HALF A CENTURY OF MODERN PALYNOLOGY

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SUMMARY

A short review of the history of palynology is presented. This branch of science received its greatest impetus from the introduction of the pollen diagram, 50 years ago. Emphasis is laid on the development of palaeopalynology, but the history of pollen morphology, medical pollen studies and melittopalynology are also briefly discussed, as well as work on chitinozoans and fossil microplankton of botanical affinity. International palynological meetings are also reported.

INTRODUCTION

In 1966, palynology celebrates its 50th anniversary. Modern palynology is considered to have come into existence at the Sixteenth Scandinavian Meeting of Natural Scientists, in Christiania (now Oslo), in 1916, where the Swede Lennart von Post presented the first pollen diagrams. This started the extensive application of pollen-and-spore studies to various geological, archaeological and palaeobotanical purposes.

Before 1916, however, various kinds of other pollen researches had already been carried out by botanists, physicians and some geologists. Therefore, the year 1916 was not an absolute starting point. But it was the geological interest in fossil pollen that brought the largest group of pollen students to the family of modern palynologists and that had a catalyzing effect also on the activities of other groups, notably the pollen morphologists. So at least, 1916 was a most significant year in the development of palynology.

The semi-centennial is a good moment to focus some extra attention on palynology. It is interesting to look back for a while at the history of this branch of science and also to pay attention, in a second paper (MANTEN, 1966b), to a number of current trends within palynology. Both contributions will serve to show the extensive and still growing value of this field for a variety of other areas of scientific activity.

This paper will, thus, concentrate on a short historical survey of the development of palynology. It should be pointed out that the purpose of such a survey is to show how palynology after half a century has reached its present position. This paper is certainly not a complete review article. Not only would there not be sufficient space for such an attempt, but also the general historical picture would tend to be obscured if too many examples and data were presented. I am sure that every specialist will find that much important work is omitted from this survey and what is mentioned is partly a personal, call it arbitrary, selection. I admit this and, where required, I do apologize. Nevertheless, I hope that the paper will serve to show the various stages of gestation, youth and puberty that this branch of science has undergone to reach the early maturity it has today. For the convenience of describing the history of palynology, the boundaries between the successive stages are set at the years 1916 (first pollen diagrams) and 1944 (coining of the name palynology).

POLLEN STUDIES BEFORE 1916

Pollen morphology

The first studies on pollen were evidently done by botanists. These started in the middle of the seventeenth century, as a result of an improvement in the construction of microscopes. Soon after, the Englishman Nehemiah Grew made the significant discovery that pollen grains in different plant species are of different size and form, but that the pollen grains of flowers belonging to the same species are all alike.

In the seventeen-sixties, notable contributions to pollen morphology were made by J. G. Kölreuter, who, despite the fact that his microscopes were only very imperfect, discovered that the outer covering of pollen grains consists of two distinct coats. In some species, he also noted the spines and sculpturing on the outer coat of the pollen grain and the elasticity of that coat.

In the years 1790–1840, Francis Bauer, working in the Royal Botanic Gardens at Kew, Great Britain, made very accurate drawings of many pollen grains. However, the majority of his work was never published and consequently, he had only very little influence on the development of pollen science.

The first successful use of pollen characters in classification appears to have been that of John Lindley, in 1830, in genera and species of orchidaceous plants.

Hugo VON MOHL, of German descent, but professor of physiology at Bern, Switzerland, published in 1834 a work entitled *Über den Bau und die Formen von Pollenkörner*, which was a major contribution to knowledge of the structure of pollen grains and the terminology needed to describe it. The greater part of the work gives a detailed descriptive classification of pollen forms.

Other significant contributions came at about that time and also later from Carl Julius FRITZSCHE, who in his later years, however, left botany to become one of the great chemists of his time. Fritzsche's pollen observations and drawings were often more accurate than those by Von Mohl, but he was less interested in drawing conclusions from his work.

In 1889, Carl Albert Hugo FISCHER obtained his doctor degree with a thesis entitled *Beiträge zur vergleichenden Morphologie der Pollenkörner*. This thesis was based on two questions: (*1*) how is the outer layer of a pollen grain formed? and (*2*) in what way do plants which are related in their outward form agree in their pollen-grain structures? To find answers to these questions, he studied thoroughly pollen grains of over 2,000 plant species from 158 families. His studies were the first to greatly benefit from the introduction, in 1884, of the apochromatic lens. Fischer's thesis could have been a most promising start to a pollen-morphological career, but unfortunately it was also the end of it, as he was later more interested in colloid chemistry, plant nutrition, soil chemistry and applied botany.

Medical pollen studies

A specialized line of pollen studies developed in medicine, in relation to the occurrence of inhalent allergic diseases, such as hay fever and hay asthma.

The first scientific paper on hay fever appeared in 1819. It was written by the Englishman John BOSTOCK, who presented his own case. A great variety of opinion about the causes and nature of hay fever was expressed, until BLACKLEY (1873) carried out the first day-to-day studies of pollen incidence, using horizontal slides, mainly. He demonstrated that the disease is due to exposure to the pollen from certain plants. His work only received scant attention, as physicians had already recognized that a sea voyage or a sojourn at the seashore often gave relief, and Blackley's theory offered nothing new in treatment. Apart from an isolated attempt by Lockwood, in the U.S.A., no further aerobiological research was carried out until 1916, when William Scheppegrell began his local sampling and counting in New Orleans. He revived the use of horizontal slides to trap pollen, the so-called "gravity slide" method (SCHEPPEGRELL, 1923).

A number of years before Scheppegrell started his pollen studies, light had also been thrown on the nature of hay fever. The Germans Weichardt, in 1905, and Wolff-Eisner, in 1906, were the first to suggest, and the Englishman Noon, in 1911, was the fiirst to prove that the disease is an anaphylactic phenomenon. This implies the destruction of a normal or natural immunity factor during an incubation period.

Observations of fossil pollen

Fossil pollen grains were only observed for the first time in February 1836. This was by H. R. Göppert, who studied the Miocene browncoal of Salzhausen in Hessen, Germany (GÖPPERT, 1836). The specific identification of seeds and other small fossils found in the browncoal required some strong magnification, and the use of a microscope naturally led to the discovery of even smaller fossils, including pollen grains.

The conservation of pollen grains is due to the resistant properties of the outer coat of the grains, when the pollen is deposited out of reach of the oxydizing action of the air. This condition is particularly fulfilled in peat bogs, with the result that pollen grains are found most abundantly in peats, browncoals and lignites, and coals.

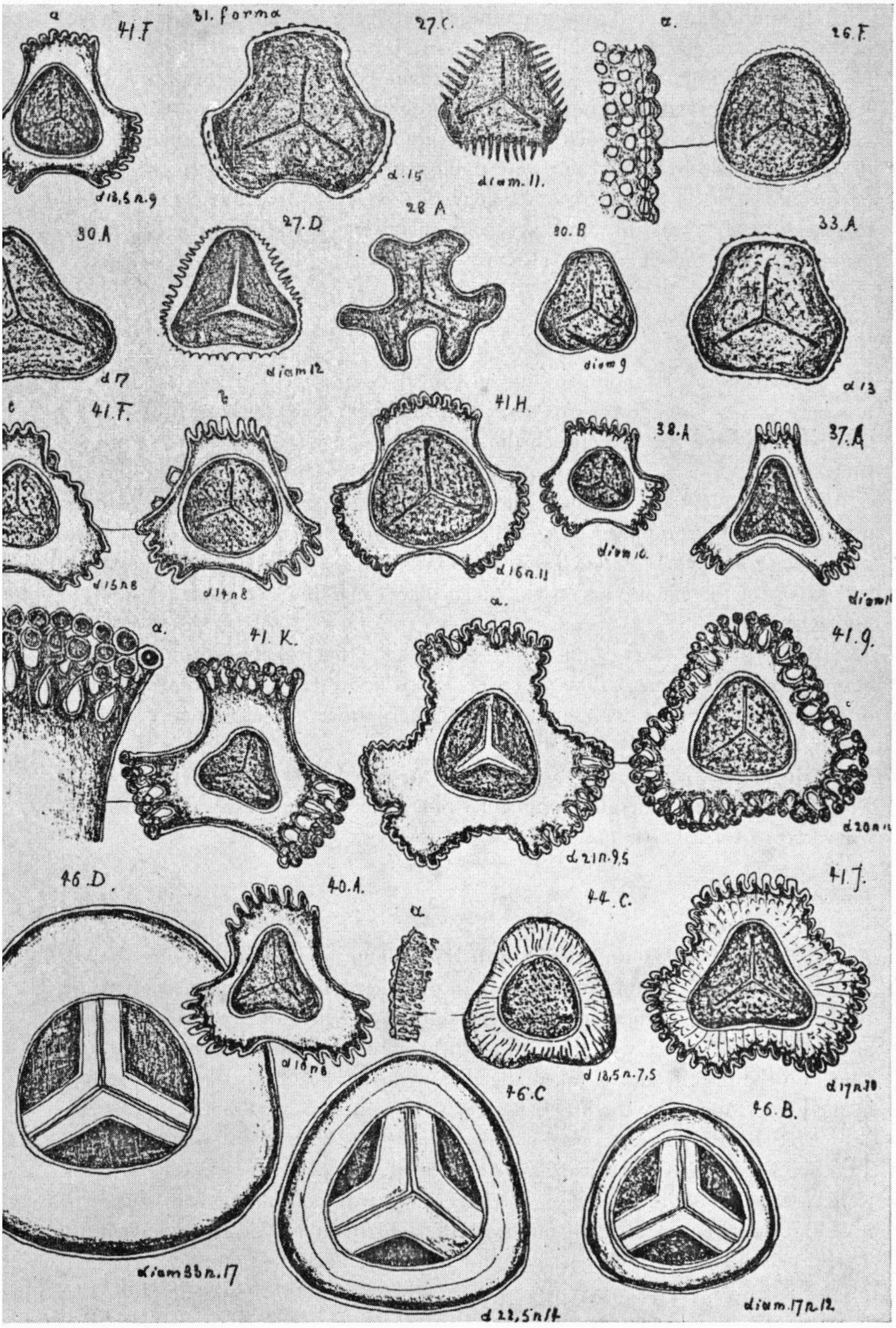
In the half a century following Göppert's first observation of fossil pollen grains, such microfossils were also studied by, among others, the famous C. G. Ehrenberg, an early pioneer of micropalaeontology, and by the Swiss workers F. E. Geinitz and J. Früh.

A very notable early contribution to the study of ancient microfloras is the two-volume work of Paulus REINSCH, *Micro-Palaeophytologia Formationis Carboniferae*, published in 1884. Most of the illustrations in this work were made in black crayon and are so clear that they are only bettered by the best modern photographs (Fig.1).

When TRYBOM (1888) encountered pollen grains of pine and spruce in a Quaternary lake deposit in Sweden, he considered these to be useful index fossils. Further important contributions were made by C. A. Weber, a German peat stratigrapher, and his school (WEBER, 1893, and later). It is in his work that a quantitative presentation of pollen-analytical data is found for the first time, and already in relative figures.

U. Steusloff, while studying certain terraces, peats and lake deposits in northwestern Mecklenburg, Germany, in the first few years of this century, took a particular interest in microfossils occurring in certain deposits of lake lime. He found that staining with Magdala red made pollen grains stand out in a brilliant red colour. He studied samples from seven strata of alternating light and dark lake marl, and counted from each sample between five hundred and seven hundred pollen grains. Steusloff believed that the banding was of seasonal origin with spring layers, poorer in lime, alternating with autumn layers, richer in lime; but the pollen content of both was nearly the same, despite the fact that he noted that the pollen grains shed during spring and early summer are entirely different from those shed later. Steusloff, therefore, suggested that pollen grains deposited in lake waters may float in the water some time before sinking down to the bottom (see further ERDTMAN, 1943, pp.6–7).

Fig.1. Plate XXII from Paulus Reinsch, *Micro-Palaeophytologia Formationis Carboniferae* (1884).


41.F
31. forma
27.C.
26.F.
d.15
diam.11.
d13,5 n.9
28 A
30.A
27.D
30.B
33.A
diam12
diam 9
d17
d13
41.F.
41.H.
38.A
37.A
diam10.
d15n8
d14n8
d16n.11
41.K.
41.G.
d21n.9,5
46.D.
40.A.
41.J.
44.C.
d16n8
d 18,5 n.7,5
d17n10
46.C
46.B.
diam33n.17
d 22,5n14
diam.17n.12

In Finland, at about the same time, H. Lindberg found that the percentages of certain pollen forms can differ in successive layers.

Another important investigator of fossil pollen was the Swede Gustav Lagerheim. Although he himself did not publish anything on pollen analysis, his contribution to this branch of science should not be underestimated. Results of analyses made by Lagerheim were published by WITTE (1905), HOLST (1909), SAMUELSSON (1910), SERNANDER (1911), VON POST (1918) and the Swedish Geological Survey. It was through Lagerheim that Von Post learnt to see the stratigraphical value of plant microfossils.

Subdivision of the Postglacial and Holocene

For a correct understanding of the historical development of pollen analysis, it is necessary to say a few words here about attempts to establish a chronological subdivision of the period between the end of the last glaciation and the present time.

As early as 1841, the Dane Steenstrup made a peat study that led him to distinguish a stratigraphical succession of a *Populus tremula* zone, a *Pinus* zone, a *Quercus* zone and an *Alnus* zone. He ascribed this zonation to a gradual improvement of the climate which has taken place since the last glaciation (STEENSTRUP, 1842).

In 1876, the Norwegian BLYTT presented a theory about climate in his country since the retreat of the ice cover. Based upon the penetration in Norway of the present flora, he distinguished a few alternating warmer and cooler, dryer and wetter periods.

His theory was further extended by the Swede SERNANDER (1908, 1910), who made it more generally applicable. Since then the successive periods have been known for a long time as the periods of Blytt–Sernander.

Pollen in honey

A fourth line of pollen studies began in 1895, when the German PFISTER showed that the geographical and botanical origin of honey can be determined by means of the pollen grains which are found in the honey. When a bee visits a flower, it also comes in contact with the anthers. As a result, some ripe pollen usually drops on the nectar, and is taken together with this nectar to the honey combs in the hive, from where the apiarist collects the honey to market it.

Initially Pfister's discovery stood more or less by itself. It was more than a decade before his work was followed up by studies of other researchers. These were YOUNG (1908) and FEHLMANN (1911), who worked on American and Swiss honey, respectively. After their publications, a hiatus again occurred in melittological pollen studies, which lasted until the early nineteen-thirties.

LENNART VON POST

One of the scientists, who decidedly influenced the life of Lennart von Post, was the colourful and stimulating Rutger Sernander. It was he, in 1902, who gave the geology student Von Post the first scientific assignment: to prepare a report about the historical development of the Mästermyr, one of the main marshes of the Baltic island of Gotland, for which a reclamation plan had been designed.

Afterwards, Von Post kept his sincere interest in peat studies. The thesis for his master degree which was presented at the University of Uppsala, in 1907, dealt with peat swamps in Norrland. In 1908, he joined the staff of the Swedish Geological Survey and began to work on swamps in the province of Närke (west of Stockholm). In this investigation he began to use pollen grains as stratigraphical indicators, and he introduced a "spruce-pollen boundary" as a basis for local correlations. This boundary, however, did not help him in later work on peat swamps in Scania, and finally the only way out appeared to study the stratigraphical distribution of all arboreal pollen. The results were so stimulating that Von Post decided also to revise his material from Närke, identifying and counting all arboreal pollen grains found therein[1].

Von Post arranged his results in graphs, extending the depths of his samples along the vertical axis and the percentages of the various pollen species found in these samples along the horizontal axis. (In a later stage, the plotted points were indicated by means of standard signs, each sign always indicating the same species.) Lines were drawn to connect the successive points. The course of each line thus was a reflection of variations in abundance of a particular tree in the course of time of peat formation. Such a graph was called a pollen diagram.

The first demonstration of pollen diagrams to a large scientific public took place in a lecture at the Sixteenth Scandinavian Meeting of Natural Scientists, in Christiania (now Oslo), in 1916.

It was not entirely coincidental that pollen analysis was developed in Scandinavia, in an area which had been glaciated during the Pleistocene and which did not exhibit topographical height differences of much importance. In that area, the forests are composed of only a limited number of tree species, each of which produces much pollen. The smooth topography meant that alterations in the composition of the forests could be recorded almost unhindered in the fossil-pollen spectra. In a mountain area, and with a much richer and more varied vegetation cover, the picture presented by fossil pollen is much more complicated. The fact that, later, successful studies have also been made of such areas is another matter entirely, as then the principles of the method were known.

Von Post's method of pollen analysis was not received immediately with general appreciation. It seemed doubtful to several people that pollen grains

[1] For a more detailed review of the development of the peat studies of Von Post, see MANTEN (1967a).

which had often been transported over long distances, could be used as a trustworthy basis for establishing a stratigraphy of the bogs in wihch they finally had been deposited and preserved.

It was mainly for other reasons that Von Post was asked to continue his peat studies. World War I was going on and Sweden was facing a difficult fuel-supply situation, since it had neither coal nor petroleum of its own. This focused attention on the peat resources of the country and Von Post had to make a survey of the peat bogs in southern Sweden, as a basis for calculations of the amount and value of the nation's peat resources (VON POST and GAVELIN, 1917). The results of pollen-analytical studies carried out in connection with this inventory and later investigations, as well as early studies by other scientists helped significantly to overcome much of the initial mistrust of the reliability of the pollen-analytical method.

THE RISE OF MODERN PALYNOLOGY

Quaternary pollen analysis

A stimulating discovery in the early days of pollen analysis was that the various periods of the Blytt–Sernander chronology of the Postglacial and Holocene showed up very well in pollen diagrams. Thus, the following periods could be distinguished, starting from the retreat of the last glaciation: a Subarctic period, a Late Glacial period, a Preboreal period, a Boreal period, an Atlantic period, a Subboreal period, a Subatlantic period, and the present time, which is often thought to be part of the Subatlantic period still. It was gradually realized, however, that no great value could be attached to the climatological importance which Blytt and Sernander awarded to their periods.

Following the example of Blytt and Sernander, several other subdivisions of the Holocene have been published, based upon standard pollen diagrams of a certain area. A well-known one is that by RUDOLPH (1931), who subdivided the forest history in central Europe into, successively: (*1*) *Betula–Pinus* period, (*2*) *Corylus* period, (*3*) *Quercetum mixtum* period, (*4*) *Fagus* period. In more restricted areas local variations may occur such as the intercalation of a *Picea* period. Other subdivisions of the Holocene are arranged with numbered zones, such as those proposed by JESSEN (1934, 1938), OVERBECK and SCHNEIDER (1938), SCHÜTRUMPF (1943), and FIRBAS (1949). As far as the subdivision of the Early Holocene is concerned, these later chronological subdivisions present no essential improvement over the classical chronology. However, the subdivision of the Late Holocene is better in these later chronologies than in that of Blytt and Sernander.

Von Post lived long enough to see the results of pollen-statistical studies extend knowledge about Quaternary plant geography in a revolutionary way and the method become an indispensable stratigraphical aid. On several occasions, he presented reviews about Quaternary pollen analysis (VON POST, 1924, 1930). In the latter contribution, he demonstrated how pollen diagrams can be used to correlate deposits from all over Europe.

In the first two decades, pollen analysts mainly followed the classical lines set out by Von Post, gradually expanding the area of investigation, especially in those parts of the world where the problems were essentially similar to those in Scandinavia. The investigators were principally engaged in solving primary problems of forest history, shore-line movements, etc.

An important improvement of the method was the suggestion by FIRBAS (1935) to pay attention also to the values of the percentages for the herbaceous pollen grains, particularly that of the Cyperaceae, Ericales and Poaceae (Gramineae). In this way it became possible to recognise, palynologically, forest-less periods with tundras and periods with a vegetation with scattered small occurrences of trees and bushes in a forest-less territory (for the latter kind of vegetation Iversen later introduced the name of park tundra), and also to study the history of the moorlands.

Firbas initially had the idea that during the last, the Würm Glaciation, the northern ice cover was surrounded by a tundra, around this a park tundra, next a subarctic forest with birches and firs, and finally around this the forests with broad-leaved trees. All these kinds of vegetation would thus have existed simultaneously, but at different places, depending on the geographical distance to the ice cap. It was also assumed that with the retreat of the land ice, in one area these kinds of vegetation succeeded each other in time.

It was shown in Denmark that this idea of a gradual improvement in climate, reflected by the succession in time of the named vegetations, was incorrect. Pollen-analytical studies made it clear that during the Late Glacial a warmer stage interrupted a period which was on the average still rather cold. This interruption was called the Allerød oscillation. Continued research showed that this oscillation had also occurred elsewhere in Europe, thereby influencing plant growth. As a result, JESSEN (1935) published a new subdivision of the Late Glacial in which the Allerød oscillation was officially included.

It should be said here that even before this, in Denmark the idea had been launched that the improvement of climate since the retreat of the land ice had not been as gradual as one might be inclined to think. HARTZ and MILTHERS (1901) had found in Late Glacial deposits an alternation in the nature of sedimentation which they believed must have been caused by a climatic fluctuation. Probably because they published their conclusion in Danish and because it came from another field of study, palynologists did not pay much attention to the article of Hartz and Milthers until they found the oscillation themselves in the pollen diagrams. Then, however, they honoured the pioneering work of Hartz and Milthers by naming the oscillation after the site from which the type deposits were first described.

Pollen analyses and archaeology

In addition to making relative datings of peat horizons, pollen analysis can also be used to determine the age of prehistoric objects found in such deposits. This made the method also of great value to archaeology. On several occasions Von Post helped to make relative-age determinations of archaeological findings by means of pollen analysis. The most well-known of these is the dating of a bronze-age mantle found at Gerumsberg, in Västergötland (VON POST, 1925).

In 1937, FIRBAS, by recognizing the pollen of cultivated cereals, showed that pollen analysis could be applied to the study of the prehistorical development of agriculture. A year later, FROMM, through a study of material collected by Lidén, succeeded in correlating the results to known geochronology.

Palynology and coal geology

New impulses were brought into palaeopalynology when it was shown that it could be used for the identification and correlation of coal seams and coal-bearing rocks as well. In 1920, the American geologist THIESSEN assumed that spores from Pennsylvanian coals might be used for stratigraphical correlation. Proceeding with this idea through a study of thin sections of the "Thick Freeport" coal, THIESSEN and VOORHEES (1922) found that, where the spore content is concerned, "there is a variation in the composition of the bed vertically, but none horizontally". They also noted that several of the spores found in the Freeport coal bed were different from the spores which they had observed in other coals. Identification of various coal deposits by means of characteristic spores and plant structures was, consequently, elaborated in later papers (THIESSEN and STAUD, 1923; THIESSEN and WILSON, 1924).

Once it had been found possible to correlate coal beds in this way, similar investigations were also carried out in other countries, and the technique was especially expanded and refined in central Europe. LANGE (1928) examined and plotted the stratigraphical distribution of Carboniferous megaspores, small spores, and fungal remains found in German and Polish coals, using thin sections and isolated-spore preparations. He obtained isolated spores by crushing the coal to about 1.5 mm, mixing it with a mixture of CCl_4 and xylol with a s.gr. of 1.5; centrifugation of this mixture resulted in the float containing the lighter spores which were freed from the coal when it was crushed. Another pioneer was ZERNDT, who in the nineteen-thirties investigated Carboniferous megaspores from Polish coals using the maceration method.

It was also particularly in central Europe that the application of palynology to the study of browncoal and lignite deposits was developed. Closely connected with this field is the name of R. Potonié.

Probably as a result of the fact that coal, browncoal and lignite represent ancient peats, and peat was the preferred deposit of pollen analysts in the first few decades after Von Post, little attention was paid to the spores-and-pollen content of the sediments underlying or overlying the coal. Once they were also included in the studies, mainly after World War II, these, particularly the clays, were often found to contain a richer and more varied microflora than the coal itself.

The nomenclature problem in Tertiary palynology

HECK (1927) seems to have been one of the first to undertake a study of Tertiary pollen in this century (cf. KIRCHHEIMER, 1940). Several others soon followed. As we shall see in later pages, it was the application of palynology in petroleum exploration that has given Tertiary palynology its greatest impetus. This began slowly in the nineteen-thirties, but the real "boom" only came after World War II.

Whereas Quaternary palynologists could identify all pollen grains which they found in terms of present-day taxa and Palaeophytic palynologists had to work throughout with organ taxa, Tertiary palynologists had to deal with an intermediate situation. As the sediments under investigation are progressively older, less and less of the pollen can be correlated, with certainty or with approximation, with modern botanical genera.

In this situation, a series of publications by Potonié and co-workers has greatly influenced Tertiary palynology (C. A. BROWN, 1957). These show many developmental changes in concepts as well as in nomenclature.

In 1931, POTONIÉ started by placing fossil spores and pollen grains in the form genera *Sporites* and *Pollenites*. Since the chances of finding fossil pollen grains or spores of a plant are at least as great as that of finding any other fossilized organ, it soon became evident, however, that two form genera were definitely insufficient and that a much higher number of form genera was required, even though pollen or spores of many species and sometimes also higher taxa are not sufficiently distinct to be kept apart. Consequently, Potonié dropped the two-form-genera system after only a few years. Instead he then began to classify fossil pollen grains and spores within the framework of a botanical classification (POTONIÉ, 1934). He initiated the system of adding "pollenites" or "sporites" as a hyphenated suffix to the generic name, as in *Alni-pollenites verus*. However, this system was not satisfactory in all respects, for in many cases he could not give a positive generic identification. He indicated the uncertainty with a question mark, as in *Coryli?-pollenites coryphaeus*.

WODEHOUSE (1933) suggested contracting the suffix "pollenites" to "pites" and to add this to the specific designation if the genus of the pollen species is known with the normal degree of accuracy, otherwise to its generic designation (e.g., *Pinus strobipites*, *Ericipites longisulcatus*).

THIERGART (1940), being faced with the same problem as Potonié, simply used existing generic names for the fossil spores and pollen grains which he felt able to correlate positively to present-day genera and used the form genera *Sporites* and *Pollenites* for the others.

Still not satisfied with the attempts then made in the classification and nomenclature of fossil spores and pollen grains, Potonié proposed in 1950, together with Thomson and Thiergart (POTONIÉ et al., 1950), the system of adding the suffixes "-oidites" to generic names and "-oides" to specific names (e.g., *Quercoidites, Fagus silvaticoides*), in this way showing to what taxonomic rank they felt reasonably certain about the identification of fossil pollen. This system has been designated the "half-natural system". In 1951 and 1959, Potonié again altered the nomenclature by altering names such as *Quercoidites* to *Quercoipollenites*; these categories he apparently considered as organ genera.

The changing of the system of classification from a form genus, *Pollenites*, to one with suggested botanical relationships, and then from a half-natural system to one using organ genera, caused much confusion. THOMSON and PFLUG (1953) recognized this, so they established a system of nomenclature based on the morphology of pollen, which is a system of form genera. But they did not preserve their type specimens. Part of their system is based on the system of classifying modern pollen into artificial sections, as proposed by IVERSEN and TROËLS-SMITH (1950; see also FAEGRI and IVERSEN, 1950).

INGWERSEN (1954) on the other hand, used present-day botanical genera to classify many of the pollen grains which he found in Danish lignites.

All these nomenclature systems together are still in use at the present day.

The haphazard application of artificial names, "half-natural" names and botanical names to fossil pollen is deplored by several palynologists. For the time being the best practical solution seems to be to use one artificial system for all Tertiary and older pollen, so that each kind of fossil pollen has only one name (MANTEN, 1958, 1965). However, such a system conflicts in some respects with the existing *International Rules of Botanical Nomenclature*. Under these rules we can, for instance, have no organ taxon which is synonymous with a taxonomic unit. A fossil pollen grain referable to, e.g., *Alnus*, is an *Alnus* pollen grain and not *Alnipollenites*; should the identification not be quite certain, the pollen grain may be called a cf. *Alnus* pollen grain.

Palynology and the petroleum industry

Most petroleum companies initially showed great reluctance to make use of palynology in their geological-prospecting work. Fossil plants had up to then never contributed much to the resolution of marine and brackish-water stratigraphical problems, and, as a result of this, more or less, petroleum geologists had seldom had any palaeobotanical training.

A change in this situation began very gradually in the middle of the nineteen-thirties. It did not become very apparent, however, until after World War II, and particularly in the nineteen-fifties.

The first attempts to find out whether palynology could be useful to the geological activities of petroleum companies seem to have started in 1934, in the U.S.A. In some areas, petroleum geologists were hampered in their work on pre-Quaternary, particularly Tertiary, series of strata, because existing palaeontological methods of determining age and correlation could not be used and also lithological methods could not be employed with sufficient results. Thus, they began to look for some other way to obtain the desired information. The suggestion was made that perhaps pollen analysis could solve the problems. The question was tackled mainly by expert consultant advice and some preliminary investigations by palaeontologists in the companies' own service. Thus, in 1938 and subsequent years, the Royal Dutch/Shell Group invited such specialists as Potonié, Florschütz, Stützer and Bode to undertake a study of Tertiary material from Mexico, Venezuela, Trinidad, the Far East and Columbia, on a consultant basis, and also had their own palaeontologist T. F. Grimsdale do some pioneering palynological work. The main problem was that knowledge of Tertiary pollen had at that time not yet reached the same stage as that of Quaternary pollen. Nevertheless, the first results were promising enough to lead the Royal Dutch/Shell Group to decide to establish a palynological section within its stratigraphical department. Because of World War II, however, this could not take place until 1946.

Botanical microplankton and chitinozoans

The same treatment as is used in the preparation of samples of fossil spores and pollen grains, can also be used for other groups of microfossils, such as microplankton of botanical affinity, chitinozoans and other types of algal and protistan entities. Gradually, study of these objects also became part of palynology. The procedure used is then taken as the boundary with older branches of micropalaeontology, which make use of the techniques of alkaline washing of disintegrated rock, such as in the study of Foraminifera or Ostracoda, or of sectioning of hard rocks.

Microplankton

Fossil microplankton organisms of botanical affinity were first described by C. G. Ehrenberg, the father of micropalaeontology, in the eighteen-thirties (cf. EHRENBERG, 1836, 1854). During the half century following his pioneering studies, such microfossils were the subject of only rather casual mention in a limited number of scientific publications. In the early decades of the twentieth century, fossil phytoplankton assemblages were recorded from several countries.

This situation only really effectively changed in the first half of the nineteen-thirties, when several European palaeontologists, among whom O. Wetzel, A. Eisenack, G. Deflandre and M. Lejeune-Carpentier, began an important series of studies of these botanical microfossils, which has continued until the present time.

For all spherical spinose remains that were found among the fossil microplankton, the name hystrichospheres was introduced. This general term, literally meaning "spiny balls", was derived from two form genera, *Hystrichosphaera* O. WETZEL and *Hystrichosphaeridium* DEFLANDRE, and was widely used in scientific literature from the nineteen-thirties until the fifties.

Chitinozoans

The discovery of the group of microfossils known as Chitinozoa is linked to the studies of Eisenack, which aimed at tracing glacial erratics found in northern Germany back to their sources. In this connection, he investigated the acid-resistant microfossils found in the erratics and in Silurian deposits of the Baltic area (EISENACK, 1931, 1932, 1934, 1938). Among these fossils, he noted a group of small (ca. 0.15–1.5 mm), thin-walled, flask-shaped vesicles, which had not been described earlier in the literature. Because of the resemblance of their wall to chitin, Eisenack named this group of fossils Chitinozoa. He also developed a systematic nomenclature, which remained in use essentially unaltered until in the nineteen-sixties. His classification was based on overall morphographical characteristics of silhouette and ornamentation, and ratios of measurements. His diagnoses did not contain information on internal structures and wall construction, for his material consisted mainly of opaque specimens. Until 1940, he recognized some twelve different genera of Chitinozoa. The systematic position of the order Chitinozoa is uncertain, but it is generally assumed that they represent remains of animals.

Pollen studies in the service of medicine

It has already been mentioned that Scheppegrell revived the "gravity-slide" method of systematic pollen trapping, in 1916, a very important year in the history of palynology. This method has been applied in the U.S.A. probably every year since and in almost every state of the country. Similar studies followed in other countries, particularly in Europe, South America, New Zealand and Australia, and South Africa. The paucity of observations from tropical areas is due presumably not to the non-occurrence of hay fever and hay asthma, but only to their relative unimportance, real or supposed.

A more ideal method than that of using a horizontal surface coated with an adhesive, as in the gravity-slide method, would be to determine at short intervals the load in pollen grains per unit volume of air and several forms of apparatus have been devised for this purpose. Most aerobiologists, however, went on trapping pollen on horizontal slides.

The aerobiological studies have given much more insight into which pollen cause inhalent allergies. Any pollen, qualifying as a probable cause of epidemic hay fever and hay asthma, must answer certain requirements: (*1*) it must be antigenic; (*2*) is must be produced in large quantities per plant by a species which is widely and abundantly distributed and is anemophilous in habit; (*3*) the pollen of such a species must be sufficiently buoyant (in practice its grains must be small enough) to become easily airborne. To these requirements must be added that for any type of pollen to be regarded as the causitive agent in a particular case of hay fever or hay asthma, its period of occurrence in the air must coincide with or include that in which the patient's symptoms are experienced, or at least are exacerbated ("time postulate") (HYDE, 1954).

The "palynological" problem presented by hay fever was to determine what kinds of pollen answering the above requirements were likely to be encountered in the air at a given place in the course of the year, during what period and in what concentration(s), and how such incidence varies from place to place.

Treatment of pollen allergies

As mentioned before, the oldest treatment of hay fever is bringing the patient to a place where the air is free of the causative pollen. A closely related treatment is that of modification of the patient's daily time table, taking into account that part of the 24-h cycle when the pollen causing the hay fever is most abundant in the air. This method gained in importance with increasing aeropalynological knowledge.

Another approach is that of desensitization of the patient to the causative pollen with pollen extracts. After he had discovered the nature of hay fever, Noon was the first to apply preseasonal treatment to his patients. WALKER (1921) noted that in cases where such treatment led to little or no improvement, pollen-extract injections may be continued, but in smaller amounts (co-seasonal therapy). WALKER (1920) was also the first to suggest that if pollen cases were treated long and consistently, many patients would possibly be entirely free from symptoms for years, if not throughout life. The first two comprehensive papers which reported good results of such perennial treatment were by A. BROWN (1927) and by VANDER VEER et al. (1927). In the next few years others reported success as well, and therefore such treatment also became an accepted procedure.

Melittopalynology

The study of the pollen found in honey began to flourish again in the early nineteen-thirties. The microscopic examination of honey was then developed mainly in Germany, by Armbruster and co-workers (ARMBRUSTER and OENIKE, 1929;

ARMBRUSTER and JACOBS, 1934–1935), GRIEBEL (1930–1931), and especially by ZANDER (1932, 1935, 1937, 1941, 1949, 1951), who through his enormous amount of work laid down the foundations of the microscopic determination of the origin of honey. During the following years, the microscopic analysis of honey was also developed in various other countries of Europe; regional types of honey and the pollen combinations which characterize them were described. Critical studies also showed the possibilities and limits of the method.

Pollen morphology

After the great advances in pollen morphology made in the nineteenth century, it was only in the nineteen-thirties when further really significant contributions to this field appeared.

In his studies of the browncoal deposits in the Lower Rhine area, Potonié found many pollen grains which were unknown in literature and, therefore, needed to be described in detail. However, there was such a variety in characteristics that he felt it necessary to give first an explanation of his terminology (POTONIÉ, 1934). This publication reveals a great insight into the construction of the pollen-grain wall. With the aid of this terminology, Potonié described the fossil pollen grains and his system is still used by several palaeopalynologists. A number of terms used by him were adopted from Fritzsche, others from Wodehouse, who had already started to publish information about pollen grains in 1928.

In contrast to Potonié, Wodehouse mainly studied recent pollen and even mainly fresh grains. His studies were made primarily to support allergy research. For North American physicians, it was most important to find out as soon as possible what kind of pollen caused hay fever in a certain area with a certain patient. This was only possible when good descriptions of the pollen grains were available. The work of WODEHOUSE culminated in a book which appeared in 1935. For his descriptions, he also developed a system of terms, some of which were again adopted from Fritzsche, but many others were new. In addition to the description of pollen grains, Wodehouse also paid much attention to the development and arrangement of apertures, and to the coherence of the pollen tetrads. Surface structures could not be studied well, as they were masked by the contents of the pollen grains (protoplasm, intine). He did not apply the method developed by the brothers G. and H. Erdtman of treating pollen grains with strong acids, which dissolved the pollen content.

G. Erdtman approached pollen morphology from quite a different angle. He was a student of Lennart von Post, and in the nineteen-twenties was mainly engaged in pollen-analytical work. He realized that the study of pollen grains from a morphological point of view had lagged behind the results of pollen analysis, which in fact was based on pollen morphology. "It is, however, true that many of the specialists most interested in the results of pollen analysis have not had a direct professional interest in pollen morphology or the fundamental theory of pollen analysis" (ERDTMAN, 1943). For this reason, in his introductory textbook, he devoted much attention to pollen morphology. The system of terms which Erdtman used was partly based on the terminologies of Fritzsche and Wodehouse, but many new terms were also introduced. For the first time all pollen grains were given consistent chemical treatment according to the acetolysis method of the brothers Erdtman. The pollen-grain wall, in particular, could thus be studied better than ever before. Recent pollen treated in this way closely resembles fossil pollen; much more so than fresh material.

First books on palynology

The first book on palynology appeared in 1935. It was WODEHOUSE's well-known *Pollen Grains. Their Structure, Identification and Significance in Science and Medicine.* In 1942, the *Lehrbuch der Pollenanalyse*, by K. BERTSCH, appeared, which treated pollen analysis in general, but also presented a guide to the fossil pollen grains and spores and leaf remains, as well as some of the more common animal microfossils. In 1943, ERDTMAN's *An Introduction to Pollen Analysis* appeared and had a good reception as a most needed treatise of the subject in the English language.

A DISCUSSION ABOUT THE RIGHT NAME

Because World War II caused the suspension of many scientific meetings and handicapped travelling, P. B. Sears felt the need for a medium to exchange information among U.S. workers in pollen analysis. On May 5, 1943, in collaboration with some others (L. R. Wilson, J. E. Potzger), he started the publication of a mimeographed *Pollen Analysis Circular.* This was the first periodical entirely devoted to pollen analysis.

In the sixth issue of this Circular, ANTEVS (1944) queried whether "pollen analysis" is the proper name for the study of pollen, and its applications. The word, he said, was used in Sweden from the beginning to signify the identification and percentage determination of the pollen grains of the principal forest trees in peat bogs and lake beds. However, its inadequacy soon became obvious. Erdtman spoke about "pollen statistics", and, after 1932, about "pollen statistics and related topics". Even the combination "statistical pollen analysis" was rejected by Antevs, since it "refers only to the *method* of getting certain data which in itself has little purpose and which does not apply to or cover all the branches of the pollen studies, much less the application of the direct results to climatic conclusions, etc. It is the *knowledge* gained from the pollen studies, be those statistical or morphological, or be they concerned with pollen-induced diseases as hay fever, etc., that has purpose and significance."

After concluding that a name like "pollinilogy" would not be very good either, Antevs ended with suggesting "pollen science", a suggestion which, according to a postscript, appealed so much to the Editor of the Circular, that he suggested renaming the periodical the "Pollen Science Circular".

In the next issue, WILSON (1944) applauded the suggested new name of the publication, but pointed out that those engaged in Palaeozoic and Mesozoic studies work with spores as much as with pollen and other microfossils. He proposed that "we could use the word 'pollen' in a very liberal sense and understand that spore studies were to be included in the Circular" (and, as he no doubt meant to say, in the science).

In reaction to this, HYDE and WILLIAMS (1944) wrote that in such a case, some word carrying a wider connotation than pollen seemed to be called for. They suggested *palynology*, derived from the Greek παλύνω (palyno), which means to strew or sprinkle, and is suggestive of παλη (palè), fine meal, which is cognate with the Latin *pollen*, flour, dust. Palynology, they defined, is the study of pollen and other spores and their dispersal, and applications thereof. They ventured "to hope that the sequence of consonants p–l–n (suggesting pollen, but with a difference) and the general euphony of the new word may commend it to our fellow workers in this field", a hope which, as history proves, has been richly honoured.

The suggestion of "micro-palaeobotany", made in the same issue of the Circular (BRYAN, 1944), has hardly been discussed.

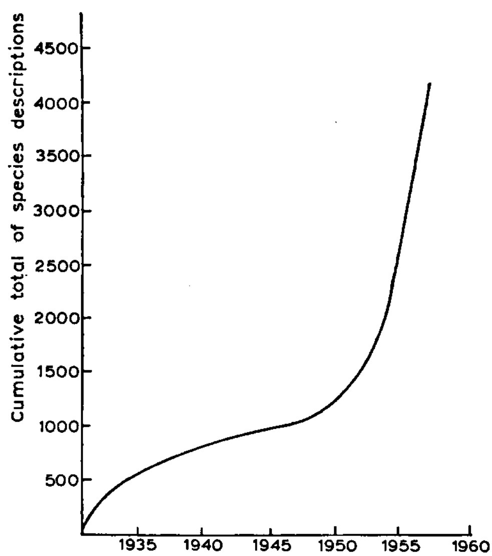


Fig.2. Rate at which new species and emendations have been added to the palynological literature in the years 1931–1956. (After KREMP et al., 1957.)

In the ninth issue, which appeared on January 15, 1945, Sears, Editor of the Circular, professed to be "intrigued with the suggestion of Professors Hyde and Williams that the term *palynology* be used to designate the whole science which deals with strewn or scattered organic particles". Recipients of the periodical seemed to be more hesitant in accepting the new name and the majority suggested calling it *Pollen and Spore Circular*, a name which it bore from the ninth to the eighteenth, and last issue.

The discussion ended in the tenth issue, when HYDE (1945) wrote that Dr. Williams and he did not intend the word palynology to have so wide an application as Sears had given it. He admitted that he could not object on logical grounds to the inclusion of fungus and bacterial spores, but would certainly not wish to include, e.g., virus particles or dead organic dusts.

THE MATURITY OF PALYNOLOGY

Palynology and the petroleum industry

There is no doubt that it is the successful utilization of plant microfossils in stratigraphical work of petroleum geology that has given modern palynology its greatest impetus. In 1946, the Royal Dutch/Shell Group added a palynological section to its stratigraphical department, and a year later the Group established its first operational palynological laboratory, in Maracaibo, Venezuela. In the period 1945–1947, also two other major companies—Creole and Carter (Jersey)—worked independently to solve stratigraphical problems by means of palynology, and were successful in establishing correlations.

Thus, the first few years after World War II opened a most important era in petroleum palynology. During the first half of this decade, the growth of palynology in the petroleum industry was still slow. It was characterized by the beginning of recruitment and training of palynologists in the full services of petroleum companies, and the attack on pre-Quaternary deposits. This led to the breakthrough in the palyno-stratigraphy of the Tertiary and the subsequent mushrooming of petroleum palynology. Vast amounts of money were spent during the nineteen-fifties in establishing palynological laboratories to assist petroleum companies all over the world. By the end of that period, almost every major company and many independents had such laboratories.

Until about 1956, the main activities of petroleum palynologists concerned the Tertiary. From 1956 onwards, however, growing interest was shown in Mesozoic and Palaeozoic sediments, but it was only in very recent years that stratigraphical work on pre-Cenozoic deposits superseded petroleum-palynological work on the Tertiary in importance. The main stimulating factors were increasing applications of palynology in petroleum-exploration work in the Middle East and in European off-shore areas.

The prolific growth of palynology in the years 1951–1959 is partly reflected by the increased output in scientific palynological literature. Whereas during the first 35 years of modern palynology (1916–1950) about two thousand scientific publications appeared, dealing with this branch of science (SELLING, 1951) an almost equal number of publications was produced by the end of the nineteen-fifties in the space of less than three years. If, in addition, we realize that to an increasing degree petroleum companies were collecting unpublished palynological information, it may be assumed that in the years 1950–1959 palynological activity expanded with a factor probably of about 10. The increase is reflected in, among other things, the rate at which new species and emendations have been added to the literature (Fig.2).

Since 1959, this rapid development of palynology has slowed down to a more normal yearly increase. Each year, roughly about 5–10% more publications are produced than in the previous year. Again taking into account unpublished work, it may be estimated that at present the total palynological activity doubles in about 5–7 years.

Acritarchs, dinoflagellates and chitinozoans

It has already been pointed out that in the decade preceding World War II fossil botanical microplankton, chitinozoans and similar entities began also to be used in palynological studies, in addition to the expanding amounts of work on spores and pollen grains. For the entire group of palynological study objects, Tschudy introduced the collective name of *palynomorphs.*

Attempts to clarify the systematic nomenclature of fossil microplankton, that had grown into a confused mass of uncorrelated data, revealed that it is possible to recognize fossil chorate cysts of dinoflagellates and to separate them from other microplanktonic bodies incertae sedis. These cysts had been described at various times by different names, such as "Xanthidia", "Spiriferites", "Palinospheres", "Ova hispida", "Hystrichospheres" and "Hystrix". The first to realize that these were dinoflagellate cysts was REINSCH (1905). Four decades later, DEFLANDRE (1947a, b) also gave evidence in favour of this interpretation; he established beyond any doubt their truly planktonic character. The matter was definitely solved by EVITT, in papers published between 1961 and 1963. It is very ironic that both the genera *Hystrichosphaera* and *Hystrichosphaeridium*, from which the group name of the hystrichosphaerids was derived, happened to be based on fossil dinoflagellates. A short historical review of the study of fossil dinoflagellates is given by SARJEANT (1967) and a bibliography of papers published on this subject up to 1963 is given by DOWNIE and SARJEANT (1964).

In order to eliminate future confusion between fossil dinoflagellates, hystrichospherous or otherwise) and other microplanktonic fossils (probably mostly of algal affinity and often with spinose ornamentation or structure), EVITT, in 1963, proposed calling the latter group Acritarcha—derived from two Greek roots and meaning "of unknown origin". This term has found ready acceptance, even though some authors used the hybrid, but more descriptive "acritarchous hystrichospheres" rather than "acritarchs". The natural affinities of the several groups within the Acritarcha are largely unknown. This is partly because few studies of Recent marine microplankton had reported the presence of bodies resembling the abundant fossil acritarchs. In fact, some palynologists were inclined to believe that acritarchs had become extinct during the Late Tertiary. This, however, has changed during the last few years. With the new stimulus given to planktology by the need to modernize and intensify the fishing industry, several isolated reports of the existence of living Acritarcha have been published. There is, thus, hope that the natural affinity of this "acritarchous" group of fossils that occur in deposits from the Precambrian onwards and are abundant since the earliest Palaeozoic, will still be learnt.

The reason why interest in various palynomorphs other than spores and pollen grains has increased rapidly especially during the last decade is roughly the same as that leading to the sudden sharp growth of pollen-and-spore analysis earlier, viz. because their potential use in stratigraphic palaeontology had become widely appreciated.

As has been mentioned before, acritarchs can be used from Cambrian deposits onwards. Although dinoflagellates are known from the Palaeozoic and perhaps were already in existence even in the Precambrian, they are mainly important tools for the correlation and dating of deposits from the Middle and Upper Jurassic, Cretaceous and Tertiary. Chitinozoa are of great and increasing stratigraphical value in deposits from Ordovician to Devonian in age.

Quaternary palynology

In 1946, IVERSEN published a new method of presenting pollen-statistical data. In his calculations, he treated the arboreal pollen on equal terms with the pollen of anemophilous herbs and Ericales. The total of the pollen grains counted for these groups together constitutes the basis for the calculation of percentages. Pollen diagrams constructed from this information, with arboreal pollen plotted from left to right and the herbaceous and Ericales pollen from right to left, immediately show variations in forest density. For statistical reasons, this method required the counting of about 500 pollen grains per sample.

Iversen also introduced the concept of arboreal-pollen frequency, that is the average number of arboreal pollen grains per slide. In this way, too, one can obtain an impression of the density of the vegetation.

Using these ingenious pollen diagrams, Iversen and his collaborators could show that the Allerød oscillation was characterized by a time in which the forest temporarily closed without an immigration of thermophilous trees. The oscillation (now preferably called an interstadial) was followed by a time with a rather open park tundra, until in the Preboreal the forest definitely closed and the Holocene Period began.

The concept of a park tundra or park landscape was introduced by Iversen to denote a grass-sedge tundra with scattered stands of dwarf birches. Alongside dwarf species of *Salix* and the arctic genera *Dryas*, *Oxyria*, *Armeria*, *Empetrum* and *Selaginella*, there were also the genera *Artemisia*, *Rumex*, *Thalictrum*, *Hippophae* and *Helianthemum*. The latter suggest a comparison with the central European alpine, rather than with northern arctic, conditions.

From his pollen diagrams, IVERSEN (1947) also came to the conclusion that once before in the Late Glacial, a temporary improvement in climate must have taken place. He called this the Bølling oscillation. This interstadial represented a time with a park landscape, which was preceded and followed by a time with a tundra vegetation. The following subdivision of the Late Glacial was thus established: Oldest *Dryas* Time—Bølling Interstadial—Older *Dryas* Time—Allerød Interstadial—Younger *Dryas* Time. The latter is succeeded by the first stage of the Holocene, the Preboreal, in which the first thermophilous trees appear.

This definitely meant the end of the earlier belief that the Late Glacial in northwestern Europe was characterized by the simple succession of times with a tundra vegetation, a park landscape and a subarctic forest. Later palynological studies of Late Glacial material from the Mediterranean area, such as by MENÉNDEZ AMOR and FLORSCHÜTZ (1962) on samples from Spain, revealed that a simultaneous plant-geographical zonation during the Pleniglacial did not exist either.

The most recent development in palynological studies of the Late Glacial is the evidence presented by VAN DER HAMMEN and VOGEL (1966), from Colombia, Kenya, Spain and France, for an interstadial which is still older than the Bølling Interstadial, and which they named the Susacá Interstadial. DREIMANIS (1966) showed that this interstadial is of world-wide significance, being contemporaneous with an interstadial described earlier from the Great Lakes region of North America, with the Raunis Interstadial in the eastern Baltic area and the Plyusna Interstadial in northwestern Russia.

Studies like those by Iversen caused a revival of interest in Quaternary palynology after World War II. Mikkelsen, stimulated by Iversen, dropped Von Post's old idea that *Corylus* pollen should never be included in the pollen sum. Iversen, in the first diagrams made according to his new method, had not included *Corylus* in his total pollen sum either. Mikkelsen demonstrated that diagrams in which *Corylus* had also been included in the pollen sum gave a more understandable impression of forest history.

Vegetation and climate

In 1960, IVERSEN published a brilliant paper about the Early Postglacial forest development in Denmark, in which the relationships between vegetation and climate are thoroughly discussed. He pointed out that it is important to distinguish between "pioneer species" and "climax species" of trees. The pioneer species have a high reproduction rate, set fruits at an early age, produce many seeds year by year and show an effective seed dispersal. Consequently these species readily appear wherever favourable new conditions for tree growth are created. On the other hand, they are weak in competition with others as they require much light and have a relatively short life. Typical pioneer trees are *Salix*, *Populus tremula*, *Betula*, and *Sorbus*. Trees of the second group, the climax species, generally have a poor reproduction rate and seed dispersal; they cannot keep pace with trees of the pioneer type in the initial stage; on the other hand, they are tenacious and they will invariably suppress and supersede the pioneer species in the long run. They have a long life, attain a great height, can endure much and also provide ample shade. Typical climax genera are *Quercus*, *Tilia*, *Fagus*, and *Ulmus*. Wherever vegetation is not in equilibrium with its surroundings, succession will set in and continue until stability is reached. The final phase of stability is called the climax vegetation. The word "climax" dces not mean that the climax species are better adapted to the climate in which they grow than any other species that thrive and reproduce there. But owing to their competitive character they may form stable communities, and not only successional stages as in the case of the pioneer species. A forest of climax trees may be superseded by pioneer trees only after forest destruction (hurricane, forest fire, man).

When interpreting pollen diagrams of the Postglacial, it should be kept in mind that forest successions are extremely slow. After the retreat of the land ice, it took thermophilous trees many centuries to migrate from south of the Pyrenees and Alps to Denmark, and in the case of *Fagus* and *Carpinus* even millenia. IVERSEN (1960), therefore, concluded that one cannot attach any climatic significance to the geochronological boundaries in the Postglacial and Early Holocene. The improvement of climate occurred faster than the immigration of the thermophilous trees. In the Early Boreal, for instance, non-arboreal pollen shows that the climate in western Europe was even more favourable than at present, although the tree vegetation was comparable with the present situation in Lapland. Only in the Atlantic period did the climax, the mixed deciduous forest, establish itself. Changes that took place thereafter mainly concerned the arrival of the slowest migrants (*Fagus*, *Carpinus*) and human activities.

IVERSEN (1960) also obtained important information about the composition of the climax forest. He realized that in pollen diagrams from peat bogs found in forests, the *Alnus*-pollen percentage is overrepresented because *Alnus* grows in and around bogs. Iversen, therefore, sought a small bog with walls steep enough to prevent the development of a peripheral vegetation of alder carr. Furthermore, the bog preferably had to be overshadowed by tree tops to prevent the pollen contribution of *Tilia*, which is insect-pollinated, being overshadowed by the pollen of wind-pollinating trees. He found the tiny bog Hertugdalen (diameter 25 m) in the Grib forest in the Danish island of Sealand and in a pollen diagram from this bog *Tilia* pollen in Atlantic time reached 118% if the total contribution of the wind-pollinating trees is taken as 100%. This shows that at that time the bog was surrounded by a forest in which *Tilia* was the major component. According to Iversen, this was the case on the high grounds; on low-lying mineral soils *Quercus* dominated and with a still higher ground-water level the mixed oak forest was superseded by an alder (*Alnus glutinosa*) carr, provided that the water is not completely stagnant. Similar results were obtained independent of IVERSEN (1960) by JANSSEN (1960) from the southeastern Netherlands.

Ice Age

Palynology also proved to be of great value in extending existing knowledge of the overall chronology of the Pleistocene.

Before the beginning of the Ice Age, large parts of the Northern Hemisphere, including Europe, were covered with the famous Sino-American flora. In its main composition, this flora is still present nowadays in Japan, China and North America.

During the Pleistocene, the advancing land ice forced this flora to move southwards. This presented no serious problems in North America and Asia, where after retreat of each glaciation the flora again recolonized the original areas if the climatic conditions permitted it. In Europe, however, the situation was different. The east–west orientated mountain ridges and the Mediterranean presented barriers against which the southwards-moving thermophilous flora was forced to halt. This meant that after each glacial the Sino-American element was less well-represented in the European flora, and consequently made Europe a very suitable continent for the palynological identification of deposits from the successive interglacials. A complicating factor, however, was that at no one place is there a complete Pleistocene succession. In order to obtain a good picture, one had to combine scraps of information from various localities, and, moreover, the deposits found in these localities had, in many cases, been deformed by the direct and indirect agents of the glaciations and had been eroded by melt water, rivers or dust storms. It required a fair dose of acumen to collect the many necessary pieces of information and to produce a general, cohesive picture out of them. Someone who certainly has this gift is ZAGWIJN (1957, 1960). He has contributed significantly to the present knowledge that in the Pleistocene there have been six glacials, separated by five interglacials. WOLDSTEDT (1958) deserves the credit for having made a representative selection from the many local names for the glacials and interglacials which had gradually been introduced in the literature, thus establishing an acceptable chronology for the whole of Europe.

Studies of various kinds have shown that climatic fluctuations have also occurred in tropical areas, where they were characterized by an alternation of wet and dry periods. Palynological data (e.g., MAARLEVELD and VAN DEN HAMMEN, 1959) suggest that the pluvials correlate with the glacials of the higher latitudes.

Palynology in archaeology

In Danish pollen diagrams, at about the transition from the Atlantic to the Subboreal period, the pollen percentages of *Quercus*, *Tilia*, *Fraxinus*, and *Ulmus* undergo a distinct, though only temporary, decline. A contemporaneous transitory increase takes place in the *Betula*-pollen frequencies, a more lasting one in those of *Alnus*, and the pollen of *Corylus* shows a pronounced maximum. IVERSEN (1941) was the first to realize that these phenomena could be attributed to forest clearance with the help of axe and fire and undertaken by Neolithic man, followed by a characteristic regeneration of the cleared area through the invasion of primarily *Betula*, *Alnus*, and *Corylus*. Iversen's pollen-analytical conclusion was supported by the occurrence of Neolithic remains and charcoal layers with the onset of the vegetational changes and the low but constant frequency of the pollen grains of cultivated cereals.

IVERSEN (1941) also pointed out that the pollen of *Plantago major* and *Plantago lanceolata* act as landmarks in distinguishing the forest clearance by European man from this Neolithic period onwards, and that the latter species probably came to Denmark with formal agriculture. GODWIN (1956) drew attention to the fact that *Plantago major*, together with certain other heliophilous plants which occurred in the open vegetation of the Late Glacial, reappear with the onset of forest clearance as ruderals.

TROËLS-SMITH (1953, 1955, 1960) followed up an idea first launched by FAEGRI (1944) that the decline of *Hedera* and *Ulmus*, which can also be observed at the Atlantic–Subboreal transition might be attributed to their use as fodder trees for stall-feeding of cattle, instead of to climatic changes, as IVERSEN (1941) supposed. Troëls-Smith pointed out that in the Danish diagrams the pollen of cultivated cereals, together with that of the ruderal *Plantago*, occurs in minute traces before the forest clearance, but never before the *Ulmus* decline. The same holds for *Allium ursinum*, which is also considered to be antropochorous. By succeeding in correlating the appearance of traces of cereal pollen in a pollen diagram with the horizon of the A ceramics of BECKER (1948), which is considered to be equivalent to the classical Ertebølle culture, Troëls-Smith and his associates showed that the *Ulmus* decline did indeed take place at a time when prehistoric man combined hunting and fishing with primitive agriculture. IVERSEN (1960) seriously contested this explanation of the major decrease in the frequency of *Ulmus* pollen and still feels that this is primarily climatically conditioned.

For a forest clearance by man, IVERSEN (1941) introduced the Danish term "landnam". When this phenomenon was also recognized in other countries, this word became internationally accepted in palynological and archaeological literature.

A typical Dutch contribution to the application of palynology is the pollen-analytical study of grave monuments, particularly by workers of the Institute for Biological Archaeology of the State University at Groningen (A. E. van Giffen, H. T. Waterbolk, W. van Zeist). Thus, spectra from Neolithic grave monuments left by the people of the Funnel Beaker and Bell Beaker cultures corroborate the type of cattle farming described by Troëls-Smith, whereas the agricultural practices of the Protruding Foot Beaker culture correspond to the so-called landnam of Iversen. A detailed review of this and similar subjects is given by VAN ZEIST (1967).

Studies like those indicated above have greatly increased the importance of palynology for archaeology. They have largely replaced the palynological dating of archaeological objects, which lost most of its importance through the discovery by W. F. Libby and his co-workers, in 1947, of the radioactivity of ^{14}C and its use as a method of dating. On the other hand, this radioactive-dating method made it possible to establish accurately with which part of the pollen diagram of a site an archaeological culture corresponds. This further improved the use of pollen analysis in obtaining information about the environment of prehistoric man.

Predominance of Cenozoic palynology

If we look at the present output in palynological literature, it appears that no less than two-thirds of this is in the field of palaeopalynology. Some specialists believe that the amount of palynological information unreleased in petroleum-company files may exceed the amount now available in all the published literature (CROSS, 1964, p.5). These two facts together lead to the conclusion that presumably over 80% of all present-day palynological activities are concerned with palaeopalynology. The geological-palaeobotanical impact on palynology is very great indeed.

Within palaeopalynology the study of Cenozoic deposits still takes a predominant place, although as was said before, the amount of pre-Cenozoic palynological work is now rapidly increasing. Over 60% of palaeopalynological literature published in the first half of the nineteen-sixties or over 40% of the total palynological literature dealt with the Cenozoic, with a ratio Tertiary: Quaternary of roughly 1:3.

Whereas initially the Cenozoic history of the earth was studied primarily by geologists and palaeontologists, after World War II other, more modern approaches to earth history—geochemical, geophysical—also contributed to an increasing extent to an understanding of the events during that era. If a yearly ratio modern/traditional is determined for the scientific publications dealing with the Cenozoic, one finds a relative decrease in the contribution from the traditional disciplines. It is interesting to note, however, that despite this, phytopalaeontology appears to have maintained a rather constant 20% of the total literature on that part of earth history. This means that it has gained in importance compared to zoopalaeontology and other classical disciplines. No doubt this is largely due to the continuously increasing importance of palynology (MANTEN, 1965c).

Extraterrestrial life

In 1961, the Americans CLAUS and NAGY found remarkable particles in a carbonaceous meteorite. They called these "organized elements" and could find no explanation for these, other than their being remains of once living microorganisms.

Palynology became involved in this controversial subject, as it was felt that this is the branch of science which should be able to throw some light on the nature of the organized elements. Since the subject has recently been reviewed in this periodical (MANTEN, 1966), readers are referred for further information to that paper.

Pollen morphology

As we have seen, initially the interests of pollen analysts working with Quaternary material was predominantly directed towards the arboreal pollen. For plant-geographical and plant-sociological reasons, however, attention was gradually being given also to the pollen grains of other plants, as these occurred in the samples. In turn, this made it possible to draw conclusions, from the collected pollen-analytical data, of a palaeoecological, palaeoclimatological and other nature. The idea was to be able to identify all pollen types which were encountered in a particular deposit. For this purpose, much larger collections of pollen of recent plants were required to enable comparisons of fossil material with pollen of known botanical origin. All these pollen grains had to be accurately described, with emphasis, of course, on the structure of the pollen wall. In this respect, important work was done especially in the palynological laboratory of the Danish Geological Survey, in Charlottenlund. A descriptive system was developed, which initially was only intended for internal use. When, however, it was planned to write a handbook of pollen analysis, Iversen decided to publish the terminology (IVERSEN and TROËLS-SMITH, 1950). In the book itself (FAEGRI and IVERSEN, 1950), pollen morphology only has a moderate part. Nevertheless, the system has had great influence on pollen morphology. The system was based on the terminologies of Fritzsche, Wodehouse, and Erdtman.

After the appearance of ERDTMAN's *An Introduction to Pollen Analysis* (1943), this author has not done further work on the subject of pollen analysis. Since then, he has concentrated entirely on pollen morphology. All plant groups were systematically subjected to detailed studies. This led to the publication of a two-volume book, of which the first volume (ERDTMAN, 1952) deals with the pollen morphology of the angiospermous plants, and the second volume (ERDTMAN, 1957) with the pollen morphology of the gymnospermous plants, the ferns (Pteridophyta) and the mosses (Bryophyta). Both volumes have become pioneering works for further pollen-morphological researches all over the world. Many plant morphologists, particularly those with a botanical background, found inspiration in these books for their own original studies.

It was said earlier that there has always been a clear relationship between the development of pollen morphology and improvements in microscopical techniques. After the introduction of the apochromatic lens, the next major improvement came from the application of electron optics. Two kinds of electron microscopical studies are to be distinguished: first, those using medium magnification (magnification about 5,000×), in which pioneering studies were carried out by FERNÁNDEZ-MORÁN and DAHL (1952) and MÜHLETHALER (1953); secondly those utilising the utmost magnification available, in which important contributions were made particularly by Erdtman and his school.

Palynological literature

Books

The books by Wodehouse, Bertsch and Erdtman, which have already been mentioned, remained in use after World War II also. In addition to these, several other important books have also appeared during the last two decades, including the *Textbook of Modern Pollen Analysis*, by FAEGRI and IVERSEN (1950) and Erdtman's two-volume work on pollen and spore morphology and plant taxonomy. This work is especially valuable because of its great number of descriptions and illustrations of pollen grains and spores from different families of plants, prepared according to a very definite and exhaustive plan (ERDTMAN, 1952, 1957). In between the two volumes, he also published a new edition of his introductory book (ERDTMAN, 1954). In addition to various books devoted entirely to palynology, there are several others in which a partial palynological content has been integrated with other scientific information.

Journals

Mention has already been made of the *Pollen Analysis Circular*, of which 4 issues were published in 1943 and an equal number in 1944. From 1945 onward, it appeared under the name *Pollen and Spore Circular*, 3 issues being published in 1945, 2 in 1946, 1 in 1947, 2 in 1948, 1 in 1949 and the last one, no. 18, not until 1954. Then, the Circular became incorporated in the *Micropaleontologist*, published by the American Museum of Natural History, New York. Soon thereafter, that journal was reorganized, to become, since 1955, the present *Micropaleontology*.

At present two international scientific journals are devoted solely to palynology. These are *Grana Palynologica*, appearing since July 1954, under the eminent editorship of Erdtman, and *Pollen et Spores*, issued since May 1959, under the guidance of Madame Van Campo, by the Muséum national d'Histoire naturelle in Paris. A third periodical, *Review of Palaeobotany and Palynology*, which will start publication early in 1967, includes in its scope not only the various fields of palynological research, but also the study of plant macrofossils. In addition, there are also some national journals and numerous other publications which regularly or occasionally present palynological articles.

Bibliography

Palynology is rather unique in possessing an almost complete bibliography. Since 1927, ERDTMAN has been publishing literature surveys in a series of papers "Literature on pollen statistics", since 1932 with the addition "and related topics". These appeared in *Geologiska Föreningen i Stockholm Förhandlingar*. In Germany, H. GAMS published bibliographies in the *Zeitschrift für Gletscherkunde und Glazialgeologie*, also since 1927. When Word War II shut off the Old World from the New, the *Pollen Analysis Circular* took over this task for the North American continent. The periodical went on publishing bibliographies throughout its existence. After the war, Erdtman resumed the work of compiling surveys of "literature on palynology", in the years 1957–1959 for the subject of palaeopalynology assisted by 3 issues of a *Palynologie, bibliographie*, issued by the Service d'Information géologique of the Bureau de Recherches géologiques, géophysiques et minières, in Paris. Madame M. Van Campo deserves special mention by compiling a section "References bibliographiques" for *Pollen et Spores*, since 1959. From 1960 onwards, she has been assisted in this by Madame N. Planchais, from which year the section has been published as a bi-annual separate supplement to that periodical.

International conferences on palynology

Palynological Conference during the Stockholm Botanical Congress

In 1950, the Seventh International Congress of Botany was held in Stockholm. After the sixth congress had convened in Amsterdam, in 1935, the seventh congress was originally scheduled to be held in Sweden in 1940. For obvious reasons, however, it had to be postponed. In 1946, the Swedish Organizing Committee decided to invite a congress to be held in 1950. In connection with the preparations for this congress, F. P. Jonker, of Utrecht, wrote a letter to G. Erdtman. In this letter, which was dated July 9, 1949, Jonker wrote that both Florschütz and he "regret that, according to Communication No. 2 of the VII International Congress, there is no section or subsection for palynology, and, as far as we can see from the preliminary outline of the program, also no session on palynology in the section of phytogeography. We especially regret this as Sweden is the classic country of palynology. We wonder whether you are in a position to draw the attention of the Executive Committee to this." Erdtman replied in his letter to Jonker of August 2, 1949, that "Palynology will no doubt be adequately dealt with at the forthcoming congress. I have brought your and Prof. Florschütz' opinion as to palynological conferences to the knowledge of the president of the congress, prof. Carl Skottsberg." Preparations started for some sort of palynological meeting.

This palynological conference in Stockholm, 1950, was the first general international gathering of palynologists. In his opening remarks of the first session, on July 10, 1950, Erdtman mentioned that only a few weeks before the meeting, the decision had been taken to organize a palynological conference in the same way as the sectional meetings. It was then too late to incorporate all palynological subjects in the palynological conference. Some subjects were, therefore, presented in the section of experimental ecology and others in the section of phytogeography. President of the Stockholm palynological conference was F. Firbas, and vice-presidents were H. Godwin, H. A. Hyde and R. Potonié. Four half-day sessions were held on July 10 and 11, in which 6, 7 (plus a demonstration of a soil sampler and two peat augers), 6 (plus a demonstration of the Palynological Laboratory, by Erdtman) and 2 lectures were presented, respectively, and which 55, 50, 70 and 40 people attended. The first international palynological conference was found to be very stimulating.

Palynological Conference during the Paris Botanical Congress

The Eighth International Congress of Botany, held in Paris in 1954, had a palynological section in its programme from the moment its organization started. The section was organized by Madame Van Campo and G. Erdtman was its president; 34 lectures were presented.

It is interesting to note that the section, by means of a resolution, expressed "the wish that palynologists working with industrial undertakings be permitted to publish their material from a taxonomic point of view, without requiring that all stratigraphical details be published."

Further meetings

The Paris congress remained the only one where palynology was represented with its own special section at an international botanical congress.

In the nineteen-fifties national meetings also began to be held in various countries, partly with restricted membership, a phenomenon which continued, even more strongly, in the sixties.

First International Conference on Palynology

At the time of the Stockholm and Paris conferences, the rapid rise of pre-Quaternary palynology had just started. Lectures on studies of pre-Quaternary deposits were presented at both conferences, but only constituted a subordinate part of the total programme. In the next years, the older deposits, however, attracted ever more interest and together with this the number of palynologists with a geological background strongly increased. The development went together with a rapid expansion of palynological activity in America.

Some of the American palynologists, notably those working at the University of Arizona, came to believe that international palynological conferences should not solely be sections of botanical congresses. Among palynologists, there are workers with geological, botanical, archaeological, medical and other backgrounds. All of these should be enabled to meet each other and be stimulated to cooperate. They obtained the support of many other North American palynologists and convened the official First International Conference on Palynology. This was held in Tucson, Arizona, in April, 1962. The president was T. L. Smiley. The conference was a significant event for this rapidly developing field of science and the excellent programme was very successful. It is unfortunate that no volume of proceedings, containing in full all the papers presented at this important palynological event, has been published. Abstracts of the contributions to the conference were published in *Pollen et Spores*, in 1962.

During the Tucson conference, an evening meeting was held, under the chairmanship of N. F. Hughes, to discuss international cooperation. The desire to have a second international conference was unanimously expressed. An International Committee was established to arrange for the next conference. F. L. Staplin was elected president, and as members N. A. Bolchovitina, M. Van Campo, G. K. Guennel, F. N. Hughes, F. P. Jonker, R. M. Kosanke, G. O.W. Kremp, L. A. Kuprianova. This committee later coopted as further members G. von der Brelie, H. A. Hyde, S. Macko, E. M. van Zinderen Bakker and B. S. Venkatachala.

Second International Conference on Palynology

It was initially hoped that the second conference could be held somewhere in the U.S.S.R. However, an official invitation failed to come. Then, in 1963, Staplin suggested Utrecht as location for the conference. Some time was allowed for suggestions of alternatives, but as none was proposed, Utrecht was officially nominated in Staplin's circular letter to the International Committee of January

7, 1964. The conference was held from August 29–September 3, 1966. A detailed report of this meeting can be found elsewhere (MANTEN, 1967b).

Towards international organizations in palaeobotany and palynology

First attempt towards a palynological organization

In 1943 and 1944, U.S. pollen analysts discussed through their *Pollen Analysis Circular* and other media, the desirability of establishing their own organization, but at that time, they did not reach any positive decision.

The International Organization of Palaeobotany

On May 12, 1948, seven palaeobotanists met at the Palaeobotanical Department of the Swedish Museum of Natural History in Stockholm. These were W. Gothan (Berlin), B. Sahni (Lucknow), Isabel Cookson (Melbourne), and T. G. Halle, G. Erdtman, O. Selling and Britta Lundblad (all from Stockholm); soon afterwards they also received support from R. Florin (Stockholm). Together they discussed the question of whether it is possible to found an International Palaeobotanical Society for the chief purpose of issuing a Journal of Palaeobotany (HALLE and SELLING, 1948).

At the 18th International Geological Congress, London, 1948, W. N. Edwards and W. N. Croft organized on August 23, a palaeobotanists luncheon, which was attended by some twenty scientists, among whom a number of palynologists. Among other topics, the foundation of an International Palaeobotanical Society was informally discussed. The following resolution was then passed and sent to Professor Halle: "That an informal gathering of palaeobotanists at the 18th International Geological Congress in London (1948) welcomes the idea of an international palaeobotanical association, and hopes that concrete proposals will be prepared for the Botanical Congress in Stockholm in 1950."

The eighth session of the Palaeobotany Section of the Seventh International Congress of Botany, in Stockholm was devoted to the present position and needs of palaeobotany. The meeting took place on July 19, 1950, under the chairmanship of H. Hamshaw Thomas, and was attended by 45 congress members. It was decided that an International Assocation of Palaeobotanists should be established to promote the advance of palaeobotany without interfering with existing institutions. To that end an organizing committee was formed, consisting of W. N. Edwards (as convenor), H. N. Andrews, R. Florin, W. Gothan and R. Sitholey as members.

It is worth mentioning here, with a view to the description of future developments, that at the Stockholm congress the two taxonomy sections (cryptogams and phanerogams) adopted a resolution "that there be established an International Association for Plant Taxonomy with a Bureau for Plant Nomenclature and Taxonomy, and that the Association and Bureau include the International

Commission for Botanical Nomenclature, the Standing Committee for urgent taxonomic needs and the International Commission for Plant Taxonomy".

The committee set up to prepare a palaeobotanical organization reported to the Eighth International Congress of Botany, in Paris, in a meeting held on July 12, 1954. At that meeting the official decision was taken to found an Organisation Internationale des Paléobotanistes (I.O.P.), which in its statutes is called International Organization of Palaeobotany (cf. *Congr. Intern. Botan., 8me, Paris 1954, Compt. Rend. Séances et Rapports et Communications, sections 3, 4, 5 et 6*, pp.111–121). The latter name became the official one. It was decided that the I.O.P. should also represent the Subsection of Palaeobotany of the International Union of Biological Sciences (which was newly established during the Paris congress) and the Committee for Palaeobotany of the International Association for Plant Taxonomy. The first president of the I.O.P. was R. Florin (Stockholm), vice-president Suzanne Leclercq (Liège) and secretary-general Ed. Boureau (Paris).

The Paris discussions about a palynological organization

In 1950, F. Verdoorn, at that time secretary of the International Union of Biological Sciences, suggested the establishment of an international commission on palynology under the I.U.B.S., with G. Erdtman, Stockholm, as chairman ad interim. The activities of that commission remained mainly restricted to the preparation of the journal *Grana Palynologica* and correspondence aimed at cooperation and dispersal of information in the field of palynology.

In order to discuss the establishment of an international commission on palynology on a broader basis, Erdtman and Madame Van Campo organized an informal meeting in Paris, September 18, 1953.

A proposal was now made to the palynological section of the Eighth International Congress of Botany, in Paris, 1954, to establish a permanent palynological section of the I.U.B.S., with Erdtman as president and Mme. Van Campo as secretary. The proposal was discussed in a special session of the section with Erdtman in the chair. This was a very uproarious meeting, as several palynologists felt that for a proposal drawn up without prior consultation of wide palynological circles, it went much too far. The proposal was voted down and the meeting closed. To appease feelings, Roger Heim, President of the congress, convened another meeting, under his chairmanship. It appeared then that several palynologists were not opposed to the idea of an international organization in itself. This led to a new general session, with F. P. Jonker as chairman, to discuss the matter. It was thought that the time was not yet ripe for an I.U.B.S. section, but some kind of international cooperation was judged useful and desirable. A committee was appointed, under P. B. Sears of Yale University, to investigate the matter and to prepare a report. Nothing was ever heard from this committee.

Tucson and Utrecht

The matter of an international organization of palynologists was again raised in a general meeting at the First International Conference on Palynology, held in Tucson, Ariz., in 1962. With the events in Paris still fresh in every one's memory, it was decided that the subject matter be handled carefully and that for the moment activities should be restricted to the establishment of an International Committee to ensure that a second international conference would be organized after a number of years.

As it was to be expected that an international organization would become a subject of discussion again at the second conference, upon his appointment, the secretary of that conference undertook as one of his activities to explore the problems and possibilities for such an organization. He worked from the premise that if an organization would be judged necessary, then this would have to be an overall association, that could act as the sole international representative of palynology and would embrace all fields of palynological activity. The possibilities of affiliation with major international unions, as those for biological sciences and geological sciences were also investigated, as well as co-operation or a possible fusion with the International Organization of Palaeobotany. A working paper was presented to all participants in the Second International Conference on Palynology, Utrecht (The Netherlands), 1966. The assembly of that conference passed a resolution that this way towards the creation of an international organization of palynologists should be further explored and they elected a working group to carry out this task (see further MANTEN, 1967b).

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(Received November 7, 1966)