# One hundred years of Quaternary pollen analysis 1916-2016

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**Abstract** We review the history of Quaternary pollen analysis from 1916 to the present-day, with particular emphasis on methodological and conceptual developments and on the early pioneers of the subject. The history is divided into three phases – the pioneer phase 1916–1950, the building phase 1951–1973, and the mature phase 1974–present-day. We also explore relevant studies prior to Lennart von Post's seminal lecture in 1916 in Kristiania (Oslo) in an attempt to trace how the idea of Quaternary pollen analysis with quantitative pollen counting and stratigraphical pollen diagrams developed.

**Keywords** Concepts · Gunnar Erdtman · History · Human impact · Johs Iversen · Knut Fægri · Lennart von Post · Methods · Palaeoclimatology · Pioneer, building, and mature phases · Pioneers · Pollen-representation studies · Relative and radiocarbon dating · Quaternary geology · Quaternary pollen analysis · Taphonomy

# Introduction

A two-day symposium entitled ‘Centenary (1916-2016) of Pollen Analysis and the Legacy of Lennart von Post’ at the Royal Swedish Academy of Sciences in Stockholm on 24–25 November 2016 celebrated 100 years of Quaternary pollen analysis (Richards 2017). The seminal lecture given by von Post in Kristiania (Oslo) in July 1916 is universally considered as the beginning of Quaternary pollen analysis as we know it.

We divide our history of Quaternary pollen analysis into three phases – the pioneer phase from 1916 to 1950, the year that Fægri and Iversen published their *Text-book of Modern Pollen Analysis*; the building phase from 1951 to 1973, the year that Birks and West published the symposium volume *Quaternary Plant Ecology*; and the mature phase from 1974 to today. As the subject first developed in Sweden, then in Denmark, Norway, and Finland before rapidly spreading to the rest of Europe and later to North America and the rest of the world, there is an inevitable bias towards Scandinavian pioneers in our history. In its hundred years, Quaternary pollen analysis has changed from being primarily a stratigraphic and relative-dating tool to a botanical and ecological tool. It has also developed close links with archaeology, landscape history, palaeoclimatology, phytogeography, and, more recently, conservation biology, landscape management, restoration ecology, phylogeography, global change biology, ecosystem science and modelling, and ecological theory. Our history concentrates on the methodological and conceptual developments in pollen analysis and its early pioneers. It makes no attempt to review the very many studies in Quaternary vegetational history. It draws, in part, on historical reviews (ESM Table 1) and on obituaries or memoirs of the early pioneers (ESM Table 2).

# Pioneer phase and Lennart von Post 1916–1950

## Lennart von Post 1884–1951

The father of Quaternary pollen analysis was Ernst Jakob Lennart von Post (Fig. 1). He was born on 16 June 1884 in Johannesberg, Lundby Parish, near Västerås in the Swedish province of Västmanland. His father, Carl Fabian von Post, was a judge-advocate in the Swedish Army, who had also worked as a civilian lawyer or as an assistant cantonal judge, as well being a farmer. Lennart von Post’s mother, Beate Jacqueline Charlotte Christiana Nisbeth (known as Jacqueline), died a year after Lennart was born. He had no brothers or sisters and he was mainly brought up by his father. He completed his secondary school education in June 1901 and became a student at Uppsala University in the autumn of 1901 (G Lundqvist 1951; Selling 1951; Manten 1967; J Lundqvist 1996).

**Fig. 1** Lennart von Post (1884–1951): (a) student in Uppsala 1906, (b) archaeological assistant, Tingstäde Lake, Gotland 1927, (c) professor in Stockholm 1929, (d) excursion leader 'Den Store' 1929, (e) field worker 1937 (Selling 1951), (f) excursion leader, Gävleområdet 1938 (Lundqvist 1951), (g) recipient of 'Till Lennart von Post' on the occasion of his 60th birthday 16 June 1944, (h) Lennart's wife Selma 'Tofsy' von Post counting pollen at the Swedish Geological Survey. She probably did much counting for Lennart. (Sources of these images are given in ESM Table 14)

Von Post planned to study zoology but he quickly became fascinated by geology through the lectures of Arvid Högbom who together with Svante Arrhenius developed the concept of the geochemical carbon cycle. von Post also established close contacts with the stimulating botanist Rutger Sernander who had extended the ideas of the Norwegian botanist Axel Blytt about Holocene climate change (Blytt 1876) to create the Blytt-Sernander scheme (Sernander 1890, 1894) for Holocene climate history that became the major paradigm of Holocene climate change until about 1960 (HJB Birks 2008). As a result of a lecture on 5 March 1902 by Sernander about

Gotland marshes, von Post began work on the developmental history of Mästermyr with Jakob Ljungqvist. This was von Post's first research project and resulted in his first two publications (von Post 1903a, b). These papers were important as they described layers of *Littorina* shells in exposures that provided estimates of isostatic rebound and evidence for Holocene transgressions in southern Sweden (von Post 1933a; Lundqvist 1951; Selling 1951; Manten 1967).

von Post earned his Fil. kand. (similar to a Bachelor's degree) in 1904 and his Fil. lic. (roughly comparable to a Master's degree) in 1907. His Fil. lic. thesis concerned mires in Norrland. In trying to develop a chronological scheme for their history, von Post encountered major problems as there were no archaeological finds or former shore-lines to provide a relative chronology. In this study, von Post extrapolated ages but he doubted if his age estimates were reliable. Despite these limitations, he was awarded the Linnaeus Prize in 1906 by the Royal Swedish Academy of Sciences at the young age of 21 (Lundqvist 1951; Selling 1951; Manten 1967). He worked as an Amanuens (= assistant) at Uppsala's Mineralogical-Geological Institute in 1903–04 and 1907. He was appointed Geologist at the Swedish Geological Survey in 1908 and later State Geologist 1914–1929 with principal responsibilities for peat inventories and assessing the economic value of Swedish peat deposits (Nordlund 2014, 2017). He left the Survey in 1929 to become Professor of General and Historical Geology at Stockholm Högskola (now Stockholm University) where he worked until his death on 11 January 1951 (G Lundqvist 1951; Selling 1951; J Lundqvist 1996; Nordlund 2017). He was awarded an honorary doctorate by Stockholm Högskola in 1927, the University of Königsberg (now Kaliningrad) in 1941, and the University of Copenhagen in 1950. He was elected a member of the Royal Swedish Academy of Sciences in 1939. He was also appointed Knight of Vasorden (1922) and Commander of Nordstjärneoden (1948). He was awarded the Sixten Heymens prize in 1941 and the Vega Medal by the Swedish Anthropological and Geographical Society in 1944 (Lundqvist 1996).

## The beginnings of pollen analysis

In his early work on mires in Norrland, Gotland, and Närke, von Post studied peat stratigraphy and entrained macrofossils (mainly wood and vegetative remains) and made detailed stratigraphical sections across mires. In his work in the province of Närke, west of Stockholm, he questioned whether Sernander's assumption that layers of tree stumps preserved in the peat were synchronous. von Post had been fascinated by the Swedish botanist Gustaf Lagerheim's (1902) observations about pollen being preserved in peat (de Klerk 2017). To resolve the synchrony or otherwise of the tree layers, von Post began to use pollen stratigraphy, leading to the identification of the 'spruce-pollen boundary' which he used for local correlations (von Post

1909; Manten 1967). Lagerheim, a skilled microscopist, analysed not only pollen but also rhizopods, diatoms, and other algal remains. His results were included in Witte (1905) and Holst (1909), who published age estimates for the Holocene. These were based in part on detailed pollen analyses by Lagerheim from the Kallsjö mire in Skurup (Scania). For two levels, Lagerheim made percentage calculations for *Pinus, Betula, Alnus,* and *Ulmus* (all decreasing upwards), for *Fraxinus, Quercus,* and *Tilia* (all increasing upwards), and for *Corylus* (not included in the pollen sum). Holst was very impressed by Lagerheim's results and wrote that "this was a certain method for following carefully, with the aid of a microscope, layer after layer of both the immigration of all plants of which pollen or spores occur fossilised and also alterations with respect to the relative numbers of these plants" (translated from Swedish by Manten 1967 pp. 17-18).

Initially von Post continued to use his 'spruce-pollen boundary' but gradually he realised that it was insufficient by itself. To study if Carl Albert Weber's peat-stratigraphic 'Grenzhorizont' really existed in Närke mires, von Post (1913) prepared a table of *Picea/Pinus* ratios in successive layers, following Weber's (1893) first ever quantitative palynological study (de Klerk 2017). When von Post tried to use the same approach in Scania, he encountered problems. He looked instead for a beech (*Fagus*) pollen boundary but this was unsatisfactory, so he started counting all the arboreal pollen. He obtained good material and satisfactory results in 1915 from Bjärsjölagård mire in southern Scania. He was so pleased with these results that he re-analysed his material from Närke (Manten 1967).

The scene was thus set, as a result of the pioneering studies of Weber, Lagerheim, Blytt, Sernander, Holst, Witte, and others, for von Post's presentation of pollen analysis to a wide audience at the 16th Scandinavian Meeting of Natural Scientists in Kristiania (now Oslo) held on 10-15 July 1916 (de Klerk 2017). The text of von Post's lecture "Skogsträdpollen i sydsvenska torvmosselagerfölder" (Forest tree pollen in south Swedish peat deposits) was not published until two years later (von Post 1918). The first pollen diagrams published by von Post are in a study of the history and development of spring mires ('Quellmoore') in southern Sweden (von Post 1916a). von Post repeated his Kristiania lecture in November 1916 in Stockholm and an extended 6-page summary of this lecture was published (von Post 1916b) along with important discussions between von Post and the Swedish forester Henrik Hesselman (Hesselman 1916; see Malmström 1943, 1944), and also with Gustaf Lagerheim, Henrik Munthe, and Gerard de Geer. The questions raised by Hesselman (1916) about how to distinguish long-distance pollen from pollen from small local tree stands (Hesselman 1919a, b; Nordlund 2014) and about the complex mathematical properties and ecological interpretations of 'closed' percentage data have been frequently revisited by pollen analysts (e.g. Fægri 1947; Fagerlind 1949, 1952; Davis 1963, 2000; Fægri and Iversen 1964; Livingstone 1968; Andersen 1970; Birks and Gordon 1985; Prentice and Webb 1986; Sugita 1994).

Von Post's 1916 lecture outlined the principles of pollen analysis, the methodology of pollen analysis, dating problems, counting statistics and presentation of results, problems of pollen transport and preservation and the differential representation of taxa, the robustness of pollen-analytical data as shown by two pollen diagrams from the same site in Scania, problems in interpretation, and approaches to synthesising pollen-analytical data including compiling an 'average' pollen diagram based on many sites ('pollen-analytical skeleton for south Sweden') (von Post 1918). The paper is a *tour de force* (Edwards 2017) and fortunately, 50 years later, it was translated into English by Margaret Bryan Davis and Knut Fægri (von Post 1967). In these lectures von Post illustrated not only the temporal dimension of pollen-analytical data but also their spatial dimension by means of a large wall-chart (Fig. 2) and associated map (Fries 1967). This wall-chart and map were not published in von Post (1918, 1967) but they are briefly described. The wall-chart presents pollen-analytical data from 13 sites on a south to north transect from north-east Denmark to southern central Sweden running through the *Fagus sylvatica* region of Denmark and southern Scania, across the southern limits of *Picea abies*, to the northern border of *Quercus*. The separate pollen diagrams from these sites were published later in different formats (e.g. von Post 1924, 1926a). The only chronological reference level to link the diagrams was Weber's 'Grenzhorizont' of about 2500 yr BP. This wall-chart (Fig. 2) or 'time–space' diagram demonstrated not only von Post's scientific motto of "think horizontally, work vertically" (Edwards et al. 2017; Richards 2017) but also the potential of pollen analysis as a means of reconstructing past vegetation patterns in both time and space. This potential was later exploited fully in the famous Itasca transect of pollen sites across the prairie–savannah–deciduous forest–coniferous forest transitions in north-west Minnesota (McAndrews 1966). von Post concluded his 1916 lecture by suggesting "I consider that this category of fossils [pollen], hitherto rather overlooked, can indeed, through systematic treatment, considerably widen our knowledge of the Late Quaternary deposits and their history" (Fries 1967 pp.12-13; von Post 1967 p.401).

In terms of the history and development of pollen analysis after the 1916 lectures by von Post, the 1920s witnessed many palynological investigations of forest history and mire development in Sweden as a result of the extensive inventory of south Swedish peatlands (von Post and Granlund 1926; von Post 1926a; Granlund 1932) conducted to assess the economic value and extent of peat resources (Nordlund 2014, 2017). von Post (1924) pioneered the mapping of pollen-analytical data using the massive amount of such data for southern Sweden. His 1924 maps for the major tree taxa agree remarkably well with the recent European-scale maps of Brewer et al. (2016). He also linked pollen analysis with archaeological investigations (von Post et al. 1925). During his last 25 years he did much research on Holocene shore displacement along the west coast of Sweden (von Post 1933a, 1947; G Lundqvist 1951; J Lundqvist 1996).

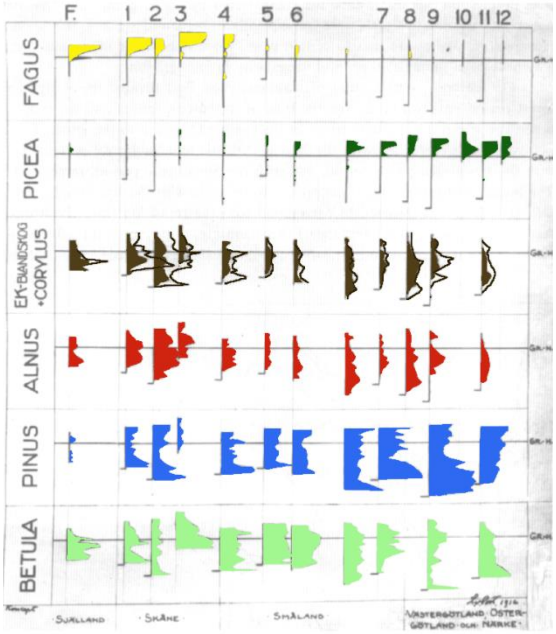

**Fig. 2** von Post's wall-chart used in his 1916 lecture of a series of pollen diagrams from north-east Denmark (site F) to Närke (sites 11, 12) in south-central Sweden. GR-H = Grenzhorizont. that separates the highly humified sub-Boreal peat from the overlying poorly humified sub-Atlantic peat. EK-Blandskog + Corylus = *Quercus* + *Ulmus* + *Tilia* + *Corylus* pollen. The four regions indicated at the bottom of the diagram are Själland (Denmark), Skåne, Småland, and Västergötland + Östergötland + Närke. von Post's signature is at the bottom left. (Sources of these images are given in ESM Table 14)

## The international 'explosion' of pollen analysis

Pollen analysis continued to evolve and it was quickly taken up in the Nordic countries of Denmark (e.g. Jessen 1920), Færoe Islands (Jessen and Rasmussen 1922), Norway (Holmsen 1919, 1920a, b), and Finland (Auer 1921). In the early-1920s pollen analysis spread rapidly outside Norden as a technique for investigating mire and forest history (ESM Table 3). This spread is described by Fægri (1973) as "the explosion" and is detailed by Erdtman (1943a). In the late 1920s pollen analysis had reached New Zealand and the Americas (e.g. Erdtman 1924a, 1943; von Post 1929; Selling 1951; Markgraf 2016). The first studies in North America were made by Auer (1927) on bogs in south-eastern Canada. The earliest North American palynologists were Patricia Draper (Draper 1929) and Ivey F Lewis and EC Cocke (Lewis and Cocke 1929), followed by Paul B Sears (Sears 1930) and others (see Davis 2004). It is testimony to the determination and skills of the early pioneers that even in the 1920s and early 1930s, pollen-analytical studies were being made on interglacial sediments worldwide (ESM Table 4).

Some of the most influential pioneering pollen analysts involved in this 'explosion' are shown in Figs. 3–5. Their obituaries or memoirs are listed in ESM Table 2.

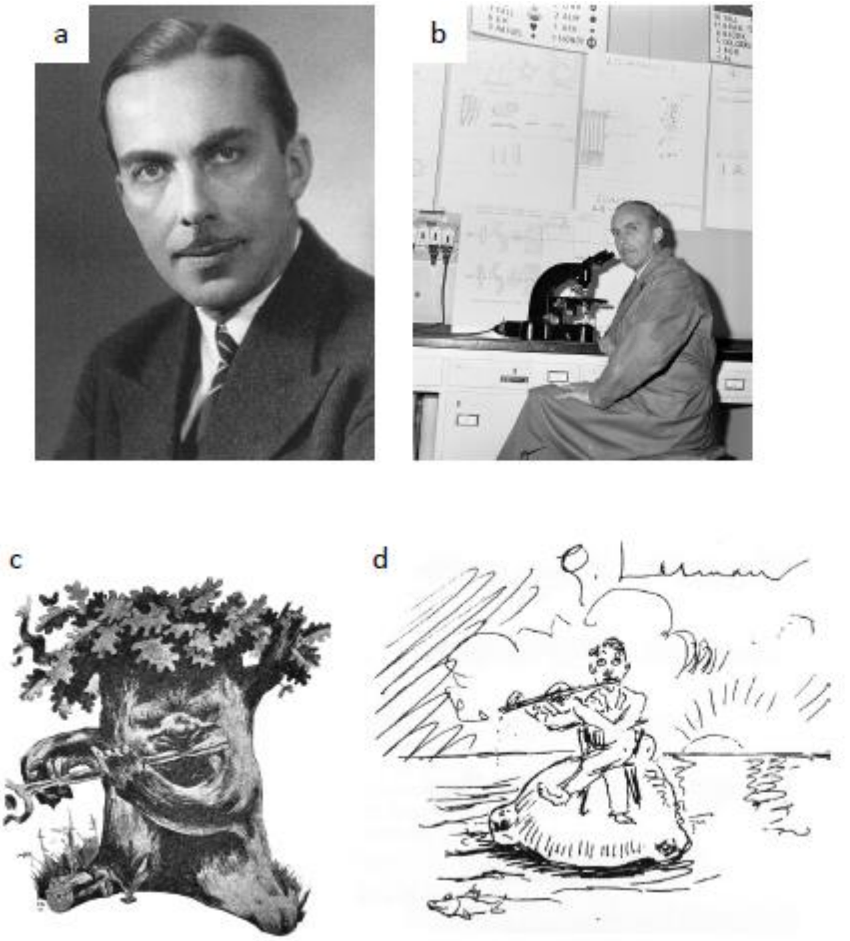

**Fig. 3** Gunnar Erdtman (1897–1973): (a) at the time of his doctoral thesis defence 1921, (b) in his newly-created Palynological Laboratory in 1950, (c) self-portrait as a wood-gnome playing a flute (Erdtman's favourite musical instrument) presented as an end-plate in his 1943 book, (d) self-portrait playing the flute whilst sitting on a *Betula* pollen grain drifting into the sunset, given as a thank-you note in 1967 to John Rowley, an American electron microscopist who worked with Erdtman in the 1960s and succeeded Erdtman as head of the Stockholm Palynological Laboratory in 1969. (Sources of these images are given in ESM Table 14)

## Gunnar Erdtman 1897–1973 – palynology's 'evangelist'

In Sweden, Gunnar Erdtman (Fig. 3) was the first to be attracted by von Post and the pollen-analytical method. In 1918 as a 21-year-old student, he was one of von Post's field assistants doing peat inventories in southern Sweden. Erdtman (1967) describes this in a characteristically lively way. Perhaps the major event in palynological history in the 1920s was the defence by Erdtman of his doctoral thesis *Pollenanalytische Untersuchnungen von Torfmooren und Marinen Sedimenten in Südwest-Schwede*n (Erdtman 1921). This and Erdtman (1920) are the first major palynological publications in an international language (Fægri 1973). In Erdtman's thesis there is a chapter on 'Die pollenanalytische Arbeitsmethode nach L. von Post'. Lagerheim and von Post were the opponents (examiners) and neither of them, according to Erdtman (1967), objected to this chapter or to much of the thesis. However, relationships between von Post and Erdtman were not good and Erdtman (1967 p.25) notes that "During the thirty years that elapsed from the publication of the thesis up to Lennart von Post's death in 1951, I had practically no contacts with him". After his thesis defence, Erdtman embarked on a 'grand tour' of north-west Europe sampling peat sections and reconstructing Holocene forest history in the British Isles (Erdtman 1924b, 1927, 1928a, 1929), north-west Germany and Holland (Erdtman 1928b), and Belgium and France (Erdtman 1928c). These papers were written in English, German, and French, respectively. Erdtman's linguistic skills and international publications contributed greatly to the internationalisation of Quaternary pollen analysis. Marshall (2005) describes Erdtman as the "palynological evangelist"! For example, as a result of Erdtman's visits in the early 1920s and his own investigations in the British Isles (Anonymous 1924; Cheetham 1925), Quaternary palynology quickly developed there by pioneers such as Arthur Raistrick (Marshall 2005; Edwards 2017), Thomas Woodhead (Woodhead 1923; Woodhead and Erdtman 1926; Edwards 2017), and Charles B Travis (Edwards 2017). At the suggestion of the English ecologist Arthur Tansley, Margaret Godwin started pollen analysis in Cambridge in 1931, and her husband Harry (Fig. 5e) soon became deeply involved (Godwin 1934a, b, 1968, 1978, 1981). Edwards (2017) discusses further the pioneering palynologists in the British Isles and the influence of Erdtman on many of these pioneers.

Erdtman's areas of study continued to widen to include parts of Russia, Canada, and United States. His last stratigraphical pollen diagram was prepared in 1931 from Twin Lakes Muskeg in north-west Minnesota (McAndrews 2006). Erdtman's site is now known as Twin Lakes Muskeg Bog D, one of the sites (Bog D) in McAndrews' (1966) Itasca study. Erdtman advised Jock McAndrews (Fig. 7c) in 1962 that "if you want to be famous you should not do pollen analysis, you should do pollen systematics" (McAndrews 2006). McAndrews remains a pollen analyst whereas Erdtman switched in 1931 to pollen morphology and systematics. Although being 'exiled' (Fægri 1973) he continued to improve laboratory techniques (e.g. Erdtman 1935, 1938). In the 1930s he taught in different high schools in Sweden (Fægri 1973; Edlund and Winthrop 2014). Fægri (1973) and Edlund and Winthrop (2014) discuss possible reasons why Erdtman was 'exiled'. Edlund and Winthrop (2014 p.6) suggest "As foreign attributions and citations of Erdtman's work grew, his relations with von Post became strained, lost cordiality, and never recovered". Fægri (1973 p.6) notes "Everything pointed to Erdtman becoming the crown prince of pollen analysis … [but] being cut off from the only laboratory where he should have been , he was doubly exiled from Academe to school teaching and also from the scientific centres of Stockholm–Uppsala". Erdtman must have had great personal strength to continue to research but he apparently believed that his predicament was only temporary (Edlund and Winthrop 2014). In his 14 years as a high-school teacher with no laboratory or administrative support but with his own much-used monocular Leitz microscope, Erdtman continued to publish important articles on pollen analysis (e.g. Erdtman 1937) and compile his invaluable bibliographies of recent palynological literature (see Erdtman 1943a for details). He built up an extensive modern pollen reference collection of 12,000 species whilst 'exiled' (Edlund and Winthrop 2014). Edlund and Winthrop (2014 p.8) suggest "von Post seems not only to have diverted the initial trajectory of Erdtman's career but to have had an ongoing and malign influence on his reputation (Fægri 1973, Hedberg 2000)". von Post even published a scathing review in Stockholm's main newspaper titled "A senseless poster series" about a high-school poster about forest history with illustrations of pollen grains by Erdtman (Edlund and Winthrop 2014).

In 1933 Erdtman and his brother Holger who was a chemist developed the acetolysis method in sample preparation (Erdtman and Erdtman 1933), a technique that is widely used today (Erdtman 1960). In 1943 he published *An Introduction to Pollen Analysis*, one of the first textbooks for Quaternary palynologists (Erdtman 1943a), a year after Bertsch's (Fig. 5a) (1942) handbook about pollen analysis appeared. Erdtman was very surprised to receive a letter from von Post in 1944 congratulating him on his 1943 book. von Post wrote "I congratulate you on your pollen bible. For the first time in my experience, I was able to identify pollen from illustrations alone, without needing reference to legends. Surely the book will come to be very useful for future research." (Edlund and Winthrop 2014 p.9). Erdtman quoted this letter in correspondence to the editor of the book series that published his 1943 book. "Godwin in his review in Nature, was very content with the book, and so is my (previously) bitter and violent antagonist Professor von Post. I am glad that I am able to say that I today received a very friendly letter from him expressing congratulations and unanimous gratitude. All people here, who know the situation between 'Erdtman' and 'von Post' must say that this means nothing less than a wonder!" (Edlund and Winthrop 2014 p.9). With the establishment of the Palynological Laboratory at Solna in 1948, Erdtman was appointed its Director and the title of Professor was conferred on him in 1954 (Gullvåg 1972; Fægri 1973; Jonsell 2007). His work concentrated on pollen morphology and pollen structure and resulted in many important monographs that form an essential part of a palynologist's library (e.g. Erdtman 1952, 1966, 1969, 1972a; Erdtman et al. 1961, 1962).

Erdtman was a person of many parts – palynologist, teacher, author, artist, and musician. He played the flute in the Academic Orchestra in Stockholm when he was a student. According to Sears (1943-54 p.7), when doing fieldwork in the muskeg bogs of northern Canada in the summer of 1930, Erdtman had his flute with him "doubtless hoping to mollify the savage mosquitoes with the sweet strains of Swedish folk music." Erdtman possessed an artist's perception of form (Fægri 1973) and there is a famous, surrealistic self-portrait as a wood gnome playing a flute at the back of his 1943 book (Fig. 3c). Erdtman's father, Elias Erdtman, was a well-known landscape painter who studied in France at the height of French impressionism. There were also artists on his mother's side (Traverse 2007; Booth 2013). There are many articles about Erdtman, his urbane personality, his evangelic zeal for pollen studies, and his many contributions to palynology and art – Gullvåg (1972), Fægri (1973), Hedberg (2000), Booth (2013), and Edlund and Winthrop (2014) are particularly interesting. He contributed greatly to the development of Quaternary pollen analysis. Fægri (1973 p.6) commented "No wonder that in wide circles [Erdtman] was considered as 'Mr Pollen analysis', shadowing out the more distant figure of the Grand Master [von Post] himself". Thinking ahead 49 years, Erdtman even extended a "hearty invitation to you, your children and grandchildren to attend the First Centenary of Modern Sporology. Welcome to Stockholm in August 2016!" (Erdtman 1967 p.29). It is not surprising that the fourth edition of the *Textbook of Pollen Analysis* (Fægri et al. 1989) is dedicated to the memory of Gunnar Erdtman.

## The 1933 Baltic Course, Knut Fægri and Johannes Iversen, and later methodological developments

An important event in the development of Quaternary pollen analysis occurred in 1933 (Fægri 1981). This was the so-called Baltic Course on pollen analysis organised by the Baltic Committee whose aim was to promote cultural interactions across the Baltic. The 1933 course was on pollen analysis with von Post as the course leader and main teacher, along with short courses by Bertil Halden (diatoms), Erik Granlund (peat stratigraphy), Gerard de Geer (sediment varves), and Rutger Sernander (botanical excursion: Fig. 6). The course participants were primarily young geologists with some botanists from Lithuania (2 participants), Latvia (1), Estonia (1), Finland (2), Sweden (2: Sten and Maj-Britt Florin), Norway (1: Knut Fægri (Fig. 4d)), Denmark (1: Johannes (Johs) Iversen, commonly known as 'Iver' (Fig. 4b)), and Iceland (1). Fægri (1981 p.42) always maintained that he had been included "more or less accidentally". This was a most fortunate accident because as a result of the course Fægri developed a life-long friendship and collaboration with Iversen, and also a close friendship with Maj-Britt Florin. Fægri and Iversen shared a room and towards the end of the course they hatched a plan to write a small monograph about pollen analysis, not primarily as a geological dating tool as it had been developed and used by von Post and taught as such on the course, but as their vision of pollen analysis – as an ecological tool for studying floristic and vegetational history, as well as long-term vegetation dynamics and human impact on vegetation. We will return to this below.

**Fig. 4** Six of the most influential Scandinavian pollen analysts in the 1930s–1990s who all made major contributions to the development of Quaternary pollen analysis. (a) Knud Jessen (1884–1971), (b) Johannes Iversen (1904–1971), (c) Tage Nilsson (1905–1986), (d) Knut Fægri (1909–2001), (e) Jørgen Troels-Smith (1916–1991), (f) Svend Th Andersen (1929–2009). (Sources of these images are given in ESM Table 14)

Soon after the course, Fægri and Iversen took up pollen analysis seriously in their respective countries and produced important and highly original publications – Fægri (1935, 1940, 1943, 1945) on the Holocene and late-glacial vegetational history of western and central southern Norway and Iversen on the vegetational history of Greenland (Iversen 1934), secondary redeposited pollen in Danish late-glacial sediments (Iversen 1936), late-glacial vegetational history of Nørre Lyngby and Bølling Sø (Iversen 1942), and perhaps most importantly, land occupation ('landnam'; land-taking) in Denmark's Stone Age and the influence of prehistoric people on vegetational development (Iversen 1941). Iversen's (1941) interpretation was generally accepted although Nilsson (1948) argued for a climatic interpretation. Iversen responded immediately (Iversen 1949) and since then early human impact on the landscape has been widely accepted. Iversen's 1941 paper is one of the first palynologial publications to apply the method of multiple working hypotheses (Chamberlin

1890). In this study, Iversen made major methodological advances including improved pollen identifications, developing stratigraphical charcoal analysis, using AP/NAP ratios (Firbas 1934a), estimating pollen concentrations, and coring lake sediments to avoid 'local' factors associated with pollen studies from peat bogs. Iversen's (1941) work was greatly inspired by Firbas (1937) who showed how cereal pollen could be determined (see Erdtman (1972b) for a perspective on Iversen's (1941) classic landnam study).

Besides the various publications by Iversen and Fægri, there were several other important developments in the 1930s and 1940s. In Sweden, Tage Nilsson (Fig. 4c) became inspired by von Post during von Post's visit to Lund in 1926 (von Post 1926b). Nilsson defended his doctoral thesis at Lund University on *Die pollenanalytische Zonengliederung der spät- und postglazialen Bildungen Schonens* in which he correlated pollen zones with the archaeological time scale to develop a complete Holocene chronology for Scania (Nilsson 1935). von Post acted as the first opponent and Knud Jessen from Copenhagen was the second opponent. von Post heavily criticised Nilsson, mainly about the chronology proposed by Nilsson whereas Jessen was very positive. The result of von Post's harsh criticisms led to Nilsson leaving Lund and going into 'exile' as a teacher in various schools in the Stockholm region. He returned to Lund in 1949 when he was appointed Laborator/Professor in Quaternary Geology. von Post was a member of the evaluation committee for this position and the committee placed Nilsson in second place. Nilsson objected and the faculty accepted his well-motivated and detailed complaint which was a great personal victory for Tage Nilsson and Lund geology. He was then able to develop teaching and research in Quaternary geology in Lund for more than 20 years. Lund is now one of the leading centres for Quaternary geology in Scandinavia. With the advent of radiocarbon dating Nilsson (1964) was able later to provide an absolute chronology for the Scanian Holocene pollen stratigraphy at Ageröds Mosse in central Scania.

In Switzerland, Welten (Fig. 5g) (1944) developed techniques for estimating absolute pollen-accumulation rates ('pollen influx') using annually laminated sediments at Faulensemoos in the Bernese Oberland (see below). He was able to demonstrate for the first time tree-pollen changes in the late-glacial and early Holocene free of the constraints of 'closed' percentage calculations (see Deevey 1946; Conway 1948; Watts 1973). Pollen analysis was increasingly being done throughout Europe (see Iversen 1967, 1973; Godwin 1968; Lang 1994 for historical reviews) and in North America (Sears 1943-54; Davis 2004) with much activity by John Potzger, Henry Hansen, Paul Sears (Fig. 5d) (e.g. Sears 1932, 1948, 1952; see Shane 2010), Stanley Cain, and Edward Deevey (Fig. 5i) (e.g. Deevey 1939, 1943).

**Fig. 5** Nine very influential non-Scandinavian pollen analysts in the 1930s–1960s who all made major contributions to the development of Quaternary pollen analysis. (a) Karl Bertsch (1878–1965), (b) Karl Rudolph (1881–1937), (c) Władysław Szafer (1886–1970), (d) Paul Sears (1891–1990), (e) Harry Godwin (1901–1985), (f) Franz Firbas (1902–1964), (g) Max Welten (1904–1984), (h) Lucy Cranwell (1907–2000), (i) Edward Deevey (1914–1988). (Sources of these images are given in ESM Table 14)

Following the basic assumption of methodological uniformitarianism (sensu Gould 1965) in historical sciences that the present is the key to the past, several important pioneering studies were made on modern pollen deposition in relation to contemporary vegetation in arctic and subarctic areas of northern Finland (e.g. Firbas 1934a; Aario 1940, 1944). They showed that modern pollen spectra corresponded well with the surrounding vegetation in the *Pinus–Picea, Pinus, Betula–Pinus,* and *Betula* forest and subarctic *Betula* scrub zones but in treeless tundra *Pinus* was the dominant pollen type despite the absence of nearby pine trees. This was one of the first demonstration of 'false presences' (sensu Birks 2014) in pollen spectra (Fægri 1981). Aario also estimated pollen concentrations of the surface peats and showed that concentrations decreased from the *Pinus* zone to the tundra. He concluded that the high *Pinus* percentages in the tundra resulted from long-distance transport of *Pinus* pollen into a landscape with a very low local pollen production. This work remains of fundamental importance in the critical interpretation of late-glacial and full-glacial pollen spectra (HJB Birks 1973a; Fægri 1981).

With the large number of pollen-analytical investigations being published in the late 1920s and early 1930s (e.g. Bertsch 1924, 1931; Rudolph et al. 1928; Rudolph 1932; Firbas 1934b, c), attempts began to synthesise the results from these studies in terms of forest history (e.g. von Post 1924, 1929, 1930; Lundqvist 1928; Rudolph 1930; Godwin 1934a, b, 1940; Firbas 1934c; Bertsch 1935, 1940) An important development in such syntheses was made by Szafer (Fig. 5c) (1935) when he introduced isopollen contours to show spatial patterns in pollen values of a particular taxon at a certain time. This approach was used by Firbas (Fig. 5f) (1949) in his synthesis of the vegetational history of central Europe and later by, for example, Bernabo and Webb (1977) for the Holocene of eastern North America; by Huntley and Birks (1983) in their pollen maps at the European scale over the last 13,000 years; and by Ralska-Jasiewiczowa (1983) and Ralska-Jasiewiczowa et al. (2004) in detailed pollen maps for Poland.

The British plant cytologist Kathleen B Blackburn (Valentine 1970; Edwards 2017) visited von Post in the early 1930s and soon began to publish results of pollen-analytical studies primarily from northern England (e.g. Raistrick and Blackburn 1932; Blackburn 1952, 1953) and also from the Outer Hebrides (e.g. Blackburn 1946; Heslop Harrison and Blackburn 1946)

The Scottish pedologist George K Fraser from Aberdeen (Edwards 2017) worked with von Post in 1936 and whilst there analysed two pollen sequences from Scotland (Fraser and Godwin 1955). Data from one of Fraser's sites, Strichen Moss (Aberdeenshire), were used by von Post in his Vega lecture publication (see below and von Post 1944, 1946). Fraser conducted a major survey of peat deposits in Scotland (Fraser 1943, 1948) and studied Scottish moorlands with respect to tree growth (Fraser 1933) and the role of tree roots on the field layer in Scottish pine woods (Watts and Fraser 1933). Given his interests in peatlands and forests, it is not surprising that Fraser went to Stockholm to learn pollen analysis from von Post.

The energetic and adventurous New Zealand ecologist, palaeobotanist, and conservationist Lucy Cranwell (Fig. 5h) (Davis 2001) was invited by von Post to visit Stockholm in the winter of 1935-36. Together they studied peat samples collected from South Island, New Zealand by Carl Caldenius in 1934 and produced the first complete Holocene pollen stratigraphies from Australasia (Cranwell and von Post 1936). Erdtman had already published results of scattered pollen counts from New Zealand (Chatham Islands, Otago district, The Snares, Antipodes Islands) in the mid-1920s (Erdtman 1924a, 1943a). Summaries of Cranwell's pollen diagrams were included in von Post's Vega lecture publications (see below and von Post 1944, 1946). Cranwell's later palynological work was on pollen morphology and pre-Quaternary pollen and microplankton (Davis 2001).

It is not known whether Blackburn, Cranwell, and Fraser were the only scientists from outside Fennoscandia or the Baltic countries to study with von Post.

On the occasion of von Post's 60th birthday on 16 June 1944, twenty colleagues from the Nordic countries presented von Post with a Festschrift volume published as a special issue of *Geologiska Föreningens i Stockholm Förhandlingar*. Interestingly there is a short paper by Erdtman (1944) on botanical pollen analysis in which he discusses ecological bases for presenting pollen-analytical results, pollen morphology of *Myrica gale* and *Corylus avellana*, and problems in interpreting *Artemisia* pollen values. Eighteen of the papers are written in Swedish or German. The two articles in English are the classics by Iversen (1944) on *Viscum, Hedera*, and *Ilex* as climate indicators and Fægri (1944) on the introduction of agriculture in western Norway. They were already planning their textbook on pollen analysis and were keen to make their innovative ideas and work accessible to a wide international readership (K Fægri 2000, pers. comm.).

## Lennart von Post and The prospect for pollen analysis in the study of Earth's climatic history

The large number of pollen-analytical studies in Europe, the Americas, and New Zealand made in the 1920s-1940s, although rather rudimentary by modern standards, laid the foundation for von Post's (1946) masterly synthesis on *The prospect for pollen analysis in the study of the Earth's climatic history* along the lines of von Post (1933b). This global synthesis was based on the lecture von Post delivered when he was awarded the Vega Medal by the Swedish Anthropological and Geographical Society in 1944 (von Post 1944). In this far-ranging and forward-looking lecture, von Post (1946 p.179) emphasised that pollen analysis is "the most complete and most realistic register of climatic fluctuations throughout the past which we now have at our disposal". By developing the concepts of revertence and regional parallelism—where the same overriding climatic change will be reflected in different ways by different taxa in different geographical and climatic regions (HJB Birks 2008)—he proposed, based on pollen diagrams from Europe, New Zealand, Tierra del Fuego, North America, and Hawaii, that there is a consistent three-fold division of Holocene pollen stratigraphies – i) a protocratic period of increasing warmth, ii) a mediocratic period of culminating warmth, and iii) a terminocratic period of decreasing warmth. Although von Post (1944, 1946) does not openly criticise the Blytt-Sernander phases of climatic stages (von Post was a former student of Rutger Sernander and a strong supporter of Sernander in the bitter 20-year feud between Sernander and Gunnar Andersson in the early 1900s (see HJB Birks 2008; Birks and Seppä 2010), as well as a co-author with Sernander (von Post and Sernander 1910)) he appears to have discretely modified his general views towards Andersson's (1902, 1909) idea of a mid-Holocene warm period. von Post (1944, 1946) recognised that there were fluctuations in climate that correspond to the Blytt-Sernander phases but these were small fine-scale precipitation changes compared with the major long-term broad-scale temperature changes proposed by Andersson. This view, obliquely presented by von Post, represents the paradigm of Holocene climatic change that began to develop in the late 1940s despite the widespread adherence to the Blytt-Sernander scheme (HJB Birks 2008; Birks and Seppä 2010).

von Post (1946 p.217) foresaw the need for international collaboration in establishing the global patterns of Holocene climate change and understanding the underlying drivers of change by writing "a plan of work of the extent here sketched can scarcely be carried out without organized international collaboration. At the head of this must stand a scientist with experience, foresight, mental acuity, and activity, and he must be young, for the task is a life's work".

Although von Post (1944, 1946) never mentioned the discovery by Iversen, Fægri, Firbas, and others in the late 1930s and early 1940s that pollen analysis has detected the early impact of prehistoric people on vegetation, he was very aware of the potential role of climate change in human societies and societal change (HJB Birks 2008). For further details of the ideas, methods, and implications of von Post (1946) in the context of Holocene climate research, see Conway (1948) and HJB Birks (2008).

At this time von Post clearly had a 'favourite' protégé, Olof Selling, who was greatly attracted by von Post's vision of Earth's climatic history. Selling and Lucy Cranwell participated on the Hawaiian Bog Survey in the summer of 1938 organised by the Swedish botanist and explorer Carl Skottsberg. The material Selling collected on this expedition formed the basis of Selling's (1948) doctoral thesis. For the thesis defence, Folke Fagerlind (Fagerlind 1949) was the first opponent and he criticised Selling for not considering the sources of error arising from long-distance transport of pollen and differential pollen preservation, for his chronology, and for his climatic interpretation with a three-fold division of the Holocene along the lines proposed by von Post (1944, 1946). Magnus Fries (Fries 1949) was the second opponent and expressed positive opinions about the thesis in contrast to Fagerlind. von Post was the chair of the evaluation committee and Selling's thesis received the highest grade despite Fagerlind's significant criticisms (Wijkander 2017).

**Fig. 6** (a) Members of the Baltic Committee and teachers and students at the Baltic Course 1933. von Post is standing in the back row, third from the right; Iversen is seated on the front row at the extreme left; and Fægri is seated on the front row, second from the right. (b) Fægri (left), Iversen (centre), and the Swedish plant ecologist Einar du Rietz (right) on the field excursion of the Baltic Course. (Sources of these images are given in ESM Table 14)

## Knut Fægri and Johannes Iversen and the Text-book of Modern Pollen Analysis

The pioneer phase in the development of Quaternary pollen analysis came to a close with the publication in 1950 of Fægri and Iversen's *Text-book of Modern Pollen Analysis*. They had planned such a monograph soon after the 1933 Baltic Course but they were both extremely busy with their own innovative pollen-analytical studies that the writing of the book kept getting shelved (K Fægri 2000 pers. comm.). Implementation of their book-writing plans was difficult in wartime Scandinavia with Fægri and Iversen unable to meet because both Norway and Denmark were occupied. Correspondence by letter was tiresome with their letters delayed by wartime censorship or totally lost. In the early post-war years, they were able to meet again regularly and to work hard on completing their book (Fægri 1971). Iversen always said (J Iversen 1969, pers. comm.) that Knut wrote most the book in the days and Iver spent the nights modifying it (and Knut admitted that 'Iver calmed my text down'!) (K Fægri 2000, pers. comm.). Iversen was responsible for the pollen key as he was working on late-glacial pollen assemblages at that time. He and Troels-Smith (Fig. 4e) produced their invaluable monograph on pollen morphological definitions and types (Iversen and Troels-Smith 1950) to provide an unambiguous terminology and to explain the various morphological terms used in the *Text-book*. The Fægri and Iversen (1950) book was dedicated to their Baltic Course teacher Lennart von Post and it represented a paradigm shift in Quaternary pollen analysis. It highlighted the critical importance of meticulous sampling and laboratory preparation, of detailed pollen identifications based on a sound understanding of pollen morphology and careful comparison with authenticated modern reference material, of understanding the statistical background to pollen counting, of rigorous and critical interpretation of pollen-analytical data, and of the need for sound botanical and ecological knowledge in all Quaternary pollen analyses. Both Fægri and Iversen worried about how von Post would receive their book (K Fægri 2000, pers. comm.). They were delighted when in his review (and last publication) von Post (1950) welcomed the new modern botanical pollen analysis and wrote "It can hardly be an exaggeration to characterise the book as the banner for a new era in the science of pollen analysis … I shall leave the pollen statistical stage." (undated translation by K Fægri). A translation of the full review is given in ESM Document 1 as this historic review is not well known amongst palynologists. An updated second edition of the book was published in 1964 retitled *Textbook of Pollen Analysis* (Fægri and Iversen 1964). Major additions included a discussion of Fagerlind's (1952) ideas on the "real signification of pollen diagrams", an expanded pollen key, and special keys for Cyperaceae, Gramineae, Caryophyllaceae, and Plantaginaceae prepared by Iversen. In response to a question on how Fægri and Iversen regarded Erdtman's (1943a) *An Introduction to Pollen Analysis,* Fægri replied "it was useful and good for its time but it was not as critical as Iver and I would have liked it to be." (K Fægri 2000, pers. comm.).

## Conceptual developments

During the 30+ years of the pioneer phase, there were many methodological advances made by, for example, Aario, Erdtman, Fægri, Firbas, Iversen, Szafer, von Post, Welten, and others, as discussed above. At the same time several important conceptual developments were also made. These included exploring modern pollen–vegetation relationships as an aid to interpret pollen-analytical results; demonstrating the impact of prehistoric people on vegetation; exploring not only temporal patterns but also spatial patterns in pollen-analytical results using a range of mapping techniques; reconstructing past climate at a broad scale from pollen-analytical stratigraphies, recognising the importance of revertence and regional parallelism in pollen stratigraphy; and realising the importance of expressing pollen counts not as 'closed' relative percentages but as 'absolute' values either as concentrations (grains per unit volume or weight of sediment) or, more meaningfully, as annual pollen-accumulation rates (grains per unit area per year). However, pollen mapping, correlation of past climatic histories, and 'absolute pollen analysis' were severely hindered by the lack of any independent absolute chronology. Despite the absence of any such chronology, by 1950 Quaternary pollen analysis as presented in Fægri and Iversen (1950) had reached a high level of sophistication in the 34 years since von Post's lecture in Kristiania. We now turn to the second phase, the building phase, from 1951 to about 1973.

## Building phase 1951–1973

### Introduction, internationalisation, and regional monographs

Following the publication of Fægri and Iversen (1950), interest and activity levels in pollen analysis greatly increased in many parts of the world. There was ever-increasing sophistication in methodology and taxonomic and stratigraphical detail. Two important events occurred soon after in 1954. First, the journal *Grana Palynologica, Nova Series* was launched by Almqvist and Wiksell under the editorship of Gunnar Erdtman. This international journal continues today under the title *Grana*. Second, *Studies in Vegetational History in Honour of Knud Jessen* was published on the occasion of Jessen's 70th birthday in 1954. Jessen (Fig. 4a) was the pioneer of pollen analysis in Denmark. His impressive monograph (Jessen 1920), although written in Danish (but with an extensive summary in English), was the first regional palaeoenvironmental synthesis based on vegetation history inferred mainly from macrofossils correlated with archaeology, Baltic Sea development, and climate changes for the last 13,000 years in south-east Denmark. He went on to study in detail freshwater interglacial deposits in Denmark and north-west Germany (Jessen and Milthers 1928). The Jessen Festschrift contains 16 papers that represented state-of-the-art Quaternary palynology in Scandinavia 63 years ago. Several of these papers (e.g. Andersen 1954; Fægri 1954; Iversen 1954; Krog 1954) are outstanding and influential; they directly or indirectly created major research agenda in Quaternary palynology in north-west Europe and eastern North America.

At about this time, two major technological developments were occurring outside pollen analysis that were to have major impacts on the subject. These were the development of radiocarbon dating by Willard Libby and great improvements in light and then electron and scanning microscopy that led to major advances in pollen morphology and identification (e.g. Fægri 1953, 1981; Fægri and Iversen 1964).

**Fig. 7** Pioneers of the Pollen Laboratory (later the Limnological Research Center) at the University of Minnesota created by Herb Wright in 1958. (a) Magnus Fries 1919–1987, the leading Swedish palynologist in the 1950s, who went to Minnesota in 1958 and helped develop the Pollen Laboratory. (b) Edward ('Ed') Cushing, one of the early PhD palynology students in Minnesota who was taught by Magnus Fries and subsequently by Svend Th Andersen in Copenhagen. (c) John ('Jock') McAndrews, another of the early PhD palynology students in Minnesota who was also taught by Magnus Fries. Jock subsequently spent a post-doctoral year with Willem van Zeist in Groningen. (d) William ('Bill') Watts 1930–2010, the leading Irish Quaternary botanist who went to Minnesota in late 1961 and developed stratigraphical plant-macrofossil analysis in Minnesota and elsewhere and made major contributions to understanding the vegetational history of the south-east US. (Sources of these images are given in ESM Table 14)

As interest in pollen analysis increased internationally, many scholars came and studied with Johs Iversen (Fig. 4b), Svend Th Andersen (Fig. 4f), and Jørgen Troels-Smith (Fig. 4e: known as 'Troels') in Copenhagen (e.g. Thomas van der Hammen, Margaret Bryan Davis, Edward J Cushing, Krystyna Wasylikowa, Donald R Whitehead, Björn E Berglund, Magdalena Ralska-Jasiewiczowa, Hilary Birks, John Birks) or with Knut Fægri (Fig. 4d) in Bergen (e.g. Donald R Whitehead, Brigitta Ammann, Sunirmal Chanda, Kazimiera Mamakova). Scandinavian palynologists also visited and worked in American laboratories. For example, Svend Andersen worked in Stanley Cain's lab in Michigan and produced the first detailed late-glacial pollen stratigraphy from the US (Andersen 1954). The American Quaternary scientist Herb Wright established a pollen lab at the University of Minnesota in 1958. On the advice of Iversen, Wright invited Magnus Fries (Fig. 7a) from Uppsala to help build up the lab and to train and advise graduate students such as Ed Cushing (Fig. 7b), Jock McAndrews (Fig. 7c), Lou Maher, Bob Bright, Tom Winter, Harvey Patten, and Anne McKnight (HJB Birks 2017). Fries went to Minnesota in 1958 (HJB Birks 2016, 2017) and was a great success there. He played a major part not only in studying Minnesotan vegetational history but also in developing an important and highly productive pollen centre in the US in the 1960s–1990s (HJB Birks 2017).

During the building phase and the following mature phase, many major monographs were published on regional vegetational history based primarily on pollen analysis (see ESM Table 5 for examples). Several of these monographs also contain valuable pollen-morphological information, as do other monographs published during this phase (e.g. Selling 1946, 1947; Andersen 1961). Such monographs, although considered by some as things from the past, remain major sources of primary data and provide unique insights into fine-scale vegetational differentiation within a region.

## Radiocarbon dating and absolute pollen analysis

There were many methodological and conceptual developments during this phase, as discussed by Birks (2005). The development of radiocarbon dating by Libby in the early 1950s provided a means of deriving an absolute chronology for events in the late-glacial and Holocene. Early radiocarbon datings of pollen-stratigraphical events were made for Allerød sediments in Denmark (Iversen 1953; Krog 1954), for Holocene pollen changes in northern England (Godwin et al. 1957) and southern Sweden (Nilsson 1964), and for late-glacial deposits in Britain (Godwin and Willis 1959). Radiocarbon dating freed pollen analysis from being a relative chronological tool (Godwin 1960; HJB Birks 2008) and allowed the temporal and spatial patterns in pollen stratigraphies to be compared rigorously (Smith and Pilcher 1973; HJB Birks 2005, 2008). If sufficient radiocarbon dates could be obtained for a sequence, sediment-accumulation rates (in cm $yr^{-1}$) could be estimated. These rates could then be used to convert pollen concentrations (in grains $cm^{-3}$) into estimates of pollen-accumulation rates ('pollen influx' – grains $cm^{-2}$ $yr^{-1}$). This was done at Rogers Lake in Connecticut by Davis and Deevey (1964) and Davis (1967a, b). Welten's (1944) pioneering study on pollen influx at Faulensemoos had relied on annual lamination counts to derive estimates of sediment-accumulation rates (Deevey 1946; Conway 1948; Watts 1973). Several studies on pollen influx followed (e.g. Fredskild 1969, 1973; Pennington and Bonny 1970; Craig 1972; Maher 1972; see Birks and Birks 1980 for a review).

## Other methodological developments

### *Field and laboratory techniques*

As pollen analysts began to use lake sediments rather than peat deposits, new lightweight piston corers were developed to permit extracting cores of lake sediment (e.g. Livingstone 1955; Cushing and Wright 1965; Wright 1967, 2010). Coring peat deposits was greatly improved by the use of the so-called 'Russian' peat sampler (Jowsey 1966). Several other coring devices were developed by, for example, Gunnar Digerfeldt, John Mackereth, Josef Merkt, Paul Colinaux, and Harmut Usinger, and continue to be refined today. Detailed and repeatable field descriptions of sediments were greatly aided by the simple but versatile system of sediment characterisation devised by Troels-Smith (1955).

Laboratory techniques continued to be developed and improved including choice of mounting medium (e.g. Andersen 1960), pollen-size statistics (e.g. Berglund and Digerfeldt 1970), and estimation of pollen concentrations (e.g. Stockmarr 1971). Many palynologists (e.g. Ed Cushing, Jock McAndrews, Lou Maher, John Flenley, Sylvia Peglar, John Birks) made improvements in preparation methodology and these were quickly incorporated into sample-preparation protocols (e.g. Fægri and Iversen 1964; Berglund and Ralska-Jasiewiczowa 1986).

### *Site selection and spatial scale*

An important methodological and conceptual development in this phase was the realisation and demonstration that mor-humus profiles and sites of different type and size receive their pollen from different sized source-areas (Birks 2005). Different sized basins and soil profiles thus reflect vegetation at different scales of ecological resolution (Tauber 1965, 1967; Jacobson and Bradshaw 1981). Studies on pollen in mor-humus profiles initiated by Firbas and Broihan (1936), Erdtman (1943b), Trautmann (1952), and Fægri (1954) were continued by Berglund (1962) in his study on heath development on Senoren and refined and expanded by Iversen (1958b, 1964, 1967, 1969, 1973) in his classic studies using mor-humus profiles to reconstruct local forest history and development in Draved Forest in Denmark (see also Aaby 1983). Fægri

(1954) pioneered the use of small (10–30 cm diameter) damp forest hollows as a source of local stand-scale pollen stratigraphies derived from a pollen source-area of about 50–100 m radius. This approach was developed by Andersen in his studies using small hollows in Eldrup forest (Andersen 1973, 1984a) and other areas in Denmark (e.g. Andersen 1975, 1978, 1989). Stand-scale palynology of small hollows (Bradshaw 1988, 2013) is now routinely used to study fine-scale aspects of forest establishment, dynamics, structure, continuity, and disturbance (e.g. Edwards 1986; MB Davis 1987; Mitchell 1988, 2005; Bradshaw and Hannon 1992; HJB Birks 1993; Davis et al. 1994, 1998; Mitchell and Cole 1998; Parshall 2002; Bradshaw and Lindbladh 2005; Overballe-Petersen et al. 2013; Bradshaw et al. 2015).

Increasing attention was being paid to project design and site selection, particularly for regional-scale studies using small- or medium-sized lakes (100–300 m diameter). Following von Post (1918; see Fries 1967 and Fig. 2) a transect of sites along marked climatic and vegetational gradients is a valuable sampling design, as pioneered by McAndrews (1966). This design was adopted by Hyvärinen (1975, 1976) and Seppä (1996) in northern Fennoscandia and by Eide et al. (2006) in southern Norway.

As Quaternary pollen analysis became more refined in terms of its methodology, concepts, and applications, several palynologists turned their attention to questions of taphonomy (i.e. pollen production, dispersal, preservation) and pollen representation. Many of these studies were published in *Quaternary Plant Ecology* (Birks and West 1973) as a result of the 14th Symposium of the British Ecological Society held in Cambridge 28-30 March 1972. The year of publication, 1973, is thus arbitrarily used here to mark the end of the 'building phase' in Quaternary pollen analysis.

## Pollen-representation studies, pollen taphonomy, and pollen-assemblage zones

Major activities centred on pollen-representation studies. Pollen analysts have long realised that there is no simple 1:1 relationship between pollen percentages (or absolute pollen influx or loading – see Davis et al. (1973)) and vegetation percentages (or biomass) (Hesselman 1916; von Post 1918, 1967; Fægri 1947; Fagerlind 1949, 1952). For example, in 1916, von Post (1918; 1967 p.390) recognised "As long as we have no indices to express the relative pollen productivity of the various trees, nor to express the different degrees to which their pollen is dispersed, we have no right to seek in the percentage figures an adequate expression of the composition of the forest communities". Hesselman (1916) emphasised that it is illogical to assume that an increase in pollen percentages of a taxon always represented an increase of the same taxon in the vegetation. Iversen (1947) proposed 'correction factors' or representation factors that could be applied to fossil pollen assemblages to derive transformed pollen values that might resemble more closely the composition of the past vegetation than the untransformed pollen values do. These preliminary factors were based largely on Iversen's intuition and what was then known about the pollen production of different trees (Birks and Birks 1980). Iversen (1945, 1952-53) did a preliminary study on pollen-representation factors in Greenland. He compared the relative pollen composition in surface muds from two lakes in the inner region of the Godthaab Fjord in western Greenland. He also recorded the composition of the surrounding vegetation in the lakes' catchments (see HJB Birks 1973a). He estimated pollen-representation factors based on these data (Fægri and Iversen 1964; see HJB Birks 1973a) and used them to transform Holocene fossil pollen assemblages from another lake in the Godthaab Fjord into estimates of past vegetation composition (Iversen 1952-53).

The idea of pollen-representation factors was formalised by Davis (1963) in the concept of R-values. She derived modern R-values from a modern surface-mud sample and vegetation data around a study lake in Vermont and applied these to derive 'corrected' pollen values for the early Holocene. These 'corrected' estimates for taxa such as *Larix* have a very large statistical uncertainty (Parsons et al. 1983) and were subsequently shown to be spurious (Fægri 1966; Davis 1967a; Livingstone 1968). The idea of correction factors was studied in detail at the local scale by Andersen (1970) in two Danish forests. This study was a major breakthrough because it distinguished between pollen-production factors (P-values), estimated from semi-absolute modern pollen counts and absolute tree-crown data, and pollen-representation factors (R-values), based on relative modern pollen and relative tree data. He recognised, for the first time, the importance of pollen from outside the immediate pollen-source area; Andersen's $p_o$ component in estimating P-values. Andersen's study led directly to the development of the so-called 'extended R-value' models for relative percentage data (Parsons and Prentice 1981; Prentice and Parsons 1983; Prentice 1986; Prentice and Webb 1986). These extended R-value models incorporate the background pollen component from outside the sampled pollen-source area in modern pollen assemblages from small- to medium-sized lakes and were initially estimated for sites in Finland (Parsons et al. 1980) and southern Sweden (Prentice et al. 1987).

Besides pollen-representation studies, interest also developed on models of pollen dispersal. These were pioneered by Henrik Tauber (1965, 1967, 1977) who developed a static, non-overload pollen collector (Tauber 1974) as part of his studies. His ideas were tested by, for example, Berglund (1973), Andersen (1974a, b), and Krzywinski (1977). Roel Janssen (1966, 1967a, 1973, 1984), working in Minnesota, partitioned pollen deposition at a single point into local, extra-local, regional, and extra-regional components and used this model to aid in the reconstruction of past vegetation from pollen data from small and medium sized sites (Janssen 1967b, 1981). Development of more detailed models of pollen dispersal and of pollen–

vegetation calibration occurred later in the mature phase of Quaternary pollen analysis (see below).

Other aspects of pollen taphonomy were also explored in the building phase such as pollen production (e.g. Flenley 1973), preservation (e.g. Sangster and Dale 1961, 1964; Havinga 1964, 1967, 1971; Cushing 1967a), sedimentation (e.g. Rowley and Rowley 1956; Salmi 1962; Davis 1967c, 1968, 1973; Davis et al. 1971, 1973, 1984; Davis and Brubaker 1973), and transportation by water (e.g. Crowder and Cuddy 1973; Peck 1973; Pennington 1973; Bonny 1976, 1978) (see Birks and Birks (1980) and Xu et al. (2016) for additional studies). As Jackson (2012) notes, "Taphonomy is an unglamorous pursuit, yet it buttresses the inferential structure of paleoecology. … Neglect of taphonomy and inattention to the processes that underline proxy-target relationships, pose risks of ignorance creep, overconfidence, underestimation of uncertainty, and inferential errors." By the 1972 Cambridge meeting on Quaternary plant ecology, pollen analysts had made significant contributions to understanding pollen taphonomy but, of course, much remained and remains to be done.

An important contribution in the handling and summarisation of pollen-stratigraphical data was the introduction to Quaternary pollen-analysts of the concept of pollen-assemblage zones (Cushing 1963, 1967b). These are defined solely on the basis of the contained pollen and spore assemblage without any preconceptions or assumptions – explicit or implicit – about inferred climate, past vegetation, or presumed time equivalence (see Birks and Gordon 1985 for further details). Pollen-assemblage zones are now used routinely in pollen analysis, often delimited numerically by clustering or partitioning methods (see below). The critical distinction between biostratigraphy and chronostratigraphy (Mangerud et al. 1974; Berglund 1982) is now clear and recognised widely in Quaternary pollen analysis.

## Interglacials and plant-macrofossil studies

Additional major methodological developments within this phase were (1) the increasing role of pollen analysis in interglacial vegetational history and hence Quaternary stratigraphy and (2) the revival of interest in plant-macrofossil analysis to complement pollen analysis.

### *Interglacial pollen stratigraphies*

Building on the classic work of Jessen and Milthers (1928), interglacial pollen stratigraphy developed rapidly with detailed studies in many parts of Europe (see EDM Table 6). Watts (1988) provides a valuable review of interglacial studies in Europe and Magri et al. (2017) explore in detail the regional extinction of tree taxa in different interglacials in southern Europe.

Pollen analysis of long (>100 m) cores covering several glacial and interglacial stages was pioneered by Lex Wijmstra and colleagues at Tenaghi Philippon in north-east Greece (Wijmstra 1969; Wijmstra and Smit 1976; van der Wiel and Wijmstra 1987a, b). This 120 m core is now thought to cover the last 1.35 million years (Tzedakis et al. 2006) and is currently the longest continuous pollen record in Europe. Long continuous cores from Colombia (e.g. Hooghiemstra 1984; Torres 2006) and Siberia (e.g. Melles et al. 2012; Andreev et al. 2014; Herzschuh et al. 2016) covering 1.2 (Colombia) or 3.6 million years (Siberia) have now been studied. An innovative aspect of the Tenaghi Philippon study was the extraction of fossil Amaranthaceae pollen for generic determination by scanning electron microscopy (Smit and Wijmstra 1970). This indicated the former occurrence in glacial stages of steppe genera *Kochia* and *Eunotia* (= *Krascheninnikovia*) that today occur in Asian cool, cold steppe in, for example, the Pamir (van der Hammen et al. 1971).

### *Plant-macrofossil studies and 'modern pollen analysis'*

Quaternary plant-macrofossil analysis started in Britain through the work of Clement and Eleanor Reid and in Scandinavia by Alfred Gabriel Nathorst, Japetus Steenstrup, Nicholas Hartz, Knud Jessen, and others (HJB Birks 2005, 2014; HH Birks 2008). With the development of 'modern pollen analysis' (sensu Fægri and Iversen 1950), there was a striking decline of interest in Quaternary plant-macrofossil analysis (Watts 1978, 2008; HH Birks 2000, 2008; Birks and Seppä 2010; HJB Birks 2014) except in archaeobotany (e.g. Jacomet 2013), central European vegetational history (e.g. Lang 1952; Ammann et al. 1985), and interglacial studies (e.g. West 1957; Jessen et al. 1959; Huckerby and Oldfield 1976; Oldfield and Huckerby 1979). A resurgence of interest in late-glacial and Holocene macrofossils began in the mid-1960s in Minnesota with the quantitative macrofossil studies by Bill Watts (Fig. 7d) and colleagues (e.g. Baker 1965; Bright 1966; Watts and Winter 1966). Their approach involved counting macrofossils in a known volume of sediment and plotting the quantitative concentration data as a stratigraphical diagram resembling a pollen diagram. It met with fierce criticism from Knut Fægri and strong disapproval from Johs Iversen at the 10th International Botanical Congress in Edinburgh in August 1964 (pers. obs.). Iversen (1969 pers. comm.) later said that macrofossils can only usefully tell us about the past local aquatic flora which is often poorly represented by pollen assemblages. Macrofossils were, in Iversen's view, uninformative about the regional upland flora and vegetation (Birks 2014). Despite these criticisms, Bill Watts continued quantitative macrofossil studies in many parts of North America (e.g. Watts and Wright 1966; Watts 1970, 1979; see HJB Birks 2016, 2017). They have been continued by Steve Jackson and others in North America (e.g. Jackson 1989, 2012; Jackson and Whitehead 1991; Jackson et al. 2014) and by Hilary Birks and colleagues in Scotland, Norway, Svalbard, Alaska, and elsewhere (e.g. HH Birks 1973, 1991, 1993, 2000, 2008, 2017a, b; Birks and Mathewes 1978; Elias et al. 1996, 1997). In all these studies from Baker (1965) and Watts and Winter (1966) up to today, plant macrofossils are studied in *conjunction* with pollen and can often help supplement, complement, and validate pollen studies (e.g. Jackson and Booth 2013; Birks 2014; Jackson et al. 2014). As Birks and Birks (2000) provocatively argue "Future uses of pollen analysis must include plant macrofossils" if more complete pictures of past flora, vegetation, landscapes, and environments are required; for example in full-glacial or late-glacial studies (e.g. Wasylikowa 1964) where the pollen record abounds in false presences (cf. Aario 1940, 1944; Fægri 1947, 1981; Birks 2014) and may have several false absences (Birks 2014). Although plant-macrofossils are not pollen, as Fægri emphatically pointed out to Watts in 1964, they are an important fossil group in Quaternary vegetational history and palaeoecology (HJB Birks 2014; HH Birks 2017a, b), especially in alpine and arctic forest-limit and tree-line reconstructions (e.g. Barnekow 1999, 2000; Wick et al. 2003; Eide et al. 2006) and in late-glacial studies (e.g. Birks and Mathewes 1978; Mortensen et al. 2011).

In his memoir of Knut Fægri, Jørgensen (2009 p.15) wrote "on his deathbed he [Fægri] felt that pollen analysis had been worthwhile in elucidating these problems [late-glacial and glacial floras] and pointed to the importance of macrofossils which in his period had been neglected."

## Conceptual developments

Between 1951 and 1973, several important conceptual developments in Quaternary palynology were made. These include the concepts of the glacial-interglacial cycle, the uniqueness of the late-glacial flora and vegetation, the interpretation of early- and mid-Holocene forest development in terms of intrinsic ecological processes, and spatial scale and resolution. Although these conceptual developments are reviewed in detail by Birks (2005), they are summarised here as some of these concepts are critically important in several current palaeoecological research agenda.

### *Glacial-interglacial cycle*

The concept of a simple glacial-interglacial cycle with its cryocratic, protocratic, mesocratic, and telocratic phases of floristic, vegetational, and soil development was proposed by Iversen (1958a). It clearly had its roots in von Post's (1944, 1946) subdivision of Holocene climatic development into protocratic, mediocratic, and terminocratic phases but with the addition of the cryocratic glacial phase and an increased emphasis on soil development. Detailed work on Danish interglacials (Andersen 1966, 1969, 1994) suggested that modifications were needed to include an oligocratic phase with declining soil base-status and fertility followed by a telocratic phase with climatic deterioration prior to the cryocratic phase of the next glacial stage (Birks 1986; Andersen 1994; Birks and Birks 2004). A glacial-interglacial cycle thus consists of a long cryocratic or glacial stage with a cold, dry climate and open treeless vegetation growing on immature base-rich soils, alternating with an interglacial stage that usually lasts for 10,000 to 30,000 years. It comprises four phases: 1) a protocratic or pioneer phase with rising temperatures and the development of a diverse light-demanding flora and vegetation on unleached soils, 2) a mesocratic phase with high temperatures and the development of closed forest and fertile mull soils, 3) an oligocratic phase with decreasing forest over and deteriorating soils, and 4) a final telocratic phase with declining temperatures, increasingly open vegetation, and infertile soils. For the Holocene, Birks (1986) added the *Homo sapiens* phase that can start, depending on local factors, in the mesocratic, oligocratic, or telocratic phases. van der Hammen et al. (1971) and Birks (1986) extended the cycle to Mediterranean environments and other areas and environments (see also Birks and Tinner 2016). Birks (1986) also showed that the plant characteristics of the different phases in the cycle have contrasting ecological attributes, life-history traits, growth forms, and population biologies. Kuneš et al. (2011) have shown that the dominant mycorrhizal types and inferred productivity and soil fertility change during the cycle in different Danish interglacials, supporting the hypothesis that long-term soil changes are important drivers of vegetation change in an interglacial (see also Wardle et al. 2004).

### *Late-glacial flora and vegetation and no-analogue pollen assemblages*

Iversen's (1954) paper on the late-glacial of Denmark was one of the first detailed reconstructions of late-glacial flora, vegetation, landscape, and environment (see also Iversen 1967, 1973). It was based almost entirely on pollen-stratigraphical data and it presented the idea in Quaternary vegetation history that there had been flora, vegetation, landscapes, and environments that have no widespread modern analogues. Later studies on the late-glacial in Sweden (e.g. Berglund 1966, 1971; Berglund and Malmer 1971), Denmark (e.g. Fredskild 1975; Usinger 1977; Mortensen et al. 2011), Norway (e.g. Paus 1988), Scotland (e.g. HJB Birks 1973b; Birks and Mathewes 1978; HH Birks 1984), Ireland (e.g. Watts 1977), Minnesota (e.g. Cushing 1963, 1967b; Birks 1976, 1981), Ohio (Gill et al. 2012), and Indiana (Gill et al. 2009) generally support Iversen's (1954) original interpretation of the unique floristic and environmental nature of the late-glacial and the absence of any widespread modern analogues. No-analogue assemblages also occur in interglacials (e.g. Jessen et al. 1959; West 1964; Hall 1980; West 1980). There are important ecological, evolutionary, and conservation implications from no-analogue floras, vegetation, and environments that are now being considered in the context of ecological theory and future global changes (e.g. Colinvaux 1974; Jackson and Overpeck 2000;

Jackson and Williams 2004; Williams and Jackson 2007; Williams et al. 2011; Veloz et al. 2012; Jackson and Blois 2015).

### *Holocene forest development and spatial scale and resolution*

Following from Iversen's (1958a) glacial-interglacial cycle, Iversen (1960) presented an ecological interpretation of the early- and mid-Holocene forest development in Denmark in terms of intrinsic ecological factors (sensu Williams et al. 2011). This interpretation was based on the known different shade tolerances, longevities, reproductive behaviour, and soil preferences of the major forest trees (see also Iversen 1967, 1973). Iversen's (1960) model of the early- and mid-Holocene forest development as being primarily a 'long-term' succession of shrubs and trees differing in their shade tolerances and longevity and driven by intrinsic factors alone provides a simple 'null hypothesis' (HJB Birks 1986, 1993) against which alternative hypotheses to explain the observed pollen-stratigraphical trends can be tested (e.g. Prentice 1983, 1988a; Bennett 1988; Bennett and Willis 1995; Shuman et al. 2004; Williams et al. 2011).

The pioneering work by Fægri (1954), Iversen (1958b, 1964, 1969), and others on local-scale vegetational history as reconstructed from pollen analysis of small forest hollows and mor-humus profiles resulted in considerations of spatial scale and the reconstruction of landscape mosaics (e.g. Iversen 1960, 1967, 1969, 1973; Janssen 1967b, 1981; Andersen 1978; Jacobson and Bradshaw 1981; Andersen et al. 1983). Questions of spatial scale were now explicitly considered by many palynologists in their project design, site selection, and interpretation (e.g. Jacobson 1979, 1988; Ritchie 1984, 1995). Concerns about the spatial resolution of pollen-stratigraphical data resulted in the development of models of pollen deposition and estimation of relevant pollen-source areas, as discussed below in the mature phase.

### *The Draved Forest experiment*

Iversen (1956, 1967, 1973) initiated another first in Quaternary palynology and palaeoecology by pioneering an experimental approach in the subject. To test his hypothesis about the early 'landnam' and its three phases presented in Iversen (1941, 1949, 1967, 1973), he and archaeological colleagues Jörgen Troels-Smith and Svend Jörgensen cleared a two-acre area in Draved Forest in September 1952. Some areas were burnt and primitive varieties of wheat (einkorn and emmer) and naked barley were sown. The floristic and vegetational changes were carefully monitored. Iversen (1956, 1973) noted "that so far our experiment has confirmed the archaeological interpretation of the pollen record on several important counts. It has been demonstrated that the forest could indeed have been cleared by the primitive tools of Neolithic man, and that in the first stage at least the reviving vegetation follows a course very like that deduced from the ancient pollen layers." (see also Smith and Willis (1961-62)).

*Johannes Iversen 1904–1971*

Sadly Iversen died on 17 October 1971 near the end of the building phase so he did not live to see how his Draved Forest experiment developed. He had planned to lecture on 'The dynamics of the forest ecosystems of Draved in ancient and recent times' at the Quaternary Plant Ecology meeting in Cambridge in March 1972. His overall contributions to Quaternary pollen analysis are immense – secondary pollen; the late-glacial; *Viscum*, *Hedera*, and *Ilex*; landnam and the influence of prehistoric people on vegetation; long-term forest dynamics; Draved Forest stand-scale history and tree dynamics; and pollen-representation factors. As Godwin (1973 p.1245) wrote "After von Post himself no-one has contributed more to the development of pollen-analytical science than the gentle softly-spoken Dane, Johannes Iversen, who, since 1931, made the Danish Geological Survey in Copenhagen a place of pilgrimage for palynologists and palaeoecologists from all over the world. … Painstaking attention to detail, which is said to be the mark of genius, can best be seen in Iver's case, in the extreme care he gave to high-grade microscopy and photographic registration of pollen-grain morphology. Over many years he set high standards for pollen identification and most happily collaborated with his life-long colleague and friend, Knut Fægri, in writing the *Text-book of Pollen Analysis* (1950, 1964), the simplicity, sanity, and erudition of which have made it indispensable throughout the world. … although we regret deeply the loss of his wisdom and knowledge, console ourselves that he left an enviable record of scientific achievement that will long continue its benefaction."

## Mature phase 1974–today

### Introduction

Quaternary pollen analysis in the last 40+ years has greatly advanced thanks to three major scientific developments that have occurred outside pollen analysis. First, developments in radiocarbon dating, particularly the use of accelerator mass spectrometry (AMS), allows the dating of very small amounts of material. AMS has revolutionised dating in Quaternary palynology in the last 30 years and has led to the development of techniques for deriving robust age–sediment depth models (e.g. Blaauw 2010; Blaauw and Christen 2011; Blaauw and Heegaard 2012). Second, continual improvements in light, electron, and scanning microscopy and the building up of extensive modern reference pollen collections have helped advance pollen morphology and identifications. These developments led to the publication of Beug's (2004) pollen flora for central Europe and of the *North-West European Pollen Flora* (Punt et al. 1976-2009), masterminded and co-ordinated by Wim Punt. In these nine volumes, he detailed pollen morphology of 90 plant families is described and illustrated, including important families such as the Asteraceae, Apiaceae, and Caryophyllaceae. In addition, illustrated guides to pollen identification in north-west Europe (Moore and Webb 1978; Moore et al. 1991) and eastern North America (McAndrews et al. 1973) were published. Third, the development and increased use of mainframe computers from about 1968 and later of desk-top and lap-top computers from the early 1980s have allowed palynologists greater access to multivariate numerical techniques, computer graphics, and data-storage facilities.

By about 1980 there were many centres of Quaternary palynological research in addition to Copenhagen and Bergen, including Amsterdam, Bern, Cambridge, Canberra, Göttingen, Groningen, Krakow, Lund, Marseille, Minneapolis, Toronto, and Utrecht.

In the mature phase there have been many developments both methodological and conceptual. It is, however, difficult to separate methodological and conceptual developments in, for example, the numerical analysis of pollen-analytical data, pollen-representation models and landscape-reconstruction algorithms, and quantitative modelling of pollen-stratigraphical results, all of which depend on computing facilities (methodological advance) but also represent conceptual advances. Methodological and conceptual developments are thus discussed together here.

## Methodological and conceptual developments

In terms of methodological developments during the mature phase, improvements have been made to many of the developments that started in the building phase such as better field sediment coring techniques (e.g. Wright et al. 1984; Renberg 1991; Wright 1991; Nesje 1992; Glew 1995; Chambers and Cameron 2001; Renberg and Hansson 2008, 2010); improved laboratory techniques (e.g. Berglund and Ralska-Jasiewiczowa 1986; Bennett and Willis 2001; Cushing et al. 2002; Myrbo 2004), counting procedures (e.g. Maher 1981a), and size statistical approaches (e.g. Andersen 1980a); greater concern about estimating analytical uncertainties (e.g. Maher 1981a, b; Maher et al. 2012) and assessing replicability within a site (e.g. Ammann 1989); and a resurgence of interest in pollen-accumulation rates (e.g. Hicks and Hyvärinen 1999; Seppä and Hicks 2006; Giesecke and Fontana 2008; Seppä et al. 2009b) despite Davis et al. (1973) showing how such rates can be highly variable from different lakes within the same vegetation type.

A major methodological innovation was the development of robust and repeatable quantitative techniques for estimating concentrations of charcoal in sediments (e.g. Clark 1988a, b; Tinner and Hu 2003; Finsinger and Tinner 2005; Higuera et al. 2007). These permit the exploration of pollen-stratigraphical changes in relation to fire events (see ESM Table 7) and the development of management plans for areas where fire is a major ecological factor (e.g. Wright 1974).

Although the identification and counting of conifer stomata on pollen-analytical slides was initiated over 50 years ago by Trautmann (1953), the full potential of fossil stomata as an indicator of tree presence (e.g. *Pinus, Picea, Larix, Juniperus*) in or near tree-line situations has only relatively recently been recognised and explored (e.g. Hansen 1995; Hansen et al. 1996; Yu 1997; MacDonald 2001; Sweeney 2004; Ammann et al. 2014). The presence of conifer stomata can help answer some of Hesselman's (1916, 1919a, b) concerns about long-distance transported pollen of conifers.

### *Palynology and the computer age*

Thanks to the computer revolution that started in the early 1980s, and the programming skills of Eric Grimm, Keith Bennett, Brian Huntley, Ed Cushing, Steve Juggins, Adam Walanus, and others, Quaternary palynologists have benefitted from the development and availability of user-friendly software for the handling, calculation, and plotting of pollen-analytical data. Widely used software include TILIA (Grimm 1990), psimpoll (Bennett 1994), and C2 and rioja (Juggins 2007, 2015). Another result of the computer revolution has been the development and application of a wide range of multivariate numerical methods to assist in the summarisation and interpretation of modern and Quaternary pollen-analytical data since about 1970 (ESM Table 8). Several of these specialised techniques take account of the sampling (stratigraphical or spatial) and numerical ('closed' percentages) properties of palynological data and have been developed by applied statisticians working in conjunction with palaeoecologists (e.g. Birks and Gordon 1985; ter Braak and Juggins 1993; ter Braak et al. 1993).

The display of the temporal and spatial patterns in pollen-stratigraphical data for many sites remains a major challenge for pollen analysts since the pioneering attempts by von Post (Fries 1967) (Fig. 2). The approach of constructing isopollen maps (Szafer 1935; Grimm 1988) displays the spatial variation in pollen assemblages at selected time intervals, including the present-day (e.g. Birks et al. 1975; Birks and Saarnisto 1975; Webb and McAndrews 1976; Bernabo and Webb 1977; Huntley and Birks 1983; Ralska-Jasiewiczowa 1983; Webb et al. 1983; Ralska-Jasiewiczowa et al. 2004; Williams et al. 2004). An alternative approach is to construct 'isochrone' maps (Grimm 1988) to illustrate the ages at which different pollen types have their first consistent appearance or expansion. Moe (1970) used such maps to reconstruct the spreading patterns of *Picea abies* in Fennoscandia. Isochrone maps have been used to illustrate presumed tree-spreading patterns in eastern North America (e.g. Davis 1976, 1983a, b) and the British Isles (Birks 1989). Recently, Brewer et al. (2016) have constructed 'basic' maps for 54 pollen taxa at 828 sites across Europe. The maps follow the design of von Post (1924) where the size of the dots at each site reflects its pollen percentage for the time being mapped. Geographic information system analyses have also been used to display geographical aspects of pollen data in varying detail (e.g. times at which particular values are first attained) and of the time intervals between particular stratigraphical features (e.g. Giesecke and Bennett 2004). An important development that allows the exploration and summarisation of the spatial and temporal patterns in large continental or sub-continental pollen data-sets (e.g. Berglund et al. 1996) has been the construction of open-access databases such as Neotoma, the European Pollen Database, and others (Mitchell 2011; Brewer et al. 2012; Giesecke et al. 2014, 2016; Goring et al. 2015), as well as the emergence of palaeoecoinformatics (Brewer et al. 2012). They are beginning to permit the use of geohistorical data (including pollen) to answer ecological questions that require a temporal dimension (e.g. Walker 1982a, b; Ritchie 1991, 1995; HJB Birks 1993; Flessa and Jackson 2005; Giesecke et al. 2017), following the advice of Deevey (1969 p.40) "when time is required to see a result, there is no substitute for history". However, as Magri et al. (2017 p.47) emphasise recently "A key message to the community is the vital importance of archiving full pollen data in public repositories, especially in the era of generally concise publication of only summary or partial pollen datasets".

## Pollen-representation models and vegetation-reconstruction algorithms

An area of major methodological and conceptual development and innovation in the last 30 years evolved logically from the work in the 1960s–early 1980s on pollen-representation values (e.g. Andersen 1970) and the extended R-value model (e.g. Parsons and Prentice 1981; Prentice 1986). This was Colin Prentice's (1985, 1988b) model of pollen deposition that attempts to quantify pollen-source area and production and dispersal biases and to predict the effect of basin size on the relative representation of different taxa. The model incorporates some of the ideas about pollen dispersal pioneered by Tauber (1965, 1967, 1977), Janssen (1966, 1973, 1984), Kabailiene (1966, 1969), Andersen (1970, 1974a, b), and Berglund (1973). The Prentice model was extended by Shinya Sugita (1993) to model pollen deposition over an entire lake surface rather than at a point in the centre of the basin. Simulations made by Sugita (1994, 1998) investigated how vegetational mosaics are reflected in modern pollen assemblages and estimated 'relevant source areas', defined as the area beyond which the correlation between pollen loading on the basin and the distance-weighted plant abundances does not improve. Only about 30–45% of total pollen deposited in the basin is derived from the relevant source area, but as the background pollen is homogenous, even in patchy vegetation, this 30–45% is adequate to reflect local vegetation. Jackson and Lyford (1999), Sugita et al. (1999), Davis (2000), and Seppä and Bennett (2003) critically review these simulation models of pollen dispersal and representation.

Using similar models, Sugita et al. (1997) performed a series of simulations to investigate the palynological reflection of disturbance by fires of different sizes and proximities to a lake. Their results suggested that fossil pollen assemblages expressed as percentages will only consistently record disturbances that are at least eight times larger than the lake and are located within a few hundred metres of the lake shore. These results are surprising at first sight and immediately raise questions of the likely spatial extent of the early forest disturbances, as envisaged by Iversen (1956, 1967, 1973) to produce the characteristic pollen stratigraphies of Neolithic 'landnam' phases (Iversen 1941, 1949). Smith and Willis (1961-62) and Pilcher et al. (1971) had queried the duration and scale of Iversen's 'landnam' phases and of the patterns within them.

The POLLANDCAL network led by Marie-José Gaillard (Gaillard et al. 2008) built on the results from a workshop on quantifying the extent of clearances in the past (Gaillard and Berglund 1998). POLLANDCAL attempted to quantify estimates of landscape openness in the past using regression and calibration modelling of modern pollen and landscape data (e.g. Gaillard et al. 1998) or historical (AD 1800) pollen and landscape data (e.g. Nielsen and Odgaard 2004) or by simulation modelling (e.g. Sugita et al. 1999; Broström 2002; Nielsen 2003, 2004).

Sugita (2007a, b) has developed a landscape-reconstruction algorithm (LRA) for the quantitative reconstruction of past vegetation composition. The LRA builds on earlier ideas of using basins of different size (e.g. Cushing 1963; Janssen 1966, 1973, 1981; Livingstone 1968; Andersen 1978; Kabailiene 1985) to quantify regional and local pollen components. Sugita's LRA consists of two parts: REVEALS and LOVE. REVEALS (Regional Estimates of Vegetation Abundance for Large Sites) (Sugita 2007a) reconstructs vegetation composition in $10^5$–$10^7$ ha ($10^4$–$10^5$ km$^2$) using pollen assemblages from 'large lakes' that have small site-to-site variations in their pollen percentages even though the vegetation can be highly heterogeneous. LOVE (Local Vegetation Estimate) (Sugita 2007b) incorporates the REVEALS estimates of regional vegetational composition into a quantitative model for reconstructing vegetation composition in smaller areas ($\leq 10^4$ ha) using pollen records from smaller sites. The LRA is currently attracting much interest and use (e.g. Hellman et al. 2008; Mazier et al. 2012; Nielsen et al. 2012; Cui et al. 2013; Overballe-Petersen et al. 2013; Marquer et al. 2014; Hultberg et al. 2015; Trondman et al. 2015; Mehl and Hjelle 2016). It is also stimulating model improvements (e.g. Theuerkauf et al. 2012, 2016), the critical testing of its assumptions (e.g. Conedera et al. 2006; Matthias et al. 2012; Matthias and Giesecke 2014; Theuerkauf et al. 2015; Baker et al. 2016; Mariani et al. 2016), and the development of alternative approaches for the quantitative reconstruction of past vegetation composition (e.g. Bunting and Middleton 2009; Paciorek and McLachlan 2009;

Dawson et al. 2016; Mrotzek et al. 2016). Approaches are also being developed to reconstruct quantitatively past vegetation mosaic patterns with an extended downscaling approach (Theuerkauf and Joosten 2009; Theuerkauf et al. 2014; Theuerkauf and Couwenberg 2016). These are exciting and important areas of major research activity at present.

## Other methodological and conceptual developments

### *Pollen trapping, non-pollen palynomorphs, and modelling approaches*

An essential part of all modern pollen-representation studies and hence quantitative vegetation reconstructions is reliable and robust data on modern pollen deposition. There are now unique long time-series of pollen-trap monitoring data from Denmark (Andersen 1980b; Nielsen et al. 2010; RHW Bradshaw 2016, pers. comm.), Finland (e.g. Hicks 1974, 1999, 2001, 2006; Autio and Hicks 2004), Norway (Birks and Bjune 2010; Bjune 2014), and elsewhere in Europe (e.g. Giesecke et al. 2010a, b; Pardoe et al. 2010; Pidek et al. 2010; van der Knaap et al. 2010).

Bas van Geel has pioneered the study of non-pollen palynomorphs (NPPs) preserved in peats and lake sediments (e.g. van Geel 1978, 1986, 2001). NPPs such as spores of *Sporormiella*-type, a dung fungus, are being used as a valuable proxy of past megafauna (e.g. OK Davis 1987; Burney et al. 2003; Davis and Shafer 2006; Gill et al. 2009, 2012). Modern studies on the abundance of dung fungal spores (e.g. Gill et al. 2013; Baker et al. 2017) show the robustness of the dung fungal spore records. Much remains to be done in NPP research.

As research questions asked of pollen-stratigraphical data become increasingly sophisticated and demanding, a major development has been fine-resolution pollen analysis (Green 1981, 1983). In conjunction with detailed chronologies (e.g. based on laminated sediments – see below), such analyses allow the exploration of past population dynamics, both expansions (e.g. Watts 1973; Bennett 1983, 1986; Chen 1988) and declines (e.g. Tsukada 1983; Peglar 1993), as well as population doubling (e.g. Bennett 1983) and halving times (e.g. Peglar 1993) and comparison of expansion rates in different geographical areas within a taxon’s range (e.g. MacDonald 1993a). Multi-species models based on reaction kinetics have also been proposed (Bennett 1990). Ecosystem-level models have been developed to help disentangle and quantify the role of abiotic and biotic drivers such as climate change, soil nitrogen, herbivore abundances, and inter-specific competition on pollen-stratigraphical changes (Jeffers et al. 2011a, b, 2012, 2014). A further development has been hindcast dynamic vegetation or landscape modelling. Past vegetation development is simulated and comparisons of simulated and ‘observed’ pollen patterns are made (e.g. Lotter and Kienast 1990; Bradshaw and Sykes 2014). This approach has been used in an attempt, for example, to decipher the potential drivers behind the Holocene spread of *Picea abies* across Fennoscandia (e.g. Miller et al. 2008; Seppä et al. 2009a), the response of the alpine tree-line and forest-limit to Holocene climate change, human impact, and fire (e.g. Heiri et al. 2006; Colombaroli et al. 2010; Henne et al. 2011), and the past and future role of *Abies alba* in Mediterranean and central European Holocene vegetation (e.g. Henne et al. 2013, 2015; Tinner et al. 2013; Ruosch et al. 2016). There are exciting prospects for further modelling studies involving pollen data as a means of testing specific ecological hypotheses. However as Bennett (1990 p.250-251) noted over 25 years ago "Further advances in the interpretation of pollen sequences as records of population change will depend on the willingness of palaeoecologists to analyse enough samples. … Models are available when there are data with which to test them". This challenge largely remains.

### *Laminated sediment*

An important methodological development in this phase has been locating, coring, sampling, and analysing continuous cores of annually laminated lake-sediments. Such sediments provide perfect material for fine-resolution palynological studies at, if required, single year or even single season resolution (Turner and Peglar 1988). Field and laboratory sampling of such sediments for fine-resolution work can be difficult and the large number of samples to be pollen counted can be extremely daunting.

Annually laminated topmost (5–25 cm) lake-sediments have been known for over a century (e.g. Heer 1865; Wesenberg-Lund 1901; Nipkov 1927). Such laminated ('varved') lake sediments extending back into the early Holocene were not studied palynologically until the classic studies of Welten (1944) at Faulenseemoos, a small former lake 600 m x 150 m and at least 15 m deep in the Swiss Bernese Oberland. Welten demonstrated the annual nature of the laminae, developed a chronology based on the laminae (Deevey 1946; Conway 1948), and invented a means of estimating pollen-accumulation rates (see Watts 1973; Lotter and Kienast 1990; Lotter et al. 1995). In the 1960s and 1970s, laminated lake-sediments were found in northern Sweden, Finland, Germany, Poland, Minnesota, and elsewhere (see O'Sullivan 1983; Zolitschka et al. 2015), usually in small- or medium-sized deep sheltered lakes.

In the late 1960s, Herb Wright, Ed Cushing, and Bud Heinselman (Birks 2016) devised ingenious coring methods to extract a continuous sediment core including the uppermost sediments from the 31-m deep Lake of the Clouds in northern Minnesota and carefully sampled, at very fine resolution, the laminae for pollen and microscopic charcoal analyses (Craig 1972; Swain 1973). These analyses were designed to reconstruct the natural fire history of the area through the Holocene and to test the hypothesis that fire was a major component of this boreal conifer-dominated ecosystem (see Wright 1974). Laminated sediments were subsequently found in other Minnesotan lakes (see Birks 2016) and fine-resolution pollen and charcoal analyses were made to compare with known recent fire history based on fire-scars of living trees (e.g. Clark 1988b, 1989, 1990, 1993). Similar laminated sediments have now been found in many parts of the world (see ESM Table 9 for examples). Coring such sediments has necessitated major developments in field coring procedures (e.g. Wright 1980; Saarnisto 1986; Lotter et al. 1997; Renberg and Hansson 2010) and laboratory sampling methods (e.g. Renberg 1981). Fine-resolution pollen analyses of laminated sediments have now been conducted to answer specific research questions (see ESM Table 10 for examples). Detailed late-glacial and Holocene pollen stratigraphies using laminae to provide a chronology have been constructed at several sites (e.g. Ritchie 1977; Lotter 1991, 1999; Ralska-Jasiewiczowa et al. 1992; Yu 2003). Lake Gościąż in central Poland (Ralska-Jasiewiczowa et al. 1998) and Elk Lake in north-west Minnesota (Bradbury and Dean 1993) probably have the most intensively studied laminated sequences anywhere in the world as detailed multi-proxy investigations have been carried out at both sites.

### *Pollen analysis of mineral soils*

At the other extreme of temporal resolution, there is pollen analysis of mineral soils. The interpretation of pollen assemblages preserved in mineral soils has been a source of heated debate since the pioneering studies by Dimbleby (1957, 1961; cf. Godwin 1958). A major development in interpretation was made by Andersen (1979, 1984b) who analysed not only pollen but also fungal hyphae and humus in different soil types. These detailed studies provide a factual basis for interpreting pollen assemblages from soils, for example, in burial mounds (Andersen 1988, 1990, 1992), and Neolithic burial rituals (Lagerås 2000), or from agricultural raised-beds (Groenmann-van Waateringe and Van Geel 2017). The uncertainties of pollen preservation in soils, within-profile palynomorph movement, and dating difficulties combine, however, to reduce the wider ecological usefulness of soil pollen analysis (K Edwards 2017, pers. comm.).

## Links with other disciplines

### *Multi-proxy studies and palaeolimnology*

Following early examples (e.g. Digerfeldt 1972; Bradbury and Waddington 1973; O'Sullivan et al. 1973) that used pollen analysis to reconstruct catchment history as an aid to understanding lake development, there has been increasing integration of pollen analysis in multi-proxy palaeolimnological studies involving, for example, diatoms, chironomids, sediment geochemistry, stable-isotope records, etc. (Birks and Birks 2006). The Kråkenes late-glacial project co-ordinated by Hilary Birks has shown the value of integrating various proxies in the context of the vegetation of the lake’s catchment as reconstructed from pollen analysis (e.g. Birks et al. 1996, 2000; HJB Birks and Birks 2008; HH Birks and Birks 2013). Other multi-proxy studies where pollen analysis has played a key role include late-glacial studies at Lobsigensee (Ammann et al. 1985; Ammann 1989) and Gerzensee on the Swiss Plateau (Ammann et al. 2000, 2013a, b), and Holocene studies at Sägistalsee in the Swiss Alps (Lotter and Birks 2003a, b; Wick et al. 2003) and at Dallund Sø in Denmark (Bradshaw et al. 2005; Rasmussen 2005; Rasmussen and Bradshaw 2005).

The range of techniques available in multi-proxy palaeoecological studies is now enormous, as illustrated by Berglund's (1986b) volume on palaeoecological techniques and by volumes 1–5 in the *Developments in Paleoenvironmental Research* series on *Tracking Environmental Change Using Lake Sediments* (Last and Smol 2001a, b; Smol et al. 2001a, b; Birks et al. 2012). New techniques are continually being developed and improved, in particular those using stable-isotopes, organic geochemistry, and biochemical markers (e.g. Francus 2004; Flessa and Jackson 2005; Leng 2006; Smol 2008; Croudace and Rothwell 2015).

### *Archaeology and landscape history in temperate and tropical regions*

Since Jessen's (1920) and Iversen's (1941) classic works, pollen analysis has always had close links with archaeology (e.g. Berglund 1969, 1985, 1986b, 2003; Fægri 1985; Behre 1986, 1988, 1990; Andersen 1988, 1990, 1992; Bottema and Woldring 1990; Lagerås 2000, 2016; Kristiansen 2002) and with the history of cultural landscapes (e.g. Wasylikowa et al. 1985; Godłowska et al. 1987; Birks et al. 1988; McAndrews 1988; Odgaard and Rasmussen 2000; Lagerås 2007; Sköld et al. 2010). The latter involves collaboration between vegetation historians, archaeologists, geomorphologists and soil scientists, plant ecologists, agricultural historians, and landscape ecologists, as shown in the detailed Ystad Project in southern Sweden (Berglund 1991). This and related projects have stimulated new attempts to quantify the openness of the landscape from pollen-analytical data (e.g. Sugita et al. 1999; Broström 2002; Nielsen 2003, 2004; Nielsen et al. 2012; Theuerkauf et al. 2014; Åkesson et al. 2015; Lagerås 2016), as discussed above and to assess the impact of human activity on palynological richness (e.g. Berglund et al. 2008a, b; Birks et al. 2016a).

Detailed pollen analyses made in the last 20 years in sub-tropical or tropical areas have provided strong evidence for human disturbance and activities over several thousand years (see Willis et al. (2004a) and ESM Table 11 for representative examples). These palynological studies contribute not only to archaeology and landscape history but also to ecological understandings of tropical vegetation dynamics and to biodiversity (Willis et al. 2004a, b).

### *Other links*

The last two decades have witnessed pollen analysis becoming increasingly linked with several new disciplines (Edwards et al. 2017). These include phylogeography and studies of DNA of extant populations (e.g. Petit et al. 2002; Jackson 2006; Magri et al. 2006; Tollefsrud et al. 2008; Hu et al. 2009; Liepelt et al. 2009). Effective links are also being established with conservation biology and management, restoration ecology, ecosystem science, global change biology, and with several aspects of population and community ecology (see ESM Table 12 for examples).

## Where are we today?

After 100 years of Quaternary pollen analysis, one can ask where has the subject reached and where is it today. In such an assessment of a non-experimental historical science, it is useful to identify three main approaches (Fægri 1974; Ball 1975; Birks 1985): 1) a descriptive exploratory approach (stage I sensu Fægri 1974) with the initial detection, description, and archiving of the basic patterns; 2) a narrative approach (stage II sensu Fægri 1974) with plausible but largely untestable inductively-based explanations for the patterns detected in the descriptive approach; and 3) an analytical approach (stage III sensu Fægri 1974) in which falsifiable hypotheses about the processes behind the observed patterns are proposed, evaluated, tested, and rejected.

## Descriptive and narrative approaches

In the 100 years of pollen analysis, particularly in the last 30 years, almost all terrestrial areas have now been explored palynologically (ESM Table 13). Tallis (1991) and some of the chapters in Huntley and Webb (1988) provide some global coverage. It is not known how many pollen stratigraphies there are worldwide. Manten (1969) in his bibliography of palaeopalynology 1836-1966 lists 12,557 palaeopalynological publications of which about 9000 concern Quaternary palynology. Simple linear extrapolation suggests about 18,000 such publications by 2016. This is possibly a serious underestimate. Eric Grimm (2016, pers. comm.) thinks that there are at least 5000 Quaternary pollen-stratigraphical data-sets in the various pollen databases at present (Mitchell 2011; Grimm et al. 2013). All these studies and their basic data represent the hard-earned results of the essential descriptive or exploratory approach.

There are, of course, many interpretations of these data. Such interpretations range from highly detailed reconstructions of past flora, vegetation, landscapes, and ecosystems at a single site (e.g. Gerzensee on the Swiss Plateau - Ammann et al. 2013a, b; Birks et al. 2016b) to continental or sub-continental syntheses based on hundreds of sites (e.g. Huntley and Birks 1983; Williams et al. 2004; Brewer et al. 2016; Giesecke et al. 2017) interpreted in terms of extrinsic and intrinsic ‘drivers’ of change, refugia, spreading rates, human impact, etc.

## Analytical approach

The analytical approach is more difficult, as it is in all historical sciences, but such an approach is possible as Iversen (1941) showed in his classic 'landnam' study. Three examples (Peglar and Birks 1993; Lynch 1998; Birks and Birks 2008) illustrate the direct testing of explicit hypotheses about the underlying 'drivers' or processes behind the observed patterns in pollen data. They exemplify what Deevey (1969 p.40) termed "coaxing history to conduct experiments". Other examples of direct hypothesis testing using palynological data include Edwards (1986), Odgaard and Rasmussen (2000), Mitchell (2005), and Bradshaw et al. (2015).

Peglar and Birks (1993) investigated possible causes for the mid-Holocene *Ulmus*-pollen decline at Diss Mere in eastern England. They considered five possible hypotheses – climate change, soil change, competitive exclusion, human impact, and pathogenic attack, as well as interactions between these causative processes. They made predictions about what patterns—especially the rate of decline—would be expected if the *Ulmus*-decline was a result of the five causes alone or interacting. By separating each annual couplet across the *Ulmus*-decline (Peglar 1993), they showed that the *Ulmus*-pollen influx had halved in five years, supporting the pathogenic attack (disease), climate + disease, disease + human impact, or climate + disease + human impact hypotheses. There was no evidence for any marked climatic change at this time as reflected by laminae thicknesses remaining constant throughout, suggesting no very warm or very cold summers or winters. The two hypotheses not falsified are disease or disease + human impact. Counting of microscopic charcoal particles showed a striking rise in charcoal 40 years before the *Ulmus*-decline, favouring the hypothesis of disease + human impact but the alternative hypothesis of disease alone cannot be rejected given the available data.

Lynch (1998) investigated the origin of a landscape mosaic of open treeless park areas and forested areas in the Wind River Range of the Wyoming Rockies. She proposed three hypotheses for the origin of the park areas – permanent site factors (e.g. soil), remnant (i.e. all areas were once park), and replacement (i.e. park areas were once forested). She studied small <30 m diameter ponds to obtain a local pollen signal in two forest areas and three park areas. The pollen stratigraphies showed that all the areas were once forested so the replacement hypothesis was not rejected. Why forest in areas that are park today was replaced by park about 2500 years ago is unclear. It might have resulted from climate change leading to changes in disturbance regime. Moreover, a positive feedback between vegetation and microclimate may have maintained the park areas once the forest had declined.

Birks and Birks (2008) tested the hypothesis that there had been no migrational lag in the spread of *Betula* trees in the earliest Holocene to Kråkenes on the coast of western Norway. Detailed pollen analyses (sample resolution of 21 years), plant-macrofossil analyses to supplement the pollen stratigraphy, chironomid analyses to provide a reconstruction of summer air temperatures independent of the botanical records, and a detailed chronology based on 72 AMS radiocarbon dates formed the basic data. The pollen and plant-macrofossil data showed that *Betula* did not arrive at Kråkenes until 670–720 years after the onset of the Holocene at 11,550 yrs BP. This contrasts with the rapid arrival of *Betula* on deglaciated areas in western Norway after the 'Little Ice Age' within 200–350 years. The chironomid-inferred temperatures suggest that summer temperatures were suitable (>10°C July air temperatures) 30 years after the onset and rose to >11°C 60 years after the Holocene began. If these inferred temperatures are correct, they suggest that climate was suitable for tree *Betula* 610–670 years before *Betula* arrived or expanded. There are several hypotheses to explain this delayed arrival – soil-forming processes; dispersal limitations; establishment limitations; interactions with other, unknown climatic variables; a no-analogue climate (e.g. greater seasonality) in the earliest Holocene; extensive fires as shown by abundant macroscopic charcoal in the early Holocene; and interactions between some or all of these factors. These hypotheses cannot be satisfactorily resolved, but the original hypothesis that there were no migrational lags in the spread of tree birch in the earliest Holocene can be rejected.

The current situation in Quaternary pollen analysis is that there are a very large number of high-quality stratigraphical data-sets from many parts of the world; there are an increasing number of syntheses and detailed narratives; but there are surprisingly few analytical studies that have attempted to test specific hypotheses. Developing an analytical approach remains a major challenge to Quaternary palynologists today (Edwards 1983; Ritchie 1984, 1991, 1995; Walker 1990; HJB Birks 1993, 2012a; MacDonald 1993b; Magri et al. 2017).

## Conclusions

The history of Quaternary pollen analysis in and around its centre of origin is now fairly well documented and is presented here as three main phases – the pioneering phase (1916–1950), the building phase (1951–1973), and the mature phase (1974–today). The distinction between the building and the mature phase is somewhat arbitrary but after 1973 there have been many fewer publications on aspects of pollen taphonomy than between 1951 and 1973. It is thus an appropriate dividing date but in reality history, like time, is a continuum and any division is inevitably rather arbitrary.

Kuhn (1970) proposed that scientific knowledge progresses by phases of 'normal science' being interrupted by periodic 'paradigm shifts' or 'revolutionary science' rather than simply progressing along a linear or monotonic trajectory. Such paradigm shifts open up new approaches and research areas that scientists may have never considered possible or were not even apparent before the shift. Science is thus thought to progress by the gradual accumulation of observations and data within a basic agreed intellectual framework (Kuhn's 'normal science') until a 'revolution' occurs and the basic research framework or paradigm of the old conceptual structure is overturned or replaced and a new research framework or paradigm rapidly develops and becomes the new 'normal' science.

Does the history of Quaternary pollen analysis follow Kuhn's proposed path? Yes, in part. There has been one **intrinsic** paradigm shift within the subject, represented by the publication of Fægri and Iversen's (1950) *Text-book of Modern Pollen Analysis*. The other paradigm shifts have all been **extrinsic** – the increasing quality of microscopes and hence improved knowledge of pollen morphology and better ability to identify more pollen types (cf. Iversen 1941); the advent of radiocarbon dating which freed pollen analysis from its predominant role as a relative dating tool in late-Quaternary science; and the development and increased accessibility of powerful computers to allow the numerical analysis of palynological data, the development of extensive databases, and the handling and display of pollen-analytical data. Perhaps a more relevant model for the development of Quaternary pollen analysis is that proposed by Toulmin (1972). It suggests that developments in science occur much more frequently and are much less dramatic than those portrayed by Kuhn's model of 'normal science' and 'revolutionary science'. In Toulmin's view, developments such as important and relevant revisions or improvements often occur during periods of Kuhn's 'normal science'. This is largely what appears to have happened during the first 100 years of Quaternary pollen analysis.

von Post's conclusion to his 1916 lecture (von Post 1918, 1967 p.401; Fries 1967 pp.12-13) that "I consider that the category of fossil [pollen grains], hitherto rather overlooked, can indeed through systematic treatment, considerably widen our knowledge of late-Quaternary deposits and their history" has, we feel, been convincingly demonstrated to be correct. Soon after the first 50 years of Quaternary pollen analysis Deevey (1967 p.65) proposed that "von Post's simple idea, that a series of changes in pollen proportions in accumulating peat was a four-dimensional look at vegetation, must rank with double helix as one of the most productive suggestions of modern times." His proposal is certainly supported by the achievements of Quaternary palynologists in the last 50 years.

We feel that Quaternary pollen analysis today with its ever-broadening links with landscape history, archaeology, phylogeography, vegetation modelling, ecosystem science and services, conservation biology and management, restoration ecology, and community and population dynamics (ESM Table 12) is in very good health and can continue to address challenging and important research questions (e.g. Flessa and Jackson 2005; Birks 2012; Jackson 2012; Bradshaw and Sykes 2014; Jackson and Blois 2015; Birks et al. 2016b; Edwards et al.

2017). We hope that it will maintain its good health and vitality and thrive for at least another 100 years!

On The Contemplative Mammoth blog, Jacqueline Gill (2013) posed the question “Is pollen analysis dead? Paleoecology in the era of Big Data”. The level of activity of primary data collection (ESM Table 13) and the increasing application of pollen analysis to different disciplines (ESM Table 12), particularly in the last 10–15 years, suggest that the answer to Gill’s question is ‘no’ and that pollen analysis is very much alive. Perhaps the suggestion by Gill (2013) that “the reports of my death are greatly exaggerated” is correct!

Lennart von Post has every reason to be immensely proud of his ‘simple idea’ of pollen analysis. It has certainly turned out to be ‘a most productive suggestion’.

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## Electronic Supplementary Material Contents

Available from https://link.springer.com/article/10.1007%2Fs00334-017-0630-2#SupplementaryMaterial

**Document 1** Translation of von Post's review of Fægri & Iversen (1950)

**Table 1** Historical reviews relevant to the history of Quaternary pollen analysis

**Table 2** Obituaries and memoirs of the most influential pollen analysts in the early phases of Quaternary pollen analysis

**Table 3** Early publications from the 1920s about pollen analysis in Holocene sediments in countries outside the Nordic countries

**Table 4** Early publications from the mid-1920s and early-1930s about pollen analysis of interglacial sediments

**Table 5** Selected examples of countries or geographical areas where detailed vegetation histories based on pollen analysis have been published, mainly, but not exclusively, during the building phase

**Table 6** Selected examples of detailed pollen-analytical studies of interglacial deposits in different European countries

**Table 7** Selected examples of detailed quantitative charcoal studies made in conjunction with pollen analysis

**Table 8** Selected examples of appropriate numerical analytical techniques for handling Quaternary pollen data (Birks et al. 2012; Birks 2013)

**Table 9** Selected examples of geographical areas where annually laminated sediments have been found and studied palynologically

**Table 10** Selected examples of research questions involving fine-resolution palynological studies of annually laminated sediments

**Table 11** Selected examples of pollen-analytical studies on prehistoric activities in sub-tropical or tropical areas

**Table 12** Selected examples of more recent applications of pollen analysis to new disciplines

**Table 13** Selected examples of new geographical areas explored palynologically, mainly, but not exclusively, during the mature phase

**Table 14** Sources of the images in Figures 1–7