once or twice.

Most of the form elements encountered in the genus are shown in the diagram (Text-fig. 1), which may be regarded as a generalized basic type of the *Vernonia* pollen-grain. For the construction of this diagram the pollen of *Vernonia jucunda* was used, because it displays most of the elements that are found in the group, and little modification was necessary to make it a generalized representation of the various forms of pattern found throughout the genus. It shows the grain in polar view—as seen when looking directly down upon one of the two centres of symmetry. When so regarded the three germinal pores appear equally spaced around the equator. In the moist condition these usually bulge and form a conspicuous and constant feature which can always be relied upon for purposes of orientation.

The surface is divided into a number of smooth areas or *lacunae*, separated from each other by a system of *interlacunar crests* or ridges, bearing on their tops a series of spines of different lengths and numbers in the different species. The lacunae are always smooth and conform to the curvature of the grain, while the ridges are always more or less undulating. This system of ridges and lacunae is nearly always radio-symmetrical and hexagonal in arrangement, conforming to the triangular system imposed upon it by the three germinal pores.

The diagram (Text-fig. 1) will serve to explain the general arrangement of the ridges and lacunae, and will serve to introduce terms useful in their description. The three pores are seen on the equator, and each is encompassed by its *poral lacuna*. In each hemisphere there is one lacuna at the pole; this *polar lacuna* is surrounded by six *circumpolar lacunae*, three of which, the *abporal lacunae*, are opposite the pores and three, the *interporal lacunae*, are alternate with the pores, thus giving two distinct sets

of circumpolar lacunae. In each polar hemisphere, flanking each of the pores, are two *paraporal lacunae*, each separated from its neighbour of the opposite hemisphere by the *equatorial crest*, a ridge which runs from pore to pore around the equator. It is broken, however, midway between the pores to include the three *equatorial lacunae* which are situated astride the equator, and consequently divided between the two hemispheres.



TEXT-FIG. 1. Diagram of the pollen-grain of *Vernonia jucunda*, a generalized form of the subechinolophate type, serving to define and illustrate terms used in the description of *Vernonia* pollen-grains. The figure represents the grain as viewed from one of the poles or centres of symmetry. When so viewed, on the equator are seen the three germinal apertures slightly bulging; the presence of these facilitates orientation. When the grain is so placed that they are all three in the same horizontal plane, the uppermost point of the sphere is regarded as the pole, and the grain is said to be in *polar view*; and the line joining the three germinal apertures is said to be the *equator*.

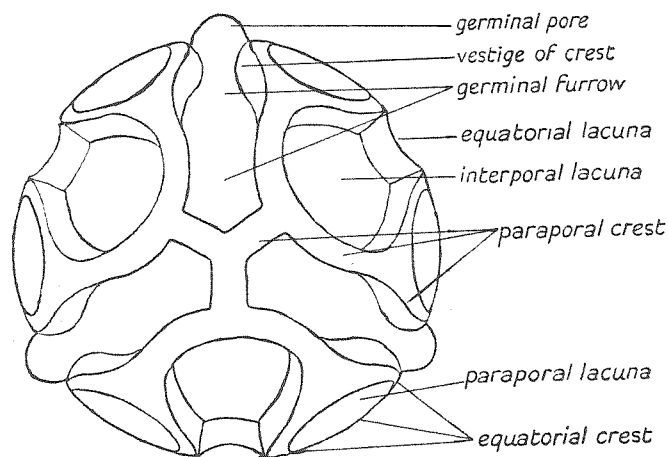
In the *Vernonia* pollen-grains the surface pattern consists of a more or less complicated system of ridges or crests enclosing depressions or lacunae. In the diagram one lacuna is represented at the pole; this is called the *polar lacuna*. Surrounding it are six *circumpolar lacunae*, so arranged that three of them, the *abporal lacunae*, are opposite the germinal apertures, and three, the *interporal lacunae*, are alternate with them. Each of the germinal pores is set in a lacuna, the *germinal or poral lacuna*. Flanking the poral lacunae, one on either side in each hemisphere, are the *paraporal lacunae*. Astride the equator and midway between the pores are the *equatorial lacunae*.

The lacunae are separated from each other by the *interlacunar crests*, some of which form prominent features that are more or less persistent in the various forms of grain found throughout the genus. For example, the *equatorial crest* reaches from pore to pore along the equator; in the diagram it is interrupted midway between the pores by the *equatorial lacunae*. The *paraporal crests* run a zigzag course from one polar lacuna to that of the opposite hemisphere, one on either side of the germinal lacuna. The significance of these crests will become apparent from Text-fig. 2.

The diagram (Text-fig. 2) shows a rather extreme but common modification of the *jucunda* type. Here the poral lacunae are joined with the abporal lacunae, thus producing the three long germinal furrows which run nearly from pole to pole, enclosing the germinal pores and bounded on either side by the *paraporal crests*. The interporal lacunae have become greatly enlarged at the expense of the paraporal lacunae, giving the pattern an entirely different appearance, though composed of essentially the same elements as those shown in the preceding figure. The diagram of this modification was drawn from the pollen of *Vernonia Wrightii*, and is characteristic of the group Sagraeanae to which *V. Wrightii* belongs. With certain further modifications, such as the presence of polar lacunae and

the absence of equatorial lacunae, it characterizes all of the leafy bracted Lepidaploa.

The relationships that the various modifications which this form undergoes bear to each other will become apparent if we consider them as displayed by the different groups (Table I). Omitting for the time being the first three sections, Stengelia, Tephrodes, and Stenocephalum, and turning our attention to the Lepidaploa, we see that in the grain of *V. gracilis* (Pl. XX, Fig. 19) the polar lacuna is present, but the poral and abporal lacunae are joined to form long and conspicuous germinal furrows. Vestiges of the interlacunar crests which in *V. jucunda* separate these two lacunae, are clearly seen. This type of long germinal furrow with vestiges



TEXT-FIG. 2. Diagram of the pollen-grain of *V. Wrightii*, a modification of the *jucunda* type. Most of the elements pointed out in that of *V. jucunda* (Text-fig. 1) can be seen. The polar lacuna is absent, and the poral and abporal lacunae are fused, forming the long germinal furrows reaching nearly from pole to pole and bounded on either side by the paraporal crests. Vestiges of the interporal crests which in the *jucunda* type separate the poral from the abporal lacunae can be seen. The equatorial, paraporal, and interporal lacunae are present, though somewhat modified in size and shape.

of the interlacunar crests more or less distinct, is the most constant feature of the entire section, Lepidaploa (Table II, p. 926). The grain of *V. gracilis* shows a further modification of the type, for here the equatorial lacunae are entirely absent, the equatorial crests continuing unbroken from pore to pore (Pl. XX, Fig. 19).

The Graciles, the group to which *V. gracilis* belongs, have no other North American representatives, but one South American representative, *V. Moritziana*, is known. Upon examination of the grains of this species it was found that they were precisely like those of *V. gracilis*, except in their somewhat smaller size and shorter spines (Table II); differences which when not extreme appear to have little significance.

The Argyropappae constitute a group of species mainly South American, but of which five have reached North America. Though their South American origin is obscure, there is ample reason for regarding them as fairly closely related to the Graciles. The pollen-grains of three species of

the *Argyropappae* have been examined, and it is found that two of them, those of *V. argyropappa* and *V. hirsutivena*, are virtually the same as those of the *Graciles*; the third, however, that of *V. remotiflora* (Pl. XX, Fig. 20), differs from them in the entire absence of the polar lacuna, in the considerably smaller size of the grain (Table II), and in the presence of spurs projecting from the paraporal crests into or, in some cases, nearly across the germinal furrows. The significance of these differences will become apparent as more forms are considered. It should be mentioned, however, that the affinities of this species to its group are stated by Gleason to be somewhat in doubt owing to the paucity of specimens; its inclusion in the North American flora is based upon a single specimen.

Lest too much importance be attached to the absence of the polar lacuna in this particular instance, it is well to mention that some individual variation is to be expected. For example, in one grain of *V. argyropappa* the polar lacuna was found to be entirely absent. In others it was pentagonal rather than hexagonal, owing to the confluence of two of the interlacunar crests in such a way that the number of radial crests abutting on the polar lacuna was reduced to five. Such irregularities, while common, are not typical and must be regarded as only deviations from the normal, which is essentially the same in the *Argyropappae* as in the *Graciles*. Nevertheless these abnormalities are interesting, giving an idea of the range of possible variation, and must be borne in mind in attempts to decide the importance of the various specific differences encountered.

The *Schiedeanae* (Table I) constitute another group, mainly South American, but with several representatives in Central America and southern Mexico (Gleason, 1923). This group as a whole is much less closely related to the *Graciles* than are the *Argyropappae*. The pollen-grains of the North American species *V. Schiedeana* and *V. vernicosa* have been examined. These are practically identical, both as to size and pattern (Pl. XX, Fig. 21), but differ from *V. argyropappa* and *V. hirsutivena* of the *Argyropappae* in the entire absence of polar lacunae, thus resembling *V. remotiflora*, which is in this respect exceptional among the *Argyropappae*.

The next seven species groups, *Arborescentes*, *Longifoliae*, *Bahamenses*, *Gnaphaliifoliae*, *Acuminatae*, *Racemosae*, and *Fruticosae*, are all rather closely related and derived from some South American species, the latter six probably directly or indirectly, through the *Arborescentes* (Table I). Quite in keeping with this, the forms of their pollen-grains are found to be all strikingly similar (Table II). All are echinolphate with the pattern sharply defined (Pl. XX, Figs. 22, 23), except *V. reducta* (Pl. XX, Fig. 24), in which the pattern shows some tendency towards the subechinolphate condition. In all the polar lacunae are present and more or less conspicuous, except in *V. longifolia* and *V. Shaferi* of the group *Longifoliae*, and possibly in *V. corallophila*, which shows extraordinary individual

variation such as the confluences of various lacunae through the absence of some of the interlacunar crests. In this form it is difficult to know what should be considered the normal condition.

The equatorial lacuna is entirely absent from the grains of all the members of these seven groups, except occasionally in those of *V. acuminata* of the last group; some of the grains of this species show the smallest visible trace of it, at the confluence of the four crests which separate the four adjoining paraporal lacunae from each other.

It is interesting that this trace of an equatorial lacuna should be found in the grains of this species belonging to the Acuminatae, since another species of this group, *V. reducta*, shows a decided tendency towards the subechinolophate condition, thus suggesting within this group a divergence from, or a convergence towards, the more highly developed echinolophate grain through *V. acuminata* on the one hand, or the much less highly developed subechinolophate form through *V. reducta* on the other hand.

Barring these differences seen in the four species, *V. longifolia* and *V. Shaferi* of the Longifoliae, and *V. acuminata* and *V. reducta* of the Acuminatae, the grains of all seven groups show a remarkable similarity of pattern (Pl. XX, Figs. 22-4).

The next group, the Sagraeanae (Table I), represents a separate stock. The pollen of the two North American species, *V. Wrightii* and *V. purpurata*, has been examined and shows no visible differences between these two species (Pl. XX, Fig. 25). Their grains are characterized by the entire absence of polar lacunae, and by well-developed and conspicuous equatorial lacunae. The interporal lacunae are exceptionally large and conspicuous, as also are the germinal furrows. Accompanying these and the development of the large equatorial lacunae has gone a considerable reduction in the paraporal lacunae, giving the grain an altogether strikingly different appearance from those of the other groups.

Gleason states, 'Eckmann would relate the group to the Bolivian *V. robusta*, Rusby . . .; also the Bolivian *V. obtusata*, Less.' An examination of the pollen of these two exotic species reveals the fact that the pattern of both is virtually identical with that of *V. Wrightii*; that of *V. obtusata* exhibits no observable differences from the North American species, while that of *V. robusta* differs only in size, measuring between three and four times the volume of the other members of the group (Table II). The plant *V. robusta*, as its name implies, is characterized by its large size and heavy construction, but otherwise exhibits no very striking differences in general aspect from *V. obtusata*, thus calling to mind such diploid forms as *Oenothera gigas*, in which Gates (16) has shown that the pollen-grains are 1.5 times as large as in the parent *Oenothera Lamarkiana*; or perhaps even more strikingly the polyploid species and varieties of wheat studied by Sax (32 and 33), who says: 'The size of

the pollen-grain is closely correlated with the chromosome number. . . The pollen-grain size may be used as an approximate measure of chromosome number in wheat species and hybrid segregates.' If this is likewise true of *Vernonia robusta*, according to the well-known relation between the size of the cell and the number of its chromosomes, *V. robusta* will be found to be diploid or tetraploid.

The next species, *V. brachiata*, is regarded as belonging to a separate evolutionary line, not related to any North American species group, but is included in the leafy-bracted Lepidaploa on account of its possession of leafy bracts, and is associated with *V. scorpioides* on account of the character of its inflorescence. Its pollen-grain, however, is in several ways quite different from any yet encountered in the Lepidaploa. Three distinct forms occur; the most usual is that shown (Pl. XX, Fig. 26). In this the germinal aperture is set in a closed lacuna resulting in the entire absence of germinal furrows, but perhaps more conspicuous than this is the pentagonal arrangement of the pattern, which, associated with the three-pored grain, gives it a remarkably unsymmetrical appearance. Another form of grain somewhat less frequent is similar to this, but hexagonal, looking not unlike that of *V. jucunda*. A third form of grain is pentagonal again, but with greatly simplified pattern and fewer lacunae, and is difficult to relate to the type. All three forms lack the germinal furrows.

In view of the fact that in the forms of grains of all the other species of the Lepidaploa the long germinal furrows are the most constant and outstanding feature, their absence from those of *V. brachiata* should be expected to be due to a rather fundamental difference in genetical constitution, and we believe is sufficient to indicate that this species should not be included in the Lepidaploa. Of similar appearance is the grain of *V. cinerea* of the section Tephrodes, with which it seems possible *V. brachiata* could be associated, or if not, possibly with some of the other South American sections which are not otherwise represented in North America.

All the species dealt with so far in this discussion are characterized by leafy bracts, and are sharply distinguished upon this basis from those that follow. In the pollen-grains of the leafy-bracted Vernonias two features are outstanding. They are all echinolophate, with ridges well developed and sharply defined, except as noted in *V. reducta*. This character marks them off from those that follow just as sharply as do the leafy bracts (Table II). A second feature in the pollen-grain is the presence of the long germinal furrow, which is found throughout the whole section Lepidaploa, except *V. brachiata*.

The next species, *V. scorpioides* (Pl. XXI, Fig. 27), is likewise regarded as belonging to a separate evolutionary line. The form of its pollen-grain introduces an entirely different type of sculpturing. It is

spiny all over, and the only ridges that can be distinguished at all clearly are the heavy crests that bound the germinal furrows, the paraporal crests. This form is accordingly subechinolophate of the lowest order, being but a slight departure from the simple echinate type seen in *Silphium* (Pl. XX, Fig. 5). One is justified in including it among the subechinolophate forms, for, besides possessing the paraporal crests, the surface is somewhat broken, showing that it has a tendency to form the ridges which are characteristic of the Vernoniaeae.

The group Stellares (Table I), as defined by Gleason, includes seven species, mostly South American in range; only one, *V. morelana*, does not grow south of Mexico. As a group they represent a separate evolutionary series of unknown origin in South America.

The pollen-grains (Pl. XXI, Fig. 28) of five of them, *V. stellaris*, *V. patens*, *V. salamanana*, *V. Aschenborniana*, and *V. morelana*, are subechinolophate, tending strongly towards simple echinate, showing only a slightly greater tendency to develop ridges and lacunae than the pollen-grains of *V. scorpioides*, and on this basis might well be regarded as having a common origin with *V. scorpioides*.

The pollen-grains of the two remaining species of the Stellares *V. canescens* (Pl. XXI, Fig. 29) and *V. mollis* (Pl. XXI, Fig. 30), are entirely different, showing no relationship to the other five members of the group. Both are fully echinolophate, with well-developed ridges sharply differentiated from the lacunae, exactly as in the leafy-bracted *Lepidaploa*. Furthermore, the pollen-grains of these two species show only a doubtful resemblance to each other, for that of *V. canescens* has a very prominent polar lacuna, and its thin delicate ridges are abundantly provided with sharp spines, while that of *V. mollis* only occasionally shows a rather indefinite polar lacuna, more frequently none at all, and the crests bear relatively few small tooth-like spines. The grain of *V. mollis* is characterized by considerable irregularity; any one or more of the interlacunar crests may be absent, the resulting confluence of the lacunae producing a lack of symmetry. The absence of a separate polar lacuna is probably to be explained in this way (Pl. XXI, Fig. 30), for it is apparently united with one of the germinal furrows. Thus it seems that these two species are not very closely related to each other, and both are strikingly dissimilar to the other members of the Stellares and, in fact, to all the bractless *Lepidaploa*.

Of these two species Gleason says in his discussion of the group, 'The Columbian species *V. canescens* and *V. mollis* retain the primitive character of acuminate involucreal scales; . . . the former also extends north into Mexico, and the latter is doubtfully admitted into the North American Flora'. This shows that there is at least one anatomical character which differentiates these two species from the rest of the Stellares. In spite of

the absence of the leafy bracts, the character upon which they are placed in the bractless subsection, these plants might conceivably belong to genetic lines more closely related to the leafy-bracted subsection, the absence of leafy bracts being then a parallelism. Of course it might with equal justice be claimed that the development of the echinolophate pollen-grain is an example of parallelism rather than the absence of leafy bracts.

There is insufficient evidence at hand, however, to settle this question, and I think it best to dismiss it for the present with the statement that the pollen-grains of these two species bear evidence that they are not related to the Stellares, evidence which is supported by the character of the involucre; and the evidence of the pollen-grain suggests that there is no very close relationship between these two species, and that their affinities should be looked for among the leafy-bracted *Lepidaploa*, evidence which must be supported by further studies.

Arising from the Stellares (Table I) is the Cuban group *Menthaefoliae*. The pollen of only one species, *V. menthaefolia*, has been examined. It is subechinolophate almost as in the Stellares, differing from *V. patens* only in the slightly better development of the paraporal crests, and in the appearance of an indeterminant equatorial ridge.

Arising also from the Stellares is the Mexican group *Umbelliformes*, and from these arise the *Texanae*, which in turn give rise to all the more northern groups (Table I), *Texanae*, *Fasciculatae*, *Angustifoliae*, *Glaucæ*, *Altissimæ*, and *Noveboracenses*.

No pollen of the *Umbelliformes* has been examined, but that of *V. texana* (Pl. XXI, Fig. 31) of the group *Texanae*, which is derived from the *Umbelliformes*, is found to be subechinolophate and strikingly similar to that of the Stellares, though somewhat less so than that of *V. menthaefolia*, for it shows a stronger tendency to develop a pattern. The paraporal ridges are prominent and more sharply defined than in the grains of *V. Scorpioides* and *V. patens*, and some of them possess a fairly well defined equatorial crest, thus showing a closer approach to the development of the echinolophate pattern.

The *Fasciculatae*, which are derived from the *Texanae*, likewise have the subechinolophate form of grain with the pattern still more highly developed. The grain of *V. corymbosa* (Pl. XXI, Fig. 32), for example, has the germinal furrows well developed and the paraporal lacunæ faintly outlined though not clearly separated from the interporeal lacunæ, thus showing a somewhat further advance towards the echinolophate condition.

The *Angustifoliae*, which have likewise arisen from the *Texanae*, have grains essentially the same in form as the *Fasciculatae*, showing about the same advance over the *Scorpioides* type. In the grains of *V. gigantea*, for example, the equatorial crest is fairly well developed. The interporeal and paraporal lacunæ appear to be confluent and are not well defined.

The *Altissimae* are derived from the *Angustifoliae*. Three species of these, *V. altissima*, *V. flaccidifolia*, and *V. ovalifolia*, have been examined; they are all essentially the same and show a slight though definite advance over the *Angustifoliae* in their well-marked equatorial crests separating the paraporal lacunae of the two hemispheres (Pl. XXI, Fig. 33).

The *Glaucæ*, according to Gleason, have been derived from the *Angustifoliae* (Table I); in keeping with this the pattern is found to be essentially the same, showing no further advance.

The *Noveboracenses* arose from the *Angustifoliae* probably at a somewhat later date than did the *Glaucæ* and *Altissimae*. In this group are only two species in North America, *V. noveboracensis* and *V. Harperi*. The pollen-grains of both (Pl. XXI, Fig. 34) are essentially the same and show still farther advance over the *Stellares* towards the echinolophate type. Here the circumpolar lacunae are well developed. Those adjacent to the pores—the abporal lacunae—are confluent with the poral lacunae forming the germinal furrows. The equatorial crests are well developed and abut upon the paraporal crests, thus definitely separating the paraporal lacunae of each hemisphere from each other.

We have seen that from a consideration of the pollen-grains alone, the species of the *Lepidaploa* fall naturally into two groups, viz. those with echinolophate grains and those with subechinolophate grains; and, with only two exceptions, these correspond to the leafy-bracted *Lepidaploa* and the bractless *Lepidaploa*. The question now arises, which of these types of pollen should be considered primitive and which advanced? Undoubtedly the leafy bracts are more primitive than the suppressed bracts, but it does not necessarily follow on that account that the forms of pollen-grain in the former group are more primitive than those of the latter. In fact, the evidence seems strongly to favour the opposite view. In the subechinolophate grained group or bractless *Lepidaploa*, *V. scorpioides* and the *Stellares* are certainly more primitive than the *Noveboracenses*, the *Fasciculatae*, and the *Glaucæ*. In fact, Gleason has shown that *V. scorpioides* and the *Stellares* on the one hand, and the *Noveboracenses* and the *Glaucæ* on the other, represent the most primitive and the most advanced extremes of the evolutionary sequence of the subsection, with such groups as the *Menthaefoliae* and the *Texanae* somewhat intermediate in position.

In keeping with this the pollen-grain of *V. scorpioides* is almost completely echinate, as in the generalized type of the *Carduaceae*, showing only the slightest tendency to develop the pattern characteristic of most of the *Vernonias*; the *Stellares* are similar, but show a more definite tendency towards the development of the pattern, while the *Noveboracenses* and the *Glaucæ* have a still better developed pattern, though not quite complete enough to be regarded as fully echinolophate.

From this there seems little doubt that the trend of evolution is from

the generalized echinate type, only slightly modified in *V. scorpioides* towards the echinolophate type, which is closely approached though not quite attained in the Noveboracenses. In the leafy-bracted or echinolophate grained subsection the course of evolution of the pollen-grain is much more obscure. It appears that in this group its development has proceeded much farther than in the bractless or subechinolophate grained group, and since these plants are more primitive otherwise, they must represent an entirely separate evolutionary stock. It seems quite possible that the leafy-bracted *Lepidaploa* are derived from an ancestor which had passed through the subechinolophate stage, long ago attaining the echinolophate condition; from such an ancestor the various groups diverge, accounting for the different forms of pattern found in the species groups of this subsection, which therefore mostly represent the ends of divergent lines of evolution.

It will be noticed that in the above discussion the sections *Stengelia*, *Tephrodes*, and *Stenocephalum* have been omitted. This is because little can be said about them at the present time; however, the little that is known regarding their pollen-grains has an important bearing on the interrelationships of the *Lepidaploa* just discussed. These sections are represented by only one species each in North America, and little is known about their South American representatives. In *Stengelia* the pollen of *V. anthelmintica* (Pl. XXI, Fig. 35) has been examined. The grain is completely echinolophate of a very high order of development. The germinal furrows are well formed. In this respect it resembles the *Lepidaploa*, but differs from them in the possession of paired equatorial lacunae, one on either side of the equatorial crest, a feature not found in any of the *Lepidaploa*.

In the *Tephrodes* the grains of one species, *V. cinerea* (Pl. XXI, Fig. 36), have been observed. Their form is completely echinolophate, as in the grains of the leafy-bracted subsection of the *Lepidaploa*, but, unlike them, the germinal furrow is not formed; each pore is set in its poral lacuna, which completely surrounds it. This feature is not found among the grains of the *Lepidaploa* except in the single species *V. brachiata* (Pl. XX, Fig. 26), which was not assigned to any species group on account of its doubtful affinities. The still more remarkable thing about the pattern of *V. cinerea* is that while the grain possesses the usual three pores, the pattern is frequently pentagonal, thus giving rise to a striking lack of symmetry, a condition likewise not found among the *Lepidaploa* except in *V. brachiata*.

Of the section *Stenocephalum* the pollen-grains of two species have been observed, namely, that of the North American *V. jucunda* (Pl. XXI, Fig. 37) and the Bolivian *V. apiculata*. Both of these grains are echinolophate with the pattern well defined, but here the resemblance to the echinolophate *Lepidaploa* ends. The pattern of the *V. jucunda* grain has already been described; it was chosen as the starting-point in the discus-

sion of the elements of the patterns, selected for this purpose on account of its highly regular and symmetrical form. The pores are each included in their poral lacunae with no trace of a germinal furrow and the equatorial lacunae are well developed. The other species of this section, *V. apiculata*, bears but little resemblance to *V. jucunda*. It appears to be characterized by a lack of constancy and great irregularity of pattern. In at least some of the grains two of the germinal apertures have well-developed furrows, while the third is enclosed in its lacuna and separated from the adjoining abporal lacuna by a well-developed interlacunar crest, so that one-third of the grain is like that of *V. jucunda*, while the other two-thirds is like that of the echinolophate *Lepidaploa*.

It is quite impossible to put any interpretation on these facts without a greater amount of material from these three sections. They are mentioned here, however, because they serve to show that the wide gaps in genetic constitution, between the sections, are fully expressed in the forms of their pollen-grains. Thus we see that the paired equatorial lacunae of the grains of *V. anthelmintica*, the only representative of the *Stengelia* examined, are not found in the other sections; the asymmetrical pattern together with the closed poral lacunae, seen in the grain of *V. cinerea* of the section *Tephrodes*, is a combination not found elsewhere except in the grain of *V. brachiata*, a species of doubtful affinities; the geometrically hexagonal pattern with closed germinal lacunae and consequent lack of germinal furrows, seen in the grain of *V. jucunda* of the section *Stenocephalum*, is not found elsewhere. It is not possible to say how constant these characters within these different sections are from the material at hand, but they serve to show that each of the sections displays characters not found in the others, nor in the *Lepidaploa*.

GENERAL DISCUSSION:

In order to distinguish any one plant or group of plants from any other it is nearly always necessary to have recourse to several, often many, characters; rarely will a single character serve. For example, in the Gramineae the two-ranked arrangement of the leaves is a good phylogenetic character, persisting, with certain modifications, throughout the entire family; but it is also frequently found elsewhere—for example, in the Iridaceae and sometimes in the Liliaceae—and is absent from the more nearly related Cyperaceae.

Another phylogenetic character of the Gramineae is the ensheathing base of the leaf completely enclosing the internode of the stem for a considerable distance above the node where the leaf takes its origin. This character, like that of the arrangement of the leaves, is present with modifi-

cations throughout the entire family, and in this case it is also found in the allied Cyperaceae.

One of the modifications of the sheath affords still another example of such characters. In most grasses the sheath is open along the side opposite the blade or the edges merely overlap. In some grasses, however, the edges are completely fused, forming a tube. This character is common to most species of *Bromus* and to some of the species of the allied genera *Festuca* and *Panicularia* of the same tribe Festuceae. It is also found in the genus *Danthonia* in the tribe Aveneae and much less closely related to *Bromus* than many other genera that do not possess it.

Still another example of such phylogenetic characters is found in the awns which, generally speaking, are characteristic of the grasses, though in many species much reduced or entirely absent. In the genus *Stipa* the awn reaches its most extreme development. For example, in *Stipa spartea* it is about eight inches long, stout, and bent at right angles above the middle, while below the middle it is twisted into a tight spiral. The remarkable thing about this awn is the sensitivity of the spiral to changes in moisture, resulting in movements which obviously serve a useful purpose in planting the seed. This character of the twisted awn is present in all species of *Stipa*. It is likewise present in the closely related genus *Aristida*; it is also found in some of the species of the much more distantly related genera *Sorghastrum*, *Avena*, and *Danthonia*.

Many more examples might be cited, but these will suffice to illustrate the general facts as to the incidence of phylogenetic characters. They usually appear in a more or less wide range of species, occur more than once, and have a strong tendency to recur several times within a phylum.

The relation of cell characters to those of multicellular organs and the degree to which they are coextensive in phylogenetic distribution indicate that they are undoubtedly as truly the result of past history as are the grosser anatomical characters of the plant body; it is at once obvious that pollen-grains of remarkable similarity are found in widely different groups. That convergence and parallelism in structure are to be encountered here as among all plant structures is of course to be expected; among pollen-grains it probably occurs with no greater frequency than in other categories. In just how far, however, pollen-grain characters are to be trusted in indicating relationships will only be settled by further extensive studies.

The bulk of diagnostic characters used in the classification of higher plants are features of many celled organs; still, characters of single cells—whether of spores or tissue cells—have long been known to be of diagnostic value; this, as noted, is obvious from their use in the liverworts, fungi, and algae, not to mention protophytes.

An interesting example of their use in classification is found in the

Hepaticae. The spores of these plants are frequently covered with ridges, spines, and various sculpturings which have long been known to have diagnostic value. For example, in the Ricciaceae, as stated by Howe (21), the spores are tetrahedral and 'the surface marked with free or most frequently mesh-forming ridges', and the various species can be distinguished by the manner in which these ridges anastomose.

Among the Fungi, particularly the Ascomycetes, the character of the sculpturing on the spores is extensively used in generic and specific determinations. In *Peziza aurantia*, Mull., the ridges enclosing hexagonal lacunae closely resemble those of the pollen of some species of Vernoniae. In *Ganoderma* among the Basidiomycetes, Colman (6) describes the formation of spines in the endospore which grow into the epispore reaching almost to, or even sometimes through, the epispore surface, and makes this the basis for a rearrangement of species from several genera.

It should be noticed that since pollen-grains are microspores that have begun their germination and possess at least two nuclei at the time of shedding, they might be regarded as plantlets. Nevertheless, the external characters of the grains are all determined during the formation of the pollen-cells as microspores prior to the division of the nucleus that denotes germination and the development of the gametophyte. It is only with the characters of the microspores as such that this discussion deals, and they are undoubted cell characters.

Tissue cells frequently exhibit characters which are only broadly or not at all phylogenetically distinctive, reflecting more their functional requirements and thus forming the basis for such conceptions of physiological plant anatomy as Haberlandt emphasized. Nevertheless, characters of tissue cells are frequently highly diagnostic, and are used in the identification of powdered drugs, commercial fibres, &c. The thickenings on the walls of the cells of the endothecium of the anthers of many plants, as shown by Purkinje (31), exhibit a wide range of specific variation. These thickenings are definitely related to the opening of the anther sacs which it is their function to accomplish at anthesis. The particular moment at which this must occur depends upon many different external factors associated with the mode of pollination or the particular species of insect concerned in pollination; the high degree of specificity in the function of these cell-walls is correlated with a corresponding specificity in structure.

The characters of pollen-grains probably possess a similar functional specificity, though it is not so accessible to analysis. In the fulfilment of their functional requirements—viz. that of carrying the male gametes, often considerable distances, to the female gametes—they are exposed to a highly diversified and varying range of environmental stimuli, and with this has come their high structural specialization.

It has been shown by Amelung (1) and others that cells from

equivalent tissues show high constancy in size, whether the organ of which they form a part is large or small. This holds not only for individual plants and plants of the same species, but in some degree for plants of related species or even genera. It has been shown that cell size is much less influenced by temporary external conditions than is the size of multicellular organs. For example, poverty of nutrition will greatly reduce the size of a leaf, while an overabundance will correspondingly increase its size; yet in either case the size of the cells of the leaf is not noticeably affected. In these size relations pollen-grains are not different from the individual cells of tissues.

Doubt has arisen among some investigators as to whether the sculpturings on pollen-grains should be regarded as really the product of the pollen protoplast, for the sculpturings frequently appear to be formed by the tapetum. It is true that long before the pattern on the surface is complete the exine upon which it is formed is cut off from direct contact with the pollen protoplast by the formation of the intine, so that the surface adornments must accomplish most of their growth without any direct influence from the pollen protoplast, and during this time they are, at first, enveloped by the special mother-cell membranes, but later in direct contact with the tapetum, making them appear to be the product of the mother-cell membrane and the tapetal cells.

Fitting (12) states that in *Isoetes* and *Selaginella* the perispore or outer layer, which carries the sculpturing, develops without contact with the pollen protoplast. He says: 'Das stark verkieselte Perispor entsteht erst nach dem Exospor, wahrscheinlich auf Kosten der Specialmutterzellmembranen.'

Fitting's observations on *Selaginella* have been confirmed by Campbell (5), who says: 'During its early stages the growth of the massive and complex membrane is almost entirely due to the activity of the tapetal cells of the sporangium . . . the extremely small amount of protoplasm in the young spore could not form the massive wall developed at a very early period.' He further strengthens this view by showing that, owing to the very rapid growth of the disproportionately large wall, a cavity is developed between it and the cell protoplast, separating them from contact with each other throughout most of their circumference.

Possibly even more convincing are Tischler's studies (40) of the pollen-grains of sterile hybrids. He shows that in *Mirabilis Jalapa* × *tubiflora*, a sterile form, the pollen-grain protoplast aborts and shrinks away from the wall, which nevertheless continues to grow and develop its characteristic pattern on the exine. He says: 'Das bedeutet aber, dass die Exinen, also die Zellwände, ohne Beteiligung des eignen Plasmakörpers gewachsen sind, denn ein Stehnbleiben auf der ursprünglichen Grösse war nie oder doch nur selten zu bemerken.'

The work of these three authors shows beyond all reasonable doubt that the sculpturing on spores or pollen-grains, in the species examined at least, can develop without being in continuous contact with the spore protoplast.

A somewhat different interpretation of the observed facts is given by other investigators. For example, Biourge (4) says the role of the tapetum is rather to nourish the tetrads by osmosis than to form the ornaments in relief on the exine of the microspore; these are already present at the tetrad stage.

A confirmation of this statement of Biourge is found in Beer's (2) studies of *Ipomoea*, in which he shows that the pollen protoplast initiates the pattern of the exine, though the early development of the intine between the exine and the sporoplast soon cuts it off from all further influence in the development of the pattern. He says: 'The young pollen-grains of *Ipomoea* surround themselves with a wall of their own—the exine. This is deposited by the pollen protoplast . . . upon the inner face of the callose-pectose wall that surrounds it . . . there can be no doubt that it is a new membrane and not one derived from the transformation of the innermost lamellae of the special wall.' This layer then becomes differentiated into a clear outer and a more densely staining inner part, and it is on its inner face that the rudiments of the spines appear. They grow outwards and through the clear layer, penetrating it at about the same time that the special mother-cell walls break down and the formation of the intine cuts off the exine from any further contact with the pollen-cell protoplast.

The spines thus complete their growth in contact with the tapetum and apparently isolated from the cell protoplast by the intine. Nevertheless, it should be borne in mind that, according to Cranmer's (7) conception of the cell-wall as a colloidal network in the meshes of which are extensions of the plasma membrane, there might still exist the mechanism for the direct control of the development of the surface sculpturings by the pollen protoplast.

It is interesting to compare the method of wall development thus described with that of the spores of *Ganoderma* described above. Judging from the descriptions of the authors, the processes are apparently analogous, the main difference being that in *Ganoderma* the spines generally do not quite penetrate the overlying layer, so that their origin and development are undoubtedly sporoplastic, while in *Ipomoea* they early penetrate the exine, so that the greater portion of their growth is accomplished in contact with the tapetum. Nevertheless, Beer (2) says of the spines and rods of *Ipomoea*, 'The origin and differentiation takes place under the direct control of the protoplast, but once formed, the further growth may continue . . . quite independently of any immediate guidance from the living protoplast, provided only the material necessary for growth be forthcoming'.

Since this pattern is initiated by and apparently morphogenetically determined by the spore protoplast, the pollen-grain in its entirety, including the external sculpturing, must be regarded as a spore and the external sculpturing as a spore character.

As a basic fact the cell characters of spores, however specialized, show no real similarity to or correlation with the characters of the many-celled plant body. Thus it does not follow that because a plant has acquired the habit of producing spines on its leaves or stems, it will likewise show a tendency to develop spines on its pollen-grains. Many of the Malvaceae are glabrous throughout, but possess pollen-grains with a double system of sharp spines, clearly showing that the organization of the many-celled plant body and that of the single cell are incommensurable.

In the same way large plants show no tendency to produce large pollen-grains, except sometimes in the case of polyploids. For example, the pollen-grains of elm, poplar, oak, and maple are $30\ \mu$, $28\ \mu$, $30\ \mu$, and $31\ \mu$ respectively, while those of *Mirabilis*, an herbaceous plant a few feet high, are $187\ \mu$ in diameter.

The Melastomaceae are conspicuous for their extremely large anthers, which in some species give the impression of being altogether too large for the flowers, yet in these enormous anthers are borne extremely small pollen-grains; those of *Meriana*, for example, are $12.5\ \mu$ in diameter, the smallest so far observed in these studies.

Just as among the Bryales, a group in which the gametophyte approaches most nearly to the sporophyte in character, the gametophyte never achieved the development of stomata in its leaves, though stomata are among the most constant characters throughout the sporophytes of the Bryales, Filicales, and Spermatophytes; the fundamental dissimilarity between the haploid and the diploid organization comes to expression. So the entire lack of parallelism between the characters of pollen-grains and those of the many-celled plant body is in keeping with the fact that the pollen-grain characters, though so highly specialized, are none the less cell characters, perhaps the climax expression of the potentialities of the morphogenic differentiation of the single cell. Certainly no other plant-cells can compare with them, except, perhaps, certain of the Desmids and Peridineae.

SUMMARY AND CONCLUSIONS.

Pollen-grain characters in the groups noted are useful for the determination of phylogenetic relationships. In most families the pollen-grains bear a general similarity throughout, proportional in amount to the closeness of interrelationship within the group. This general similarity is the composite of a limited number of more or less independent characters, such as the size and shape of the grain, the number and arrangement of germinal

apertures and expansion folds, the character of ridges and spines, and the texture of the surface. These, like most phylogenetic characters, occur individually in varying degrees of similarity throughout somewhat restricted groups of plants and have a strong tendency to recur in similar or different associations within the family or order, or even in entirely unrelated groups. In these respects the characters of pollen-grains behave just as do the phylogenetic characters of multicellular plant organs.

A special application of these principles is found in the genus *Vernonia*. The pollen-grains of the species of this genus, in common with those of the majority of the *Carduaceae*, are characterized by the possession of spines, but are distinguished from those of the other tribes of the family by the manifest tendency to develop the echinolophate condition, in this respect resembling those of most of the other genera of the *Vernonieae* and the family *Cichoriaceae*.

The section *Lepidaploa*, to which all except three North American species of *Vernonia* belong, is characterized by the possession of long germinal furrows extending nearly from pole to pole, except in the single species *V. brachiata*, which is included in this section of the genus, though of doubtful affinities.

The leafy-bracted subsection of the *Lepidaploa* is characterized by a completely echinolophate grain. The pattern assumed by the crests and lacunae of this grain is always radiosymmetrical and the distribution among the species of the various modifications assumed by it coincides with the genetic lines of the species groups as far as understood.

The pollen-grains of the species of the bractless subsection of the *Lepidaploa* are characterized by the subechinolophate form, excepting the two species *V. canescens* and *V. mollis*, which have acuminate involucre bracts but are included in the bractless subsection because they do not have leafy bracts below the head. In the most primitive members of this subsection the grain shows the least development of crests and lacunae, while in the most advanced members of this subsection it shows the most highly developed crests and lacunae. In no species, however, do these attain the completely echinolophate condition found in the leafy-bracted subsection.

The pollen-grains of the other three sections of the genus, from the limited material available, show only that each possesses characters not found in the others nor in the *Lepidaploa*.

From these considerations of the pollen-grain it seems certain that the *Lepidaploa* are made up of two distinct evolutionary stocks, probably both derived from the same echinate grained ancestor. One of these, the leafy-bracted subsection, achieved early in its history the completely echinolophate condition; the other, the bractless *Lepidaploa*, has not yet achieved the echinolophate condition, but closely approaches it in its most highly developed members.

The major portion of the material used in these studies was obtained from the herbarium of the New York Botanical Garden, and the author wishes to extend his sincerest thanks to the Director, Dr. N. L. Britton, for his many courtesies and the unrestricted use of the herbarium and laboratories. The writer also wishes to thank the members of the Garden staff for many kindnesses, and particularly Dr. P. A. Rydberg, Dr. A. B. Stout, and Dr. H. A. Gleason for much valuable assistance wherever the problems of this work touched upon their respective fields.

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Table I shows the interrelationships of the species of *Vernonia* of which the pollen-grains are discussed. The vertical line represents the division between North and South America, south of which no attempt is made to trace the genetic lines.

The arrangement is a graphical representation of the different groups, showing their probable origin, as developed by Gleason (19). Four sections of the genus are represented. Sections 1 to 3 are primarily South American, having but a single species each in North America. The fourth section, *Lepidaploa*, includes all the other North American species. Those that are 'so closely related in form and structure and so similar in distribution that they must be akin genetically' are segregated into species groups. 'Most of the groups present strong evidence of their relation to, and their probable origin from, each other.' These interrelationships are indicated by the connecting lines.

The section *Lepidaploa* is divided into two subsections on the basis of the presence or absence of leafy bracts below the heads.

A study of the pollen-grains reveals the fact that the development of their complicated pattern follows closely along the genetic lines indicated in this table and which were established by Gleason on evidence other than that of pollen-grains.

TABLE I.

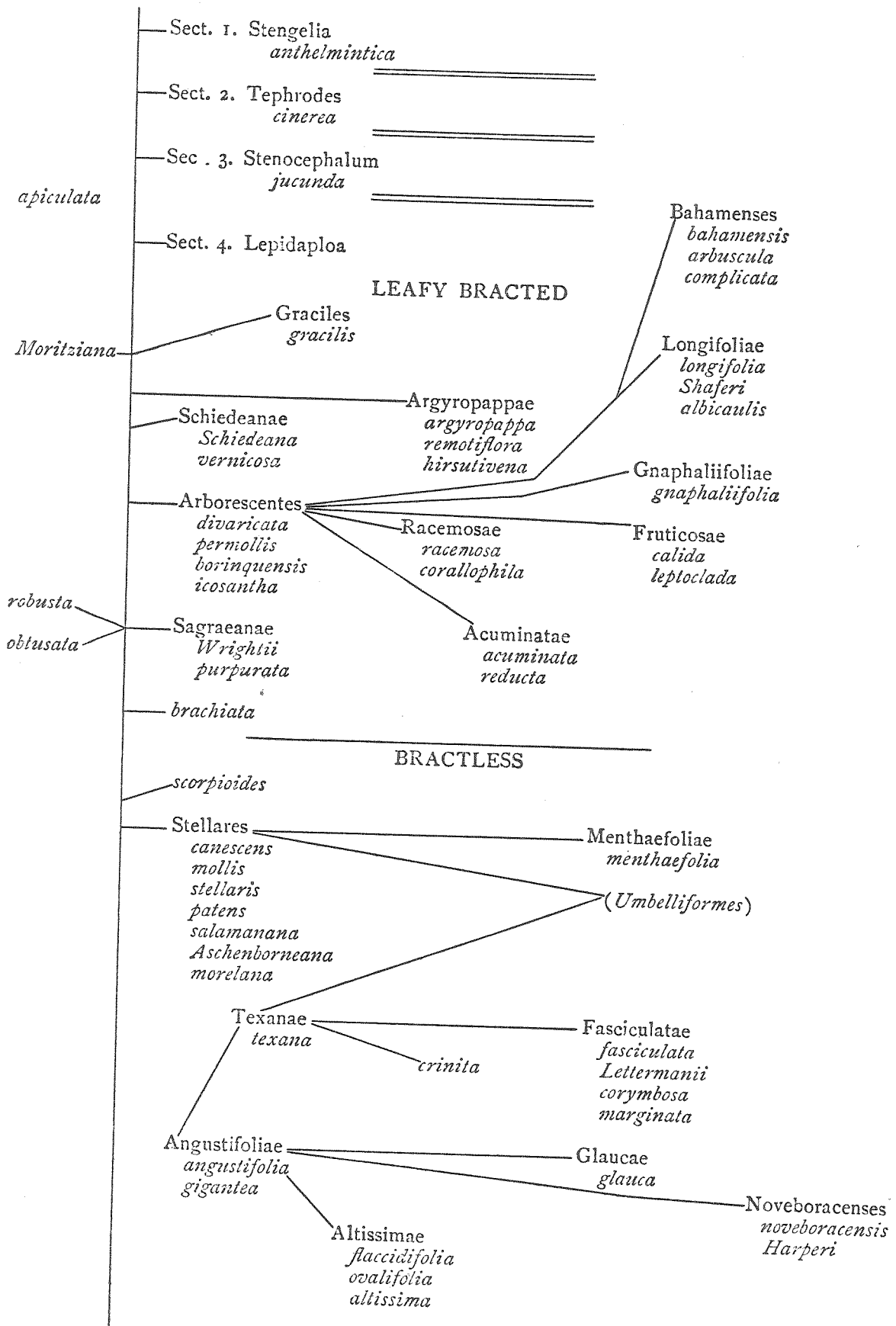


Table II displays the salient characters of the pollen-grains of the different species of *Vernonia* that have been examined. Four sections of the genus are represented, and of the fourth section, Lepidaploa, representatives of nineteen species groups and three species not assigned to any group are included.

The table shows that the germinal furrows are present in the pollen-grains throughout the section Lepidaploa, except *V. brachiata*, but are absent from the grain of *V. cinerea* of the section Tephrodes and *V. jucunda* of the section Stenocephalum.

The form of the pollen of all the leafy-bracted Lepidaploa is echinolophate with, only in *V. reducta*, a tendency towards the subechinolophate condition; but in the bractless Lepidaploa it is subechinolophate in all except *V. canescens* and *V. mollis* of the Stellares, but which have acuminate involucre bracts.

The polar lacuna is present in some groups but absent from some others that are closely related, so that it is difficult to put an interpretation on its occurrence. It should be noted, however, that in the group Longifoliae it is absent from *V. longifolia* and *V. Shaferi* and present, but small and poorly developed, in *V. albicaulis*, while in the remaining six groups, the Arborascentes and its derivatives, it is present and well developed. This makes it appear to be a late development in the group. It is absent from all subechinolophate grains.

The equatorial lacuna is doubled in *V. anthelmintica* of the section Stengelina. It is double or single in *V. apiculata* and single in *V. jucunda* of the section Stenocephalum. In the section Lepidaploa it is absent throughout except in the group Sagraeanae, in the four species of which it is single but well developed.

TABLE II.

Characters of *Vernonia* found in the different Species groups.

<i>Species.</i>	<i>Type of Pattern.</i>	<i>Germinal Furrow.</i>	<i>Polar Lacuna.</i>	<i>Equatorial Lacuna.</i>	<i>Size μ.</i>
Sect. 1. <i>Stengelia anthelmintica</i> , Willd.	echinolophate	present	present	double	40.0
Sect. 2. <i>Tephrodes cinerea</i> , (L.) Less.	"	absent	"	"	30.8
Sect. 3. <i>Stenocephalum apiculata</i> , Mart.	"	present	"	double or single	33.7
<i>jucunda</i> , Gleason	"	absent	"	present	3
Sect. 4. <i>Lepidaploa</i> , leafy bracted					
Graciles					
<i>gracilis</i> , H. B. K.	"	present	"	absent	38.8
<i>Moritziana</i> , Sch.-Bip.	"	"	"	"	31.9
Argyropappae					
<i>argyropappa</i> , Buek.	"	"	"	"	33.0
<i>hirsutivena</i> , Gleason	"	"	"	"	33.0
<i>remotiflora</i> , Rich.	"	"	absent	"	22.0
Schiedeanae					
<i>vernica</i> , Klatt.	"	"	"	"	37.5
<i>Schiedeana</i> , Less.	"	"	"	"	37.5
Arborescentes					
<i>icosantha</i> , DC.	"	"	present	"	37.5
<i>divaricata</i> , (L.) Sw.	"	"	"	"	33.4
<i>permollis</i> , Gleason	"	"	"	"	35.2
<i>borinquensis</i> , Urban	"	"	"	"	38.5
Longifoliae					
<i>longifolia</i> , Pers.	"	"	absent	"	
<i>Shaferi</i> , Gleason	"	"	"	"	40.0
<i>albicaulis</i> , Pers.	"	"	present	"	35.3
Bahamenses					
<i>bahamensis</i> , Griseb.	"	"	"	"	38.5
<i>arbuscula</i> , Less.	"	"	"	"	40.0
<i>complicata</i> , Griseb.	"	"	"	"	39.6
Gnaphaliifoliae					
<i>gnaphaliifolia</i> , A. Rich.	"	"	"	"	38.5
Fruticosae					
<i>calida</i> , Gleason	"	"	"	"	
<i>leptoclada</i> , Sch.-Bip.	"	"	"	"	44.0
Racemosae					
<i>racemosa</i> , Delponte	"	"	"	"	27.5
<i>corallophila</i> , Gleason	"	"	"	"	33.0
Acuminatae					
<i>acuminata</i> , Less.	"	"	"	absent or trace	
<i>reducta</i> , Gleason	echinolophate to subechinolophate	"	small	absent	34.1
Sagraeanae					
<i>Wrightii</i> , Sch.-Bip.	echinolophate	"	absent	present	39.4
<i>purpurata</i> , Gleason	"	"	"	"	49.4
<i>obtusata</i> , Less.	"	"	"	"	42.0
<i>robusta</i> , Rusby	"	"	"	"	61.5
<i>brachiata</i> , Benth.	"	absent	present	"	35.2

TABLE II (continued).

<i>Species.</i>	<i>Type of Pattern.</i>	<i>Germinal Furrow.</i>	<i>Polar Lacuna.</i>	<i>Equatorial Lacuna.</i>	<i>Size μ.</i>
Sect. 4. <i>Lepidaploa</i> (contd.), bractless					
<i>scorpioides</i> , (Lan.) Pers.	subechinolophate	present	absent	absent	34.9
Stellares					
<i>stellaris</i> , Llave & Lex.	"	"	"	"	30.0
<i>patens</i> , H. B. K.	"	"	"	"	28.5
<i>salamanana</i> , Gleason	"	"	"	"	28.5
<i>Aschenborniana</i> , S. Sch.	"	"	"	"	27.5
<i>morelana</i> , Gleason	"	"	"	"	33.2
<i>canescens</i> , H. B. K.	echinolophate	"	present	"	35.2
<i>mollis</i> , H. B. K.	"	"	absent or trace	"	31.9
Menthaefoliae					
<i>menthaefolia</i> , Less.	subechinolophate	"	absent	"	31.9
Texanae					
<i>texana</i> , (Gray) Small	"	"	"	"	34.9
Fasciculatae					
<i>fasciculata</i> , Michx.	"	"	"	"	40.0
<i>Lettermanni</i> , Engelm.	"	"	"	"	37.5
<i>corymbosa</i> , Schw.	"	"	"	"	37.0
<i>marginata</i> , (Torr.) Raff.	"	"	"	"	37.4
Angustifoliae					
<i>angustifolia</i> , Michx.	"	"	"	"	34.6
<i>gigantea</i> , (Walt) Trel.	"	"	"	"	36.0
Glaucæ					
<i>glauca</i> , (L.) Willd.	"	"	"	"	38.5
Altissimæ					
<i>altissima</i> , Nutt.	"	"	"	"	36.4
<i>ovalifolia</i> , T. & G.	"	"	"	"	38.5
<i>flaccidifolia</i> , Small	"	"	"	"	33.0
Noveboracenses					
<i>noveboracensis</i> , (L.) Michx.	"	"	"	"	35.0
<i>Harperi</i> , Gleason	"	"	"	"	32.8
<i>crinita</i> , Raf.	"	"	"	"	38.5

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EXPLANATION OF PLATES XX AND XXI.

Illustrating Dr. R. P. Wodehouse's paper on the Phylogenetic Value of Pollen-grain Characters.

All drawings are freehand, made with the aid of a Zeiss 2 m. apochromat objective, N.A. 1.3, and a 10 x (K. 8) ocular giving a magnification of about 900 diameters.

The relative sizes of the figures bear no relation to the sizes of the pollen-grains; instead, the diameter of each grain is given as determined by a micrometer scale used with the same objective as above and a 15 x (K. 12) ocular. Magnification about 1,300 diameters.

PLATE XX.

Fig. 1. Pollen-grain of *Phleum pratense*, L., 31 μ diam. This type of grain, smooth without adornments of any kind except the single germinal aperture closed by an operculum, called monopored psilate, is characteristic of all the Gramineae, and is not found in any other family.

Fig. 2. Pollen-grain of *Phleum pratense*, L., in the dry condition. The operculum is drawn deeply into the germinal aperture, and shrinkage has taken place without the formation of any well-defined folds.

Fig. 3. Pollen-grain of *Sarcobatus vermiculatus*, Torr. (Chenopodiaceae), 25.3 μ diam. This type of grain, distinguished by the possession of a number of germinal apertures cut sharply into the exine, a condition described as cribellate, is characteristic of the families Chenopodiaceae and Amaranthaceae.

Fig. 4. Pollen-grain of *Salsola pestifer*, A. Nels. (Chenopodiaceae), 25.4 μ diam. Compare with Fig. 3. Shows the kind of variation in the cribellate form of grain encountered in the Chenopodiaceae and Amaranthaceae.

Fig. 5. Pollen-grain of *Silphium perfoliatum*, L. (Heliantheae), 27.5 μ diam. Equatorial view. This type of grain provided with three germinal apertures enclosed in three furrows or expansion folds—in this case short and inconspicuous—and with the rest of the surface covered with prominent sharp spines, tricolpate echinate, may be regarded as the basic form of the Carduaceae, but undergoes various modifications in the different tribes.

Fig. 6. Pollen-grain of *Ambrosia elatior*, L. (Ambrosiaceae), $26.4\ \mu$ diam. Equatorial view. Similar to that of *Silphium*, but with the spines greatly reduced and rounded on their tops, subechinate. This type of grain is characteristic of the family Ambrosiaceae, though in some species the spines are more prominent and sharper, and in others still further reduced.

Fig. 7. Pollen-grain of *Xanthium speciosum*, Kearney (Ambrosiaceae), $26.4\ \mu$ diam. Equatorial view. A subechinate form showing the extremest reduction of the spines exhibited by the grains of any of the Ambrosiaceae.

Fig. 8. Pollen-grain of *Inula Helenium*, L. (Inuleae), $28.6\ \mu$ diam., showing the development of the subechinate condition in the tribe Inuleae, also the conspicuous germinal furrow. Not all the members of this tribe are subechinate, but most show a decided tendency towards reduction of spines, though considerably less than in the Ambrosiaceae.

Fig. 9. Pollen-grain of *Tanacetum camphoratum*, Less. (Anthemideae), $29.7\ \mu$ diam. Polar view, showing the long conspicuous germinal furrows characteristic of all the Anthemideae and the low sharp spines characteristic of all except *Artemisia* and its allies.

Fig. 10. Pollen-grain of *Artemisia tridentata*, Nutt. (Anthemideae), $29.7\ \mu$ diam. Equatorial view, showing the three prominent germinal furrows or expansion folds characteristic of the genus *Artemisia* and its allies, and its nearly smooth exine; in this latter respect it is quite different from the rest of the tribe Anthemideae. This form of grain is known as tricolpate psilate.

Fig. 11. Pollen-grain of *Crossostephium artemisioides*, Less. (Anthemideae), $20.9\ \mu$ diam. Polar view, showing the tricolpate psilate grain similar to that of *Artemisia* except for the possession of specks on the surface which may be regarded as vestiges of the spines found in most of the Carduaceae.

Fig. 12. Pollen-grain of *Chuquiragua oppositifolia*, Don. (Mutisieae), $42.5\ \mu$ diam. (a) Polar and (b) equatorial view, showing the tricolpate psilate grain with long germinal furrows reaching from pole to pole. This type of grain is characteristic of most of the Mutisieae, except those of *Barnadesia*.

Fig. 13. Pollen-grain of *Barnadesia spinosa*, L. (Mutisieae), $65.0\ \mu$ diam. Polar view. Characterized by the possession of well-developed ridges entirely lacking spines—psilolophate—in this respect characteristic of the genus but differing from all other members observed of the Mutisieae.

Fig. 14. Pollen-grain of *Cichorium Intybus*, L. (Cichoriaceae), $45.0\ \mu$ diam. Polar view, illustrating the well-developed crests abundantly provided with spines—echinolophate—characteristic of almost all of the Cichoriaceae, but differing from the pollen form of *Barnadesia* principally in the possession of spines.

Fig. 15. Pollen-grain of *Catananche caerulea*, L. (Cichoriaceae), $33.5\ \mu$ diam. Equatorial view. Subechinolophate, possessing only the rudiments of the pattern characteristic of *Cichorium*. This form represents a possible link between the simple echinate and the echinolophate types of grain.

Fig. 16. Pollen-grain of *Struchium sparganophorum*, (L.) Kuntze (Vernonieae), $28.6\ \mu$ diam. Polar view. An echinolophate type of grain with the spines greatly reduced.

Fig. 17. Pollen-grain of *Stokesia laevis*, (Hill) Greene (Vernonieae), $55\ \mu$ diam. Equatorial view. Echinolophate, with the spines even more reduced than in the pollen-grain of *Struchium*. These two species represent possible links between the echinolophate and psilolophate types of grain.

Fig. 18. Pollen-grain of *Pacourina edulis*, Aubl. (Vernonieae), $49.5\ \mu$ diam. Polar view. A psilolophate form genetically related to and similar to the two preceding forms except for the total absence of spines.

Fig. 19. Pollen-grain of *Vernonia gracilis*, H. B. K. (Graciles), $38.8\ \mu$ diam. Polar view. Echinolophate, with ridges and lacunae well developed and sharply defined. Germinal furrows are present, but show vestiges of the interlacunar crests which in the *jucunda* type separate the abporal from the germinal lacunae. The polar lacuna is present and large. This grain is exactly like that of *V. Moritziana*, a South American representative of the Graciles, except that the latter has somewhat shorter spines. It is likewise essentially the same as that of *V. argyropappa* and *V. hirsutivena* of the Argyropappae.

Fig. 20. Pollen-grain of *V. remotiflora*, Rich. (Argyropappae), $22.0\ \mu$ diam. Polar view. Differs from the grains of the Graciles in the absence of the polar lacuna. In this respect it also differs from the other members of the Argyropappae, *V. argyropappa* and *V. hirsutivena*, but resembles those of the Schiedeanae. A peculiar character of this grain is that it frequently bears spurs on the paraporal crests projecting out into and sometimes nearly crossing the germinal furrow,

not to be confused, however, with the vestiges of the interlacunar crests which separate the abporal from the poral lacunae, and which are also present in this grain.

Fig. 21. Pollen-grain of *V. vernicosa*, Klatt. (Schiedeanae), 37.5μ diam. Polar view. Shows the absence of the polar and equatorial lacunae, thus resembling the grain of *V. remotiflora*. The projecting spurs, however, are much reduced or entirely absent.

Fig. 22. Pollen-grain of *V. icosantha*, DC. (Arborescentes), 38.5μ diam. Polar view, showing the pattern characteristic of all the Arborescentes and their six derivative groups, except *V. reducta* of the Acuminatae. It differs from the grains of *V. vernicosa* and *V. remotiflora* in its possession of well-developed polar lacunae, in this respect resembling *V. gracilis*.

Fig. 23. Pollen-grain of *V. arbuscula*, Less. (Bahamenses), 40.0μ diam. Polar view, showing great similarity to pollen-grain of *V. icosantha* of the Arborescentes, from which the Bahamenses are derived. It possesses a well-developed polar lacuna which is characteristic of the species group Arborescentes and all the species of the six groups derived from it, except *V. longifolia* and *V. Shaferi* of the Longifoliae.

Fig. 24. Pollen-grain of *V. reducta*, Gleason (Acuminatae), 34.1μ diam. Similar to that of *V. icosantha* in pattern, but with its crests greatly thickened and with sloping sides. This form presents what might be regarded as a reversion to, or a recent deviation from, the subechinolophate form.

Fig. 25. Pollen-grain of *V. Wrightii*, Sch.-Bip. (Sagraeanae), 39.4μ diam. Polar view. Shows the absence of polar lacunae, but differs from those of *V. remotiflora* and *V. vernicosa*, which are likewise without polar lacunae, in the possession of well-developed equatorial lacunae, seen only in side view.

The grains of the other members of the Sagraeanae (*V. purpurata*, *V. obtusata*, *V. robusta*) are exactly the same as this, except that the grain of *V. robusta* is much larger, viz. 60μ in diameter.

Fig. 26. Pollen-grain of *V. brachiata*, Benth., 35.2μ diam. Polar view, showing the entire absence of the germinal furrows, in this respect differing from all the other Lepidaploa. The figure shows the pentagonal type of pattern which predominates among the grains of this species, though two other forms are found; one is hexagonal, closely resembling the *jucunda* type, the other a simplified pentagonal form with fewer lacunae and difficult to relate to the *jucunda* type. All three forms lack the characters which are distinctive of the Lepidaploa.

PLATE XXI.

Fig. 27. Pollen-grain of *V. scorpioides*, (Lan.) Pers., 34.9μ diam. Polar view. A subechinolophate type of grain, characteristic of the bractless Lepidaploa. Only the paraporal crests are at all well developed. The germinal furrows, however, are well developed, as in all the Lepidaploa except *V. brachiata*.

Fig. 28. Pollen-grain of *V. patens*, H. B. K. (Stellares), 28.5μ diam. View about 45 degrees from polar, showing the subechinolophate type of grain only slightly in advance of that of *V. scorpioides*. This grain is practically the same as those of the four other members of the Stellares, *V. stellaris*, *V. salamanana*, *V. Aschenborneana*, and *V. morelana*, but is entirely different from the two members of the group which are echinolophate, *V. canescens* and *V. mollis*.

Fig. 29. Pollen-grain of *V. canescens*, H. B. K. (Stellares), 35.2μ diam. Polar view, showing completely echinolophate grain with pattern almost as in *V. gracilis*, *V. icosantha*, and *V. arbuscula*, despite the fact that this species is included in the Stellares among the bractless Lepidaploa, all others of which have subechinolophate grains except *V. mollis*.

Fig. 30. Pollen-grain of *V. mollis*, H. B. K. (Stellares), 31.9μ diam. Polar view, showing completely echinolophate grain but with irregular pattern. This species is included with *V. canescens* in the Stellares among the bractless Lepidaploa, of which all others have subechinolophate grains.

Fig. 31. Pollen-grain of *V. texana*, (Gray) Small (Texanae), 35.5μ diam. Equatorial view, illustrating the subechinolophate type of grain with the crests somewhat better developed than in *V. scorpioides*.

Fig. 32. Pollen-grain of *V. corymbosa*, Schw. (Fasciculatae), 37.0μ diam. Polar view. Subechinolophate, but with the crests somewhat better developed than in *V. scorpioides*.

Fig. 33. Pollen-grain of *V. ovalifolia*, T. and G., 38.5μ diam. (Altissimae). Polar view. Subechinolophate, but showing well-developed parapolar crests and prominent, though incomplete equatorial crests.

Fig. 34. Pollen-grain of *V. noveboracensis*, (L.) Michx. (Noveboracenses), 35.0 μ diam. Polar view. Subechinolophate, but with crests fairly well developed. This species and *V. ovalifolia* represent the climax of the development of the crests in the bractless Lepidaploa.

Fig. 35. Pollen-grain of *V. anthelmintica*, Willd. (sect. Stengelia), 49.0 μ diam. Polar view, showing the well-developed polar lacuna, germinal furrows, and paired equatorial lacunae, the latter a character not found in the Lepidaploa.

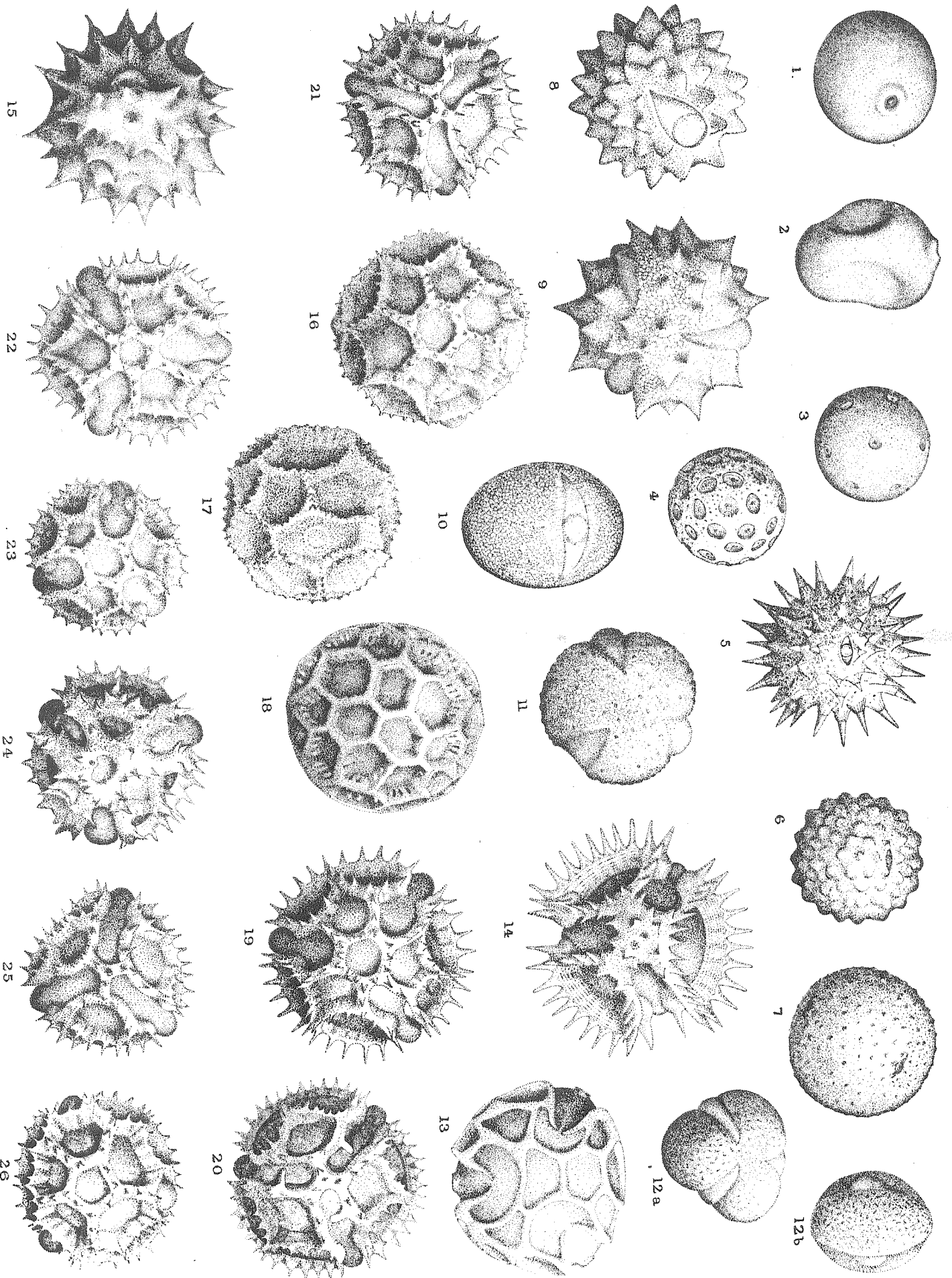
Fig. 36. Pollen-grain of *V. cinerea*, (L.) Less. (sect. Tephrodes), 30.8 μ diam. Polar view, showing a symmetrical pattern and closed polar lacunae and consequent absence of germinal furrows, characters not found in the Lepidaploa except in *V. brachiata*.

Fig. 37. Pollen-grain of *V. jucunda*, Gleason (sect. Stenocephalum), 36.3 μ diam. Polar view, showing the absence of germinal furrows, each germinal pore being set in its own lacuna. The polar, parapolar, and equatorial lacunae are well developed; the pattern is hexagonal and radiosymmetrical. No other species observed in the genus possesses this combination of characters except sometimes *V. brachiata*. This grain was used as the starting-point in our discussion of the genus *Vernonia* on account of the regularity of its pattern and its complement of units.

GLOSSARY.

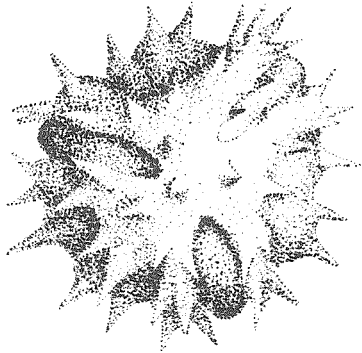
- Abpolar lacunae.* Those of the circumpolar lacunae, generally three in each hemisphere, which are opposite the germinal pores in lophate grains. Example: *Vernonia jucunda*.
- Circumpolar lacunae.* The lacunae, generally six in each hemisphere, surrounding the polar lacuna in lophate pollen-grains. Example: *Vernonia jucunda*.
- Cribellate.* Possessing a number of germinal apertures appearing as rounded and sharply delimited thin areas, equally spaced and generally more or less deeply sunken in the exine. Examples: *Salsola pestifer*, *Sarcobatus vermiculatus*.
- Echinate.* Adorned with prominent sharp spines more or less evenly distributed. Examples: *Silphium perfoliatum*, *Tanacetum camphoratum*.
- Echinolophate.* With the surface thrown into ridges, anastomosing or free, provided with more or less prominent spines. Examples: *Cichorium Intybus*, *Stokesia laevis*.
- Equatorial crest.* A ridge or interlacunar crest extending from pore to pore along the equator in lophate grains. It may be continuous or interrupted to admit the equatorial lacunae when present. Example: *Vernonia anthelmintica*.
- Equatorial lacuna.* A lacuna in lophate grains, situated midway between the pores and astride the equator when single, or on either side of the equator when double. Examples: *Vernonia Wrightii*, single; *V. anthelmintica*, double.
- Expansion fold.* A longitudinal thin-walled area, generally present in heavy-walled grains and serving to accommodate changes in volume. Example: *Inula Helenium*.
- Germinal aperture, Germ pore, Germinal pore.* The point of emergence of the pollen-tube.
- Germinal furrow.* A longitudinal area surrounding the germinal pore, differing from the remainder of the surface generally in the unadorned and thinner character of the exine; usually serving as an expansion fold. Example: *Inula Helenium*.
- Interlacunar crest.* A ridge separating lacunae from each other in lophate grains. Examples: *Cichorium Intybus*, *Pacourina edulis*.
- Interpolar lacunae.* The circumpolar lacunae, generally three in each hemisphere, which are alternate with the germinal pores in lophate pollen-grains. Examples: *Vernonia jucunda*, *V. gracilis*.
- Lacunae.* Areas in lophate pollen-grains, bounded by crests and generally smooth. Examples: *Barnadesia spinosa*, *Vernonia jucunda*.
- Lophate.* With the outer surface thrown into ridges, anastomosing or free. Examples: *Barnadesia spinosa*, *Vernonia jucunda*.
- Monopored.* Possessing a single but clearly defined germinal aperture. Example: *Phleum pratense*.

- Paraporal crests.* The ridges bounding the germinal furrows in lophate and sublophate grains.
Examples: *Vernonia Wrightii*, *V. texana*.
- Paraporal lacunae.* The lacunae adjacent to the poral lacuna and flanking the germinal furrow or abporal lacuna, generally four—two in each hemisphere—about each poral lacuna. Example: *Vernonia gracilis*.
- Polar lacuna.* The lacuna at the pole or centre of symmetry, in lophate grains, in which the pattern formed by the ridges is radiosymmetrical or nearly so. Examples: *Vernonia jucunda*, *V. gracilis*.
- Poral lacuna.* The lacuna enclosing the germ pore. Example: *Stokesia laevis*.
- Psilate.* Unadorned—without spines, ridges, or projections other than germinal apertures. Examples: *Phleum pratense*, *Artemisia tridentata*.
- Psilolophate.* With the outer surface thrown into ridges which lack spines or conspicuous adornments. Examples: *Pacourina edulis*, *Barnadesia spinosa*.
- Subechinate.* As under Echinate, but with spines small and rounded on top. Example: *Ambrosia*.
- Subechinolophate.* With a spiny surface partially thrown into ridges which are not sharply defined; intermediate between Echinate and Echinolophate. Examples: *Catananche caerulea*, *Vernonia noveboracensis*.
- Sublophate.* With the surface partly thrown into ridges or crests which are imperfectly defined. See Subechinolophate.
- Tricolpate.* Possessing three longitudinal furrows or expansion folds, generally enclosing germinal pores. Example: *Tanacetum camphoratum*.

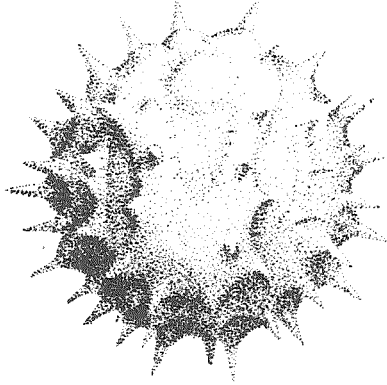


WODEHOUSE—POLLEN GRAIN CHARACTERS.

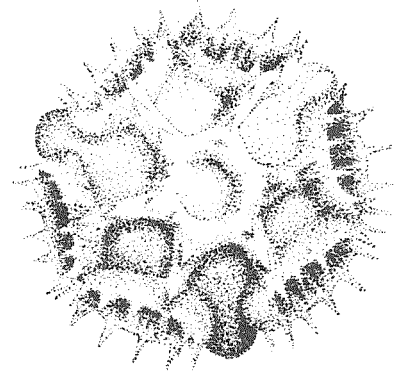
Hugh, London.



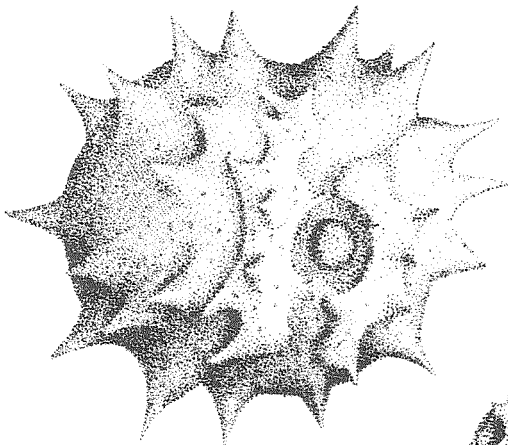
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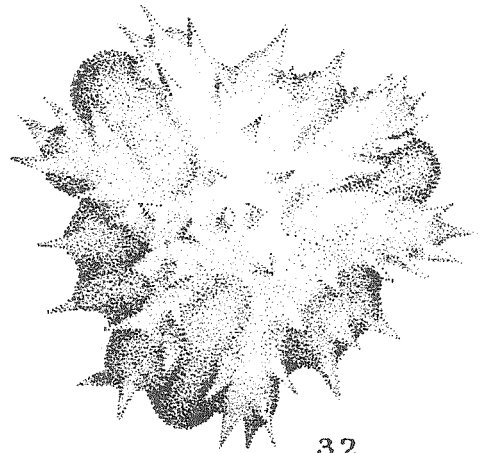
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29



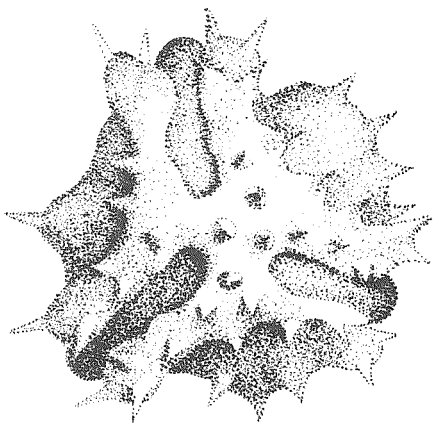
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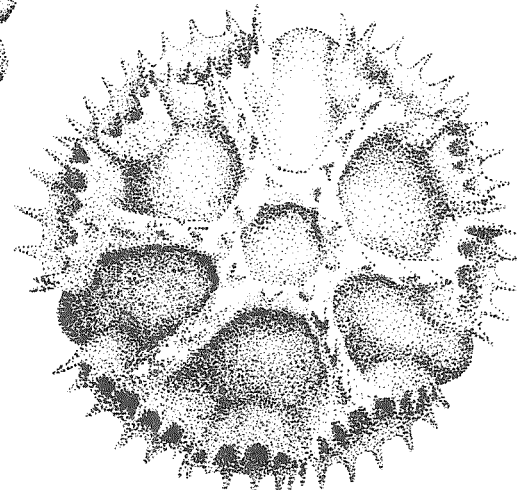
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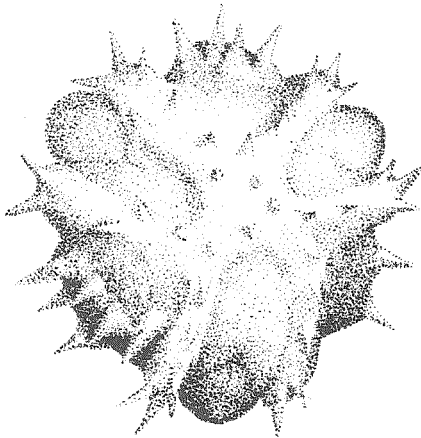
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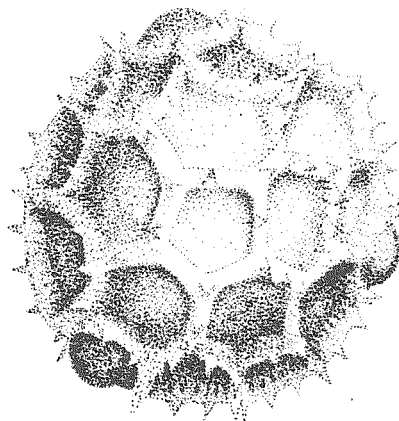
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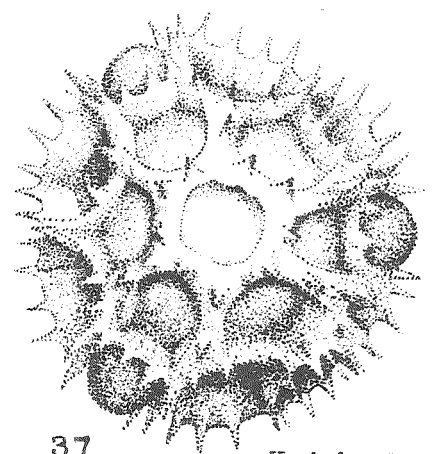
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