0014-4754/93/110931-12$1.50 + 0.20 © Birkhäuser Verlag Basel, 1993

Multi-Author Reviews

Human biometeorology, Part II

Pollen

R. M. Leuschner

Dermatology Division, Research Department, Kantonspital, Hebelstrasse 20, CH-4031 Basel (Switzerland)

Abstract. This review deals first with basic knowledge about pollen, especially its biology, morphology and physiology, and then discusses the connection of pollen with medical problems such as hay fever (pollinosis). The next sections cover the historical development of methods for trapping and counting airborne pollen grains to produce reliable quantitative data, and the development of a European network of pollen-reporting stations.
Key words. Airborne pollen; hay fever; pollen collectors; pollen count; pollen network.

Introduction

Pollen can be considered from various points of view. First of all, there is the biology and morphology of the pollen grain. In addition, the collection of pollen plays a certain role in the activities of both animals and humans. A matter of central interest is pollen in connection with the illness which is commonly known as 'hay fever' – despite the fact that fever is usually not a symptom. It is because of this characteristic of pollen that studies of the occurrence of airborne pollen are carried out in most countries of the world. Here, studies in Europe will be emphasized.

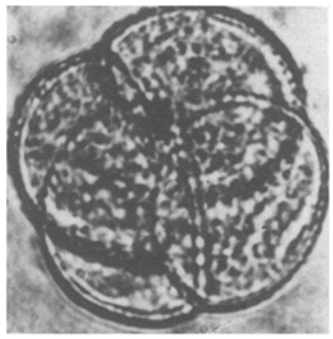


Figure 1. Tetrade of *Erica spec.* pollen. (Photo by R. M. Leuschner.)

Basic knowledge of pollen

The biology of pollen

The pollen cells are the male gametes or microspores of flowering plants. The pollen cell contains half the diploid chromosome number of the plant it comes from. In contrast to the microspores, which are set free, the egg cells or megaspores (also haploid) normally remain attached to the parent plant below the style and stigma in the ovary. The pollen cell is formed in the pollen sacs (microsporangia) of the anthers. Usually the anther is divided into two lobes (thecae) which are attached to the filament.

A pollen cell arises from a microspore mother cell, which undergoes meiotic division to form a tetrad of four haploid cells, known as microspores. According to Stanley and Linskens[57], the term 'pollen grain' should only be used for the mature microspore, in which a further process of maturation has taken place, beginning with a mitotic division which gives rise to a vegetative cell and a generative cell. The nucleus of the latter subsequently divides to give two generative male nuclei. The vegetative nucleus is responsible for the growth of the pollen tube towards the egg cell; the generative nuclei serve for fertilization and seed-formation. In angiosperms there are two fertilizations, namely of the egg-cell and of the endosperm. At this stage, when it is no longer a single cell, the pollen grain is comparable with the prothallus of ferns.

The separation of the cells after the various division steps may be incomplete, so that a pollen-grain may contain several cells attached to each other. In *Drosera*, *Epilobium*, the Juncaceae and the Ericales this structure is referred to as a tetrad (fig. 1). If the separation after cell-division is interrupted even earlier, as in the Mimosaceae, the pollen grain can consist of 8, 16 or even 32 cells. In *Acacia*, for example, 16 cells are present (fig. 2). Pollen grains of this type are not to be confused with the pollinia or pollinaria which occur in the Orchidaceae and the tropical Asclepiadaceae. These structures consist of individual pollen grains stuck together by a substance called pollenkitt, and represent the contents of one or more pollen sacs. They become attached to the heads of pollinating insects and are thus carried to other flowers.

Figure 2. Acacia pollen, 16 parts. (Photo by G. Boehm.)

Two types of pollen are differentiated, according to the type of fertilization process they are involved in: the wind-borne (anemophilous) or the insect-borne (entomophilous). Morphologically, these two main types are distinguished by the fact that the wind-borne types mostly have a relatively smooth outer surface, so they can easily move in air-currents, whereas insect-borne pollen is generally covered with pollenkitt[17], which makes the surface sticky so that the grains more easily adhere to the insect that carries them. The composition of this substance is not yet completely known.

Pollen morphology

The ripe pollen grain is surrounded by a wall, called the sporoderm[16]. This is divided into a hard outer layer, the exine, and a softer inner layer, the intine. The exine can be subdivided into further layers, which are given different names by different authors and research groups.

Pollen grains are classified on the basis of their outward appearance – shape, size and possibly colour, and above all the structure of the outer surface of the exine. The size as seen under the microscope may vary somewhat according to the amount of swelling caused by the mounting medium. Table 1 (from Stanley and Linskens[57]) gives average values. It is not mentioned in the table that the pollen of the forget-me-not (*Myosotis*) – probably the smallest pollen grain that exists – is about 5 μm in diameter, and the smallest type of airborne pollen commonly collected is that of the stinging nettle (*Urtica*) with a diameter of about 13 μm (fig. 3). The exine can vary enormously in appearance. In gymnosperms the outer surface of the pollen grain tends to

Table 1. Variations in pollen size

Species	Dimensions in microns (μm)			Volume in 10^{-9} cm^3	Weight 10^{-9} g
	Length	Width	Height		
Abies alba	97.8	102.9	62.7	499.4	251.6
Abies cephalonica	97.1	98.6	86.2	422.6	212.2
Picea abies	85.8	80.5	66.3	278.2	110.8
Pinus sylvestris	41.5	45.9	36.0	35.5	37.0
Larix decidua	76.0	72.0	50.0	180.2	176.3
Pseudotsuga taxifolia	84.8	81.1	54.8	219.2	188.8
Acer saccharum	32.5	23.6	24.6	16.5	6.6
Aesculus hippocastanum	31.0	16.4	18.2	4.8	0.9
Alnus glutinosa	26.4	22.8	13.7	4.4	1.4
Betula verrucosa	10.1	10.1	16.8	2.9	0.8
Fagus silvatica	55.1	40.5	41.1	50.3	26.0
Quercus robur	40.8	26.1	21.5	13.3	5.7
Tilia platyphyllos	40.5	40.1	20.6	15.0	6.5
Ulmus laevis	33.4	32.7	17.7	12.8	6.8
Zea mays	116.3	107.3	107.3	702.4	247.0
Cucurbita pepo	213.8	213.8	213.8	5,117.0	1,068.0

(Reprinted from Stanley and Linskens[57]; with permission.)

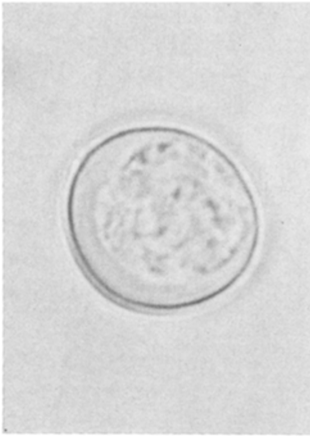


Figure 3. Pollen of *Urtica dioeca*. (Photo by R. M. Leuschner.)

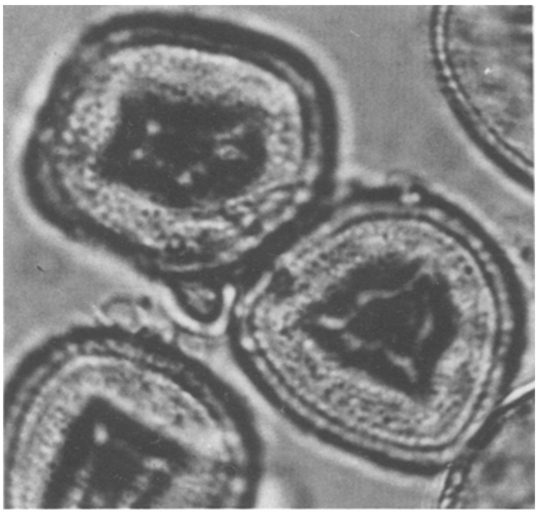


Figure 4. Taxus pollen. (Photo by G. Boehm.)

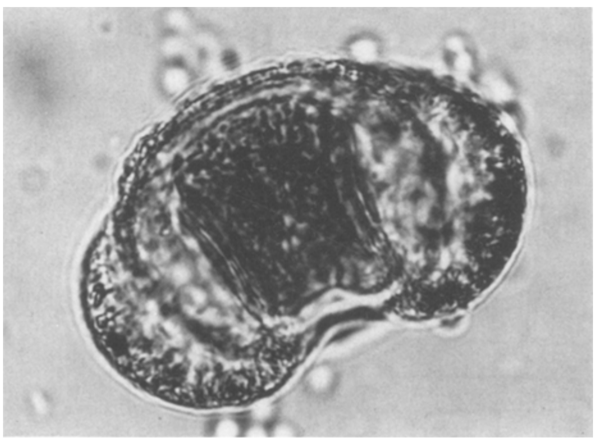


Figure 5. Pinus pollen. (Photo by G. Boehm.)

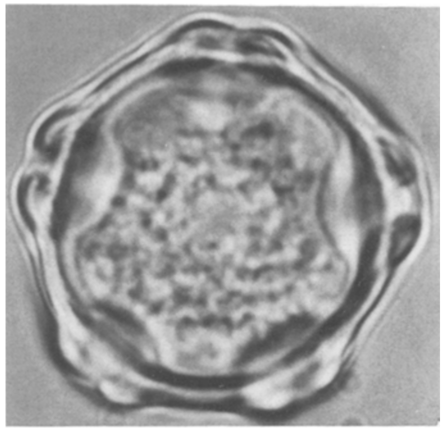


Figure 6. Pollen of *Alnus glutinosa*, 5 pores. (Photo by R. M. Leuschner.)

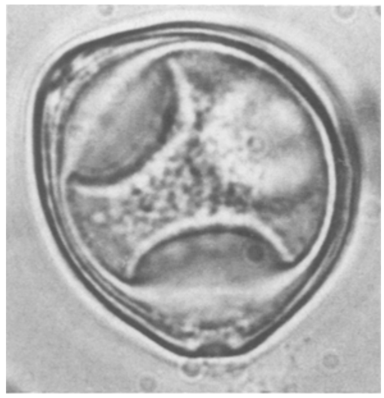


Figure 7. Pollen of *Corylus avellana*, 3 pores. (Photo by R. M. Leuschner.)

Figure 8. Pollen of *Quercus robur*, 3 slits. (Photo by R. M. Leuschner.)

be simpler in structure, though the pollen of many coniferous trees has air-sacs. There are pollen grains with and without pre-formed apertures. In the latter, there is often a part of the outer wall which is thinner, where an opening will subsequently form for the outgrowth of the pollen tube. This occurs, for example, in yew (*Taxus*) (fig. 4) and pine (*Pinus*) (fig. 5). In pollen grains from flowering plants there are often pores, for example in the alder (*Alnus*) and the hazel (*Corylus*), or slits, as in the oak (*Quercus*), or a combination of both, as in the ivy (*Hedera*) (figs 6–9). The pollen grains of grasses (Poaceae) have only one pore; a 'lid' is often to be seen beside it (fig. 10). The presence of pores in the exine seems to be a more recent development than that of slits.

Figure 9. Pollen of *Hedera helix*, 3 slits with pores. (Photos by Ciampolini and Cresti, cf. ref. 9.)

Figure 10. Grass pollen (*Dactylus glomerata*), 1 pore. (Photo by R. M. Leuschner.)

Figure 11 (from Stanley and Linskens[57]) shows various surface features which enable pollen grains to be identified. Surface features include spines, networks, trabeculae or cones. Not all these surface patterns can be clearly seen in the light microscope at a 500-fold magnification. Among the examples shown, the surface structures of *Gossypium* (cotton), *Hisbiscus* and *Lilium* (lily) are already visible in the light microscope, whereas in the others the raster electron microscope (REM) shows the details better. A palynologist working on airborne pollen only occasionally has an opportunity to use a REM picture, whereas the pollen morphologist or the palaeopalynologist can benefit from the higher enlargement that the technique offers.
The outer wall of the pollen grain, the exine, consists of a substance called sporopollenin, which is a polyterpene. The sporopollenins are chemically scarcely degradable, and are therefore highly weather-resistant. This is why it is still possible to identify pollen grains by their wall structure even after periods as long as 15,000 years in moorland soils. In deposits in rocks the structures are even more durable; in extreme cases it has been possible to demonstrate pollen up to 200,000 years old. The intine, or inner pollen wall, consists basically of pectin and cellulose, which form the pollen tube at fertilization. During this process enzymes are liberated.

The content of pollen grains

The content of pollen grains varies greatly from genus to genus. Proteins, starch, sugars, lipids, carotenoids and ascorbic acid are found, and there are additional special substances in some cases. Pollen is used as food by many fertilizing insects, but some kinds are injurious to them. Pollen from certain plants can be toxic for humans. In India, for example, honey is sometimes found with sufficient pollen from one of these plants (*Lasiosiphon eriocephalus*) to cause nausea and vomiting[57].
Pollen is frequently advocated by proponents of dietary reform and in the cosmetic industry as a tonic or an especially nourishing food. It is also said to have been used by American Indians to increase their strength[36].

Collection of pollen and fertilization

There are a number of techniques for collecting pollen from the plant for use for pollination or fertilization. It is always necessary to know at what time of day the anthers of a particular plant – for example, a fruit tree – open to shed the pollen. Collected pollen is important for plant-breeding. It can be stored for a limited time under carefully-controlled conditions of temperature, humidity and air pressure.
The collection of pollen from the air involves different methods, because the objective here is not to use the pollen, but to determine the kinds and quantities that occur, in order to correlate them with the time of year, the weather and the occurrence of disease.

Pollen and hay fever

Most publications on airborne pollen are not simply concerned with the botany and distribution of pollen, but also with inhalation allergy – hay fever or pollinosis – or with the study of biometeorology and aerobiology. The anemophilous (wind-distributed) types are especially important in the investigation of allergies – although the entomophilous types can occasionally be taken up and cause reactions in patients.
Anemophilous plants have inconspicuous flowers, which can be greenish, yellowish or even grey in colour, and produce large quantities of pollen (table 2, after Pohl[50]). The pollen of entomophilous plants rarely causes allergic reactions, though there are exceptions, such as the pollen from various composites (Asteraceae – previously called Compositae) and probably the lime tree (*Tilia*). A more detailed discussion of allergic reactions is to be found in Rapp and Frankland[53], translated into German, supplemented and amplified by Boehm[53]. A magnification of

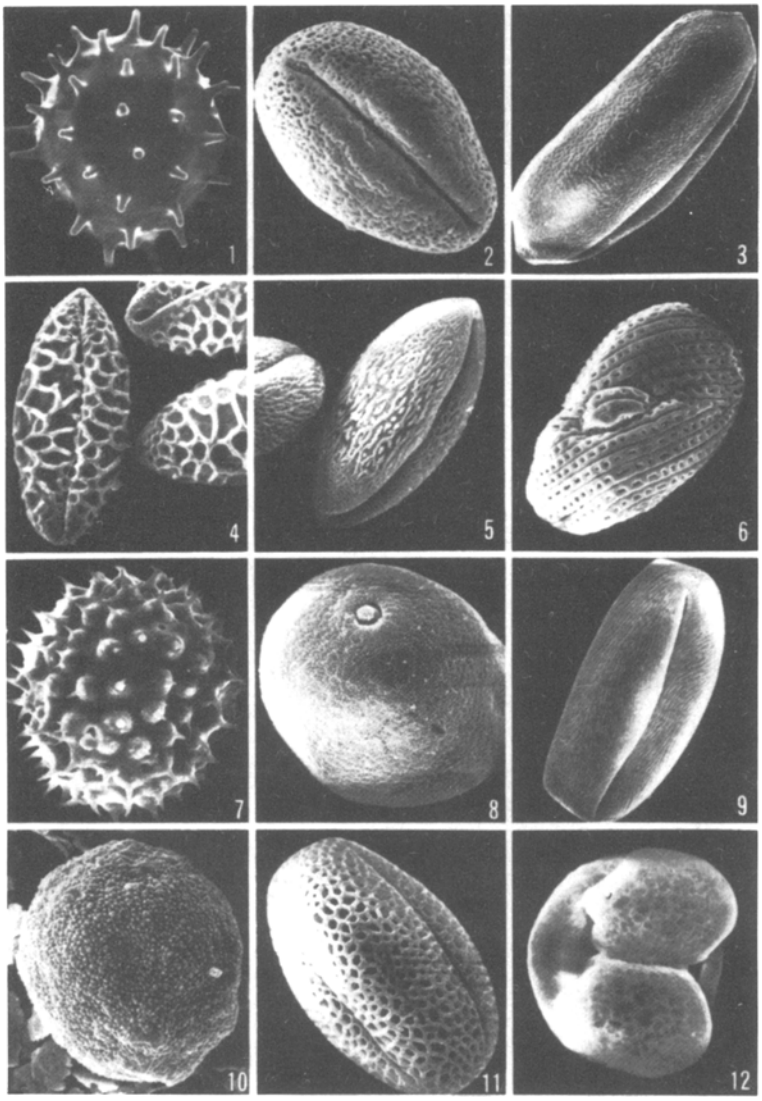


Figure 11. Pollen grains illustrating exine wall patterns, differences in size, form, and germination pore. 1) Hibiscus 420 ×; 2) Vitis 2000 ×; 3) Tradescatia 1500 ×; 4) Lilium 400 ×; 5) Petunia 1350 ×; 6) Sanchesia 450 ×; 7) Gossypium 500 ×; 8) Paspalum 2200 ×; 9) Pyrus 1000 ×; 10) Populus 1700 ×; 11) Jasminum 2000 ×; 12) Pinus 940 ×. (Scanning electron micrographs by courtesy of M. M. A. Sassen and A. W. Dicke). From Stanley and Linskens[57].

400–500 times is used for the microscopic examination of samples of pollen from the air.

Hay fever is a seasonal phenomenon. Many patients already show reactions in January or February to hazel (*Corylus*) or alder (*Alnus*) pollen. Later the pollen of the Salicaceae is found; this includes pollen from willows (*Salix*) and poplars (*Populus*). The elm (*Ulmus*), whose pollen is the next to appear, is not considered to be an especially important cause of hay fever. For many patients birch (*Betula*) pollen is a greater cause for anxiety. Pollen from a number of other trees follows: ash (*Fraxinus*), hornbeam (*Carpinus*), sycamore (*Acer*), plane (*Platanus*) and oak (*Quercus*).

The pollen from grasses (Poaceae, previously Gramineae), which is responsible for most pollinosis in Central Europe, is particularly to be feared in our latitudes from the middle of May through June and July. Almost at the same time we also find pollen in the air from the plantain (*Plantago*), dock (*Rumex*), goosefoot and other *Chenopodium* species, and stinging nettles (Urticaceae). These last species are all rather less important in causing allergies. In contrast, in the late summer some patients have a short but violent reaction to the pollen of the mugwort (*Artemisia*). A calendar of airborne pollen (fig. 12[29]) illustrates the flowering sequence of the important pollinosis-causing plants. (In the summer and early autumn, inhalation allergies can also be caused by fungal spores.)

Studies of pollen in the air

Collecting airborne particles

A case of hay fever was described early in the last century by a doctor in the United States[7]. The cause of

Table 2. Pollen production

		per anther	per flower	per inflorescence	per herbaceous plant
W	*Rumex acetosa*	30 000	181 000	393 000 000	393 000 000
T	*Aesculus hippocastanum*	26 000	181 000	42 000 000	–
W	*Secale cereale*	19 000	57 000	4 200 000	21 000 000
W	*Fraxinus excelsior*	12 500	25 000	1 600 000	–
W	*Betula verrucosa*	10 000	20 000	5 400 000	–
W	*Plantago lanceolata*	7 700	31 000	2 000 000	–
W	*Sanguisorba minor*	7 300	169 000	2 500 000	63 000 000
W	*Arrhenatherum elatius*	6 200	18 600	3 700 000	75 000 000
T	*Plantago media*	6 000	24 000	3 300 000	–
W	*Quercus sessiliflora*	5 000	41 000	554 000	–
W	*Mercurialis annua*	3 900	39 000	–	1 352 000 000
W	*Zea mais*	3 000	10 000	18 500 000	18 500 000
T	*Cucurbita pepo*	3 000	15 000	–	2 500 000
T	*Sanguisorba officinalis*	2 800	11 000	589 000	3 500 000
T	*Calluna vulgaris*	2 000	17 000	–	–
W	*Acer platanoides*	1 000	8 000	238 000	–
T	*Polygonum bistorta*	700	5 700	2 900 000	2 900 000
Wa	*Vallisneria spiralis*	36	72	-	-
T	*Papaver rhoeas*		2 636 000	–	298 000 000

W wind-pollinated; T animal-pollinated; Wa water-pollinated.
(Reprinted from Pohl[50]; with permission.)

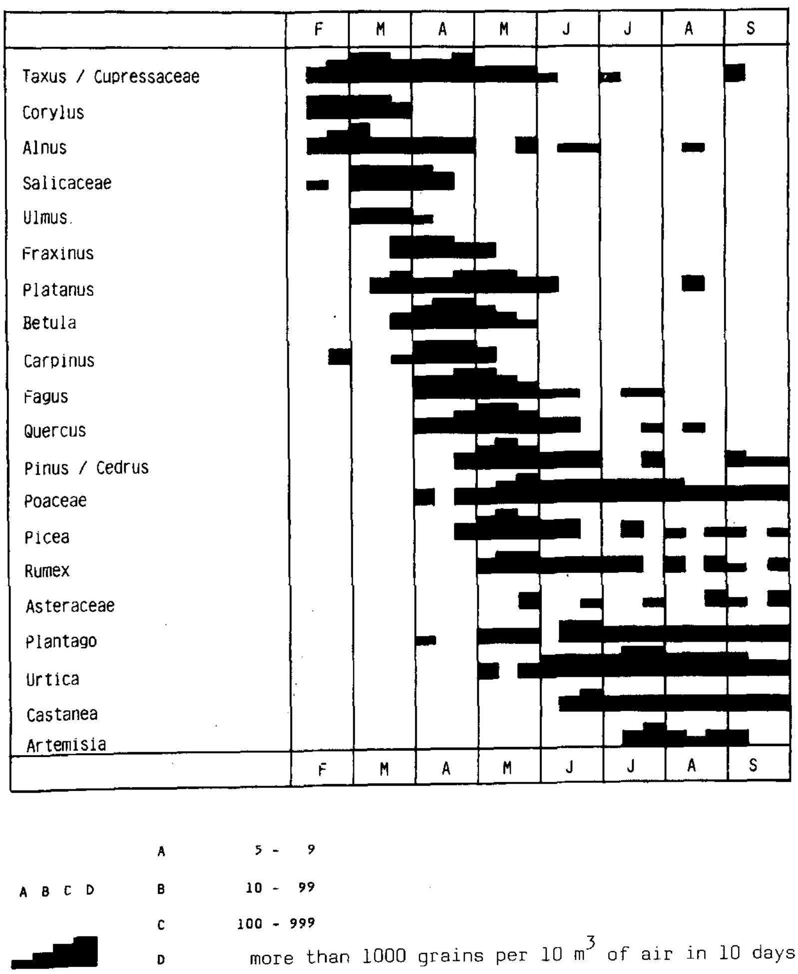


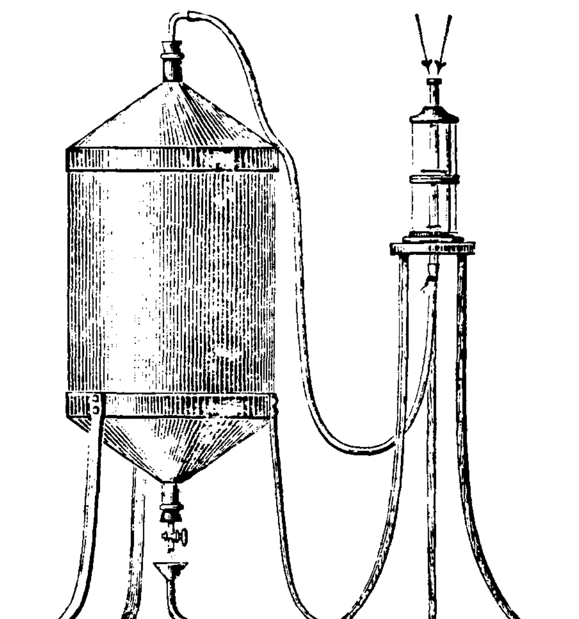
Figure 12. Pollen calendar, Basel 1992.

the disease was suspected, but it was nevertheless half a century before the theory was experimentally proved. This proof we owe to the English doctor Charles Blackley[2], who was himself a sufferer from 'summer catarrh', as hay fever used to be called. Blackley not only rubbed grass pollen on to the conjunctiva of his own eyes, to demonstrate that this could cause an attack, but also demonstrated that there was pollen in the air by collecting it on microscope slides with an adhesive coating – and even with a specially-adapted paper kite. He was almost certainly the first person who recorded the occurrence of airborne pollen from May to August in two successive years, and drew curves to compare his observations[2].

After him, many authors in many countries, for example Liefmann[35] in Germany, exposed microscope slides coated with adhesive to collect airborne pollen. There are now publications from almost all the countries in Europe, and also from Australia, India, South Africa and the USA.

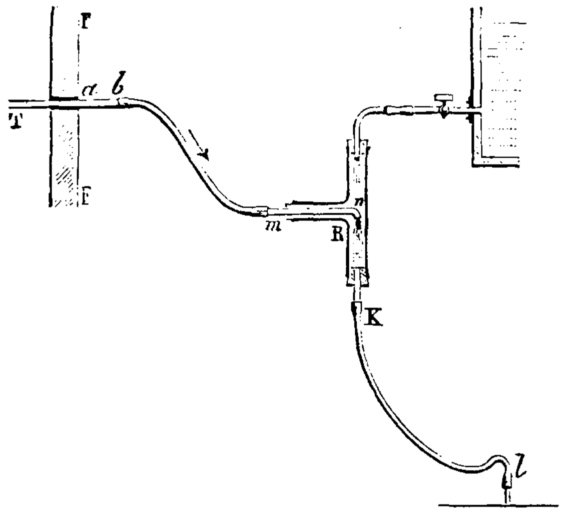
Around 1860 – that is, shortly before Blackley published the results of his experiments – two French scientists, Pouchet[51] (fig. 13) and Pasteur[43] (fig. 14) designed apparatus to collect particulate matter from the air. The main objective of their experiments was to demonstrate bacteria. An English doctor called Cunningham[11], working in Calcutta, also constructed an 'aeroscope', as such devices were then called (fig. 15).

While Pouchet, Pasteur and Cunningham wanted to investigate all kinds of particles that are ubiquitous in the air, Blackley's apparatus was constructed to look especially at airborne pollen[2] (fig. 16). His apparatus



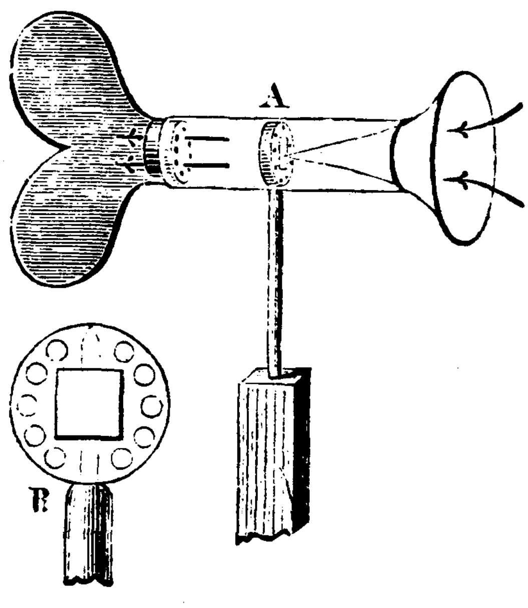
Aéroscope de A. Pouchet.

Figure 13. Pouchet's aeroscope (ca. 1860), cf. refs. 29a and 51. (Reprinted with permission *.)



Trompe de M. Pasteur.

Figure 14. Apparatus used by Pasteur (1862), cf. refs. 29a and 43. (Reprinted with permission *.)



Aéroscope du Dr Cunningham.

Figure 15. Aeroscope constructed by Dr Cunningham (1874), from refs. 11 and 29a. (Reprinted with permission *.)

had some features similar to the Burkard apparatus used today, and its predecessor, both designed by Hirst[19] – especially the wind vane, which orientates the part of the apparatus where particles are caught, or sucked in, towards the prevailing wind. The modern equipment, which uses an air-pump, will be described below.

Airborne pollen has thus been collected with more and more sophisticated methods for the past hundred years. Another method of collection is still in use in palaeobotanical investigations: samples of moss are examined to find out what kinds of pollen can be found in them, so that this can be compared with the pollen found in

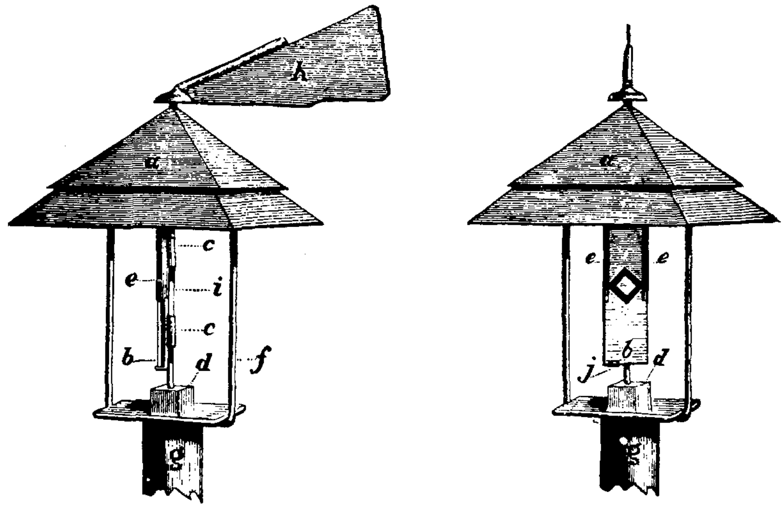


Figure 16. Pollen trap constructed by Blackley[2]. Views from the front and from the side with a microscope slide in position. On this slide an area of 1 mm^2 is marked in which pollen will be examined under the microscope.

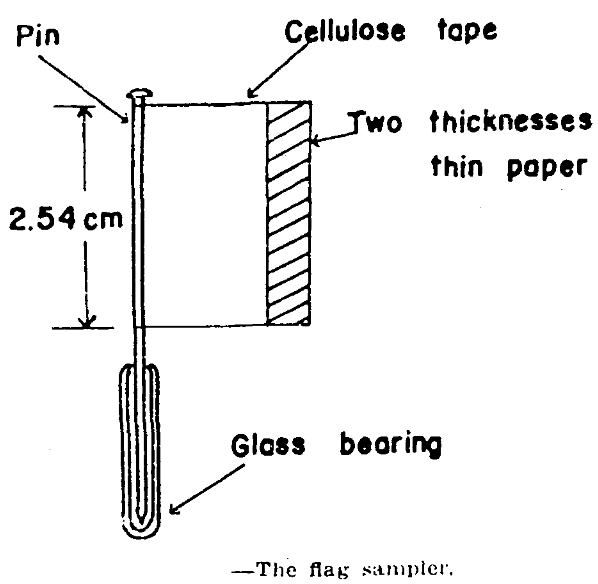


Figure 17. "Flag-sampler", from Sakagami[56]. (Reprinted with permission *.)

samples from drill-cores from moorland soil. Examples of the use of this method are in references 38, 40 and 63. Pollen can also be found on snow and on glaciers, as described, for example, by Pouchet[52] and Heusser[18] in the USA. Pollen grains can also be demonstrated in the sea, in lakes, ponds and pools; in water-tanks and in rivers (see, for example, references 6, 55, 61 and 62).

Many investigators have collected airborne particles by setting out vessels – usually filled with a mixture of water and glycerine. A particularly well-known example is the 'Tauber trap', developed by Tauber[60] in Denmark. Other workers have used different techniques for collecting airborne pollen, for example a nylon stocking soaked in a glycerine-gelatine mixture and hung on a tree[1]; Risbeth[54] used pieces of muslin; Eisenhut[15] used strips of adhesive tape (Tesa-film); Liefmann[35] and also Maunsell[39] employed different kinds of respirators. The Individual Pollen Collector developed by Boehm (fig. 18) should also be included here. This apparatus enables the patient's exposure to pollen to be investigated, for example on a Sunday outing in an area some distance away from the nearest large pollen-trap[3,4,30–33].

A number of researchers have investigated the occurrence of suspended particles at higher levels of the atmosphere. In this work, it has always been especially important to take into account the current weather conditions. The kite-flying experiments of Blackley belong in this category. Cristiani[10] studied bacteria in the air from a balloon. In 1986 Linskens and Jorde[37], also working from a balloon, investigated the occurrence of pollen at different levels in the atmosphere. They established that there is less pollen to be found in the air near the ground than at 2,000 metres; that is, the pollen-density increases with increasing altitude. This finding explains the long distances over which pollen can be transported; particles that have been carried to a high altitude may sink to earth again a long way away, sometimes in a locality where the plant they came from cannot even grow. The equipment used by Linskens and Jorde included Boehm's 'individual pollen collector'.

Among more recent types of pollen-collecting equipment, the Durham[14] apparatus enjoyed considerable popularity for some time (fig. 19). It consists of a support for a microscope slide, protected by a roof to keep off the rain. This apparatus is usually set up on a building in as exposed a position as possible. Much of the work using this equipment has been done in North America, though the apparatus has also been used in Europe, Asia and Australia. In Frankfurt, a study compared the results obtained with equipment similar to the Durham apparatus with those from small

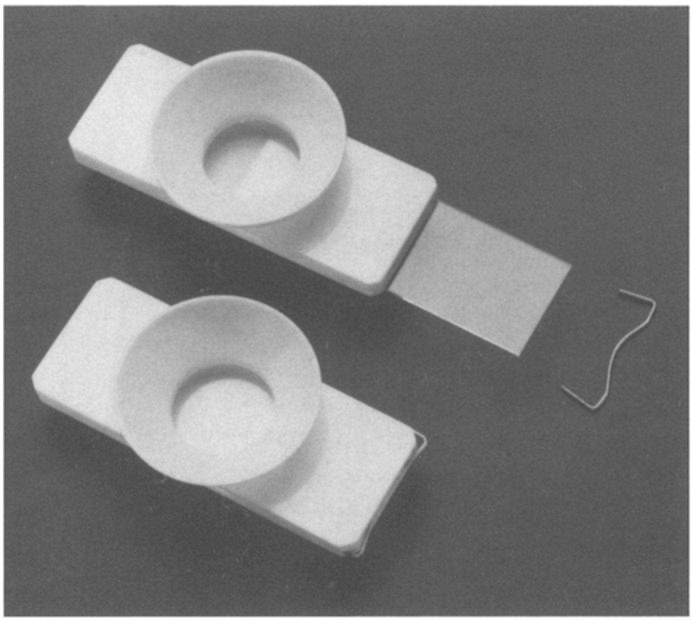


Figure 18. Individual pollen collector after G. Boehm. It contains a Vaseline-covered microscope slide which can be pulled out (upper picture). This collector can be worn attached to clothing. The patient should wear the device for 24 or 48 hours, of which at least 4 must be spent outdoors. (From Boehm and Leuschner[4], photo taken by D. Hund, Cantonal Hospital, Basel.)

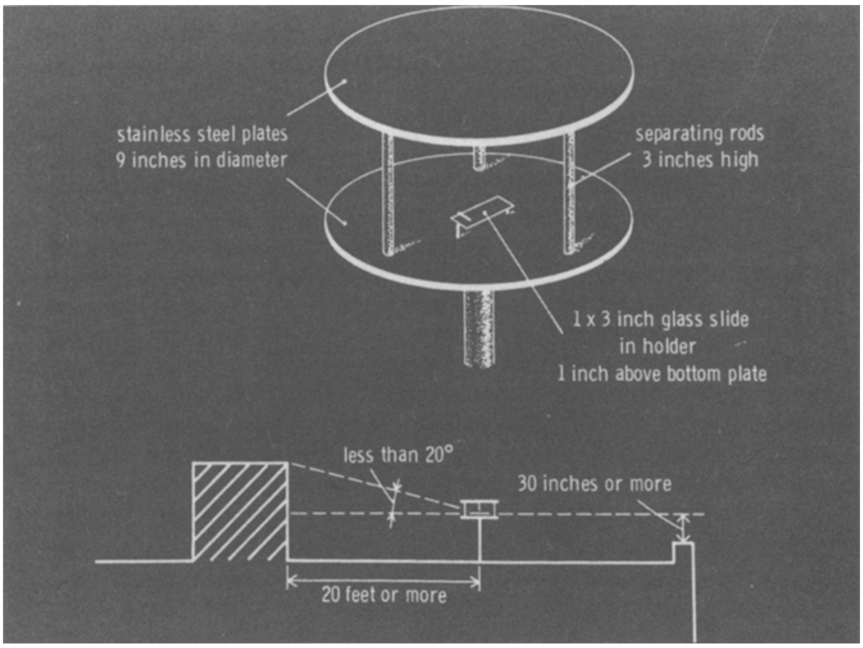


Figure 19. Durham apparatus, from Durham[14]. (Reprinted with permission *.)

'flag-samplers'[56] (fig. 17). The usefulness of these small pieces of equipment was emphasized by Philippi[49].
In recent years, the Burkard apparatus, based on that designed by the phytopathologist Hirst[19,20], has won the 'competition' with Durham's apparatus. Its use has spread from England throughout Europe. The apparatus constructed by Hirst works with a pump which takes in an exactly measured volume of air. This means that the results of the microscopic evaluation of the captured airborne particles can be compared not only from day to day and from year to year but also from place to place, provided that identical equipment is used. The functioning of the Burkard apparatus, also called the Burkard pollen-and-spore-trap (fig. 20) is described in detail by Leuschner[24,26].

Studies using the Burkard apparatus

A large number of studies have already been carried out using the Hirst and Burkard apparatus, and doubtless there will be more in the future. Comparisons from year

Figure 20. Burkard pollen-and-spore trap (designed by Hirst). From Leuschner[27]. (Photo by R. M. Leuschner.)

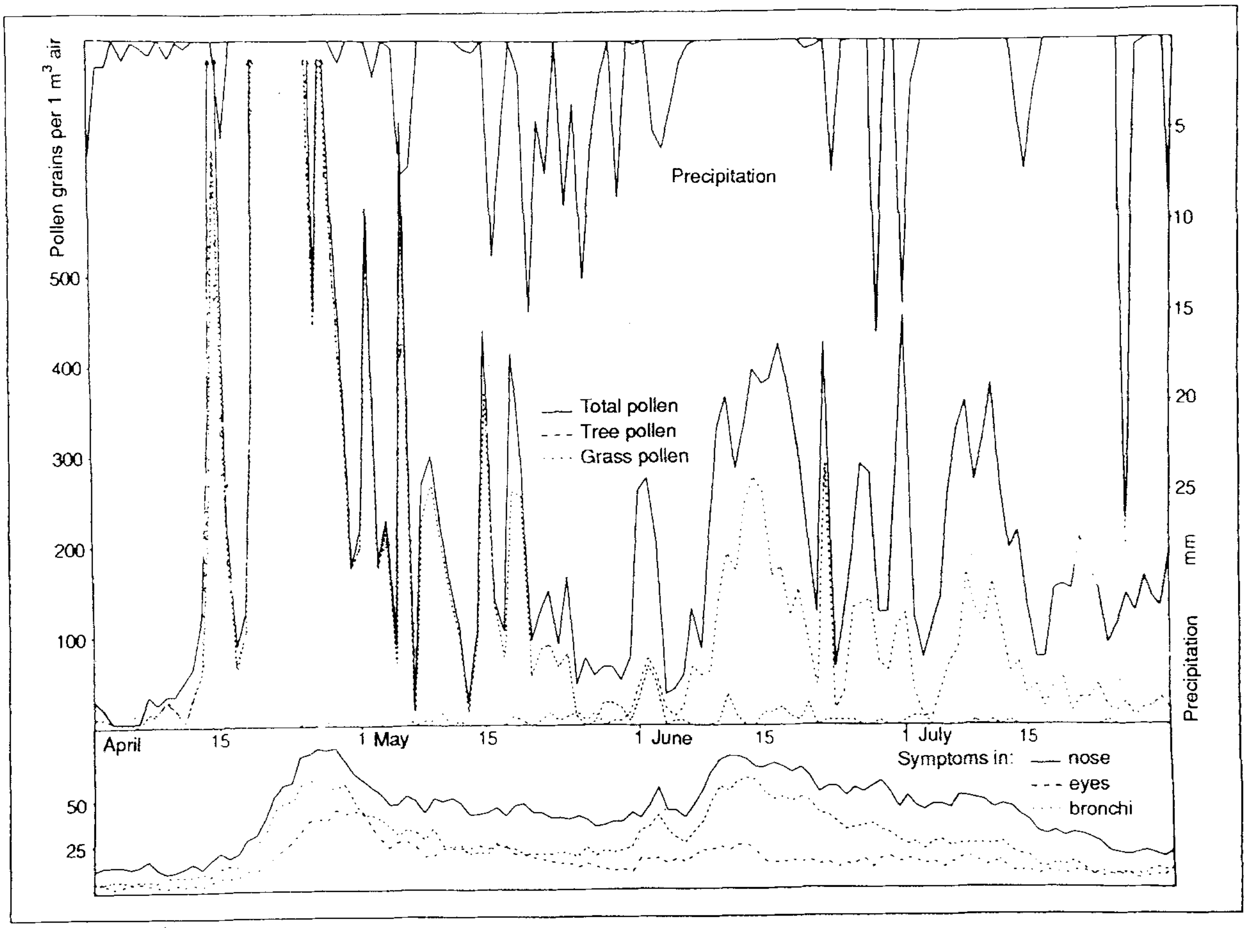


Figure 21. The occurrence of pollen from April until the end of July 1984 in Basel. Tree pollen and grass pollen are shown separately. The volume of precipitation allows conclusions to be drawn about marked variations in the quantity of pollen. The lower part of the figure shows symptoms affecting nose, eyes and bronchial tubes noted by 145 patients of the Allergy Clinic of the Basel Cantonal Hospital. There is a clear correlation between levels and allergy symptoms[27].

to year were reported by Stix[58]. She found particularly for the alder, but also for other trees and shrubs, that there were great differences in the beginning of the flowering period, and also that the amount of pollen produced varied from year to year. Such data can be used to complement phenological observations. Studies of the relationship between the quantity of pollen and hay fever attacks in patients have been made, for example by Leuschner[24,27] (fig. 21). The influence of climatic inversions on pollen levels and the symptoms of patients with allergies has also been investigated by Leuschner et al.[34].

Comparisons of studies of airborne pollen in different places

The great advantage of measurements made using the Burkard type of apparatus is that in all the places where it is used, the pollen-content of one cubic metre of air per day is evaluated. Therefore it is possible to make comparisons of the results from measuring-stations that have quite different climatic conditions, which can influence the prevalence of pollen; for example, Basel at 273 m above sea-level and Davos at 1,600 m[5,28,32]. Comparisons can be made not only within one country, but between measuring-stations in different countries. One of the first publications that attempted to survey the occurrence of pollen in the whole of Europe was the 'Atlas of European Allergenic Pollens' by Charpin et al.[8], published in French and English.

Other publications have concentrated on particular countries. In 1979, a book with a lot of information about the seasonal prevalence of pollen, mostly in France, was brought out by the Laboratoire Fisons[23]. In Germany, Stix[51] published an account of the work of her group. Nilsson et al.[41] published a pollen atlas for Sweden in 1977, and Driessen et al.[13] a similar work for the Netherlands in 1988. In Italy there have been many publications describing results obtained with this volumetric method; for example those of d'Amato and Melillo[12], who used equipment built by Lanzoni on the lines of Hirst's apparatus. An atlas of the appearance of airborne pollen in Italy was already published in 1981 by Ciampolini and Cresti[9].

Information networks

A 'Pollen Information Service' has existed in Germany since 1981. It now records and publishes the pollen-counts from 55 measuring-stations (reference 22, see also Puls and Bock in this issue). In Switzerland, comparisons of the results of various measuring-stations have been made by Leuschner[25,27,28], and reports are also published regularly by the 'Working group for Aerobiology'[44–48]. From 1993 onwards the responsibility will be taken over by a special division of the Swiss Meteorological Institute (SMA) called 'Napol' (national pollen research programme). Large and small networks of pollen-measuring stations have also been built up in France, Spain, Italy, Austria, the Netherlands, Belgium, Great Britain, Denmark, Norway, Sweden and Finland.

To take advantage of the existence of these networks, and to register the movement of the beginning of the hayfever season across Europe, Jäger and Mandrioli[21] drew maps of the prevalence of grass pollen at weekly intervals for the whole of Western Europe. Such a procedure is, of course, only possible when comparable data can be obtained from all the measuring-stations. The Burkard apparatus, or Lanzoni's modification, is suitable for this purpose. To help hayfever patients to plan their holidays, Nilsson in Sweden and Spieksma in the Netherlands have produced a useful brochure[42] showing where and when grass pollen is most abundant, based on information from the pollen-calendars of various Eruopean countries.

More and more, the countries of Europe are approaching the point when co-operative work on the occurrence of airborne pollen will cover the whole of the continent.

*Note: Figures 13, 14, 15, 17 and 19 have been reprinted with the kind permission of: Dustri Verlag, Dr. Karl Feistle, Munich-Deisenhofer, Germany (cf. ref. 29a).

1 Ammann, K., Versuche zur Ermittlung des rezenten Pollenniederschlags und seiner Abhängigkeiten. Bot. Inst. Univ. Bern (1967, not published).
2 Blackley, C. H., Experimental Researches on the Causes and Nature of Catarrhus Aestivus (Hay fever or Hay Astma), pp. 202. Balliere, London (1873). Reprinted by Dawson's of Pall Mall, London 1959.
3 Boehm, G., and Leuschner, R. M., Observations with an 'Individual Pollen Collector', in: Berichte Umweltbundesamt *5/79*. Proc. Int. Conf. on Aerobiology, pp. 411–419. Erich Schmidt Verlag, Berlin 1980.
4 Boehm, G., and Leuschner, R. M., Experiences with an 'Individual Pollen Collector', developed by G. Boehm, in: Advances in Aerobiology, Birkhäuser, Basel, pp. 3–8, EXS *51*, 1987.
5 Boehm, G., and Leuschner, R. M., Les polluants aérien à diverses altitudes. Revue int. Pédiatrie *193* (1989).
6 Bonnefille, R., Analyse pollinique d'un sédiment récent: Vases actuelles de la rivière Aouache (Ethiopie). Pollen et Spores *11* (1969) 7–16.
7 Bostock, J., (1819) citation after Stanley/Linskens, Med. Chir. Transact. (London) *10* (1974).
8 Charpin, J., Surinyach, R., and Frankland, A. W., Atlas Européen des Pollens allergisants/Atlas of European allergenic Pollens, p. 229. Ed. Sandoz, Paris 1974.
9 Ciampolini, F., and Cresti, M., Atlante dei principali pollini allergenici presenti in Italia, pp. 190. Università degli studi di Siena, 1981.
10 Cristiani, H., Analyse bactériologique de l'air des hauteurs puisé pendant un voyage en ballon. Annls Inst. Pasteur, Paris *7* (1893) 665–671.
11 Cunningham, D., Microscopic Examination of Air. Reviewed in 'Nature' *9* (1874) 330–331.
12 D'Amato, G., and Melillo, G., Le aerospore di importanza allergenica in Italia. Atti XVI Congr. Nazionale Società Ital. Allergol. (1983) 291–305.
13 Driessen, M. N. B. M., Derksen, J. W. M., Spieksma, F. Th. M., and Roetman, E., Pollenatlas van de Nederlands atmosfeer, p. 237. Ed. Drukkerij Onkenhout, Hilversum, Nederlands 1988.

14 Durham, O. C., The contribution of air analysis to the study of allergy. J. Lab. clin. Med. *13* (1928) 967–976.
15 Eisenhut, G., Untersuchungen über die Morphologie und Oekologie der Pollen einheimischer und fremdländischer Waldbäume, Forstwiss. Forschungen, Beih. forstwiss. Centbl. *15* (1961) 68.
16 Erdtmann, G., Pollen Morphology and Plant Taxonomy. Angiosperms, pp. 553. Hafner Publ. Comp., New York and London 1966.
17 Hesse, M., Cytology and morphogenesis of pollen and spores. Progress in Botany *52* (1991) 19–34.
18 Heusser, C. J., Palynology of the Taku Glacier snow cover, Alaska, and its significance in the determination of glacier regimen. Am. J. Sci. *252* (1954) 291–308.
19 Hirst, J. M., An automatic volumetric spore trap. Ann. appl. Biol. *39* (1952) 257–265.
20 Hirst, J. M., The capabilities and limitations of the HIRST spore trap. Acta allerg. Suppl. *VII* (1960) 149–150.
21 Jäger, S., and Mandrioli, P., Airborne grass pollen distribution in Europe 1991. Aerobiologia 7 (1991) (Suppl.) 3–36.
22 Kersten, W., Bongers, W. F., and Puls, K. E., Pollen- und Sporenbulletin für Birke, Gräser, Beifuss sowie Alternaria und Cladosporium, p. 119. Ed. Deutscher Polleninformationsdienst, Krefeld, 1988.
23 Laboratoires Fisons, Les pollinoses. Lab. Fisons, p. 433. Ecully, France (1979).
24 Leuschner, R. M., Luftpollenbestimmung in Basel während der Jahre 1969 und 1970 mit Uebersicht über die Methoden der Luftpollenuntersuchungen. Verh. naturf. Ges. Basel *84/2* (1974) 521–626.
25 Leuschner, R. M., Pollenzählungen und Informationsdienst über Pollen und Pilzsporen in der Luft. Schweiz. Aerztezeitung, *64/44* (1983) 1798–1804.
26 Leuschner, R. M., The Burkard Trap, in: Atlas of Moulds in Europe causing Allergy, pp. 55–56. Eds K. Wilken-Jensen and S. Gravesen. ASK-Forlaget, Copenhagen 1984.
27 Leuschner, R. M., Zwanzig Jahre Luftpollenbestimmung. Der informierte Arzt *10* (1989) 367–374.
28 Leuschner, R. M., Comparison of airborne pollen levels in Switzerland at four recording stations in Davos, Lucerne, Nyon and Basle during 1989. Int. J. Biometeorology *35* (1991) 71–75.
29 Leuschner, R. M., Pollenflugkalender 1992. 1992 (Not yet published).
29a Leuschner, R. M., Von Messgeräten für Partikel in der Luft zum Europäischen Polleninformationsnetz Präv.-Rehab. *4/1* (1992) 30–36.
30 Leuschner, R. M., and Boehm, G., Ueber ein Pollenfanggerät für Einzelpersonen. Schw. med. Wschr. *107* (1977) 57–59.
31 Leuschner, R. M., and Boehm, G., Individual pollen collector for use of hay-fever patients in comparison with the Burkard trap. Grana *16/3* (1977) 183–186.
32 Leuschner, R. M., and Boehm, G., Pollen and inorganic particles in the air of climatically very different places in Switzerland. Grana *20* (1981) 161–167.
33 Leuschner, R. M., and Boehm, G., Schadstoffe in der Luft in verschiedenen Höhenlagen. Präv-Rehab. *1/2* (1989) 67–74.
34 Leuschner, R. M., Boehm, G., and Brombacher, Ch., Influence of inversion layers on the daily pollen count and the allergic attacks of patients, in: Advances in Aerobiology, Birkhäuser, Basel, pp. 19–23, EXS 51 (1987).
35 Liefmann, H., Ein Beitrag zur Frage nach der ätiologischen Bedeutung gewisser Pflanzenpollenkörner für das Heufieber. Hygiene *47* (1904) 153–178.
36 Linskens, H. F., Pollen als Lebensmittel. Ref. Mönchengladbacher Allergie-Seminar. Will be published in 1993.
37 Linskens, H. F., and Jorde, W., Pollentransport in grossen Höhen – Beobachtungen während einer Fahrt mit einem Gasballon. Allergologie *9/2* (1986) 55–58.
38 Lüdi, W., Der Pollengehalt von Oberflächenproben am Katzensee bei Zürich. Ber. Geobot. Forsch. Inst. Rübel, Zürich *1946* (1947) 80–82.
39 Maunsell, K., Respirator Spore Trap. Acta allerg. *17*, 447–450.
40 Mullenders, W., Les relations entre la végétation et les spectres polliniques en forêt du Mont Dieu. Bull. Soc. r. Bot. Belg. *94* (1962) 131–138.
41 Nilsson, S., Praglowski, J., and Nilsson, L., Atlas of Airborne Pollen Grains and Spores in Northern Europe, p. 159. Natur och Kultur, Stockholm 1977.
42 Nilsson, S., and Spieksma, F. Th. M., Traveller's Allergy Service, p. 120. Palyn. Lab. Swed. Museum of Natural History and Fisons Sweden AB Stockholm 1992.
43 Pasteur, L., Examen au microscope des particules solides disséminées dans l'air atmosphérique. Annls Chim. Phys. 3e sér. *64* (1862) 5–110.
44 Peeters, A., Pollenflug in der Schweiz 1988, p. 55. Ed. Schweiz. Arbeitsgruppe für Aerobiologie, Zurich 1988.
45 Peeters, A., Pollenflug in der Schweiz 1989, p. 72. Ed. Schweiz. Arbeitsgruppe für Aerobiologie, Zurich 1989.
46 Peeters, A., Pollenflug in der Schweiz 1990, p. 52. Ed. Schweiz. Arbeitsgruppe für Aerobiologie, Zurich 1990.
47 Peeters, A., Pollenflug in der Schweiz 1991, p. 54. Ed. Schweiz. Arbeitsgruppe für Aerobiologie, Zurich 1991.
48 Peeters, A., Pollenflug in der Schweiz 1992, p. 41. Ed. Schweiz. Arbeitsgruppe für Aerobiologie, Zurich 1992.
49 Philippi, E., Ueber den Blütenstaub in der Luft von Frankfurt a.M. Diss. Frankfurt 1-66 (1960).
50 Pohl, F., Die Pollenerzeugung der Windblütler. Eine vergleichende Untersuchung mit Ausblicken auf die Bestäubung der tierblütigen Gewächse und die pollenanalytische Waldgeschichte. Untersuchung zur Morphologie und Biologie des Pollen VI., Beih. Bot. Centbl, *56/A* (1937) 365–470.
51 Pouchet, F. A. (ca. 1860), Bau eines Aeroscopes zur Luft-Partikel-Untersuchung. Described in Miquel, P., Les Organismes Vivants de l'Atmosphère. Gauthier-Villars. Paris 1893.
52 Pouchet, F. A., Corps organisés recueillis dans l'air par les flocons de neige. C.r-Acad. Sci. *50* (1860) 532–534.
53 Rapp, D., and Frankland, A. W., Allergie, Fragen und Antworten, translated, completed and enlarged by G. Boehm with collaboration of R. M. Leuschner, G., pp. 299. Thieme Verlag, Stuttgart/New York 1988.
54 Risbeth, J., Detection of viable Airborne Spores in Air. Nature *181* (1958) 1549.
55 Rossignol, M., Sédimentation palynologique récente dans la mer morte. Pollen et Spores *11* (1969) 17–38.
56 Sakagami, J., On the structure of atmospheric turbulence near the ground. Cited after: Harrington, J. B., Gill, M. A., and Warr, B. R., High efficiency pollen-samplers for use in clinical allergy. (J. Allergy *30* (1959) 357–375).
57 Stanley, R. G., and Linskens, H. F., Pollen, Biologgy, Biochemistry, Management, p. 307. Springer Verlag, Berlin 1974.
58 Stix, E., Vorkommen von Pollen und Sporen in der Luft, in: Allergie durch Pollen und Sporen. Ed. Landes, E., and Ziegler, H., Kommission zur Erforschung der Luftverunreinigungen der deutschen Forschungsgemeinschaft, Mitt. *VI* (1971) 46–73.
59 Stix, E., Pollenkalender. Regionale und jahreszeitliche Verbreitung von Pollen, p. 56. Wissenschaftliche Verlagsgesellschaft, Stuttgart 1981.
60 Tauber, H., A stativ non-overload pollen collector. New Phytol. *73* (1974) 359–369.
61 Traverse, A., and Ginsburg, R. N., Pollen and associated microfossils in the marine surface. Sediments of the Great Bahama Bank. Rev. Palaebot. Palynol. *3* (1967) 243–254.
62 Wasmund, E., Pollenregen auf die ostoholsteinischen Seen und seine Bedeutung für die Pollenanalyse. Centbl. Miner. Geol. Paläont. *B* (1931) 603–617.
63 Welten, M., Beobachtungen des rezenten Pollenniederschlags in alpiner Vegetation. Ber. Geobot. Forsch. Inst. Rübel, Zürich *1949* (1950) 48–57.