TEXT-BOOK

of

MODERN POLLEN ANALYSIS

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To Lennart von Post

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PREFACE

The object of this book is to present to our colleagues a summary of those methods and principles which have guided us in our pollen-analytical work. Pollen analysis is still a very young science and far from reaching perfection; nevertheless we consider it useful to sum up our present position. We hope that this book will provoke discussion, and contradictions if necessary, thus serving as a stimulus for the development of pollen analysis into a more refined instrument of research. We also hope that our treatment of the subject is sufficiently simple to be understood by the beginner, and that this book may serve as an introductory text-book.

It is not without its predecessors. The principles and methods of pollen analysis have been set forth in a number of more or less authoritative text-books. However, some of them are old and out of date—pollen analysis has developed swiftly during the last 10 years—and others have been written by investigators who—writing mainly with other objects in view—have not given the same attention to some of the aspects we consider to be of prime importance.

It has been our aim to make our treatment of the theme as generally applicable as possible. As both of us have carried out our work in Northern Europe (and the Arctic), and as the pollen-analytical history of that part of the world is much better known than that of any other part, most of our examples have been taken from investigations dealing with that area. They should, however, not be considered as anything more than they are meant to be: examples illustrating the application, and the applicability, of the principles laid down in the main text. We are convinced that these principles are generally applicable wherever pollen-analytical investigations are to be carried out. But the investigator has to find out for himself the way in which these principles are to be practised within his special area; no fixed rules can be laid down to help him out of that difficulty. A thorough knowledge of the dynamic aspects of the vegetation of the area under investigation is the only stable foundation on which to base the work.

We also want to point out that no key, however ingenious, and no illustrations, however masterly executed, can replace the personal knowledge of pollen forms acquired from working with actual preparations. Every pollen analyst should have access to a well-stocked "pollen herbarium" for comparison of any problematic form that may occur in his preparations. If properly executed, keys and illustrations may serve as a guide in the identification of a pollen grain, but all identifications should be verified by comparison with recent pollen material. To the experienced worker a key may substantially serve as an aid to the memory, to the beginner it may serve as an instruction in the very difficult art of observing pollen-morphological features. This is the reason why we have published a specimen key, with a few diagrammatic illustrations to render the key more easily applicable.

Although the term "pollen analysis" is in this book taken in its most restricted sense, i.e. the pollen-analytical investigation of Pleistocene deposits, we hope that the book may be of some interest to those who deal with pollen grains from other points of view. The chapters dealing with the theoretical foundations are therefore relatively comprehensive.

We have dedicated this book to the grand old man of pollen analysis, Dr. LENNART VON POST, professor at the university of Stockholm, our teacher and friend whom we want to thank in this place and in this manner for all his inspiration, when first we came—each from his own country—to study under his direction the principles of the science that is his, also later when we returned to discuss our common problems in the field, in the laboratory, or in the lecture-room. Teacher and friend indeed, in the best possible sense of this phrase.

We want also to thank Dr. KNUD JESSEN, professor at the University of Copenhagen, another of the pioneers of pollen analysis, for all that he has meant to us and to the science of pollen analysis. His claims to exactness in the establishment of facts and to common sense in their interpretation should be leading principles for all pollen analysts.

It is self-evident that the opinions laid down in this book have been discussed with a great number of our colleagues, especially during the last four years when the book has been under preparation. We are indebted to almost all the leading pollen analysts in Northern Europe for some suggestion or some criticism during our discussions. However, only one more name shall be mentioned here, that of Mr. J. TROELS-SMITH of the Danish Geological Survey, with whom we have had many heated discussions on technical matters and practical problems.

We have endeavoured to take into account all literature having reference to our subject which has appeared until spring 1949; we stress, however, that we deal exclusively with methods of pollen analysis, not with results. As to the latter we refer to comprehensive treatises, e.g. the great work of FIRBAS on Middle Europe[1]. Similarly, our list of references does not constitute a complete bibliography of pollen analysis, but we hope to have covered most of the field dealing with pollen-analytical methods.

We are most grateful to the Danish CARLSBERG and RASK-ØRSTED FUNDS, as well as to DET AKADEMISKE KOLLEGIUM, Bergen, for their generous contribution to the cost of printing this book.

To the Danish Geological Survey we are indepted for the use of the blocks for the plates in this book.

For linguistic advice we are indebted to Miss JEAN ALLISON and Mr. PHILIP TALLANTIRE who have assisted in the proof-reading of manuscript and printed text, respectively—but we want to stress that the final responsibility in this respect rests with us.

Bergen and Copenhagen, August 1949.

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[1] FIRBAS, F. 1949: Waldgeschichte Mitteleuropas I.—Jena (Fischer). This book deals also with general problems, unfortunately it appeared to late for its discussions to be incorporated into our text.

OUTLINE OF THE HISTORY OF POLLEN ANALYSIS

The observation that certain remains of the former vegetation are preserved in peat bogs is certainly as old as the practice of peatcutting itself. Nobody cutting peat, e.g. in a de-forested region, can help noticing the big trunks and roots or pine cones preserved in the bogs and reflecting upon the changes in vegetation. A closer inspection will soon reveal that the remains differ in different depths of the bog, and whereas some of these differences are due to the natural development of the deposit itself, e.g. the filling up of a lake, others demand a more radical explanation, e.g. climatic changes.

The method of investigating late-quaternary changes of vegetation and climate by determining the individual fossils—ranging from tree trunks to bud scales or seeds—and arranging them according to their occurrence in different layers of the deposits, was that of the so-called palaeo-floristic school. However, at the same time, another school, the palaeo-physiognomic, tried to investigate the climatic changes, not by utilising the fossils directly, but by reconstructing the so-called mother-formation, i.e. the plant community, represented at each level, and by drawing conclusions from the changes of mother-formations. In their original form both schools now belong to history, and we mention them here because they—and especially the polemics between their distinguished leaders GUNNAR ANDERSSON and RUTGER SERNANDER—form the back-ground to pollen analysis.

The specific determination of seeds and other small fossils found during the examination of peat required the use of some magnification, and using strong magnification quite naturally led to the discovery of even smaller fossils, i.a. pollen grains. Oddly enough fossil pollen grains were apparently first observed in pre-quaternary deposits, by GÖPPERT (1836 and later) and EHRENBERG (1838 and later, both quoted after KIRCHHEIMER 1940). The first to utilise systematically the occurrence of pollen grains in post-glacial deposits were, as far as we know, C. A. WEBER and his school (1893 and later), whereas ANDERSSON, the leader of the palaeofloristic school in Northern Europe, apparently never attached much importance to the occurrence of pollen grains in the deposits (cp. ANDERSSON 1898 p. 87). There is, however, a difference in principle between these early, qualitative registrations (quantitative in STEUSLOFF 1905) and pollen analysis proper, i.e. the percentage calculations. The first percentage calculations seem to have been carried out by LAGERHEIM (in WITTE 1905), and later by C. A. WEBER himself (1910, quoted in H. A. WEBER 1918 although it is not quite clear if the actual calculations were carried out in 1910, cp. l.c. p. 259). As pollen analyses these early works are of historical interest only, even if HOLST (1909 p. 30) evidently realised the great importance of LAGERHEIM's calculations.

The real potentialities of the method were, in fact, not realised until LENNART VON POST, then state geologist, took it up with LAGERHEIM as his micro-morphological instructor. v. POST presented the first modern percentage pollen analyses in a lecture to the Scandinavian scientists' meeting at Kristiania (now Oslo) in 1916, repeated later the same year in Stockholm. A rather short abstract of the latter was published in 1916, whereas the report of the Kristiania meeting was not published until 1918.

In the meantime v. POST's students and collaborators had continued his work, SANDEGREN, HALDEN, and SUNDELIN publishing (1916 and 1917) bog monographs including pollen-analytical data. As these papers were all published in Swedish, pollen analysis passed rather unnoticed outside the Scandinavian language region (quoted by C. A. WEBER in H. A. WEBER 1918), and the first pollen-analytical investigations outside Sweden were published in Denmark (JESSEN) and also in Norway (HOLMSEN) in 1919 and 1920. The first time v. Post's methods were published in a congress language, was in 1921 (ERDTMAN). After that they were adopted almost everywhere, supplanting the older methods, and the pollen-analytical literature grew rapidly—in quantity, not always in quality. ERDTMAN publishes a regular series of extremely valuable bibliographies (in Geologiska Föreningens i Stockholm förhandlingar, beginning with vol. 49), comprising the entire pollen-analytical literature.

From the middle twenties pollen analysis has been the dominant method for investigation of late-quaternary vegetational and climatic development, and it has also been used for older deposits. It has been perfected into a very refined instrument of research, highly versatile and giving surprisingly intimate glimpses into the conditions of life during earlier periods. It has thus become one of the most important auxiliary sciences for archaeology, adding to the picture given by human relics. Still, the macro-fossils have their story to tell, and even if it is poorer than that told by the pollen grains, it may elucidate points not covered by the pollen diagrams. On the other hand the pollen-analytical control serves to increase the value of the information given by macro-fossils, and especially to lend a previously unexpected exactitude to palaeophysiognomy.

As a consequence of its different demands, pollen analysis cannot always utilise the same deposits as the other methods. Spring bogs, which give the most perfect palaeophysiognomic results, are practically worthless for pollen analysis owing to the bad state of preservation of pollen grains in that type of bog. Where conditions are best, pollen analysis is not influenced by the mother formation and the sites of investigation must be chosen to obviate this effect. It should always be remembered, that for pollen analysis peat bogs are much inferior to lake deposits; the predilection still shown by many investigators for bogs instead of lakes is historically conditioned and has no relevance to facts. Whereas the older workers preferred the marginal zones of deposits, where the chances of finding the most varied macro-fossil flora were best, the pollen analyst prefers the central parts where local influence is reduced to a minimum. Pollen-analytically the best sections are palaeophysiognomically rather uninteresting, and vice versa. As palaeophysiognomy still has information to give that the pollen diagrams cannot convey, one is frequently obliged to investigate both types of sequence.

THE POLLEN GRAIN, ITS FORM AND FUNCTION

The pollen grain[1] is formed in the male apparatus of the flower, that is, in the anther. The interior of the anther consists of a sporogeneous tissue from which originate the so-called pollen mother cells. With few exceptions each of these gives rise to 4 pollen grains that are in most plants ultimately free from one another. In some genera they remain together, forming tetrads, or other rarer types (dyads, polyads) of composite grains (cp. list in ERDTMAN 1945 b p. 286). Even if the grains are eventually isolated from each other, the tetrad stage constitutes an important step in their development, and the surface pattern shows a distinct relation to the orientation of the grain in the tetrad (WODEHOUSE 1935 p. 159). The part of the pollen grain which is nearest to the centre of the tetrad is called the *proximal* (WODEHOUSE 1935), the line between the proximal and the distal pole of the grain is called the *polar axis*, and the plane perpendicular to this axis through the middle of the grain the *equatorial plane*. Positions on the surface of the grain can be identified by their *latitude*, corresponding to the latitude on a regular sphere. Similarly surface features perpendicular to the equatorial plane are called *meridional*. The terms *interior* and *exterior* refer to the distance from the centre of the individual grain.

The sporogeneous tissue or, as the case may be, the mass of pollen grains, is surrounded by a wall, the structure of which is rather complicated. When the pollen is ripe, this wall breaks down in some way, and the pollen grains are liberated for transfer to the female apparatus (generally of another flower) where fertilisation takes place.

The pollen grain is built up of 3 concentric layers. The central part is the living cell, which germinates on the stigma and forms the pollen tube that penetrates the style and brings the fertilising nuclei down to the ovum.

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[1] The word *pollen*, meaning originally "fine flour" (cp. SKEAT 1910) signifies the substance and ought not to be used in the plural, "pollen types" and "pollen grains" being the correct terms.

The middle layer is the *intine*. It is always present and envelops the whole of the pollen grain. It consists chiefly of the same substances that form the bulk of the ordinary cell-walls of the plant. If the pollen grain does not reach its destination, it soon dies, and cell contents and intine are easily destroyed and disappear.

The third layer, the *exine,* is formed of one of the most extraordinarily resistant materials known in the organic world. Apparently unchanged spore walls (consisting of the same or a closely related substance) are found in Paleozoic rocks where all other organic remains have been carbonised and distorted. Recent pollen grains can be heated to almost 300° C (ZETZSCHE 1929 p. XXIX) or be treated with concentrated acids or bases with very little effect on the exine. According to ZETZSCHE (l.c.) and VICARI (1936) the substance is less resistant to oxidation. As a consequence of this great resistance the chemical composition of the exine is very inadequately known. According to VICARI (l.c.) the so-called sporopollenins are N-free substances, which are specifically different, as is the quantity of sporopollenin in different pollen species. It is interesting to note that the very resistant *Pinus* pollen also possesses the greatest quantity of sporopollenin.

Pollen exines (and spore walls) are generally excellently preserved in peat and sediments even when all other organic constituents are reduced to a structure-less and indefinable substance. There are, however, peat types in which pollen exines are more or less corroded. This seems to take place especially in aerated peats formed at or above the ordinary water level, near springs, etc.

The exine is highly variable. In some few pollen types (hydrogamous species) it seems to be absent altogether. Apart from these the simplest cases are those where the grain is enveloped in a thin, continuous cover, apparently consisting of one homogeneous sheet (*Larix*).

Where the exine is more complex, it is possible to distinguish between two layers (FRITZSCHE 1837), an inner and an outer, which are called, respectively, ***endexine*** and ***ektexine***. The inner layer forms a continuous, homogeneous membrane, corresponding to the simple exine of the above-mentioned pollen type[1]. In contrast the outer layer always seems to consist of small elements (*granula,* FRITZSCHE l.c.), the development and distribution of which cause the extreme variability of the structure of the exine.

In very simple grains the ektexine is confined to isolated small knobs,

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[1] In some grains the pores (cp. later) seem to form true holes in the endexine. However, it is very difficult to ascertain this, nevertheless, the continuous endexine may have thinner areas equivalent to fully perforate pores.

which are scattered on the inner membrane (*Juniperus*). In other types these projections are more densely crowded (*Populus*) or have the form of rather conspicuous clubs (*Ilex*). More elaborate structures are formed when the granules are grouped into various patterns and fused laterally more or less completely, forming an open net-work (*reticulum, Armeria*). A contrast to the open structure of the above-mentioned exines is formed by those pollen grains in which the outer ends of the granules fuse, forming another, outer sheet which envelopes the whole grain covering all the other exine elements. If the granules assume the form of radially placed prismatic elements that are fused along their whole length, the ektexine is compact, but in most cases a very careful examination (preferably of sections) discloses that the granules are fused at their tips, or at their tips and bases, thus forming an outer membrane which is separated from the inner one by a cavity and is borne by small columns (*columellae*), which may in some cases fuse to form an inner reticulum (*Alisma*). In some pollen types the outer part of columellae is branched, forming intricate patterns (*Stellaria,* cf. plate IV: 1-5).

Pollen grains in which the ektexine elements, if present, are free and isolated (*Ilex*) or form an open pattern (*Armeria*) are called *intectate* (Iversen and Troels-Smith 1950)[1]. If the ektexine forms another membrane outside the endexine (*tectum*), the grains are called *tectate,* notwithstanding whether the tectum is separated from the endexine by a cavity or not.

These are the two principal types of pollen structure. It is self-evident that they are not completely distinct, but are linked by transitional forms. In some pollen grains the granula have the shape of densely crowded small rods, which sometimes seem to be isolated, sometimes fused (*Taxus*). Many *Liliiflorae* possess a reticulum with very narrow meshes. As long as the diameter of the holes (*lumina* Potonie 1934) is more or less equal to the breadth of the walls (*muri* Potonie l.c.), the grains may still be considered intectate. If the holes are distinctly smaller, we may consider the grain to possess a *perforate tectum* (*Silene maritima*) and consequently classify it as tectate. In the *Liguliflorae* the tectum is broken by a limited number of rather large openings (*lacunae* Wodehouse 1928), which are arranged in a symmetric pattern. As this highly developed pollen type derives from types with a complete tectum, we class it as a tectate pollen of a special type (*fenestrate* i.e. equipped with windows), even if the

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[1] Most of the following morphological discussion is a simplification of the more elaborate system published l.c.—Plate I-VIII illustrate the morphological terms discussed in this chapter.

lacunae occupy a greater area of the total surface of the grain than the tectate parts of the exine. Similar types are found also in other groups.

In accordance with Potonie (1934) we distinguish between the *structure* (*texture*) and the *sculpturing* of the exine. The term structure comprises all those characters which are due to the form and arrangement of the exine elements inside the tectum. It also comprises the form and arrangement of the individual elements in intectate types. All those ektexine characters that have been dealt with above, thus belong to the structural features.

The term sculpturing on the other hand comprises the external geometrical features without reference to their internal construction. Thus a spine may consist of a single granule, but it may also be a highly complex structure comprising a number of granules. We shall later in this chapter deal with the sculpturing in more detail, but we want to emphasize here that unless one is very careful, it is easy to confuse structure and sculpturing. E.g. in *Fritillaria* structure and sculpturing are identical (reticulate), whereas *Galeopsis tetrahit* (cf. plate IV, 6-8) possesses tectate-reticulate pollen grains, in which the sculpturing only is reticulate, whereas the structural elements are evenly distributed. On the other hand it is self-evident that sculpturing is in any case due to the arrangement and form of ektexine elements, e.g. the striation of the pollen grains of most *Rosaceae* are just as much a structural feature as a sculpturing type.

The chemical composition of the different layers of the exine varies. Whereas the ektexine is stained intensely by fuchsin, the endexine is only stained very faintly. The endexine seems to be less resistant than the rest with regard to some chemicals, and more resistant to others (cp. Fischer 1890 p. 15, Jentys-Szafer 1928).

The structure and sculpturing of the exine furnish characters of great diagnostic value. There are, however, many other characters which are of equal or even greater importance in the identification of pollen grains. Before stating our opinions we want to point out that we only take into account characters that pertain to fossilised grains. Cnaracters that disappear during fossilisation (colour and structure of cell contents, intine features, colour of oil on the exine, etc.) are purposely omitted. When dealing with recent material for comparison purposes we have always endeavoured to produce a state resembling that of fossil grains. As the images of cell contents, extra-exinous oil, etc. obscure the exine characters, it is important to get rid of all superfluous matter.

In most pollen grains one can distinguish between polar axis and equatorial plane. In the original tetrads the polar axes point towards the

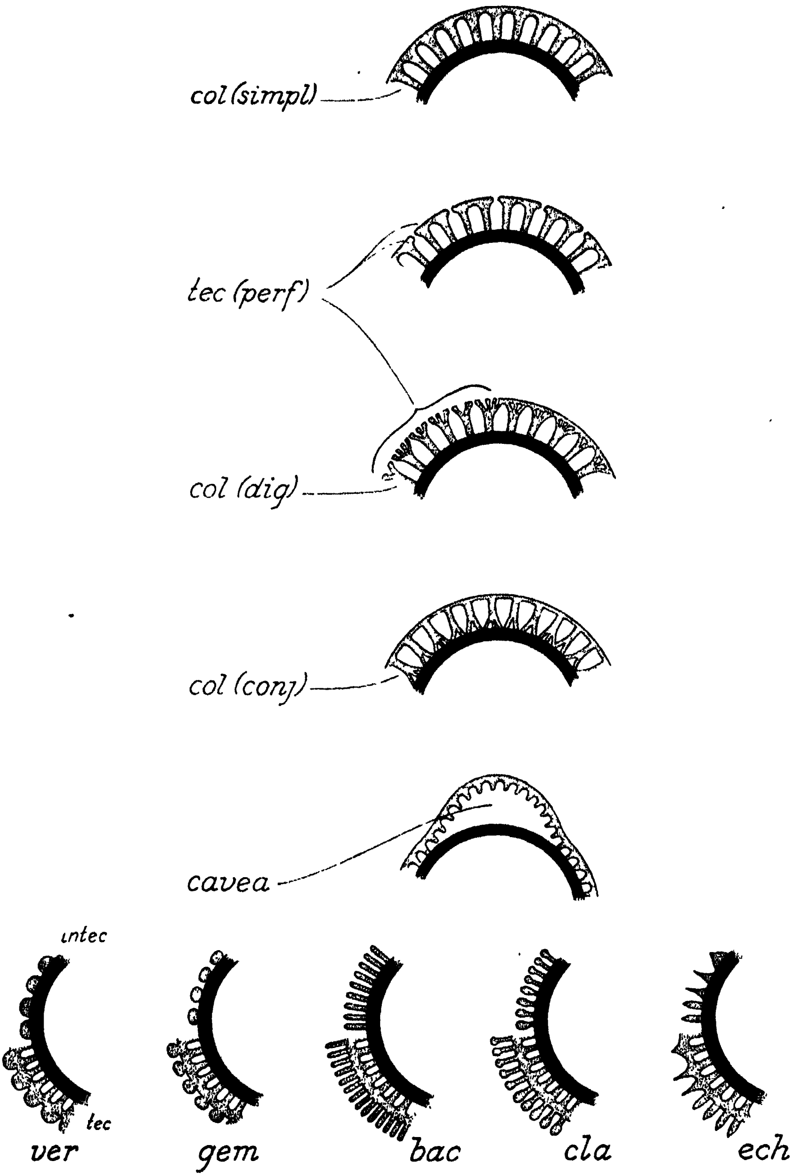

Plate I. Structural and sculpturing types I.
Endexine black; ektexine dotted. col = columellae (simpl = simple; dig = digitate; conj = joined). tec (perf) = perforate tectum. intec = intectate; tec = tectate. Verrucate, gemmate, baculate, clavate, and echinate sculpture.

Drawings by B. Brorson Christensen from Iversen & Troels-Smith (1950).

centre of the tetrad. In single pollen grains this cannot be observed directly, but with the exception of the regularly globular grains (where the distinction is of minor importance) one is rarely left in doubt as to the position of the axis, which is the axis of symmetry of the grain. Generally pollen grains can be regarded as more or less regular rotation ellipsoids, the polar axis being that of rotation.

Most pollen grains possess openings in, or thin parts of the exine, through which the pollen tube emerges. Two different types of apertures can be recognised, which are generally called *pores* and *furrows* (*colpi* WODEHOUSE 1935). In many cases the furrows also function as *harmomegathi* (WODEHOUSE 1935: mechanism which accomodates the changes in volume of the semi-rigid exine).

Furrows are with few exceptions boat-shaped parts of the exine where this membrane is much thinner than in the rest of the grain. The ektexine is reduced, even to absence, whereas the endexine is less affected. The furrows thus form no holes through the exine, and if no pores are present, the pollen tube must force its way through the thin membrane. The volume of the dry, living grain is comparatively small, the exine is contracted and the furrows appear as narrow slits. When the grain is moistened, it expands and the thin membrane of the furrows bulges out (this is the state generally depicted by WODEHOUSE 1935). When the cell contents have been removed —by fossilisation or by chemical action—the furrows generally appear as rather open grooves in the exine.

In contrast to the furrow the pore is generally isodiametric and, if it is somewhat elongated (not boat-shaped!), the ends are rounded. For practical purposes the limit between pore and furrow may be defined by a length/breadth ratio of $^2/_1$. The endexine of the pore is thinner than that of the rest of the grain; we are not competent to state whether it in any case really is absent in the living grain. In many fossil grains pores appear as genuine holes in the wall, but this may be a secondary phenomenon. It is obvious that as soon as a pollen grain is wetted and its contents swells out, the very thin membrane of the pore is in danger of being ruptured.— The pore is the natural place of emergence of the pollen tube. In pollen grains that possess furrows, but not pores, and where the pollen tube must force its way through the thin membrane of the furrows, it frequently leaves an irregular hole with tattered edges.

Pores and furrows may appear as simple holes or slits in the exine, but generally they are surrounded by distinctive parts of the exine. A pore is frequently surrounded by an annular area (*annulus*), the exine of which is characterised by differences in the outer layer, the endexine

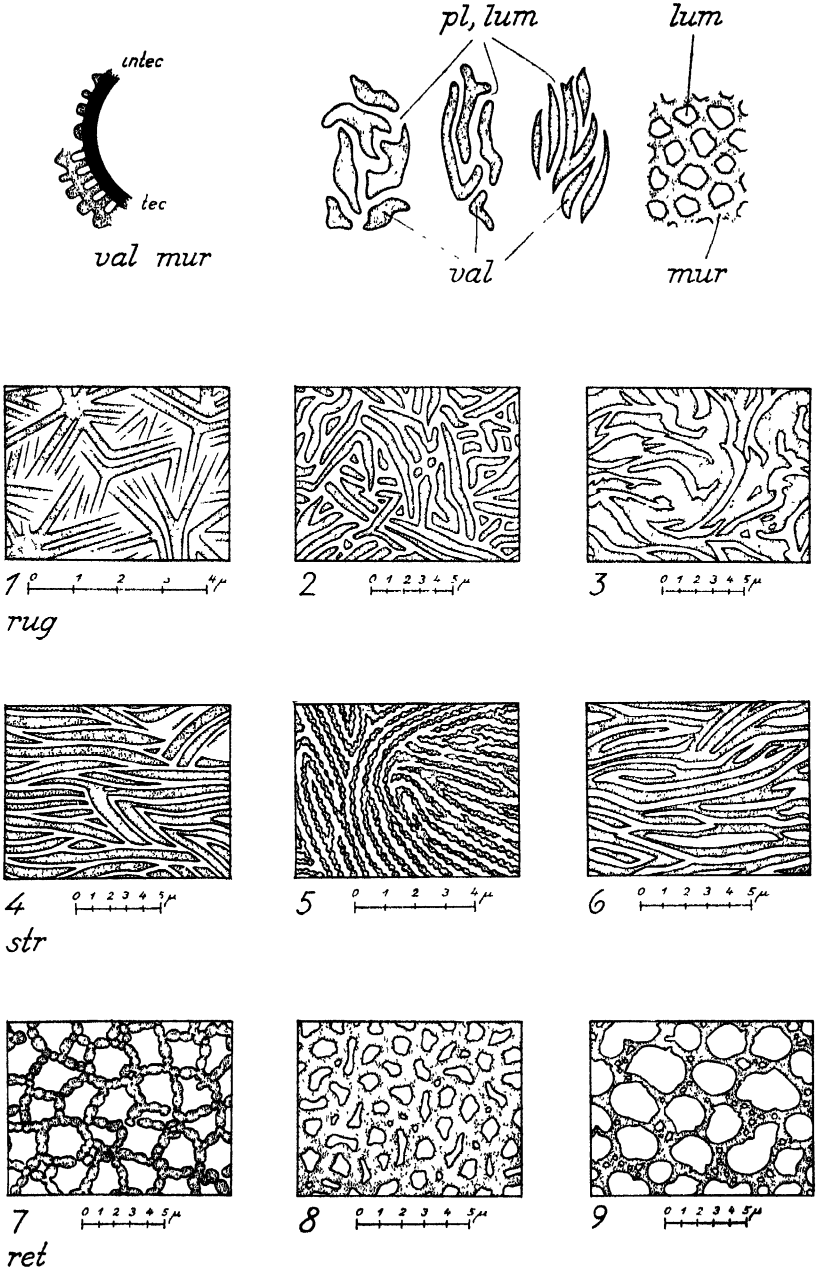

PLATE II. Structural and sculpturing types II.
Sculptural elements dotted. tec = tectate ; intec = intectate ; rug = rugulate ; str = striate ; ret = reticulate ; val = vallae ; mur = muri ; lum = lumina.

sometimes being thicker, sometimes thinner. A similar area (*margo*) may often be found surrounding the furrows, and in this case the ektexine is nearly always reduced in thickness. This is the part of the exine, which carries out the harmomegathic movements. The sculpturing of the margo is different from that of the rest of the grain, the ektexine elements decrease. This development is accentuated in the furrows, where tectum and in some cases all granula disappear. Thus, the margo, represents the transition zone between the furrows and the remainder of the exine.

There are also frequently thickenings of the endexine edging the furrows (*costae colpi*), but these are often difficult to observe directly, and they are most easily recognised by their effect on the furrow, the harmomegathic function of which is impeded (*Rumex*). Similar thickening, of the endexine may also be found edging the pores (*costae pori*).

When both pores and furrows occur together (*colporate* pollen, ERDTMAN 1945) the pores are always located in the furrows, one pore per furrow[1]. But a number of pollen types is known, in which the number of pores is regularly smaller than (most frequently ½ or ¼ of) that of furrows (*heterocolpate*). In *Platycarya* all pores are located outside the furrows (*extraporate*). The homology of these furrows with the regular colpi may be questioned.

In colporate pollen grains the thin exine of the furrows is even thinner in the pore area, and it is characteristic that this thinning is most distinct in the endexine. These thinner parts of the endexine may assume the form of internal *transversal furrows* (*colpi transversales*) which may fuse together to one single internal furrow along the equator of the grain. The internal furrows may be accompanied by thickened edges (*costae transversales*, resp. *costae aequatoriales*).

The effect of a preformed exit place on the form of the furrow varies. If the rim of the pore is reinforced by a thickening of the endexine (a *costa pori*), the regular slit or boat shape of the furrow is not much influenced. On the other hand, if there is no such thickening, the middle part of the furrow either collapses or, less frequently, the membrane blows out forming a tattered collar (*Sorbus*).

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[1] The pollen grains of *Myoporum* have furrows provided with 2 pores or transversal furrows each (CRANWELL 1942, SELLING 1947). Somewhat similar but more irregular features appear in *Ribes grossularia*, where short furrows, provided with one pore each, fuse in pairs. In *Anthyllis vulneraria* each pore seems to be connected with 3 furrows, a smaller lateral one on each side of the main furrow. However, we do not consider the lateral fissures as real furrows.

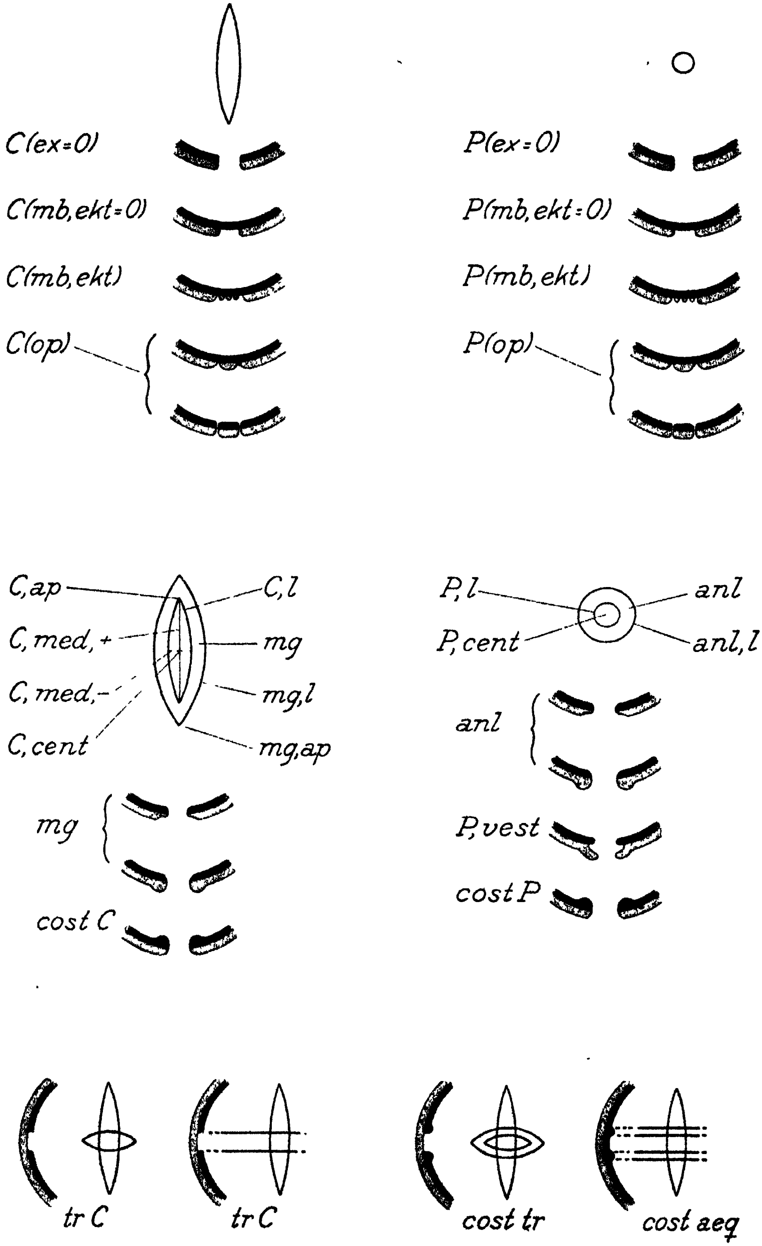

Plate III. Furrows and pores. Endexine black; ektexine dotted. C = furrow (colpus); P = pore; ex = exine; ekt = ektexine; mb = membrane; op = operculum; mg = margo; anl = annulus; cost = costae; vest = vestibulum; tr = transversales; aeq = aequatoriales.

In living grains both pores and furrows may be covered by an *operculum* (Wodehouse 1928), an isolated part of the ektexine which is separated from the rest by a narrow zone in which the ektexine is missing or greatly reduced. As this zone forms an area of least resistance, the grain is generally ruptured along it when pressure is exerted from within, and especially in fossil material, pore opercula are frequently lost. If the furrow operculum is preserved, the effect may simulate that of a double furrow, separated in the middle by a boat-shaped part. Sometimes the two parts of the primary furrow are definitely separated from each other and may even coalesce with the adjacent furrows (*Sanguisorba officinalis*).

The arrangement of normal furrows and pores varies from species to species. In most cases 3 furrows and/or pores are arranged equidistantly from each other and meridionally along the equator of the grain. If more than 3 are present, they may be arranged in the same way (*stephanocolpate/stephanoporate*). In other cases the apertures are evenly distributed over the whole surface of the grain (*isometric* distribution, Wodehouse 1935[1]), *pericolpate/periporate*). A special type is the single furrow of the great majority of monocotyledoneous grains (pore e.g. in *Gramineae*), which is placed at the distal end of the polar axis.

The number of apertures varies from 0 to 30-40 or even more. The most frequent number in dicotyledons, viz. 3, corresponds to the points in which the grain has been in contact with the other grains of the tetrahedral tetrade (Wodehouse 1935 p. 182). Next to the equidistant equatorial arrangement comes the isometric (which is most frequent with the higher number of apertures) and then the completely irregular. The polar arrangement is practically exclusive to the monocotyledons, where it is dominant. A special case is that of *syncolpate* grains, in which two or more furrows are combined into rings or spirals surrounding the whole or parts of the grain (cf. plate VI, 8).

The number and arrangement of apertures are easily observed and can be described exactly. These characters are of great diagnostic value and we have based our main groups for practical classification on them even if they are less constant than some other characters (e.g. *Ranunculus* which fluctuates between tricolpate, isometric hexacolpate, etc.). We hope that the main key given on p. 128-129 will serve to put all pollen grains into their proper pigeon-holes of morphological classification.

Each of the groups of the main key comprises a number of types, and other characteristics must be taken into account to differentiate between

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[1] For a discussion of the geometrical pattern governing the different isometric distributions we refer to Wodehouse l.c.

them. As mentioned above, most pollen grains can be referred to a rotation ellipsoid. The form of this ellipsoid is frequently a very important characteristic of the pollen grain, e.g. the *oblate* types of *Betulaceae* or the *prolate* of most *Umbelliferae*. ERDTMAN (1943 p. 15) has proposed a series of shape classes, based upon the relation between the length of the polar axis (Lg) and of the equatorial diameter (Lt) of the rotation ellipsoid corresponding to the pollen grain, ranging from perprolate ($Lg/L>2$) to peroblate ($Lg/L<\frac{1}{2}$). It must be remembered, however, that the shape of the pollen grain is also dependent on its history and on the treatment it has received (CHRISTENSEN 1946 p. 12).

Departures from the strict ellipsoid forms are frequently met with. In pollen grains with equidistant equatorial pores (no furrows) the equatorial plane is frequently distorted to assume the shape of the corresponding polygon (the sub-triangular outline of *Corylus* or the subquadratic of 4-pored *Alnus*, etc.); in many cases this distortion is increased by the addition of strong pore rims to the ground-form (*Epilobium*). In some few cases the 3 axes of the ellipsoid are of different size (*Myriophyllum alterniflorum*)[1]. In other cases the shape of the grain is that of a (triangular) prism rather than that of an ellipsoid (e.g. *Centaurea cyanus*). This state[2] is brought about by the unequal thickness of the exine in different parts of the grain (much thickened between the furrows).—Finally there are some few types that are completely irregular, e.g. the pear-shaped pollen of *Cyperaceae*, the subprismatic of *Impatiens*, or the winged grains found in *Pinaceae* and *Podocarpaceae*.

The sculpturing of the pollen grain is generally a fairly constant character and is in most cases an excellent means of recognition of pollen. It is, however, frequently difficult to describe in exact terms, and consequently somewhat unsatisfactory for analytical description. This is also the reason why we use as few terms as possible, and only distinguish between the following types, which are based upon the form and arrangement of *sculpturing elements*, i.e. those elements which project beyond an imaginary even surface, either the endexine in intectate pollen or an imaginary surface touching the lowermost parts of the tectum[3].

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[1] The triaxial pollen described from living material (RISCH 1940) do not seem to keep that pattern on fossilisation.

[2] It should be remembered that we always refer to grains without cell contents. Dry, living grains are frequently subprismatic owing to contraction of the exine, but the empty exine assumes the ellipsoidal shape.

[3] These terms refer to sculpturing only. Corresponding structure types are sometimes designated as *intra*-reticulate, *intra*-striate, etc.

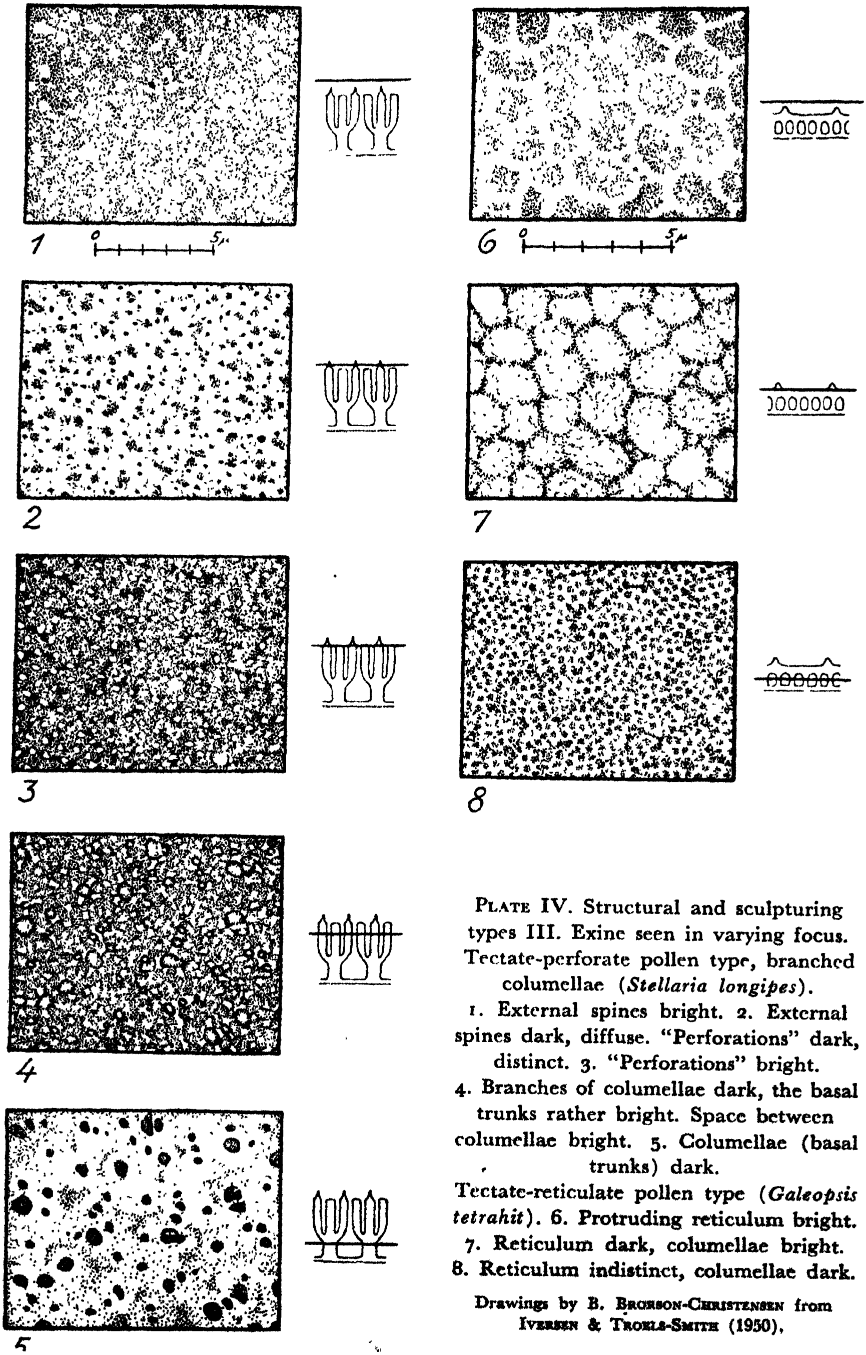

Plate IV. Structural and sculpturing types III. Exine seen in varying focus. Tectate-perforate pollen type, branched columellae (*Stellaria longipes*).
1. External spines bright. 2. External spines dark, diffuse. "Perforations" dark, distinct. 3. "Perforations" bright. 4. Branches of columellae dark, the basal trunks rather bright. Space between columellae bright. 5. Columellae (basal trunks) dark.
Tectate-reticulate pollen type (*Galeopsis tetrahit*). 6. Protruding reticulum bright. 7. Reticulum dark, columellae bright. 8. Reticulum indistinct, columellae dark.

Drawings by B. Brorson-Christensen from Iversen & Troels-Smith (1950).

TABLE OF SCULPTURING TYPES[1]

A. Sculpturing elements s.s. absent.
  B. Surface even or diameter of pits $< 1\ \mu$ .... *psilate* (*Betula*)
  BB. Surface pitted, diameter of pits $\geqq 1\ \mu$ .... *foveolate* (*Lycopodium Selago*)
  BBB. Surface with grooves .... *fossulate* (*Ledum palustre*)
AA. Radial projection of sculpturing elements ± isodiametric.
  B. No dimension $\geqq 1\ \mu$ .... *scabrate* (*Artemisia campestris*)
  BB. At least one dimension $\geqq 1\ \mu$.
    C. Sculpturing elements not pointed.
      D. Greatest diameter of radial projection greater than height of element.
        E. Lower part of element not constricted ...... *verrucate* (*Plantago major*)
        EE. Lower part of element constricted .... *gemmate* (*Juniperus*)
      DD. Height of element greater than greatest diameter of projection.
        E. Upper end of element not thicker than base ... *baculate* (*Nymphaea*)[2]
        EE. Upper end of element thicker than base .... *clavate* (*Ilex*)
    CC. Sculpturing elements pointed .... *echinate* (*Malva*)
AAA. Radial projections elongated (length at least twice the breadth).
  B. Elements irregularly distributed .... *rugulate* (*Nymphoides peltatum*)
  BB. Elements ± parallel .... *striate* (*Menyanthes*)
  BBB. Elements forming a reticulum .... *reticulate* (*Fritillaria*)

The smallest pollen grains measure about 5 μ, the biggest more than 200 μ. However, the size is even more dependent on the history of the grain than is the shape. The living pollen grain has no definite size, expanding and contracting according to the quantity of available moisture. The empty exine—as found in sediments under optimal conditions of preservation—seems to have a rather constant size, which is one of the characteristics of the species, and which is not appreciably affected by the boiling of the sediment with 10 % KOH. The same size is reached if recent pollen grains are boiled with 10 % KOH for some hours (the concentration must be kept constant by the addition of some distilled water from time to time during the process).

As the prolonged KOH boiling is rather an unpleasant process, needing constant supervision, other methods of preparation of recent pollen have been proposed. The simplest is undoubtedly to leave the pollen in concentrated H_2SO_4 for some days, followed by heating in KOH. Size is not affected. Treatment with anhydrous acetic acid (ERDTMAN, cp. p. 62) is quicker than the other two; structural features are better brought out, but the size of the grain changes (FÆGRI 1945 p. 108) and, what is more important, the change is different in recent and fossil grains (cp. also CHRISTENSEN 1946 p. 15, WENNER 1948 p. 89). As a method of preparation for general

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[1] Cp. plate I-II.

[2] Mixed with clavae and echinae. We know no purely baculate pollen type.

morphological inspection we recommend acetolysis, but it must be borne in mind that pollen grains which have been treated in this way cannot be used for the purpose of size statistics. According to CHRISTENSEN (l.c. p. 17) the behaviour of recent pollen grains that have been boiled with KOH before acetolysis is more or less like that of fossil grains treated in the same way. If this holds true for a greater number of species (so far, *Corylus* only has been investigated) acetolysis after KOH treatment will undoubtedly be the best way of preparation of recent pollen.

Another method for preparation of recent pollen has been described by JIMBO (1933): The material is moistened with a drop of concentrated hydrochloric acid on a slide. The acid is evaporated carefully and replaced by a very small drop of KOH, which is also evaporated. The material is then ready and can be kept in glycerine or glycerine jelly. In cases when very little material is available, the method certainly presents some advantages. We have found it easier to carry out the procedure in a small watch-glass and evaporate over a water-bath.

According to SCHOCH-BODMER (1940) the size of pollen grains is dependent on the state of nutrition of the plant. It is not known, however, if this applies to empty exines as well. On the whole the important question of the constancy of the size of pollen grains deserves much closer attention than it has received until now— ENEROTH's unfortunately unpublished investigations on *Betula* excepted. It is self-evident that such investigations are of very limited value unless the exines have been treated in such a way that permits control of all factors of importance.

Dealing with the more complicated floras of the western hemisphere American pollen analysts have to a great extent utilised size statistics in an attempt to differentiate between species, especially species of conifers[1]. CAIN and CAIN (1948) arrive at a most extraordinary result with regard to *Pinus echinata,* which seems to exhibit a geographical cline, "with the grains of the northeastern half of the area of the species having consistently larger mean values than those of the southern half of the area of the species" (l.c. p. 330). If this conclusion is not invalidated by circumstances of which we are at present unaware (e.g. different taxonomic relations), it is certainly of great importance and should serve as another warning against indiscriminate use of size statistics as a means of recognising pollen.

According to their meridional length furrows reach a higher or lower latitude on the surface of the pollen grain. As *polar area* we define that part

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[1] It is imperative that fossil samples must be treated in such a manner that their size can be directly compared with that of recent material, e.g. they must not be acetolysed (cp. CHRISTENSEN, WENNER). Unfortunately this has not always been considered.

of the pollen grain which is situated in higher latitudes than all apertures, annuli, or margines. The relative size of this area is of considerable diagnostic value and can be expressed by the angles formed by the latitudes. For practical reasons we have, however, measured the greatest distance between the ends of two furrows[1], and expressed the "*polar area index*" as the ratio between this measure and the greatest breadth of the pollen grain.

A number of other measurements and indices will be found to be of great practical value in the identification of pollen grains, cp. p. 150-151 (cp. also IVERSEN and TROELS-SMITH 1950).

By means of the characters dealt with above pollen grains can be classified. The units of classification, "pollen species", are of very different taxonomic values, sometimes comprising most or all of a large family (*Cyperaceae*), sometimes a single or some few closely related species only (e.g. *Polygonum amphibium*). If it is necessary to subdivide the unit further, this can sometimes be done by statistical treatment of quantitative characters which are in themselves insufficient for identification. v. POST has (1929 p. 561) used a statistical treatment of the number of apertures for the distinction between *Nothofagus* species, and ENEROTH has developed the statistical treatment of pollen grain size for the distinction between Scandinavian *Betula* species. As the size of a pollen grain is a rather indefinable quantity, as the method is always extremely laborious, and as the reliability of the results is generally rather dubious, the method should be used only when no other is available (for a discussion of the method, cp. FÆGRI 1945 p. 103). Only when the state of preservation is almost perfect—which seems to be the case in acid sediments only—can size-statistical determinations be carried out with some hope of success. It is obvious that the treatment both of samples and of comparison material must be carried out with the utmost care. BRORSON CHRISTENSEN (1946) has suggested that one should use the dimensions of one, or more, indicator pollen grains of known "real" size in the same preparation (recent or fossil) as a factor of correction. Thus, in many northwest European samples the size of the *Corylus* grains (which are considered uniform) will show whether the pollen grains of a given preparation are of "normal" size or not. Further, the index of expansion, resp. diminution of the *Corylus* grains of the preparation may be used as a correction coefficient. It should be taken into account that different exines react in slightly different ways to the same treatment.

A common characteristic of all statistical methods is that whereas the individual grain cannot be classified, the percentages of the different

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[1] In the case of a well-delimited margo, we have measured the distance between the ends of the margines.

species within the total can be calculated. Border-line cases are those in which the variation curves of the components are almost completely separate (e.g. Cereals and ordinary grasses, cp. FIRBAS 1937).

Pollen grains are always difficult to determine whether from illustrations or from a key. As many grains can be recognised at once from one outstanding feature, which cannot, however, be brought into the ordinary key except at a very late point, it is expected that the principle of perforated multiple-entry identification card keys (cp. CLARKE 1938) will prove more useful than ordinary keys for the purpose of identification of unknown pollen grains. A proposed form for such cards is given in fig. 16, p. 150.

During an early phase of Northern European pollen analysis a number of "doubles" was reported, e.g. *Quercus--Viola, Salix—Fraxinus, Fagus—Helianthemum—Hippophaë,* even *Corylus—Myrica—Urtica—Betula.* Further experience has proved that most of these are comparatively easily kept apart, but there still are some troublesome pairs, first and foremost *Corylus—Myrica* and *Hedera—Lysimachia vulgaris.* We want to emphasise again that the optical equipment for pollen analysis must be adequate. It is impossible to distinguish between difficult, often badly crumpled pollen grains without proper equipment. It should be pointed out, too, that the microscope should be of binocular type, both because of the strain on the eyes and because of the difficulties in realising the stereoscopic relations of pollen grain characters with a monocular microscope.

More difficult structures may be impossible to unravel without sections through the exine. The technique of microtome sections has been described by BRORSON CHRISTENSEN (1949). It differs from the ordinary preparation of recent pollen material mainly by the washing with conc. acetic acid instead of water after acetolysis. Cutting is carried out in refined carnauba wax as an embedding medium into which the material is passed at 80° C. in the centrifuge tube via a 50/50 xylol-carnauba mixture after repeated washing in xylol to remove the acetic acid. Primitive sections can also be made by embedding prepared pollen grains in gum arabic to which is added a little glycerine. After the medium has dried, it can be cut with a razor. With some luck parts of sections can be obtained that show the structures.

THE PRODUCTION AND DISPERSAL OF POLLEN GRAINS

The way in which pollen is transferred from anther to stigma is of great importance for the evaluation of pollen-analytical data. Some few aquatic plants are pollinated under water. Per se, there should be excellent opportunities for pollen of these species to be embedded in sediments and fossilised. Unfortunately such pollen grains have—as far as is known—no exine and therefore no remains are left. The small group of hydrogamous species are missing from pollen analysis altogether.

Another group which is also heavily under-represented, is that of the obligate autogamous flowers. In extreme cases the flowers are cleistogamous, never opening, and the pollen germinates on the stigma within the closed perianth. No pollen is exposed. In other cases the flowers open, but only after the pollen grains have germinated and the pollen mass is woven through and glued to the stigma by the pollen tubes. Usually no pollen grains are liberated in that case either; besides which, the number of pollen grains is frequently heavily reduced owing to the great effectivity of the pollination process. Even in such autogamous plants where some pollen grains are at last exposed, e.g. in ordinary wheat, the number is almost infinitely small compared with that of related allogamous species, e.g. rye (cp. I. MÜLLER 1947).

There is a very comprehensive group of zoogamous flowers, in which the pollen is carried from the anther of one flower to the stigma of another by some animal, insect, bird, bat, even slug. In extreme cases these flowers are highly specialised and the pollen is released only when the right animal visits the flower and behaves correctly. The pollen is then firmly deposited on the animal, and is removed by the stigma only. Unless the pollen-bearing animal itself perishes in a lake or bog, or whole flowers (or anthers) drop accidentally into the water, pollen grains from this type of flower have equally small chances of being preserved as fossils.

Pollen grains of zoogamous species frequently possess a heavily armed surface. Layers of sticky oil on the surface of the grains cause them to stick better to the body of the animal. Extreme cases are the massulae of orchids and *Asclepiadaceae* or the viscin threads binding together smaller pollen masses e.g. in *Rhododendron*. As such masses are spread as a unit, their existence tends to reduce heavily the number of "pollination units". In some cases at any rate pollen-analytical experience indicates that such masses become broken up in fossilisation.

Although pollen grains of obligate zoogamous species are occasionally found in peat or sediments, they are always infrequent, and their occurrence rather irregular.

Consequently they should not be treated on a par with anemogamous species. Their occurrence may furnish indications of the greatest value, but nothing can be concluded from their absence.

The more specialised and the more effective the zoogamous pollination, the smaller the production of pollination units and the fewer are liberated in the air. On the other hand there are zoogamous species that produce such great quantities of pollen that their production is fully comparable to that of the wind pollinated species, e.g. *Tilia* (HYDE and WILLIAMS 1945 p. 457) or *Calluna* (POHL 1937 p. 440). Their pollen is to a great extent "lost" in the air and behaves like the pollen of wind pollinated species. It is noteworthy that in some cases such pollen grains possess a coating of oil, e.g. *Tilia* (ZANDER 1935 p. 218), whereas in other cases they are dry, e.g. *Calluna* (l.c. p. 241). It is also noteworthy that this high pollen production occurs in typical nectar flowers like those of the above-mentioned plants. It is self-evident that the production is also high in the so-called pollen flowers, e.g. *Filipendula ulmaria,* where surplus pollen is the lure, leading the animals to visit the flower.

Accordingly the group of zoogamous flowers comprises all types from species which are never to be expected in pollen analysis to those that form important constituents of the pollen rain and that are calculated in ordinary analysis.

The last, and for our purposes most important, group is that of wind pollinated species, which produce very great quantities of pollen which are liberated into the air and scattered all over the surroundings as the "pollen rain". A very small fraction of this settles on the stigmata, the great majority is lost, *int. al.* on bogs and in lakes. The pollen of wind pollinated species is dry and the individual grains fall apart, thus producing the maximum number of pollination units and securing a regular distribution of the grains over a wide area. WODEHOUSE (1935 p. 351) has pointed out that pollination by wind tends to bring about a reduction of the exine "with an attendant loss or reduction of its structure such as furrows, pores, and sculpturing" (cp. KNOLL 1930 p. 629). Most of the pollen types of Northern European wind pollinated species are smooth or almost so, the strong sculpturing being characteristic of zoogamous species.

Whereas the anthers of zoogamous species are more or less concealed, the more so the more perfect the pollination mechanism, those of anemogamous species are generally freely exposed, projecting beyond any perianth. Flowering frequently takes place before the development of the foliage. A number of mechanisms tends to scatter the pollen grains as effectively as possible.

The tendency of pollen grains to stick together has been investigated by REMPE (1937 p. 103, cp. also KNOLL 1930, 1936). In most of the typical wind-pollinated species, *Picea, Fagus, Corylus, Alnus, Betula, Carex* (*montana*), *Secale,* in *Erica carnea* (tetrads) and *Calluna* (tetrads), and, rather surprisingly, in *Acer platanoides* and *A. pseudoplatanus,* there is practically no clumping of the pollen grains. In the rest of those forest trees that are included in routine analysis: *Quercus, Tilia* (2 spp.), *Ulmus* (2 spp.), *Acer* (2 spp.), *Larix, Salix* (2 spp.), *Castanea,* and, most unexpectedly, *Pinus,* 25-40 % of the grains stick together to form comparatively small clumps. In typical insect pollinated species: *Salix* (3 spp.), *Malus, Pyrus, Galanthus* (cp. TROLL 1928, KNOLL 1930 p. 662), and *Taraxacum,* clumps are both more frequent and bigger. The same pertains to a few wind-pollinated species, e.g. *Mercurialis.*

The pollen grains of wind pollinated species constitute the bulk of the pollen rain, and pollen analysis is primarily concerned with these species. There are 3 factors that serve as the factual basis for pollen analysis, viz. 1. Pollen grains of different taxonomic groups are different and can be recognised. 2. The great resistance of the exine which permits pollen grains to be embedded in sediment or peat and still be recognisable. 3. The extremely even distribution of the enormous quantities of pollen grains of the most important species in the air and—consequently—on the ground, or water, as the case may be.

One single anther of hemp may contain 70,000 pollen grains. In Northern European forest trees the number is considerably lower, e.g. ca. 10,000 in birch. Usually insect pollinated species produce much smaller numbers, ca. 1,000 in *Acer* (all seq. POHL 1937); in *Linum catharticum* (frequently autogamous) the number is ca. 100, and in autogamous species it may be even smaller.

As each flower usually possesses a number of anthers, and each shoot many flowers, the figures for total production reach enormous dimensions. One shoot of hemp produces more than 500 million pollen grains whereas a male plant of *Rumex acetosa* produces 400 millions, but even a large plant of *Linum catharticum* hardly reaches 20,000. The forest trees produce great quantities, a 10-year old branch system of beech produces more than 28 millions, birch, *Picea,* and oak a little more than 100 millions, and pine ca. 350 millions (nearly as much as a male plant of *Rumex acetosa*). The production per hectare of forest runs into billions (all seq. POHL l.c.), and HESSELMAN (1919 p. 41) concludes that the *Picea* forests of Southern and Middle Sweden produce ca. 75,000 tons of pollen annually when flowering freely.

These enormous quantities of pollen are liberated, float in the air for a shorter or longer period, and are eventually sifted over the surroundings as the dense and even pollen rain. Studies on the quantity and composition of the pollen rain have been undertaken in several localities, usually in connexion with hay-fever studies. Most of the results suffer, however, from weaknesses of method that make them less useful for our purpose. The only technique that corresponds to the state prevailing in nature is to collect the pollen on horizontally exposed, unprotected surfaces. All other methods (protected surfaces, e.g. microscope slides, horizontal or vertical, vacuum cleaner, etc.) may give better information of the pollen grain content of the air, but they are less adapted to answer the question of pollen sedimentation, which is the important question in pollen analysis. HESSELMAN's experiments in 1919, those of LÜDI and VARESCHI (1936) and FÆGRI (unpublished, cp. also FIRBAS & SAGROMSKY 1947, DYAKOWSKA 1948) have been carried out by a technique corresponding to natural pollen sedimentation. HESSELMAN trapped his pollen grains in Petri dishes, the bottoms of which were covered by a glycerine-drenched filter-paper. To prevent over-flowing the dishes had to be closed when rain began, the values are therefore minimum values. LÜDI and VARESCHI used cylindrical glass jars with a little glycerine; after being exposed the jars were washed with distilled water and the pollen contents concentrated on the centrifuge. FÆGRI used cylidrical zinc vessels with conical bottoms and a glycerine-drenched filter-paper, excess water was drained off through a cock in the bottom of the vessel. The methods suffer from the disadvantage that pollen-bearing insects sometimes perish in the vessels; in such cases the numbers are too high. The quantity of pollen of anemoganous species should not, however, be appreciably influenced by this.

HESSELMAN exposed his dishes in two lightships in the Bothnian Gulf (which is surrounded by heavily forested country) with the following results:

Distance offshore	35 km	50 km	flowering
Picea...........	700	400	profuse
Betula	700	350	„
Pinus...........	200	100	medium

All numbers indicate pollen grains per cm² per season.

In the Davos valley, which is situated at fairly high altitude, LÜDI and VARESCHI found (cp. LÜDI 1937 p. 108) the following quantities of pollen (all per cm² per season):

	1934	1935	
Picea	4.7	4.6	
Pinus	5.0	49.1	
Betula		2.5	
Alnus		8.3	
Corylus		2.7	(not growing in the valley)
Gramineae	16.7	150.3	

The numbers are fluctuating, but on the whole much lower than those of HESSELMAN, although the lower 500 m of the valley sides are forested, mainly with *Picea* (LÜDI and VARESCHI l.c. p. 52).

In the three localities Nesbyen (forest region), Haugastøl (timberline), and Slirå (regio alpina media) FÆGRI (unpubl.) found the following numbers of *Pinus* pollen grains, all per cm² per season:

	1942	1943	1944
Nesbyen	172	230	1050
Haugastøl	3	24	—
Slirå	13	4	1

The numbers are intermediate between those of HESSELMAN and of LÜDI quoted above. Nesbyen is located in Hallingdal and Haugastøl at the upper end of a continuation of that valley, whereas Slirå is located practically at the water-divide between East and West Norway, some 30 km west of Haugastøl and 50 km west of the continuous conifer forests of Hallingdal.

A similar investigation was carried out in the summer of 1949 at the Atlantic weather ship station M, lat. 66° N, long. 2° E Greenwich, 450 km from the Norwegian coast, and some 1700 km from the Middle European oak region. In that place the following numbers of pollen grains fell per cm^2 and season (1949):

Picea	0
Pinus	5.5
Betula	4.7
Quercus	0.8
Gramineae	5.5

Considering the great transport distances the figures are unexpectedly high.

Observations indicate that pollen grains are dispersed with air currents across wide distances. Pine pollen has been recovered in recent samples from the Arctic (WILLE 1878 p. 15). The journal of the "Michael Sars" expedition of 1914 records the observation, on 24th June at 17.30 hrs of a *Pinus* pollen rain on the surface of the Arctic ocean, ca. 100 km from the nearest coniferous forest. The number of pollen grains was calculated as 2,500 per cm^2, which is certainly too high owing to the method of sampling. One must also take into account that the pollen grains may have been brought together from a wide area by surface currents.

Studies on the rate of sedimentation of pollen grains in calm air give figures ranging from ca. 40 cm/sec for heavy wind-borne pollen to ca. 2 cm/sec for the smallest, most buoyant types (KNOLL 1932, DYAKOWSKA 1937). However, according to DURHAM (1946) such values suffer from great experimental errors and are on the whole rather useless. By means of SCHMIDT's formula one can calculate the "mean dispersal distance" (i.e. the limit reached by 1 % of the grains) which—under given conditions—varies between ca. 1 and ca. 500 km (KNOLL, DYAKOWSKA l.c.). These maximum figures are, however, only of limited practical value, as a wind very rarely lasts sufficiently long to carry a pollen grain so far at one stretch. On the other hand pollen grains are frequently redeposited several times before their final destruction or incorporation in a sediment (cp. the find of *Zea* pollen in Middle Sweden at Christmas ERDTMAN 1938 p. 130). Thus the combined distance can theoretically be much longer than that calculated by SCHMIDT's formula.

The above mentioned figures for the sedimentation rate of pollen grains are, however, of great value in another connexion: It is well known that the vertical component of air movements can be very strong: thermic or orographic "up-winds" frequently reach the velocity of many metres per second, and even the vertical component of air movements connected with frontier passages may be sufficiently strong to carry at least some of the most buoyant types up into the air.—As anthers normally open in dry and warm weather, the thermic up-winds, especially those under cumulus clouds, are of the greatest significance for the transport of pollen grains into the upper air masses and thus for long-distance dispersal. REMPE (1937 p. 134) has shown that the upward air current under a cumulus cloud took a *Picea* pollen rain from the Harz mountains 34 km south west to Göttingen, where the pollen dropped in a beechwood district when the cloud dissolved.—39,610 of HESSELMAN's 44,625 pollen grains were trapped during two of the 40 days of observation; it is probable that this concentration may be due to similar transport with cumulus clouds.

Airplane reconnaissances on the pollen grain content of the atmosphere (REMPE l.c.) have demonstrated that pollen grains carried upward during the day fall comparatively rapidly during calm nights. The heavier grains especially are more or less completely eliminated, whereas the more buoyant types, owing to their smaller rate of fall, are concentrated in the lower air layers and may thus easily be carried upwards the next day. It must not be forgotten, however, that the thermic up-winds are compensated by corresponding descending airmasses, which may bring pollen grains from the upper layers down again.

Considering the meteorological control of the opening of the anthers, the longevity of cumulus clouds and the maximum distance they travel before being dissolved, are major factors in the problem of pollen transport. According to information this distance is of the order of 50-100 km. Other types of warm, dry winds generally cover similar distances.

The distance 50-100 km thus forms a natural limit of pollen dispersal. It is self-evident that the greatest quantities are deposited long before this limit has been reached, and on the other hand there are, of course, those other grains which remain in the air for more than one day, and which can therefore be transported over wide distances. It is evident that there is in that respect a great difference between those buoyant pollen types that are not completely eliminated during the night and the others. The long-distance transport problem for species like *Fagus* or *Picea* is quite different from that of *Pinus* or *Betula*. Later (p. 92) the long-distance transport problem will be taken up from the pollen-analytical point of view. In this place we shall confine ourselves to dealing with the problem from the pollination view-point. Even if maximum transport distances are very large, only a very small fraction of the pollen will have any chance of reaching outside the region of production, i.e. beyond the frequently rather insignificant area covered by the day's horizontal transport. ERDTMAN's observations show that the atmosphere over the Atlantic ocean does contain pollen grains, even as definite pollen rains, several hundred kilometers from the nearest shore (ERDTMAN 1937 p. 189), but also that the numbers met with are insignificant as compared with those of a forested area (6 grains per 100 m^3 of air vs. 18,000).

Pollen analysis is based upon the great quantity and uniform dispersal of pollen grains. The occurrence of macro-fossils is always more or less accidental, most of the macro-fossils found in sediments or peat are remains of the local vegetation, which is frequently climatically indifferent. Species of dry ground are heavily under-represented or usually not represented at all. The find of a macro-fossil is a rather certain indicator that the species in question occurred in the locality at the time of deposition of the sample, but nothing can be concluded from its absence. On the other hand: if a wind-pollinated species flowers in the neighbourhood, its pollen grains will be sifted over the whole region, including bogs and lakes, they will be embedded and can be recovered. If no pollen is found, there is only a very small chance that the species grew in that locality at that time. The quantity of pollen deposited per unit area will depend upon a number of factors, viz.:

1. The frequency of the species in the region.
2. Its absolute pollen production, which varies both specifically and individually according to the conditions under which the specimen grows. Thus many species that produce great quantities of pollen when growing in an open position, produce very little when growing in dense stand. Pollen production is also dependent upon the frequency of flowering years. Some forest trees flower freely at intervals only. This is partly due to morphological reasons, the flowers or inflorescences being situated in such a position that no flower can be formed in that place in the following year, and partly to physiological factors, a period of "rest" being necessary before the next profuse flowering. The nearer one comes to the limit of the area of distribution of the species, the longer the periods of "rest" between flowering.—Dendrological literature gives information about the years of rich seed-setting, which is, however, not necessarily the same as years of rich flowering. The various authorities do not always agree, but there seems to be a general agreement that *Betula* and *Alnus* flower and fruit

freely every year, and that there are intervals between the flowering years of *Picea, Fraxinus, Fagus,* and *Quercus.* The position with regard to *Pinus* is more obscure; at any rate in *P. silvestris* flowering seems to be more regular than seed-setting, which is less certain because of the long ripening-period.

3. The dispersal mechanism of the pollen also influences its deposition in the region. Dry pollen is better dispersed because of the smaller size of the particles, and the greater number of pollination units. It is also more widely scattered than pollen grains whith stick together in lumps because of oil coating, etc.

Provided we can compensate for the factors mentioned under 2 and 3, above, the quantity of pollen per unit area is a measure of the frequency of any wind-pollinated species in the region. Fortunately almost all Northern European forest trees are wind-pollinated. During the flowering season enormous quantities of pollen are scattered over the whole area and can be recovered from the contemporaneous surfaces of bogs and sediment deposits. There are some few Northern European forest trees that are pollinated by insects, the most important being *Tilia* and *Salix* species which, however, produce such great quantities of pollen that they behave more or less like wind-pollinated species. These genera are therefore not seriously under-represented in relation to many wind-pollinated species.

In a forested region the under-growth plays a rather insignificant part in the pollen rain. Many of the plants of the forest floor flower sparsely, and in the calm between trees wind pollinated flowers are in rather unfavorable position. Other pollination types are relatively more important. If, however, the forest cover disappears, conditions change: the increased amount of light favours flowering of the lower vegetation, and wind can disperse the pollen. Per se the pollen production per unit area of lower vegetation is not small. According to Pohl (1937 p. 440) the pollen production of a rye field per m^2 is higher than that of *Carpinus; Arrhenatherum elatius* produces more pollen per unit area than oak or beech, and *Calluna* twice as many units (8 times as many pollen grains) as *Pinus silvestris.* It is noteworthy that *Calluna* is zoogamous, but at the end of the flowering season great quantities of pollen are liberated in the air. Most of this pollen is, however, almost immediately deposited on the ground (cp. Hesmer 1933 p. 631). Within the same climatic region the pollen production of an area is more or less the same whether that area is forest-clad or covered by lower vegetation, and the relation between the pollen produced by forest trees and that produced by the ground vegetation is an indication of the density of the forest.

The total pollen production in different climatic regions is highly variable (cp. AARIO 1940), and the intensity of the fossil pollen rain would furnish a very fine instrument for the analysis of the character of former vegetation and climate. This instrument is, unfortunately, not available, as we always measure the number of pollen grains in a given *volume* of substance. The rate of growth of the deposit thus constitutes another unknown factor that—in all but the rarest cases (WELTEN 1944)—makes our equation insoluble. Methods have been proposed to calculate the so-called absolute pollen frequency (APF) i.e. the number of pollen grains per unit quantity (by weight or volume) of deposit. Apart from the fact that the weight or volume of a sample is dependent on the water content, the APF suffers from the fundamental error of giving the number of pollen grains in a volume of the deposit, instead of on a surface. On the other hand there is no doubt that the APF numbers may in some cases (especially in late-glacial analyses) give indications of great value. However, one must always investigate whether a given variation of the APF is due to a different rate of sedimentation or to different pollen production— or to both, as both are climatically conditioned. The simplest indications of the APF values are obtained by noting the number of pollen grains per unit area of microscopic preparation. If the preparations for pollen analysis are all made by the same person working in the same manner, this simple method gives comparable figures. The figures are more reliable if based upon many small preparations; if one only is used, accidental errors may have an undue influence. A better, although more complicated method consists in boiling the sample with water[1] and centrifuging it in a graduated centrifuge tube under constant conditions. The volume of samples treated in this manner are comparable, and the pollen contents of part or all of such a sample may be counted, after acetolysis or other treatment. The method thus gives APF per volume unit, but owing to the highly variable rate of growth of deposits, these figures are only of limited value (cp. v. POST 1929 p. 547).

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[1] Not KOH, which will dissolve the "humic acids" and reduce the volume in acid deposits.

PEAT AND SEDIMENT TYPES

Before proceeding further with the main theme of pollen analysis, we shall have to deal quite summarily with the matrix in which the pollen grains are embedded. In agreement with previous authors we distinguish between *peat* which is mainly autochthonous, consisting of remains of the vegetation that once lived in that particular place where the sample is recovered, and *sediments* which are mainly allochthonous, consisting of material that has originated elsewhere and been deposited or redeposited in the place where it is recovered. Organogenic sediments are chiefly formed in open water, more exceptionally also above the low-water level, e.g. diatom mud in the inundation zone of rivers. Peat on the other hand is formed both below low-water level (*limnic* peat), in the periodically submerged zone between low-water and high-water levels (*telmatic* peat) and also above high-water level (*terrestric* peat). It must be remembered that the realisation of these peat types is to some extent dependent on the correlation between seasonal submergence/emergence and the production rhythm of the plant community.

"It is hardly possible to establish a peat type classification that is directly applicable under all circumstances" (v. POST and GRANLUND 1926 p. 41), but the distinction between these three primary hydrologic classes is of fundamental importance for the understanding of the development of a deposit. The ordinary sequence during the filling up of a basin passes through the stages: sediment—limnic peat—telmatic peat—terrestric peat. The types of sediment and peat differ according to the chemical and physical conditions under which they have been formed, but the above sequence (or some abbreviated type) is always recognised if the filling up has proceeded in the normal manner. On the other hand a reversion of this sequence indicates that the ordinary hydrosere has been interrupted, and further investigations may disclose whether this interruption is due to climatic irregularities or not. The distinction between the main classes is therefore of primary importance.

All sediment and peat types divide themselves into two ecological series, one oligotrophic and one eutrophic[1], with some intermediate types. This distinction is purely ecological and—with the exception of the general oligotrophication in humid climates—rarely permits any climatic conclusions being drawn, but they furnish a firm basis for further classification.

The oligotrophic lake is generally also dystrophic, and its sediment is the *dy* (Swedish) or gel-mud (GODWIN 1938), a blackish-brown, colloidal precipitate that is dissolved by treatment with KOH. In extreme cases pollen grains form almost the only solid particles left after such treatment. Other types of oligotrophic sediments are less frequent, at least in NW Europe. The eutrophic sediment is the *gyttja* (Swed.) or nekron-mud (GODWIN l.c.). Its colour varies. Pure gyttja consists of microscopic and submicroscopic remains of the flora and fauna of the basin. As this flora and fauna varies, the gyttjas vary, but they have in common that they are insoluble in KOH and that the extract is never dark brown, but colourless, greenish, yellowish, etc. The actual sediments observed in nature frequently occupy an intermediate position between the extreme types, and they are characterised by their origin from a special community or by having been deposited under special conditions; resultant variants are lake marl, clay gyttja, alga gyttja, diatom gyttja, detritus gyttja, etc. How far one goes in dividing the sediments, depends upon the special problems under consideration. Whereas it is in some cases sufficient to characterise the sediment as gyttja or dy, it may in other cases be neccessary to distinguish between a long series of finely divided types. It all depends on the problems to be investigated (cp. LUNDQVIST 1938).

A practical method for the investigation of the quantitative relations between the components of sediments (or peats) is to use the ordinary eye-piece micrometer and note how many of the index lines touch the different constituents. After having done that for a sufficient number of fields of vision, one gets a good percentage estimation of the composition.

The peats are even more variable in composition than the sediments, each bog community producing its own peat type. The main types from subcontinental Northern Europe have been summarised by v. POST and GRANLUND (1926), in other parts of the world other types will be found. It should, however, always be possible, and desirable, to distinguish between the main hydrologic types.

Among the terrestric peats one series deserves a special comment, viz. the regenerative types, which are in Northern Europe represented by some *Sphagnum* peats. The principle of regeneration was first described by

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[1] These terms refer to the available quantities of plant nutrients only.

v. Post and Sernander (1910); it consists of a cyclic succession between wet and dry communities that form a mosaic on the surface of the bog. As the rapidly growing peat is light and slightly humified[1] whereas the small quantity of peat formed by the drier communities is dark and highly humified, the resulting section of the bog will show an alteration between broad, lens-shaped layers of bright, and narrow undulating bands of dark, peat ("bacon peat"). In this way the bog grows up above the general groundwater level until its margin reaches a maximum gradient that—within the same climatic area—is entirely dependent upon the quantity of precipitation (Granlund 1932). The more the bog approaches this stage, the more important are the dry communitites in relation to the wet ones until the bog is completely dominated by the so-called stand-still complex (Osvald 1923) when no more peat is formed. Correspondingly the peat section is gradually dominated by the dark bands, the brighter parts thinning out and disappearing. This gradual development from dominant bright, slightly humified peat to dominant dark is the normal development of a regenerative peat, just as development from limnic to terrestric peat is the normal within the hydrosere, and reversions may be of climatic significance. In Swedish domed bogs[2] Granlund (1932) has demonstrated the existence of 5 different reversions of general distribution. Each of these "recurrence surfaces" ("rekurrensytor", RY) represents a climatic change from drier to wetter conditions, permitting the establishment of another regeneration complex instead of the previous stand-still. Other RY's have since been discovered. The much-debated Grenzhorizont of Northern German bogs is obviously the same phenomenon (Overbeck 1947).

Reversions of the normal development may be due to some non-climatic cause, e.g. a small land-slide damming a basin up to a higher level than it was previously, but if such causes can be ruled out in the particular case under consideration, the sequence of layers can give very important informations about the climatic development—as a matter of fact this was the objective of the old palaeophysiognomic school. By means of pollen analysis such climatic events can be dated and their synchronity—and general significance—established.

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[1] The degree of humification can be easily and fairly accurately judged by squeezing a piece of peat in the closed hand (cp. v. Post and Granlund p. 29). More elaborate methods are discussed by Overbeck (1947), their result is not much superior to that of the less exact method.

[2] We prefer the term "domed bog"—proposed by Mrs. Marguerite Bulman née Fearnsides—to the slightly ambiguous and somewhat compromised "raised bog" as a translation of the Swedish "högmosse", ombrogenous bog. It should be noted that there is no logical necessity for ombrogenous bogs always to be regenerative.

Reversions of bog development should always be followed in a profile across the deposit, as the evidence from a single section may be misleading.

Besides a determination of the peat type and the degree of humification many other characteristics of deposits can be noted and expressed more or less quantitatively. We refer to v. POST and GRANLUND (1926) and to LUNDQVIST (1938).

SEDIMENT AND PEAT SYMBOLS

If one wants to utilise the information given by bog development, the stratification of the bog must be represented in a diagrammatic profile. All pollen diagrams should be accompanied by a schematic section representing the composition of the deposit where samples were collected. For the evaluation of pollen-analytical data it is indispensable to know something about the deposit; percentages in a carr peat and in a sediment mean different things. This holds even for the arboreal pollen, whilst an analysis of non-arboreal pollen in an unknown deposit is of very restricted value.

One can write the names of the peat and sediment types in lettering on a diagrammatic drawing—it is the easiest way out for the author and the least satisfactory for the reader who, besides the omnipresent language difficulties, must take the trouble of forming a mental image from a complicated text. It is therefore preferable to use a symbol system that gives an immediate impression of the structure of the deposit. Most symbol systems have been made to cover immediate needs, the consequence is that one and the same symbol may mean different things in different publications. This is, of course, highly inconvenient; symbols are conventional and their effectivity is dependent upon the universality of their acceptance.

FÆGRI and GAMS (1937) have proposed the following general principles: Symbols for (a) sediments, (b) limnic and telmatic peat, and (c) terrestric peat should be immediately recognisable in the diagrams. This is obtained by varying the general direction of the symbol lines. Sediments should have symbols consisting of crossing lines, peat symbols of parallel lines; limnic and telmatic peat symbols having vertical lines, and terrestric peat symbols consisting of horizontal lines.—The degree of humification should be immediately recognisable by the distance between symbol lines (modified later, cp. below), the darker, highly humified peat being represented by dark signatures thus imitating the natural conditions. Adoption of these rules will allow any investigator to follow at least the main features

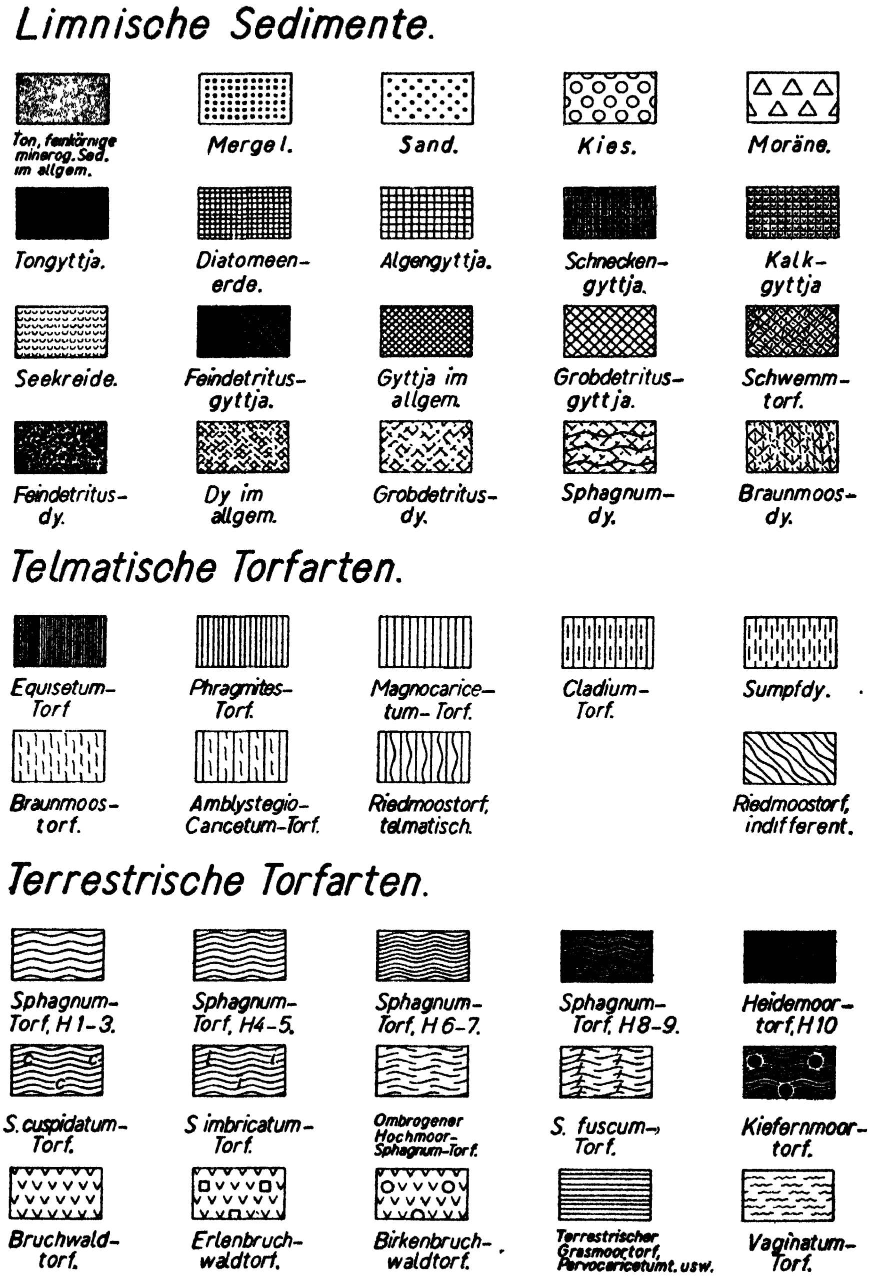

FIG. 1. Peat signatures proposed by FÆGRI and GAMS.

of bog development even if the peat and sediment types and their mother formation are completely unknown to him.

Troels-Smith and his collaborators (cp. Troels-Smith 1947) have introduced a third principle besides the two proposed by Fægri and Gams: As most sediments and many peats are not pure types, but mixtures, it is preferable to indicate this in the symbols. The degree of admixture is classified by a 1 to 4 scale, 4 being the pure type. To each degree corresponds a specific distance between symbol lines, which permits different symbols to be combined to form 4/4. In telmatic and some terrestric deposits it is found convenient to indicate the degree of destruction—corresponding to the humification of moss peat. In contrast to humification destruction cannot for technical reasons be indicated by the distance between lines, but must be indicated by the thickness of the lines, which gives the same visual effect. If this principle is adopted, humification should be indicated in the same way. Troels-Smith's sediment system is very elaborate, cp. fig. 2-3. For general use this system is much too complicated, we quote it as an example of how far one can and for the solution of certain problems must, differentiate. For a representation of the hydrosere one single sediment symbol would in some cases be sufficient, but in most cases one will want to be able to differentiate a little more.

Sediments are comparatively uniform all over the world, and the same symbols ought therefore to be used everywhere in the same way. The applicability of peat symbols is less general, owing to the great regional differences between mother formations and consequently between peats. Fig. 1 comprises some of the more important peat types of Northern Europe. In other regions the same signatures may, of course, be used for different, but preferably corresponding peat types. One should be careful to reserve the broken wave-line for regenerative peat, which certainly does not mean that it should always be reserved for *Sphagnum* peat.

Lüdi (1939) has objected that the system proposed by Fægri and Gams forces the investigator in every case to classify his deposits as belonging to one of the groups mentioned above, thus in certain cases introducing an apparent exactness in the classification of deposits which is neither justified nor intended. To cover such cases Fægri and Gams introduced "neutral" symbols of parallel lines, the main direction of which runs at 45° to the horizontal and vertical (not of course to be confused with those sediment symbols, the *crossing* lines of which have the same main direction). For generalised diagrams it will also be necessary to use symbols meaning peat in general etc., but such symbols are easily extemporized, and in such simple diagrams consistency is not of the same importance as in the more complicated types.

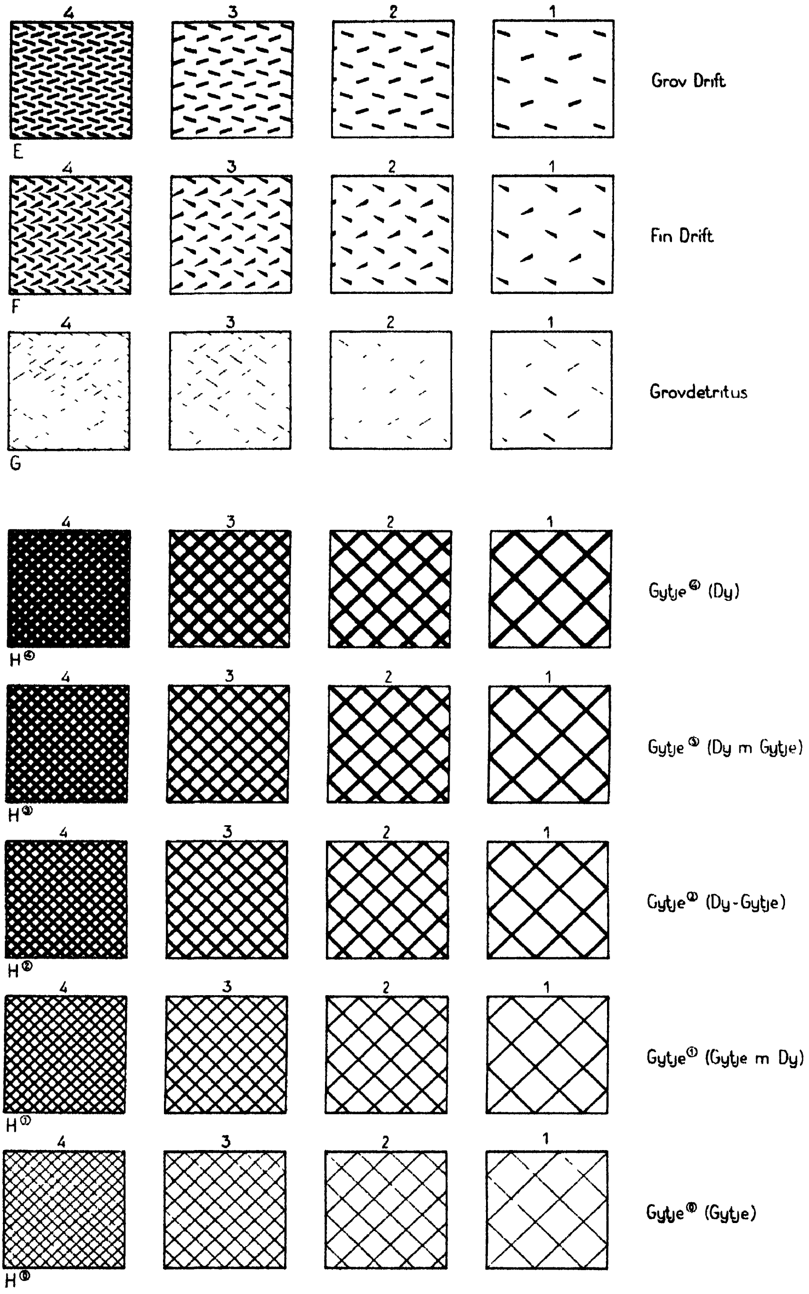

FIG. 2. Part of the peat signature system proposed by TROELS-SMITH, cp. p. 47. (Borrowed from J. TROELS-SMITH).

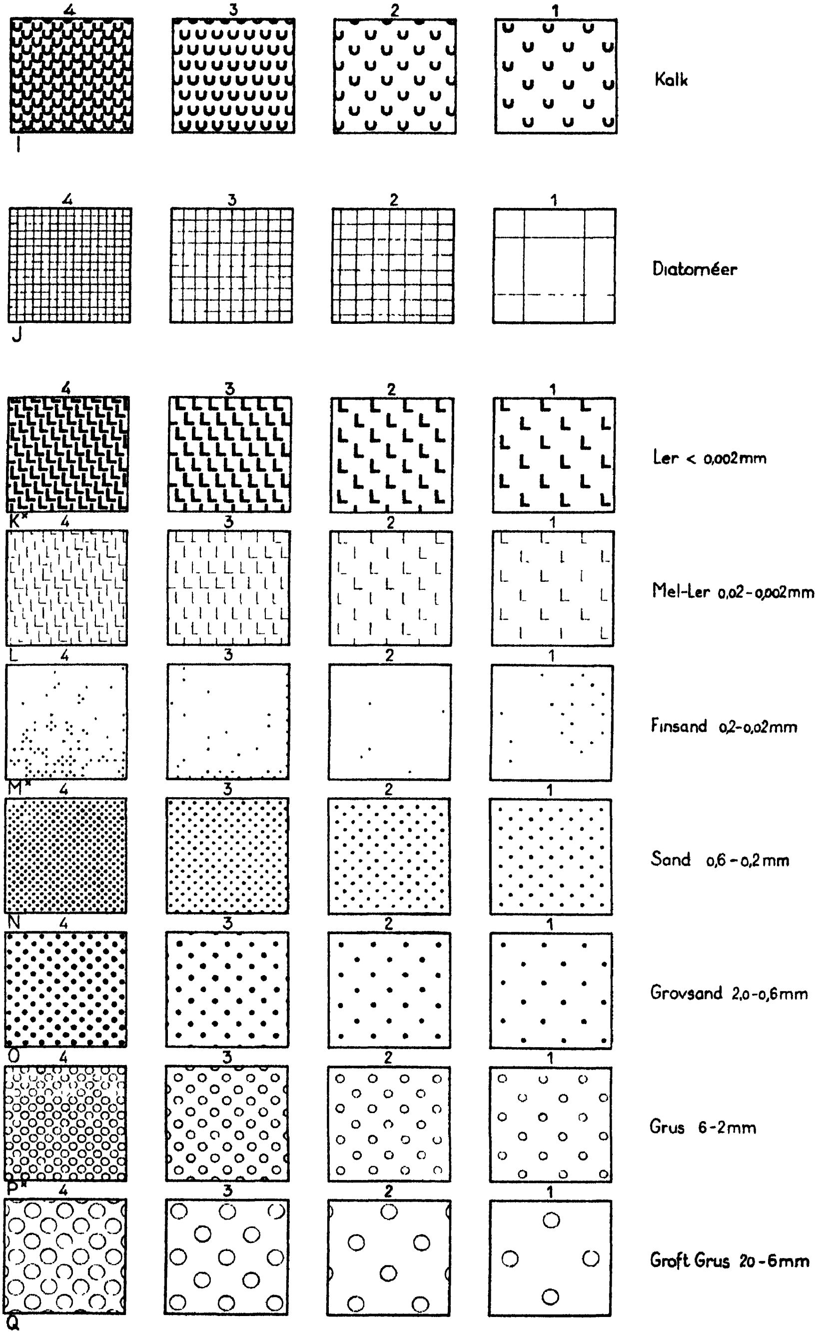

FIG. 3. Conf. Fig. 2.

FIELD TECHNIQUE

The technique of pollen analysis has two widely different aspects: field work and laboratory work, and unless both are executed with the greatest care, the results will be uncertain, in extreme cases having no value at all.

The aim of field work is to collect samples of the deposit, to define as exactly as possible the conditions under which the samples were taken, to determine the types of sediment, and to explain the stratigraphy. The first condition is that samples must be *absolutely pure,* they must contain nothing but material from the layer they are supposed to represent. To attain this, great care is necessary when samples are taken out of the deposit. Never touch a sample with your fingers, it must be handled with a pair of smooth forceps (the ordinary, milled type is worse than anything) and/or a spatula. Forceps are best for peats, whereas sediments are better treated with a spatula or even better with two. All instruments must of course be thoroughly cleaned between samples—the easiest way of doing this, is to rub them on the dress, which should be suitable for such purposes.

Usually one must work from the surface of the bog. In that case it is rarely profitable to dig to any depth. The surface samples, down to 15 or 20 cm, are usually taken out of a sod that is cut for the occasion, the others are then taken by some kind of peat sampler[1].

The general principle of these is that a closed chamber is pushed down through the deposit to the required depth, where it is opened. In the Hiller type of samplers this is accomplished by turning the apparatus anti-clockwise. An outer, loose jacket with a projecting lip remains stationary while the inner chamber turns so that the longitudinal slits of jacket and chamber coincide. By further anti-clockwise turning the jacket is rotated as well, the

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[1] As all extra turning of the instrument tends to make a mess of the deposit, the instrument should be *pushed* down through the layers, not screwed; consequently we have prefered the neutral term "sampler" instead of the usual, but misleading "borer" or "auger".

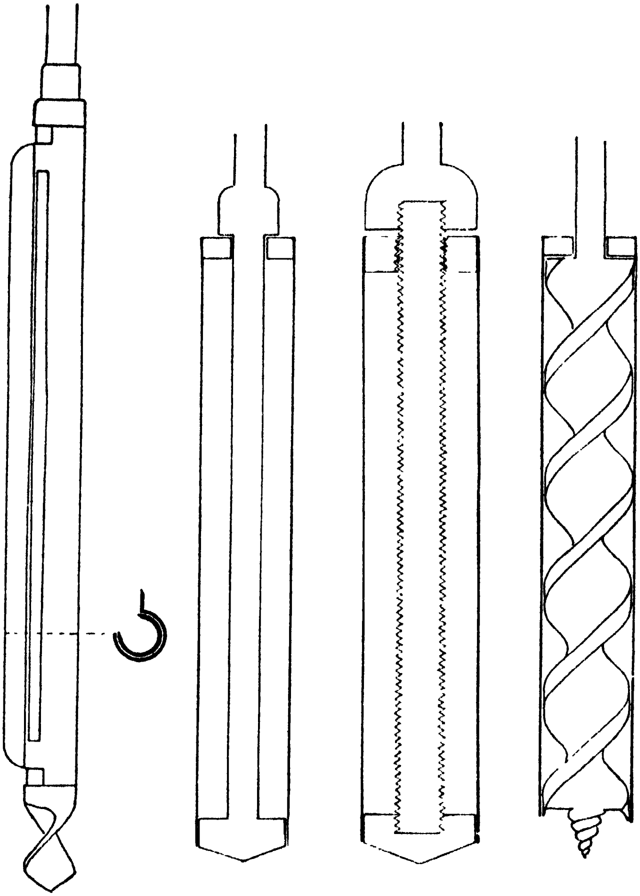

Fig. 4. Types of peat samplers. From left: Hiller, Dachnowsky, Reissinger, Douglas (Reissinger modification).

chamber fills with sediment and is then closed by turning the other way before pulling up. After the sampler has been taken up, the chamber is again opened and the samples taken out. It is difficult to preserve the undisturbed sequence if one tries to remove the sample in its entirety (Erdtman 1935 p. 111 has for this purpose proposed a thin, removable zinc lining of the chamber). It is better to take out smaller samples at regular intervals with forceps or spatula. Before opening the sampler, one must clean the surface with a knife (not a cloth). Those parts of the sample that are in contact with the inner walls of the chamber, must be considered contaminated and must be avoided. The exposed surface must be cleaned most carefully. It is better to remove too much than too little!

A serious error may be caused by the gradual sinking of the sampler during the operation in the bog. If one is careful at this point, and cleans chamber and jacket thoroughly between each sample, the Hiller apparatus is a very reliable instrument[1]. In some types of deposits, especially fibrous or undecomposed peat, it is the only instrument to give any samples at all, even if in such peats the samples are never absolutely free from contamination. In sandy sediments the results are not reliable, and in sticky muds it may be necessary to use an extra broad lip on the jacket (FÆGRI 1944). The same may be the case in very loose or watery mud.

Another principle is represented by the Dachnowsky sampler. Its main parts are a core and a jacket. When the instrument is pushed down, the core fills the jacket. When the right depth has been reached, the core is pulled up into the upper part of the jacket, which is pushed further down its own length and thus filled. The core is prevented from sliding down again either by a snap spring or by a bayonet fastening. A modified type has been proposed by REISSINGER (1936 p. 17) in which the core remains at the same level while the jacket is screwed further down by turning the instrument anti-clockwise.—By carefully pushing out the core[2], it may be preserved in its entirety, thus permitting the reconstruction of the whole section in the laboratory. The drawback of this type is that it does not work well except in homogenous fine-grained sediments.

Some samplers have the shape of a screw with a very coarse thread, in which the deposit is left when the instrument is *screwed* down. When it is *pulled* out again, the sediment from the deepest part is supposed to be left in the screw. We have little practical experience with this type, which, however, does not seem to give a sufficient guarantee against contamination. REISSINGER (1941 p. 34) recommends this type with a loose outer jacket ("Douglas sampler") for penetrating otherwise impervious sandy layers. When the instrument is bored down, the jacket remains in a raised position; on pulling up, it is pushed downwards and protects the contents of the screw. The construction is worth trying, as sandy sediments represent one of the major difficulties in sampling work, especially if important layers are expected under the sand, which should therefore be penetrated.

J. T. WILSON uses a much simpler instrument for piercing sand layers and obtaining samples from same, viz. an ordinary ½-inch pipe. It is

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[1] Two different sizes are manufactured and sold by the firma Beus & Mattson, Mora, Sweden.

[2] In difficult cases by pumping air into the upper part of the chamber.

closed at the bottom by a snugly fitting cork, and is brought down to the sand layer through a hole made by the ordinary peat sampler. The cork and sand are then forced into the pipe by pounding the latter with a sledge hammer (WILSON & POTZGER 1943 p. 388)[1].

Especially when using the Hiller sampler one should always work two holes alternately, as the deposit is disturbed by the screw under the chamber during the turning back and forth.

In those cases when the contents of the sampler are not preserved in their entirety, small samples should be taken at regular intervals. Whereas the standard interval during the early days of pollen analysis was 25 cm, it is now for general work 5 cm—which does not, however mean that all 5 cm samples must be analysed in all cases. On the other hand, near transitions between different deposit types, or in deposits which have accumulated very slowly, the sample distance must be reduced to 2.5 or even 1 cm. As a general rule one should always take more samples than one expects to need for analysis, but it is self-evident that in very rapidly growing deposits the distance between samples may generally be increased above the usual standard.

The samples should be preserved in glass tubes. Flat-bottom tubes are generally thin-walled and easily broken. Round-bottom tubes are stronger, but have the disadvantage that they will not stand on the table. Tubes with cork stoppers in both ends are well protected against breaking, but are more difficult to seal effectively. Recent experiences have demonstrated that samples should be kept moist until they are analysed, as the more fragile pollen grains are easily destroyed if the sample dries out, and are therefore partly over-looked by subsequent routine analysis[2]. We therefore warn against wrapping samples in cellophane or other material in which they dry up rapidly. To keep samples moist in the tubes, stoppers should be sealed with paraffin or other wax and/or some glycerine added to the samples to prevent desiccation.—It is very difficult to keep larger samples (entire chamber contents) moist for any length of time. They must be wrapped in many layers of cellophane or parchment paper and kept moist in a cellar or some similar place or be enclosed in paraffin. Precautions must be taken to prevent moulding.

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[1] We have not tried the water-hose arrangement used by the authors for organogenic sediments, but we are afraid that too heavy disturbance of the layering may be the result of the process.

[2] According to information from Mr BRORSON CHRISTENSEN of the Copenhagen National Museum this difficulty is overcome by soaking the sample in 5 % KOH ca 1-2 months before preparation.

All samples must be clearly marked. Tube samples are most conveniently marked with consecutive numbers written with copying pencil on the cork stopper. In the note-book the corresponding depth is recorded together with notes on the nature of the deposit. It is more difficult to mark the larger samples. The top must be clearly indicated. It must be remembered that paper slips which have been in contact with wet peat or sediment for some time, are usually so corroded that notes written on them are unreadable.

Ordinary opaque paper should never be used for wrapping up samples, not even temporarily, as its cleanness cannot be checked.

After samples for pollen analysis have been taken, the rest of the contents of the sampler should be investigated macroscopically for determination of the type of deposit and should be searched for macro-fossils. All plants cannot be identified pollen-analytically, and among the indeterminable ones there may be important indicators, the macroscopic remains of which are more easily detected.

Frequently it is desirable to obtain samples from the bottom of lakes. The sub-aquatic technique has been developed to high perfection (STRØM 1935, KULLENBERG 1947, JENKINS & MORTIMER 1938, the same and PENNINGTON 1941); unfortunately the most effective apparatus is too complicated and heavy to be transported to small lakes and worked from the small boats or rafts available there. In many cases one must work from the ice where it is practicable, or from a raft. A pontoon raft is usually preferable; especially when working in inaccessible places it is imperative to have light pontoons (inflated rubber!) that can easily be transported. The raft must be securely anchored, either by 3-4 grapnels or by strong wires to the shores (of very small lakes). If there is any depth of water, the unprotected stem of the sampler is likely to bend, thus making the depth indications uncertain and making it difficult or impossible to penetrate more compact layers. REISSINGER (l.c. p. 4) proposes to make the lowermost extension rods heavy, the upper ones buoyant (by means of floats), in this way the stem keeps straight by itself. In order to reach the same hole each time REISSINGER uses a funnel that rests on a piece of sheet-iron on the sediment surface. It is very difficult to obtain samples from the uppermost, loose flocculent sediment layers. SIGURD OLSEN (unpubl.) has used a pump with very narrow intake that is lowered to the correct depth and there filled. The narrow opening prevents sediment entering from other levels.

In very small bogs or lakes one single profile point may be sufficient. It must then be located as near the sedimentation centre (not always identical with the geometrical centre) as possible. If the deposit studied is a uniform series of fine-grained sediments that have been deposited under uniform conditions, one section may also be sufficient in larger basins. Usually one ought to investigate a *profile* across the bog. A series of sections must be taken with the sampler for the determination of the nature of the deposits, the horizontal and vertical distances between points of investigation being determined with appropriate instruments. Some simple levelling outfit is therefore necessary. The different sections are combined to give a profile of the deposit. Samples for analysis are taken from that part of the bog where the deposit is most complete and homogeneous; for the investigation of special problems, additional samples may be taken from other points.

The more complicated the sequence, the shorter the distance between sections (cp. fig. 5). If the sequence is very intricate, e.g. in domed bogs with more than one RY, and especially in such cases where archaeological objects or other traces of human activities are preserved in the deposit, open profiles are necessary. Such open profiles should have at least one vertical wall, where all important points are marked with matches or in a similar way. Afterwards the whole profile is levelled and the position of the marked points either levelled directly or measured by tape-measure from the levelled surface of the bog or a levelled reference line. This is necessary to secure sufficient detail to identify former bog surfaces etc.

It is much easier to take samples from exposed profiles than from samplers. When a suitable spot has been selected, the peat-wall is cleaned with a knife (horizontal cuts, not carrying material from one layer to another). A tape-measure is then stretched along the section and the glass tubes pressed into the wall (tubes open at both ends, otherwise the air cushion will impede the entry of any substance), or small pieces can be taken out with forceps and spatula and transferred to tubes. For more exact work a pillar of the deposit can be cut out and brought into the laboratory to be investigated in detail. In this case the problem is to keep the pillar suitably moist until it can be worked up.

Even in apparently homogenous sediment series erosion may have caused great lacunae (cp. LUNDQVIST 1924), especially in the littoral parts. Samples should always be collected centrally, where the sequence is presumably most complete. Very sharp contacts between different types of deposit frequently indicate erosion. In other cases erosion contacts are indicated by thicker or thinner—in some cases exceedingly thin—layers of sand.

One very treacherous type is the redeposited peat or sediment. Redeposition takes place where former peat-bogs or littoral accumulations are eroded, either because of lowering of the water-level or because of changes

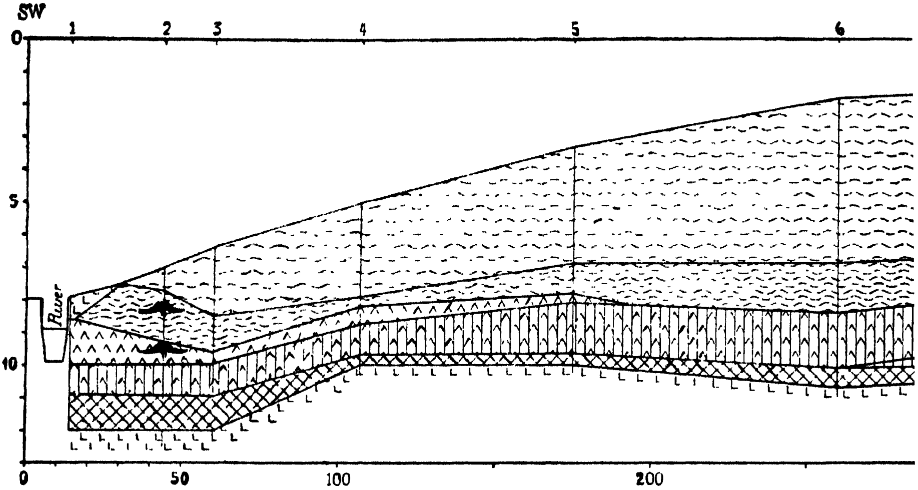
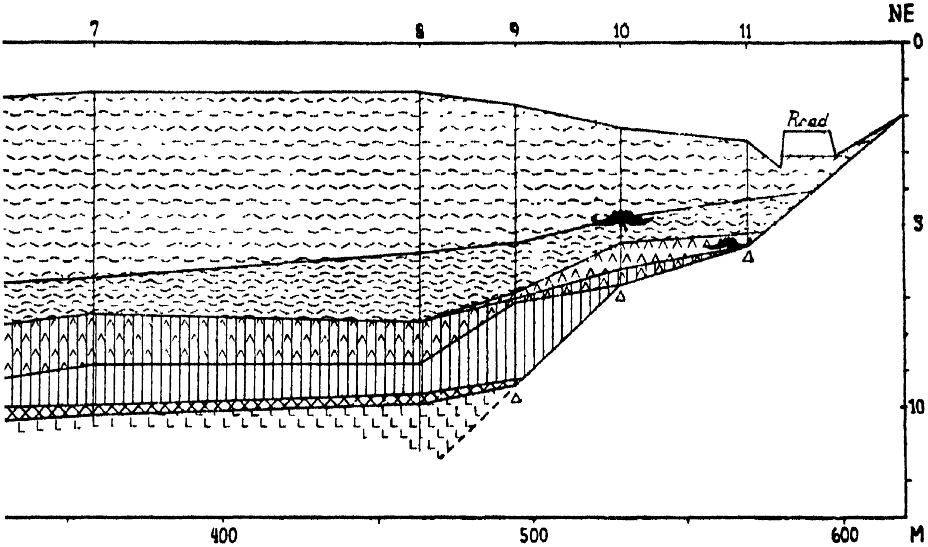


FIG. 5. Peat-bog profile from Cloughmills, Co. Antrim, Ireland (from JESSEN gradually filled in (*Phragmites* coming in from the right-hand shore) and was c Subsequently, peat mosses occupied the area and built up a domed bog. The lowe the upper layers were formed under more humid conditions. The angular outlines lines as curves between the in

in the prevailing wind-direction. Redeposited sediments contain a mixed pollen flora, partly dating the time of the original deposition, partly dating the redeposition. Typical redeposition sediments are often recognisable by an abnormally high content of coarse particles, the finer ones being carried further away. In the extremely oceanic blanket bogs small peat slides frequently cause small-scale redeposition; the inconvenience of this is, however, reduced by the fact that blanket peats are on the whole not well suited for pollen analysis.

Besides the numbering of samples and their position and the data for construction of profiles, records of field-work should contain a short description of the recent vegetation of the bog and its surroundings, especially an enumeration of plants flowering at the time the samples were taken —for control in case recent contamination is suspected. Furthermore for studies of transgressions etc, one must note the altitude above sea level.— With varying aims of the investigation the accuracy of the macroscopical analysis of the deposit in the field will vary, degree of humification, water content, fibrosity, contents of wood etc. may be noted for different layers, especially if no samples are preserved.

In rainy weather field work is impossible or practically so. The note-



og rests on clay and has started as an open lake (gyttja bottom layer) which
a birch forest with *Phragmites,* later by a drier birch forest without *Phragmites.*
obably formed under comparatively dry conditions (high degree of humification)
rofile are customary in Denmark. Other investigators prefer to draw the boundary
of observation (vertical lines).

book becomes wet, the pencil tears holes in the paper, rain drops into the sample and splashes the substance all over, the copying pencil dissolves, and everything becomes hopelessly dirty in a short time. Under such circumstances it is almost impossible to work with sufficient exactness and to obtain really pure samples; the only possible hope consists in taking the samples out of the apparatus under some kind of permanent or improvised roof, but even then it is very difficult to avoid contaminations. If one is compelled to work under such conditions that absolute purity of samples cannot be guaranteed, the only way is to take relatively large samples and to work up all of each sample; under those circumstances one may hope that the contaminations may play a relatively small part as compared with the quantity of the deposit to be analysed.

Days when pollen production and dispersal are especially active, are, of course, also very unfavorable for pollen-analytic field work.

LABORATORY TECHNIQUE

To examine pollen grains under the microscope, one must prepare the sample in some way; methods of preparation differ according to the type of deposit and to a certain extent with the aim of the investigation.

The simplest method of preparation—the one originally used by von Post—consists in boiling the sample for a moment with 10 % KOH. The substances that cause particles to stick together, are dissolved and the sample can be worked into a suspension to which is added some glycerine to prevent desiccation. The viscosity of the suspension depends upon the ratio between glycerine and water. Pollen grains must frequently be turned in the preparation by application of slight pressure on the cover slip, in order to be examined from the different angles which may be necessary for the identification. This turning is easier to carry out if the viscosity of the suspension is rather high, consequently one may prefer to let most or all of the water evaporate from the sample before the cover slip is applied.—It should be noted that tap-water may contain pollen grains; consequently distilled, or at least filtered water should always be used.

In ordinary deposits very little substance is necessary to provide a sufficient number of pollen grains for analysis. von Post boiled a few cubic millimeters of substance on a microscope slide that was held over a spirit flame by means of an ordinary clothes-peg. If the field-work has been carried out properly, this method is perfectly safe—provided some water is added during the boiling to prevent too high KOH concentrations. In pollen-analytic work the KOH concentration should never rise much above 10 %. Others have preferred to use greater quantities and boil them in a porcelain basin or some similar vessel—in that case the influence of possible impurities will be reduced. Others again boil in water and add the KOH afterwards, etc. The last-mentioned procedure does not possess any advantages as compared with the simpler ones.

By all methods the sample is converted into a suitable suspension, a small

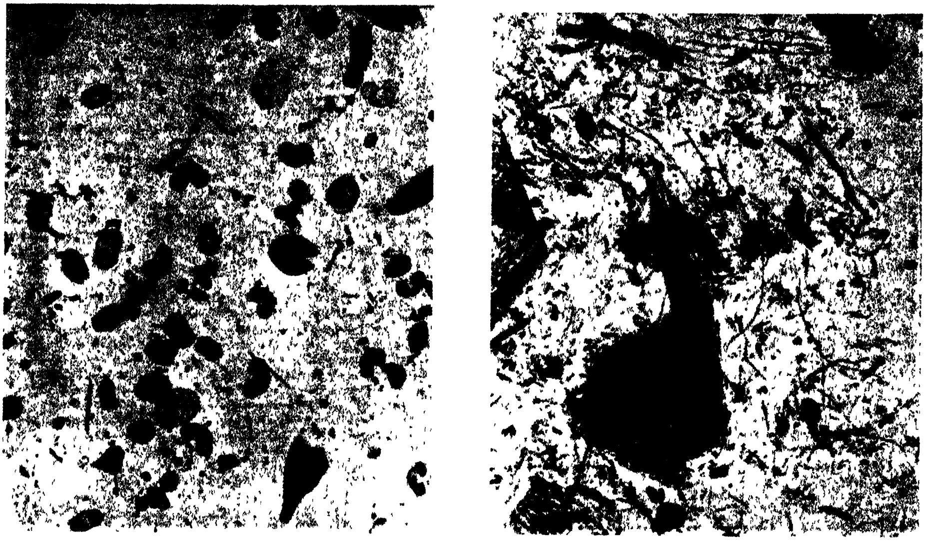


Fig. 6. The effect of sieving a sample of *Sphagnum*, cp. text.

quantity of which is transferred to a slide and covered. Care should be taken that the amount of substance is sufficient to fill all the space under the cover slip and that nothing is pressed out. It has been maintained—even if no statistical proof has been given—that when the cover slip is applied, a sorting of the pollen grains take place, the smaller ones floating towards the edges. If the analysis does not comprise the whole of a preparation, this must be taken into account (cp. WENNER 1948 p. 107).

If there is much "humic acid" in the sample, the resulting fluid will be dark-brown. As it is rather unpleasant to work with such a dark preparation, one may in that case boil the sample with a larger amount of KOH either in a basin or a test tube. When all "humic acid" has been dissolved, the suspension is transferred to a centrifuging tube and the solid particles centrifuged down. In some cases it may be necessary to repeat the treatment, which may at last result in a sediment consisting of practically nothing but pollen grains. Many investigators prefer this method as a standard treatment of all samples (provided more elaborate treatments can be dispensed with). It has the advantage of giving more uniform preparations and of affording an opportunity to wash off excess KOH.

Samples frequently contain much coarse detritus, small pieces of wood or bark, moss leaves, etc. In such cases it will be beneficial to boil comparatively large samples ($\frac{1}{2}$ cm^3 or more) with KOH in a tube and shake vigorously (a few drops of alcohol remove the froth) and strain the suspension on a fine metal (copper) or china strainer, mesh size ca 0.2 mm. The residue on the strainer must be washed with a powerful jet of (distilled) water, e.g. from a wash-bottle. The fine suspension that has passed the strainer is then concentrated by centrifuging (in such cases it is a great help to possess an electric centrifuge capable of handling ca 100 cm^3 at one time). By grinding the wet sample in a mortar before straining one may be able to get some more pollen out of the substance. This technique, if carried out carefully, separates fine and coarse particles almost quantitatively, as is shown by fig. 6. It shows the result of straining a recent *Sphagnum* that had previously been boiled with KOH. Very little passed through the sieve, and the volume was only reduced to ca ¼ by acetolysis. The remains on the sieve measured some 10 cm^3; after not wholly complete acetolysis it had dwindled to some mm^3. In spite of this enormous reduction in volume practically no pollen grains were observed in the latter fraction, whereas the former one was extremely rich in pollen.

In those cases where it is considered desirable to keep the preparations permanently, it is important to get rid of all KOH or other reagent. This is accomplished by "washing" with water in a centrifuging tube, i.e. shaking vigorously and centrifuging down again; the process should be repeated. Permanent preparations should be made up in pure glycerine, and can be sealed by a sealing-wax, the following composition for which has been found the best:

65 % beeswax
34 % gum dammar
1 % venetian turpentine[1]

In such cases the preparations should not exceed 18 × 18 mm. Better preparations are obtained by using glycerine-jelly or even canada balsam, but such preparations are unsuitable for analysis as the pollen grains are fixed and cannot easily be turned if necessary.

Preparations should always be stained (cp. FÆGRI 1936) otherwise small or thin-walled pollen grains are frequently overlooked. The exine absorbs a number of stains, many of them are, however, rather ineffective in alkaline solution. Gentian violet or safranin have been recommended by some investigators. We have found basic fuchsin more convenient. In some cases, especially if the sample contains many moss leaves etc., the result may be improved by the addition of some methylene blue.

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[1] The formula has been placed at our disposal by Mr. J. TROELS-SMITH.

Most pollen grains are then stained dark violet, whilst other constituents vary between yellowish green and greyish lilac.

The staining keeps well and improves by being left for some time to differentiate. A very practical method is to leave one sample to differentiate while the preceding one is analysed. This method has the advantage that relatively weak staining solutions may be used, and added to the suspension until a satisfactory intensity has been reached, which is easily judged by experience. Surplus water evaporates during the differentiation period. After treatment with other reagents samples should be heated with KOH to boiling point and washed with water before staining.

Coarse mineral particles can be removed either by repeated decanting between two test-tubes or beakers or simply by "lifting" the suspension carefully from the slide with the spatula. The coarse particles are not carried along with the rest. Another method consists in boiling the sample with a fair amount of liquid in a beaker which is afterwards kept in a rotating motion. The heavy particles very soon collect in the middle and the liquid with the organogenic material can be drained off.

Heavy liquids (spec. gravity ca. 2.0) will differentiate between organic particles—that float—and inorganic ones. The most convenient liquid is H_2SO_4 conc. (WENNER 1944, 1948 p. 84). However, no mechanical method is at present known that effect a separation of the colloidal inorganic substance of clayey samples from the organic particles.

The advantages of the KOH method are 1. its simplicity, which permits its use practically without any laboratory equipment and 2. the excellent condition of the grains after treatment since no change in the size of fossilised grains takes place. We do not agree with POTZGER (1932) that the KOH treatment induces distortion of the pollen grains (NB. as long as the concentration is kept about 10 %); on the contrary, it frequently causes crumpled grains to expand and resume their original size. The alcohol preparation method introduced by GEISLER (1935) to prevent this alleged inconvenience of the KOH method seems to be superfluously complicated and ineffective as well.

The chief drawback of the KOH method is that with the exception of "humic acids" the matrix is not removed from the sample, consequently the concentration of pollen grains in the preparation may be rather low. If the sample is very poor in pollen, one is generally obliged to concentrate its pollen contents by some other chemical treatment, especially by acids and bases, which attack the other constituents of the sample more vigorously than the exines.

The treatment of samples containing excess $CaCO_3$ is very simple. Cold

10 % HCl or HNO_3 dissolves the lime, best results being obtained after the sample has been boiled for a moment and then brought into suspension form. After treatment with acid and washing on the centrifuge, the sample is treated in the usual manner, e.g. with KOH.

Siliceous matter is removed by HF treatment. The method was introduced by **ASSARSON** and **GRANLUND** (1924) and is practised by us as follows[1]:

1. Boil the sample with KOH, remove coarse particles by mechanical means (straining, decanting, etc.). If free lime is present, it should be removed by acid. Centrifuge.
2. Wash with water and centrifuge.
3. Boil (ca. 3 min.) with ca. 30-40 % HF in a platinum or copper crucible.
4. Tranfer to a Pyrex glass centrifuging tube. If no such tube is available, the reagent mixture must be cooled before being transferred to ordinary glass centrifuging tubes. Centrifuge.
5. Heat with 10 % HCl without boiling to remove colloidal SiO_2 and silicofluorides. Centrifuge while still hot. The process must generally be repeated once or more if the original sample contained much SiO_2. In extreme cases the HF treatment should be repeated, followed by another short HCl treatment.
6. Boil with KOH (15 seconds) and centrifuge.
7. Wash with water and centrifuge. Add a drop of glycerine. Stain.

The HF necessary to remove minerogeneous matter does not, or only to a small degree, attack organic remains (inclusive of pollen grains). It has proved more difficult to find ways of getting rid of excess organic matter without attacking the pollen grains. Cellulose, e.g. *Sphagnum* leaves, may be removed by cold H_2SO_4 conc. (24 hours or more), but the method is not very effective. **ERDTMAN** (**ERDTMAN** and **ERDTMAN** 1933, **ERDTMAN** 1934 and later) has introduced the use of anhydrous acetic acid for the dissolution of cellulose, combined with oxidation with Cl_2O for the removal of lignin etc. The procedure as practised by us may be summarized thus:

1. Boil the sample with KOH, remove coarse particles by mechanical means, remove lime by acid. Centrifuge.
2. Wash with water. Centrifuge.

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[1] It is practical to write directions like these on a piece of cardboard that is mounted over the laboratory desk for reference as required.

3. Dehydrate with glacial acetic acid. Centrifuge.
4. Treat with a fresh mixture of 9 parts anhydric acetic acid and one part H_2SO_4 conc. Heat gently in a waterbath to the boiling point. Centrifuge.
5. Wash with glacial acetic acid. Centrifuge. (Direct transfer to water causes the cellulose acetate to precipitate again).
6. Wash with water. Centrifuge.
7. Boil (15 seconds) with KOH to permit staining. Centrifuge.
8. Wash with water. Centrifuge. Add a drop of glycerine. Stain.

If HF-treatment is necessary, it comes in before acetolysis.

The oxidation is carried out by:

1. Adding to the sample 4 cm^3 glacial acetic acid, 5-6 drops $NaClO_3$ solution (30 %) and 1 cm^3 HCl conc.
2. When the sample is bleached (after some seconds to one minute) centrifuge and wash with water.

All operations are carried out in the centrifuging tube.

Whereas acetolysis is a comparatively safe process, oxidation is very dangerous, because sporopollenins are not very resistant to oxidation[1]. As much of the material that is to be removed by oxidation, can be removed much more easily by KOH treatment before acetolysis, we practically never employ oxidation. If oxidation must in special cases be resorted to, it should be carried out before other treatments.—The advantage of ERDTMAN's method is the great concentration of pollen grains obtained. Its principal draw-back (apart from possible destruction of pollen by oxidation) is the increase of size of fossil grains (cp. p. 27) by acetolysis, an increase which makes size statistics impossible. If, however, size statistics are unnecessary—which they are in most cases—acetolysis is an excellent means of concentrating the pollen contents of not too rich samples. (Acetolysis after KOH treatment for the preparation of recent pollen for comparison purposes, cp. p. 28).

Scarcity of pollen grains in a given sample may be due to the following 3 causes: 1. Rapid growth of the deposit, the pollen rain is highly "diluted" by matrix substance. 2. Subsequent destruction of pollen grains during fossilisation in aerated deposits. 3. Low pollen production of the surrounding vegetation. Deposits of the first type are easily dealt with by acetolysis if

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[1] Treatment with fuming HNO_3 afterwards (REISSINGER 1941) hardly improves the situation. It is noteworthy that the advocate of the method (l.c. p. 40) characterises the rather resistant *Fagus* pollen as being "somewhat tender". What then about the really fragile ones?

simpler methods are not sufficient. Deposits of the second type should be discarded altogether, as their pollen flora most probably is not representative of the contemporary pollen rain. Besides, the matrix is in this case generally so resistant against chemical treatment that very radical measures are necessary with consequent danger of further distortion of the pollen flora. Deposits of the third type present real difficulties, especially as they are frequently of great interest, e.g. late-glacial samples. Concentration by chemical treatment must in these cases be carried out as far as possible without attacking the pollen grains themselves. Even after such treatment the analysis can be extremely trying to one's patience.

Other methods of preparation have been proposed, but are evidently of little importance in pollen analysis. Some of them will be described in a later chapter (p. 120 seq.).

When the sample is prepared, the analysis proper can begin. The pollen grains are so small that a magnification of ca. 300 × is a minimum for routine work. More difficult types need ca. 1000 ×, and a very high numerical aperture (above 1.2), too. It goes without saying that an immersion objective of the best quality is necessary in all advanced pollen-analytic work. Many identifications represent insoluble problems if one works with low-power objectives or with objectives of too low numerical aperture, whereas the same identifications are easily carried out with proper optical equipment. Cover-slips must be sufficiently thin to permit the use of high-power objectives. In order to make the change between objectives easy one should use anisol or some other immersion fluid that is easily removed from the cover-slip after the high magnification has been used and routine work is to proceed. A piece of blotting-paper is sufficient to remove all traces of such fluids in contrast to the cedar wood oil that must be washed away with other liquids.

By means of the mechanical stage the preparation is moved slowly from one side to another under the microscope, and all pollen grains observed are noted. The preparation is then shifted at least 1½ diameters of the field of vision perpendicularly to the first direction of movement and then moved back again. In this way one proceeds until a sufficiently great number of pollen grains (cp. below) have been noted. The work is facilitated if some kind of table is used where at least the more important pollen types have their regular place. Tables should contain the space necessary for calculations etc. It is also practical to note how many strips of the preparation have been investigated. This will give an approximate indication of the frequency of pollen grains in the preparation, and it will also show which way one was moving the preparation if the work is interrupted in any way.

During this part of the work the principal problem is that of recognising the pollen grains. It is chiefly a question of practice, and the beginner cannot learn very much about this part of the work from books. The best thing for him to do is to start his work in the laboratory of some more experienced colleague. One must possess a well-stocked "pollen herbarium" containing all the more important types. The preparation of such a collection from recent material either by acetolysis or by some hours' boiling with 10 % KOH is an excellent practice for beginners. A number of comprehensive illustrated pollen floras exist, most of them intended for the use of European investigators, (ERDTMAN 1943 and earlier, MEINKE 1927, WODEHOUSE 1935 and 1942, ZANDER 1935-37). The quality of these illustrations is rather variable, (they have not improved by being repeated in BERTSCH 1942), but even the best of them can hardly serve as more than a "remembrancer" to more experienced workers. The beginner will have great difficulties in interpreting the morphology of a pollen grain by means of illustrations alone.

During laboratory work samples may be contaminated in different ways, and the cleanliness in a pollen-analytical laboratory must equal that in a bacteriological one. Some sources of impurity are especially dangerous: During spring and summer the air of the laboratory will contain quantities of pollen grains, which may be caught in the preparations (cp. WENNER 1948 p. 104). If the KOH method alone is used, recent pollen grains may be recognised by their cell contents, in other cases it is more difficult. Sometimes it is tempting to ascribe the finding of single pollen grains of southern species in Arctic deposits to such laboratory contaminations, especially if no statement to the contrary is to be found in the publication in question. It is self-evident that to prevent contamination one should keep utensils used for the preparation of recent pollen apart from those used for deposits. Especially when working with samples that are in themselves poor in pollen, one must be very careful about "air pollen" and other sources of impurity. The same applies if one is on the look-out for infrequent pollen types. On the other hand, by careful treatment of the samples from the moment they are taken out of the sampler till the analysis is completed, contaminations should be precluded, and in most cases such which may occur, are not of great importance. If some few pine pollen grains are added to a sample containing thousands of them, it does not affect the results materially, but if oak grains are added to an Arctic sample with no oak, the effect is rather unpleasant. Even worse is the contamination of pre-agricultural samples by weed and cereal pollen which are generally very frequent in the surroundings of the laboratory.

Important finds should always be preserved in some way or other for future reference and control. Unfortunately documentation in pollen analysis has so far been largely neglected and pollen-analytical literature—especially the older—abounds in statements which it would be highly desirable to check, but which are not open to control since no attempts at documentation have been made.

The easiest control method is preserve the actual preparation by sealing. If the place of a special pollen grain is marked on the cover slip (with Indian ink), it is usually possible to recover it for later reference.

The easiest control method is to preserve the actual preparation by in picking the pollen grains out of the preparation and keeping them as single-pollen preparations (cp. Fægri 1939). With some practice one may do that rather easily either by "fishing" the grain on a piece (not a drop) of glycerine-jelly on the tip of a needle or by sucking it into a micro-capillary tube. Both processes must be carried out under low-power microscopic control. The glycerine-jelly method works best in comparatively dry preparations; if too much liquid is present, the pollen grain will float away, but in that case it can be collected by means of the capillary tube. Afterwards the pollen grain is transferred to a larger piece of glycerine-jelly with the piece used for "fishing" or blown out from the capillary to the larger piece, which is afterwards melted and covered (preferable by a very small coverslip). Care should be taken that the grains do not shrink or crumple when being transferred; the glycerine-jelly should be rather soft, and the whole left to evaporate for a day or two before melting and sealing. If the pollen grain is found during ordinary analysis, one must slide (not lift) the cover-glass off under low-power microscopic control.

Photographs are also good means of documentation, and have the great advantage of being reproducible. However, it is often difficult to give an adequate picture of the general form of a pollen grain by means of photographs. By the use of high magnification and by focusing at different levels structural details may be brought out with admirable distinctness, cp. fig. 17.

Drawings are less useful for documentation purposes. It takes a very high degree of observation power and artistic skill to make a good drawing of a pollen grain, and even if the very best drawings are on a par with, or even surpass, a photograph, especially for presenting the general form of the grain, indifferent or poor ones are of very little value for future reference.

THE PRINCIPLE OF POLLEN ANALYSIS

Per se, pollen analysis is palaeofloristic: there is in principle no difference between determining pollen grains and determining seeds, cone-scales, etc. However, there is one important difference: The fossils dealt with in pollen analysis are all comparable, consequently their relative frequency can be expressed as percentages of a total. It is not possible to do the same with macro-fossils, as they are not comparable: one cannot make a total sum of leaf impressions, seeds and twigs, but it makes good sense to state that the pollen rain preserved in a sample consists of 50 % *Pinus*, 40 % *Betula* and 10 % *Quercus*. The variations of the percentages can be followed through the section of a peat bog or a sediment deposit and give a quantitative expression of the changes which the vegetation cover has undergone during the period of formation of the deposit.

One very important point is the pollen sum that forms the basis for the calculation of percentages. The pollen sum should comprise *all* species forming the topmost layer of the vegetation under investigation. Thus, in an area where the history of the forest is the primary object, the pollen sum should only contain the pollen of forest trees; in a mixed steppe area those of the steppe grasses and herbs as well, whereas tree pollen should be excluded if the steppe alone is under consideration. The reason why only the topmost layer should be represented is that the curves of the pollen diagram should represent separate *areas*, and the variations of the curves should demonstrate the relative changes of the areas occupied by the different vegetational types. Consequently only one layer can be represented in each place. viz the topmost layer of the vegetation that covers that particular spot. Besides the flowering of the plants of the lower layers is usually much reduced and the pollen grains of wind-pollinated species in the lower layers are not adequately represented in the regional pollen rain.

In the forested parts of Northern Europe, where pollen analysis was inaugurated, the pollen types that are of importance are those of *Pinus, Picea, Populus, Betula, Alnus, Fagus, Carpinus* and the so-called mixed-oak forest constituents, *Ulmus, Tilia, Quercus,* and *Fraxinus,* which have in this area more or less the same climatic demands and therefore to a certain extent can replace each other. With the exception of late-glacial diagrams (where *Salix* is a major constituent) it is immaterial whether or not *Salix* is included, theoretical considerations speak in favour of its inclusion in post-glacial diagrams as well. The same applies to *Hippophaë,* which always constitutes the topmost layer of the vegetation wherever it occurs. With regard to *Corylus* the situation is somewhat different: when publishing his first pollen analyses, v. POST (1918 p. 442) stated that he had not included *Corylus* in the pollen sum "as the hazel generally occurs in the shrub layer of the mixed oak forests and under exceptional circumstances only forms separate communities that compete with the other forest types" (orig. Swedish). It has therefore been customary to calculate *Corylus* "outside" the ordinary percentages, the only exception seems to be BERTSCH (cfr. l.c. p. 38). Unfortunately, VON POST's statement is only partly correct, as the hazels of the shrub layer in unthinned forest do not flower or flower very sparsely. The *Corylus* pollen met with in pollen analyses partly represents forest margins (BORSE 1939 p. 129), partly specimens forming part of the upper canopy, partly areas where *Corylus* enters into the regular succession cycle of the vegetation. If we want a Northern European pollen sum to give an adequate representation of the composition of the topmost layer of vegetation, *Corylus* cannot be excluded[1]. We shall return to this question later (p. 88).

The pollen sum mentioned above is adapted to conditions in forested Northern Europe during the post-glacial period. In other regions and other periods the pollen sum should be calculated in different ways, and the establishment of a proper pollen sum is one of the most important points in dealing with the vegetational history of a previously unknown region. It is especially important to obtain the correct balance between the pollen of forest trees (AP: arboreal pollen) and that of field vegetation (NAP: non-arboreal pollen).

During pollen analysis many other micro-fossils are observed in the preparations. Pollen analysis is just one special branch of general microfossil analysis, by far the most important branch. The occurrence of many other types of micro-fossils that are mutually comparable, can be expressed quantitatively in a similar manner to that of the pollen grains. In some of the following chapters we shall return to some other cases of microfossil analysis.

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[1] This necessity becomes particularly flagrant in, the much discussed "hazel period" in Western Europa. From Ireland maxima of over 1700% *Corylus* are reported (MITCHELL 1942). It is obvious that the classical treepollen curves in these circumstances are quite misleading.

THE POLLEN DIAGRAM

After the pollen sum has been established, the results of analyses can be expressed as percentages. The simplest way to reproduce these percentages is, of course, in a table. However, such tables are too unwieldy to be of any real use to the reader, and the results must therefore be represented in a simpler form, as a diagram. The drawing of the diagram is the last link in that chain of technical processes that starts by the taking of the samples.

The diagram is a conventional technical aid, and its usefulness is directly proportional to the universality of the conventions. On the whole the use of symbols is now quite well standardised (cp. GAMS 1938 and fig. 7), and there are only two main types of diagrams in general use to-day. Fortunately local "schools" are gradually abandoning their aberrant diagram types which make the understanding of the results much more difficult than it would otherwise be. Two principles should always be kept in mind in the construction of pollen diagrams, viz. the legibility and the comparability with other diagrams. Unnecessary changes should therefore be strictly avoided, even if they are to a certain extent desirable.

The first diagram type may be called the composite diagram, the principle of which was introduced by v. POST in his first publication. An example of a composite diagram is given on plate IX. The left vertical column represents a diagrammatic section through the deposit. Next comes the diagram proper, in which each sample is represented by a horizontal line at the corresponding level. The percentages are set down on the sample line and each species is marked by means of conventional symbols. Those which are generally in use in Europe were chosen by VON POST (cp. 1929 p. 556) to indicate the order of immigration of the respective species in Middle and South Sweden. Outside that area the signature system is purely conventional, as the order of immigration changes from region to region, but the symbols are generally accepted. It is self-evident that the use of these symbols in a definite sense in European literature does not preclude their

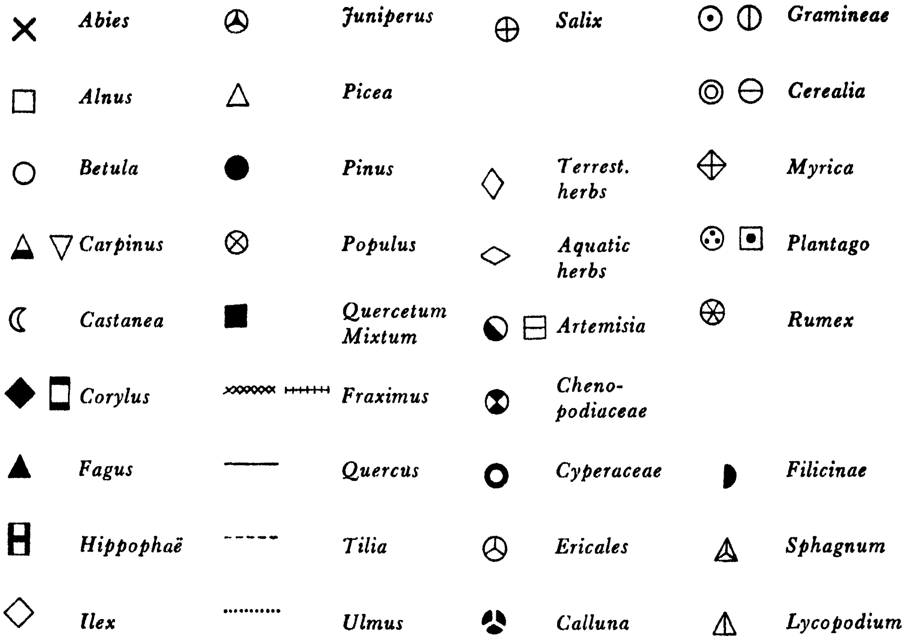


FIG. 7. Symbols of pollen signatures used in northern Europe.

use in different senses in other floristic areas. However, the same genus, wherever it occurs, should always be represented by the same symbol.

Each horizontal sample line with its symbols is called a *pollen spectrum,* and the *diagram* consists of a number of such spectra from different levels. To demonstrate more clearly the trend of vegetational development the symbols for the same species or genus are connected from one spectrum to another by *pollen lines,* which then form the *curves* of the diagram. It is very important that those pollen curves that represent species forming part of the basic pollen sum, and those only, are drawn as continuous lines, whereas all others should be represented by dashes. This rule is of paramount importance for the legibility of the diagram: if it is not strictly adhered to, the result will be a great deal of trouble on the part of the reader to find out what the author has meant.

Not infrequently some or even all of the curves of a diagram are crowded together and are difficult to follow individually. In most cases this inconvenience is not too serious, but if one of the curves is especially important, it can be set off from the others by hatching of the area between it and the zero line or in some similar way. It can, however, also be represented in a separate diagram. The latter method must also be resorted to for those constituents, the quantity of which is so small, that the curves would not be of any use if drawn to the same scale as the others. If it is statistically significant a change of a curve from 1 to 2 % or even less may be as important as the change of another curve from 30 to 60 %, but it is self-evident that they cannot be represented on the same linear scale.

Logarithmic scales are not to be recommended, the scale should be linear and consistent throughout, and those of auxiliary, partial diagrams should not vary too much. The area of the main diagram should always correspond to 100 %, even if no single curve reaches above 40-50 %. The extra space is a very cheap price for greater legibility and greater comparability with other diagrams. Furthermore the main diagram should have vertical lines at each 10 % of the scale. Corresponding lines should be found in the auxiliary diagrams as well. The main diagram should preferably comprise all those pollen types that are part of the basic sum, but care should be taken not to bring too much together in one diagram, as legibility soon suffers if the diagram is too complicated. The number of possible auxiliary diagrams is almost unlimited. The illustrations will show some examples.

The AP diagram, which is based upon tree pollen as the basic sum, may be sufficient as the main or only diagram if forest history is the object of investigation. Where there is a succession between forest and tundra, steppe or cultivated areas, the vegetation of the forest-less area must be accounted for as well. The NAP diagram portrays the changes of the vegetation within the forest-less area as the AP diagram covers the changes of the forest area. The principle of the NAP diagram is the same as that of the AP diagram: The basic pollen sum is made up of the pollen from wind-pollinated herbs, grasses, and shrubs that constitute the topmost layer of vegetation. Insect-pollinated species should normally not be included, as their pollen is presumably not evenly distributed over the area. Insect pollinated species, the pollen of which form part of the pollen rain (e.g. *Calluna*) should, of course, be included.

The NAP diagram suffers, however, from more complications than the AP diagram and demands great botanical knowledge. As many peat-forming plant communities produce NAP, but no AP, the NAP flora is even more dependent on the composition of the mother formation than the AP flora. E.g. in a heather peat *Calluna* pollen will contribute 80-90 % or even more of the total NAP rain. NAP diagrams from deposits the mother formation of which have themselves produced NAP, are generally useless for the purpose of regional analysis. Such diagrams are easily recognised by the excessive dominance of one pollen type and by violent changes in the course of the curves. If the NAP diagram is to be of any real value, the locally produced NAP must be eliminated, which can be done in limnic (and marine) deposits where the locally produced pollen, viz. that of the aquatic species, is more or less recognisable and can be excluded. Especially in oligotrophic lakes where the surrounding grasses and sedges are insignificant, the NAP flora of the sediments will represent the vegetation of the surrounding open land without much distortion due to locally produced pollen. In any case the NAP diagram will be more local than the AP diagram, and in a forested or mainly forested area it does not represent much more than the open land bordering on the basin. For the solution of general problems the NAP diagram is in such areas of limited interest only, but it may be important for the solution of special problems. The quantity of NAP in a forested area is generally small (ca 10 % AP or generally less in limnic deposits), consequently one will not get sufficient material for a NAP analysis without much extra work. In areas with little or no forest cover the relative quantity of NAP is so high (50 % AP or more) that sufficient material is generally obtained in connexion with the AP analysis.

In such cases where the NAP flora is subject to strong local influences, and a NAP diagram is consequently of little interest, some information may be gained by expressing the occurrence of more important NAP types in percentages of AP. Those curves which represent constitutents of the changing mother formations will show excessive variations whereas curves of other types will be smoother and may furnish information as to the density of forests. A better method is to include these pollen types, and these only, in a total diagram (cp. below).

Whereas the AP and NAP diagrams separately represent the variation of forest, and vegetation outside the forest respectively, the relation between the two main vegetational types is best seen in a third diagram type, the "total" diagram, in which the pollen sum consists of both AP and NAP (and in special cases even of other constituents). It is self-evident that the value of such a diagram is dependent on the same factors, which determine the value of the two other diagrams. If the NAP diagram is subject to strong local influences, the total diagram will also be rather valueless. Sediments should therefore be used wherever possible and peat analysed only in those cases where the problem in question calls for an analysis of that special deposit.

Within an area where, or during a period when, forest covers all dry ground, the total diagram from a sediment series will be more or less identical with the AP diagram (and consequently not very necessary), as the

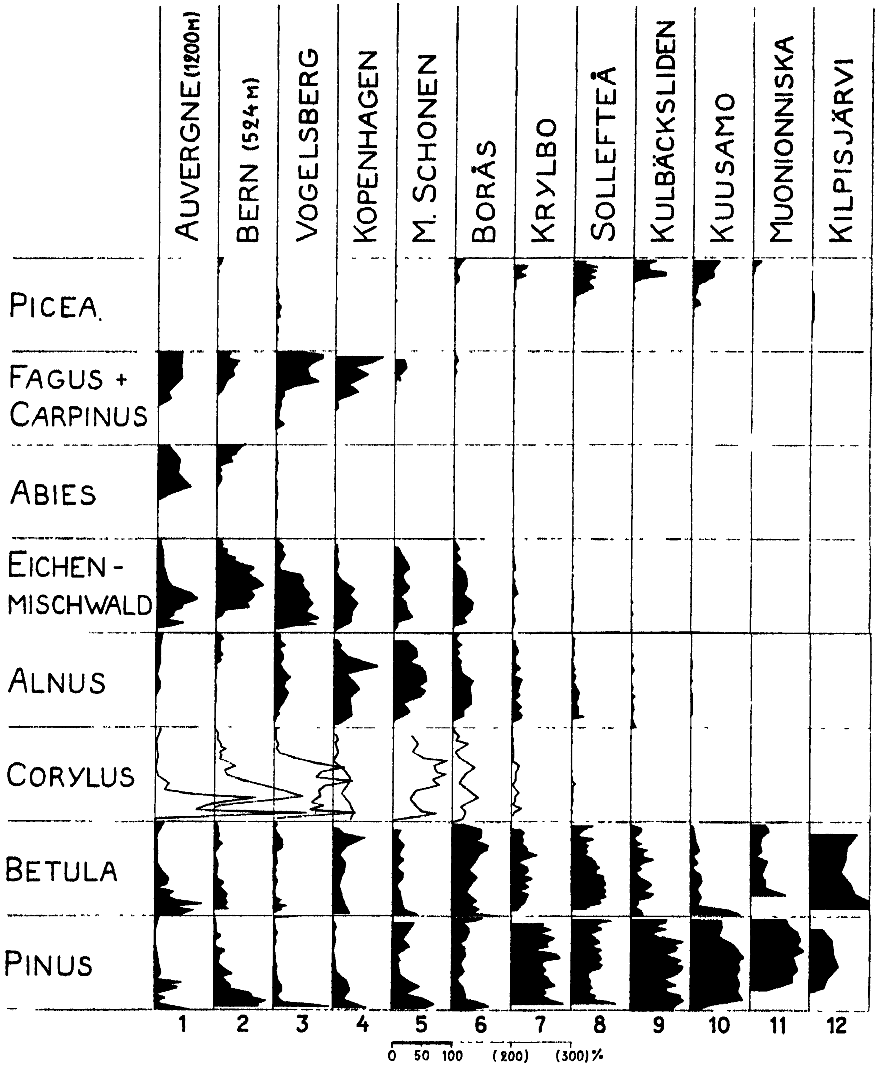


FIG. 8. A series of dissolved diagrams ("saw-blades") illustrating the main features of the vegetational development in a transect through Europe from S to N. It will be seen how the climatic optimum is registered in pure broad-leaf forests in the south, passing through mixed forests and birch forests to pine forests in the north. *Corylus* has been drawn as a line—not as a silhouette, because the species was not part of the 100 % sum. If a curve is calculated in that way, it should always be accounted for by a different signature, but as we have stated p. 68, such calculations should not be made. (From v. POST 1929).

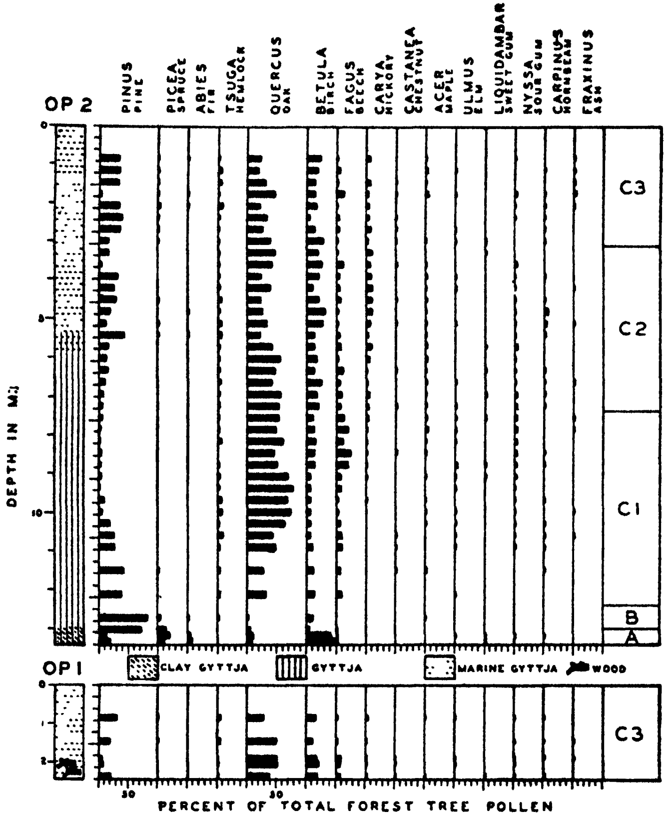


Fig. 9. Dissolved pollen diagram (histogram). The distance between samples in this diagram (1 foot?) is adequate for a first summary of the vegetational development, but it is self-evident that at a more advanced stage of the investigation this wonderful material should be utilised more intensely by samples taken not more than 5 cm apart. (After Deevey 1948).

ground flora of the forest delivers practically no pollen. The NAP present registers the vegetation of wet ground: fen, rush thickets, etc. A difference between AP diagram and total diagram is found where and when forest-less areas occur, and in these cases it is necessary that the latter areas be represented in the diagram as well as the forest. This claim is especially imperative in late-glacial diagrams and in sub-alpine or sub-arctic areas, but the total diagram is also of great importance if the disappearance of forest is due to cultivation, *int. al.* because it serves as a warning that the AP curves must be considered with a certain suspicion, as the composition of the forest has been interfered with by cultivation. In NW European late glacial diagrams the difference between AP and NAP is more or less illusory (*Betula* *nana, Salix herbacea, Juniperus*) and the total diagram is the only means of an adequate representation. An AP diagram would be misleading and should be avoided altogether even if the post-glacial part of the same deposit is to be represented in the same diagram series.

Both the NAP and the total diagram can be constructed in the same manner as the composite AP diagram with symbols and connecting curves. It will be found almost impossible to draw these complicated diagrams in any other manner, as they need too much space and the legibility suffers because of the great distance between the curves. The advantage of the composite diagram lies in the wealth of information given in a compact form and in the clear demonstration of the interrelationship of the curves. The disadvantage is that the diagram may become so crowded that it is difficult to follow the courses of the individual curves.

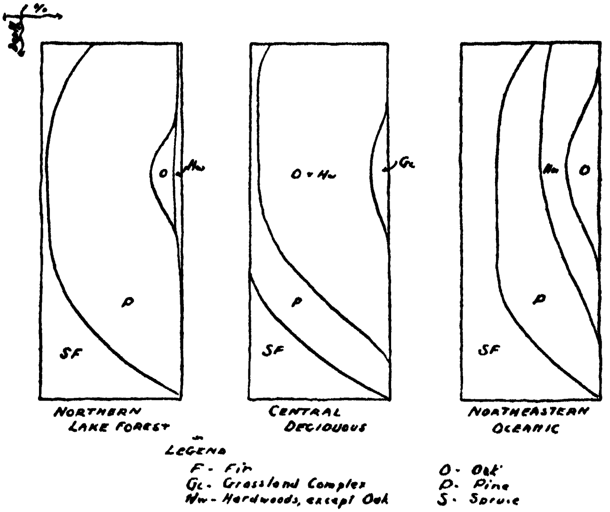
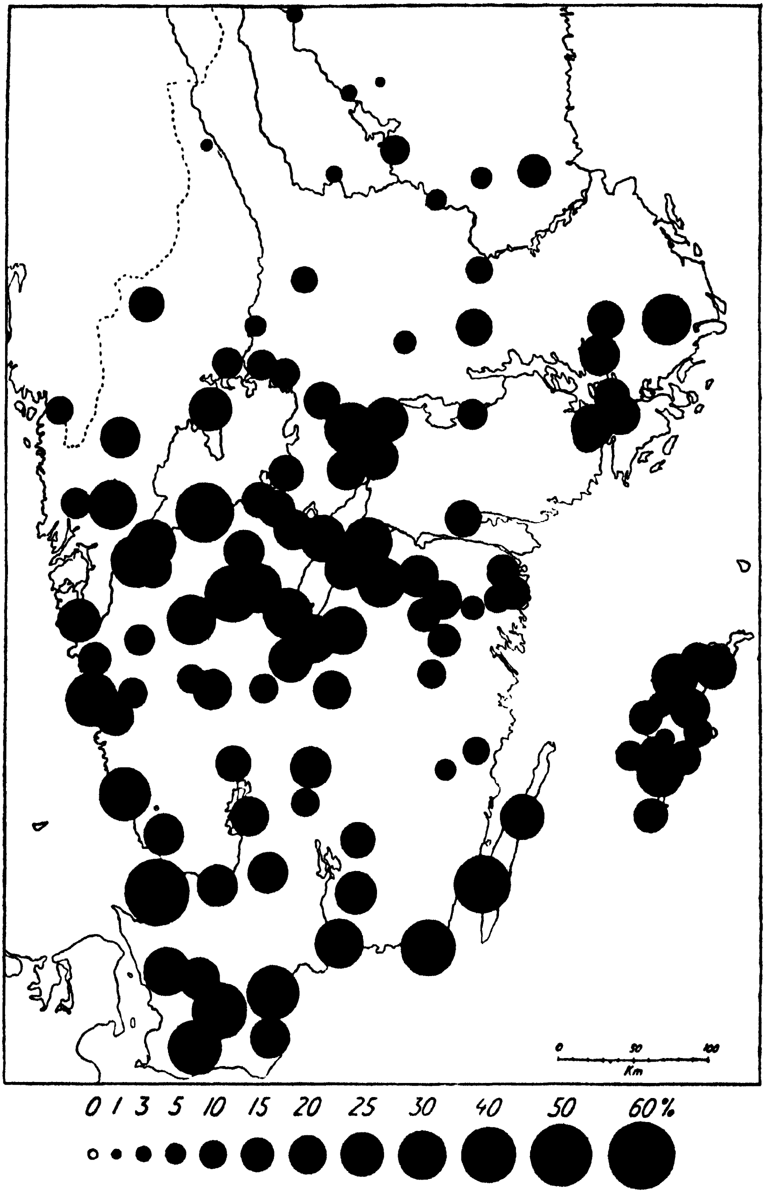
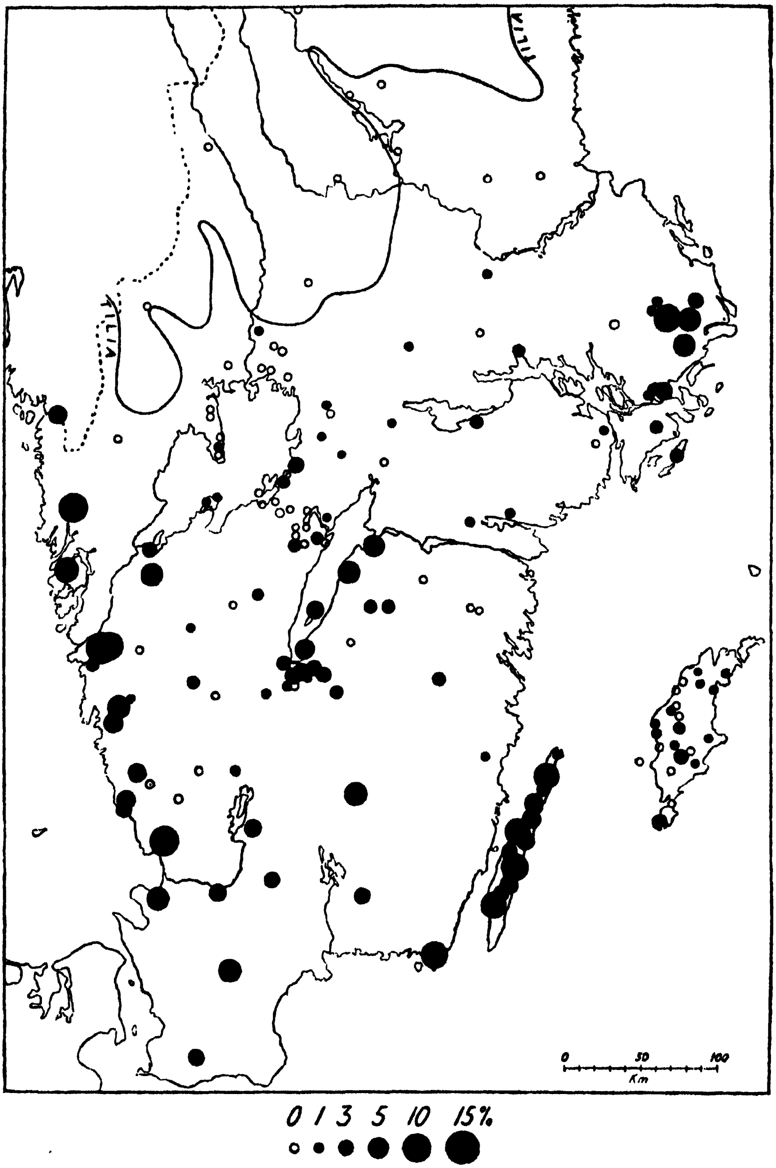


FIG. 10. "Schematic types of pollen profiles such as are often found in the United States east of the Rockies" (SEARS 1938 p. 180). For schematic illustrations this type of pollen diagrams (all curves added to form 100 % in each spectrum) is very convenient—but the execution of the drawing might have been more careful.

The easiest way to remedy this drawback is to let each curve stand apart, and thus we are lead over to the other main type, the "dissolved" diagram, of which fig. 8-9 give examples. What is combined in one single composite diagram, is in this case drawn in as many partial diagrams as the former possesses curves. A dissolved diagram is obviously much easier to read, most symbols are more or less superfluous, and there is no crowding of the



FIGS 11-12. Dissolved maps, showing the quantity of elm + lime + oak pollen in



ıd M Sweden during the climatic optimum (Fig. 11) and now. (From v. POST 1929).

curves; on the other hand it needs much more space and it is difficult to follow the interrelationship between the individual constituents. The composite diagram is therefore best suited for the close analysis of the development within the individual basin. The dissolved diagram is of greater advantage for regional comparison where the finer details are of less importance than the general features. Fig. 8 demonstrates the use of dissolved diagrams for a regional comparison; the appearance of new species (*Picea, Fagus*) is particularly clearly brought out. The curves of the dissolved diagrams may be constructed as "saw-blades" (fig. 8) or as histograms (fig. 9). The former are easier to draw, but the latter give a much more objective expression of the course of the curves. If small samples are taken at some interval, the individual columns of the histograms should be kept apart, otherwise a continuous histogram should be made.

The curves of those constituents that are included in the pollen sum should be clearly different from those that are not, e.g. by being filled in in black. The sample levels and percentage lines should be included in the dissolved diagrams as well as in the composite ones. On the other hand one should not reproduce too much of the grid, as the general picture is rather unsatisfactory if the grid is too compact. Whereas it may be impractical to let the area of all partial diagrams cover 100 %, ranges should not vary too much: a few standard ranges should be used, e.g. 100 %, 50 %, 25 %, 10 %, 5 %, 2.5 %, etc. The range of each partial diagram should be clearly indicated, especially as it is in many cases necessary to use different scales in order to bring out salient points.—If diagrams are used for regional comparisons, their vertical scales should be regulated so that the same periods are represented by diagrams of the same length, even if one may represent 50 cm of deposit and another several metres.

The dissolved diagram it most suitable for relatively simple cases. If diagrams are too complicated, they will soon assume a monstrous breadth. In such cases it may be necessary to combine the types, using one or more composite main diagrams and giving the occurrence of important indicators by means of partial diagrams.

It is self-evident that different purposes require different diagram types, and one cannot lay down strict rules. However, original material should, if possible, be published in one of the generally accepted ways whereas diagrams summarising the results of one or more investigations can be treated more or less freely, cp. the very simple, but illustrative diagram given by SEARS (1938), here reproduced as fig. 10.

Such diagrams serve to illustrate an opinion, but they are inadequate as representations of the material upon which that opinion is founded.

FOSSIL FOREST MAPS

The pollen diagram gives the changes in the composition of the forest in one definite locality during a certain span of time. The opposite problem is to give a representation of the composition of forests within a certain area at a definite point of time. A diagram series like that in fig. 8 gives the necessary information, but is rather difficult to read from that point of view.

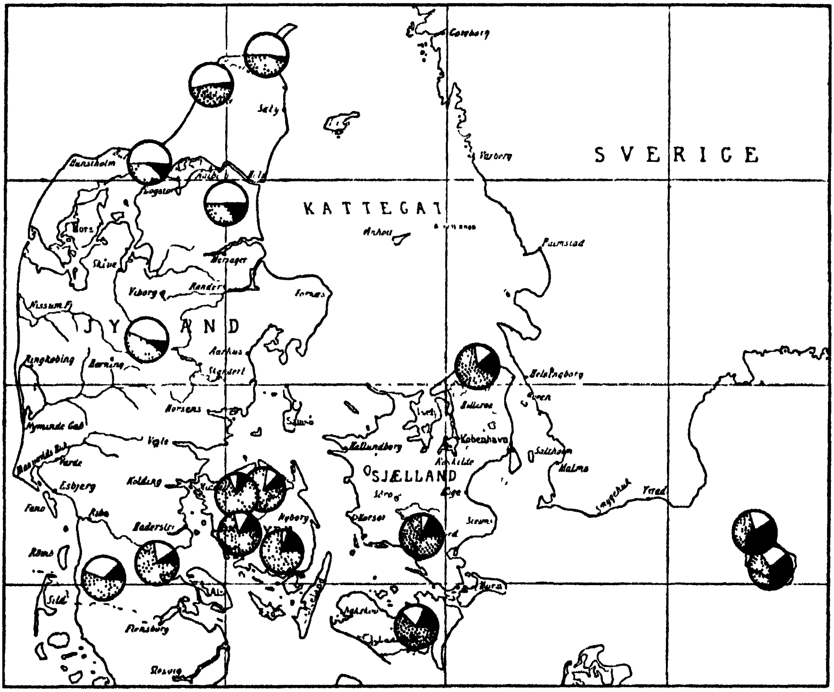


Fig. 13. Sectorial map showing the distribution of vegetation in Denmark during the Allerød period. Black: *Pinus,* dotted: *Betula* + *Salix,* white: anemophilous grasses and herbs + *Ericales.* From Iversen (1947 b). The map indicates prevailing tundra in the north, an intermediate birch belt and some pine forest in the south-east.

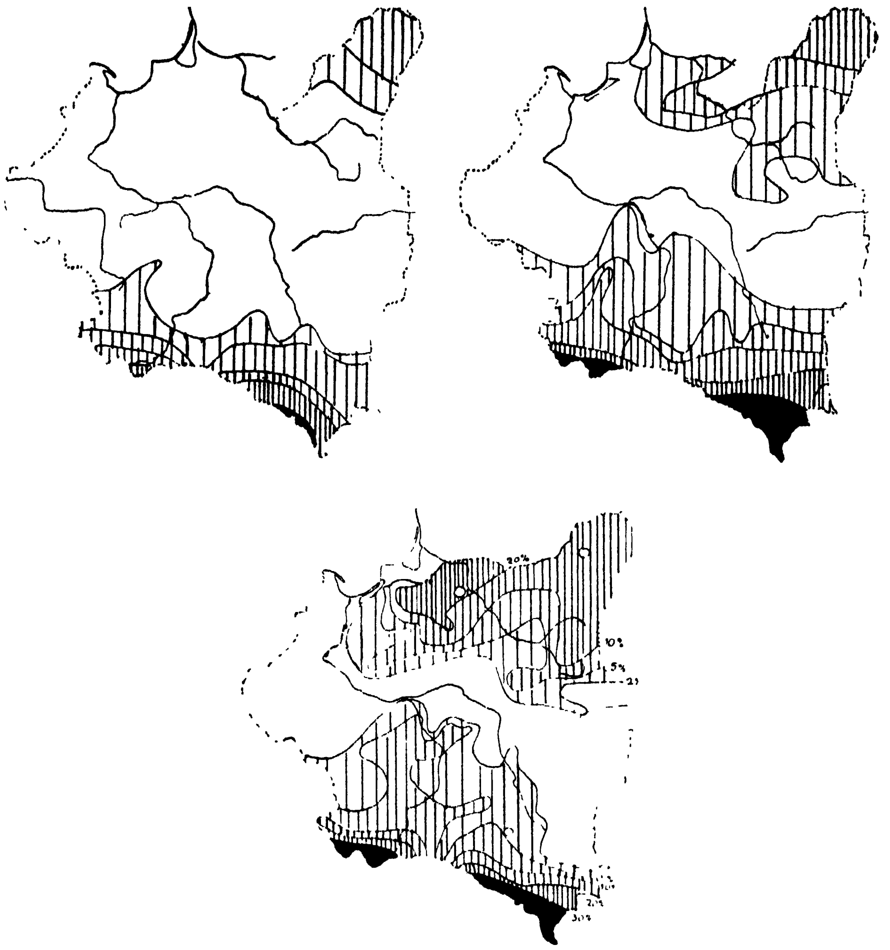


FIG. 14. Isopollen maps of three stages in the migration of *Picea* into pre-war Poland and East Prussia. From SZAFER (1935), simplified. The stations upon which the maps are based should be indicated at least in one map of each series.

The remedy is to construct fossil forest maps corresponding, as closely as possible, to the recent ones. Such maps are valid for one particular period only, and it is imperative for their usefulness that the diagrams utilised for their construction are accurately dated. A metachronous map is worse than none.

Fossil forest maps can also be divided into composite and dissolved types. The composite maps give an indication of the total composition of the forest (alternatively of the vegetation as a whole) during the period in question, whereas the dissolved maps give the importance and distribution of each individual forest constituent. When dissolved maps are used, a whole series is necessary, one for each species, to give a complete picture of the vegetation cover of the area.

The usual type of composite maps has circular symbols, in which the relative importance of the constituents is indicated by sectorial division of the circle cp. fig. 13. As this type of map has not been widely used (it is not always easy to read), the use of symbols has not been very consistent. GAMS (1937, cp. 1938) has proposed a standardised symbol system for Europe.

Unless the composition of the forests is very simple, better representation of facts is achieved by use of dissolved maps, where the part played by the species in question in contemporary forests is indicated by the size of the symbol, usually black circles, cp. fig. 11-12.

If the number of localities is very great, the circular symbols may become too crowded and overlap. FIRBAS has (1939) used small lines instead of circles, but even such maps are rather complicated and difficult to read. SZAFER has suggested (1935) the use of iso-pollen lines, i.e. synchronous lines delimiting areas with the same percentages of a given species, in the same way as isotherms delimit areas having the same temperature. Isopollen lines give a cartographic representation which is equivalent to that of recent forest maps—even though the figures must, of course, be read in another way, cp. fig. 14. Whereas the isopollen maps give excellent comprehensive summaries, they are generally less suited to documentation purposes unless very carefully executed.

THE INTERPRETATION OF POLLEN DIAGRAMS

The work that has been dealt with in the preceding chapters, is all of a technical kind and much of it may be left to laboratory assistants: as a matter of fact much of it is regularly left to such technically trained persons without scientific qualifications. This should only be done in the case of routine analyses, never when dealing with an unknown deposit, where a routine worker will most probably overlook unexpected irregularities that may be of the greatest importance for the interpretation of the diagram. Schematic routine work is always dangerous in pollen analysis, even in the early stages of the work, but it is absolutely fatal when it comes to the interpretation of the diagrams. One must never for one moment forget that the pollen diagram is a representation of the *vegetation* of the locality in question. The pollen diagram has no *direct* bearing on anything else: climate, nor soil, nor exposition, nor anything else. The pollen diagram must first be translated into terms of vegetation and only after that has been done one may try to find the reasons for the observed vegetational changes. It is a corollary to this that the pollen analyst should be a trained field botanist, pollen analysis without a strong botanical foundation is sooner or later certain to lead to incongruous results.

As the main object of pollen analysis is usually to infer the climatic changes, it is of prime importance that the investigator should be able to recognise such non-climatic features that are likely to occur in pollen diagrams, e.g. those that are due to the ordinary succession in a fen area, cp. also the almost identical, but highly metachronous regression diagrams published by FLORIN (1945). Such objections as those raised by L. R. WILSON (1938)[1] against the application of pollen analysis to Wisconsin demon-

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[1] "... there were several narrow belts of unlike vegetation which interpreted in the usual sense of plants as climatic indicators would call for distinct narrow climatic belts bordering the lake shore." etc.

strate the necessity of botanical training in the interpretation of the diagrams, not imperfections of the method.

It is also obvious that the regional parallelism between diagrams from the same area will be greatly influenced by edaphic conditions. As the recent vegetation of a sand and a clay area will be different, so were the former vegetation types, and so will be the pollen diagrams, but if any climatic change has taken place during the period comprised by the diagrams, the corresponding effect on vegetation will show in both areas, but not necessarily in an identical manner. An experienced botanist will usually be able to distinguish between edaphic and climatic influences in pollen diagrams. Nothing is more dangerous than the habit of considering the pollen diagram curves as independent phenomena and to discuss them as such: they are registrations of vegetation and any attempts to consider them as anything else is bound to lead to confusion.

Elevation will also influence the pollen diagram. Unfortunately very little is known about the influence of altitude. The vertical transport of pollen grains is of relatively greater importance than the horizontal one, and tends to carry lowland grains up into regions where they do not belong (cp. RUDOLPH and FIRBAS 1927, LÜDI 1937, FIRBAS and LOSERT 1949). However, very little is known about the quantitative relationships.

Other effects can also influence the composition of pollen rains and conceal or imitate the effects of climatic changes. The varying distance of the area of investigation from the glacial refuges of a slowly or intermittently spreading species causes the immigration of that species into different areas to be highly metachronous. The beginning of e.g. the beech curve in European diagrams, locally a highly important indicator level, is thus of very different age in different areas. Cultivation of the area may distort diagrams and substitute e.g. a long-distance transport diagram for a local one if cultivation is sufficiently intensive. Change of sediment or peat type may introduce changes in the curves—especially those of NAP, but even of the AP curves if trees are members of the mother formation. Forest fires may cause changes—under natural conditions these are probably reversible, except in regions of vegetational instability where a forest fire may cause the realisation of inherent tendencies in the development. All these and many other factors must be taken into account during the interpretation of any pollen diagram.

We emphasise that pollen diagrams from peat are almost impossible to interpret in all their details if they cannot be controlled by comparison with sediment diagrams. The local pollen production of peat does not influence NAP alone, but may also influence the AP spectra in many unpredictable ways. For ordinary work one should never analyse peat if any sediment is available.

The simplest case is, of course, that of a completely forested area, where all information is contained in the AP diagram. If the diagram is to be translated adequately into terms of vegetation, one must take into account the different pollen production of different species. As pine produces great quantities of pollen, 10 % pine pollen is almost of no account, pine hardly grew at or near the site at the time of deposition of the sample. As beech produces very little pollen, 10 % beech is highly significant and generally means that beech must have played a prominent part. If we use the production figures quoted p. 34, cp. p. 87 (their significance and applicability must not be exaggerated) a pollen spectrum registering 33 % each of pine, oak, and beech should represent a vegetation consisting of 5 % pine, 35 % oak, and 60 % beech. This is a theoretical example only, in nature conditions are much more complicated, *int. al.* because the pollen grains of different species are transported over longer or shorter distances.

It is hardly possible to give transformation factors of general applicability. One must also take into account the variations in pollen production according to the density of the stand; one tree in an open position produces as much pollen as dozens of trees of the same species in dense stand (cp. BORSE 1939 p. 129)[1]. It is probable that the area-production figures are more constant than those of production per tree, but this subject is so far very incompletely known.

It is also very important to keep in mind that as the numbers of the pollen spectrum are relative, the curve of each species is not only dependent on the occurrence of that species, but also on the composition of the rest of the forest. If we imagine a forest consisting of equal parts of oak and pine, and we use the pollen production numbers quoted, we find that the corresponding spectrum will contain 15 % oak, 85 % pine. If the pine is replaced by beech (apart from the botanical improbability of that succession) the same quantity of oak will give 60 % of the pollen against 40 % beech. If the beech is then replaced by *Populus tremula,* we get 100 % oak pollen, although the quantity of oak has not changed at all[2]

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[1] Road-side trees in cultivated areas, especially elms, produce enormus quantities of pollen and distort the composition of the recent pollen rain. Surface samples from cultivated areas frequently exhibit too high percentages of the species of road-side trees in that region.

[2] This is provided that *Populus tremula* pollen grains are not recognised in the preparations. As a matter of fact they can be recognised and counted like those of other forest trees, even though they are delicate and easily overlooked, especially if the preparation is not stained (cp. IVERSEN 1946 p. 223).

(cp. Erdtman 1932 p. 15). It is necessary to take into account not only the curve under discussion, but the other ones as well.

By the use of absolute figures for the pollen rain instead of the relative ones these difficulties could be prevented. Unfortunately such figures are generally unobtainable. The absolute pollen contents of any peat or sediment sample are too dependent on the nature of the deposit to be of general applicability: the drawbacks are usually greater than the advantages even if APF figures have in some cases been used with advantage to elucidate special problems (Welten 1944, Aario 1944).

The last example given above opens up another, very important problem: If the forest is to a great extent composed of species, the pollen of which is not found in fossil deposits e.g. because the species in question are exclusively insect pollinated, the pollen flora will not only give an incomplete, but an essentially false picture of the composition of the forests. In Europe this source of error is hardly of any significance, but in Northern America the difficulty of recognising *Populus* pollen in the deposits represents a serious imperfection (Erdtman 1932), which can, however, be overcome by careful examination. Conditions in tropical regions are unknown, but one may fear that the greater number of zoogamous species may cause difficulties. If the vegetation of an appreciable, but incalculable, part of the area is not represented in the pollen rain, the pollen-analytical discussion of the remainder of the vegetation is of limited interest only.

One important problem has not been discussed very much in pollen-analytical literature, viz. the question of how large an area an average pollen diagram represents: the vegetation of which area is distinctly represented in the diagram or, in other words, where is the transition—which is, of course, very gradual—between "normal" pollen transport, and long-distance transport, the latter term referring to pollen grains coming from other areas. The question can hardly be answered without much more empirical material. In the next chapter we shall show that the long-distance transport usually plays a very small part, but nothing is at present known about the part played by the immediately adjacent vegetation, e.g. 0-500 m from the site of investigation as compared with that of a wider neighbourhood, e.g. up to 10 km distance. The relation will vary with the species represented: in species with buoyant pollen grains the gradient will be smaller than in species with heavy, rapidly sedimenting grains. It will also vary with orography and, above all, with the size of the basin. If the nearest trees are close to the point where samples are collected, the local influence will be very great (cp. Hoffmann-Grobéty 1946 p. 27); if samples are taken from the middle of a great basin, the local influence of the nearest trees will be negligible. The extent of the littoral forests along the basin is also a factor of great importance, as the composition of the littoral forests in most cases differ materially from that of the ordinary dry-ground forests. The theoretical deductions about the average transport of pollen grains are of limited value in practical work as conditions vary from case to case. Ordinary pollen transport should cover ca. 50 km, but judging from pollen-analytical experience we suppose that the forests beyond the 10 km limit are of very little importance for the ordinary pollen diagram, and most of the material will be derived from much nearer sources (cp. RUDOLPH & FIRBAS 1927 p. 114).

The best control of the representativity of a pollen diagram is obtained by comparing the topmost sample with recent conditions. One should therefore take care to obtain samples from the topmost recent and sub-recent layers of the deposit. It must be admitted, though, that the recent spectra suffer from the draw-back that contingent differential destruction of pollen grains has not yet taken place. Theoretically such a spectrum may contain pollen grains which would not have been recovered if the same sample had been allowed to fossilise. In practice this objection is rather immaterial, and recent pollen rains as they are preserved in sediments under formation, are fairly good representatives of the conditions as found by analysis of fossil deposits.On the other hand recent samples have frequently been collected from moss cushions etc. As these do, however, represent a much drier substratum than the peat or sediment that is analysed, it is to be expected that differential destruction will go further than in deposits that are used for regular analysis. Consequently one must expect accumulation of the relatively resistant grains. Besides, recent moss cushion spectra will in many cases suffer from local NAP over-production which is different from that of the deposits.

A number of investigators have tried to establish a relation between the representation of a species in vegetation and in pollen diagram. STEINBERG (1944 p. 535) has within a restricted area in Middle Germany established the following relations between the percentage of trees in the surrounding forests and of pollen in the sub-recent deposits:

Betula	8
Pinus	7·7
Quercus	1.8
Picea	1.1
Fagus	0.21

The *Fagus* figure seems to be too low, but otherwise the table gives a clear distinction between the two main groups of the large and small pollen producers. Other investigators have arrived at corresponding figures, e.g. P. Müller (1937):

Pinus	6
Picea	0.9
Abies	1.0
Fagus	0.6

It is also indicative that in Finland the sub-recent pollen spectra reproduce the actual composition of the forests comparatively well—because they are totally dominated by *Betula* and *Pinus,* which are equally strong pollen producers. However, *Picea* seems to be under-represented in this case too (Aario 1940 p. 56 seq.).

Pohl has (1937 p. 431) used his pollen production values (cp. p. 34) for calculating the quantities of pollen produced by one ha. of pure forest taking into account the frequency of flowering of the different species, and arrived at the following relative figures, which (except for *Picea*) correspond to those found by Steinberg and Müller:

Alnus	17.7
Pinus silvestris	15.8
Corylus	13.7
Betula	13.6
Picea	13.4
Carpinus	7.7
Quercus	1.6
Fagus	1.0

Thus it is obvious that if the percentages of the pollen diagrams are to represent adequately the percentage composition of forests, the figures quoted above must be taken into account. Iversen has proposed (in lectures, cp. 1947 p. 242) to divide the pollen types into three groups, A, B, and C. The A group comprises those species which contribute the great quantities of pollen, i.e. (in Northern Europe) *Pinus, Betula, Alnus, Corylus.* The B group comprises those which contribute small quantities: *Picea, Tilia, Quercus, Fraxinus, Fagus,* etc. The C group comprises pollen types that are so scarce that it is immaterial whether or not they are included in the pollen sum. The species in question are both scarce and small pollen producers besides. Many of them may be of great indicator value, e.g. *Ilex, Hedera, Viscum, Vitis, Lonicera periclymenum,* and if used as indicators they must always be represented by special diagrams.—

In the construction of diagrams the fraction of the A group must be reduced, e.g. by a division of the pollen numbers by four before they are added to those of the B group to make up the pollen sum. The principle is illustrated by the following table:

	Number of grains	Percentage	Number after reduction	Percentage after reduction
Pinus	120	60	30	30
Betula	24	12	6	6
Querc. mixt....	32	16	32	32
Fagus	24	12	24	24
	200	100		
Corylus	32	16	8	8
			100	100

It is obvious that such a reduced spectrum, in which *Corylus* must be included in the pollen sum (cp. p. 68), gives a more adequate representation of the actual composition of the forest, as is demonstrated by IVERSEN (l.c.) in the case of the fossil Kaas forest (cp. also IVERSEN 1949). To what extent such reduced spectra should replace the ordinary ones, is a matter for discussion.

When discussing the position of a pollen type in relation to these groups one must, besides pollen production, also take into account the effectivity of dispersal of pollen (*Tilia, Picea*), the periodism of flowering, the relation between male and female flowers, etc., especially if NAP is also included, because the factors mentioned above counteract each other, e.g. *Calluna:* great production, ineffective dispersal. Whereas the reduction figure 4 has proved to give adequate results in the case of most Danish forest trees, there are of course some species of genera that occupy an intermediate position.

Even if it is quite obvious to anybody who realises that the interpretation of pollen-analytic data must take place in terms of vegetation, many investigators overlook the fact that the same climatic event may express itself in quite different ways in pollen diagrams from different areas. If climate is classified by its corresponding climax vegetation, the effects of a climatic fluctuation in different areas can be represented in a diagram like fig. 15. In the locality represented by curve A the climatic fluctuation will manifest itself in a glacier retreat followed by a readvance before the final retreat. In locality B the forest will invade the tundra and disappear again. In locality C the outward sign will be a change between birch and

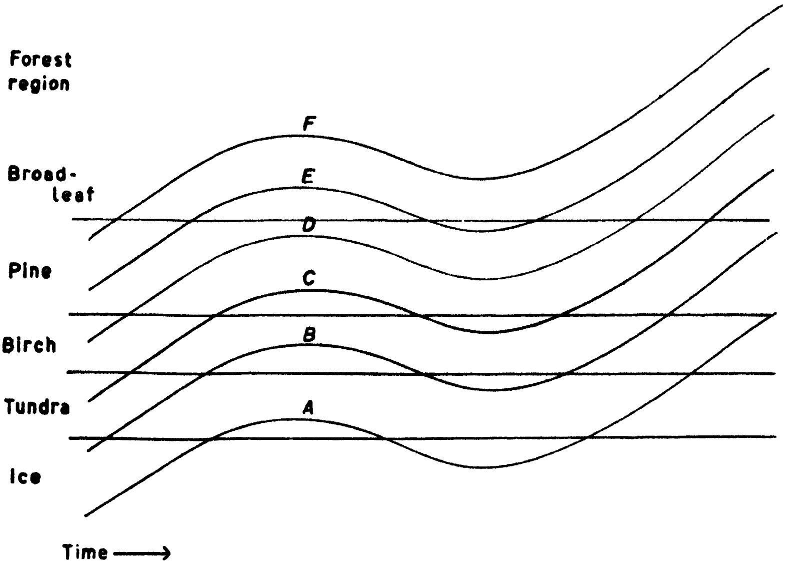

Fig. 15. Different pollen-analytic registrations of the same climatic oscillation in different regions in an imaginary transect from a centre of glaciation outwards. Close to the centre (curve A) the oscillation is represented by a glacier retreat and readvance. Curve B is the classical Allerød: tundra—birch forest—tundra. Further outwards the oscillation is registered by other vegetational changes. NB! In the curves D and F no major change is to be observed.

pine forest, and in locality E between pine and oak forest, whereas a pollen diagram from locality D will show minor quantitative changes in the composition of the pine forest. Nevertheless it is the same climatic fluctuation.

Fig. 15 can serve as an illustration of the effects of the Allerød oscillation on the European pollen diagrams. Curve B represents the classical case, Denmark, whereas conditions further south are represented by the curves C-E. A development like that in locality A cannot, of course, be traced by means of pollen analysis. Two conclusions can be drawn from this, viz.: (1) that the pollen-diagrammatical representation of the Allerød, or any other climatic, oscillation must be different in different climatic areas, and (2) that if an identical representation is found in two sufficiently different climax areas, it cannot be the same fluctuation. Thus, if a "classical" Allerød (curve B) is found e.g. in the lowlands of southern Middle Europe, one can be certain that it represents an older climatic fluctuation than the Allerød[1].

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[1] The tendency on the part of some investigators to call every and any supposed late-glacial climatic fluctuation an Allerød, is certain to cause unnecessary confusion.

SOURCES OF ERROR

In the preceding chapter we have dealt with some aspects of the interpretation of the diagrams and with those difficulties which are inherent in the method. There are, however, a series of errors which may occur under certain circumstances, and which can distort a pollen diagram completely making it more or less useless.

First there are some pitfalls that are common to all stratigraphical work, viz. hidden erosion contacts and redeposition. LUNDQVIST (1924) has demonstrated that apparently continuous deposits may conceal a hiatus comprising a very long period. The explanation is that the sediment in question has been removed by some change of the current system of the basin. Such cases are rather frequent in large, shallow basins, where the mechanism of filling-up is very complicated and may cause other irregularities as well. Similar errors may be caused by the drying up of the basin for a period during which no sediment is formed. Usually a hiatus is recognisable by the very sharp contact between two types of deposit, and conversely sharp contacts are always to be suspected, but it can occasionally be invisible at any rate in the sampler. The investigation of more than one series from the area under consideration will generally disclose such invisible breaks of the sequence.

The material removed by erosion will generally be distributed over such an extensive surface that the contamination of contemporaneous pollen diagrams is negligible, but in serious cases a layer may be dominated by redeposited peat or sediment of a different age and its pollen flora completely distorted (cp. examples in ERNST 1934 p. 304). The remedy is the same as in the preceding case: more diagrams from the same area (plus a little common sense).

Then there are those errors which are particular to pollen analysis. During the first decade of pollen analysis these errors were much discussed, more, however, on the basis of theoretical considerations of what *could* happen than on the basis of actual knowledge of what *does* happen. Some of the supposed errors, e.g. downwash of pollen grains through the strata, have been proved to be without significance (MALMSTRÖM 1923 p. 149).

There are three classical sources of error, which have been known and feared during the whole history of pollen analysis. The first and simplest is that of *differential destruction of pollen grains* already mentioned in the preceding chapter. As the composition of the exine and its resistance against corrosion differ specifically, it is an obvious conclusion that if pollen grains are subject to corrosion of more than a minimum amount during or after fossilisation, the composition of the pollen flora will change, the more resistant types apparently accumulating because of the disappearance of their counterparts, the weaker grains. Fortunately it is in most cases very easy to control this error as corrosion of pollen grains is, according to our experience, easily observed whenever it occurs. If corrosion has proceeded so far that some pollen grains have disappeared altogether, there will be many grains, the exine of which has assumed a peculiar, pitted surface which is easily recognisable and which is the first stage in corrosion. If more than 50 % of the pollen grains of deciduous trees (conifer pollen is more resistant) show traces of corrosion, the sample should be discarded, as one must suspect that the spectrum has been distorted by the total disappearence of part of the pollen flora. In normal diagrams, which are to be used as a standard for the area, corrosion should not be tolerated at all. In some cases, e.g. for dating purposes, one may be obliged to analyse deposits, the pollen contents of which are more or less corroded; in such cases the diagram must be taken for what it is worth and its features considered with due suspicion. The extent and degree of corrosion should be stated. In sediments corrosion will generally be unimportant, but in aerated peat it is a grave source of error.

Problem number two is the *local over-representation* due to the occurrence of some heavy pollen producer in the immediate proximity of the locality where the sample was taken. Local over-representation is especially dangerous in peats where the pollen producer is part of the mother formation, e.g. pine forest peat formed on a dried-up bog covered with pines, or alder carr peat. In these cases the deposit itself will serve as a warning and if possible such deposits should not be analysed. Other cases are more serious e.g. when a tree on the bank has dropped pollen or whole catkins into water, where they have been deposited within a small area. It is important to note that the number of pollen grains left in the falling catkins may be greater than that which has been dispersed in the air during flowering time (REMPE 1937, p. 114). In such cases no remains of the tree occur in the deposit (profiles may give the solution) but usually the pollen grains will adhere in lumps, thus indicating what has happened. Even if such pollen lumps are counted as units, the percentage of the species in question will in many cases be abnormally high. If this is the case in one or very few samples only, the over-representation can be compensated for simply by assuming that the percentage of the species in question has changed continuously between the two adjacent "normal" spectra. The other percentages can then be calculated from the following formula:

$$p_1 = a_p \frac{100 - r_1}{S - a_r}$$

where p_1 is the "corrected" percentage that is to be calculated, a_p the number of pollen grains of that species in the count, r_1 the "fixed" percentage of the over-represented species, a_r the number of grains of that species, and S the total of all pollen grains included in the sum (FÆGRI 1944 b p. 456)[1].

Owing to the small transport distance of most of the NAP the danger of local over-representation in the NAP diagram is even greater than in the case of AP, but on the other hand it is generally easier to check the occurrence of pollen producers in the mother formation, especially in sediments.

Local over-representation can make a diagram totally unfit as an expression of the general vegetational history of a region. Such a diagram may nevertheless be of great value, as it can form the basis of a palaeophysiognomic analysis, which may disclose climatic influences not revealed by ordinary methods. As a matter of fact each pollen diagram represents an antagonism between the regional and the local pollen, and sound botanical judgment is needed to determine which is dominating in each case.

The third of the classical sources of error is the *long-distance transport,* which in the first years of pollen analysis was taken very seriously (HESSELMAN 1919). Later experiences have shown that it is in most cases a subordinate factor. Considering the data given p. 35, especially HESSEL-

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[1] E.g. Pinus 480, Betula 566 and total 1070 grains. Betula is overrepresented, the correct percentage is supposed to be 10; the Pinus percentage will then be $p_1 = 480 \frac{100 - 10}{1070 - 566} = 85\frac{1}{2}\ \%$.

MAN's results from the light-ships, this might seem rather unexpected. The explanation is that the quantity of pollen produced by the local vegetation is so immense that the quantities due to long-distance transport are in relation insignificant in spite of their absolute magnitude. It is self-evident that if long-distance pollen is caught in a place where no AP is produced, the whole AP sum will be due to long-distance transport, and the AP diagram will, of course, be totally misleading as a representation of the local vegetation. However, there will generally be a local NAP production (lichen heaths are frequently extremely unproductive), and the AP/NAP ratio will show the character of the AP, whether it is local or long-distance transported. The "normal" NAP percentage in sediments from a forested area in West Norway is ca. 5, whereas it is in a forest-less area 50 % of the total diagram. Consequently the local NAP production is of the same order of size as the long-distance AP supply, which again means that if the same relation between NAP and long-distance AP holds true in a forested area, the latter should also be some 5 % of the AP met with. Such a calculation is, of course, highly conjectural, but it gives an idea of the order of size of the long-distance contamination of the ordinary pollen diagram. This is not realised generally, as most of the long-distance AP consists of the same pollen types as the local ones, but in the case of species which did not grow locally, the influence can be read directly from the pollen diagram. Results obtained by such calculations support the conclusions arrived at here.

In the diagram as a whole the long-distance pollen is of little significance, but it is highly unpleasant when the question of immigration of a species arises. Is a small percentage of a pollen type due to a small local occurrence or to long-distance transport? The question cannot be answered by a single formula. Formerly it was supposed that when the curve rose above some few percent (the so-called rational limit), one might be fairly certain that the species did occur within the area. In many, perhaps most cases, this is certainly correct in forested areas, but here dogmatism is more fatal than ever. The association plays a very great part: a curve in a diagram chiefly composed of prolific pollen producers (our group A, p. 87) means something quite different from one in a group B diagram. The curve of A species—in whatever association—may be continuous and even reach great values without any local or regional representation of the species. For *Pinus* in a forested area the limit seems to lie at 10 %: under ordinary circumstances values below 10 per cent do not indicate the presence of *Pinus* in the immediate neighbourhood of the deposit. On the other hand a single grain of a group C species may be sufficient to indicate the presence of that species with great certainty, e.g. *Ilex,* the pollen grains of which are produced in small quantities only and are not adapted for wind transport. This presumes of course, that all contamination of the sample can be precluded.—The smaller the total local pollen production, the greater the demands made on the representation of a species in the pollen diagram before it is accepted as an indication of the actual presence of the species. On the other hand, in a densely forested area even low percentages may indicate presence, but, unfortunately, it is impossible to lay down fixed limits, and many cases most probably for ever remain uncertain. It is hardly possible to date exactly the immigration of a forest tree by means of pollen analysis alone. Absolute certainty can be acquired by the find of macro-fossils only, and even they may in some cases be wind-transported, e.g. pine needles blowing on and with snow above the timber-line.

The above pertains mainly to forested areas. With increasing distance from the forest the importance of long-distance pollen increases, and at a sufficient distance, some 10 km from the nearest forest, all AP must be counted as belonging to that category. This is where difficulties arise: one and the same pollen type may, even in the same diagram, sometimes be produced locally and indicate a warmth period and— in other diagram zones—be long-distance transported and indicate the absence of forests, i.e. unfavorable conditions. A typical example is afforded by the *Pinus* pollen in Northern Finland (Aario 1940 p. 60): The pine representation falls off from 80 % in the S to 50 % at the northern end of the pine area and further to 20 % in the birch belt. Then it rises again to 80 % in the AP diagram in the tree-less tundra[1]. The same applies to *Picea* and *Alnus.* No general directives can be given until we posses more experience. Until then one must solve each problem independently by botanical judgment (and common sense!).

The occurrence of NAP obeys quite different rules, if any rules can be laid down to-day. These pollen types are less subject to long-distance transport than AP, simply because they are released at a much lower level above the ground, and their occurrence is therefore more local. Just at the border of the forest zone the NAP production per area is highest (apart from clearings within the forest zone), and then it falls off with increasing distance from the forest. Experience seems to indicate that this fall-off may in certain cases be stronger than the corresponding fall-off for AP,

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[1] In a total diagram, where the tundra is also represented, this secondary and misleading rise will be suppressed.

consequently one may find AP dominance again at a sufficiently great distance from the forest. The respective dominance of AP or NAP is conditioned by a complicated set of mutually interdependent and interfering factors, and no hard-and-fast rules can be laid down. An intimate knowledge of the vegetation types is the only possible foundation for the solution of these problems.

AARIO (1944) has discussed the possibilities of evaluating the density, or non-existence, of forest by pollen analysis. He concludes that it is possible by means of the AP/NAP ratio and by the APF, which is much lower in the tundra samples than in those from the forest region. Unfortunately AARIO has investigated peat only; the NAP/AP relations give a much clearer picture in sediments, and we are convinced that many of the difficulties met with in peats, above all the extreme variability of figures, will disappear if the investigation is carried out in sediments only. AARIO has pointed out that high NAP values (in peat) are of little importance as indicators of the absence of forests if they are due to one NAP type only, or in some cases to the simultaneous occurrence of some types which are together characteristic for one plant community, e.g. *Empetrum* and *Rubus chamaernorus* in northern Finland (1940 p. 69). These "disharmonic" high NAP values are characteristic of peat, we have always found that in typical sediments the NAP flora is harmoniously developed, containing representatives of all major NAP types. Even if their mutual relation varies, these variations are subordinate to those of the NAP/AP relations as a whole. For the local, single-type NAP maxima that are of no indicator significance it is characteristic that they dominate the NAP/AP relations (cp. the Andalstorvmyrane diagram FÆGRI 1944 a pl. 8).

Other sources of error have since been recognised. IVERSEN (1936) has demonstrated that moraine (boulder clay) may contain great quantities of pollen from pre- or interglacial deposits. These pollen grains are redeposited in late-glacial clays, thus giving rise to a mixed pollen flora in which the "secondary" pollen frequently predominates. Any pollen spectrum from a clay or a clayey sediment must be considered with great suspicion until the presence or absence of secondary pollen has been thoroughly investigated. The contaminated spectra may nevertheless give an adequate picture of the composition of contemporaneous vegetation if the secondary pollen can be subtracted from the total sum. The principle is comparatively simple: The composition of the secondary pollen flora can be obtained by analysis of a *fresh* boulder clay—this is very important, as the pollen contents of moraines are easily destroyed by subsequent weathering. The secondary pollen flora consists partly of pollen types which cannot be separated from those that could be expected in the clay sample, partly, however, of pollen types which are obviously secondary either because the species in question did not grow in Europe after the Ice Age, or because their climatic demands are such that they could not be satisfied under the prevailing conditions, e.g. lime pollen in glacial clay. This second group constitutes N % of the moraine pollen. In a given clay sample the same group constitutes n %. It can be inferred that $\frac{n}{N}$ of the percentages of the species belonging to the first group must be represented in the late glacial clay. These percentages are subtracted from those found in the clay and the rest then gives the "primary" pollen spectrum of the clay.

Regular local winds in mountainous districts or on the coasts may cause disturbances in the diagrams (cp. Brinkmann 1934 p. 388). This source of error is in most cases insignificant, but may in special cases prove fatal if over-looked.

In Northern European diagrams *Pinus* is over-represented for several reasons. The pine over-representation in deforested areas has been mentioned previously. It is the combined effect of the great quantities produced and the great ease with which pine pollen is transported. The so-called secondary rise of *Pinus* in Middle European diagrams after cultivation has been thoroughly discussed in a series of publications. It is, of course, the same effect as the above. Another case of *Pinus* over-representation is that frequently found in marine deposits. The most likely explanation is that the pine pollen falling on the ocean surface drifts towards the shores and is at last deposited in the sediments of shallow coves or lagoons, whereas the pollen of deciduous trees sinks to the bottom before reaching the shores. This explanation suffers, however, from certain weaknesses: The pine over-representation is not always realised, and other pollen grains also float, at least sometimes (cp. Overbeck and Schmitz 1931 p. 86). The problem of pine over-representation in marine deposits is not yet fully solved. In practical analytical work it means that one must always expect irregularities in marine deposits. In Eastern Sweden the *Pinus* over-representation in marine deposits is followed by one of *Alnus* in the following lagoon sediments (Florin 1945). Whereas the pine over-representation obviously does not represent any vegetational reality, that of *Alnus* reflects the actual carr vegetation round the lagoon. Thus, if pollen analysis is used for the investigation of land/sea relations one may in certain cases get a diagram the main features of which are no indication of the regional history of vegetation, and consequently cannot be used for synchronisation. There will usually, however, be other features of the diagram which will permit this. In all such cases where one pollen type is over-represented, correlation with other diagrams can be obtained by means of the relation between the other constituents of the diagram . In extreme cases one may be obliged to construct auxiliary diagrams from which the over-represented species is omitted (cp. v. POST 1947 p. 234). It must be emphasised that such diagrams are even less representative of the actual vegetation of the area than the original ones: they are only to be used for correlation purposes.

STATISTICAL ERRORS

Pollen analysis is essentially a statistical technique, and as such it is subject to the rules that govern all statistical relations. It is remarkable that the statistical problems of pollen analysis have been largely neglected, both in sampling design and in the evaluation of data.

The two types of statistical problems that are of principal interest to pollen analysis are (1) sampling errors, and (2) irregular fluctuations of the curves, both of which interfere with, and in extreme cases conceal, the long-term movements which are of interest in the investigation.

Sampling errors have been discussed by a number of previous investigators. No statistical training is necessary to realise that the more pollen grains counted, the more is the sample representative of the "real" composition, i.e. for the universe of numbers as a whole. Experience has that if ca. 150 AP are counted in each spectrum, the main AP diagram curves are comparatively safe (cp. BOOBERG 1930 p. 226), but experience alone cannot give any quantitative evaluation of the errors. One fact has, however, emerged from these and other experiences: If less than 150 pollen grains are counted per spectrum, the variations of the pollen curves must be very pronounced for one to be certain that the observations are "real" and do not represent sampling errors. Nevertheless, some investigators still count quite inadequate numbers of pollen grains[1].

The easiest way to obtain an idea of the errors is by gradually increasing the samples, i.e. by counting increasing numbers of pollen grains from the same preparations and observing the gradual "settling" of the percentages. Most pollen analysts have done this at some time, and some of

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[1] A deplorable example is that of an otherwise highly esteemed colleague who has published spectra based upon 4 and 7 pollen grains. Even more remarkable: In the 7 grain spectrum *all* curves reach zero. If it proves impossible to establish a proper spectrum from one sample, one must either pool the numbers from more spectra or give the actual figures from the count, not calculating percentages which would only be misleading.

these tables have been published. One of the more comprehensive is that published by Bowman (1931 p. 698), giving the composition of 20 samples from the same preparation, totalling 100 AP each. The results indicate that after 800-1000 grains have been counted, the percentage are generally fairly constant. With regard to the exceptional case of *Alnus* l.c. we consider it highly improbable that sampling errors alone have been active in this case (cp. Wenner 1948 p. 107).

Practical experience and tables like the one published by Bowman can give certain indications as to how many pollen grains must be counted in order that contingent regularities shall not be hidden by sampling errors, but mathematical treatment of the material is the only way in which one can obtain more definite answers. Barkley has studied the question of sampling errors and concludes that "there is little significant shifting of relative percentages beyond the 200 count" (1934 p. 288). Unfortunately the criterion used by Barkley, viz. 90 % correlation between parallel samples, is of little value in actual analysis, as it gives no information about the maximum variations of individual percentages. Besides, no attempt is made to discuss results in relation to the value of the percentages themselves: Small percentages require much higher counts than percentages of medium order, even though the absolute sampling error is highest for a density of 50 % and decreases symmetrically towards both extremes.

Ording (1934) and Westenberg (1947) have subjected the sampling error to a formal statistical treatment, presuming a binomial distribution of values. That this presumption is in accordance with facts, was proved by Fægri and Ottestad (1948. The following discussion is based upon that paper). Consequently the limits of the sampling error are defined by the standard variation of the binomial function (σ), which is dependent on the value of the observed percentage and on the number of grains counted, cp. tab. 1, which shows the 95 % confidence interval. This means that if the observed percentages are as indicated in the left column, it can with 95 % confidence be stated that the "real" value will be found within the interval indicated by the table. The observed value is situated in the middle of the interval.

It will be seen that the nearer the percentage approaches 50, the less certain are the observations, and the wider the limits of error. However, the numerical value of these limits are in pollen analysis less significant than the relation between the observation and the error, i.e. between the numerical value of the observation and the corresponding confidence interval; we may call it the relative confidence interval. Tab. 2 gives an approximate indication of the number of pollen grains that must be counted to give two definite relative confidence intervals. The table is not symmetrical about 50 %, but the higher values are of little practical interest.

TABLE I

Width of the 95 % confidence interval of P.

Pencentage density	Number of pollen grains counted				
	50	100	200	500	1000
1 (99)	9,2	5,4	3,4	2,0	1,3
3 (97)	11,7	7,6	5,1	3,2	2,2
5 (95)	13,9	9,3	6,4	4,0	2,8
10 (90)	17,4	12,1	8,6	5,4	3,8
20 (80)	22,2	15,9	11,2	7,2	5,1
30 (70)	25,1	18,1	12,9	8,2	5,9
50 (50)	27,2	19,2	14,0	8,9	6,3

The table shows that even such moderate demands for exactness are fulfilled only in very few pollen spectra, and as soon as the percentages approach low values, the demands are practically impossible to satisfy.

Two other questions of sampling errors are equally pertinent, viz. the questioh if values also distribute themselves binomially (1) if new preparations are made from the same major sample for each count, and (2) if samples are taken individually over the surface of the bog. Both questions have been investigated by WOODHEAD and HODGSON (1935)—who have, however, not tested the significance of their results statistically—and by FÆGRI and OTTESTAD. The answer to the first question is that no departure from the binomial distribution can be demonstrated.

The second question is more complicated, it pertains to the distribution of pollen grains over synchronous surfaces, i.e. the composition and distribution of the pollen rain. WOODHEAD and HODGSON analysed 10 surface samples taken from places up to 60 ft. apart (l.c. p. 268). FÆGRI analysed 50 samples belonging to an apparently synchronous layer, the maximum distance between samples being 1 m. In both cases the observed data were consistent with hypothetical values for random distribution and one may therefore conclude that over small surfaces the distribution of pollen grains in synchronous layers does not depart appreciably from the binomial; consequently the sampling error is in this case also defined by the standard

TABLE 2

Approximate minimum numbers of pollen grains

"Relative 95 % confidence interval"	$^2/_5$		$^1/_1$	
Density	Interval	Nr. of pollen grains	Interval	Nr. of pollen grains
50	30—60	100	25—75	16
20	16—24	400	10—30	64
10	8—12	900	5—15	144
5	4—6	1900	2.5—7.5	300
2	1.6—2.4	4900	1—3	780
1	0.8—1.2	9900	0.5—1.5	1600

variation of the binomial function. On the other hand it is self-evident that—especially in areas of variable vegetation—different parts of the bog may receive different types of pollen rain (some striking examples have been published by Lüdi 1947), but this is a case of over-representation, not of sampling error.

If the binomial sampling errors were the only ones, the practical requirement would simply be that samples should be made as great as possible—or rather, sufficiently great to reduce the confidence interval below a given level, consequently the sequence of percentage numbers of pollen grains will approach the "true" sequence with increasing size of the samples. However, it must be presumed that pollen curves may—like all empirical curves—contain irrelevant fluctuations which distort the picture. In such cases the limit to which the sequence of the percentage numbers approaches with increasing size of the samples, will contain maxima and minima that are irrelevant and misleading because they are consequences of local factors working within relatively short spans of time and space, factors which are of no interest to the investigation in hand. There may, of course, also be cyclical fluctuations which can be mistaken for irrelevant short-term ones. However, it is evident that it is more dangerous to use an irrelevant short-term maximum (or minimum) as a real one, e.g. for synchronisation purposes than it is to refrain from using a real maximum (or minimum) if there is some doubt about its reality.

The concept of short-term fluctuations must be defined, as it is obvious that every vegetational fluctuation which may reflect a climatic one, is of interest to a pollen analyst. However, a diagram contains a certain number of details only, has a limited "resolution power", and only a decrease of distances between samples can give more details. The distance in time between two pollen spectra is not of constant magnitude, either from diagram to diagram or even within the same diagram. It depends primarily on the method of sampling and on the rate of deposition of the peat or sediment to be analysed. In modern routine work the ordinary distance between samples is 5 cm; these 5 cm may represent 50 years or less in a rapidly growing peat, 500 years or more in a slowly accumulating sediment. In any case, if a more or less pronouncedly cyclical development has taken place, and we want a satisfactory representation of the development around a maximum or minimum, the full recurrence should generally be represented by ca. 8 samples (4 samples per maximum or minimum). In the first of the two cases mentioned above, where distance in time between samples was on an average 50 years, the diagram cannot profitably be utilised for the study of a recurrent development of shorter duration than 400 years: the "resolution power" of such a diagram will be 400 years. If shorter fluctuations are observed, they will—even if they are regularly recurring—occur as irrelevant fluctuations which cannot be analysed properly by means of the ordinary diagram. Similarly, the resolution power of the diagram in the second case mentioned above will be of the order of 2000 years per maximum or minimum (4000 years per full cycle).

It is obvious that by increasing the number of samples one can analyse progressively shorter cycles. This involves a great deal of work, and if our main object in this connexion is to control the influence of short-term fluctuations and irrelevant maxima and minima, this can be done by interpolating between the "ordinary" spectra a set of controls, which are separated from the former by an adequate span of time, i.e. vertical distance, in other words by *paired samples*. If the distance between the two samples of a pair is $^1/_5$ of that between pairs, i.e. between "ordinary" samples, we possess a means of evaluating the effects of fluctuations, the duration of which is $^1/_5$ of the minimum duration of those variations that can be properly analysed by means of the diagram in question. This again corresponds to a maximum or minimum equalling the distance between two "ordinary" samples, or in other words: single-spectrum maxima or minima.—It should be kept in mind that the concept of short-term fluctuations is a relative one: it comprises those details of the curves that are of too short duration to be analysed properly by means of the ordinary samples of the diagram, whatever their duration in years.

In practical work the "controls" can be taken from the core of the sampler, or from the exposed wall of the deposit at the same time as the "ordinaries". They can most conveniently be put into—another part of—the same receptacle (glass tube) as the "ordinary" and receive the same serial number. If one works systematically, the relative position of the two samples in the receptacle will always be the same—this question is, however, chiefly of academic interest, as it is in practical work irrelevant which sample is considered "extra". Some investigators practise continuous sampling, taking the whole core into the laboratory. The method—which has its practical difficulties—has the great advantage that the distance between samples can be regulated according to demands during the work, However, the practice of *analysing* continuous pieces of the core instead of discrete samples cannot be recommended from a statistical point of view. It must be admitted that some fluctuations are certainly integrated and disappear, but the possibilities of control are not so good as with ordinary treatment.

The introduction of paired samples does not entail a much heavier burden of work, as the counting of n pollen grains from each sample of a pair gives a more reliable estimate of the "true" value than the counting of 2n grains from one of the samples. The extra work in using paired samples is consequently restricted to the preparation of another sample for analysis—which may, however, in some cases be troublesome. We therefore find that the following procedure will most probably produce the safest results without causing much extra labour:

1. Samples are analysed at e.g. 40 cm intervals[1]. In this way a "skeleton diagram" is worked out, and— at any rate in areas of known vegetational development and not too compressed sequences—certain inferences may be made with regard to the character of the diagram.
2. Samples are intercalated at every 20 cm. Former conclusions are controlled.
3. Samples are intercalated at every 10 cm. Further control of conclusions. In many cases parts of the diagram now exhibit smooth curves, which presumably describe the corresponding events satisfactorily without further probing. Other parts still exhibit sudden changes that must be worked out to further detail. This is done by
4. intercalating samples at every 5 cm in these parts. If variations are not even now equalised,

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[1] In this case it is presumed that samples have been taken with 5 cm interval. If intervals are smaller or greater, these values may be changed.

5. the other pair of each sample within that part of the diagram is analysed. In this way the number of pollen grains counted in critical parts of the diagram is automatically doubled (with consequent reduction of sampling errors), and at the same time material is produced to show whether the variations observed in these parts of the diagram must come under the heading of short-time fluctuations. Later in this chapter we shall show how to control this point statistically by means of the data from the paired samples.—

Whereas the formulae based upon the assumption of binomial distribution are the only ones that can give information about the individual percentages as they occur in ordinary analysis work, other methods yield better results when more samples are to be compared, which is the case if we want to examine statistically the variations of a pollen curve. As long as samples are treated individually without being compared with each other, sampling errors are the only errors that can be evaluated (by means of the binomial formulae, cp. tab. 1 and 2). If more samples are to be compared, other methods can be used to study other possibilities.

One of the most frequent problems met with in practical pollen analysis, is when one of the pollen curves exhibits a more or less distinct maximum in a certain spectrum—and in this one only. Such a maximum, if "real", is of great value for the synchronisation of diagrams, as it may correspond to a significant, long-period maximum observed in other diagrams. If no additional data are obtainable, one may test the statistical significance of the observation by means of the χ^2 method, which is described in all modern statistical text-books (e.g. BONNIER-TEDIN, MATHER). The individual spectra are then compared with the average for the—generally three — spectra comprising the maximum or minimum, and the zero hypothesis is that there is no significant difference, i.e. all three samples can be considered random samples of the same universe. If the observed number of grains of a pollen type is o_i, the total number n_i, the average is

$$p' = \frac{o_1 + o_2 + o_3}{n_1 + n_2 + n_3}$$

which gives $$\chi^2 = \frac{(o_1 - p'n_1)^2}{n_1p'(1-p')} + \frac{(o_2 - p'n_2)^2}{n_2p'(1-p')} + \frac{(o_3 - p'n_3)^2}{n_3p'(1-p')}$$

with 2 degrees of freedom. The value of χ^2 is compared with a χ^2 table in a text-book or the graphical χ^2 table by PÄTAU (1943) to test the probability of our zero hypothesis.

This test can be used as a negative control only. If the observed value of χ^2 corresponds to a significant value of P, there is a *possibility* that the maximum is due to something other than sampling errors, but we have no proof. As the samples were not chosen at random, but were chosen just because of their excessive variability, the occurrence of values exceeding a given confidence level ("improbable values") will be much higher than in the tables, which are calculated for random samples. Plain, pollen-analytic reasoning may in such cases give some clue, other changes taking place in the diagram at the same time will indicate if the vegetation underwent other changes at the same time. Such negative controls are of great value for eliminating, irrelevant cases, but it should be kept strictly in mind that they can do no more.

By means of paired samples we may evaluate the influence, not only of sampling errors, but also of short-term fluctuations. A χ^2 test between the samples of each pair will show the contingent presence of short-time fluctuations. Analysis of variance will show the significance of the trend of the curves as a whole. The formulae to be employed are the following:

$$V_1 = \frac{1}{c - k} \Sigma\Sigma n_{ij} (p_{ij} - p_j)^2$$

$$V_2 = \frac{1}{k - 1} \Sigma n_j (p_j - p_o)^2$$

$$F = \frac{V_2}{V_1}$$

where k is the number of sets (pairs) and c the total number of samples, n_{ij} is the total number of pollen grains in an individual sample, p_{ij} the percentage of the species in question in the same sample. n_j is the total number of pollen grains in a set (pair), p_j the average percentage of the same species in the same set, and p_o the total average of all percentages of the species in question. If the χ^2 analysis shows that there is no difference between the two samples of a pair, p_j and p_o, should be calculated as weighted averages:

$$p_j = \frac{\Sigma n_{ij} p_{ij}}{n_j} \qquad p_o = \frac{\Sigma\Sigma n_{ij} p_{ij}}{\Sigma n_j}$$

If, on the other hand, there is a significant difference between samples, unweighted averages should be employed:

$$p_j' = \frac{1}{c_j} \Sigma p_{ij} \qquad \text{and} \qquad p_o' = \frac{1}{c} \Sigma\Sigma p_{ij}$$

where c_j is the number of samples per set (in our case: pair, $c_j = 2$).

By means of the value F arrived at in this way we can test our zero hypothesis, viz. that in this case the samples can be considered random samples from the same universe (in other words: identical). The F tables (cp. statistical text-books) give the values of F corresponding to different levels of probability with different degrees of freedom presuming random sampling. If two pairs only are compared, the degrees of freedom are, respectively, 2 and 1 (c-k and k-1). The formulae will in this case assume the following forms:

$$V_1 = \tfrac{1}{2} \left[n_{11} (p_{11} - p_1)^2 + n_{12} (p_{12} - p_1)^2 + n_{21} (p_{21} (p_{21} - p_2)^2 + n_{22} (p_{22} - p_2)^2\right]$$

$$V_2 = n_1 (p_1 - p_o)^2 + n_2 (p_2 - p_o)^2$$

These formulae can only be used for a comparison between two samples. It is an advantage of the analysis of variance that more than two samples can be compared at the same time, e.g. both spectra adjacent to a single-spectrum maximum. The corresponding formulae are then

$$V_1 = {}^1/_3 \left[n_{11} (p_{11} - p_1)^2 + n_{12} (p_{12} - p_1)^2 + n_{21} (p_{21} - p_2)^2 + n_{22} (p_{22} - p_2)^2 + \right.$$
$$\left. + n_{31} (p_{31} - p_3)^2 + n_{32} (p_{32} - p_3)^2\right]$$

$$V_2 = \tfrac{1}{2} \left[n_1 (p_1 - p_o)^2 + n_2 (p_2 - p_o)^2 + n_3 (p_3 - p_o)^2\right]$$

The quotient gives F with 3, resp. 2 degrees of freedom. The F values that are of principal interest in connexion with the application of these formulae in analysis, are summarised in tab. 3.

TABLE 3

Significance of F (variance ratio)

Confidence probability	Degrees of freedom (V_1 and V_2)			
	2 and 1 (2 pairs)	3 and 2 (3 pairs)	4 and 3 (4 pairs)	5 and 4 (5 pairs)
0.2	3.6	2.9	2.5	2.24
0.05	18.5	9.6	6.6	5.2
0.01	98.5	30.8	16.7	11.4
0.001	998.5	148.5	56.2	31.1

This means that if we e.g. compare 3 pairs and find F equal to 40, we have got a confidence probability between 0.01 and 0.001; it is hypothetically a very unlikely value and indicates that our zero hypothesis was not satisfactory, i.e. that our samples cannot be considered random samples of the same universe. If the samples tested were selected at random, we could feel confident that the registration in our diagram was significant, i.e. due to long-time movements. However, this control is also purely negative. As our samples were tested just because of their deviation from the normal, the frequency of higher F values will be much greater than that indicated in tab. 3, which gives, of course, the distribution by random sampling. If F is, however, lower than the value corresponding to $P = 0.05$, there is little reason to take our maximum seriously.

In all scientific work of this kind it is necessary to use statistical tests with common sense. In pollen analysis this is emphatically so. The variance analysis amounts to a comparison of two variances expressed by V_1 and V_2. The latter is a measure of the contingently existing long-term movement, and it is balanced against V_1, which is the square error, and which should embody all other variation. But a significant ratio between them (F) does not always mean that the existence of a long-term movement has been demonstrated. A significant F value only implies that there *may* exist a long-term movement, provided the total irrelevant short-term fluctuations are accounted for by V_1. This, in turn, depends upon the mutual relationship of distances between samples (cp. above). Great caution must therefore be exercised.

Within a diagram—or part of a diagram—under discussion long-time movements will more or less assume the character of a trend, and we think that pollen-analytic experience will in most such cases make complicated statistical methods less necessary. After all, *vegetational* changes can only be evaluated by a mental integration of the whole diagram; the curves are not variables to be discussed as such, they are registrations of vegetation and no mathematical statistics, however complicated, can replace botanical common sense.

There are, however, some cases in which statistical control is of a certain value. As, for example, when the diagram falls into parts characterised by a greater or smaller frequency of some indicator species. The curve of the indicator exhibits short-term fluctuation within the different parts of the diagram, and the problem to be tested is whether or not the variance between diagram parts is greater than that within the individual parts, in other words if the division of the diagram is statistically permissible. It is easily seen that this is another aspect of the short-term versus long-term movement controversy, only in this case we need no control samples because the short-term fluctuations are represented already in the variance within the parts into which we have divided our diagram (each part must contain at least 2 samples). The confidence probabilities are read out of a comprehensive F table. Such a calculation has been carried out by FÆGRI (1945). It must be remembered, however, that again we have a case of negative control only: the samples, i.e. diagram parts, were not chosen at random.

Another case may be illustrated by the following problem: At a specific level something takes place in a pollen diagram, e.g. the introduction of agriculture as indicated by the occurrence of *Plantago lanceolata* pollen grains. It is asked if this event has influenced other curves as well, e.g. causing a sudden decrease of the *Ulmus* curve, as elm twigs are preferred for cattle fodder. This can be tested by balancing the variance of the curve of this second constituent *(Ulmus)* within the two parts of the diagram against the variance between them by means of this same formula. As the criterion upon which the original sampling (i.e. division of the diagram into parts) was carried out, in this case the *Plantago* curve, was not included in the material to be tested, viz. the *Ulmus* curve, the sampling of the *Ulmus* curve may be considered fortuitous and the confidence probability values may be used without reservation. Such a calculation has been carried out by FÆGRI (1944 b) to examine—by a similar test—the behaviour of *Fraxinus* in parts of a diagram that had been divided by means of the *Quercetum mixtum, Betula, Alnus,* and *Corylus* curves. It should be kept in mind that if the curves dealt with, especially the indicator curve, reach high values, there will be a certain interdependence of the curves, which will to some extent interfere with probabilities of the F table.

It has been customary in pollen analysis to calculate certain genera "outside" the pollen sum. The classical example is *Corylus* which was from the beginning excluded from the pollen sum on the—fallacious—ground that "die normale Rolle des Hasels nur die eines regelmässig vorhandenen Unterholzes innerhalb ... Baumverbände gewesen" (v. POST 1929 p. 550). Later on, NAP types etc. have been calculated in the same way. The principles for this have been discussed in previous chapters. Logically the calculation of "extras" is rather dubious, and mathematically it is even worse. For a statistical approach the calculation of pollen types as "extras" is not to be recommended in any case. Indeed the real circumstances with which pollen analysis is concerned make this concept very unsound. As the species delivering the "extra" pollen practically always compete for space with the "ordinaries", the two groups are mutually exclusive: If there is a great deal of NAP, this means that forest, i.e. AP-producing species, is excluded from a greater part of the area under investigation. As a negative correlation thus exists between the densities of "ordinaries" and "extras", the variations of the latter group will be greatly exaggerated. The calculation of pollen categories as "extras" should therefore be avoided, it is merely traditional and has no background of vegetational fact. The traditional AP diagram (*Corylus* included!) is a means of studying the composition of the forests, the NAP diagram of studying the forest-less areas, but the only adequate means of studying the whole vegetation is the total diagram. There is, of course, nothing to prevent an investigator excluding from the calculation any species for whatever reason—the diagram then tells what happened in those parts of the area which were not covered by the species in question; but the calculation of such species as "extras" is of very limited value (cp. the rather ineffective representation of results in WENNER 1948). It should be the general rule in pollen analysis that the occurrence of any pollen category should be expressed in percentages of a universe of which it forms part. Thus, if it is desirable to express quantitatively e.g. the occurrence of fern spores, this should be done by means of a special diagram comprising the spores + AP + NAP or whatever will form an adequate universe for the calculation of these percentages.

To sum up: The procedure of statistical evaluation of a pollen diagram should proceed by the following steps:

1. Sampling errors are judged by means of tab. 1 and 2.
2. Maxima and minima are tested by χ^2 tests of unpaired samples.
3. Paired samples are analysed if this has not been done.
4. Short-term fluctuations are tested by means of χ^2 analysis of the two samples of each pair.
5. The trend of the curve is tested by analysis of cariance.

We want to point out that the exposition of statistical methods in pollen analysis given in this chapter is far from exhaustive, and especially we want to warn against an uncritical application of the formulae given above. Unless an investigator possesses a certain knowledge of the principles of modern statistical theory, it is very dangerous to use statistical formulae. The pitfalls are numerous and treacherous, and an unskilled worker very frequently makes tests that are of no value whatever, or even worse: that are directly misleading.

POLLEN-ANALYTICAL ZONES

A pollen diagram covering some thousands of years is generally a rather complicated structure, and in order to deal with it more easily the investigator has to subdivide it into zones. As all further work with the diagram is dependent on these zones, the division must be carried out most carefully. First and foremost the zoning must be based on a "normal" diagram exhibiting a minimum of local influences. In practice this means that the diagram should be from a homogeneous sediment series from the middle of a not too small basin where the influence of erosion, redeposition and other stratigraphic irregularities on the one side, and of local anomalies of littoral vegetation on the other, are reduced to a minimum. Normal AP diagrams may be obtained from large peat-bogs as well, provided there has been no forest on the bog. However, peat-bogs produce great quantities of NAP and cannot be used in such cases where the NAP values are of importance, e.g. for investigating the clearing of the land, etc. In many cases it will be necessary to piece the normal diagram together by means of diagrams from a number of basins, as no single diagram of sufficient quality comprises the whole period under consideration.

The normal diagram should always be checked by comparison with all other diagrams from the area. Zoning refers to the diagram *type,* not to any single diagram, however regular. No individual diagram is in reality *the* normal diagram, just as no individual is *the* species.

For the zones one must demand criteria which cannot be misunderstood: from one zone to another the diagram must be subject to changes of fundamental character, preferably by the appearance or disappearance of some forest type, or by fundamental changes in the dominance. Thus one should in ideal cases be able to determine at a glance to which zone even an isolated spectrum belongs, provided it is fairly regularly developed. It is much better to establish few, but properly defined zones than a greater number, which give an impression of a very exact division, but which are in reality vaguely defined. But on the other hand one must take into consideration that zoning is an instrument for dealing with the features of the diagram. If zones are too few, the instrument will be awkward.

Those changes in the diagrams that form the definitions of zone borders should preferably take place rather rapidly, giving sharply defined borders. It is self-evident that they are never point-sharp. In some cases zone boundaries have been defined by the crossing of two pollen curves. This is, however, most unpractical, as the point of intersection is subject to fortuitous fluctuations. If one of the curves for some local, e.g. edaphic, cause is a little higher or lower than usual, the crossing will take place in another part of the diagram, even if the trend of the curves, which is the important feature of a diagram, is unchanged.—The diagram zones form the firm structure upon which every treatment of the diagram must be founded, consequently each must be unmistakable.

Some investigators (e.g. VON POST) begin their zoning from above; other, however, from below with the oldest zone, I, at the base (JESSEN 1935, GROSS 1935). The latter procedure is more natural and convenient than the former.

The zones can be subdivided into subordinate units. If the curve of a forest type within a zone gradually rises to a maximum and then falls off again, one may base upon it a subdivision into 3 parts: *a:* rising curve, *b:* culmination, and *c:* falling curve. Whether such a course of the curve is conditioned by climate or by the immigration of another forest type or both it is obvious that such changes of the diagram have a definite, ecological meaning and must be common to the vegetation of the whole region, even if the local conditions modify the picture in each individual case. One may take it for granted that such changes of the curves are synchronous within a reasonably large area.

It is much more difficult to interpret the short-term changes of the pollen diagram which manifest themselves as a minimum or maximum of one or only very few samples. What do such short-term fluctuations mean in terms of vegetation? Is it possible that the whole vegetation of an area is subject to small synchronous variations? Certainly, some years of profuse flowering of one species may theoretically be sufficient to cause an appreciable maximum of the corresponding curve. But a maximum may be due to quite different causes. If the pine forest surrounding our basin has become over-ripe and blows down in a storm, it may be succeeded by a generation of birch, causing a birch maximum before the reappearence of pine. Maxima of the latter type—and unfortunately it is not possible to see any difference between them and the former in a diagram—are isolated features of no regional distribution. Even the fact that a corresponding maximum is found in another diagram from the same area, is no proof, as the succession between birch and pine may be a regular feature in the regeneration of the forest, and we have no reason to presume that this regeneration is simultaneous over the whole area; the opposite is more likely. In our opinion it is rather dangerous to correlate diagrams and establish synchronous levels by means of short-term fluctuations, the ecological significance of which is not exactly understood. A long-term change of dominance relations, a slow rising of a curve with a subsequent decline, can be interpreted ecologically with a certain degree of probability, and so can a sudden, but irreversible change. Such diagram features are therefore excellently suited for correlation purposes. Apparently accurate correlations by means of curve details, the ecological significance of which is obscure—to say the least—are of little value. After the introduction of agriculture and consequent clearing and forest destruction, the difficulties of interpretation and correlation are, of course, even worse than before, cp. the highly characteristic, but methachronous "clearance phase" in Danish pollen diagrams (IVERSEN 1941). There has been a tendency among pollen analysts in different countries to consider curves of pollen diagrams as phenomena per se, as a kind of index fossils, and to utilise them independently of their botanical background. Needless to say, such a procedure is bound sooner or later to lead to incongruous results.

THE APPLICATIONS OF POLLEN ANALYSIS

The "normal" diagram is the primary product of a pollen-analytical investigation. Per se it is a very valuable result as it gives the history of the vegetation of the area, from which can be inferred the history of the climate. However, vegetation is no meteorological universal instrument, and those climatic factors that first and foremost affect vegetation, are only part of the climatological complex, viz. those climatic elements which are at minimum. E.g. in moist, cool Northwest Europe moisture is generally available in sufficient quantity, but temperature is too low for optimal development of the more exigent vegetation types. Consequently vegetation will react very strongly to changes of temperature: with increasing temperature the warmth-demanding species will spread from their local stations in favourable positions and on favorable soil, and conquer greater areas. With decreasing temperature they will again recede. The climatic fluctuations registered in a pollen diagram from such a region are therefore chiefly those of temperature. Temperature and precipitation do not vary independently of each other—in spite of many geologists' apparent belief to the contrary—however, the laws of this interpendence are far from understood and we cannot infer from the one to the other. If we want information about precipitation in an area like northwestern Europe where there has always been plenty, we must resort to phenomena which are not, or at any rate are less conspicuously, represented in the diagrams. On the other hand a diagram from a semi-arid regon will in the varying dominance of forest and steppe elements in the pollen diagram give a representation of variation of moisture (i.e. precipitation — evaporation) whereas the influence of temperature is less conspicuous.

However, secondary phenomena may give additional information about the fluctuations of climatic factors not conspicuous in the normal diagram. Palaeophysiognomic methods may show the influence of varying moisture. We have previously (p. 43) already dealt with some of the main lines of investigation in such cases. The pollen diagrams from deposits that exhibit features which are caused by changing hydrologic conditions may be nearly normal, e.g. the AP diagram from a domed bog with recurrence surfaces. On the other hand the diagram may be greatly distorted by over-representation etc. If it can be checked with a normal diagram, the differences between them may give important clues as to the character of climatic development. In most cases the hydrologic fluctuations can be dated pollen-analytically, i.e. placed in their proper place in the time-scale of forest history.

Besides climate another set of factors influence pollen diagrams directly, viz. cultivation. As soon as a tract of land is cleared for agricultural or other purposes, the quantitative composition of the flora changes materially, and a number of species which were either unknown in the region, or occupied very restricted areas, come into dominance as weeds, and their pollen is incorporated in the pollen rain. Similarly crop plants may deliver part of the pollen rain even if the most important of them, viz. most of our cereals, are self-pollinating and release very little pollen. Even if pollen of weeds and crop plants are quantitatively insignificant, they are of the greatest indicator value, and besides the direct information they convey, their appearance may explain otherwise inexplicable changes in the diagrams. The appearance in northwest European pollen diagrams of *Plantago lanceolata* and *P. major* pollen together with those of Cerealia and some rare types mark the introduction of agriculture, and also the introduction of a non-climatic factor in forest development. By botanical analysis of cultivation diagrams one may gain surprisingly intimate glimpses of rural life in the past.

The general procedure for the dating of an event that has left its mark in the development of a peat bog is as follows: One or more diagrams are prepared from the bog in question, from sections as near the finding-place as possible, preferably including the find. If the find is an object that has been removed from the deposit, its exact location is ascertained by measurement and *controlled pollen-analytically.* Like the surfaces of recent bogs those of ancient ones were not necessarily absolutely flat, and we have no guarantee that any synchronous level is a horizontal plane in the deposit. Once the object has been removed and its impression in the deposit disappeared, even the most exact indications of the depth are only of limited value, not to mention information given in that unit of measure with which all peat investigators are acquainted: spades' depths ("mumps" CLAPHAM and GODWIN 1948). Besides, small objects frequently fall out of the peat cutting and are recovered in a secondary place—or in the peat drying grounds. In such cases no direct information is available. However, with the exception of highly polished stone and metal objects, most of those objects that are found in pollen-bearing deposits will contain in some crevice or hole sufficient material for analysis[1]. If the possibility of contamination can be ruled out, the pollen spectrum, or preferably spectra, from the object can be fitted into its proper place in the diagram of the deposit. The easiest way to carry out this process is to draw the spectrum near the edge of a slip of paper and slide this along the reference diagram until the place of best coincidence is found. Because of statistical uncertainty it is not possible to define the place exactly; a better understanding of the statistical possibilities is obtained if "zones of uncertainty" of both diagrams are indicated by shading on both sides of the curves.

In this way the place of the object in the local sequence and the local diagram can be established. In many cases this local diagram will be badly distorted by over-representation, selective destruction, etc., and the next problem is the fitting of the local diagram into the normal one. Only after that has been solved—and here again no fixed rules can be laid

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[1] According to circumstances of recovery the reliability of information referring to peat finds can be classified as follows:

A. Contamination improbable.
- A 1. Samples collected by specialist in the field at the time of recovery.
- A 2. Samples collected by specialist in recently recovered material. In this case samples must be taken from interior cavities, etc., not from the outside of the object, which may be contaminated during the handling by non-specialists.
- A 3. As the preceding, but sample collected by non-specialist after thorough instruction.

B. Contamination possible.
- B 1. As A 2-3, but the material has been recovered some time before and has in the meantime not been adequately protected.
- B 2. Metachrony possible between object and sediment (sinking down during embedding).

C. Contamination probable. The material has been recovered in too superficial layers (contamination by recent pollen), it has been buried in the deposit, the sediment is redeposited, the object has been found very long ago and kept in a collection, etc.

Pollen analysis of objects in the C category must be considered a waste of time, as no reliable information can be gathered from such material. The B type may give positive results, but one must be very careful in discussing their reliability. Before undertaking any pollen-analytical dating the investigator should decide about the reliability of information pertaining to circumstances of recovery and about chances of contamination.

down to cover all cases—can our object be dated in relation to the forest history of the region.

The majority of objects to be dated pollen-analytically are archaeological ones. In the preceding paragraphs we have sketched the procedure necessary to date such an object in relation to forest history. Necessary are: 1. Spectra from the object, 2. local diagram, and 3. regional diagram type. It follows that in a pollen-analytically unknown area very much work is connected with such a dating. If the regional diagram type has been worked out previously, the amount of work is greatly diminished, but even in such cases the dating of an object may involve the work of weeks or months. It may prove impossible to date objects found in bogs, the pollen contents of which are corroded and destroyed.

One should always have a definite problem in view before undertaking—or demanding—a pollen-analytical dating of any archaeological object. Such objects fall into two groups: 1. Those which cannot be dated by archaeological, i.e. typological methods. Such objects are e.g. wooden implements for which no typology has been established. If one can determine the position of such an object in relation to forest history, a relative chronology can be established. 2. Those objects the archaeological age of which is well known. Such datings are apparently of little interest to archaeologists and it is frequently difficult to persuade them to submit such objects for analysis. To pollen analysts the fitting in of such objects in the diagrams are of the greatest importance as they provide definite archaeological dates (in many cases referable to absolute chronology) to the different phases of forest history, i.e. to synchronous levels which can be recognised all over the area. A few objects of this type and of suitable age will be sufficient to date the main phases of forest history—and this in its turn works back again to the problems raised by the objects of the first group. Such objects can then be dated to archaeological periods, which is, of course, the aim, and need not be referred to forest history alone.

If one is certain that the spectrum from the object is pure, not contaminated with foreign peat during and after the uncovering, and if the zoning of the normal diagram has been carried out in a sensible manner, even an isolated spectrum may be of some value for dating objects the age of which cannot be ascertained in any other way. The spectrum can be referred to its zone and thus dated even if it is not possible to decide to which part of the zone it belongs.

There are many pit-falls in the pollen-analytical handling of archaeological objects. In many cases objects have been dropped accidentally either in the water or on the surface of a wet bog. If sinking down through the layers can be ruled out, the case is usually fairly simple. In other cases, however, the object has been put down in an artificial hole in the bog—and may even have been covered with old peat material. Unless the investigator is very careful, such cases may lead to grossly erroneous conclusions. If the object and the material for analysis are taken out of the peat wall by the pollen analyst, most pit-falls of this type should be detectable, but, especially in the case of bog dwellings, sequences may be so distorted by peat cutting etc. as to be uninterpretable without a very close, extremely time-wasting and rather tedious analysis of the whole cutting. It is naturally impossible to solve such problems by means of the peat sampler.

Properly dated refuse layers from a prehistoric dwelling are more valuable than a number of isolated objects. The refuse layer can usually be followed from the shore into the former lake or bog, where it dovetails with the ordinary strata. It is obvious that the dating of such strata is much safer than that of concrete objects, which may or may not have sunk down into or been buried in older deposits.

The practice of analysing objects that have been resting in museums for years and the exact finding-place of which cannot be ascertained, may give correct results, but it may also give directly misleading results. In any case the actual finders and the museum officials must control their disastrous desire to wash their objects, until it has been decided whether or not the find shall be submitted to pollen-analytical investigation. It is too late when all evidence has disappeared down the sink. It should be routine work of any archaeologist in whose charge a peat-bog find is placed, to take care that samples are secured for pollen-analytical investigation, even if this is not imminent. If it is not done, one is just as certain to throw away information as by excavating carelessly. Even if this additional information is of no value in that particular case, nobody can know beforehand whether or not it may become highly necessary.

The principles outlined above also pertain to finds of animals (or plants) that have perished naturally and the remains of which have been embedded in peat or sediment deposits. Some of the complications met with in archaeological work are of less importance in this case. On the other hand the danger of the objects' sinking down in the mud is certainly greater.

In other cases the events to be dated pollen-analytically manifest themselves in the sequence and form part of the latter. The hydrologic fluctuations and their climatic interpretation have been referred to above. Other cases are the changes of sediment types due to transgressions and regressions that cause alternation between lacustrine and marine deposits, in most cases with intermediary brackish-water deposits. The age of the contacts between sediments is determined pollen-analytically in the same manner as the age of objects, at first one establishes the place in the local sequence, then by means of the normal diagram the change is dated in relation to forest history.

If one can investigate a number of basins at different altitudes within a restricted area, the established age of different marine-lacustrine contacts will permit the investigator to construct a curve of displacement of the shore-line. Such curves are easier to construct in areas of predominant regression than in those of dominant transgression where most of the deposits in question will be submarine.—It should be noted that if a basin extends for some distance across the general isobase direction, isostatic movements will cause unilateral transgressions and regressions in those parts of the basin that are opposite to the outlet. Mutatis mutandis the same refers to basins without outlet, but in this case the phenomenon is complicated by the superposition of multilateral changes of level due to climatic fluctuations. In all cases, however, pollen analysis furnishes a much firmer factual foundation for shore-line investigations than can be obtained by other methods.

So far we have dealt primarily with pollen types of our categories A and B (p. 87). Those of type C also convey important information, first and foremost about the immigration of the flora. In an earlier chapter (p. 93) we have discussed that aspect of pollen analysis with regard to the A and B pollen types. For such species one can generally establish an *earliest* date of immigration, but it is difficult to decide if the first faint traces are due to long-distance transport or to local production. With type C pollen the case is generally the opposite: they produce so little pollen and it is so unsuitable for long-distance transport that one may be fairly certain that it has been produced locally. On the other hand its occurrence is so accidental that nothing can be concluded from its absence. Thus the find of such a pollen establishes the *latest* date of immigration. To quote one example: the fact that pollen grains of *Lonicera periclymenum* in Western Norway have not been found in pre-subboreal periods does not mean that the species has immigrated at that late date; on the contrary it must be judged fairly probable that it is an old member of our flora. Such "incidental" information about the occurrence of species that are not regular contributors to pollen rain suffer from many of the disadvantages that characterise macro-fossils as compared with the A and B pollen types, but nevertheless it may prove to be of the greatest value. This refers especially to such species that are otherwise rarely met with as fossils, but the pollen grains of which can be relied upon to appear if the species has been present and if a sufficiently large number of pollen grains are counted. *Viscum* in Denmark (IVERSEN 1941 p. 15) is a good example of this. Once the occurrence of a species outside its present area has been ascertained (by macro- and microfossils), one may draw climatic conclusions, provided the distribution of the species is conditioned by climate and not by non-climatic, e.g. historic, factors.

Various methods have been proposed for the transformation of cartographic to climatic data. We refer to IVERSEN (1944) which gives the most objective of the methods so far proposed. Unfortunately it is not possible to give an absolute answer to the questions of climatic inference from distribution data. Owing to the interchangeability of ecological factors, the answer will always have to be given in alternatives, but even then it may prove to be of the greatest value. Pollen analysis comes in as an important method here owing to the many distributional facts which can be inferred from the diagrams and analyses.

It is hardly feasible to enumerate all possible applications of pollen analysis. To a person who is able to interpret pollen diagrams botanically, the field of applicability is great and ever increasing. This pertains not only to fossil pollen—Quaternary as well as pre-Quaternary, in the latter case the specific identity of the individual pollen or spore types will be more or less uncertain—but it pertains to recent pollen as well. Recent pollen analysis is a very important aid in a number of sciences and techniques, honey investigations (ZANDER 1935-37), hay-fever investigations (WODEHOUSE 1935, 1945), pollination ecology (HØEG 1924), glaciology (VARESCHI 1942), etc. Problems of criminal investigation have also been solved by pollen analysis.

SOME OTHER MICRO-FOSSILS

A pollen-analytic preparation contains much material besides pollen grains: how much, depends on the nature of the deposit and the treatment of the sample. In acetolysed samples the quantity of extra material is frequently negligible and chiefly consists of spore walls etc. which have a chemical composition comparable to that of pollen exines. The chemical resistance of spore walls varies; whereas the spores of *Sphagnum* are easily corroded and to a great extent disappear by acetolysis, those of *Lycopodium* and *Botrychium* are extremely resistant, even more so than pine pollen.

It is obvious that there is no great difference in principle between spores and pollen grains, and spores should be counted when samples are analysed. In many cases the spore-producing species represent a separate area of vegetation, in which cases the spores are indispensable for the interpretation of vegetation. In other cases, however, the spores will be of strictly local origin. Owing to the position of the spore-producing organs (generally under a leaf, a pileus, etc.) cryptogam spores do not on the whole seem to be so well distributed in the air as are the pollen grains of wind-pollinated trees. Spore curves are therefore more local in origin and frequently very irregular. There are, however, important exceptions, e.g. *Pteris* in the post-glacial of western Europe.

Illustrations of spores of most European and a number of exotic *ferns* have been published in different connexions, i.a. in some of the publications mentioned previously, but illustrations are, as usual, of rather limited value. Some of the most indicative and easily recognised spores are regularly counted. In some vegetational types, e.g. as they occur in the late-glacial of Denmark, fern spores (*Dryopteris Linnaeana* C. Chr. *Botrychium* a.o.) are frequently produced in great numbers and certainly represent an important part of vegetation. There is no doubt that fern spores may in many cases supply the pollen analyst with additional information, they may even in some cases be included in the NAP and total diagrams.

Unfortunately in *Polypodiaceae* the outer layer of the exosporium which furnishes the diagnostically important characters, is very thin and loosely connected with the inner and heavier layer. It is frequently lost, and the resulting "bald" spore is with few exceptions (e.g. *Dryopteris Linnaeana*) indeterminable.

Spores of *Lycopodium* (some of which can be determined to species) and the easily recognised microspores of *Selaginella* should also be counted and may be of use for conclusions about the history of vegetation. The enormous spore production of *Lycopodium* must be taken into account.

Equisetum spores are frequently met with, especially in hydroseres in shallow lakes. They are spherical and resemble *Larix* pollen grains, but are usually provided with an outer, crumpled and colourless "envelope".

Whereas the spores of vascular cryptogams are to a certain extent known, those of the lower plants have with few exceptions been ignored by pollen analysts. *Sphagnum* spores are easily recognised as such, and the characteristic double teleuto spores of *Puccinia* are also old acquaintances of most pollen analysts together with the conidia of *Helotium Schimperi* (*Tilletia sphagni*), but the rest—and there are others even if they are in most cases less frequent—are generally neglected. Some of them may have important information to communicate.

Plant *tissue fragments* are especially important in peats, where they constitute most of the deposit. Very few of them survive acetolysis treatment, the object of which is, of course, to remove them. Easily recognised fragments like epidermis of *Carex* or *Phragmites* rootlets, *Sphagnum* leaves, etc. serve to determine the character of the mother formation. In those cases when tissue fragments are removed from the sample by chemical treatment one should always make a KOH preparation to obtain an idea of the original composition of the deposit.

Among the tissue fragments that can be recognised are stomatar cells of *Pinaceae*, but it is not known how far specific determination can be carried out in an area with many species. Other cuticular fragments can certainly be determined, and it is not improbable that a cuticular analysis similar to that developed by palaeobotanists could be used with advantage in micro-fossil analysis as well. However, little work has been carried out along these lines (cp. KATZ and KATZ 1933, ISTOMINA, KORENEWA and TJUREMNOW 1938).

Plant *trichomes* are in many cases well preserved and easily determinable. In "Pollen analysis circular" nr. 3 L. R. WILSON has made sketchy illustrations of some of those encountered in N American deposists. Among those important in Europe are the easily recognised peltate hairs of *Hippophaë rhamnoides*. Such tissue fragments corroborate pollen finds and show that the species in question grew very near the locality of the deposit. In cases where the representation of a species in a pollen diagram may be due to long-distance transport, the occurrence of such fossils as trichomes or stomatar cells is of great value as giving evidence of local origin.

Different *algae* may form important constituents of the deposit, *Scenedesmus* gyttja, *Pediastrum* gyttja, and, above all, *Cyanophyceae* gyttja are well-known types. *Botryococcus* is rarely missing in limnic deposits, etc.

More important than these are, however, the *diatoms*. They occur practically everywhere in open water or very moist places, and their great importance is due to this fact as well as to the facts that diatoms are (1) very sensitive to the chemical composition of the medium in which they live, and (2) in the possession of siliceous "shells" (frustules) that are very resistant against decay—even if they are easily destroyed by mechanical action in sandy deposits. Above all diatoms are indispensable for the analysis of the halinity of the mother formation, the different species being more or less exclusively bound to a specific degree of halinity. Such halinity analyses are indispensable in the investigation of former positions of the shore-line.

A complete diatom analysis is a very complicated job that can be undertaken by a few specialists only. The average pollen analyst will have to rely on the occurrence and distribution of a small number of easily recognisable indicator species. Their occurrence can be expressed as percentages of a certain basic sum, similar to the occurrence of pollen grains. As some diatoms, especially the epiphytic ones, are highly gregarious, the basic sum must be made up with some care. One good basic sum is formed by the naviculoid diatoms, which are easily recognised, present in all halinity types, and show no marked tendency to mass-occurrence. The number of shells of indicator species are then expressed in percentages in relation to the total number of naviculoid diatoms of the sample.

The preparation methods for diatom analysis vary according to the ultimate object of the analysis. For such simple analyses as will be carried out by most pollen analysts the following method will be sufficient (for other methods cp. Brander 1936):

1. A small quantity of substance is boiled (bleached) with perhydrol in a beaker until practically all organic matter has been removed.

2. The siliceous matter is concentrated by centrifuging. If coarse sand particles are present, they can be concentrated in the middle of the beaker bottom by careful rotation of the beaker with the hand. The remaining material is then drained off in suspension.

3. After being washed with water on the centrifuge, the diatom suspension is transferred to cover-slips and left to evaporate at ordinary room temperature. This will give more even preparations than evaporating over a flame. The addition of some alcohol to the suspension will make it easier to spread it over the whole of the cover-slip. The proper concentration of the suspension must be learned by practice.

4. To be clearly visible the diatom shells must be embedded in a matrix with sufficiently high refractive index. Styrax resin forms a very convenient matrix, hyrax is even better but less easy of access. It is best applied as a solution of resin in xylene or some similar fluid, which is afterwards evaporated over a very weak flame. When the resin is sufficiently thick, the cover-slip with the adherent diatoms is placed on a slide and is ready for examination.

The diatom literature is, unfortunately, widely scattered, and there is no modern comprehensive flora. For European workers HUSTEDT's two works (1930 and 1930-37) are the most convenient. However, the first contains no truly marine species and the second so far covers only part of the diatom system.

Animal remains are very frequently met with in pollen-analytic preparations. Chitinous skeletal remains especially are often beautifully preserved.

Rhizopods. Monothalamine foraminifera belong to fresh water, and their easily recognised remains are especially charateristic of *Sphagnum* peat. They have been dealt with by HOOGENRAAD (1935). The calciferous shell of the marine polythalamine species usually disappears by fossilification, but in some cases an inner *Discorbina*-like chitinous shell remains and gives evidence of the marine origin of the deposit.—Theoretically remains of other rhizopods (*heliozoa, radiolaria*) should be found as well, but so far they have played no practical role.

Remains of sponges (spiculae), tardigrades, *acarinae, entomostraca,* chironomids, etc. are frequently met with, but very few attempts have been made at a systematic treatment of these micro-fossils, which are generally neglected by the pollen analyst. The so-called *Hystricosphaeridae* ("Hystrix"), marine cysts of unknown origin, are in some cases important as indicators of an inter- or preglacial origin of part of the material of the fresh-water deposit in question (cp. IVERSEN 1936).

It is obvious that pollen-analytic samples in some cases include an accidental small macro-fossil, big spores (*Characeae, Selaginella* macrospores) or small seeds. It lies outside the scope of the present work to deal with these objects.

Whereas mineral particles in pollen-analytic samples are generally a nuisance, the occurrence of volcanic dust is of great importance, offering means of dating and correlating deposits very exactly, cp. investigations in Iceland by THORARINSSON (1944) and in Fuegopatagonia by AUER (1941).

POLLEN KEYS

In the following chapters we present 3 keys. viz.:

A. A master key defining the 22 groups into which all pollen grains can be arranged as far as we know. A somewhat different edition of this key has been published in "Pollen and spore circular" nr. 26. It will be seen that some of the concepts have changed slightly since then.

B. A key comprising those pollen types that can be expected in North West European pollen analyses. This key is based on a thorough investigation of the pollen of more than 1000 plant species, embracing among others the great majority of all recent trees and shrubs, water- and bog plants, and windpollinated plant species within the area. The key comprises also some of the more important tertiary pollen types, which appear as secondary pollen in lateglacial clays, and some cultivated plants and weeds.

C. A discussion of a perforated multiple entry key.

The beginner especially cannot expect to be able to use these keys for immediate identification of unknown pollen types. We have frequently been obliged to rely on subtle characters, which can only be perceived after some practice (and with a first-rate optical equipment!). One should therefore prepare a series of known pollen types and follow them through the keys. Especially within the keys for tricolpate and tricolporate grains the differentiation requires great attention. We want to emphasise that unfortunately critical pollen types cannot be determined in other ways. If one is not able to use the characters employed in the keys (or characters which are equally subtle) one cannot identify such pollen grains. Some pollen types can easily be recognised without that; and in our flora fortunately most of the quantitatively important types can be distinguished from each other without great difficulty. It is, of course, perfectly possible to work on such grains alone, but if more exact results are required, there is no alternative but to make accurate identifications, and to take into account all possible "doubles". If they cannot be ruled out, the identification is of no value whatsoever. One should always make such statements that the reader can judge about the reliability of identifications.

Our key B is not exhaustive, i.e. it is in many cases possible to identify smaller units than those in the key, which practically always lead to the family, sometimes to the genus or species. In a few cases we have proposed alternatives (e.g. *Myrica-Corylus)* either because it is only possible to distinguish between the units after long experience if they can be separated at all, or because we have considered the differentiation of secondary importance. If it is desirable to carry out more exact identifications than our key permits, it is decidedly more practical to make special keys for the occasion than to use a general one. An investigator is generally able to eliminate a number of species within the group because their occurrence at that particular place and date is extremely unlikely, e.g. it is impractical to make a complete key for composites because in each locality a limited number only may be expected.

Our key B is intended for North West Europe, outside this area it is of limited value. Keys for general use in other regions have been published e.g. by WODEHOUSE (1935), CRANWELL (1942), SELLING (1947). Besides a number of special keys dealing with a single family or smaller group have been published. We refer to some of them in the text. The illustrations published by ERDTMAN (1933), WODEHOUSE (1935), and ZANDER (1935) may serve as a help in the identification of the general shape of the pollen types in question. (E), (W) and (Z) in the key refer to these publications.

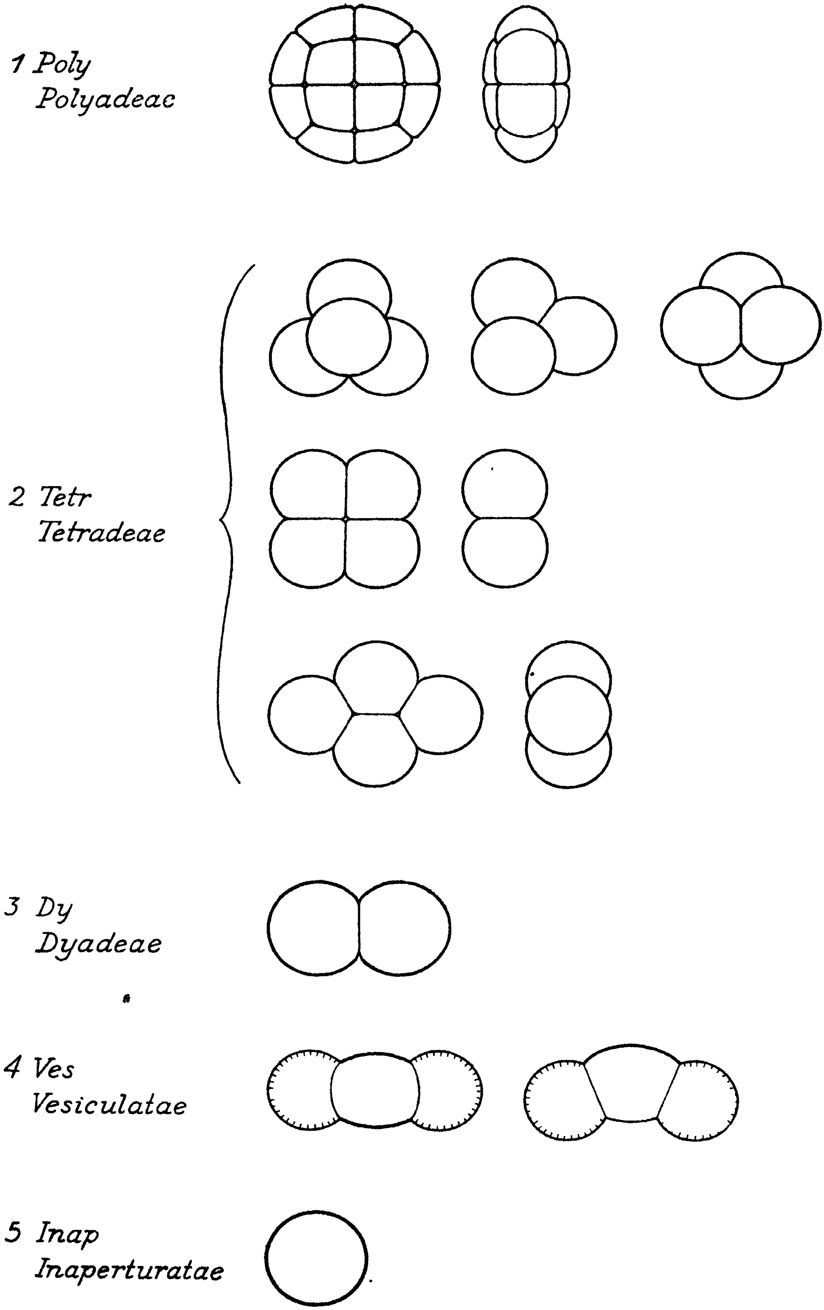


PLATE V. Principal types of pollen grains : 1-5.
Drawings by B. BRORSON CHRISTENSEN from IVERSEN & TROELS-SMITH (1950).

MASTER KEY TO POLLEN CLASSES

- A. Pollen grains united in groups.
  - *B.* More than 4 grains in each group …… 1 *polyads*
  - *BB.* Groups of 4 …… 2 *tetrads*
  - *BBB.* Groups of 2 …… 3 *dyads*
- AA. Pollen grains free from each other.
  - B. Apertures 1 or none.
    - C. With air-sacks …… 4 *vesiculate*
    - CC. No air-sacks.
      - D. No furrow.
        - E. Pore rudimentary or absent …… 5 *inaperturate*
        - EE. One distinct pore present …… 6 *monoporate*
      - DD. One furrow present …… 7 *monocolpate*
  - BB. Two or more distinct apertures.
    - C. Lacunae (pseudocolpi or pseudopores) absent.
      - D. Furrows present, no free pores.
        - E. Furrows fused to spirals, rings, etc. …… 8 *syncolpate*
        - EE. Furrows not fused.
          - F. Two furrows …… 9 *dicolpate*
          - FF. More than two furrows.
            - G. Furrows without distinct pores or transversal furrows.
              - H. All furrows meridional.
                - I. Three furrows …… 10 *tricolpate*
                - II. More than 3 furrows …… 11 *stephanocolpate*
              - HH. Some or all furrows not meridional 12 *pericolpate*
            - GG. Furrows with pores or transversal furrows (sometimes missing in one or two furrows).
              - H. All furrows meridional.
                - I. 3 furrows …… 13 *tricolporate*
                - II. More than 3 furrows …… 14 *stephanocolporate*
              - HH. Some or all furrows not meridional 15 *pericolporate*
      - DD. Free pores present, no furrows.
        - E. Pores restricted to the equatorial area.
          - *F.* 2 pores …… 16 *diporate*
          - *FF.* 3 pores …… 17 *triporate*
          - *FFF.* More than 3 pores …… 18 *stephanoporate*
        - EE. Pores outside the equatorial area …… 19 *periporate*

CC. Lacunae present.
D. Pseudopores present .... 20 *fenestrate*
DD. Pseudocolpi present.
E. Some furrows with, others without pores, free pores absent .... 21 *heterocolpate*
EE. Free pores present .... 22 *extraporate*

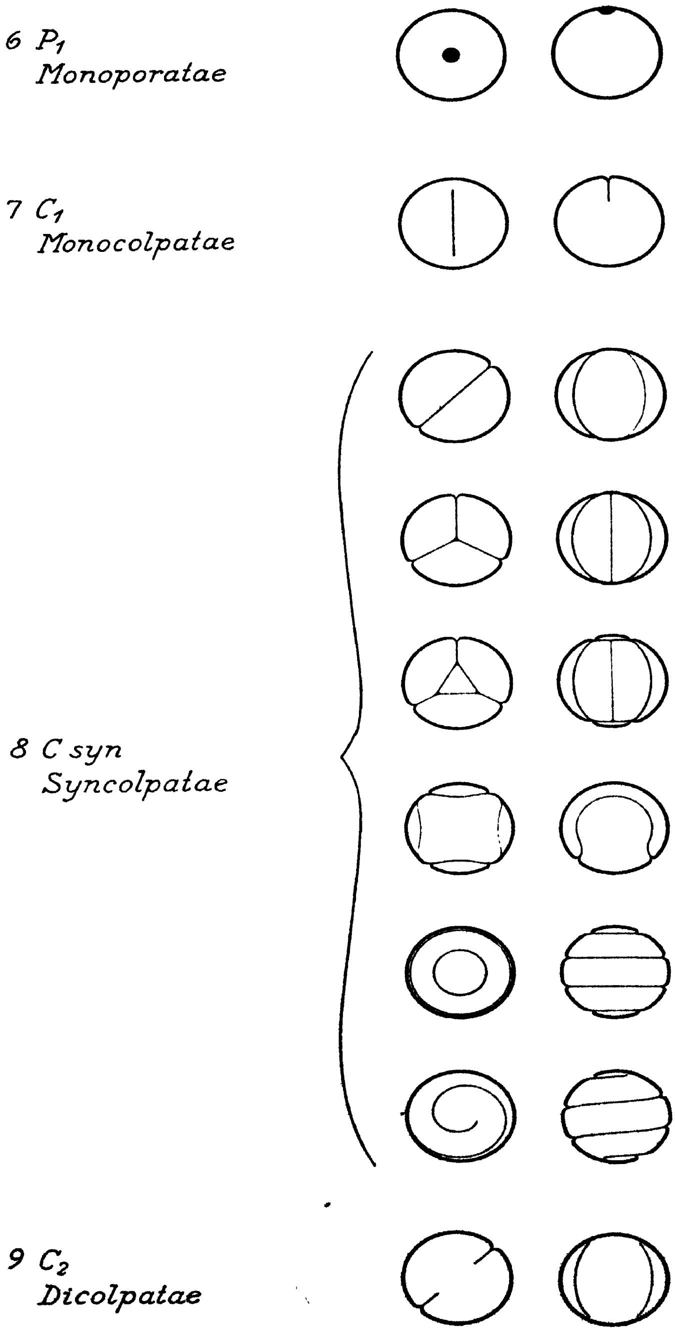
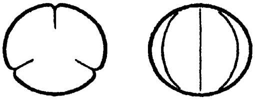
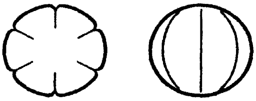


PLATE VI. Principal types of pollen grains : 6-9.
Drawings by B. BRORSON CHRISTENSEN from IVERSEN & TROELS-SMITH (1950).

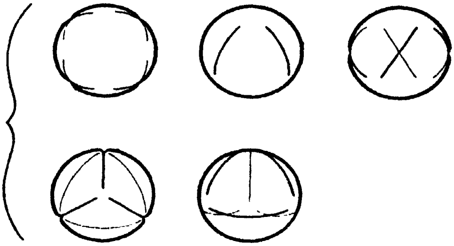
10 C_3
Tricolpatae



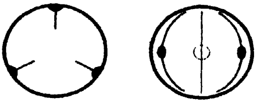
11 Cstp
Stephanocolpatae



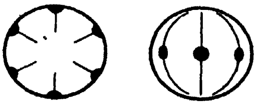
12 Cperi
Pericolpatae



13 C_3P_3
Tricolporatae



14 CPstp
Stephanocolporatae



15 CPperi
Pericolporatae

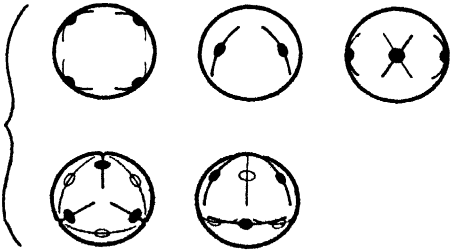


Plate VII. Principal types of pollen grains : 10-15.
Drawings by B. Brorson Christensen from Iversen & Troels-Smith (1950).

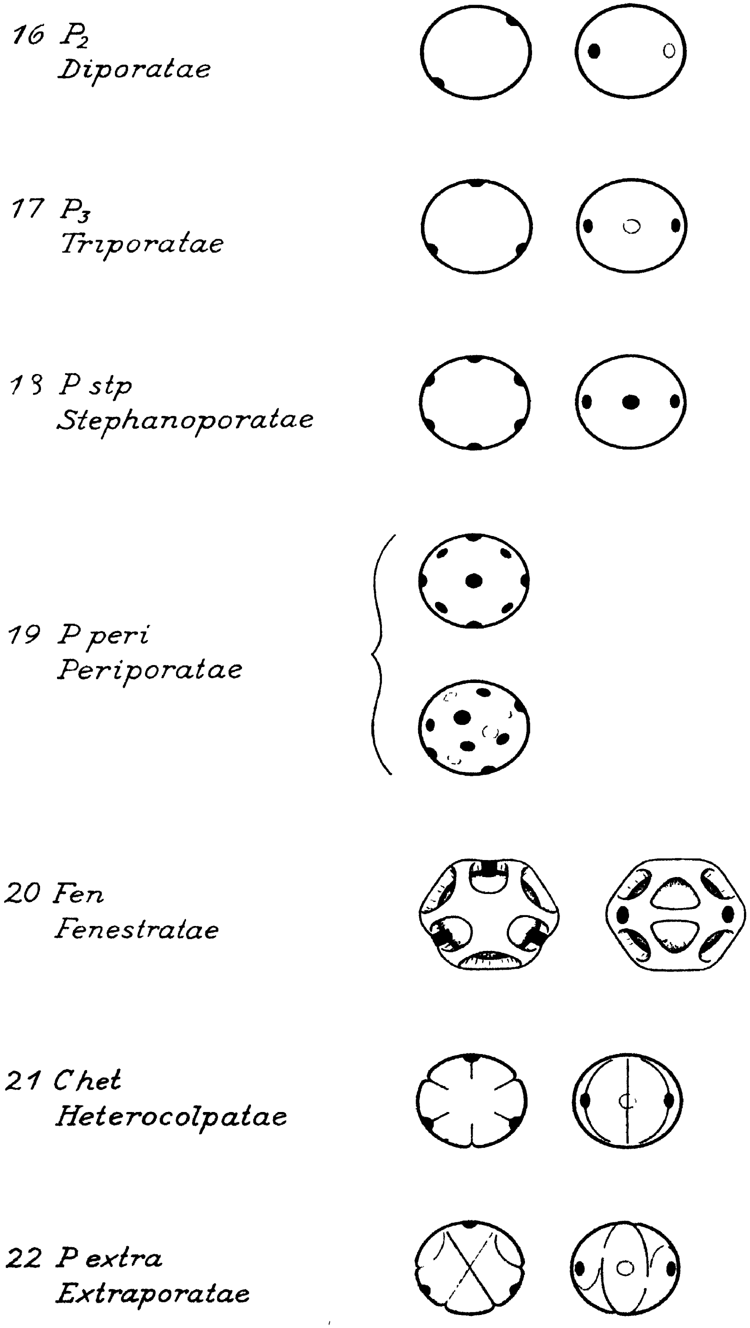


PLATE VIII. Principal types of pollen grains.
Drawings by B. BRORSON CHRISTENSEN, from IVERSEN & TROELS-SMITH (1950).

KEY TO NW EUROPEAN POLLEN TYPES

This key follows the divisions of the master key above. We emphasize that in many cases the keys are not dichotomous, which must be kept in mind when they are to be used. Index letters are in italics when there are more than two entries in the same group.

Dimensions refer to measurements made on recent pollen that has been acetolysed after KOH-treatment.

In order to carry out an identification of an unknown pollen grain it is generally necessary to investigate it from all angles. Pollen grains should therefore be embedded in a liquid medium where they can be turned to show all faces. If the medium is solid and the grains locked in a definite position, the identification will in some cases prove impossible.

1. Polyads.

E. g. *Acacia*. No example within the area.

2. Tetrads.

Inaperturate, exine extremely thin, smooth	***Juncaceae*** (W)
Monocolpate	***Helleborine palustris***
Tricolpate	***Ericales***[1]
Monoporate	***Typha latifolia*** (E, W)
Triporate	***Epilobium*** (s. l.)
Stephanoporate, echinate	***Drosera*** (E, W)

3. Dyads.

Scheuchzeria (E) is the only known example. Teratological grains of many species may occur as dyads. Fægri once observed a specimen of ***Empetrum nigrum*** which produced dyads exclusively.

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[1] Cp. Overbeck 1934.

4. *Vesiculate.*

Pinaceae and ***Podocarpaceae*** are the only known representatives of this group, cp. the comprehensive treatment in WODEHOUSE (1935).

5. *Inaperturate.*

(Grain heteropolar, one pole echinate-clavate, the other psilate-verrucate—cp. monoporate!	***Nymphaea*** (E, W))
Grains not heteropolar	
A. With a well-marked exitus papilla	***Taxodiaceae*** (E, W)
AA. No exitus papilla.	
B. Psilate.	
C. Grain tectate, irregular, pear-shaped, with rudimentary pores	***Cyperaceae*** (E, W)
CC. Grains intectate, usually regular	
D. Grain very big, usually more than 60 μ	***Larix, Pseudotsuga***
DD. Grain smaller, usually ruptured (cp. *Juniperus*)	***Cupressus*** (E)
BB. Scabrate-gemmate.	
C. With scattered, deciduous gemmae; exine normally ruptured	***Juniperus***
CC. Projections crowded.	
D. Projections uniform. Intectate (cp. *Cyperaceae*!)	***Populus*** (E)
DD. Sculpturing slightly irregular	***Taxus*** (E)
BBB. Verrucate; cavate; grain big, more than 60 μ	***Tsuga***
BBBB. Echinate	***Hydrocharis*** (E)
BBBBB. Reticulate-clavate.	
C. Grain subcylindric; sculpturing finer at the ends	***Ruppia*** (W)
CC. Grain subsphaeroidal; sculpturing uniform.	
D. Granules widely separated; reticulum indistinct	***Potamogeton sect. Coleogeton***[1]
DD. Granules closely spaced; reticulum distinct.	
E. Granules in most cases perceptible; reticulum slightly irregular	***Potamogeton sect. Eupotamogeton*** (E, W)
EE. Granules imperceptible; reticulum uniform	***Triglochin***

6. *Monoporate.*

(With a well-marked exitus papilla	cp. ***Inaperturate***)
Without exitus papilla.	
A. With distinct annulus; psilate-scabrate	***Gramineae***[2]
AA. Annulus absent.	

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[1] ***P. pectinatus*** and ***P. filiformis.***

[2] Cp. FIRBAS 1937.

B. Reticulate .... *Typhaceae* (E)[1]
BB. Not reticulate.
C. With deciduous gemmae; exine generally ruptured; pore faint .... *Juniperus*
CC. Not so.
D. Projections (spines) uniform, 1½ μ long, no operculum .... *Lemna*
DD. Projections polymorph (echini, clavae, baculi or verrucae); operculum present .... *Nymphaea* (E, W)

7. *Monocolpate.*

A. Verrucate.
B. Verrucae uniform .... *Sciadopitys* (E)
BB. Verrucae not uniform .... *Nymphaea*
AA. Psilate—foveolate—scabrate.
B. Furrow narrow, distinct .... *Liliaceae* p. p.
BB. Furrow ± broad, ± indistinct .... *Araceae* p. p.
AAA. Reticulate.
B. All lumina less than 1 μ .... *Liliaceae* p. p.
BB. Some lumina more than 1 μ.
C. Size of lumina uniform.
D. Grains > 70 μ .... *Iris* (E)
DD. Grains < 50 μ .... *Butomus* (E)
CC. Size of lumina variable .... *Liliaceae* p. p. (Z)
AAAA. Echinate-clavate (with short, crowded, barely perceptible projections between the long ones).
B. Sculpturing regular, echinate.
C. Long spines ca. 10 μ long .... *Nuphar* (E)
CC. Long spines ca. 3 μ long .... *Stratiotes* (E)
BB. Sculpturing irregular, echinate-clavate .... *Nymphaea* (E, W)

8. *Syncolpate.*

A. Furrows fused to spirals .... *Eriocaulon* (E)
AA. Furrows (2) fused to a single ring.
B. Ring broad with distinct granules .... *Ranunculus Ficaria*
BB. Ring narrow, no granules .... *Pedicularis* p. p.
AAA. Furrows not fused to spirals or a single ring.
B. With 3 or 6 meridional furrows; grain regular.
C. With 3 furrows; grain distinctly triangular.
D. With small transversal furrows; meridional furrows very narrow .... *Myrtaceae* (E)

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[1] The two genera are difficult to separate in fossil material, as some *Sparganium* species are extremely like *Typha angustifolia.*

DD. No transversal furrows.
E. Scabrate .... *Loranthus*
EE. Rugulate .... *Nymphoides*
CC. With 6 furrows .... *Sanguisorba officinalis*

BB. Furrows not meridional; rather irregular.
C. Pitted; furrows narrow, no pores .... *Berberidaceae*
CC. Not pitted; furrows fused in pairs, each pair with 2 distinct pores .... *Ribes*

9. *Dicolpate.*

A. Furrows broad, indistinct; exine psilate, perforate ... . *Calla palustris*
AA. Furrows narrow; exine reticulate, intectate.
B. Granules distinct .. .. *Tamus*
BB. Granules indistinct . ... *Tofieldia*

10. *Tricolpate.*

For the sake of convenience this key is divided in sections according to the sculpturing type. ***Verrucate*** grains are restricted to ***Ranunculus*** and ***gemmate*** to ***Linum usitatissimum***. The following sculpturing types are represented in the key: a) psilate, b) scabrate, c) clavate, d) echinate, e) rugulate-striate, and f) reticulate. Cp. also the unique, cavate, crested pollen grain of *Trapa* (E).

It should be remembered that tricolpate and tricolporate pollen types have a tendency to occur in a pericolpate modification with 6 or more furrows. Sometimes the hexacolpate grain becomes by reduction tetracolpate, cp. WODEHOUSE (1935 p. 170). Stephanocolpate and stephanocolporate grains may become tricolpate or tricolporate by reduction. The opposite change seems to be more rare.

a. Psilate.

A. Structure of middle part of each intercolpium finer than nearer the edges, intercolpium flattened; furrow narrow, without granules .... *Melampyrum*
AA. Not so.
B. Furrow without equatorial constriction.
C. Columellae indistinct or ± united in irregular groups *Scrophulariaceae*
CC. Columellae isolated, distinct.
D. Columellae branched; grain $> 50\ \mu$ .... *Convolvulus*
DD. Columellae not branched; grain $< 50\ \mu$.
E. Tectum imperforate .... *Ranunculus* p. p.
EE. Tectum minutely perforate .... *Spergularia* (E)
BB. Furrow with equatorial constriction.
C. Edge of furrow (in equatorial projection) rough or undulating[1] .... *Rosaceae* (E)

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[1] Caused by folding in of the relatively thick exine into the furrow.

C. Edge of furrow straight.
D. Exine pitted.
E. Columellae perceptible .... *Lobelia, Scrophulariaceae (Digitalis* type)
EE. Columellae not perceptible .... *Elatine*
DD. Exine not pitted.
E. Both polar areas medium (index > 0.25) .... *Myricaria*
EE. At least one polar area small.
F. Grains distinctly heteropolar, less than 25 μ *Gratiola*
FF. Grains slightly heteropolar, more than 25 μ *Viola*

b. Scabrate.

A. Operculate.
B. With margo (exine thinner near furrow) .... *Teucrium*
BB. Margo absent (exine slightly thicker near furrow) ... *Saxifraga (hirculus* type) (E)
AA. Inoperculate.
B. Sculpturing irregular, scabrate-verrucate.
C. Polar area medium-great (index higher than 0.35) . . *Quercus* (E)
CC. Polar area smaller .... *Ranunculaceae* p. p.
BB. Sculpturing uniform; minute, regularly scattered spines.
C. Furrow with equatorial constriction; with distinct costae colpi .... *Cornus* (E)
CC. Furrow without equatorial constriction or costae colpi
D. Columellae forming an indistinct reticulum on the lower surface of tectum .... *Papaver* (E)
DD. Columellae evenly distributed, no reticulum on lower surcace of tectum .... *Ranunculaceae* (*Caltha* type)

c. Clavate.

A. Clavae branched, half-way out fused to a reticulum; grain very big (more than 80 μ) .... *Geranium* (E)
AA. Clavae not branched.
B. Margo distinct; clavae polymorph, small clavae predominantly in margo, ca. ¼ of the large ones .... *Ilex* (E)
BB. Margo absent.
C. Clavae dimorph, a few large ones regularly scattered between densely crowded ones of ca. ½ their height; the lower frequently fused to a tectum .... *Viscum*[1]
CC. Clavae uniform; no tectum.
D. Endexine as thick as or thicker than height of clavae; outer face of clavae flattened, arrangement extremely regular .... *Linaceae*
DD. Endexine thin; sculpturing less regular .... *Callitriche*

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[1] Cp. IVERSEN 1941.

d. Echinate.

- A. Spines constricted basally ...... *Rubus chamaemorus* (E)
- AA. Spines not constricted basally.
  - B. Polar area medium; each spine on a shield-shaped projection ...... *Valeriana* (E)
  - BB. Polar area great (index > 0.5); spines not on projections.
    - C. Exine more than 5 μ thick; very fine, crowded spines between the coarse ones ...... *Dipsacaceae* (E, Z)
    - CC. Exine less than 5 μ thick; smooth between the spines.
      - D. Columellae densely crowded, indistinct ...... *Linnaea* (E)
      - DD. Columellae distinct, their lower parts separated *Lonicera*

e. Rugulate-striate.

- A. Furrow granulate, inoperculate, regularly boat-shaped, without equatorial constriction.
  - B. Sculpturing fine.
    - C. Striate.
      - D. Vallae predominantly meridional ...... *Acer* (E, W)
      - DD. Vallae in equatorial area not meridional ...... *Saxifraga* (*oppositifolia* type) (E)[2]
    - CC. Sculpturing very fine, direction of vallae variable . . *Trollius*
  - BB. Vallae coarse, diffuse; minutely echinate ...... *Ranunculus* p. p.
- AA. Furrow equatorially constricted or ruptured.
  - B. Inoperculate ...... *Rosaceae* p. p.
  - BB. Operculate.
    - C. Exine medium (less than 3 μ thick) ...... *Saxifraga* (*cernua* type)
    - CC. Exine thick (3-4 μ thick) ...... *Alchemilla alpina*

f. Reticulate.

- A. Tectate (cp. *Salix polaris* type), columellae minute, sometimes indistinct, evenly distributed.
  - B. Furrows with equatorial constrictions or indistinct pores *Papilionaceae* p. p.
  - BB. Furrows without constrictions or other irregularities ... *Labiatae* (*Galeopsis* type)[1]
- AA. Intectate (lumina sometimes with isolated granules).
  - B. Lumina less than 1 μ (visible in immersion objectives only!), cp. *Sambucus nigra*.
    - C. Sculpturing slightly irregular, limb rough ...... *Limosella*
    - CC. Sculpturing uniform, limb smooth.
      - D. Polar area tectate, perforate ...... *Chrysosplenium*
      - DD. Sculpturing of polar area not different ...... *Saxifraga* (*nivalis* type)[2] (E), *Samolus*, *Hypericum*

---

[1] Plate IV: 6-8. Cp. Risch 1940.

[2] Arctic-alpine species!

BB. At least some lumina more than 1 μ.

C. Grains large (more than 50 μ).

D. Granules not branched, echinate; furrows long; polar area index ca. 0.5 .... *Plumbaginaceae*[1]

DD. Granules branched, top smooth; furrow short; polar area very great (index more than 0.75) ... *Geraniaceae* (E)

CC. Grains smaller.

D. Margo present.

E. Muri with 1 row of coarse granules; exine 3-4 μ thick; polar area index 0.4-0.5 .... *Ligustrum* (E)

EE. Granules minute; exine thinner.

F. Furrows with pronounced equatorial constrictions, sometimes bridge-like. Endexine thick .... *Sambucus*

FF. Furrows without or with less distinct constrictions, endexine thinner .... *Salix* (E)[2]

DD. Margo absent

E. Furrows short; polar area rather great (index more than 0.4).

F. Granules minute, forming a genuine reticulum, lumina uniform.

G. Furrow with granules .... *Platanus* (W)

GG. Furrow without granules .... *Fraxinus* (E)

(FF. Granules distinct, isolated, but may appear as a reticulum under objectives with low aperture .... *Callitriche*)

EE. Furrows long; polar area smaller.

F. Furrows not constricted equatorially; granules very distinct, only their topmost parts united in a reticulum .... *Cruciferae* (E)

FF. Furrows with equatorial constriction, frequently with an equatorial bridge; granules minute .... *Hottonia*

11. Stephanocolpate.

A. Psilate-scabrate.

B. Furrows short, pore-like, with thickened rim . ... cp. *Stephanoporate*

BB. Furrows longer, no thickened rim.

C. 6-10 narrow furrows .... *Rubiaceae* (E)

CC. 4-6 broad furrows .... *Hippuris* (E)

AA. Reticulate.

B. Polar area great, granules indistinct.

C. Grain regular, intectate; 5-10 furrows .... *Primula*

---

[1] IVERSEN 1940, SZAFER 1945.

[2] The *Salix polaris* type differs in having rather irregular muri with knob-like thickenings, isolated granules in lumina coarser than usual.

CC. Grain irregular, tectate; 4 furrows ……………… *Impatiens* (Z)
BB. Polar area medium, granules often distinct ……………… *Labiatae* p. p.[1]

12. Pericolpate.

A. Reticulate.
B. 30 short furrows; tectate ……………… *Polygonum amphibium*[2]
BB. 4-6 furrows; intectate ……………… cp. *10. Tricolpate*
AA. Not reticulate.
B. 12 furrows; columellae finer near the furrow ……………… *Montia*
BB. 4-12 furrows; columellae uniform.
C. Sculpturing irregular, rugulate-verrucate-scabrate; tectum non-perforate ……………… *Ranunculus* p. p.
CC. Sculpturing regular, scabrate with minute spines and pits[3] ……………… *Spergula arvensis*

13. Tricolporate.

Together with the tricolpate grains these are the most cumbersome of the list, and the key presumes a very close observation. Unfortunately a certain subjectivity cannot be avoided, and some readers may disagree with our treatment of some species or other. In many cases we have endeavoured to cover all opinions by entering the same pollen type in different places in the keys. We want to emphasize that some of the types placed by us among the tricolpate with equatorial constriction of the colpus might perhaps with the same right be considered tricolporate. The constriction is in itself an indication that the colpus membrane is pierced in the exitus.

For the sake of convenience this key is divided into sections according to the sculpturing type, viz. a) psilate-scabrate, b) echinate, c) striate-rugulate, and d) reticulate-foveolate.

a. Psilate-scabrate.

A. Operculate, polar area great ……………… *Sanguisorba minor*
AA. Inoperculate.
B. With costae equatoriales (and transversal furrows).
C. Exine very thick (more than 4 μ); columellae coarse, branched, equatorial limb pronouncedly triangular ……………… *Centaurea cyanus* type (Z)
CC. Exine thinner; columellae finer ……………… *Polygonum convolvolus* type[2]

---

[1] Cp. Risch 1940. *Brunella* (tectate) and sections *Monardeae* and *Satureieae* (intectate).

[2] Cp. Hedberg 1946.

[3] By focusing on the outer part of the exine one sees the spines as bright points, the pits as dark ones *at the same time*. This is the only safe criterion for *Spergula* (visible under immersion objectives only!)

- BB. Costae equatoriales absent or indistinct, with or without transversal furrow.
  - C. Thickness of ektexine varying, thickest in the median of the intercolpium at different latitudes (sometimes in the polar area); grain consequently angular, equatorial limb subtriangular; grain often prolate, usually prismatic .... *Umbelliferae* (E)
  - CC. Not so.
    - D. With transversal furrow.
      - E. Endexine thicker than ektexine, transversal furrow narrow .... *Glaux*
      - EE. Endexine not as thick as ektexine.
        - F. Prolate.
          - G. Polar area index more than 0.4 . . . . *Lotus*
          - GG. Polar area index less than 0.4 .... *Castanea* (E)
        - FF. Subsphaeroidal. ....
          - G. Grain medium, ± apiculate, intercolpium flattened .... *Rhus* (E)
          - GG. Grain small (< 25 μ).
            - H. Micro-echinate, pore scarcely protuberant .... *Filipendula* (E)
            - HH. Smooth; pore distinctly protuberant .... *Solanum dulcamara*
    - DD. No transversal furrow.
      - E. Intercolpium flattened or concave; equatorial limb subtriangular.
        - F. Columellae distinct; grain 30-40 μ; pore large, 4-5 μ .... *Nyssa*
        - FF. Columellae indistinct; grain 20-30 μ ...... *Frangula alnus* (E)
      - EE. Intercolpium convex.
        - F. Furrow edged by heavy costae colpi; grain regularly micro-verrucate .... *Cornus*
        - FF. Not so.
          - G. Pore distinct, elongated equatorially.
            - *H*. Pore protuberant; grain scabrate; polar area small .... *Hippophaë* (E)
            - *HH*. Pore protuberant, with equatorially elongated vestibulum; polar area great .... *Ludwigia*
            - *HHH*. Pore not protuberant, psilate, polar area great .... *Lotus*
          - GG. Pore isodiametric or indistinct.
            - H. Grain more than 30 μ.
              - I. Prolate, exine thick .... *Polygonum* (*bistorta* type)[1]

---

[1] Cp. HEDBERG 1946.

II. Subsphaeroidal, exine medium ... *Fagus* (E)
HH. Grain less than 30 μ.
I. Exine thick, micro-echinate .... . *Artemisia*[1]
II. Exine medium, psilate.
J. Furrow slit-shaped .... *Rumex* (*Oxyria* type)
JJ. Furrow boat-shaped, grain ca. 15 μ .... *Tillaea*

b. Echinate.

Bases of spines constricted .... *Rubus chamaemorus* (E)
Bases of spines broad .... *Compositae* (*tubuliflore* type) (W)

Within this type a further differentiation is possible by taking into account presence of transversal furrows (*Centaurea jacea* type), the relation between the monogranulate apices and the polygranulate bases of the spines, character of columellae, the mutual distance between spines, whether cavate or not, etc. Whereas most *Liguliflorae* pollen grains are fenestrate, those of *Scorzonera humilis* are completely covered. They are easily recognised by the arrangement of spines corresponding to the pattern of crests in the ordinary *Liguliflorae* pollen.

c. Striate-rugulate.

A. With transversal furrow.
B. Apiculate; costae transversales distinct .... *Rhus*
BB. Non-apiculate; no costae transversales .... *Rosaceae* (*Geum* type)
AA. Transversal furrow absent.
B. Operculate .... *Rosaceae* (*Potentilla* type)
BB. No operculum.
C. Pores indistinct; furrows frequently with equatorial constriction.
D. Vallae straight, forming intercrossing groups (immersion objective!). Cp. plate II, 1 .... *Crassulaceae*
DD. Vallae curving.
E. Arrangement of columellae coincident with sculpturing pattern .... *Rosaceae* s. l.
EE. Columellae evenly distributed .... *Gentianaceae*
CC. Pore distinct.
D. Furrow with coarse, spine-like granules .... *Aesculus*
DD. Furrow without coarse granules.
E. Oblate; polar area great; finely rugulate ...... *Ludwigia*
EE. Not oblate; polar area small; striate.
F. Apiculate .... *Helianthemum*
FF. Non-apiculate .... *Gentiana pneumonanthe* (E), *Swertia*

---

[1] Cp. Erdtman 1949.

d. Reticulate.

- A. Intectate.
  - B. Furrow interrupted by equatorial bridge (cp. *Sambucus nigra*!).
    - C. With transversal furrow; granules almost isolated, only outermost ends united to an indistinct reticulum ...... *Mercurialis*
    - CC. Indistinct pore; granules united in a fine, but distinct reticulum, only their bases isolated .... *Hottonia*
  - BB. No transversal bridge across furrow.
    - C. No transversal furrow, pore generally meridionally elongated or isodiametric.
      - D. Pore broader than furrow.
        - E. Equatorial limb circular; polar area great; margo absent .... *Rumex sect. acetosa*
        - EE. Equatorial limb subtriangular, polar area small, margo present (cp. *Rhamnus*!) .... *Vitis*[1]
      - DD. Furrow as broad as or broader than pore.
        - E. Grain large (more than 40 μ) .... *Gentiana* (*campestris* type)
        - EE. Grain smaller (less than 40 μ).
          - F. Lumina much smaller at the poles .... *Parnassia*
          - FF. Lumina uniform.
            - G. Lumina relatively large, pore ca. 6 μ ... *Euonymus*
            - GG. Lumina smaller, pore smaller .... *Scrophularia*
    - CC. With transversal furrow (or pore equatorially elongated).
      - D. Exine thick; muri consisting of a single row of rather coarse granules, lower part of granules isolated; endexine thick; polar area small; transversal furrow short .... *Viburnum*
      - DD. Exine thinner, granules finer.
        - E. Polar area medium (index 0.3-0.5); the greatest lumina in the polar area 2-3 μ, muri frequently with a double row of granules .... *Hedera*[2]
        - EE. Polar area small (index 0.15-0.3); the greatest lumina in polar area less than 2 μ.
          - F. Shape slightly angular .... *Sambucus nigra*
          - FF. Shape regularly ellipsoidal .... *Lysimachia*
- AA. Tectate, muri low.
  - B. Furrows very short, foveolate-reticulate sculpture .... *Tilia*

	Rhamnus	*Vitis*
[1] Equatorial projection ("meridional limb")	angular	circular
Pore	protuberant	sunk
Margo	indistinct	broad

[2] Cp. IVERSEN 1941.

BB. Furrows longer.
C. Foveolate-reticulate; columellae coarse (ca. 1 μ diameter), ektexine thick.
D. Granules branched; margo indistinct .... *Fagopyrum*
DD. Granules simple; margo distinct .... *Euphorbia*
CC. Columellae fine; ektexine thin.
D. Intercolpium flattened, equatorial limb subtriangular; grain broader than long, small .... *Rhamnus cathartica*
DD. Intercolpium not flattened, equatorial limb subcircular, grain longer than broad .... *Papilionaceae*

14. Stephanocolporate.

A. Polar area with lacunae .... *Polygala* (E)
AA. No polar lacunae.
B. Polar area very great (index more than 0.75) .... *Boraginaceae* p. p.
BB. Polar area smaller.
C. Psilate, tectate.
D. More than 10 furrows .... *Utricularia* (E)
DD. 6 furrows .... *Sanguisorba officinalis*
DDD. 4 furrows .. .. *Viola tricolor*
CC. Reticulate, intectate . ... *Pinguicula*

15. Pericolporate.

A. Intectate, finely reticulate.
B. Polar area great to medium (index 0.50 or more); furrows very narrow with distinct pores, usually 4 ... . . . *Rumex sect. acetosa* (W, E)
BB. Polar area small (index less than 0.25); pore indistinct *Limosella*
AA. Tectate.
B. Echinate .... *Tubuliflorae* p. p. (W)
BB. Not echinate.
C. With internal transversal furrows .... *Polygonum*[1]
CC. No transversal furrow.
D. Furrows very narrow; pore distinct, small .... *Rumex* sect. *Eu-Rumex*
DD. Furrows medium-broad; pore rather indistinct ... *Rosaceae* p. p.

16. Diporate.

Colchicum is the only regular representative of this group. Exceptionally grains of ***Betula, Myrica, Myriophyllum,*** etc. are diporate.

---

[1] Cp. Hedberg 1946.

17. Triporate.

Whereas the tricolpate and tricolporate pollen types generally occur in isometric modifications if the number of apertures becomes more than 3, the triporate types appear in stephanoporate modifications. And on the other hand stephanoporate types not infrequently occur in a triporate modification.

A. Foveolate-reticulate, oblate, exine very thick near the apertures, pores meridionally elongated	*Tilia* (E, W)
AA. Echinate.	
B. Spines dimorphous, crowded; grain large (more than 50 μ); exine thick (more than 5 μ)	*Dipsacaceae* (E, Z)
BB. Spines uniform, scattered; grain medium (25-50 μ); exine medium	*Campanulaceae* (E)
AAA. Psilate-scabrate-rugulate.	
B. Vestibulum distinct, cylindric, covered; grain large (more than 50 μ)	*Oenotheraceae* (E, Z)
BB. Vestibulum conical, open or absent; grain small-medium (less than 50 μ).	
C. Equatorial limb subtriangular.	
D. Pores not exactly in the equatorial plane; grain slightly heteropolar	*Carya* (E)
DD. All pores in the equatorial plane	*Myrica, Corylus, Engelhardtia*[1]
CC. Equatorial limb circular, with or without protruding pores.	
D. With minute, scattered spines	*Campanulaceae*
DD. Spines absent.	
E. Pores distinctly protruding	*Betula, Ostrya*[1]
EE. Pores not or slightly protruding; ektexine forming an intruding edge round the pore	*Urticaceae, Cannabaceae* (E)

18. Stephanoporate.

A. Echinate, 4 pores	*Campanulaceae*
AA. Reticulate-rugulate, 4-6(-7) pores, grains heteropolar	*Ulmus* (E)[2]
AAA. Psilate-indistinctly verrucate.	
B. Grains with thickened bands connecting the pores, 4-6 meridionally elongated pores	*Alnus* (E)

---

[1] Cp. JENTYS-SZAFER 1928, WODEHOUSE 1935, ERDTMAN 1943 o. a.

[2] According to recent comprehensive material collected by IVERSEN (unpubl.) we want to emphasize that a specific diagnosis of elms by means of pollen grain characters has so far proved impossible. Neither number of pores nor type of sculpturing show any consistent specific difference.

BB. No thickened bands.	
C. Equatorial limb subpolygonal.	
D. With endexinous rims around the pores, 3-5 meridionally elongated pores	*Myriophyllum* (E)
DD. Ektexine slightly protruding around the pores, not thickened	*Pterocarya* (E, W)
CC. Equatorial limb elliptic, pores strongly protruding	*Myriophyllum alterniflorum* (E)
CCC. Equatorial limb subcircular, one or more pores generally outside the equatorial plane, exine thin, pores not elongated.	
D. Pollen grain small (less than 25 μ)	*Urticaceae, Cannabaceae* (E)
DD. Pollen grain medium	*Carpinus* (E)

19. Periporate.

A. Verrucate	*Plantaginaceae*[1]
AA. Striate-rugulate	*Polemonium*
AAA. Echinate.	
B. Grain large (more than 100 μ), ca. 100 pores	*Malvaceae* (Z)
BB. Grain medium (20-40 μ), 8-20 pores.	
C. Spines slender, pores elongate	*Koenigia*[2]
CC. Spines broadly conical, pores isodiametric	*Sagittaria* (E)
AAAA. Reticulate.	
B. Pores surrounded by annuli	*Caryophyllaceae* p.p.
BB. Annuli absent or indistinct.	
C. Tectate; pore smaller than lumina of reticulum	*Polygonum sect. Persicaria*[2]
CC. Intectate; pore and lumina of the same size	*Daphne*
CCC. Intectate; pore much greater than lumina.	
D. Edge of pore prominent	*Liquidambar* (E, W)
DD. Edge of pore not prominent	*Buxus*
AAAAA. Psilate-scabrate.	
B. Heteropolar (pores aggregated towards one pole) or irregular.	
C. Grain irregular, pear-shaped, pores indistinct	*Cyperaceae* (E, W)
CC. Grain regular, pores distinct.	
D. One or two pores outside the equatorial plane, less than 8 pores	cp. *Stephanoporate*
DD. Most pores outside the equatorial plane, 8-14 pores	*Juglans* (E, W)

---

[1] Cp. Iversen 1941, I. Müller 1947.

[2] Cp. Hedberg 1946.

BB. Not heteropolar or irregular.
C. More than 50 pores .... *Chenopodiaceae* (E, W)
CC. Less than 50 pores.
D. Pores surrounded by an area without tectum ...... *Ribes*
DD. No such areas without tectum.
E. Grain large (ca. 80 μ), exine thick (ca. 5 μ)... *Calystegia*
EE. Grain smaller, exine thinner.
F. Annulus distinct, without structure .... *Caryophyllaceae* (E)
(G. Columellae branched: *Stellaria* type[1]
GG. Columellae not branched: *Lychnis* type)
FF. Annulus diffuse, structure finer than in the rest of the grain; grain subpolyhedric, intra-reticulate .... *Alismataceae* (E)
FFF. Annulus imperceptible, grains subsphaeroidal.
G. Pitted, no spines .... *Liquidambar* (E, W)
GG. Not pitted, with minute spines .... *Thalictrum* (E)

20. *Fenestrate.*

A. Psilate.
B. Polar area with lacunae; more than 8 furrows .... *Polygala* (E)
BB. Polar area without lacunae; 3 furrows, 3 lacunae ...... *Peplis* (E)
AA. Echinate .... *Liguliflorae* (E, W)[2]

21. *Heterocolpate.*

A. 9 furrows, 3 pores (cp. *Anthyllis* p. 22) . .. . *Verbena*
AA. 6 furrows, 3 pores.

B. Grain very small (ca. 5 μ) .... *Myosotis* (Z)
BB. Grain small-medium (more than 10 μ)
C. All furrows approximately equally long; polar area great (index more than 0.50) .... *Mertensia*
CC. Aporate furrows slightly shorter than the porate ones; polar area medium (index ca. 0.25) .... *Lythraceae*

22. *Extraporate.*

Platycarya (W) is the only known representative of this type.
3 pores, 2 furrows.

---

[1] Cp. plate IV: 1-5.

[2] Cp. the very exhaustive treatment in Wodehouse 1935.

THE PERFORATED CARD KEY

The disadvantage of a key like the preceding one is that the user is obliged to follow the sequence of characters which is laid down in the key. Sometimes a primary distinction must be made by means of rather subtle characters, which creates uncertainty from the outset. Many of the grains contained in a key, however, may be comparatively easily recognised by means of striking features which are, systematically, less important, and which cannot therefore be entered in the key until a later stage.

This disadvantage does not pertain to the perforated card key of the type in fig. 16. In a key of this type the characters can be used in any sequence, and it is consequently possible to utilise straightway a striking, special character which may very rapidly lead to a correct identification.

The principle is, in short (cp. CLARKE 1938), that all diagnostic features are written round the margin of a card, each being represented by a submarginal perforation of the card. If a pollen grain possesses a certain character, the hole representing that character is notched, e.g. the cards of all thick-walled pollen grains are notched for the character "thick exine". All cards are placed behind each other in a box. A steel rod is run through the hole representing "thick exine", and the whole pack lifted and gently shaken. Those cards which are notched for that special feature, drop out of the pack. A second sorting of this much smaller number of cards is then carried out by means of some other, less striking feature, until one single card remains, viz. the correct one, or so few are left that further identification can be carried out comparatively easily by comparison with preparations of recent material.

Besides the possibility of choosing the most striking and least ambiguous characters for identification, this type of key possesses some other advantages which are very important when dealing with such difficult objects as pollen grains. Ambiguous characters can easily be disposed of by notching the holes representing both alternatives. An erroneous decision will then not be of any significance, as the card will anyhow fall out of the pack. As compared with other perforated card systems this one has the advantages that it is (1) technically very simple, all that is needed is a box and a steel rod, and (2) that the sequence of cards is absolutely irrelevant, only all cards must be put into the box right side up. This is secured by cutting off one corner of the cards.

The card represented in fig. 16 closely follows the morphological scheme of IVERSEN and TROELS-SMITH (1950). The left-hand side of the card gives the 22 main pollen types and the sculpturing types dealt with in previous parts of this book, represented by easily decipherable abbreviations. So are also the features of the lower side, which is tripartite. First come the two main types, tectate and intectate with a special hole for perforate tectate grains. Then comes a section consisting of measurements of the greatest dimension of the grain, of the greatest diameter of the lumen (in reticulate grains), of the height of the sculpturing, of the thickness of the exine, and of the diameter of columellae. If columellae cannot be distinguished, they are grouped under "incertae". The last part gives some indices, first the shape of the pollen grain in different classes from prolate to oblate, then the polar area index, and lastly the exine index, expressing the thickness of the exine in relation to the equatorial diameter of the grain. In all these measurements the largest elements only are measured, as these are of much greater diagnostic value than the ± omnipresent smaller ones.

The upper side deals with the characters of pore (P) and furrow (C), viz. α form, β delimitation, γ structure and Σ number of apertures. Of these the last group is self-explanatory. The others signify:

P(C) α 1: Pore (furrow) in the level of the exine (*Urtica, Melampyrum*).
P α 2: Pore intruding (*Stellaria*)
C α 2: Furrow in- or protruding (*Quercus*).
P α 3: Pore protruding (*Carpinus*)
C α 3: Furrow equatorially constricted (*Menyanthes*).
P α 4: Pore vestibulate (*Betula*)
C α 4: Furrow with equatorial bridge (*Mercurialis*).
P α a: Pore meridionally elongated (*Ulmus*).
P α b: Pore isodiametric (*Fagus*).
P α c: Pore equatorially elongated (*Daucus*).
P α d: Pore equatorially elongated, constricted (*Anthyllis vulneraria*).
P(C) β 1: Delimitation wholly or partly diffuse (*Plantago major, Batrachium*).
P(C) β 2: Delimitation distinct (*Plantago maritima, Melampyrum*).
P(C) β 3: Pore with annulus, furrow with margo (*Plantago coronopus, Salix*).
P(C) γ 1: Pore (furrow) membrane structureless (*Corylus, Melampyrum*).
P(C) γ 2: Pore (furrow) membrane with ektexine elements (*Plantago major, Ranunculus*).
P(C) γ 3: Pore (furrow) operculate (*Gramineae, Potentilla*).

M fos
L ret
K str
I rug
H ech
G cla
F bac
E gem
D ver
C sca
B fov
A psi

Typus Sculpturae

22 Pext
21 Chet
20 Fen
19 Pperi
18 Pstp
17 P3
16 P2
15 CPperi
14 CPstp
13 C3P3
12 Cperi
11 Cstp
10 C3
9 C2
8 Csyn
7 C1
6 P1
5 Inap
4 Ves
3 Dy
2 Tetr
1 Poly

Typus Pollinis

I Intec	Typus Structurae	
II Tec		
Tec perf		
< 10μ	Pollinis M+	Magnitudo
10-25μ		
25-50μ		
50-100μ		
> 100μ		
< 1μ	Luminum Lum-D+	
1-4μ		
>4μ		
< 1μ	Sculpturae Sculp-Alt+	
1-4μ		
>4μ		
< 1μ	Exinae Ex-M+	
1-4μ		
>4μ		
incertus	Columellarum Col-D+	
<0.5μ		
0.5-1μ		
> 1μ		
> 2	Pollinis Lg/Lt+	Index
2-1.33		
1.33-0.75		
0.75-0.50		
<0.50		
0	Areae Poli Pol.area-M/Lt+	
<0.25		
0.25-0.50		
0.50-0.75		
>0.75		
<0.05	Exinae Ex-M+/M(+)+	
0.05-0.10		
0.10-0.25		
>0.25		

Nomen: **Senecio palustris.**

Nomen X-Pollinis.

Loc. Aamosen 1942

Columellae not branched
Ectexine partly loosened
from entexine, cavate.
Spines not crowded
Spine concave, angle ca.
45°
Monogranulate apex ca. 2/3
of total height of spine

Praep Nr.: G I 56
recent.
Mat Nr.:
Mic:

Magnitudo:
35-37μ
δ 1.25μ
Corylus
– M+:
Σ– . :
δ
Fot.: NMM 23
Det.:

K. F. & J. I.

Forma (α) et Limes (ρ) et Structura (γ) et Multitudo (Σ) Aperturarum

Pα 1
- 2
- 3
- 4
- a
- b
- c
- d
Pρ 1
- 2
- 3
Pγ 1
- 2
- 3
Cα 1
- 2
- 3
- 4
Cρ 1
- 2
- 3
Cγ 1
- 2
- 3
ΣP 4
-5-6
-7-12
-13-24
-25-48
->48
ΣC 4
-5-6
-7-12
-13-24
->24

Atypica 30 29 28 27 26 25 24 23 22 21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1

Fig. 16. A perforated key card for *Senecio palustris*. The notches represent (running counter-clockwise from the left-hand side): 13 C3P3: tricolporate. H ech: echinate. II Tec: tectate, perforation of the tectum could not be observed. 25-50 μ: Size of pollen: medium. As the pollen is not reticulare, there are no lumina. Magnitudo sculpturae > 4 μ: The height of the sculptural elements (spines) is measured from the lowermost part of the tectum (the valleys between spines) to the top of spines. M. exinae > 4 μ: The thickness of the exine is measured from the inner side of the endexine to the lowermost part of the surface (intercolpium). M. collumellarum: Width of columellae. Index pollinis, index areae polaris: cp. p. 25, 29. Index exinae: ratio between the thickness of the exine and the breadth of the grain. C γ 2: Furrow with granules. C β 2: Furrow delimitation distinct, no margo. C α 2: Furrow intruding. P γ 1: Pore nudate. P β 2: Pore delimitation distinct, no annulus. P α 1: Pore in level with the rest of the furrow. The card is also notched for *COM(positae)*.—Compare fig. 17.

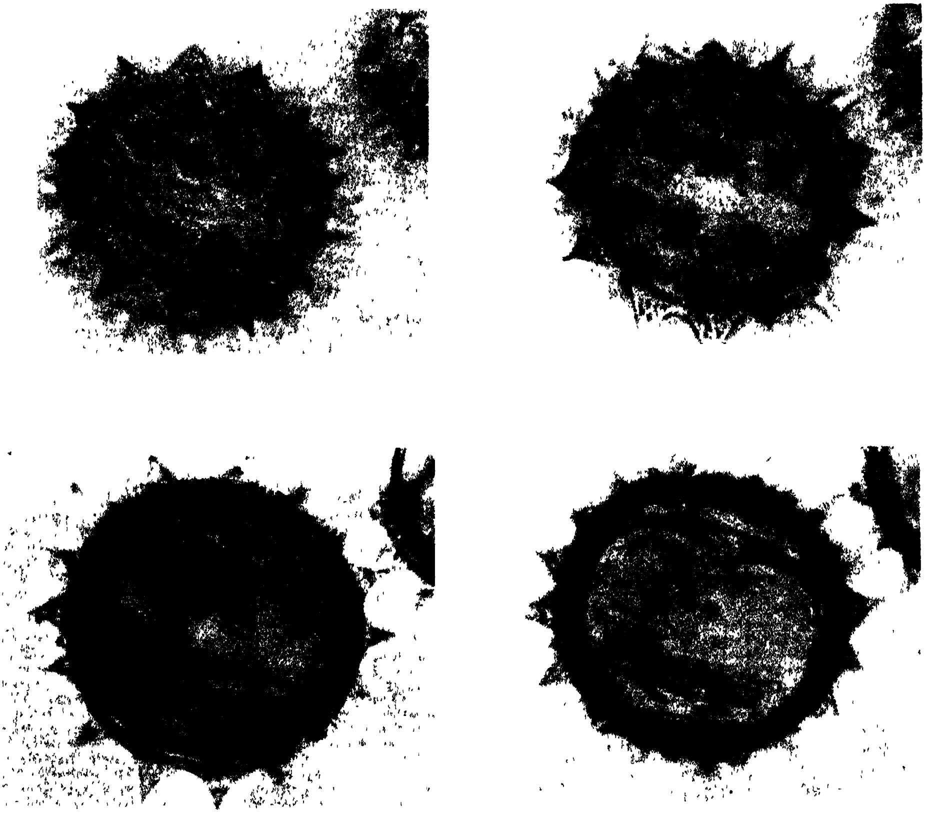

Fig. 17. A pollen grain of *Senecio palustris* photographed at different levels. a: In the level of the continuous tectum. b: In the level of the pore. c: Through the middle of the grain, optical longitudinal section. d: Below the middle, through another pore. (Phot. J. Troels-Smith).

With the exception of nr. 30, which is reserved for atypical pollen grains, the right-hand side has so far not been used. It represents a reserve, which may be used in the future, either for a general key if experience shows that more features can be added, or it may be used for specialised keys within smaller groups, where characters may be used, which do not belong in a general key. There is also another reserve of holes at the ends of the long sides, for which the text may be written on the back of the card.

The rest of the card leaves room for other information mainly of a non-morphological kind, a short characteristic of the grain, the name, or in the case of unidentified grains, the laboratory nick-name under which it is known, information about locality, serial number of preparation, of sample in the case of fossil material, the microscope used, the exact size (δ is the micrometer unit value), the size of *Corylus* grains in the same preparation and the contingent correction factor, photographs, name of investigator and all other relevant information.

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GLOSSARY OF MORPHOLOGICAL TERMS

Terms which are used in this book, are italicised.

Acolpate (Wodehouse 1935) = inaperturate.
annulus 20
apiculate: with slightly protuberant poles.
apolar (Erdtman 1947): without distinct polarity, e.g. *Chenopodium.*
apsilate (Erdtman 1947): sculptured.
arcus (Potonie 1934): band-like parts (thickenings?) of the exine, extending in sweeping curves from pore to pore, e.g. *Alnus.*
areolate (Erdtman 1947): with small areas, separated by small grooves.
aspidate, aspidoporate (Erdtman 1947) cp. seq.
aspis (Wodehouse 1935): shield-shaped subexineous thickening surrounding a germ pore.

Baculate (bacula, Potonie 1934, sculpturing) 27
Baculate (Erdtman 1947): tectate with isolated columellae = intra-baculate.

Canaliculate (Potonie 1934) = rugulate + striate p.p.
cavate: ektexine loosened from endexine, columellae sticking to the under surface of the tectum, e.g. the vesiculi of *Pinus* (Potonie 1934), the crests of *Trapa,* the verrucae of *Tsuga.*
cicatricose (Potonie 1934) = rugulate + striate p.p.
clavate (sculpturing) 27
colpus (plur.: colpi) 20

Although the term is rather meaningless in fossil grains, in which the furrows do not bulge out (like the living grains studied by Wodehouse), we have kept it because of the very useful derivations. It should be noted that, being derived from Greek *kolpos,* the correct Latin form is *colpus* (pl. *-i*), not *colpa* (pl. *-ae*), which has been used by some authors.

colpate (Wodehouse 1935): originally comprising *all* pollen types with furrows, after Erdtman (1945 a) only when there is no pore in the furrow.
colpodiporate (Selling 1947): with two pores in each furrow = colporate p.p.
colporate 22
columella (cf. plate I) 17
corrugatus (Erdtman 1947) = rugulate p.p.
costae colpi, costae pori, costae transversales, costae equatoriales 22

cribellatus (Wodehouse 1928) = periporate p.p.
cristae (Potonie 1934) = muri p.p.

Demicolporate (Selling 1947) = heterocolpate pollen, in which every second furrow has a pore
dicolpate, diporate 128
distal 15
dyad 15, 128

Echinate (Wodehouse 1928, sculpturing) 27
ektexine 16
ektonexine (Erdtman 1948) v. nexine.
endexine 16
endonexine (Erdtman 1948) v. nexine.
equatorial ridge (Wodehuse 1935), cp. lophate. NB! is *not* identical with costae equatoriales!
exine 16
exitus (Potonie 1934): that part of the aperture through which the pollen tube leaves the grain.
exoexine = ektexine
exolamelle (Potonie 1934) = tectum.
extraporate 129

Fenestrate 17, 129
fossulate (Erdtman per lit.) 27
fovea (Potonie 1934): badly defined pore without annulus.
foveolate (Erdtman 1947, sculpturing) 27
furrow 20

Gemmate (sculpturing) 27
grana (Potonie 1934) = gemmae + verrucae.
granula (Fritzsche 1837) 16
granulate (Erdtman 1947) = gemmate.

Harmomegathus 20
heterocolpate 129

Inaperturate 128
insulating layer (Isolierschicht Potonie 1934) = cavity between endexine and tectum.
intectate 17
intercolpium: the part of the exine between neighbouring furrows.
intexine = endexine.
intra(-reticulate etc.): structure, refers to the arrangement of granules *below* the tectum. Ref. the significance of terms, cp. the corresponding sculpturing terms.
isometric distribution of apertures 24

Lacuna: regularly distributed large openings in the ektexine. Wodehouse (1928) originally uses the term in a somewhat wider sense, comprising also great lumina in coarsely reticulate grains (cp. Erdtman 1943). Ref. lacuna terminology, cp. Wodehouse (1935).
lophate (sculpturing): "with the outer surface thrown into ridges, anastosmosing or free" (Wodehouse 1935).
lumen (pl. lumina) 17

Maculatus (Potonie 1934): with structure, the elements of which can be measured by 400 × magnification.
margo 22
mesexine (Erdtman 1943) = part of ektexine.
mesonexine (Erdtman 1948) v. nexine.
monocolpate (Wodehouse 1935) 128
monoporate (Wodehouse 1928) 128
muri 17

Nexine (Erdtman 1948) seems to correspond more or less to endexine.
nonaperturate (Erdtman 1947) = inaperturate.

Oblate: shape class (q.v.), index 0.75—0.5.
operculum 24
ornamentatum (Potonie 1934) = structure + sculpturing.
— (Erdtman 1943) = sculpturing.
os (plur.: ora) (Erdtman 1943) = equatorial pore.

Pattern (Muster Potonie 1934) = structure + sculpturing.
paxillate (Erdtman 1948) = intrabaculate (+ baculate?).
perforate 17
pericolpate 24, 128
perine (Erdtman 1948): that part of the ektexine which is presumed to be deposited by a periplasma.
periporate 24, 128
peroblate: shape class (q.v.), index less than 0.5.
perprolate: shape class (q.v.), index more than 2.0.
pilae (Potonie 1934): small rods with rounded, swollen ends = clavae p.p.
pilatus (Erdtman 1947) = clavate.
polar area 28
polar axis 15
pole 15
polyad 15
pore 19
prolate: shape class (q.v.), index 2.0—1.33.
proximal 15
pseudocolpus (*pseudopore*)*:* differs from a normal furrow (pore) in that it is not an exit for the pollentube.
psilate (Wodehouse 1928) 27
punctatus (Potonie 1934): structure, the elements of which are too small to be measured by 400 × magnification.

reticulate (sculpturing) 27
rimula (Potonie 1934) = slightly elongated pore.
rod (Stäbchen Potonie 1934) = columella.
rugae (Potonie 1934) = furrow p.p.
 — (Erdtman 1945) = isometrically distributed furrows.
rugate (Erdtman 1945) = pericolpate.
rugosus (Potonie 1934) = rugulate p.p.
rugulate (sculpturing) 27

Saccatus (Erdtman 1947) = vesiculate.
scabrate (sculpturing) 27
scrobiculate (Potonie 1934) = foveolate.
sculptine (Erdtman 1948) seems to correspond more or less to ektexine.
sculpturing 18
sculpturing element 25
setosus (Erdtman 1947): with bristles = echinatus p.p.
sexine (Erdtman 1948) seems to correspond more or less to ektexine.
shape class 25
shape class index is expressed by the relation between the length of the polar axis and that of the greatest equatorial diameter (Erdtman 1943).
spina (Potonie 1934) = echina.
stephanocolpate, stephanocolporate, stepanoporate 24, 128
striae: grooves between elongated sculpturing elements in striate grains.
striate 27
structure 18
subsphaeroidal: shape class (q.v), index 1.33—0.75.
sulcus (Potonie 1934) = short furrow, e.g. in *Tilia.*
 — (Erdtman 1945 a) = distal furrow in *Monocotyledones.*
syncolpate 24, 128

Tectate 17
tectum 17
tetrad 15
transversal furrow 22
tricolpate, tricolporate, triporate 128
tuberosus (Erdtman 1947): with projections lower than in verrucate, more rounded, and very densely placed. (Potonie 1934): "höckerig".

Vallae: ridges in striate and rugulate sculpturing types.
verrucae (Erdtman 1947), *verrucate* 27
 — (Potonie 1934) = gemmae + verrucae with irregular radial projections.
vesiculate 128
vestibulum: cavity forming the pore and being separated from the interior of the grain by a low rim or by a separation between different layers of the exine, e.g. *Betula* or *Circaea.* Originally used by Potoine (1934) with a slightly different definition.

Zonate (Wodehouse 1935): syncolpate with one, or more, parallel, encircling furrow(s).

INDEX

Morphological terms are not included in this index, cp. the preceding glossary. Where a plant-name stands alone, the entry refers to the morphology of the pollen grain or spore. Asterisks indicate illustrations.

Plate IX. Composite total diagram from a late glacial section near Akkerup, Denmark (after DEGERBØL & IVERSEN 1945).

The diagram is divided into four parts, all of which correspond, however, analysis by analysis. The basis of calculation for all pollen curves is the total pollen of trees, shrubs, anemophile herbs and *Ericales* (including *Empetrum*).

A. This part of the diagram shows the proportions between the pollen of the above three categories, the pollen of trees and shrubs (white area) representing forest and scrub, the herb pollen (hatched area) grassland, and *Ericales* pollen (stippled area) the oligotroph heath (*Empetrum-Vaccinium* heath). The curves for birch (including *Betula nana*), pine, and willow are inserted on the left; together they form the collective curve for trees and shrubs.

B. Contains the curves or silhouettes for the more important anemophile herbs and for *Empetrum*.

C. Silhouettes for *Hippophaë*, *Helianthemum* and *Selaginella*, which are not included in the pollen total that forms the basis of calculation. They should have been.

D. The hatched area represents the percentage of rebedded pollen. Here the basis for the calculation of the percentages is the total pollen sum, the rebedded pollen in this case being—exceptionally—included.

n Pollen total (rebedded pollen subtracted).

N Pollen total (rebedded pollen included).

On the extreme left is the zonal division according to KNUD JESSEN's system: I Early Dryas, II Allerød, III Late Dryas, IV Preboreal.