ON THE ORIGIN OF NUMBER AND ARRANGEMENT OF THE PLACES OF EXIT ON THE SURFACE OF POLLEN-GRAINS

BY

P. M. L. TAMMES.

(With plates I—III).

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Introduction.

An observation on the pollen of *Lythrum Salicaria*, where beside the normal grains with three there also occurred grains with four places of exit, gave rise to this research.

This phenomenon is also known to occur in other species; so investigators as Fischer (1890) and von Mohl (1834) mention a varying number of places of exit in the pollen of various species of plants belonging to different families. Besides pollen-grains with a varying number of places of exit may arise in case of irregularities of the reduction-division, which Michaelis (1926) described for the pollen of *Epilobium hirsutum*. It is likewise known of a number of polyploid plants that the pollen possesses a greater number of places of exit than the pollen of the normal form, e.g. the diploid pollen-grains of the gigasforms of *Solanum* (Winkler 1916) and *Oenothera* (Boedyn 1925—1928).

Now the question rose in how far by this variability an insight could be gained into the way in which the arrangement of the places of exit is brought about in the pollen and what causes can play a part in the formation, the variation of number and the arrangement of these places of exit.

For this reason this publication has been divided into the three following parts:

1. The morphology of the normal pollen.
2. Variations in the pollen-morphology.
3. The causes of the variability and the arrangement.

CHAPTER I.

THE MORPHOLOGY OF THE NORMAL POLLEN.

§ 1. The form of the pollen in the tetrade.

In tracing the development the great variety of form in pollen-grains may be reduced to two types: the radial and the bilateral symmetrical forms, which are closely connected with the way of division and wall-formation in the pollen-mother-cell. A short summary of this follows.

According as in the pollen-mother-cell a wall is formed

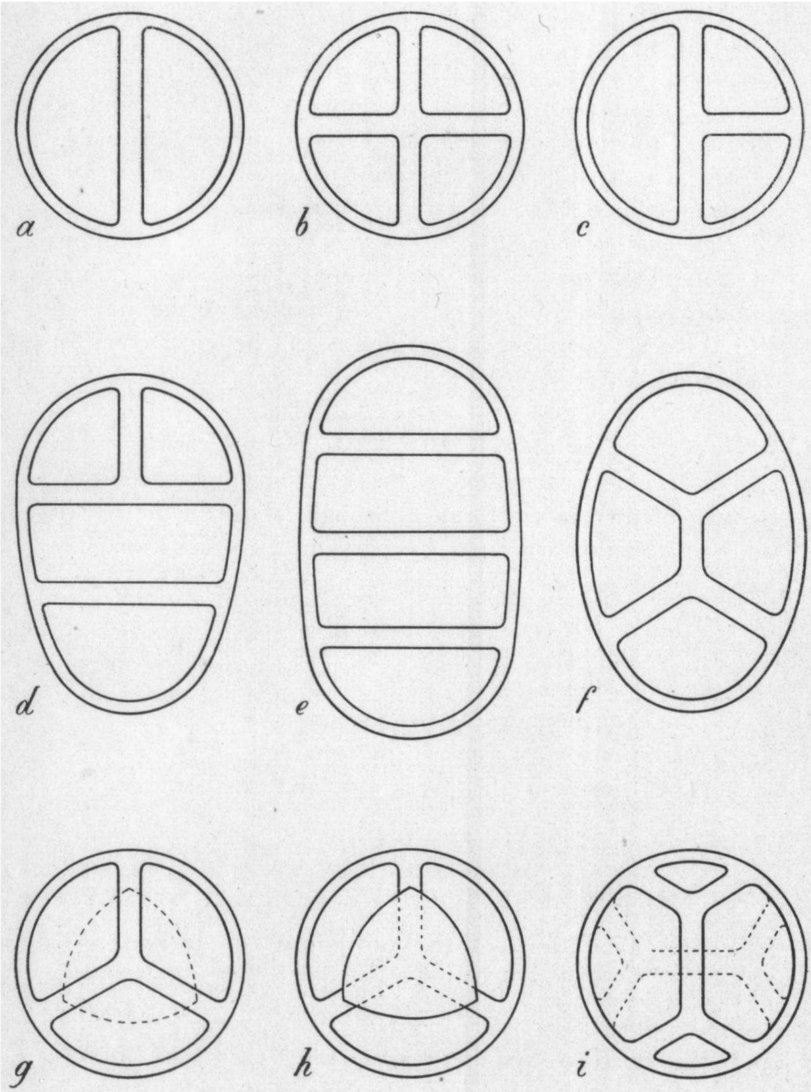

Fig. 1. The arrangement of daughtercells in a tetrade; a, b, c, d, e, belonging to the succedanic type f, g, h, i belonging to the simultanic type.

directly after the reduction-division, or that not until after the homeotypical division a wall is formed between the four daugther-cells, we can speak of two types of tetrades, the succedanic and the simultanic type. The daughter-cells of a tetrade of the succedanic type can have two different arrangements, that is parallel (fig. 1*a*, *b*) or cross-wise (fig. 1*c*). The two arrangements may occur side by side with transitions between them. Fig. 1*d* is an illustration of a rare arrangement, as was observed by Täckholm and Söderberg (1918) in a few pollen-tetrades of *Cinnamomum*. The same arrangement and also another as illustrated in fig. 1*e* was observed by myself in a tetrade of *Aechmea fulgens*.

The arrangement of the daugther-cells of a tetrade of the simultanic type is connected with the arrangement of the nuclei in the mothercell, before the wall-formation took place. If in this arrangement the nuclei lie in one plane, there arises a parallel arrangement much resembling that of the succedanic type, but differing from it in the way in which the walls meet in the centre (fig. 1*f*).

If the nuclei are not in one plane, but in two directions perpendicular to each other, that is according to the angular points of a regular *tetrahedron*, a so-called *tetrahedrical* arrangement arises (fig. 1*g*, *h*, *i*), in which each cell gets the form of a *tetrahedron*, the base of which is rounded spherically, while the apex points to the centre of the tetrade, a *sphaero-tetrahedron*. The two arrangements of the simultanic type can, though the case is rare, occur side by side; usually, however, only the *tetrahedrical* arrangement is present. Transitions may also occur and greatly resemble the various possibilities in which four equally large soapbubbles can be joined.

For that reason Thompson (1917, pp. 396—398) assumes that the directing influence in the formation of the simultanic tetrade may be due to surface-tensions.

The part these play, however, should not be overrated, because the nuclei divide in a way exactly corresponding with the subsequent arrangement of the daughter-cells; so the cause of the arrangement may be better looked for in the direction of the division of the nuclei and a secondary part be attributed to surface-tensions. In connection with this the formation of longitudinal walls in the very long cells of the cambium (Beyer 1927) must be pointed out, where the wall-formation is the reverse of what would be expected according to the rule of the *Surfaces minimae areae.*

In the daughter-cells of special mother-cells, as they are called by Nägeli (1842), pollen-grains are developed

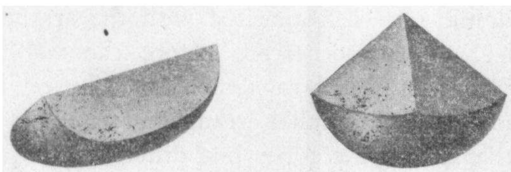

Fig. 2. Spherical-wedge and sphaero-tetrahedeon.

which have initially preserved the form of the cells from which they arose. This form which the pollen gets, when developing in the tetrade, I shall call the primary form of the pollen. In the parallel arrangement of the two tetrade-types and in the cross-wise arrangement of the succedanic type, there arises a bilateral symmetrical form, approaching a spherical-wedge (fig. 2 to the left). From the tetrahedrical arrangement of a tetrade of the simultanic type develops a radial-symmetrical form: the *sphaero-tetrahedron* (fig. 2 to the right).

As a rule the primary form of the pollen is not preserved long; in the tetrade there appear dislocations, the cells fall apart, grow rounded and the primary form gets lost.

In a few cases, however, the primary form can persist, that is in those plants in which the ripe pollen continues to cohere in tetrades, the so-called tetrade-pollen, which Fischer (1890, p. 18) described for the following species of plants: *Typha, Apocynum, Periploca, Phylidrum, Drimys, Anona, Podophyllum, Empetrum, Jussieua, Salpiglossis* and *Catalpa,* moreover it is characteristic of most *Ericaceae* and is further found in part of the *Orchidaceae, Juncaceae* and *Epacridaceae.*

Tetrahedrical arrangement occurs a.o. in the tetrade-pollen of *Erica,* parallel and tetrahedrical in *Neottia,* parallel and crosswise in *Typha* and *Vellosia.* Data on division and arrangement in the tetrade are to be found in Farr's work (1915), where a list was made of the observations which various authors made on this subject.

If the pollen coheres in the tetrade for a long time or if the structure of the pollen admits of few alterations, the primary form can be but little modified. The preservation of the primary form is found in a great measure in the spores of ferns and *Lycopodinae,* where the tetrade-formation proceeds in the same way as in the Angiosperms. With respect to the ferns Sadebeck (1902, p. 15) describes this as follows: „In der äuszeren Gestalt der Sporen findet man im wesentlichen zwei Modifikationen, die der radiären und die der bilateralen Sporen, welche durch die Art und Weise der Entwickelung der Spore aus der Sporenmutterzelle bedingt sind. In dem ersteren Falle wird der Inhalt der Sporenmutterzelle nach Art von Kugeltetraedern zerlegt, in dem letzteren Falle teilt er sich in Kugelquadranten; es entstehen also aus der Sporenmutterzelle stets 4 Sporen. In beiden Fällen aber runden sich die bei dem Teilungprozesse entstandenen Kanten weiterhin noch ab, und die radiären Sporen werden daher kugelig, die bilateralen dagegen mehr oder weniger nierenförmig. Die *Hymenophyllaceen, Cyatheaceen* und *Osmundaceen* bilden nur radiäre Sporen aus die *Polypodiaceen, Schizaeaceen* und

Gleicheniaceen dagegen bilden sowohl radiäre als auch bilaterale Sporen aus."

Some exceptions which may give rise to a deviating primary form of the pollen occur, where more or fewer than four daughter-cells have developed in one pollen-mother-cell. More cells appear in *Acacia chloranta* with eight and *Acacia laxa* with sixteen cells (Mohl 1834), fewer cells appear in Scirpus where three of the four nuclei disappear and all the contents of the mothercell fuse into one pollen-grain; further in case of abnormal reduction-division when fewer, but also more than four cells can lie in a tetrade. So Warth (1925 p. 212) observed a number of daughter-cells varying from one up to and including eight in the pollen-tetrades of *Fuchsia Lycoides*.

§ 2. The secondary modifications of form and the form of the ripe pollen.

After the breaking up of the tetrade the primary form undergoes a number of modifications. The angular form which had already become rounded more or less in the tetrade disappears more and more; from the *sphaero-tetrahedron* develops a sphere, from the spherical-wedge an ellipsoid or in case of stronger stretching also a sphere. Besides rounding there now appear other modifications of form closely connected with the structure of the wall of the pollen-grains and dominating over the preceding form. The exine of the pollen-grains has not the same thickness throughout, but it is thicker in some places, thinner in other places. In the thin places the wall stretches more and bulges out, while the pollen shows an inclination to become angular according to the number and the arrangement of these thinner places of the exine (fig. 3).

Herewith the development of the pollen-wall is finished and further modifications of shape only occur in consequence of desiccation or swelling of the grains. In the dry pollen the thinner places of the exine are folded inwards, in a swollen state the thinner places are stretched or bulging. If there occur no thinner places in the wall, but it is equally thick throughout, the pollen may shrivel up irregularly when drying up, e.g. in *Taxus*. It may also occur that though thinner places are present, the form is but little altered in desiccation, because the protoplasm withdraws from the wall, e.g. *Alnus*.

Besides the thinner places, the places where the exine bears strong thickenings can contribute to a modification of form. These exine-thickenings which occur as bands or as projecting crests, have the reverse effect of the thinner places. In the dry pollen they project, in the swollen pollen they enclose the grain tightly.

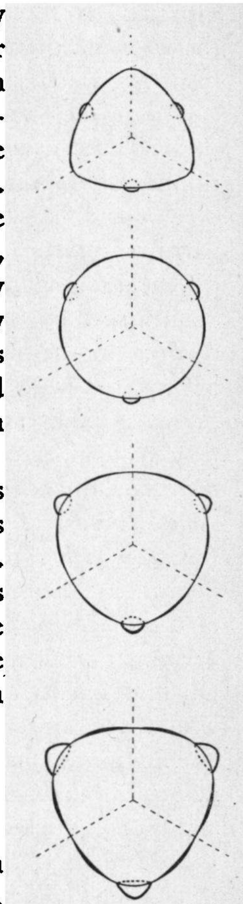

Fig. 3. Lythrum Salicaria. Secondary modifications of the primary form of a grain.

§ 3. The connection between cell-wall, structure and form.

In the previous section a connection was occasionally mentioned between form, structure and surface. Anatomy and morphology are so much interwoven in the pollen, that only an artificial separation can be made. Therefore a discussion of the anatomy of the wall has been given here as far as it is connected with form and surface of the pollen.

Beside Fischer (1890) and von Mohl (1834) it was especially Schacht (1860) who described the structure of the wall and therefore the following data have been derived from his work.

The exine can be of the same thickness throughout (*Canna, Phrynium, Streliza* and *Musa*), or locally show thinner or thicker areas. The thinner areas form the places of exit and the grooves, the thicker form broad bands or narrower crests or less clear-cut flat thickenings. Besides by the bulging places of exit the surface of the exine is determined by small projecting parts of the exine. According to their nature the surface varies; the exine may be covered with warts (*Viscum, Campanula, Canna* and *Persea*), spines (*Calendula*), palissades (*Geranium*), which may be connected together (*Cobaea* and *Cichoraceae*) or reticulate thickenings (*Passiflora, Himantoglossum, Opuntia, Abies, Picea* and *Podocarpus*). A perfectly smooth exine is found in *Phrynium, Streliza, Saccharum, Larix* and *Cupressus*. Further round thickenings may occur in the centre of the places of exit, which are thrust off when the grains germinate and which have been given the name of lids. On the inside of the exine sculptures may also occur, which may be classified like those on the outside.

The intine may be equally thick throughout (*Canna, Musa, Streliza, Larix* and *Cupressus*) or bear lenticular and warty thickenings (*Malvaceae, Campanula, Cucurbita* and *Mirabilis*); the thickenings may also be less clear-cut (*Yucca* and *Gladiolus*). The intine may be relatively thick or thinner; a thick intine is found in the pollengrains of *Canna, Phrynium, Cucurbita* and *Passiflora*, a thin one occurs in *Mirabilis, Agrostemma, Cobaea* and *Astrapeae*.

For the rest the connection between exine and intine may be more or less loose; in *Mirabilis, Agrostemma* and *Oenothera* the exine is separated from the intine, whilst in *Cucurbita, Passiflora* and in the *Malvaceae* the exine is firmly connected with the intine.

§ 4. The places of exit of the pollen.

In literature a number of different terms are known all referring to the places of exit of the pollen; those are the places where a pollen-tube can develop. Von Mohl (1834) distinguishes two kinds of such thinner places of exit, viz. grooves and pores according as the form of the places of exit is slit-like or circular. He assumes that the exine at the places of exit is only thinner and never appears to be quite absent, as contrasted with Schacht (1860) and Fischer (1890) whose opinion is that a place of exit can very well exist as a hole in the exine. Schacht (1860) describes three kinds of places of exit: holes, thinned places and pore-canals; the last-mentioned he derived from little pores in the exine functioning as places of exit *(Mirabilis, Ipomoea)*.

Likewise connected with the structure is a distinction which Fischer (1890) uses for a classification of pollen-grains. Here the places of exit are distinguished in „Austrittstellen" and „Keimporen", in the former case the exine is locally thinned, in the latter locally deficient. According to the structural properties of the exine and the form of the places of exit Fischer divides the pollen-grains into seven classes, as enumerated below:

1. A. The exine is lacking.
   B. The exine is present.
2. *a.* the same thickness throughout.
   b. with „Austrittstellen".
3. α „Austrittstellen" circular.
4. β „Austrittstellen" like grooves.
   c. with „Keimporen".
5. α in grooves.
6. β freely spread over the surface.

Tho these may be added a separate group, viz.

7. The exine is thinned in one or more circular lines;

the piece bounded by these is pushed off like a lid on germination.

An objection to this classification, however, is that the arrangement of the places of exit which is the most easily perceptible characteristic is found here only in the third place and that a classification is made according to nicer differences of structure, which are but faintly discernible in the morphology of the pollen. Fischer himself already saw the objections to his system: „Die Hauptschwierigkeit dieser Einteilung liegt darin, dass es nicht immer durchführbar ist, die Klassen 3. und 6. einerseits, und 4. und 5. andrerseits, die unter sich sehr ähnliche Formen aufzuweisen haben, streng auseinander zu halten; denn zu entscheiden ob die Exine nur äuserst dünn ist oder ganz fehlt, ist bei der Kleinheit der fraglichen Stellen oft äuserst schwer, ja zuweilen unmöglich!"

For the purpose aimed at in this publication, in which we have only to deal with the arrangement and the variation of the places of exit, a classification as given above can easily lead to confusion of ideas. With a view to external morphology it suffices to speak of form and arrangement of the places of exit and to broach the structure only then, when this is necessary to a proper insight.

§ 5. The arrangement of the places of exit in the ripe pollen.

In the previous section the significance Fischer (1890) attached to the arrangement of the places of exit in the classification of the pollen was already mentioned. According to the possibilities which present themselves, he divides his classes into separate groups, which may be parallel in the different classes. Summarizing his data we find the following possibilities:

A. For pollen with circular places of exit.

1. With one place of exit.

2. With two opposite places of exit.
3. With more places of exit lying in one plane.
4. With more places of exit spread regularly over the surface.

B. For pollen with slitlike places of exit (grooves).
1. With one place of exit.
2. With two opposite places of exit.
3. With more parallel places of exit (meridian grooves).
4. With more places of exit, regularly spread over the surface.

Essentially A. and B. are equal and if instead of a whole groove only the centre is regarded, all possibilities meet the requirements summed up for category A; so in excluding the form of the places of exit one can distinguish four possibilities of arrangement.

The strict regularity in the arrangement of the places of exit has led some authors to look for an explanation. Pohl (1928 p. 59) sees in the pollen with one place of exit the primitive state, „Während meiner Pollenuntersuchungen wurde es mir jedoch immer klarer, dasz wir in dem einfach längsgefalteten Pollenkorn nicht nur ein Gruppenmerkmal, sondern auch ein ausgezeichnetes entwicklungsgeschichtliches Merkmal besitzen". Vesque (1883) sees in number and arrangement of the places of exit an adaptation to an easier germination on the stigma; of the other exine-sculptures which frequently correspond with the arrangement of the places of exit, however, he takes quite another view: „La disposition des pointes, des lames, des réseaux qui orment la surface du grain de pollen ne paraît pas dépendre du mode de développement du grain; elle semble obéir uniquement à une loi géométrique qui ne serait autre que la phyllotaxie étendue à tous les organes saillants de la plante et à la loi d'économie".

A discussion of this will be given later; for the present it can only be determined that there are some four different possibilities of arrangement and that in these cases the places of exit take up a regular position with respect to each other.

§ 6. The arrangement of the places of exit in the tetrade.

At the daughter-cells of a tetrade two poles have been distinguished, viz. the basal and the apical pole. The basal pole or base of the developing pollen-grain or spore lies on the outside of the tetrade, whilst the apex or apical pole points to the centre of the tetrade. In pollen-grains with one place of exit it is usually found at the base of the grain, in spores of *Pteridophyta* on the contrary at the apex. Therefore in considering the arrangement of the places of exit it is of importance to pay attention to the position of the basal and apical poles. The same holds good for pollen-grains possessing more than two places of exit.

If therefore for a pollen-grain the direction of the edges and the position of the poles is indicated, the situation in the tetrade is completely determined, and at the same time a standard is found to compare the various ways of arrangement of the places of exit with each other.

About the situation of the places of exit of the grains in the tetrade little is known, some data may be found in Pohl (1928) and Goebel (1923) and for the rest this arrangement may be seen in descriptions or illustrations of tetrade-pollen, in which the initial condition was preserved. In the case of the spores of the *Pteridophyta* orientation is much easier, because the primary form alters but little and consequently the form of the ripe spores directly reveals the situation of the edges and the poles.

§ 7. The pollen-scheme.

Just like the arrangement of the floral parts the arrangement of the places of exit may be synoptically represented in a schematic representation. Such a schematic representation for the pollen I have called pollen-scheme and it will be added to the descriptions of the grains as often as possible.

The pollen-scheme consists of a basal- and a side-view of the primary form of the pollen-grain in which the form and the arrangement of the developing places of exit are indicated entirely black; thinner places of the exine as far as they cannot give exit to a pollen-tube are hatched,

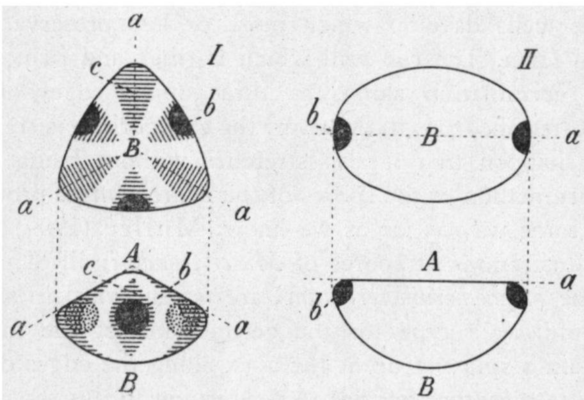

Fig. 4. Pollen-scheme of *Lythrum Salicaria* (I) and of *Nidularium Carolinea* (II). A apex, B base, a edge, b place of exit, c groove,

whilst the places of exit found on the reverse side are dotted. As there are two types of primary form, we get two kinds of pollen-schemes, viz. those representing the radial symmetrical type (fig. 4 I) and those representing the bilateral symmetrical type (fig. 4 II). For the radial type the side-view has been chosen in such a way, that one of the edges with which the daughter-cells adjoin, points backwards just as if it was mirrored in a plane parallel one of the faces lying at the backside of the form that was pictured above; for the bilateral type in such a way that we look perpendicularly on the longitudinal axis of the grain. The edges, indicated *a* in Fig. 4 are usually omitted, because their position can be gathered from the form. In the side view the apex is designed pointing upwards as is also to be seen in fig. 4.

§ 8. The arrangement of the places of exit on the spores of Bryophyta and Pteridophyta.

Schiffner (1909) gives data on the formation of the spores in the *Jungermannieae,* where four tetrahedrically arranged daughter-cells develop which more or less preserve their original form. The cell-wall which is thick and firm splits up on germination along the three apical edges of the sphaero-tetrahedron; if, however, the exosporium is thinner, it may happen that it also stretches without being torn. The germination of the spores of the *Marchantieae* proceeds in the same way as far as we know. Muller (1909) gives some illustrations of spores of *Musci frondosi*; all of which save one *(Ephemerum serratum)* are tetrahedrical in shape. Therefore, as a type for the germination of the mosses we obtain a splitting up at the apex along the edges of the *sphaero-tetrahedron* (fig. 5*a*). An exception to this, however, has still to be discussed: Goebel (1918) gives an illustration of the germination of the spores of *Sphaerocarpus terrestris,* which remain firmly united in a tetrade and do not split up at the apex, but break out irregularly at the base.

Among the spores of the *Pteridophyta* both types of a primary form occur, as may be seen in illustrations of them given by von Mohl (1833). On leaving the strongly specialised spores (e.g. Equisitum) out of discussion, we can draw up the rule that the dehiscence-bands, that are the places where the exosporium splits up or tears open on germination, are turned towards the apex and lie along the edges of the primary form (figs 5*a* and *b*).

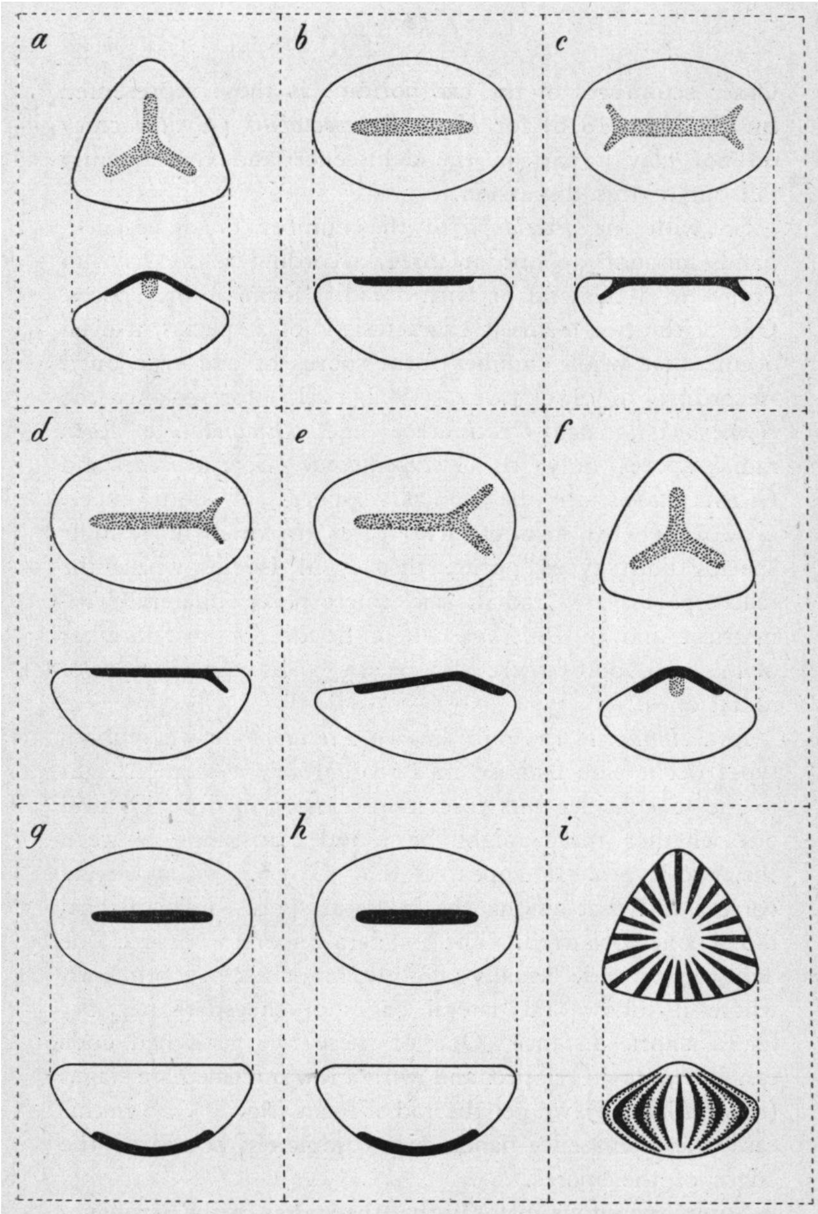

Fig. 5. Schemes of spores a, b, c. d, e, f, and pollen-grains g, h, i. a *Lycopodium selago*, b *Polypodium vulgare*, c, d, e *Psilotum triquetrum* bilateral, f the same but radial, g *Zamia muricata*, h *Pinus montana*, i *Welwitschia mirabilis*.

Other sculptures of the exosporium, as those represented by Bauke (1876) for *Hemitelia spectabilis (Cyatheaceae)* do not play a part in the dehiscence and consequently fall out of this discussion.

So with the *Pteridophyta* the number of dehiscence-bands amounts to one or three, according as we have to deal with a bilateral or with a radial form of the spores. One of the two forms is characteristic of a species, it even occurs that whole families form spores of one type only. According to Sadebeck (1902 p. 15) for instance the *Hymenophyllaceae, Cyatheaceae* and *Osmundaceae* form radial spores only, the *Polypodiaceae, Schizaeaceae* and *Gleicheniaceae* on the contrary spores of both types. Goebel (1918) mentions two cases in which in a single species both types occur, that is in Isoetes where the macrospores are radial, the microspores bilateral-symmetrical and in *Psilotum,* where besides a great number of bilateral spores there also occurs a slight percentage of radial ones.

As *Psilotum* is the only known *Pteridophyte* where both types occur side by side in a *sporangium,* it seemed right to me to consider this case more closely in order to find out whether there might be found transitions between the two types. It appeared that Goebel's data were correct and that among the bilateral spores an occasional radial one occurred. The bilateral spores possess one dehiscence band, usually slightly branched at both ends where it follows the lateral edges of the spore (fig. 5*c*) for a short distance. One of these two branched ends can be more developed and with a few intermediate stages (figs 5*d* and *e*) we get the radial form (fig. 5*f*). So in this case the dehiscence-bands are completely bound to the edges of the spores.

Summarizing we may say that the spores of the *Bryophyta* and *Pteridophyta* are in possession of a single place of exit which barring one exception, is found at the apex of the spore, and that the form of this place of exit is connected with the symmetry of the spores. In the radial spores the place of exit has the shape of a triradiate star, in the bilateral spores the shape of a straight slit which may be slightly branched at the ends; in both cases this form is determined by the position of the edges of the spore.

§ 9. The arrangement of the places of exit in the Gymnospermae.

On germination of the pollen-grains of the *Gymnospermae* the exine is torn open after which a pollen-tube can develop. The tearing of the exine can happen irregularly, e.g. in *Taxus*; or the exine is torn open in a place which takes up a definite position on the grain, e.g. *Pinus* and *Welwitschia*. In the first case the exine is of the same thickness throughout, in the second case one or more thinner places occur in the exine.

Data on the orientation of these thinner areas in the exine with regard to the position of the poles are to be found in Goebel (1923 p. 1538), who treats of the polarity of the microspores and gives two illustrations: of *Cycas* and of *Pinus*, in which the position of the poles has been given. Both the pollen tube of *Pinus* and the haustorium-tube of *Cycas* which is considered homologous with it, develop on the basal side of the grain, which has been schematically represented in fig. 5*g* for *Zamia* and fig. 5*h* for *Pinus*.

In the Gnetinae there appear for the first time pollen-grains with more than one place of exit. These places of exit are parallel grooves, the number of which amounts to about 6 in *Ephedra*, about 20 in *Welwitschia*. How their arrangement has been in the tetrade cannot be found in literature. This is probably owing to a late differentiation of the exine after the tetrade had already been broken up.

Thompson (1916) noticed this in *Gnetum*. In this case therefore we shall not be able to determine the arrangement in the tetrade in this way; there are, however, some arguments which make us suppose that we have to deal with meridian grooves of the primary form. The primary form is radial-symmetrical, so is the form of the mature pollen; if the axes of the two forms are the same, the grooves are meridian with respect to the primary form. A second argument for this orientation may be obtained from the arrangement of the nuclei in the pollen. In *Cycas* and *Pinus* the nuclei lie in the axis which joins the two poles, and if we assume the same for the *Gnetinae* the grooves lie parallel to the line passing through the nuclei and the orientation of places of exit has presumably been meridian with respect to the primary form. However in the orientation of these nuclei some complications occur, which may be explained as follows. For *Ephedra* Land (1904—1907) described the development of nuclei in the longitudinal axis of the pollen, followed by a shifting occurring during the germination, by which the prothallium-nuclei, however, maintain their original arrangement, the other nuclei stand perpendicular to the longitudinal axis of the grain. Different and less pure is the condition in *Welwitschia* and *Gnetum* where but two nuclei develop in the axis, as may be seen in Pearson's (1906) and Thompson's (1916) figures; subsequently they arrange themselves in a direction perpendicular to the longitudinal axis of the grain, that is the direction in which the pollen-tube develops.

Summarizing we find that the following holds good for the pollen of the *Gymnospermae*: the pollen can possess one or more places of exit; if there is one place of exit, it lies at the base of the grain (*Cycas* and *Pinus*), are there more places of exit (*Ephedra* and *Welwitschia*), they run parallel and should probably be taken as meridian grooves of the primary form.

§ 10. The arrangement of the places of exit in the Angiospermae.

In discussing the arrangement of the places of exit in the mature pollen in § 5 I already gave a short summary of the possibilities which occurred and now the question is in how far this arrangement is orientated with respect to the primary form of the pollen. The various possibilities mentioned sub § 5 will be discussed separately.

A. *Pollen with circular places of exit.*

1. With one place of exit. According to Fischer (1890) this occurs in *Typhaceae, Sparganiaceae, Gramineae, Restiaceae* and *Pandanus.* Warth (1925) describes the occurrence of very small abnormal pollen-grains with one place of exit in *Fuchsia.* It can likewise occur in the *Orchidaceae* by the side of species with a slit-like place of exit and in Drimys (figs. 6*a* and *b*).

2. With two opposite place of exit. According to Fischer's data only in the pollen of *Nidularium* and *Fuchsia.* As an exception it may occur in pollen which has normally three places of exit. In figs 6*c*, *d* and *e* the arrangement has been schematically represented according to observations of my own on tetrades of *Nidularium, Fuchsia* and *Myrica.* In all three cases the places of exit lie in an equatorial plane of the primary form.

3. With more places of exit lying in one plane. This case is very common with the dicotyledones whilst in the monocotyledones it rarely occurs, it occurs here according to Fischer only in *Anthurium.*

As far as known the arrangement of these places of exit in the tetrade is always in an equatorial plane of the primary form, which according to my own observation applies to the following plants: *Epilobium hirsutum, Myrica gale, Alnus glutinosa, Platycodon grandiflorum* and *Campanula carpatica.* Also in literature some data on this subject are known, a.o. for *Oenothera* (Warth 1925),

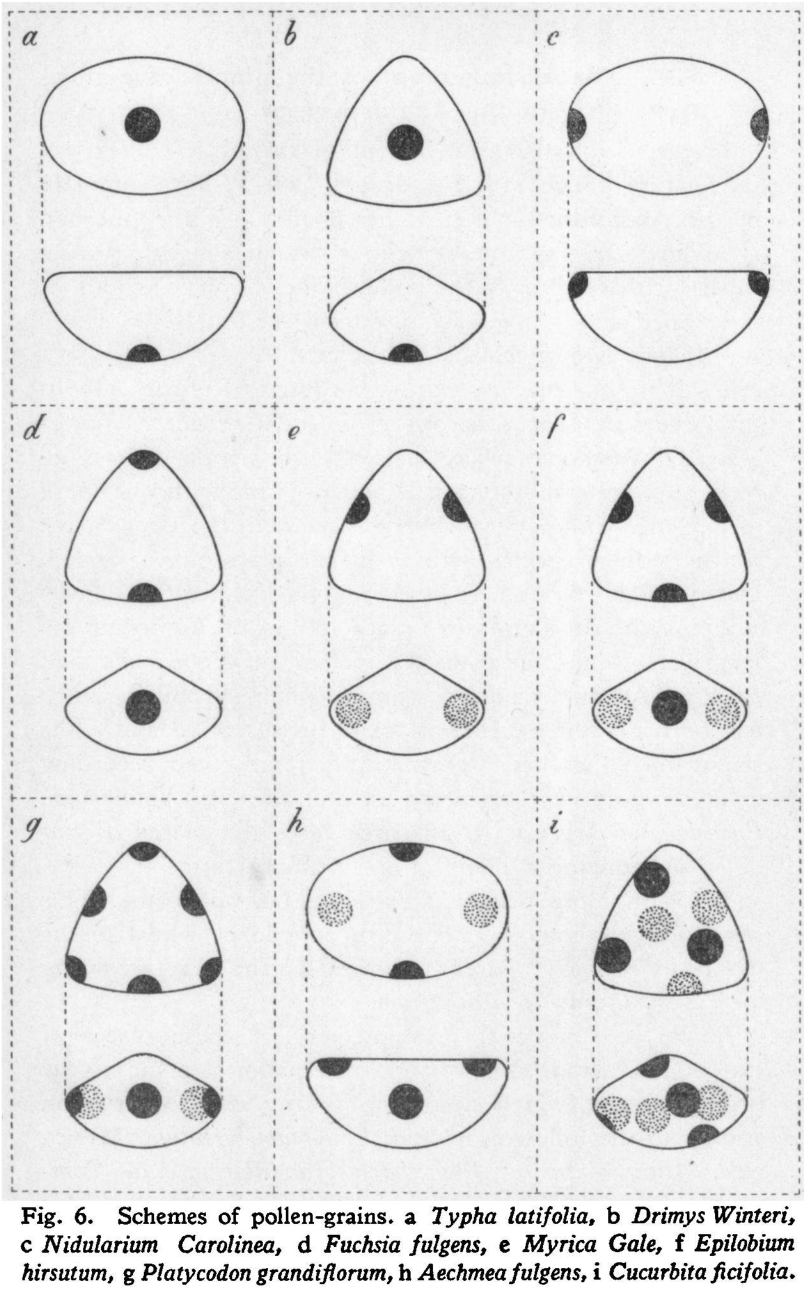

Fig. 6. Schemes of pollen-grains. a *Typha latifolia,* b *Drimys Winteri,* c *Nidularium Carolinea,* d *Fuchsia fulgens,* e *Myrica Gale,* f *Epilobium hirsutum,* g *Platycodon grandiflorum,* h *Aechmea fulgens,* i *Cucurbita ficifolia.*

Epilobium (Michaelis 1926) and for the tetrade-pollen of *Drosera* (Fischer 1890). In figs 6*f* and *g* this arrangement has been given for *Epilobium* and *Platycodon*.

4. With more places of exit spread regularly over the surface. In the pollen with a low number of places of exit the arrangement in the tetrade can as a rule be correctly determined, as soon, however, as we have to deal with numbers higher than ten, little can be determined and it can no more be decided whether we have to deal here with a fixed arrangement of the places of exit in the tetrade. For two cases I have determined the arrangement in the tetrade, viz. in *Aechmea fulgens* with four places of exit and *Cucurbita ficifolia* with six places of exit (Figs 6*h* and *i*). In *Cucurbita* the places of exit lie according to the faces of a cube, no definite arrangement, however, is to be observed in the tetrade. If small numbers of places of exit occur, they are mostly corresponding with elements of regular polyhedra.

In the pollen-grains with a greater number of places of exit the distances between them are about equal, only in some *Malvaceae* there is a visible variation in this distance. With the regular arrangements with a great number of places of exit each place of exit is surrounded by a definite number of others, usually six to five. This will be reverted to afterwards (photo 1).

B. *Pollen with slit-like places of exit (grooves)* in which are also included grooves which do not function as places of exit themselves, but bear a circular place of exit in the centre.

1. With one place of exit. Pohl (1928) gave a full description of this pollen, because he sees a phylogenetic characteristic in it; at the same time he also determined the orientation in the tetrade for one species, viz. *Curculigo* (fig. 7*a*). According to my own observation the same orientation occurs in the tetrades of Vriesea. It may

also occur in tetrade-pollen; so Schacht (1860) gives an illustration of a tetrade-grain of *Fourcroya gigantea*, where the groove lies on the basal side.

2. With two opposite places of exit. This case is very rare in normal pollen. According to Fischer's data, l.c. it was observed in the following species of plants: *Justicia*, *Crinum*, *Pontederia* and *Eichhornia*. The arrangement in the tetrade is not known.

3. With more parallel places of exit (meridian grooves).

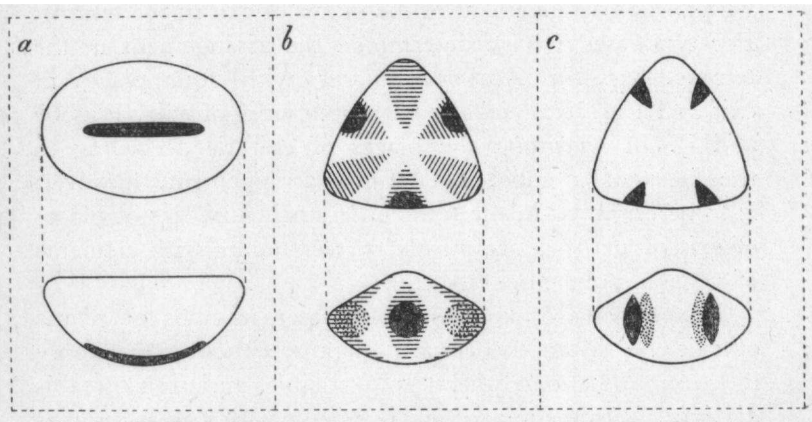

Fig. 7. Pollen-schema's of a *Curculigo spec.*,, b *Lythrum Salicaria*, c *Impatiens Sultani*.

This is very common with the *Dicotyledones*; with the *monocotyledones* it is according to Fischer only known in three varieties of the tulip, of which the arrangement in the tetrade is not known. In the observed cases in the *Dicotyledones* the orientation is such that the poles of the mature pollen coincide with the poles of the pollen in the tetrade, as I observed myself in the pollen of Impatiens and *Lythrum* (Figs 7*c* and *b*). Further this orientation occurs in the tetrade-pollen of *Ericaceae* and *Empetrum*.

4. With more places of exit spread regularly over the surface. According to Fischer l.c. this arrangement oc-

curs in some species of the following families: *Santalaceae, Phytolaccaceae, Portulacaceae, Ranunculaceae, Papaveraceae, Fumariaceae* and *Cactaceae*. A few cases excepted these grooves lie along the elements of regular polyhedra. According to Fischer we find along the six edges of a tetrahedron or the faces of a cube a.o. the pollen-grains of: *Thesium intermedium, Thesium alpinum, Epiphyllum truncatum, Caltha palustris, Adonis aestivalis, Papaver refractum, Corydalis ochroleuca* and *Corydalis nobilis*. Along the 12 edges of a cube or the faces a rhombic-dodecahedron would lie a.o. pollen-grains of *Rivinia humilis, Talinum patens, Ranunculus lanuginosus, Hepatica angulosa, Pulsatilla alpina, Corydalis capnoides* and *Platycapnos spicatus*. Along the thirty edges of a *pentagonal-dodecahedron Portulaca oleracea, Portulaca grandiflora* and according to von Mohl's data also *Fumaria spicata* and *Rivinia brasiliensis*.

A very common arrangement frequently occurring in pollen with four parallel grooves is according to Fischer the case in which the grooves converge towards the poles in pairs and lie in the faces of a regular tetrahedron, which is frequent a.o. in *Ranunculaceae*.

Exceptions to the arrangement in regular *polyhedra* seldom occur; the following possibilities are taken from the cases given by Fischer: *Platycapnos spicatus*, sometimes with 15 grooves following the edges of a regular pentagonal prism; *Sempervivum arachnoidum* normal with four parallel grooves, sometimes however, with eight grooves following the edges of a tetrahedral pyramid.

At present some exceptions remain to be discussed which deviate somewhat from the groups enumerated above. Two exceptions are to be found in Fischer, the first is *Neurada procumbens*, where in each of the meridian grooves two places of exit occur; the second exception form some grains, in which the grooves run over the surface in a faint spiral, or proceed parallel to each other in several rings. These cases may be regarded as deviations from the arrangement with meridian grooves, since we usually find transitions, as von Mohl (1837) described a.o. in *Hypericum, Oxalis crassicaulis* and *Mimulus moschatus.* The possibility of existence of pollen-grains with spiral grooves, however, has not been explained by this; it will be further discussed later.

Summarizing the data on the arrangement of the places of exit and the orientation of the pollen-grains in the tetrade, going by the few data which are known, we could state as follows: Three arrangements occur, viz.

a. with a basal place of exit.

b. with a number of places of exit which take up an equivalent position with respect to the two poles (equatorial or meridian arrangement).

c. with a number of places of exit regularly spread over the surface; of these no hard and fast rules are to be found concerning the arrangement in the tetrade; this arrangement often corresponds with the arrangement of the elements of regular polyhedra.

The orientation of the places of exit with respect to the edges of the primary form is usually determined most accurately for a low number of places of exit, though in variating or higher numbers this relation was not observed.

CHAPTER II.

VARIATIONS IN THE POLLEN-MORPHOLOGY.

§ 1. Material, method and mode of description.

From the groups mentioned in the previous section one or more examples, which have been described below, were selected in order to get an impression of the variations of the pollen-grains in one and the same species this selection, however, involved some difficulties, because no pollen-grains were to be found which varied in this respect when they normally possessed one or two places of exit. From the remaining groups the following species were selected, described in the sequence given below.

A. With more circular places of exit in an equatorial plane.
Alnus glutinosa,
Oenothera Lamarckiana,
Oenothera gigas,
Fuchsia globosa.

B. With more circular places of exit regularly spread over the surface.
Fumaria capreolata.

C. With more places of exit as meridian grooves.
Lythrum Salicaria,
Impatiens Sultani.

The material was taken from the Gardens of the botanical Laboratory of Groningen, except the material from *Oenothera* for part of which I am indebted to Prof. Stomps of Amsterdam, and from a number of plants of *Lythrum Salicaria* for statistical research, which came from the so-called Elsburger Onland in the neighbourhood of Groningen. The gathering of the material took place during the years 1928 and 1929, attention being paid to the fact that only pollen of sound, robust plants should be used; with a view to statistical research e.g. in *Lythrum* I also looked to it that the samples of pollen to be compared, were taken from flowers which took up an equivalent place in the inflorescence.

The pollen was examined in a dry and in a swollen state. The dry pollen was at once imbedded in Canada-balsam, a method Bodmer (1927) described for *Lythrum*; it also appeared to be practicable for most other species of pollen. In a desiccated condition pollen contains so little water that it does not make the Canada-balsam turbid, so that the balsam can be directly applied to the pollen. If need be the grains may be slightly stained by a previous fixation with iodine-alcohol 1 %, which is allowed to evaporate before the canada-balsam is added.

From the pollen which was examined in a swollen state the fat was first extracted with xylol and subsequently the pollen was stained with Fuchsin according to Fischer (1912). I set to work as follows: a thin layer of glycerine-albumen is spread over the centre of a slide and the pollen is stuck upon it; by this means the pollen is glued sufficiently to the slide and is not washed off during the staining. Next a drop of xylol was added to remove eventual oil-drops from the pollen; the xylol was made to drip out and for ten minutes the whole slide was put into a solution of fuchsin in alcohol (1 part of fuchsin in 10000 parts of alcohol 96 %); the fuchsin was made to drip out thoroughly; subsequently the preparation was imbedded in glycerine-jelly.

If the grains might have become too dark in staining or the colour too uniform, differentiation can be obtained by boiling the preparation under the cover-glass for a moment. This staining enables us to clearly distinguish the thicker and thinner places of the exine. With a view to difference in the state of swelling in different preparations the measures for statistical research were always taken of a single preparation.

The tetrade-stages were examined in water, glycerine, Sudan III (solution of ½ % Sudan III in a liquid consisting of equal parts of alcohol and glycerine) or fuchsin-glycerine 1 to 1000; the latter stain was used because it is extremely difficult to stain tetrades in the alcohol-fuchsin mixture.

The description of the pollen of the various species of plants was made from the subjoined scheme, for which I am indebted to Prof. Dr. J. W. Moll; before long it will be published by him elsewhere. The description of the contents of the pollen, however, was immaterial to me, so that the latter part of the scheme which for the sake of completeness has been rendered here entirely, was omitted in the description; so were communications concerning the germination.

Guiding scheme for the description of pollen.

1a composition of pollen.
- *2a* dusty powder.
- *2b* more coherent powder.
- *2c* diplopollen.
- *2d* tetrade-pollen.
- *2e* pollen sectile.
- *2f* pollinium.
  - *3a* pollinium proper.
  - *3b* caudicle.
  - *3c* adhesive disc *(rostellum)*.

1b external characters of pollen-grains.
- *2a* general shape, dimensions, colour and statistical data.
- *2b* surface.
  - *3a* general characters.
  - *3b* grooves.
    - *4a* a single one.
    - *4b* more than one.
      - *5a* meridian.
  - *3c* bands and creste of more considerable dimensions.
  - *3d* slighter projections: warts, spines, etc.
  - *3e* places of exit.
    - *4a* number, one, two, three or larger numbers
    - *4b* arrangement.
      - *5a* one place of exit.
        - *6a* acrosiphonic.
        - *6b* basisiphonic.

5b more than one place of exit.

6a equatorial arrangement.

6b scattered over the surface.

1*c* organographic contents.

2a prothallium of numerous cells.

2b a single prothallium cell and a single antheridium cell, the latter ultimately producing a tube cell and two spermatozoids.

2c two prothallium cells and a large cell, the latter producing a tube cell and two male cells or nuclear cells.

2d a large tube cell and a antheridium mothercell, ultimately producing two male or generative cells, prothallium cells lacking.

1*d* germination.

2a pollentube branches and functions as a haustorium.

2b pollentube unbranched and forming a passage for the male cell towards the egg-cell.

If the arrangement of the pollen in the tetrade is known, a pollen-scheme will be added to the description; at the same time the bibliographical data will be given.

The dimensions of the pollen-grains were taken in a 450 × magnification with the aid of a drawing-prism and a measure. In the radial-symmetrical pollen the length of the symmetry-axis was measured (axis) and the diameter of the equator of the grain (diameter), which has been rendered in fig. 8*a*; if, however, the grains were spherical only a diameter was given without further data. In the bilateral symmetrical pollen I likewise measured the length of the symmetry-axis (axis) and further the longest and the shortest diameter of the equator (diameter 2 × 3); all three dimensions have been given in fig. 8*b*, respectively 1, 2, 3. If not otherwise stated the measures have been taken on grains which after fuchsin-staining were imbedded in glycerine-jelly. The primary form in the tetrade was measured in the same way as the ripe grains.

For the description of the grains in the tetrade, however, the above scheme did not suffice; it was supplemented by me with a separate brief scheme for the tetrade.

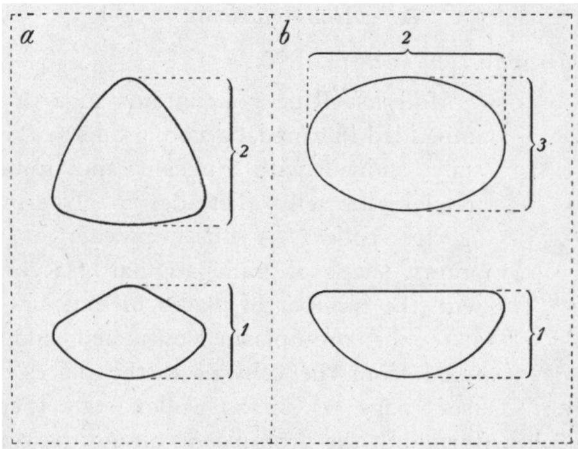

Fig. 8. Dimensions of pollen-grains.
1 axis, 2 and 3 diameter.

Guiding scheme for the description of tetrades.

1*a* partition.
- 2*a* simultanic.
- 2*b* succedanic.

1*b* arrangement.
- 2*a* parallel.
- 2*b* crosswise.
- 2*c* tetrahedrical.

1*c* daughter-cells description as in ripe grains.

Finally some remarks on the photographs made of the preparations stained with fuchsin.

A Zeiss' Homal was used; to prevent chromatic aberration Kodak-filters were employed, that is a green-filter (B), if a strong contrast was desired, and a yellowfilter (G), if less strong contrasts were desired. The photographs were taken on Eosin-silber-plates of Perutz.

§ 2. Descriptions of pollen-grains with a variating number of places of exit.

A. *Alnus glutinosa.*

Bibliography. Fischer, 1890.

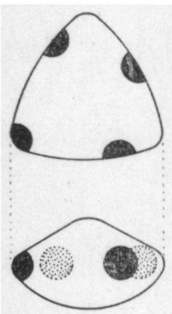
Fig. 9. Pollen-scheme of *Alnus glutinosa.*

Material. Ripe pollengrains in a dry state imbedded in canadabalsam, grains in a swollen state stained with Fuchsin and imbedded in glycerine jelly. Tetrades in glycerine.

Ripe pollen. A dusty powder of single grains, shape of grains angular in accordance with the number of places of exit; in a dry state the protoplasm contracted and separated from the cellwall at the places of exit (see page 9), in a swollen state the same form but the protoplasm joining the cellwall. Dimensions taken in a dry state lying between 20 to 25 μ. One grain with 6 places of exit with a diameter of 30 μ. Colour of grains yellow.

Surface smooth. Places of exit 4—6 in the following percentage:

4 places of exit .... 48,55 %
5 places of exit .... 51,27 %
6 places of exit .... 0,18 % Total counted 552 grains.

Arrangement of places of exit equatorial (see scheme).

Tetrade. Partition simultanic, arrangement tetrahedrical. Daughter-cells having the form of a spherical tetrahedron. Places of exit equatorial; no relation to the edges observed.

B. *Oenothera Lamarckiana.*

Bibliography. Mohl, 1834. Fritsche, 1837. Renner, 1919. Boedyn 1925—1928. Fischer, 1890.

Material. Grains in a dry state imbedded in canada balsam and grains in a swollen state stained with fuchsin and imbedded in glycerine-jelly. Dimensions were taken without places of exit, because their variation in arrangement and size might probably complicate statistical data. Tetrades in water and fuchsin-glycerine.

Ripe pollen. Grains cohering by a fibrous substance. Single grains in two modification viz. as normal swollen fertile grains and wrinkled sterile grains. The percentage being about 50 % after Boedyn (1925). Shape angular according to the number of places of exit. Colour yellow. Surface smooth with a circular band round the base of each place of exit. Exine consisting of two layers, separating only in wrinkled grains.

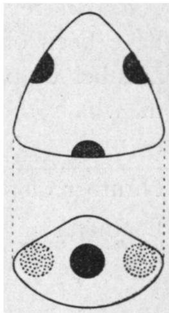

Fig. 10. Pollen; scheme of *Oenothera Lamarckiana.*

Places of exit:

a. In wrinkled grains 1—3 places of exit have been observed, though one case must be mentioned of a grain by which no place of exit at all was observed; the diameter of this grain was about 70 μ. Dimensions in relation to the number of places of exit are given in the following table in which the dimensions of single grains are rounded to multiples of 5 μ.

Number of places of exit	1	2	3
Diameter in μ	4 × 20 7 × 25 5 × 30 4 × 35	4 × 35 2 × 40 6 × 45 5 × 50 2 × 55 1 × 60	5 × 55 7 × 60 7 × 65 1 × 70
	545	910	1220
Average dimensions	27,25	45,5	61

Form of places of exit, if not wrinkled, semi-spherical with a diameter of about 40 μ, with exception of the grains with one place of exit where it may be down to 20 μ. and than having the same dimensions as the grain itself and only to be distinguished from it by the band round its base and the thinner exine at the apex.

Arrangement of places of exit equatorial, see scheme.

b. In fertile swollen grains only three places of exit have been observed by me. Dimensions in relation to the number of places of exit are given in the following table, in which the diameters of the single grains are rounded to multiples of 5 μ.

Number of places of exit	3
Diameter in μ	1 × 85
	6 × 90
	9 × 95
	3 × 100
	1 × 105
	1885
Average dimension	94,25

Form of the places of exit is semi-spherical with a diameter of 50—70 μ. Arrangement of places of exit equatorial.

Tetrade. Partition simultanic. Arrangement of daughter-cells tetrahedrical. Primary form of pollen a spherical tetrahedron, though sometimes more than four daughter-cells occur, than resulting in a different primary form for some grains. Arrangement of places of exit equatorial, placed between the edges (see scheme), diameter about 18 μ., axis about 15 μ.

C. *Oenothera gigas.*

Photo 2, 3, 4, 5, 6.

Bibliography. Renner, 1919. Warth, 1925. Boedyn, 1925—1928.

Material. Pollengrains in a dry state imbedded in canadabalsam and grains in a swollen state stained with fuchsin and imbedded in glycerine-jelly. Dimensions were taken without the places of exit because they vary in arrangement and size so that they may complicate statistical data.

Ripe pollen. Grains cohering by a fibrous substance. Single grains in two modifications, viz. as normal swollen fertile grains and as wrinkled sterile grains. Shape angular according to the number of places of exit. Colour yellow. Surface smooth with a circular band round the base of each place of exit. Exine consisting of two layers which may separate only in wrinkled grains.

Places of exit:

a. In wrinkled grains 1—5. Dimensions in relation to the number of places of exit are given in the following table in which the dimensions of the single grains are rounded to multiples of 5 μ.

Number of places of exit	1	2	3	4	5
Diameter in μ......	4 × 20	3 × 35	2 × 45	3 × 65	1 × 70
	5 × 25	5 × 40	3 × 55	4 × 70	4 × 75
	10 × 30	6 × 45	5 × 60	4 × 75	2 × 80
	1 × 35	5 × 50	6 × 65	3 × 80	3 × 85
		1 × 55	3 × 70	2 × 85	3 × 90
			1 × 80	2 × 90	4 × 95
				2 × 95	2 × 100
					1 × 105
	540	880	1235	1555	1740
Average dimensions.	27	44	61,75	77,75	87

Of each group 20 grains were measured. The form of places of exit, if not wrinkled is semi-spherical with a diameter of about 40 μ. with exeption of the grains with one place of exit where it can be down to 20 μ. In grains with such a low number of places of exit the places of exit may have the same diameter as the grain itself. Arrangement of places of exit equatorial.

b. Fertile swollen grains with 3—5 places of exit and a maximum of grains with 4 places of exit (photo 5, 6). Dimensions in relation to the number of places of exit are given in the following table, in which the dimensions are rounded to multiples of 5 μ.

Number of places of exit	3	4	5
Diameter in μ	1 × 90	2 × 95	1 × 100
	8 × 95	2 × 100	2 × 105
	5 × 100	1 × 105	1 × 110
	4 × 105	4 × 110	4 × 115
	1 × 110	1 × 115	4 × 120
	1 × 115	4 × 120	2 × 125
		3 × 125	4 × 130
		3 × 130	1 × 135
			1 × 140
	1995	2295	2405
Average dimensions	99,75	114,75	120,25

From each group were taken 20 grains. Form of places of exit semi spherical with a diameter of 50—70 μ. Arrangement of places of exit equatorial, sometimes, one or two small places of exit are formed (15—25 μ.) lying not in the equator but in a plane parallel to it, or instead of one normal place of exit two smaller places of exit are formed lying close to each other.

Such cases as mentioned above are drawed by Boedyn (1925), These exeptions, though rare, occasionally also occur in wrinkled grains.

Tetrade. No tetrades were observed by me, but according to Warth (1925) an irregular reduction-division often takes place; the daughtercells in this case are not of the same size. To that reason fig. 11 has been copied from Warth (1925); it shows a tetrade with six daughtercells in which the places of exit are equatoriably arranged.

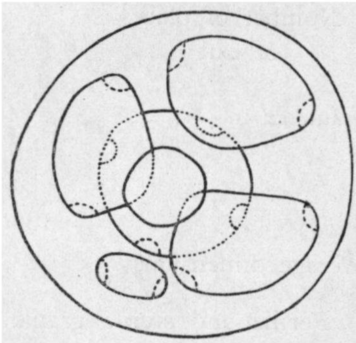

Fig. 11. Tetrade with 6 daughtercells from which the places of exit are visible (after Warth).

D. *Fuchsia globosa.*

Photo 7, 8.

Bibliography. Fischer, 1890. Beer, 1921. Warth, 1925.

Material. Ripe pollengrains in a swollen state stained with fuchsin and imbedded in glycerine-jelly. Tetrades in fuchsin-glycerine. Dimensions of the ripe grains were taken without the places of exit.

Ripe pollen. Single grains slightly cohering. Shape depending on the numberof places of exit, equatorial plane polygonal in accordance with the number of places of exit. Dimensions, axis 10—50 μ. diameter 10—60 μ. Colour grayish-white Surface smooth with 0—4 semi spherical places of exit arranged in an equatorial plane.

The dimensions of the grains in relation to the number of places of exit are given in the following table. Only ten grains of each group were counted because the pollengrains with no places of exit were very rare. Dimensions were rounded to multiples of 5 μ.

Number of places of exit	0	1	2	3	4
Diameter in μ	3 × 10 7 × 15	3 × 15 6 × 20 1 × 25	4 × 30 5 × 35 1 × 40	3 × 40 4 × 45 3 × 50	3 × 50 4 × 55 3 × 60
	135	180	335	450	550
Average dimensions ..	13,5	18	33,5	45	55

Fertile and sterile grains can not be distinguished in preparations stained with fuchsin and imbedded in glycerine jelly, because they are all in the same normal, swollen state.

Tetrade. Partition simultanic; reduction-division according to Beer (1921), by which a varying number of daughtercells are formed in a tetrade.

According to Warth (1925) there also occur so called „Riesenkörner" formed out of the whole pollenmothercell and distinguished from the other grains by their size and the occurrence of 4 places of exit. In my pollensamples, however, there was a transgressive variability as is to be seen in table above and therefore I do not see any reason to treat them separately, though I can share Wart's opinion that there may occur pollengrains that take up nearly the whole or the whole contents of the pollenmothercell.

Arrangement of daughtercells in accordance with their number.

E. *Fumaria capreolata.*

Photo 9, 10, 11.

Bibliography. Fischer, 1890.

Material. Ripe pollengrains in a dry state imbedded in canada-balsam and grains in a swollen state stained with fuchsin and imbedded in glycerine-jelly. Tetrades in water and sudan III.

Ripe pollen. Grains slightly cohering. Shape polyhedrical in connection with the number of places of exit. Diameter 25—50 μ. Colour white. Surface smooth with a thick band round the base of each place of exit. Places of exit semi spherical, number 6—12 in the following percentage, counted from 200 grains.

Places of exit...	6	7	8	9	10	11	12
Percentage	62,5	3	14,5	2,5	1,5	1	15

In the grains with 6, 8 or 12 places of exit, the arrangement is in accordance with the faces of endospherical or less regular polyhedra, respectively cube, tetragonal trapezohedron, octahedron, rhombic dodecahedron and pentagonal dodecahedron. In the other cases the same arrangement can occur with the absence of one or more places of exit, in the remaining cases not such an arrangement could be observed and here the places of exit regular spread over the surface in that way that each place of exit has about the same distance to the nearest ones. In the following table the relation between the dimensions and the number of places of exit is given for the grains with 6, 8 and 12 places of exit. Dimensions were taken without the places of exit and rounded to multiples of 5 μ.

Number of places of exit ..	6	8	12
Diameter in μ.	1 × 25 2 × 30 14 × 35 3 × 40	1 × 30 8 × 35 10 × 40 1 × 45	13 × 40 6 × 45 1 × 50
	695	745	840
Average dimensions	34,75	37,25	42

Tetrade. Partition simultanic, arrangement parallel or tetrahedrical, no places of exit could be observed in this stage.

F. *Lythrum Salicaria.*

Photo 12, 13, 14.

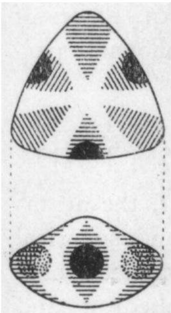

Fig. 12. Pollen-scheme of *Lythrum Salicaria.*

Bibliography. Mohl, 1834. Darwin, 1892. Tischler, 1918. Bodmer, 1927. Schoute, 1928.

Material. Ripe pollen-grains in a dry state imbedded in canada-balsam and grains in a swollen state stained with fuchsin and imbedded in glycerine-jelly. Tetrades in water and in sudan III. Dimensions were taken from the protoplast and not from the external shape in accordance with Schoute (1928). The different sorts of pollen will be indicated as follows:

pollen-grains from longest stamens of short-styled form .... Kl
pollen-grains from mid-length stamens of short-styled form .... Km
pollen-grains from longest stamens of mid-styled form .... Ml
pollen-grains from shortest stamens of mid-styled form .... Mk
pollen-grains from midlength stamens of longstyled form .... Lm
pollen-grains from shortest stamens of longstyled form .... Lk

Ripe pollen. A dusty powder of single grains. Shape in a dry state ellipsoidical with 6, sometimes with 8 and rarely with 4 meridian grooves; every other groove with a circular place of exit in the middle. In a swollen state spherical with 6, sometimes with 8 and rarely with 4 meridian bands, dividing the grain in a number of area with a thinner exine. Every other thin place with a circular place of exit in the middle. Bands mostly but not always meeting at both poles of the grain.

Dimensions:

Ml and Kl axis 31—35 μ, diameter 30—35 μ.
Lm and Km axis 20—22 μ, diameter 20—23 μ.
Lk and Mk axis 17—20 μ, diameter 17—21 μ.

The following table of the diameters of pollen-grains after immersion in glycerine is copied from Schoute (1928).

Average dimensions; one anther was taken of each of four plants and from each anther measured 12 grains.

Lm.... 21,3 μ.	Ml ....30,6 μ.	Kl .... 32,2 μ.
Lk .... 19,7 μ.	Mk.... 19,7 μ.	Km.... 21,4 μ.

Colour of Kl and Ml green, pollen of other stamens yellow. Surface smooth. Places of exit 3, sometimes 4 or rarely 2. Four places of exit are especially found in Kl and Ml and are rare in the grains of other stamens; two places of exit occur now and than in short stamens; and one case must be mentioned in which I found a grain with two places of exit in a mid-length stamen. The percentage of grains with four places of exit was counted from nine flowers of every form, these flowers were taken from different plants. From each sample 50 grains were counted. In the following table the samples belonging to the same flower are placed in pairs in a vertical direction.

Kl:	2 %	0 %	6 %	0 %	28 %	0 %	0 %	0 %	0 %
Km:	0 %	0 %	2 %	0 %	0 %	0 %	0 %	0 %	0 %
Ml:	0 %	12 %	0 %	0 %	0 %	0 %	0 %	0 %	12 %
Mk:	0 %	0 %	0 %	0 %	0 %	0 %	0 %	0 %	0 %
Lm:	0 %	0 %	0 %	0 %	0 %	0 %	0 %	0 %	0 %
Lk:	0 %	0 %	0 %	0 %	0 %	0 %	0 %	0 %	0 %

From this we may not conclude that grains with four places of exit do not occur in mid-length and shortest stamens; for instance they are found in Mk from a plant growing in the botanical gardens of Groningen, which shows some grains with four places of exit in Mk and a large number of such grains in Ml.

Tetrade. Partition simultanic. Arrangement of daughtercells tetrahedrical. Primary form of pollen a spherical tetrahedron, grooves meridian, places of exit equatorial and between the edges. No arrangement in relation to the edges could be observed, if four places of were formed. Tetrade of Ml axis 10 μ., diameter 18 μ.

G. *Impatiens Sultani.*

Photo 15, 16, 17.

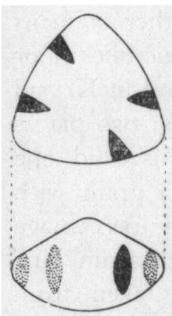

Fig. 13. Pollen-scheme of *Impatiens Sultani.*

Bibliography. Fischer, 1890. v. Mohl, 1834.

Material. Ripe pollen-grains in a dry state imbedded in canada-balsam and grains in a swollen state stained with fuchsin and imbedded in glycerine-jelly. Tetrades in fuchsin-glycerine.

Ripe pollen. Single grains slightly cohering. Shape depending on the number of places of exit. If four places of exit are existing, the equatorial plane is rectangular, the sides proportionally 1 : 2 : 1 : 2, see photo 15. If five places of exit occur the equatorial plane is pentagonal, the sides proportionally 1 : 1 : 2 : 1: 1, see photo 16. If six places of exit occur the equatorial plane is hexagonal, the sides all equal, see photo 17. Meridian planes oval or circular, axis 35—40 μ. diameter 25—45 μ. × 40—55 μ. Colour pink. Surface reticulate with 4—6 slitlike places of exit arranged in an equatorial plane. The percentage is to be seen in the following table:

number of places of exit ...	4	5	6
number of grains counted ..	158	98	19
percentage	57	36	7

275 grains were counted.

The sides of the equatorial plane always take up about $^1/_6$ or $^1/_8$ of the circumference, though there was some variation as may be seen in the following table, in which the dimensions of the sides of 20 grains with four places of exit are given. Dimensions rounded to multiples of 5 μ.

50	25	50	25.
50	20	50	20.
40	20	40	20.
40	20	40	20.
45	20	45	20.
50	20	50	20.
45	25	45	25.
45	20	45	20.
45	20	45	20.
35	15	35	15.
45	20	45	20.
50	20	50	25.
40	20	40	20.
45	20	40	20.
50	20	50	20.
50	25	55	20.
45	20	45	20.
50	25	50	25.
45	25	45	25.
50	25	50	25.

Average long side 45,75 μ. Average short side 21,25 μ.

A curve of this table is to be seen in fig. 17. Possibly a part of the variation is due to the fact that it is impossible to know of each grain if the equatorial plane is exactly horizontal.

Tetrade. Partition simultanic; arrangement parallel or tetrahedrical, form of pollen a spherical wedge or a spherical tetrahedron, axis 15 μ. diameter 15 × 25 μ. Places of exit equatorial, but no connection with the edges has been observed, see scheme.

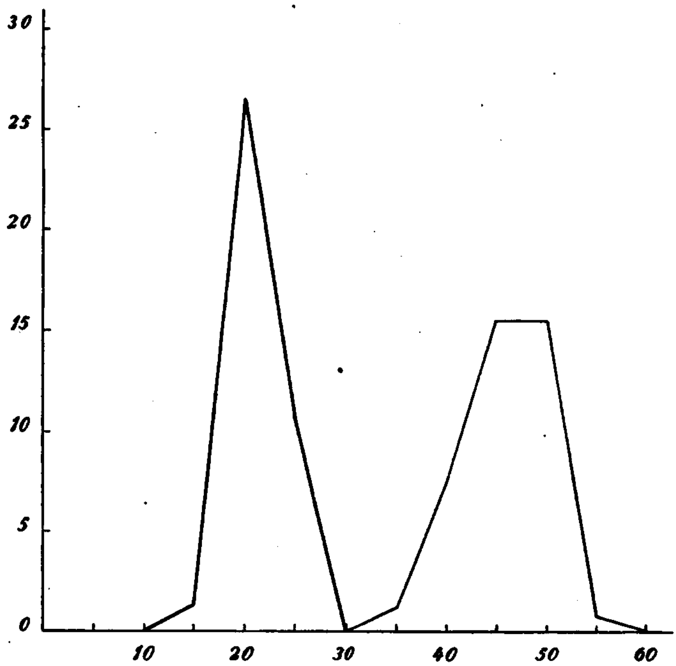

Fig. 14. Impatiens Sultani. Curve of the side-length. On the abscis the length of a side in μ on the ordinate the number of cases observed.

§ 3. The possible variations.

Before discussing the data more fully, I wish to conclude some general rules concerning the course of development of the variations, as they appeared in the various species.

In the first place the fact that with variation in number of places of exit, regularity is preserved, that is, that the distance between every two places of exit remains about equal. If, for instance, we have to deal with a variation of 3—5 places of exit in an equatorial plane, the places of exit of the pentamerous and tetramerous grains are as well equidistant as the trimerous ones, or expressed differently: the trimerous axis of symmetry which is perpendicular to the equatorial plane passes respectively into a tetramerous or pentamerous axis, when variation occurs. Also with pollen-grains, in which the places of exit are regularly spread over the surface the equidistance with respect to the nearest places of exit is preserved. Herewith the conditions necessary for arrangements according to the elements of regular polyhedra (endospherical symmetrical group) may have been established. Afterwards this will be discussed more fully.

The rule of equidistance, though there can be a little variation in distances, which could be observed in the variation of the seven described forms, holds also good for nearly all pollen-grains which possess more places of exit, irrespective the presence or absence of variation. This appears from the accurate descriptions Fischer (1890) and Mohl (1834) gave of a great number of pollen-grains. Of the very few varying species to which this rule apparently did not apply, as *Myrica Gale* and *Impatiens Sultani*, I selected *Impatiens Sultani* and included it into the other descriptions. It appeared that the grains which are normally provided with four places of exit in the equator, situated at distances in the ratio 1 : 2 : 1 : 2, may also vary, in which case they are, when 6 places of exit occur, perfectly equidistant in an equatorial plane (photos No. 15, 16, 17). This indicates an initially regular arrangement, in which for some reason or other one or more places of exit did not develop, so that the spot in question was left vacant. In this case we had better speak of a complication than of an exception to the regular arrangement. The same phenomenon may occasionally occur in a grain of *Fumaria*; for instance a regular arrangement according to the faces of a dodecahedron is present, while one of the 12 places of exit are lacking, leaving one place vacant. Taking into consideration that we find an occasional grain in which instead of a single place of exit there are two small coherent ones *(Oenothera gigas)*, we have in my opinion, brought tot the fore all complications of the regular equidistant arrangement.

A second point of discussion is a variation not in number, but in arrangement of the places of exit in pollen-grains. It may occur that an equal number of places of exit is grouped in a different way, as for instance grains with four equatorial places of exit in which occasionally grains appear in which the places of exit lie according to the planes of a tetrahedron. Among the forms described we find this variation in *Fumaria*, in which in the grains with 12 places of exit two arrangements are possible, that is according to a pentagonal-dodecahedron and a rhombendodecahedron.

Therefore the rule of equidistance may be defined about as follows: *If a pollen-grain has two places of exit, they are diametrically opposed; if there are more, they may either be regularly spread over the surface with equal mutual distances between them or the arrangement is in an equatorial plane with equal distances between them and an equivalent position with respect to the poles.* If grains occur with an arrangement according to various parallels of latitude on both sides of the equator, transitions are found between the equatorial arrangement and the arrangement in which they are regularly distributed. Equidistance, therefore, is the rule for pollen-grains with more places of exit, irrespective as to whether this number is fixed or varying.

§ 4. Connection between the size of the pollen and the number of places of exit.

In species of a varying number of places of exit there usually exists a strong correlation between the size of the grains and the number of places of exit, in that sense that the grains with a greater number of places of exit possess a greater diameter than the grains with a smaller number of places of exit. Fischer (1890) also observed this and remarks as follows: „Gewöhnlich sind Körner mit verminderter Faltenzahl kleiner, mit vermehrter Faltenzahl grösser als die typischen; so fand ich bei *Arnica Chamissonis* dreifaltige Körner von 24 μ. Durchmesser an, mehrfaltige bis zu 64 μ."

One need only look at the photographs of *Oenothera* and *Fuchsia* to convince oneself of this correlation. The question, however, is what value must be attached to this correlation and for this reason I worked out quantitatively the data for the two forms of *Oenothera* for *Fuchsia* and for *Fumaria*.

Of each group of grains respectively containing 1, 2, 3, etc. places of exit an equal number of grains were measured, which has been represented in the following tables. The measures of a table have all been taken of one preparation, because the state of swelling may vary in the different preparations. The number of grains measured, therefore, was limited by the group which was in the minority.

The mean error of the various tables was now computed for each group and next the mean error of the difference between the groups. For the mean error we have the following formula.

$$m = \frac{\sqrt{\dfrac{\Sigma p \times Dev^2}{\sqrt{n-1}}}}{\sqrt{n}}$$

In this formula *m* is the mean error, *p* the number of individuals of one length-interval, *Dev* the deviation of a length-interval from the average and *n* the total number of individuals of the group. For the mean error of the difference of two groups the following formula was used: $m(\text{diff}) = \sqrt{m_1^2 + m_2^2}$, the difference lying between plus or minus 3 times the mean error. The calculations were made with a sliding-rule.

Subjoined are found the values as computed from the various tables.

Page 33.

Oenothera Lamarckiana. Wrinkled grains.

Number of places of exit	Average dimensions
1	27,25 ± 1,1 μ.
2	45,5 ± 1,6 μ.
3	61 ± 1 μ.

Page 34.

Oenothera Lamarckiana. Swollen grains.

Number of places of exit	Average dimensions
3	94,25 ± 1,1 μ.

Page 35.

Oenothera gigas. Wrinkled grains.

Number of places of exit	Average dimensions
1	27. ± 1 μ.
2	44 ± 1,3 μ.
3	61,75 ± 1,5 μ.
4	77,75 ± 2,2 μ.
5	87 ± 2,1 μ.

Page 36.

Oenothera gigas. Swollen grains.

Number of places of exit	Average dimensions
3	99,75 ± 1,3 μ.
4	114,75 ± 2,6 μ.
5	120,25 ± 2,4 μ.

Page 38.

Fuchsia globosa.

Number of places of exit	Average dimensions
0	13,5 ± 0,7 μ.
1	18 ± 1 μ.
2	33,5 ± 1 μ.
3	45 ± 1,3 μ.
4	55 ± 1,3 μ.

Page 39.

Fumaria capreolata.

Number of places of exit	Average dimensions
6	34,75 ± 0,8 μ.
8	37,25 ± 0,8 μ.
12	42 ± 0,7 μ.

For the wrinkled grains of the two forms of *Oenothera Lamarckiana* and *Fuchsia globosa* the differences and their mean errors have been united in the subjoined table:

Oenothera Lamarckiana, pag. 33.

Difference between 1 and 2 places of exit	18,25 μ.	± 2,0 μ.
Difference between 2 and 3 places of exit	15,50 μ.	± 2,0 μ.

Oenothera gigas, pag. 35.

Difference between 1 and 2 places of exit	17 μ.	± 1,6 μ.
Difference between 2 and 3 places of exit	17,75 μ.	± 2,0 μ.
Difference between 3 and 4 places of exit	16 μ.	± 2,6 μ.
Difference between 4 and 5 places of exit	9,25 μ.	± 3,0 μ.

Fuchsia globosa, pag. 38.

Difference between 0 and 1 place of exit	4,5 μ.	± 1,3 μ.
Difference between 1 and 2 places of exit	15,5 μ.	± 1,5 μ.
Difference between 2 and 3 places of exit	11,5 μ.	± 1,6 μ.
Difference between 3 and 4 places of exit	10 μ.	± 1,8 μ.

In the wrinkled grains of the two forms of *Oenothera,* therefore, the difference, V, amounts to circa 17.5 μ and in *Fuchsia globosa* circa 13,5 μ. Starting from one of the middle groups and every time diminishing the average diameter with the full amount of this difference, V, we find as a theoretical average diameter of grains with 0 places of exit an amount about equal to half the value of V and for 1 place of exit the value of $1\frac{1}{2}$ V, so that the following equation may be drawn up for the average diameter of a group:

Diam. aver. = $V \times (a + \frac{1}{2})$, in which *a* represents the number of places of exit of the group in question.

Seeing that grains with 0 places of exit must have an average diameter of $\frac{1}{2} \times V$ and grains with one place of exit a diameter of $1\frac{1}{2} \times V$, we have obviously to associate a diameter from $0 \times V$ up to $1 \times V$ with the occurrence of 0 places of exit and likewise a diameter of $1 \times V$ to $2 \times V$ with the occurrence of 1 place of exit.

In the subjoined table this has been synoptically represented and at the same time the value of the diameter has been given when *a* places of exit occur.

Length of the diameter in V	Number of places of exit.
$0 \times V$ to $1 \times V$	0
$1 \times V$ to $2 \times V$	1
$2 \times V$ to $3 \times V$	2
$3 \times V$ to $4 \times V$	3
$a \times V$ to $(a + 1) \times V$	a

This relation between the length of the diameter of the pollen and the number of places of exit deduced from the above data may be tested at a correlation-graph, in which the theoretical line has also been given. Figs. 15 and 16.

It only remains to be explained why the average value of the groups lying at the extremities of the range of variation, approximates more or less the total average, which in my opinion is not only possible, but necessarily following from the curve for the variability of the length of the diameter of the grains. Fig. 17.

In fig. 17 the length of the diameter and the number of individuals have been plotted on the coordinates and

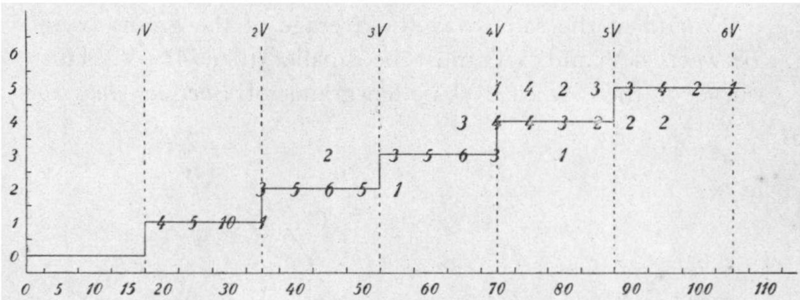

Fig. 15. *Oenothera gigas,* wrinkled grains. Correlation table between the diameter of grains and the number of places of exit. In accordance with the theoretical formula, Diam. = (a to a + 1) $\times$ V, a theoretical line has been given. On the abscis the diameter of grains in μ on the ordinate the number of places of exit.

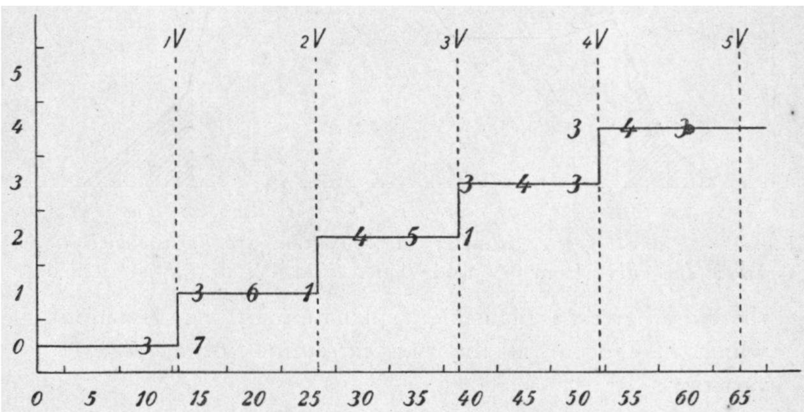

Fig. 16. *Fuchsia globosa.* Correlation table between the diameter of the grains and the number of the places of exit. In accordance with the theoretical formula, Diam. = (a to a + 1) $\times$ V, a theoretical line has been given. On the abscis the diameter of the grains in μ, on the ordinate the number of places of exit.

further the length of 1 × V, 2 × V, 3 × V, etc. is indicated with a vertical dotted line.

It is now obvious that the average of a number of grains lying between 0 × V and 1 × V must be greater than ½ V and in the same way the average of the grains lying between 4 V and 5 V must be smaller than 4½ V. This curve of the size of 100 pollen-grains of *Fuchsia globosa,*

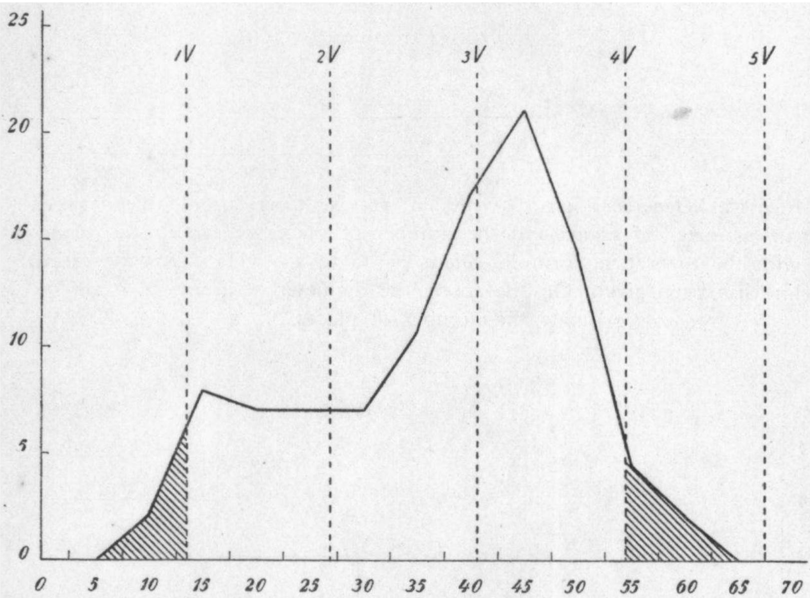

Fig. 17. Curve of the diameter of 100 grains of *Fuchsia globosa.* A part of the curve from 0 V to 1 V and from 4 V to 5 V is hatched.

therefore, gives a plausible explanation of the deviations which may occur at the two extremities of a range of variation.

This removes the objection that might be raised against the deviation from the fixed difference in the extreme variation-groups and from this it follows at the same time, that in determining the fixed difference (V) we should start from the middle groups of a range of variation.

If the variability is very slight, so that there are e.g. a great number of grains with *a* equatorial places of exit and a small number with $a+1$ equatorial places of exit, we had better, with a view to the deviations discussed above, not compute *V* from the average diameter, but deduce a theoretical *V* from the limit formed between the diameter of the large grains with *a* and the small grains with $a+1$ places of exit. The calculations can for instance be made according to the following formula:

$$V = \frac{\text{Diam.}_{\text{(l.a. aver.)}} + \text{Diam.}_{\text{(sm. a + 1 aver)}}}{2 \times (a+1)}$$ in

which Diam. (l.a.aver.) represents the average diameter of a number of large grains with *a* places of exit and Diam. (sm. (a + 1) aver) the same for a similar number of small grains with $a+1$ places of exit. It should, however, be borne in mind that this *V* is never so accurate as the one obtained according to the other method.

Now the question is in how far the typical relation described above between the size of the pollen and the number of places of exit obtains for other species with equatorial arrangement. I traced this in *Lythrum* and *Alnus*; in *Lythrum* because it shows a difference in size of the pollen-grains connected with *heterostylism* and I initially thought that this did not tally with the variability. I also chose *Alnus*, because of its showing little difference in size in relation to variability.

In *Lythrum* we notice that beside the ordinary trimerous grains there also occur tetramerous ones. They specially belong to the Ml and Kl. groups. In his material Schoute (1928) observed a frequent occurrence of such tetramerous grains in Ml, a rare occurrence in Kl, Lm, Mk and absence in Lk and Km. As it appeared to me that the different plants rather varied in this respect I composed a table (pag. 38) from which it appears that tetramerous grains only occurred here in Ml and Kl and one exceptional case in Km; for the rest the greater part of the samples of pollen possessed no tetramerous grains. Seeing that Ml and Kl forms the group with the largest grains, one might theoretically expect that the averages of Ml and Kl approximate the value 4 × V and since these averages lie at circa 30 μ, 3 × V must approximate 22 μ, that is about the size of *m* and *k*; therefore we may here expect the occurrence of dimerous grains, as far as difference in size is due to differences in the tetrade grains and not to differences in size originating after the formation of places of exit. I was indeed much surprised not to find them in the beginning, but on close inspection it appeared, that dimerous grains do occur in *m* and *k*-pollen; that the longitudinal axes of these grains, however, lay horizontally and on account of that they were not to be distinguished from the trimerous ones. When the grains are rolled under the cover-glass of a liquid preparation, they may be recognised (see photo 12). Of the percentage little can be said, seeing the difficulties attending the finding of the grains. *Lythrum*, [1]) therefore, does not make an exception to the relation between size of the grains and number of places of exit observed in *Oenothera* and *Fuchsia*, nor is this the case in *Alnus*.

Alnus has grains with 4 and 5 places of exit in an equatorial plane, the tetramerous and pentamerous grains which occur in about an equal proportion hardly differ in size: diameter 20 to 25 μ. Only one grain with 6 places of exit occurred and this was distinctly larger, viz. 30 μ, which again lies within the bounds of theoretical possibility (*V* is in this case about 4½ μ).

It must be mentioned here that if grains are varieing in the number of places of exit and do not vary much in size for the reason mentioned above, one must be very careful

[1]) It is possible that a part of the difference in size is originating after the tetrade formation.

in statistical data, because the arrangement of the places of exit can be the origin of systematic faults in measuring. Than they may complicate the data, especially when the difference between the size of the grains is small; when we take for instance grains with 3 and 4 places of exit with the same diameter, than the latter ones will have a greater circumference etc.

This is the reason why I made no statistics of the grains with four and five places of exit of *Alnus glutinosa.*

On turning to the forms in which not all the places of exit have the same position with respect to the poles, but are regularly distributed over the surface, we see that in the described form of this group, that is *Fumaria capreolata* the number varies from 6 up to and including 12 places of exit, the grains with 6, 8 or 12 places of exit being most common. On computing the averages of these three groups, we arrive, just as with *Oenothera* and *Fuchsia,* at a positive difference; this difference, however, does not fit in with the formula: Diam. aver. $= V \times (a + \frac{1}{2})$. This may be easily understood considering that the equatorial circumference of a sphere is directly proportional to the diameter, while a spherical surface is directly proportional to the squared diameter. Indeed it appears that this applies to the table of *Fumaria* and the relation between the diameter of the pollen and the number of places of exit may be represented in this case by the following formula:
Diam. aver. $= V \times \sqrt{a + \frac{1}{2}}$; at the same time we may say with regard to grains with *a* places of exit, that the diameter must be found between the values $V \times \sqrt{a}$ and $V \times \sqrt{a + 1}$. In the correlation-table fig. 18 just as in the other correlation-tables the theoretical line has been given.

It should, however, be borne in mind that in the range of variation 6 to 12 only 6, 8 and 12 places of exit are common, so that the average value of all grains with 6 places of exit lies between 6 and 8 or Diam. aver. = $\pm$ V $\times$ $\sqrt{7}$.

Finally a special case should be discussed here. It may occur in the large grains of *Oenothera gigas*, that beside a number of places of exit in an equatorial plane, either some are added lying between this equatorial plane and the poles, or the places of exit do not lie so exactly in the equatorial plane as is the case with grains of the

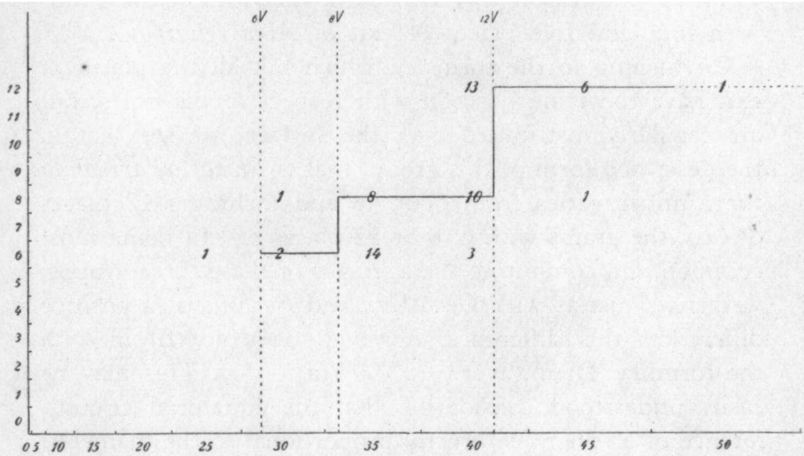

Fig. 18. *Fumaria capreolata.* Correlation-table between the number of places of exit and the squared diameters. In accordance with the theoretical formula for 6-8, 8-12 and more than 12 places of exit a line has been given. On the abscis the squared diameters of the grains, on the ordinate the number of places of exit.

same species with a lower number of places of exit. So it appears that greater proportions of space at the equatorial zones may run parallel with a less exact equatorial arrangement or with the occurrence of an arrangement which already begins to resemble a distribution of the places of exit over the whole surface.

Summarizing we may say that the variation in number of places of exit in the above-mentioned pollen-grains with equatorial arrangement, viz. *Oenothera* and *Fuchsia* is directly proportional to the diameter or to the equatorial circumference of the grains; and that when the places of exit are regularly distributed over the surface *(Fumaria)* the number is proportional to the square of the diameter or to the surface of the grains.

§ 5. The genetic base of the number of places of exit and its variation.

The occurrence of some grains with 2 or 4 places of exit beside the normal grains with three places of exit in *Oenothera Lamarckiana* leads Boedyn (1925—1928) to decide on a fluctuating variability. The grain being trimerous he takes as a genetic character: „Die dreieckige Pollenform mit einer grossen Keimpore an jeder Ecke ist typisch für die *Oenotheraceae* und ebensogut ein erbliches Merkmal, wie z.b. die gelbe Blüthenfarbe bei den *Subgenera Oenothera* und *Onagra*." The fact that in the Gigas-form an average of 4 places of exit occurs instead of 3 or of double the number, that is 6, Boedyn tries to explain by picturing to himself that two trimerous ones cohere along one of the sides.

The reverse of Boedyn's opinion is Warth's (1925) derived from observations on pollen-grains of *Fuchsia*; he sees a close connection between the number of chromosomes and the number of places of exit. Various species from the genus *Fuchsia* were examined by him, from which it appeared that species with 22 chromosomes formed pollen with two places of exit, species with circa 44 chromosomes on the other hand pollen with three places of exit, sometimes mingled with tetramerous grains. Further he observes, just like Beer (1921) a thing which in my opinion is of great importance: that variation is associated with abnormal reduction-division. Then the chromosomes are unequally distributed and the result is the occurrence of tetrades with a deviating number of daugther-cells differing in size (Beer 1921 in *Fuchsia*). This phenomenon is confirmed by an observation of Michaelis (1926) on *Epilobium*, where on exposure to extremely low temperatures an abnormal reduction-division can artificially be obtained, while grains occur with a number of places of exit deviating from the normal number. As such abnormal reduction-divisions were also observed in *Oenothera Lamarckiana* and *gigas*, (Davis 1911), it is easily understood that Warth p. 242 ascribed the variation to them. „Daraus scheint mir hervorzugehen, dasz, was Boedyn als fluktuierende Variabilität bezeichnet, nichts anderes ist als Unregelmäszigkeiten der Reduktionsteilung." Warth traced this in *Oenothera gigas* and actually found that tetrades occurred with more than 4 daugther-cells and that these daugther-cells which varied in size, also varied as to the number of places of exit (see fig. 11, borrowed from Warth p. 243). Of the direct or indirect relation between number of chromosomes and number of places of exit Warth writes as follows: „Es ist vielmehr durchaus möglich, dasz für die Erhöhung der Keimporenzahl ein anderes kausales Moment vorliegt. Bei der Entstehung der Gigas-Formen scheint dies aber immer gleichzeitig mit der verdoppelten Chromosomenzahl zustande zu kommen. Inwieweit es selbständig ohne gleichzeitige Verdoppelung der Chromosomenzahl auftreten kann, müssen erst weitere Untersuchungen lehren."

The pollen-grains of *Lythrum Salicaria* seem to me to be a case in which the number of chromosomes and the genetic constitution is the same for the two sorts of pollen of a flower, East (1927), while a distinct numeric variation occurs in the places of exit: 2 to 3 places of exit in the pollen from the short and mid-length stamens, 3 to 4 places of exit in the pollen of the long stamens. In this case, therefore, an important variation occurs without change in the number of chromosomes or differences in the genetic constitution. The correlation between the size of the pollen and the number of places of exit, however, is preserved as well in this case, as in the species with abnormal reduction-division or polyploidy.

According to Fischer (1890 p. 54) different numbers of places of exit can also occur between the pollen of both sorts of stamens of *heterodistylic Primulaceae*, the grains themselves also differing in size. In his description of pollen with more than 3 meridian grooves he describes this phenomena as follows „Die Faltenzahl bei den um etwa ein Dritteil kleineren Körnern der kurzen Staubfäden geringer als bei den grösseren. Es besitzt der grosse Pollen von *Primula elatior* 6, auch 5 oder 7, *P. acaulis* 7, auch 8 oder 6, *P. officinalis* 7 oder 8, *P. anglica* 9, auch 8, selten 10 Falten; der kleine Pollen hat 5 bis 6, selten 7 Falten bei *P. officinalis* und *elatior*, 6, selten 5, bei *P. anglica*, 5, auch 6 oder 4 bei *P. acaulis*." This is much resembling the facts that are observed in *Lythrum*, though in comparing the pollen-grains of *Primula* we always must take pollen from genetically different plants, so this differences are not so proving as in the case of *Lythrum* were pollen from both sorts of stamens can be taken from the same flower.

As the size of the grains and the number of places of exit are so typically correlated they may be substituted for each other in some cases and in polyploidy or abnormal reduction-division the chromosomes-plasmrelation becomes an important factor in determining the number of places of exit. Seeing, however, that the number of places of exit varies discontinually and the size of the pollen more continually, we have a worse standard for judging the number of chromosomes in the number of places of exit than in the size of the pollen. When in gigas-forms a circa twofold increase in volume of the cells is found, we may expect that the number of places of exit of the pollen-grains of the gigas-form is about $\sqrt[3]{2} \times$ that of the normal form, when the places of exit lie in an equatorial plane. If a represents the number of places of exit of the normal haploid pollen, we might expect a number of (a to $a + 1$) $\times$ 1,26 in diploid grains. If, for instance, we have to deal with haploid grains bearing three places of exit in an equatorial plane, we may expect in the diploid grains of the same species a number amounting to 3 up to and including 5, which tallies with the data on *Oenothera* (Boedyn 1925), *Solanum nigrum* and *Solanum Lycopersicum* (Jörgensen 1928), *Cleome spinosa* (Ufer 1929).

So when with abnormal reduction-division the grains with a lower number of chromosomes are smaller and bear fewer places of exit than those with a higher number (Warth 1925, Michaelis 1926), it is most probable that the chromosome-plasm-relation is expressed in the same way as with the occurrence of polyploidy, that is $\frac{Chr}{Chr_1} = \frac{Vol}{Vol_1}$. Substituting we can give the ratio of the number of chromosomes and the number of places of exit as follows: $\sqrt[3]{\frac{Chr}{Chr_1}} = \frac{a \text{ to } a+1}{a_1 \text{ to } a_1+1}$, for grains with an equatorial arrangement. From this we may compute for a definite species how many places of exit a pollen-grain must possess, which has received but one chromosome in the reduction-division, representing, therefore, the smallest grain imaginable for that species. For *Oenothera* this value lies between 1 and 2 places of exit, in *Fuchsia* between 0 and 1 places of exit, which might serve as an explanation of the fact that in *Oenothera* we never find grains with 0 places of exit, in *Fuchsia*, however, we do. It must, however, be pointed out that the ratio of chromosomes and size of the cell does by no means always satisfy the ratio underlying the above formulas (v. Wettstein 1927), and that the above values should only be regarded as a very rough approximation.

In the described species, in which a strong variation was observed, which might run parallel with changes in the number of chromosomes *(Oenothera)* or with difference in a physiological respect *(Lythrum)* one thing remained constant in a definite species, viz. the proportion between the size of the grain and the number of places of exit, that is the value V for pollen-grains with places of exit in an equatorial plane, and V^2 for grains where the places of exit are regularly distributed over the surface. With a view to this I should wish to supplement Boedyn's conception (1928) this the number of places of exit is genetically determined, in that sense, *that the proportion between the size of the pollen and the number of places of exit is genetically determined and that a great variation in the number of places of exit especially comes about in such cases where factors are present which greatly influence the size of the pollen,* as, for instance, a change in the number of chromosomes or a difference in size of the pollen in heterostylism.

In the normal pollen in which the size of the grains does not vary much, but little variation of the number of places of exit is to be expected. In my opinion, therefore, it is easily understood that the number of places of exit was considered the most important character. As soon, however, as abnormal reduction-division or polyploidy were observed, this view could not be maintained and this gave rise to attaching a great value to the number of chromosomes (Warth 1925) with the occurring variation of the number of places of exit, or to finding another explanation, as in my opinion, Boedyn (1928) does, when he considers the possibility that the pollen of *Oenothera gigas* has risen from the coherence of two haploid trimerous grains.

Finally it should be observed that views concerning polyploidy and number of places of exit can only be applied to polyploid-varieties and not to polyploid-species, in which the genetic constitution may already vary considerably. This, for instance, appears from some observations by W a r t h that species of *Fuchsia* with an equal number of chromosomes and an equal number of places of exit may possess pollen-grains rather divergent in size.

CHAPTER 3.

THE CAUSES OF THE VARIABILITY AND THE ARRANGEMENT.

When in the preceding sections the correlation between the size of the pollen and the number of places of exit is considered more closely, it follows from the theoretical formulas that no additional place of exit arises before a certain exess of space is available in the equatorial circumference or on the whole surface. If one further considers that all places of exit are at about equal distances from their neighbours (equidistance), the idea naturally suggests itself that each place of exit takes up a certain space. Calling this space which is controlled by a place of exit an area, we might assume, *that the number and the arrangement of the places of exit on a pollen-grain depend on the way in which a maximal quantity of areas can be distributed in the equator or over the surface.*

If the above view is correct, the number of places of exit occurring in nature and their arrangement will have to correspond with constructions of point-systems on a sphere or on a body approaching nearest to the somewhat rounded primary form of the pollen, for instance a flattened rotation-ellipsoid in case of the sphaero-tetrahedron and a lengthened rotation-ellipsoid in case of a spherical wedge. We shall now begin with a discussion of the point-systems possible on the sphere. After that it will be considered in how far these point-systems will deviate when constructed upon the above-mentioned rotation-ellipsoids.

§ 1. The point-systems possible on the sphere.

A point-system on a sphere satisfying the condition that each point must be at an equal distance from the surrounding ones, may be represented best by touching circles, the centres of which form the points of the system. There are two kinds of systems to be considered for pollen-grains: firstly systems for a number of points which are at equal distances to the nearest points and all points of which are at equal distances from two places in the system (the poles), that is with an equatorial arrangement and secondly systems in which the points are regularly distributed over the surface at equal distances from the nearest other points.

The different values may be indicated by the following letters: p is the radius of the touching circles on the sphere, R is the radius of the sphere and a the possible number of places of exit or points of the point-system.

I. Point-systems in an equatorial plane. The condition for each point is an equal distance to two diametrically opposed points of the sphere: the poles, and equidistance. The result is a number a of circles in the equator according to the formula $\frac{\pi R}{p} = a.$, when the minimum diameter is assumed for that number of circles (for p the spherical radius has been taken). The symmetry of the point-system is here an „a-merous" symmetry-axis, passing through the two poles and a symmetry-plane perpendicular to it and coinciding with the plane in which all points of the point-system lie, while moreover each point of the point-system sends out a dimerous symmetry-axis and lies in a symmetry-plane passing at the same time through the „a-merous" axis. With the symbols used in crystallography fig. 19 gives the symmetry-elements for a system in which $\frac{\pi R}{p} = 3.$

II. Point-systems over the entire surface of the sphere, as only condition equidistance of the nearest points. In order to get an idea of this we had best start from one point of the system and see how many other points can lie around it, when $\frac{R}{r}$ is made to vary from 0 to infinite, if *R* represents the radius of the sphere, when a minimum diameter is assumed for that number of circles and *r* the linear distance from the spherical centre of a circle to the circumference. Up to and including three places of exit this runs parallel with the previous group. If $\frac{R}{r} = 0$ to $\frac{1}{2}$ not a single circle can be drawn, if $\frac{R}{r} = \frac{1}{2}$ to $\frac{1}{2}\sqrt{2}$ one circle is possible, if $\frac{R}{r} = \frac{1}{2}\sqrt{2}$ to 1 two circles are possible, which may touch over their entire circumference, if $\frac{R}{r} =$ exactly $\frac{1}{2}\sqrt{2}$. If $\frac{R}{r} = 1$ up to and including 1.1, each circle can only be touched by two others. If $\frac{R}{r} = 1.1$ to 1.3, each circle can maximally be touched by 3 others. If $\frac{R}{r} = 1.3$ to 1.8 each circle can maximally be touched by 4 others; from 1.8 upwards 5 touching circles are possible. Six touching circles are only possible in a plane, that is if $\frac{R}{r}$ is infinitely great.

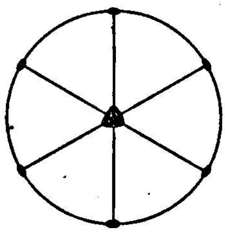

Fig. 19. Symmetry-elements for a system in which $\frac{\pi R}{p} = 3$.

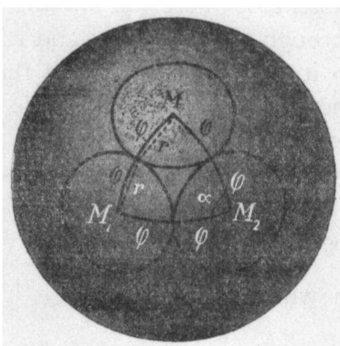

Fig. 20.

In fig. 20 this has been represented once more. If two circles with radius *r* (in this case the distance from the spherical centre to the circumference) touch on the sphere with radius *R*, the arc-distance of the spherical centres M_1, M_2 has a certain value $2\ \varphi$ which grows smaller according as *R* (*r* constant) increases. When 2 such circles with centres M_1 and M_2 touch both each other and the circle with M_3 as centre, these centres form an equilateral spherical triangle with sides $2\ \varphi$. The angle α of this spherical triangle only depends on φ and decreases according as φ decreases, so R increases.

Special values and limits of α are:

$\alpha = \frac{2\ \pi,}{6}$ for R = ∞ and likewise $\frac{R}{r} = \infty$.

$\alpha = \frac{2\ \pi,}{5}$ when M_1, M_2, M_3 are centres of adjoining lateral faces of a regular dodecahedron. $\frac{R}{r} = \pm 1.81$.

$\alpha = \frac{2\ \pi}{4}$ when M_1, M_2, M_3 are centres of adjoining lateral faces of a cube. $\frac{R}{r} = \pm 1.30$.

$\alpha = \frac{2\ \pi,}{3}$ when M_1, M_2, M_3 are centres of adjoining lateral faces of a regular tetrahedron. $\frac{R}{r} = \pm 1.09$.

$\alpha = \frac{2\ \pi,}{2}$ when M_1, M_2, M_3 are centres of an equilateral triangle, which can be described in a large circle. $\frac{R}{r} = 1.00$.

For $\frac{R}{r} = \frac{1}{2}\sqrt{2}$ two touching circles are possible, each taking up half a sphere.

$\frac{1}{2}\sqrt{2} = \pm 0.71$.

When $\frac{R}{r} = 0.5$ there is just room for 1 circle on the sphere; when, however, $\frac{R}{r}$ grows still smaller not any circle with radius *r* is possible.

The total number of circles imaginable on the sphere, of course also depends on the ratio $\frac{R}{r}$, in this way, that when a great number of circles are possible, the number may be roughly approximated by the value $4\left(\frac{R}{r}\right)^2$, which therefore gives the proportion of the size of the surface of the sphere and the surface of a circle. This proportion, of course, does not quite hold, because πr^2 does not exactly represent the surface of a circle on the sphere and moreover there always remains a certain vacant space between the touching circles. Further the arrangement of the circles is of great importance, especially as there are certain very advantageous possibilities of arrangement for circles on a sphere, which for the lower numbers often correspond among others with regular polyhedra, viz. tetrahedron, cube and pentagonal-dodecahedron. [1])

This even goes so far that when there is room on a sphere for five circles, six may always be constructed according to the faces of a cube. This can be proved when it is demonstrated that five circles are impossible for $\frac{R}{r}$ between 1.09 and 1.30, which is again proved when we can demonstrate that when $\frac{R}{r}$ is smaller than 1.30, not more than 4 circles are possible. This may be conceived as follows: Supposing there was room for 5 circles with $\frac{R}{r} < 1.30$, the centres of the touching circles must have a spherical distance of

[1]) Together with Octahedron and Icosahedron, these are the only five possible regular so-called endospherical polyhedra. Jaeger (1917).

$2\varphi < \frac{\pi}{4}$, that is the radii of the sphere passing through two centres of touching circles form an angle $> 90°$. If we adopt the centre of one of the circles as Southpole, the southern hemisphere and the equator are excluded for the rest of the centres M_2, M_3, M_4 and M_5 and all these centres must lie in the northern hemisphere. If M_2 is a centre touching the circle with M_1 as centre, we can, taking M_2 as a pole, mark out another area within which M_3, M_4 and M_5 must lie. For these three centres a space is left smaller than a spherical quadrant. If we assume a circle with M_3, touching M_1 and M_2, a space is left for M_4 and M_5 smaller than a spherical octant, in which no two points can occur for which a radius passing through these points forms an angle larger than 90°. So a maximum of 4 touching circles is possible. As soon, however, as the above-mentioned angle diminishes to 90° or less, so $\frac{R}{r} > 1.30$, 6 circles are possible.

So the total number of circles possible on a sphere with *r* constant and *R* varying depends not only on these two but also on the most advantageous arrangement of the circles on the surface of the sphere.

The possible number of circles up to 13 with varying *R* has been represented in a graphical representation (fig. 21), which was obtained by experimentally describing touching circles on a rubber sphere. In this we see that the greatest space of the range of variation is occupied by 1, 2, 4, 6 and 12 possible circles, further in a less degree by the possibility of 8 and 3 circles and a very small space by the remaining 7, 9, 10 and 11; some of these latter numbers were not obtained at all, which of course, does not prove that these, as was the case with the number 5, are lacking.

In connection with Fig. 21 we might assume that if we had 1000 spheres the radius of which varied with regular intervals from 0 × r to 2 ×r; on every sphere touching circles are drawn with *r* as radius (distance spherical centre

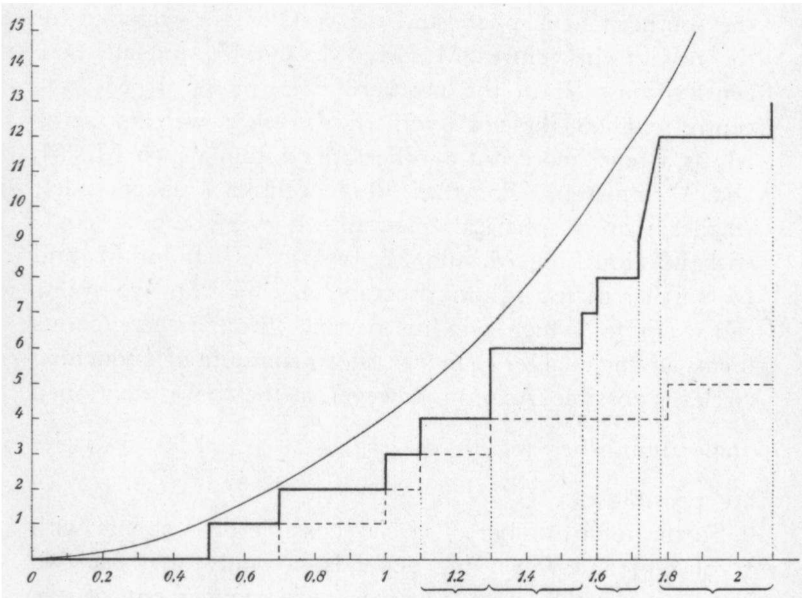

Fig. 21. On the ordinate the number of circles, on the abcis the ratio $\frac{R}{r}$. The dotted line gives the maximal number of circles that is possible touching to one. The thick line gives the total number of circles possible on the sphere. The thin line gives the relation between the surface of the sphere and the surface of a circle. The range of the value $\frac{R}{r}$ corresponding with 4, 6, 8 and 12 circles has been indicated with accolades.

to circumference) and the question is asked what percentage of these spheres can be provided with respectively 0, 1, 2, 3, etc. touching circles. The percentages will about have to correspond with the subjoined table, derived from fig. 21.

25 % with 0 circles.
10 % with 1 circle.
15 % with 2 circles.
5 % with 3 circles.
10 % with 4 circles.
0 % with 5 circles.
14 % with 6 circles.
1 % with 7 circles.
6 % with 8 circles.
4 % together for possibilities from 9 up to and including 11 circles.
10 % with 12 circles.

Of the arrangement of these circles on the sphere we can say that up to and inclusive of 3 circles this point-system corresponds in number and arrangement with the above-mentioned point-systems in an equatorial plane. With 4 up to and including 12 points, however, it behaves quite separately, and as far as 4, 6, 8 and 12 points occur, we get arrangements which more or less approximate to an arrangement of the faces of one of the regular polyhedra as tetrahedron, cube, octahedron, pentagonaldodecahedron or other polyhedra as rhombic-dodecahedron, tetragonal trapezohedron and possibly others.

From 12 upwards there is little to be said about the arrangement; round each circle on the sphere there is too little room for six others and ample room for five. On the above-mentioned rubber sphere I made a construction for a value $\frac{R}{r}$ = ca 7.2, from which it appeared that a maximum of 156 circles could be described on this sphere. It appeared that every circle on this sphere was touched by a maximum of 5 other circles, as might be expected, but that on our examining the centres of these circles my first impression was quite different. Though each circle can have only 5 touching circles, there is so

much room left that a sixth circle can come very near the central circle. On estimating the distance from the centres of the surrounding circles to the central circle with the eye, these distances seem perfectly equal and we think we have to deal with an arrangement of 6 points situated at equal distances from one central point. To the eye the points on this sphere lie in groups of 6 or 5 or 4 points around each other; usually, however, 6 or 5, while the theoretical amount varies from 2 to 5 with an optimum of 5.
III. Transitions between the systems on the whole surface and the systems in an equatorial plane. By these I understand those systems in which points are only possible above a certain distance from the poles. If this distance approaches to the equator the system quite satisfies the conditions of systems in an equatorial plane. If this distance, which will be called q for convenience' sake, amounts to 0, the system satisfies the same conditions as a system regularly spread over the surface of the sphere. The only thing that can be said of these systems is, that they can be the cause of a seemingly irregular arrangement of the points somewhere near an equatorial plane, or the occurrence of points on various parallels of latitude.

With a view to the primary form of the pollen we shall also have to ask ourselves in how far the above-mentioned systems can deviate, when we picture them on a body corresponding more with the primary form of the pollen than the sphere does; so for instance a flattened rotation-ellipsoid for the radial symmetrical primary form of the pollen and a lengthened rotation-ellipsoid for the bilateral symmetrical primary form of the pollen. For the systems expressed in I and III, so with equatorial or sub-equatorial arrangement the deviation will not be worth mentioning, only the proportion to the axes is no more so simple. For the systems expressed sub II occupying the whole surface of the sphere this may cause slight modifications, so that for instance an arrangement with a maximum of 5 can actually exist without six touching circles being imaginable. Further we may expect here that an arrangement with 2 or 3 points on the surface will lie in a plane intersecting the ellipsoid according to the greatest circumference. In a flattened rotation-ellipsoid this plane lies perpendicular to the rotation-axis, for a lengthened rotation-ellipsoid the rotation-axis itself lies in this plane. With respect to the higher numbers it seems to me, that, but for some slight modifications in arrangement, these systems fairly correspond with those which were described in the above-mentioned group II, especially as to numbers of points above 12, when again the same questions arise of the number of touching circles possible for one single circle.

The arrangement of the circles, as is mentioned above, is always regular when a minimum R for a certain number of circles is given, when however R is to large for a circles and to small for $a+1$ there is some space vacant on the surface of the sphere. This space can now more or less regular be divided between the cirkels. When there are many circles the space, which is then very small in relation to the whole surface, will not cause visible changes in the arrangement of the points of the system. When however smaller numbers occur, it is possible that the distribution of this space causes visible irregularities in the arrangement. If we suppose that there is room for 4,9 circles on the surface, only four circles can be formed and a space according with the remaining part must be divided between those four circles. In the majority of the cases this will not cause visible changes in the arrangement of the points, it can however occur that the whole or nearly the whole space is divided between only two circles and than beeing visible to the eye and causing an irregularity in the regular arrangement.

§ 2. The correspondence of the point-systems with the number and the arrangement of the places of exit of the pollen-grains.

In accordance with the point-systems in an equatorial plane we may expect in pollen-grains with equatorial arranged places of exit or places of exit as meridian grooves, that all whole numbers to start with 0 are among the possibilities, the arrangement is regular, though the occurrence of some grains with irregularities especially in lower numbers is possible. As to the second group of point-systems distributed over the whole surface we may expect, that the number of places of exit as far as it does not exceed 12, will most probably be among one of the numbers of the following series: 0, 1, 2, 3, 4, 6, 8, 12, of which the places of exit up to and including 3 lie in one plane, hence correspond with the equatorial systems, while upwards of 3 the places of exit are distributed over the surface, and up to and including 12 they frequently approach to the arrangement of regular and symmetrical polyhedra. Upwards of 12 we can only say that every place of exit may be surrounded by a maximum of 5 others, that, however, owing to the proportion of space a sixth circle which nearly touches, cannot be told from the others with the eye, so that the observation of the grains must satisfy the condition that no more than 6 places of exit may occur at equal distances from a central one. For the grains with a sub-equatorial arrangement we may expect that the arrangement in outline satisfies the conditions of the equatorial systems; that the arrangement, however, will be more irregular and that we may also expect the occurrence of places of exit according to one or more parallels of latitude.

These possibilities I have compared with the descriptions Fischer (1890) gave of the pollen of about 2200 species of plants. About 1720 of them possess 0 up to and including three places of exit, of which the di- and trimerous ones are arranged as equatorial circular places of exit or as meridian grooves. There are about 210, having more than three places of exit equatorially arranged or as meridian grooves. In about 260 species the places of exit are distributed over the surface. The rest, about 15, partly consist of forms the meridian grooves part of which are fused into one or more rings encircling the grain; and forms in which, though the centre of a groove has an equatorial position, yet the direction of the grooves is not meridian but more or less spiral. The numbers of places of exit and the arrangement which Fischer gives, square on the whole very well with the numbers and the arrangement of the points of the point-systems described; this also obtains for the data and the illustrations which von Mohl 1834 gives of a great number of pollen-grains.

I shall restrict myself, however, to giving some examples from Fischer's descriptions, of pollen-grains admitting of the same possibilities as the point-systems described above; and next mention which possibilities are common or rare, or have not been observed at all, and finally discuss those pollen-grains which do not satisfy the above-mentioned possibilities.

a. Pollen-grains with a single place of exit, either circular or slitlike. These are frequent in the *Monocotyledones*, for instance, in *Gramineae*, *Liliaceae* with cognate families, etc.; further in some *Coniferae*; in the *Dicotyledones* they are only mentioned in *Piper decurrens*, *Nuphar luteum*, *Magnolia obovata*, *Talauma pumila*, *Drimys Winteri*.

b. Pollen-grains with two opposite places of exit occur in *Nidularium* and in *Fuchsia fulgens*, in *Pontederia cordata*, *Eichhornia azurea*, *Crinum asiaticum*, *Justicia elongata* and some others. They also occur as exceptions in the grains where there are normally three places of exit, for instance *Phaseolus vulgaris*.

c. With three circular places of exit in one plane or three places of exit as meridian grooves. They are very common with the *Dicotyledones* and very rare with the *Monocotyledones,* where they have only been given for the following species: *Tulipa oculis solis, Clusiana, Gesneriana* and some *Araceae*. Among the *Dicotyledones* Fischer observed about 1350 species in which this occurred.

d. With more than three places of exit in an equatorial plane or more than three places of exit as meridian grooves. Fischer describes about 210 cases, all of which belong to the *Dicotyledones* except a few *Araceae* and two *Gnetaceae*. So *Alnus glutinosa* has 4 to 5, *Platycodon grandiflorus* 5 to 6, rarely 7, *Pinguicula vulgaris* 6 sometimes 7 to 8, *Galium boreale* 7 or sometimes 6, *Galium Mollugo* 8, *Asperula orientalis* 9, *Sherardia arvensis* 10, *Richardsonia scabra* 10 also 11 and 12, *Polygala vulgaris* 11 to 12, *Polygala Chamaebuxus* 11 to 19 as a rule 15 to 17, *Polygala myrtifolia* 21 to 24 places of exit.

e. With four places of exit regularly distributed over the surface of the grain: *Scirpus, Aechmea fulgens* and besides the normal grains with three places of exit of some *Ranunculaceae,* among others *Ficaria ranunculoides*. Arrangement approximating the faces of a tetrahedron.

f. With five places of exit regularly distributed over the surface. Not found, only as an exception in *Aechmea fulgens*.

g. With six places of exit regularly distributed over the surface, among others in *Basella rubra, Ranunculus lingua, acer, repens, granatensis, Corydalis ochroleuca, glauca, nobilis*. The arrangement is according to the faces of a cube, or expressed differently as the angular points of an *octahedron* or the edges of a *tetrahedron*.

h. With 7 places of exit regularly distributed over the surface. Not given as a normal number of any species, only here and there where the number is varying, as for instance in *Sida triloba* 4 to 8 and also according to my own observation in a small percentage in the grains of *Fumaria capreolata.*

i. With 8 places of exit regularly distributed over the surface. Occurring among others in *Clematis patens, Macleya cordata, Sida herbacea, Gossypium herbaceum.* A variable number can also occur, as for instance in *Cucurbita Pepo* with usually 6, sometimes, however, 7 to 8.

j. With 9 up to and including 11 places of exit regularly distributed over the surface. No special numbers given; some examples, however, mentioned as for instance *Sagittaria montevidensis* 8 to 10, *Gypsophila paniculata* 10 to 12.

k. With 12 places of exit regularly distributed over the surface. *Tunica prolifera, Dianthus nitidus, Gypsophila repens* and some other *Caryophyllaceae*; further *Rivinia humilis, Talinum patens, Corydalis lutea, Platycapnos spicatus.* Arrangement, when given, always according to the faces of a pentagonal or rhombic-dodecahedron.

l. With more than 12 places of exit regularly distributed over the surface. Frequent among others in *Chenopodiaceae, Caryophyllaceae* and *Malvaceae.*

m. With a number of places of exit distributed over the grain, but leaving the poles clear. To those may perhaps be reckoned some grains of *Oenothera gigas* which sometimes tend to form a number of smaller places of exit according to parallels of latitude and also the grains of *Gilia multicaulis* and *canadensis* which can likewise show places of exit according to various parallels of latitude and *Gilia* tricolor having about 12 places of exit in a twice rising and falling curved line.

The above numbers and different modes of arrangement of the places of exit of the pollen-grains correspond very well with the theoretically constructed point-systems on the surface of the sphere and it only remains to be seen whether grains occur which do not correspond with these point-systems, and whether arguments can be inferred from them pleading against the view that number and arrangement of the places of exit in pollen-grains necessarily follow from the occurrence of a maximum of areas on the whole or on part of the surface of the grains. The pollen-grains which deviated for some reason I have recorded and two of the principal ones I mentioned with the forms described in this publication: viz. *Alnus* and *Impatiens*. *Alnus glutinosa* represents a phenomenon which is rather frequent: that with slight variation there exists no clearly perceptible difference in size between the grains, which is theoretically possible, when the size lies just between (a and $1 + a$) $\times$ V (in the case of *Alnus* this would be between 4 and 5 times V). That this is indeed the case may appear from the observation of a single much larger grain with 6 places of exit. *Impatiens Sultani* represents a second group, the grains of which are formed according to the number a, though one or more of these places of exit have not or but partly been developed. This appears in the case of *Impatiens* from the variation. Neither *Alnus* nor *Impatiens* present any further difficulties to the above view.

Two other cases must be mentioned which I can not discuss fully in lack of material. The first case are the grains from which the grooves are more or less spirally wounded for instance *Berberis vulgaris, Thunbergia fragrans, Oxalis crassicaulis*. The second case shows a phenomena rather frequent in the pollengrains of a few *Ranunculaceae*. The grains of these species usually show three meridian grooves; beside those there also occur grains varying in number and possessing 4 alternately converging grooves, so as the faces of a tetrahedron, and grains with 6 grooves according to the faces of a cube or expressed differently according to the edges of a tetrahedron. This corresponds very well with the point-systems, but there also occur forms, in which the variation leaps from 3 to 6, without observing grains possessing the intermediate number of four places of exit.

In connection with the facts accumulated in this publication, I think I can bring forward some arguments in favour of the following view. When in pollen-grains there exists a tendency to form places of exit over the whole surface or over part of it, the arrangement respectively the symmetry and the number follow necessarily from the arrangement of a maximum of areas in that part of the surface where the formation is possible.

This research was made during the years 1928—1929 in the Botanical Laboratory of the State University of Groningen. I am much indebted to Prof. Dr. J. C. Schoute for his suggestions and criticisms.

SUMMARY AND CONCLUSIONS.

Three factors appeared to be very suitable for the research into the way in which the number and the arrangement of the places of exit in pollen-grains is brought about; they are: 1°. the simple form usually to be reduced to two types only, which the pollen possessed when the places of exit were formed on the surface. 2°. the fact that pollen-grains are pre-eminently suitable for statistical ends. 3°. the occurrence of variations in number and arrangement of the places of exit.

The variation in number of places of exit was statistically traced and a typical correlation appeared to exist between the size of the pollen and the number of places of exit, in that sense that the diameter of a grain was about expressed by the following formula. Diam. = (a to $a + 1$) × V when the number of places of exit lay in one plane or as meridian grooves and Diam. = $(\sqrt{a \text{ to } a+1}) \times V$, when the places of exit are distributed over the whole surface, *Diam.* representing the diameter of the grain, a the observed number of places of exit, and *V* a constant for pollen-grains of one species being under equal circumstances.

With polyploidy or abnormal reduction-division a great variation in the number of places of exit can often be observed; in these cases it appears that an increase or decrease in the number of chromosomes runs parallel with variations in the size of the grain and the number of places of exit. Yet a variation in the number of places of exit correlated with the size of the grain can also occur without there being any differences in the number of chromosomes or in genetic constitution, which can be observed in the differences in size which can be found in the pollen of heterostylic plants (among others *Lythrum Salicaria*).

To the arrangement of the places of exit in the pollen, however variable it may be, yet a general rule obtains: that equidistance is observed in which the distance from a place of exit to the nearest places of exit is nearly equal in value.

From the equidistance of the places of exit and from the fact that with the correlation between the size of the pollen and the number of places of exit, a place of exit is not observed to appear before a certain space is cleared for it on the surface, we might infer that the arrangement and the number of places of exit only depends on the closest covering of the space occupied by the places of exit over the entire surface or that part of the grain that allows of formation of places of exit.

If this view is correct, the numbers observed and the arrangement of the places of exit of the pollen-grains will have to nearly correspond with the constructions of point-systems on the sphere drawn up on equal theoretical conditions. It appeared that such constructions not only correspond well with the numbers and arrangement observed in nature, but that moreover from such point-systems we could more or less infer which numbers would be preferred in nature, and which not, which again tallied with the facts observed.

Therefore I think that I possess in the above some arguments pleading for the view that the number and the arrangement of the places of exit and consequently the symmetry of the pollen-grains arises from the closest possible arrangement of a number of areas on that part of the surface where this formation is possible.

In my opinion, therefore, the symmetry of the pollen is not previously extant in the protoplasm, but arises only consequent on the junction of as great as possible a number of equivalent parts.

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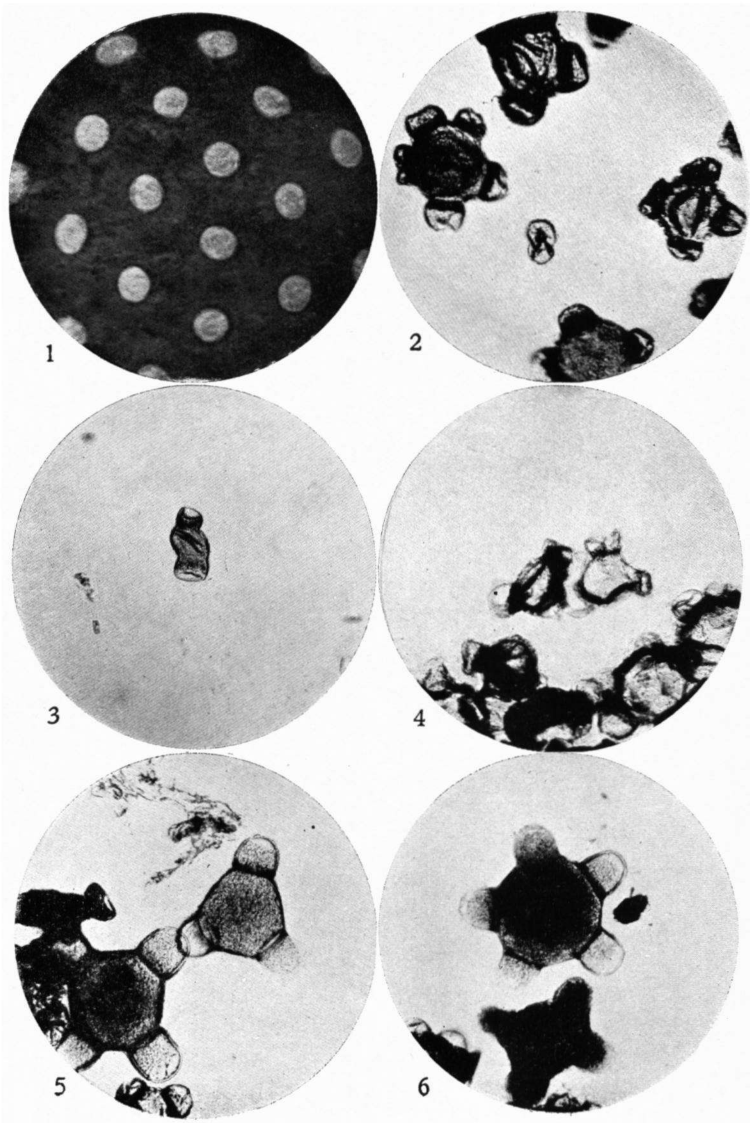
EXPLANATION OF MICROPHOTOGRAPHS.

(Pl. I—III).

1. *Ipomoea purpurea*. Surface of grain with numerous places of exit each place of exit surrounded by 5—6 others. Magnification 600 ×.
2. *Oenothera gigas*. Wrinkled grains with 1, 4 and 5 places of exit. Magnification 120 ×. The grain with one place of exit in the centre.
3. *Oenothera gigas*. Wrinkled grain with 2 places of exit. Magnification 120 ×.
4. *Oenothera gigas*. Wrinkled grains wit 3 places of exit in the centre. Magnification 120 ×.
5. *Oenothera gigas*. Fertile swollen grains with 3 and 4 places of exit. Magnification 120 ×.
6. *Oenothera gigas*. Fertile swollen grain with 5 places of exit. Magnification 120 ×.
7. *Fuchsia globosa*. Grains with 0, 1, 3, and 4 places of exit. Magnification 120 ×. In upper half of photo grains are visible respectively with 1, 0 and 3 places of exit.
8. *Fuchsia globosa*. Grain with 2 places of exit near the centre. Magnification 120 ×.
9. *Fumaria capreolata*. Grain with 6 places of exit arranged as planes of a cube. Magnification 600 ×.
10. *Fumaria capreolata*. Grain with 8 places of exit arranged as planes of a tetragonal-trapezohedron. Magnification 600 ×.
11. *Fumaria capreolata*. Grain with 12 places of exit arranged as planes of a rhombic-dodecahedron. Magnification 600 ×.
12. *Lythrum Salicaria*. Grain with 2 places of exit. Magnification 600 ×.

13. *Lythrum Salicaria.* Grain with 3 places of exit. Magnification 600 ×.
14. *Lythrum Salicaria.* Grain with 4 places of exit. Magnification 600 ×.
15. *Impatiens Sultani.* Grain with 4 places of exit. Magnification 600 ×.
16. *Impatiens Sultani.* Grain with 5 places of exit. Magnification 600 ×.
17. *Impatiens Sultani.* Grain with 6 places of exit. Magnification 600 ×.



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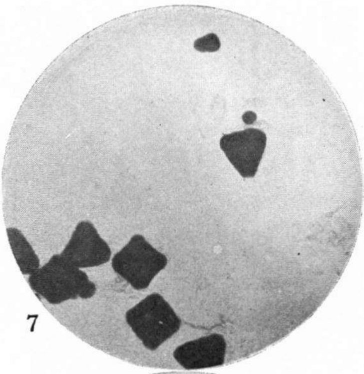
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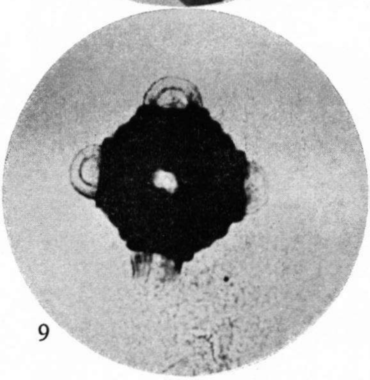
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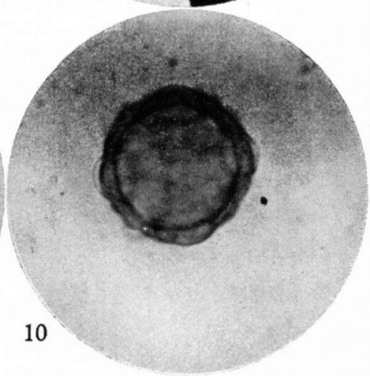
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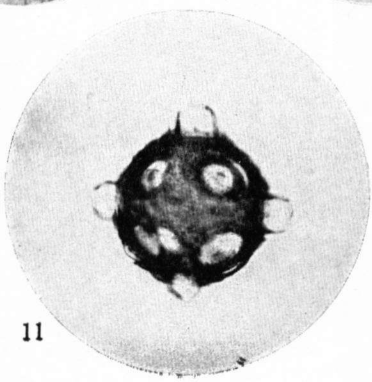
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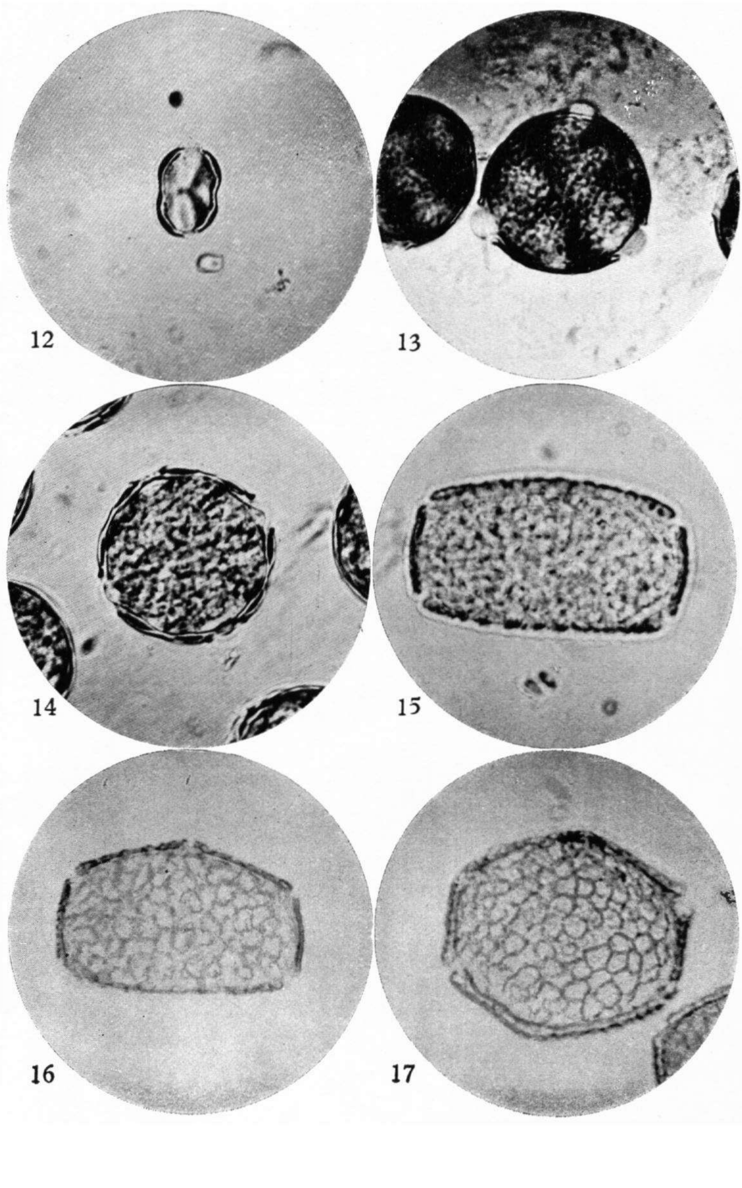
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