Quaternary Vegetation Dynamics of Europe

Gerhard Lang
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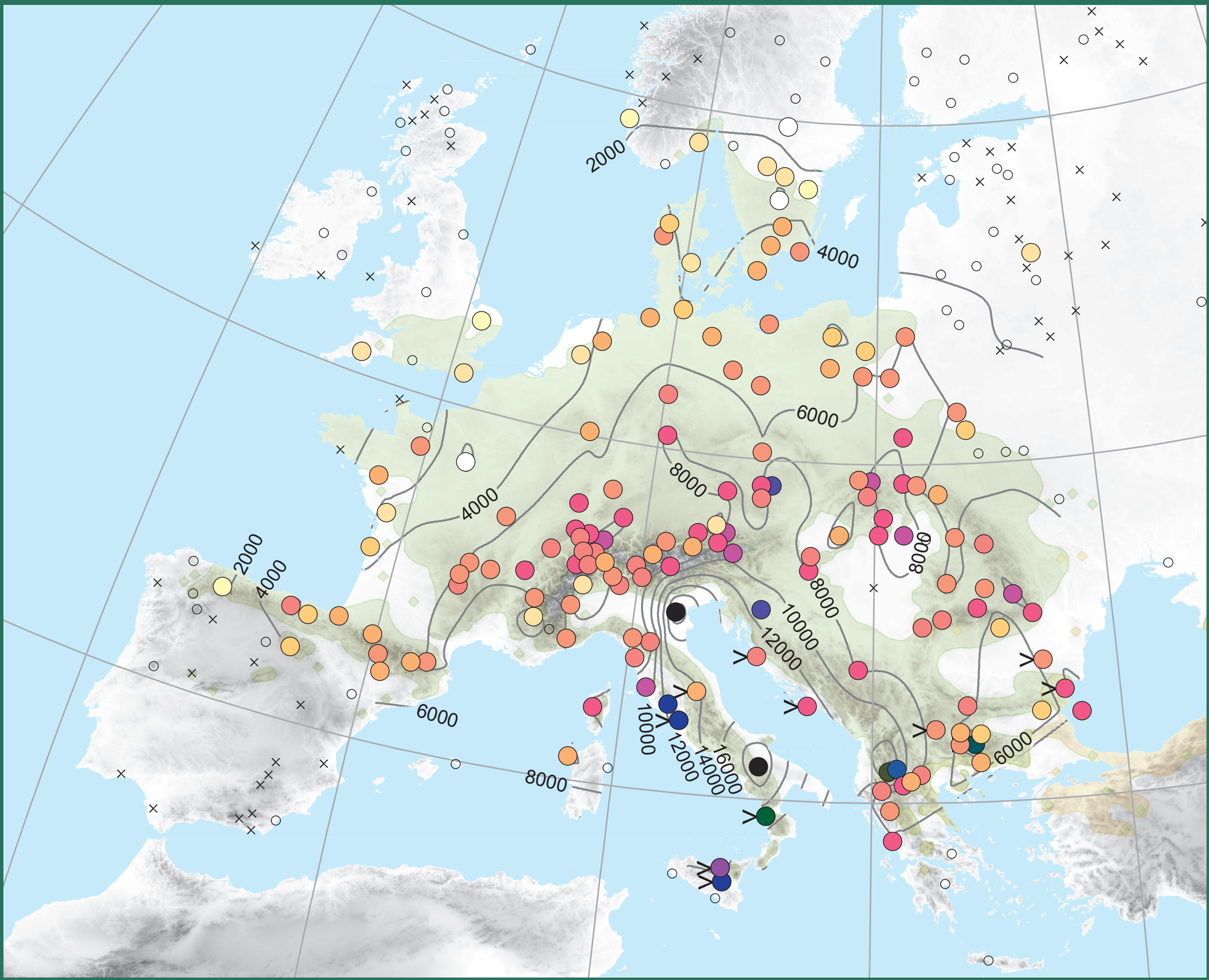
Willy Tinner
(Editors)



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Preface

To the memory of Max Welten (1904–1984) and Werner Trautmann (1924–1989)

A summary overview of the Quaternary history of European vegetation had been lacking until 1994, if one disregards geographically or temporally narrower or much broader surveys. However, during the 20th century, Quaternary botanical research, including neighbouring fields, had brought so many new insights that in the 1990s the time seemed ripe to attempt a synthesis in the form of a basic outline. For one person, however, this was an ambitious undertaking in view of the enormous amount of material, if all aspects needed to be even half covered. Nevertheless, fully aware of the risk of such an inevitably subjective presentation for the whole of Europe, Gerhard Lang undertook this venture. After decades of his own research in a geographically limited framework, he felt the need, to broaden the horizon of vegetation history and palaeoecology and to communicate this to others in as comprehensible a form as possible. The result was the book "Quartäre Vegetationsgeschichte Europas", published in 1994 in German by the publisher Gustav Fischer in Jena. His attempt at a synthesis was intended as an introduction primarily for palaeoecologists and neoecologists, but also served as a source of information for researchers from neighbouring disciplines.

In the structure of his book Gerhard Lang followed the outline which, in his opinion, had proved didactically successful in the lectures he gave at the Universities of Karlsruhe and Bern. This began with a concise overview of the most important events in the history of vegetation in the European Quaternary and was followed by an orientation on the main methods which are important for understanding them. Then came the central part covering the major periods of the Quaternary with the emphasis on the Late-glacial and the Holocene, followed, in conclusion, by a consideration of various general problems of fundamental importance for palaeoecology and neoecology. In accordance with the title of the book, the focus of interest was on the plant world itself and its changes. Thus, vegetation and floral history did not primarily serve as an instrument for determining other, climatic or landscape-historical

Fig. I. Gerhard Lang (*21 October 1924 , †19 June 2016) on the "International Moor-Excursion" to the Bodensee and Oberschwaben - 1985.

events. These were, therefore, only followed insofar as they were important for understanding plant responses. Gerhard Lang attached great importance to rich and meaningful illustrations. If possible, no section of the text should remain without graphic illustration. To this end, many illustrations taken from original publications were redrawn, usually in a somewhat modified form, or completely new drafts were produced. He designed almost all the final artwork for his book himself – at that time without computer graphics - and drew it by hand. This was certainly a method that seems old-fashioned today, but it gave him great pleasure, although it also took much more time than originally planned. A basis of Gerhard Lang's book were the excursion meetings of the European Quaternary botanists in various European countries, which Gerhard Lang attended from 1954 onwards. Of particular interest were the field meetings of participants in the IGCP 158 (International Geological Correlation Programme) led by Björn Berglund and Leszek Starkel, which started in the second half of the 1970s. Finally, the "International Moor-Excursions" to important regions of Europe, organised every year since 1976 by the Institute of Geobotany of the University of Bern, deepened his horizon of vegetation history. All these events provided opportunities for personal contacts and discussions, many of them in the field at the study sites.

Students and teachers of many disciplines welcomed his comprehensive book, which in the German speaking countries of Europe is still an important reference. In 2006 Brigitta Ammann, Karl-Ernst Behre, Pim (W.O.) van der Knaap and Willy Tinner made the ambitious plan to republish Gerhard Lang's book, in expanded form, in English. This long-term publication project proved to be extremely demanding. Very sadly Gerhard Lang (1924-2016) passed away before our project came to an end, after 6 years of common work.

The new English version relies in numerous parts on the original book of Gerhard Lang. New text, topics and figures have been added to reflect the progress achieved in palaeoecology during the past now almost 30 years. We would like to thank all our colleagues, in particular the co-authors of this book. Among others, very special thanks go to Pim (W.O.) van der Knaap, who designed and drew the great number of pollen diagrams and Christoph Schwörer, who made many new colourful figures and compiled the first version of this new book from a myriad of text fragments. Linguistic corrections and proofreading by Sheila Hicks and Cathy Jenks as well as technical corrections by Lieveke van Vugt are gratefully acknowledged. We would also like to thank our colleagues at Institute of Plant Sciences and Oeschger Centre for Climate Change Research at University of Bern, Peter von Ballmoos, César Morales del Molino, Erika Gobet, Martin Grosjean, Andy Lotter and Thomas Stocker for their great support and suggestions. Special thanks go to Haupt Verlag Bern and its managing director Matthias Haupt, for their favourable reception of the book and their almost infinite patience until the completion of the manuscript. We also thank Katarina Lang and her team for carefully designing and typesetting this book. The Oeschger Centre for Climate Change Research of University of Bern, the Fondation Johanna Dürmüller-Bol, the Burgergemeinde Bern, the Sebastiana Stiftung and the UniBern Forschungsstiftung are gratefully acknowledged for their financial support.

In his original book of 1994 Gerhard Lang wrote: "At the end of many years of work, the work still seems to me to be highly incomplete, apart from the fact that it can of course never be finished at all because of the ongoing research". We still have just this same feeling. New literature is only included up to 2020, in some parts to 2018. Some researchers may be disappointed to find that their work has been included too little or not at all, but due to the limited scope of the work and the huge body of literature, a selection had to be made which is in no way intended to be taken as a judgement on the quality. Any criticism and suggestions for improvement are welcome.

Bern and Wilhelmshaven, March 2023

Brigitta Ammann, Karl-Ernst Behre
and Willy Tinner

1.

An overview of the general framework of the development of flora and vegetation

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1.1

Geology and geomorphology

The Quaternary is the latest stage of Earth's history. As the name implies, there were three preceding periods in the old nomenclature, the Primary (now Palaeozoic), the Secondary (now Mesozoic) and the Tertiary (now Cenozoic) but, according to modern knowledge, there was still a very long phase before the Palaeozoic. Compared with the older stages, the Quaternary is extremely short and comprises a timespan of only 2.6 million years (Ma).

According to modern knowledge, Earth was formed around 4.5 billion years ago. Isolated continents soon formed on its surface and moved on the Earth's crust. Several times they collided or met and reshaped into large supercontinents where all the world's landmasses were joined together. The position and contours of these early supercontinents are still vague and open to discussion. The penultimate supercontinent, however, broke up and its parts later re-assembled to the better-known supercontinent called Pangaea by Alfred Wegener. It was he, who already as early as 1915 proposed the theory of continental drift, the details of which were largely worked out on the basis of palaeobotanical and palaeozoological investigations (Wegener, 1915).

This theory, however, was strongly disputed and eventually rejected by the scientific community. Only in the 1960s, when the theory of plate tectonics arose, did geologists once more become aware of Wegener's ideas and nowadays the moving of continents is accepted without question.

The Pangaea supercontinent existed from around 250 Ma BP and comprised all continents including Antarctica. Around 200 Ma BP Pangaea began to split up and its parts became the modern continents that moved around the Earth's surface to their present positions. The time of separation of the various continents can be determined by the distribution of fossil plants and animals and the different development of their taxa. The *Glossopteris* flora, which denotes the southern part of this supercontinent, Gondwana, is well known in this respect.

Now that the theory of plate tectonics has gained acceptance it is recognized that there are eight large and many minor plates that comprise not only the mainlands but also the marine areas where sea-floor spreading takes place. Europe is a part of the Eurasian plate, which borders to the south on the African plate. As at other plate boundaries, strong volcanic activity and mountain-building took place along this boundary. Of eminent and long lasting importance was the formation of a huge oceanic trench between the two plates. It is called Tethys and during the Cretaceous extended as far as East Asia. In the course of the Tertiary it became reduced to the Mediterranean sea in the west, while other remnants are the Black Sea and the Caspian Sea. The calcareous deposits in the Tethys and its surrounding shelf seas and bays constitute the huge areas of limestone which extend northwards to the Alps that still determine large parts of the modern landscape.

During the Tertiary, these broad-scale processes continued and formed the geology of Europe with notable consequences for the following Quaternary period. Due to the tectonic movements of the plates north of the Tethys, the long west–east running range of the alpidic mountains was formed, which became a strong barrier for the migration of plants during the subsequent climate changes of the Quaternary. Another outcome of the plate tectonics in southern Europe is the volcanic activity that led to the emergence of many volcanoes, not only in the Mediterranean but as far north as France and central Germany, where they have long been inactive but often form isolated mountains with a specific vegetation. Several crater lakes formed in the Pleistocene became excellent archives for vegetation history.

The severe climatic deterioration at the start of the Quaternary – the Ice Age – led to strong morphological changes on top of the Tertiary subsoil. Huge ice sheets were formed in the north as well as smaller ice caps on the Alps and several other mountain areas. The movement of these ice masses led to intense glacial erosion and the removal of bedrock and soil material: large areas of northern Europe and of the mountainous areas became periodically completely bare until new soils developed or even remained bare. The adjoining areas

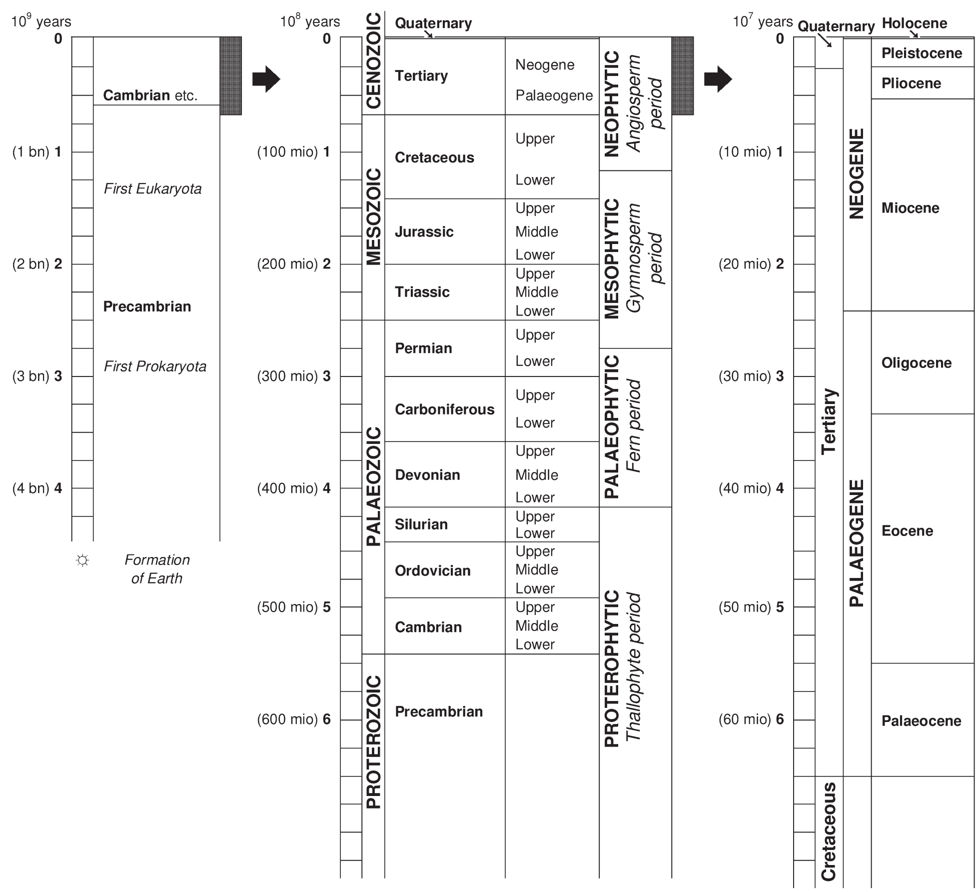

Fig. 1-1. Geochronological subdivision of the Earth's history. The scale between the three parts differs by a factor of ten (after Lang, 1994, modified and updated).

of the formerly glaciated regions were covered with thick layers of till and at their boundaries, end moraines were formed, sometimes more than a hundred metres in height. Large numbers of lakes were formed in the glaciated areas ranging from small kettle-hole depressions, which came into existence by the melting of dead ice, up to large ones formed behind moraine dams, for instance. Areas that were glaciated during the last glaciation (Weichselian or Würmian) usually display existing lake landscapes, for example in Finland, Sweden or north-east central Europe, while the lakes of earlier glaciations were filled up during the following interglacials and glacials. Nowadays these are very important as archives for Pleistocene vegetation history.

Outside of the glaciated region there was a large periglacial area, where various cold-climate processes created special landscapes. Large quantities of gravel, sand and clay were deposited and formed outwash plains or sandurs immediately adjacent to the glaciated areas. Along the rivers, Rhine or Rhone for example, fluvial accumulation with elevated river banks took place for several hundred kilometres. All these geological processes formed a great variety of different environments which resulted in vegetation units adapted specifically to those conditions. Another important feature along the rivers are the terraces that were formed due to interglacial down-cutting through the deposits aggregated during glacial periods.

The most important deposit in the periglacial area and beyond is loess – windblown dust – finer than sand. It was formed during dry and cold steppe phases and often attains many metres in thickness. The loess belt stretches from western Europe across central to eastern Europe and is particularly well developed in Austria and large regions of the Ukraine and southern Russia. Its nutrient content is high and, therefore, the loess areas are preferred for farming.

The stratigraphy of the loess often shows buried palaeosoils, reflecting interstadial or interglacial phases. This indicates that soil formation, not only in loess, takes place only in warm periods. During cold phases there is no development of soils: the surface in the permanently frozen areas, the so-called permafrost region, is constantly disturbed by frost action such as squeezing and upheaval of the uppermost layers, called cryoturbation, and the downslope movement of sediments, called solifluction.

The formation of soils is an important precondition for the development of vegetation. At the beginning of the warm phases many plant species, which could grow in the area given the climatic conditions, are unable to spread due to the lack of mature soils while others, such as several pioneer plants, are already able to occupy the raw habitats and so contribute to the formation of productive soils.

1.2

Early development of flora and vegetation

After the formation of the Earth it still took a very long time until the first traces of life, single-celled bacteria, appeared around 3.8 billon years ago (Fig. 1-1). It took, however, more than another billion years before multicellular life began. After this very long Precambrian period, the Palaeozoic started at around 542 Ma ago with the Cambrian and from this point onwards it is mainly palaeontology, the science of plants and animals, that is used for the subdivision of the geological development.

Fossil spores have been found as early as the late Ordovician and, in the late Silurian, the land plants started their development. The following Devonian was already dominated by lycopods and early ferns, which represent the earliest woody plants. They proliferated strongly in the tropical climate of the Carboniferous (which existed in most parts of Europe) and dense woodlands spread over wide areas forming the coal deposits that we see today. They consist mainly of species of the ancient lycopods such as *Sigillaria* or the scale tree *Lepidodendron* that produce tall trees. Also the tree-like *Calamites*, which belongs to the Equisetaceae, became quite common in the coal forest flora.

Eventually, towards the end of the Carboniferous, the first seed plants appeared. The first step was made by the Pteridospermae, followed by the Progymnospermae and the Cordaits, closely related to the gymnosperms.

Most of the coal-forming trees became extinct during the Permian: *Glossopteris*, a prominent genus of the seed fern, appeared while the lycopods were replaced by the conifers, which soon evolved into many systematic groups. In addition to many extinct genera, *Ginkgo* and *Cycas* appeared: living fossils in our present flora. Evolution proceeded further with the Benetittales, seed plants and early progenitors of the angiosperms.

In the following Triassic and Jurassic, conifers dominated the vegetation and became highly diversified. Already at that stage all modern families of the conifers existed. The ensuing Cretaceous is characterized by the development of the angiosperms, which must have come into being earlier but, apart from their pollen found in the Jurassic, specific fossils are still missing. As early as the Lower Cretaceous, the angiosperms split up into the Monocotyledoneae and Dicotolydoneae and from

Fig. 1-2. Contours of last glacial ice margins and Early Holocene shorelines, in cal ka BP (modified after Lang, 1994).

the Middle Cretaceous, angiosperms dominated the vegetation worldwide (Kadereit, 2008).

From the Upper Cretaceous until the Upper Miocene the European vegetation is characterized by paratropical rainforests, which are closely related to tropical rainforests but include members of some genera typically thought of as 'temperate' such as *Alnus, Acer* and others. In some regions, subtropical rain- and laurel forests, as well as temperate laurel forests, were present in accordance with the climatic conditions with high temperatures in the Eocene and later in the Miocene (see Fig. 3.1-1). During these two periods most of the huge brown coal deposits were formed.

Overall, during the Tertiary the vegetation of Europe evolved from paratropical to warm-temperate and temperate forms in response to a progressive but undulating cooling. There were mainly two separate ecological units: the evergreen, laurophyll 'palaeotropical geoflora' and the deciduous, broadleaved 'Arctotertiary geoflora'. During the Tertiary, the Arctotertiary geoflora occupied the northern parts of the Holarctic, the 'Greenland region' and has advanced into Europe in waves since the Palaeocene. This flora formed the basis for the Tertiary mixed mesophytic forests and became the roots of the Quaternary temperate mixed oak forests. Considerable differences in their composition allow us to separate several floral regions in Eurosiberia so that there are four well-defined floral regions by the end of the Pliocene. A Mediterranean region, however, cannot be recognized although Mediterranean floral elements appear from the Eocene onwards and the Mediterranean xeromorphic vegetation has its origin in the Tertiary laurophyll vegetation. The Mediterranean sclerophyll forests, in their present form, are a very young phenomenon and probably arose only after the destruction of the laurophyll forests during the Pleistocene (Mai, 1989, 1995).

1.3

Quaternary climate development and the consequences in terms of the position of coastlines

The Quaternary flora and vegetation are determined by climatic oscillations at a much higher magnitude than during the Tertiary. There were alternating cold periods (glacials) and warm periods (interglacials). Oscillations at a smaller scale, with cool to slightly temperate climate conditions, occurred during the glacial periods and are called interstadials. By definition the interglacials are classified as temperate periods with a climatic optimum at least as high as the present interglacial (Holocene) in the same region. Interstadials are assumed to have been either too short or too cold to reach the climate level of interglacial status in the same region (Litt et al., 2008). On the basis of the marine isotope record (see Fig. 3.3-1) there have been around 100 climate oscillations since the beginning of the Quaternary.

Within the Quaternary there has been an overall shift to cooler conditions. During the long Lower Pleistocene the cold phases became gradually colder and the amplitude of the oscillations increased: during the Middle and Upper Pleistocene the temperatures in the cold phases became very low, resulting in extensive ice advances in the north and smaller ones in and around high mountains in more southern areas such as the Alps, Carpathians and Pyrenees.

The duration of the cold phases in the Lower Pleistocene was also markedly shorter than in the Middle and Upper Pleistocene when the warm periods lasted around 15 000 years while the cold phases exceeded 100 000 years. Taken as a whole the Pleistocene was a cool to cold period with intercalated warm phases.

Penck and Brückner (1901–1909) were the first to present a chronological order for the Alpine glaciations and called them Günz, Mindel, Riss and Würm, but even before that Penck (1879) had denominated the large north European glaciations as Elster, Saale and Weichsel. There are also indications of one or more preceding glaciations in northern central and eastern Europe as well as in the Alps. Large areas of Europe were, nevertheless, spared from an ice cover and, therefore, the term 'cold stage' is often used instead of glacial.

Knowledge of the last glaciation in Europe, the Weichselian (Fig. 1-2), is good. It did not extend as far as the preceding large glaciations but is clearly the geological basis for large parts of central and northern Europe. Several ice advances formed clear end moraines such as the Pomeranian, Frankfurt and Brandenburg phases and the lakes and outwash plains of this glaciation created diversified landscapes across large areas. This is complemented by a huge loess belt covering large parts of Europe outside the glaciated regions.

The glaciations mentioned above were, however, not the first in Earth's history. A very early Permo-Carboniferous glaciation is known from the Gondwana continent and there were also Pliocene glaciations, but these were restricted to the polar regions.

During the glaciations huge amounts of water were shifted from the sea into the glaciers, which often reached up to 3000 m in thickness, and this resulted in global sea-level changes of great magnitudes. This kind of sea-level oscillation is called eustatic. Very little is known about the older fluctuations of sea-level but the evidence increases from the Upper Pleistocene to the Holocene, in particular with respect to the North Sea and the Baltic Sea. During the glaciations, most parts of the North Sea and the Baltic Sea basins became dry or temporally glaciated. The fall in global sea-level around the maximum of the last glaciation is estimated at about 130 m.

The melting of the glaciers led to the refilling of the shallow North Sea and Baltic Sea basins during the interglacials. The coastlines of these periods, however, deviate from the modern ones such that the area of the Holsteinian Sea extended far into northern Germany but did not reach the western Netherlands (Ehlers, 1994). The coastline of the Eemian Sea was similar to that of the modern North Sea (Streif, 1990). There was, however, in southern Jutland a connection to the Baltic Sea (Konradi et al., 2005) which did not come into existence during the Holocene. The configuration of the Eemian Sea in the Baltic was very variable as it is in the Holocene and the position of the coastlines is still uncertain. During the first 2000 years of the Eemian interglacial there was, however, a connection to the White Sea so that Scandinavia became an island for a time (Andrén et al., 2011).

In addition to the eustatic sea-level changes the coastlines were displaced by another factor: isostasy. Due to the very heavy ice load in the glaciated regions, in particular in Scandinavia, the Earth's crust sank considerably. The unloading of this weight in the interglacials, due to the ice melting, caused uplift which is still occurring at a magnitude of around 100 cm per century in the centre of the Scandinavian shield. These two factors determined the varied configuration of the Baltic Sea in the past. Thus its coastline is mainly determined by both the eustatic sea-level change and the glacio-isostatic adjustment (Harff et al., 2017).

These opposing trends result in various stages of the Baltic Sea, with or without connections to the North Sea, and that means fresh or brackish-marine. Five main stages of the Baltic are distinguished:

- Baltic Ice Lake (freshwater) from around 14 500 to 9700 BC
- Yoldia Sea (brackish) from 9700 to 8800 BC
- Ancylus Lake (freshwater) from 8800 to 6550 BC
- Littorina Sea (brackish-marine) 6550 BC to AD 1500
- Mya Sea (marine-brackish) from AD 1500 (after Björck, 2008).

As a consequence of the isostatic uplift of the Scandinavian shield in the postglacial, the area around it is sinking and, in particular, the southern coastline of the Baltic in north-east Germany was, and still is, displaced by the sinking coast together with the general eustatic rise in sea-level.

In contrast to the special development of the Baltic Sea, the North Sea is a marginal sea, open to the Atlantic Ocean. In the Early and Mid Holocene, when parts of the North Sea basin were still dry, forests occupied those areas, but these were later drowned in the course of the rising sea level.

For the Holocene North Sea there are many investigations to reconstruct former sea-levels and shorelines (Shennan and Andrews, 2000; Behre, 2007a). Both basal and intercalated peats provide sea-level points to construct a sea-level curve from around 10 000 BC to the present. After a long strong increase, sea-level rise decelerated around 5000 BC and from 3000 BC there occurred temporary drops in sea-level, during which large areas fell dry and became influenced by fresh water so that peat formed, which was later covered again with marine sediments. Altogether, seven of these regressions of various magnitudes have been identified in the southern North Sea during the course of the last 5000 years, all having severe consequences for the coastal vegetation as well as habitation.

In accordance with the rise in sea-level, shorelines moved very fast. After 8000 BC the Dogger Bank was cut off and became a large island in the middle of the North Sea: it was inundated around 2000 years later. Around 7000 BC, Britain was separated from the European mainland and as early as around 6000 BC the sea reached the foreland of the Frisian Islands (Fig. 1-2). While for a long time the coastal habitation reacted only passively to the shoreline changes, people started active resistance against the sea in the late 11th century by building dikes. They started with ring dikes which were interconnected in the 13th century to a continuous closed dike line. For the coastal vegetation this was a dramatic change. Prior to diking, the coastal zone was characterized by a great variety of vegetation units ranging from salt marshes to freshwater communities with many intermediate forms. Now the dikes sharply separated the seaward marine and brackish area from the landward freshwater area (Behre, 2002).

Similarly in the Mediterranean Sea, eustatic sea-level changes resulted in shoreline displacements, in particular in wide parts of the shallow Adriatic Sea the rising sea level disconnected the Italian Peninsula from the Balkans. Similarly, Malta was disconnected from Sicily, also Sardinia and Corsica became two separate islands. Numerous other displacements have been described as well-defined raised beaches at fixed levels in several coastal areas around the Mediterranean Sea. The Mediterranean basin, however, is a tectonically strongly disturbed region and many of the suggested sea-level fluctuations can be explained by differential tectonic movements rather than by local relative sea-level changes (Pirazzoli, 1991).

Great progress has been made during recent decades in dating the organic and inorganic layers of the Quaternary. For the younger periods, mainly the Holocene, the radiocarbon method has been refined to be used for very small samples. More precise dating started earlier with varve counting, particularly in the Baltic region, and this was later extended to the investigation of annually laminated sediments in many freshwater lakes in all parts of Europe. With the addition of dendrochronological data, very precise dating of many Holocene sites is now possible. Quite a number of physical and chemical methods have been developed in order to date Pleistocene sequences. In particular they have been applied to the key profiles for modern Quaternary records: the deep sea cores and the long ice cores from Greenland and Antarctica. These continuous cores span large parts of the Quaternary and allow global correlations of the climatic sequence. The Marine Isotopic Stages (MIS) that now cover the whole Quaternary have become the framework for the detailed subdivision of the Quaternary period.

1.4

Changes of vegetation belts and decrease of floral elements in the course of the Pleistocene

The numerous climate oscillations during the Pleistocene resulted in multiple radical changes of the European flora and vegetation. During the cold phases the forests were pushed to the south or south-east while treeless tundra or steppe spread onto the non-glaciated regions. During the extreme cold glacials of the Middle and Upper Pleistocene there were no longer forests north of the Alps. Some woody species survived in favourable or sheltered areas in southern and south-eastern Europe, while others withdrew much further. The manifold repeated expansions of cold periods of increasing strength over time, forced the thermophilous species to migrate to far and sometimes remote areas and some of them failed to come back to the European areas they had occupied before. A very severe obstacle for plant migrations was the long west–east running mountain range from the Pyrenees to the Carpathians and many species did not manage to cross this barrier at each climate change. This is one reason why the number of plant species is much higher in America or east Asia where the direction of the mountain ranges is north–south instead of west–east. As a consequence the flora of the various interglacials show considerable differences. Many species of the Pliocene flora had already become extinct in Europe at the Tertiary/Pleistocene boundary but persisted in other parts of the world. Thus in Europe, *Sciadopitys,* for example, did not survive the oldest part of the Pleistocene while *Eucommia* reached at least the lower Middle Pleistocene: both trees are nowadays native only in east Asia. Another tree, *Pterocarya*, nowadays very popular in European parks and naturally occurring in the Caucasus and east of it, was common in European forests until the end of the penultimate interglacial and became an important indicator for the Holsteinian interglacial. The same is also true for herbs and aquatics: for instance, *Brasenia schreberi (=purpurea)*, a well-known aquatic that occurs all over the world except in Europe, disappeared here only at the end of the last interglacial. Other components of the Plio-Pleistocene flora, such as *Fagus*, have a varied history in that they occurred in some interglacials but were absent at least over large regions in others.

Overall, the number of tree and other species began to decrease in the Lower Pleistocene, at first slowly but at an increasing rate towards the Upper Pleistocene (see Table 3.3-1). One has to take account, however, of the very limited amount of data from the Lower Pleistocene. Future sites may well reveal that some 'old' species survived longer than is assumed today.

1.5

The Holocene

The current interglacial – the Holocene – began about 11 600–11 700 cal yr BP. According to Table 4.1-2 the Holocene starts at 11.7 cal ka BP (e.g. Litt et al., 2008) and so has about the same duration as the last interglacial but, in contrast to that interglacial, it has strong climatic and vegetational oscillations during the immediately previous Late-glacial. The Holocene started with a strong climatic improvement, so that particularly north of the Alps many species could not immediately use the climate possibilities because of a time lag in their remigration.

In addition to the barriers formed by the mountain ranges, the development of the coastal configuration caused by sea-level changes also had strong consequences for the spreading of plant and animal species. A good example is provided by the British Isles. In the Early Holocene they were connected to the European mainland and there were no obstacles for plants and animals to spread into this region. Once Britain was separated from the continent, around 7000 BC, the possibilities for spreading became reduced and the late-comer trees from the south, such as *Acer pseudoplatanus* and *A. platanoides* as well as *Picea* and *Abies,* were no longer able to reach the British Isles. Other trees, such as *Fagus* and *Carpinus* reached Britain in spite of their late expansion, probably with the help of Bronze Age people, but they did not reach Ireland which had already been separated earlier so that *Tilia* is also lacking there. Similar effects must have occurred in earlier periods as can be seen by the Pleistocene distribution of plants and animals.

After the *Betula/Pinus*-phase of the Early Holocene, mesocratic deciduous forests soon spread northwards and beyond their present distribution areas. While *Fagus* advanced to the north slowly and late, the important trees *Abies* and *Picea* did not even reach the North Sea coast as they had done earlier in the Eemian. *Picea*, however, found its way into Scandinavia from north-western Russia. The climatic optimum was reached in the Atlantic period, when *Tilia* or the aquatic *Trapa natans* reached their northernmost distribution, far beyond their modern boundaries. In the course of the climatic deterioration in the younger Holocene, the natural vegetation adapted to the changing conditions. Another consequence of the climatic deterioration was the formation and extension of huge raised bogs around the southern North Sea as well as in the Alpine foreland which led to distinctive changes in the landscape.

The increasing activity of humans became the main factor influencing the vegetation development in the course of the Holocene and created vegetation types and landscape features that had never occurred before. At first the hunter, gatherer and fishers acted only passively as permanent settlements did not yet exist. The resulting impact on the vegetation was very small and often invisible.

A totally new epoch started with the immigration of the first farming cultures: now the human relationship to the natural environment changed abruptly – passive adaptation changed to active encroachment. Arable farming with the domestication of the first cultivated plants was developed at about 9000 BC in the Near East in the so-called Fertile Crescent and, at about the same time, the domestication of the first animals took place. This new economy had, as a precondition, the establishment of permanent settlements, so this signifies the beginning of a non-nomadic life-style. This total change in the economic base, from hunting and gathering to farming, was called very appropriately the "Neolithic Revolution" by Childe (1951) and the term Neolithic is bound to this form of economy, not to a particular time. Consequently the date for the beginning of the Neolithic is metachronous and varies between regions, depending on when animal and plant husbandry were first initiated.

The new form of economy soon spread across the Balkans to central Europe and another movement took place westwards across the Mediterranean Sea. The expansion of the Neolithic economy led to an increasing opening of the wooded landscapes by arable farming, forest grazing and general woodcutting. So many new biotopes were created and gave native species as well as introduced weeds, which arrived together with their cultivated host plants, the chance to spread. The number of plant species increased steadily and this became still stronger after the contact with America and the establishment of modern trade routes all over the world.

Agriculture, forest grazing, burning, shredding, pollarding (see Rackham, 1976) as well as selective wood cutting and the introduction of exotic, mainly American, trees changed the composition of the forests in many ways. Even more consequences ensued from several special types of economy that led to the formation of large heaths and dry grasslands. Until around AD 1900 the hugely widespread Atlantic dwarf-shrub heaths that existed from Belgium to the Netherlands, Germany and Denmark were regarded as natural, but it transpired that they were of anthropogenic origin (see Behre, 1988) and this also applies to areas in Great Britain (Pennington, 1974) as well as Brittany and the 'lands' in the north-west of France (van Zeist, 1964) and along the coasts of the Iberian Peninsula. The same is true for the Norwegian coastal heaths, where fire was an important factor for their formation (Kaland, 1986; Prøsch-Danielsen and Simonsen, 2000). The huge unwanted areas of sclerophyll woodlands with macquis and garrigue in the Mediterranean also came into existence as a result of people's activities and meadows and pastures all over Europe, except for salt marshes and above the tree line in the mountains, would not exist without human activities.

The transformation of the landscapes from natural to anthropogenic occurred steadily but with peaks, for example in the Roman period, but the final disruption of landscapes and vegetation started in the medieval period and reached its maximum in modern times.

Compared with preceding interglacials, the Holocene is a period on its own. The strong human impact in this period could account for most of the phenomena mentioned above. As can be shown by physical palaeotemperature investigations as well as by pollen analysis, there were also climatic changes. Both had considerable and manifold impact on the vegetation but the real cause of some change is often difficult to illucidate.

1.6

Fauna and humans

Dramatic changes also occurred in the animal kingdom during the Quaternary in that faunal assemblages are closely related to the climate and certain types of vegetation. This is particularly visible in the large mammals that followed the environmental changes and migrated northwards during warm periods and southwards during colder ones. Over the long period of the Quaternary there were extinctions as well as evolution of species. A good example of the latter is shown by the elephant's lineages from the *Mammuthus meridionalis* to *M. trogontherii* and finally *M. primigenius* (van Kolfschoten, 1992).

The interglacials are characterized by a forest fauna consisting of, for example, the straight-tusked elephant *Palaeoloxodon (Elephas) antiquus,* Kirchberg's rhinoceros *Stephanorhinus kirchbergensis*, wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, fallow deer *Cervus dama* and also water buffalo *Bubalus murrensis* and even the Mediterranean immigrant hippopotamus *Hippopotamus amphibius*, which occurred along the Rhine and as far north as England and indicates relatively high winter temperatures there.

During the cold phases there were steppe or tundra faunas in central Europe, including the steppe mammoth *Mammuthus trogontherii*, the ancestor of the later woolly mammoth *M. primigenius*, reindeer *Rangifer tarandus*, musk oxen *Ovibus mos-*

chatus as well as lemmings, various species of *Lemmus* and *Dicrostonyx* of the small mammal fauna.

A striking and much discussed phenomenon is the extinction of many of the large mammals at the end of the Pleistocene after the Eemian and around the end of the Weichselian, including both herbivores and predators. Most authors blame people for these extinctions but others blame climate change. However, similar changes in climate had happened several times before without such consequences.

The first humans appeared in Europe relatively late. The evolution of humans took place in Africa. After various forms of development *Homo erectus* was the first to be accepted as a real human in that they were able to produce artefacts: they came into being almost two million years ago. In Europe, finds of *Homo erectus* are very sparse and are lacking in the long Lower Pleistocene. The oldest bones in Europe have been found in Spain and are dated to around 780 000 years BP while the oldest find from north of the Alps was discovered at Heidelberg in Germany with an age of 600 000 years BP. Around 300 000 years BP, Neanderthals (*Homo neanderthalensis*) evolved from *Homo erectus* and this group spread far across Europe until Neanderthals disappeared around 30 000 years BP. Several millennia before that, modern humans, *Homo sapiens,* had immigrated to Europe, also coming from Africa via the Orient. These people evolved independently from *Homo erectus* and gradually replaced the Neanderthals (Terberger, 2009). Now a cultural revolution took place, expressed in tool industries as well as in artistic cave paintings and sculptures and leading gradually to modern periods. Only much later did the sharp increase in population result in anthropogenic environmental changes.

2.

Palaeoecological materials and methods

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2.1

Introduction

"At one extreme are its philosophical underpinnings. At the opposite, practical end of the spectrum, are the techniques used to obtain scientific results – radioactive tracing, remote sensing, controlled laboratory experiments, the deployment of instrumental arrays or pollen analysis, for example." Oldfield (2005)

The spectrum of methods used in Quaternary palaeoecology and vegetation history is very broad and can only be briefly summarized in this chapter. A number of more detailed books and book chapters exist for various specific topics. A comprehensive introduction by Birks and Birks (1980), reprinted in 2004, offers much more than methods: namely principles, research questions and results. Decades ago the need to standardize methods across Europe was felt and, within the International Geological Correlation Programme, the project on Palaeohydrology (IGCP 158a on rivers, IGCP 158b on lakes) first produced a handbook on methods edited by Berglund (1986), reprinted in 2003, and subsequently a synthesis by Berglund et al. (1996a). These, in turn, led to the establishment of the European Pollen Database (EPD). More recently two new major methodological sources have become available: (1) Tracking Environmental Change Using Lake Sediments now published in the Developments in Paleoenvironmental Research series, especially volumes 1, 3 and 5 and (2) the sections about pollen and plant macrofossils in volume 3 of the Encyclopedia of Quaternary Science (2007 and 2nd edition in 2013 edited by S.A. Elias and C.J. Mock).

Methods help to address the basic questions of 'where', 'how', 'when' and 'why' did changes in flora and vegetation occur? In other words, what and where are the natural archives, how do we extract botanical information from them, how can we develop a chronology and what processes may explain the changes (or the stability)? Answers to these questions will help to formulate the next research questions of why, where and how to continue. Concise introductions to the principles are offered for pollen analysis by Seppä (2007a, 2013) and for plant macrofossil analysis by H.H. Birks (2007a, 2013), Jackson and Booth (2013) and Birks (2014).

2.2

Where: natural archives and their sampling

2.2.1

Deposits in lakes and mires

In cultural archives we hate humidity because it destroys paper and paintings through fungi, microbes and other agents. In natural archives, however, water conserves the plant remains (pollen, macrofossils and wood, all of which are susceptible to oxidation) by reducing or even excluding oxygen from the air. Therefore, the best natural archives are the wettest spots in a landscape, for example lakes and mires.

Site selection depends primarily on the research question being asked. In addition, it is worth considering what is the origin of the lake or mire basin. Hutchinson (1957, 1975) provides an overview of 76 types of lake origin, of which we show a selection in Table 4.6-1. Concerning the importance of these possible origins there is a difference between number and relevance: most lakes are of glacial origin (as in Fennoscandia and northern North America) but lakes of special relevance to studies of environmental history may be those outside formerly glaciated areas, either because of their spatial coverage (such as lakes of karstic, deflational, fluvial or geomorphological origin) or because they hold long records (volcanic lakes or meteoritic impact craters).

Basin analysis may be useful for choosing the best coring sites. Even basins that look simple from a landscape perspective may turn out to be more complex. Depending on the research question (and often in accordance with the available coring equipment), we may want to choose littoral or profundal coring spots. For tracing lake-level changes, littoral cores are more informative but for complete sequences (that is without hiatuses) the profundal

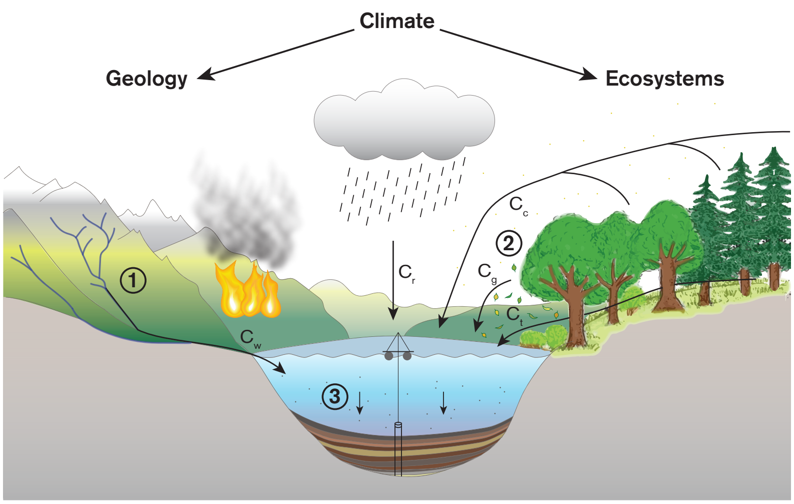

Fig. 2.2-1. Lake basins are natural archives for abiotic and biotic particles that record geological and ecological conditions and their changes over time. Biotic remains of both terrestrial and aquatic origin are deposited in lakes. The processes of pollen (and macrofossil) production, dispersal and deposition are highly complex, and some of them are taxon-specific: for example pollen productivity of entomophilous plants is usually much smaller than that of anemophilous plants; pollen dispersal to the free atmosphere (and the fall-out curve) is higher for tall trees than for small herbs. Tauber (1965) distinguished five ways of pollen transport: Cg = gravity component, Cc= canopy component, Cr= wash-out by rain, Ct = trunk-space component, Cw= runoff component. The ultimate goal is to reconstruct flora and vegetation (and their patterns) around the lake at various distances and to understand the causative factors for change (see chapters 4 and 5). Plant macrofossils are more heterogenous than pollen in several respects: various parts of the plants can be found (fruits, seeds, bud-scales, wood and more), accordingly their dispersal and preservation are complex, but the possibility to identify macrofossils to the species level and their more local origin makes them very valuable for palaeoecology, see Box 1 by Hilary H. Birks. In addition non-pollen palynomorphs (NPPs) may be important, see Box 2 by Bas van Geel below.

is more appropriate (see vol. 1 of Tracking Environmental Change Using Lake Sediments: Scholz, 2001; Moorman, 2001; King and Peck, 2001). Differences in sediment accumulation may also be found between wind-exposed and sheltered parts of the basin as has been demonstrated by Odgaard (1993).

Some lakes may become completely filled and then overgrown by peat, usually first by fen peat and later by *Sphagnum*-dominated raised bog (see Fig. 2.2-2 and chapter 4.7). Ombrotrophic peat can be used as a special archive for purely atmospheric input (that is without input from surface run-off): this is important for the reconstruction of atmospheric pollution history (Shotyk et al., 1998, 2000; Martínez-Cortizas et al., 1999; Weiss et al., 1999; Roos-Barraclough et al., 2002).

2.2.2

Other archives

In addition to lakes and mires many other archives exist, such as marine sediments, glacier ice or cave deposits. Each type brings its own possibilities and difficulties.

Marine cores are very important for timescales longer than the Holocene. Their lower sedimentation rates have an advantage – reaching further back in time – and a disadvantage – even refined sampling may not provide high temporal resolution. In spite of the vast pollen-source area of marine cores their comparability to terrestrial records has been shown in some cases, for example by Tzedakis et al. (1997) or Sánchez-Goñi et al. (2002).

Cores in glacier ice can provide very interesting records if the pollen concentration can be enhanced by appropriate laboratory treatments (Brugger et al., 2018a). Again the pollen-catchment area is very large but landscapes can be studied that otherwise have hardly any archives (Brugger et al., 2018b).

In archaeological contexts, samples within excavations are often compared with records from outside the settlements (on-site records versus off-site records; see chapter 4.5).

Soils of certain types such as mor (raw-humus top of podzols) or shallow organic layers formed in small forest hollows without permanent open water can provide refined spatial records, namely the stand-scale development of vegetation. Whereas the source area for pollen and macrofossils may be large for lakes and mires (see chapters 4.6 and 4.7) it is often small and spatially restricted for small forest hollows due to the very local deposition of

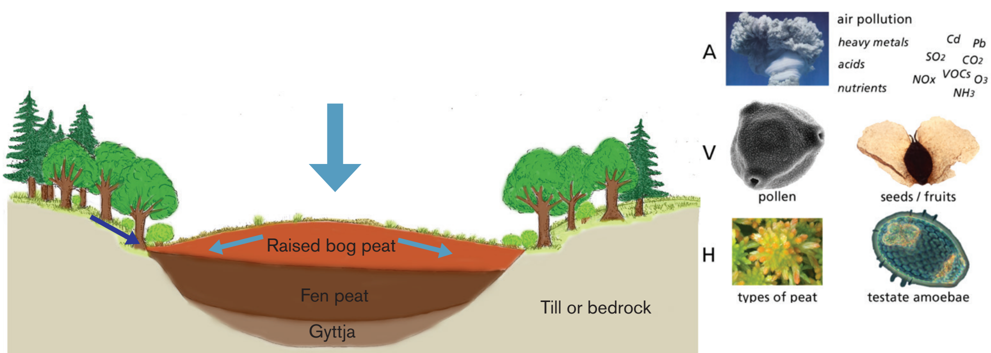

Fig. 2.2-2. Schematic system of how a site may develop from a lake to a fen and a raised bog, incorporating environmental components through time: A from the atmosphere, V from vegetation, H from hydrology and aquatic ecosystems. Mires can also have other origins than lakes, see chapter 4.7. Because raised bogs are in their centre disconnected from the hydrology of the surrounding landscape they offer the possibility of separating atmospheric input (large blue arrow) from erosional input; thus studies of air pollution are possible ("pollution history", see Box 4 by Neil Rose). Hydrological changes may be recorded in the composition and preservation of the peat and in the biostratigraphy of the testate amoebae, see Box 3 by Katarzyna Marcisz.

plant remains (Iversen, 1964; Andersen, 1970; Aaby, 1983; Bradshaw, 1988, 2013; Bradshaw et al., 2005).

Cave deposits may be difficult because of poor pollen preservation but of great interest because they often represent long and/or archaeologically important periods. Cave sediments may include pollen, plant macrofossils, charcoal and fossilized animal droppings (coprolites, see Gale and Carruthers, 2001).

In rare cases **archives controlled by animals** can be used, for example droppings from bats or other mammals, as shown by van der Knaap (1989) or Yll et al. (2006). Fossilized droppings can be important in archaeological contexts, be it for the Palaeolithic or the Neolithic (Rasmussen, 1993; González-Sampériz et al., 2003; McGarry and Caseldine, 2004; Carrión et al., 2008). In caves, coprolites and sediments may provide complementary evidence. By comparing pollen spectra in surface samples with those in dung pellets from goat, sheep, rabbits and other animals, Carrión (2002a) could show that a high diversity of insect-pollinated species (rare or absent in lake sediments) can be traced in this way. Birds and mammals as collectors of modern pollen by means of their feathers and coats were studied by Groenman-van Waateringe (1998): if such pollen is brought into lakes or bogs and becomes incorporated in the sediment it may provide a chance to record rare taxa but it may also be a source of long-distance contamination.

Table 2.2-1. Components of lake sediments and peat after Troels-Smith (1955) and Aaby and Berglund (1986, 2003).

1. Turfa (T)		Peat: Macroscopic, mainly subterranean parts of phanerogams and mosses
	T. bryophytica (Tb)	Moss-peat: T. sphagni, T. hypnacea, T. polytrichi
	T. lignosa (Tl)	Wood, roots, twigs of trees, shrubs (e.g. Ericaceae)
	T. herbacea (Th)	Rhizomes, roots of non-woody plants (e.g. ferns, *Phragmites,* Cyperaceae)
2. Detritus (D)		Above-ground parts of phanerogams
	D. lignosus (Dl)	Fragments of wood and bark, > 2 mm
	D. herbosus (Dh)	Fragments of herbaceous parts, > 2 mm
	D. granosus (Dg)	Fragments of woody and herbaceous parts, 2 – 0.1 mm
3. Limus (L)		Gyttja: Remains of micro-organisms (animals, plants), < 0.1 mm
	L. detrituosus (Ld)	Detritus-gyttja, algal gyttja: organic remains of micro-organisms (animals, plants, silica exclusively of organic origin)
	L. siliceus organogenes (Lso)	Remains of micro-organisms built of silica (diatoms, needles of spongi)
	L. calcareus (Lc)	Marl: precipitated calcium carbonates, particles < 0.1 mm
	L. ferrugineus (Lf)	Precipitated Fe-oxides or Fe-sulfides, if reduced: black, if oxydized: yellow or red
4. Substantia humosa (Sh)		Strongly decomposed organic matter, without structure, blackish, not peat, detritus or limus
5. Argilla (A)		Clay and silt: Mineral particles, < 0.06 mm
	A. steatodes (As)	Clay: Mineral particles, < 0.002 mm
	A. granosa (Ag)	Silt: Mineral particles, 0.06 – 0.002 mm
6. Grana (G)		Sand and gravel: Mineral particles, > 0.06 mm
	G. minora (Gmin)	Sand: Mineral particles, 2 – 0.06 mm
	G. majora (Gmaj)	Gravel: Mineral particles, 60 – 2 mm

2.2.3

Coring and core description

A clean and complete core is a *conditio sine qua non* for a successful palaeoecological study as mistakes during the coring operation may be very difficult to discover and impossible or time-consuming to mend. Glew et al. (2001) present more than 10 hand-operated types of corer (for lake sediments) together with their advantages and disadvantages. Wright (1991) offers good advice for frequently encountered problems. Some of the corer types (Fig. 2.2-3) may also be used on peat (piston corers on rods, chamber-type samplers such as the Russian-Belarusian peat sampler). In many cases the top of a sequence is especially difficult to recover as an undisturbed core. In lakes, freeze-corers usually provide a clean sediment-water interface, while in peat sections the top may best be collected as a monolith (for example in a long, square sided box) because the fibres of only partially decomposed *Sphagnum* or other mosses make undisturbed coring difficult. If basins in remote or hardly accessible areas are cored a trade-off between light and/or fancy equipment becomes obvious (unless helicopters or mules are available). More technical coring techniques for deep lakes are described by Leroy and Colman (2001). A general overview including coring, sampling and much more is reported by Glew et al. (2001) and Coleman (1996).

The **storage** of cores is an important concern. Ideal storage conditions can be summarized as 'wet, cool, and dark'. The material must be protected against drying out and against fungi and other microbes. Therefore, proper wrapping in plastic contact-foil and 'sleeves' and storage at cool temperatures (c. 4°C, not below zero) are essential. Dark storage is important because, when stored in the light, algae may develop that capture modern CO_2 from the air thus contaminating the sediment with respect to radiocarbon sampling.

Description of sediments and peats

The description of the cores obtained is a strong basis for any further studies. Aaby (1979), based on Troels-Smith (1955), provides a strong and inexpensive tool which is orientated towards the estimation of the mineral and biological components of sediment or peat. Aaby and Berglund (1986) offer a somewhat refined form and Birks and Birks (2004) provide the connection between the sediment or peat types and hydrological conditions, especially water depth and trophic state. Our figures 2.2-4 and 2.2-5 and Table 2.2-1 visualize the components and their origin. Colour description can be standardized by using the colour charts developed by Munsell for soil descriptions (Munsell, 1975).

2.3

How: analysis of samples

Strategies for laboratory sampling of the cores must be planned carefully to provide enough material for all the studies envisaged (e.g. pollen, plant macrofossils, loss-on-ignition, diatoms, chironomids, Cladocera and radiocarbon or other dating techniques). Non-destructive methods such as photography and geochemistry by XRF should be carried out before the core is subsampled, that is, on the intact core (just cleaned on the surface). If possible, sampling should be done on a single core or a composite master based on the correlation between parallel and overlapping cores. Some analyses, however, require large sample volumes, for example for plant macrofossils and especially for beetles, so, in those cases, the correlation of additional neighbouring cores may become necessary. In addition, a variety of mineralogical and geochemical techniques are very useful.

Samples for analyses of pollen (and plant macrofossils) should be taken as known volumes rather than weights (even if volumes are less precise). The volume needed per sample depends on the pollen concentration (which is not known beforehand). In sediments or peat of Holocene age, 1 cm^3 (ml) is usually enough for pollen, and 10–100 cm^3 for plant macrofossils. Before any chemical treatment, marker grains should be added to samples for pollen analysis as described by Stockmarr (1971) and Maher (1981). This is important because, with a well-established chronology and age-depth model, we may later want to calculate pollen (or macrofossil) influx (grains per surface and year), also known as PAR (pollen accumulation rates). Its advantage compared to percentages is that it is not closed data (not internally dependent). For optimal calculations the number

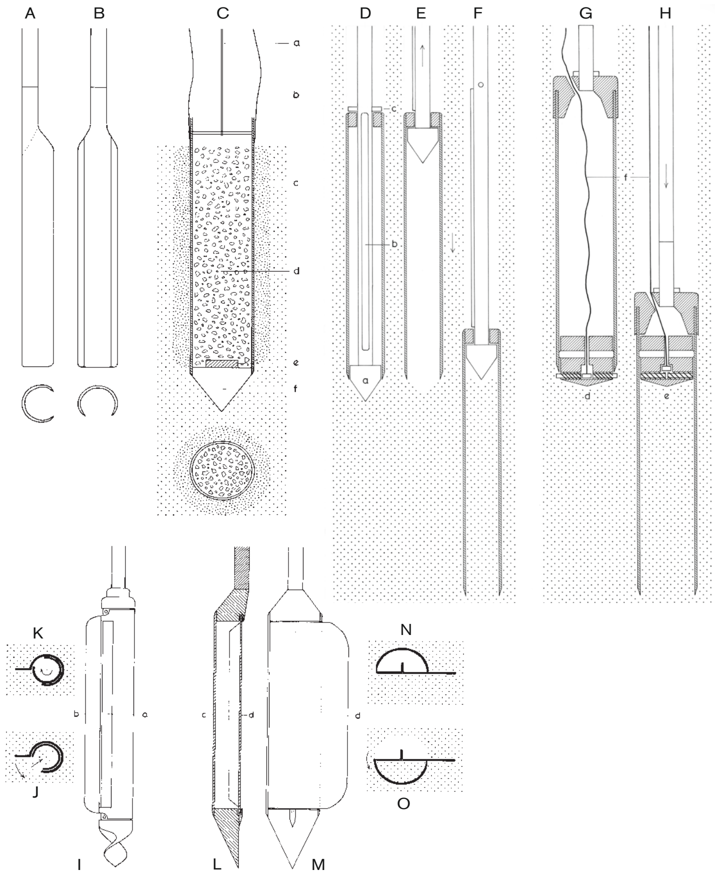

Fig. 2.2-3. Different corer types. **A** and **B:** Dutch 'marsh-spoon' in side view and front view. **C:** 'fridged finger' or 'frozen finger' in side view and cross-section; a: metal cable. b: soft plastic tube fixed to the metal tube; c: frozen sediment; d: refrigerating mixture of dry ice and a mixture of alcohols (ethanol, butanol, trichloraethylene); e: lead weight; f: point of corer that is not affected by cold temperatures. **D, E, F:** Piston-sampler Dachnowski, D: position at the beginning of coring; a: piston; b: fixing-rod for the piston; c: pin to fix the chamber. E: tube with piston fixed after withdrawal to the upper position (chamber open). F: corer in lowered position (chamber filled). **G, H:** Livingstone corer, G = corer empty, before coring; d: piston fixed by rubber stopper and springs at the lower end; f: steel cable (loose in G and tight in H); H = corer with filled chamber; e: piston unlocked, fixed by the tight cable, allows gliding of the chamber into the sediment by pushing the rods. The metal parts in the cross-section are hatched. **I, J, K:** Swedish side-sampler or Hiller-corer, I = side view; a: chamber (inner tube, fixed to a rod at the top and with an auger point at the bottom); b: external tube with slit and sharpened flange (rotating between pins). J = cross-section when open, K = cross-section when closed (as in I). **L, M, N, O:** Russian-Belarusian side-sampler, L = side view as cross section; c: chamber (half-tube fixed to a rod at the top and with a point at the bottom); d: metal-plate that can be turned. M = front view with d = metal plate, on which the sediment will remain after turning (opening). N = cross-section when chamber is empty, the position in which it is pushed into the sediment. O = cross-section with chamber full of sediment after the corer has been turned. The metal parts in the cross-section are black or hatched.

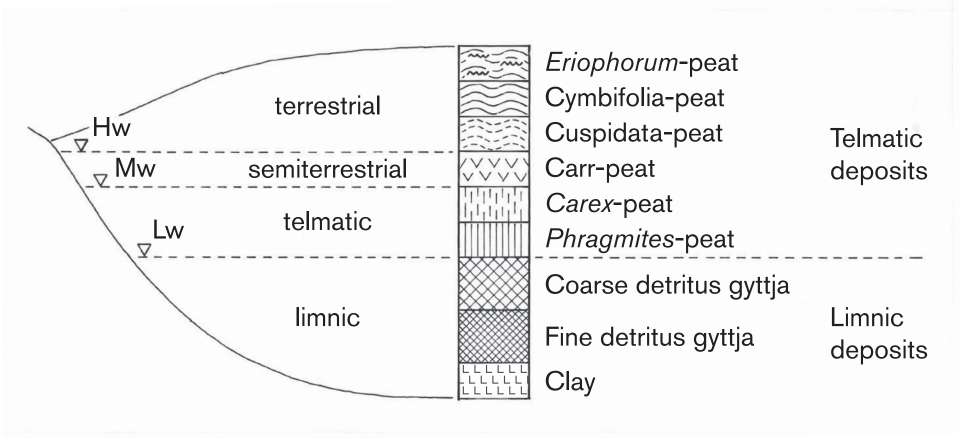

Fig. 2.2-4. Types of sediment and peat in a basin and the relationships to low, middle and high water (Lw, Mw, Hw) and their signatures in the Troels-Smith system (Troels-Smith, 1955)

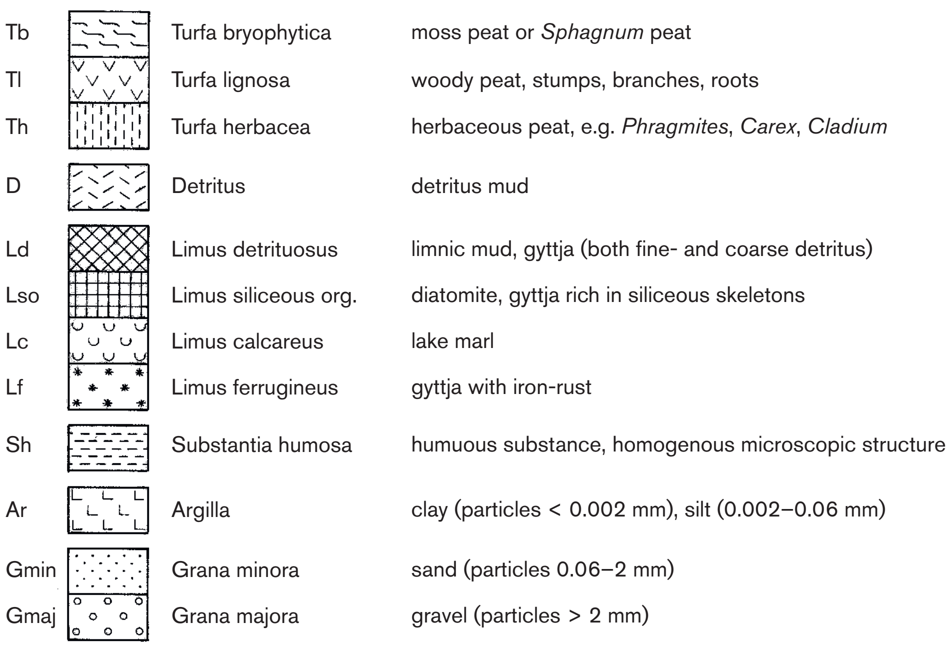

Fig. 2.2-5. Signatures for sediments and peat according to Troels-Smith (1955) and Aaby and Berglund (1986).

of added exotic markers should be similar to the number of pollen and spores in the same volume of sample residue (which cannot be known at the beginning but can be initially estimated and later adapted).

The sampling resolution depends on the research question and the processes that need to be understood. Often, sampling resolution is refined in an iterative approach, but re-opened and re-sampled cores frequently provide less certainty about the exact position of the samples (if the sediment was disturbed during the initial sampling). A good way out of this dilemma is to cut the core lengthwise in two halves, one of which goes to a cool archive, the other one gets completely sub-sampled in as fine a resolution as possible for as many types of analyses as wished. A device for refined sub-sampling was introduced by Joosten and de Klerk (2007).

Laboratory preparation techniques (and safety concerns) are described for pollen by Moore et al. (1991) and Bennett and Willis (2001) and for plant macrofossils by Birks (2001). All preparation techniques aim at concentrating the biological particles to be identified (e.g. pollen, plant macrofossils, charcoal, stomata and other cells) by either dissolving unwanted parts of the sediment or wet-sieving according to size classes. In order to potentially overcome the problems associated with pollen percentages, marker grains in known concentrations must be added (see above).

A puzzling biological paradox is if the living cells within the pollen grain can survive for only hours or days, why do plants invest in substances (sporopollenin) in the outer wall of the pollen grain (ektexine) that can survive for millions of years and resist such violent chemical treatments as being immersed in hydrofluoric acid? It is pertinent to remember that there may be evolutionary reasons for this, such as the development from isospores in ferns, to heterospores in, for example Lycopods, to pollen and ovules in Angiosperms.

For the analysis of plant macrofossils H.H. Birks (2007a, 2013) provides a list of relevant literature grouped into manuals, books and papers on seeds and fruits, on mosses, on wood and on cuticles, bud scales and leaves (see also Box 1 by Hilary Birks).

For the analysis of pollen a strong understanding of morphology is needed for the best possible identification. Europe is in a privileged position in having a number of good reference books for pollen morphology, especially the series of the Northwest

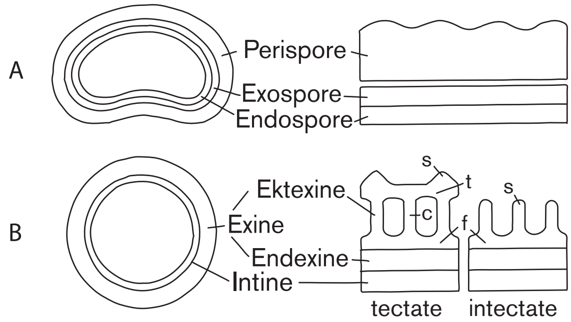

Fig. 2.3-1. Structure of the cell walls in spores (A) and pollen (B). c: columella, f: foot layer, s: sculptural element, t: tectum. Pollen-morphological nomenclature after Iversen and Troels-Smith (1950) and Fægri et al. (1989).

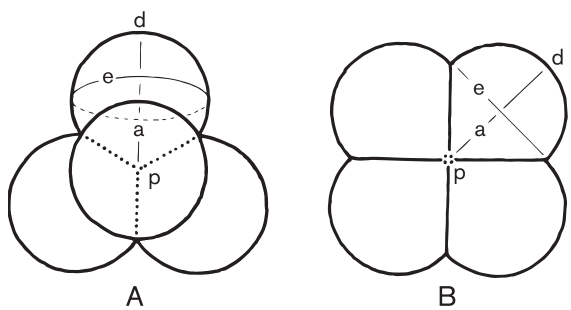

Fig. 2.3-2. Two types of tetrads after meiosis in Cormophytes. A: Tetraedric tetrad (two cell divisions at right angles to each other) in Bryophytes, Pteridophytes and most Dicotyledons. B: Tetragonal tetrad (two cell divisions in the same plane) in Pteridophytes, Gymnosperms, Monocotyledons and primitive Dicotyledons. a: polar axis, d: distal pole, e: equatorial plane, p: proximal pole. Modified from Birks and Birks (1980).

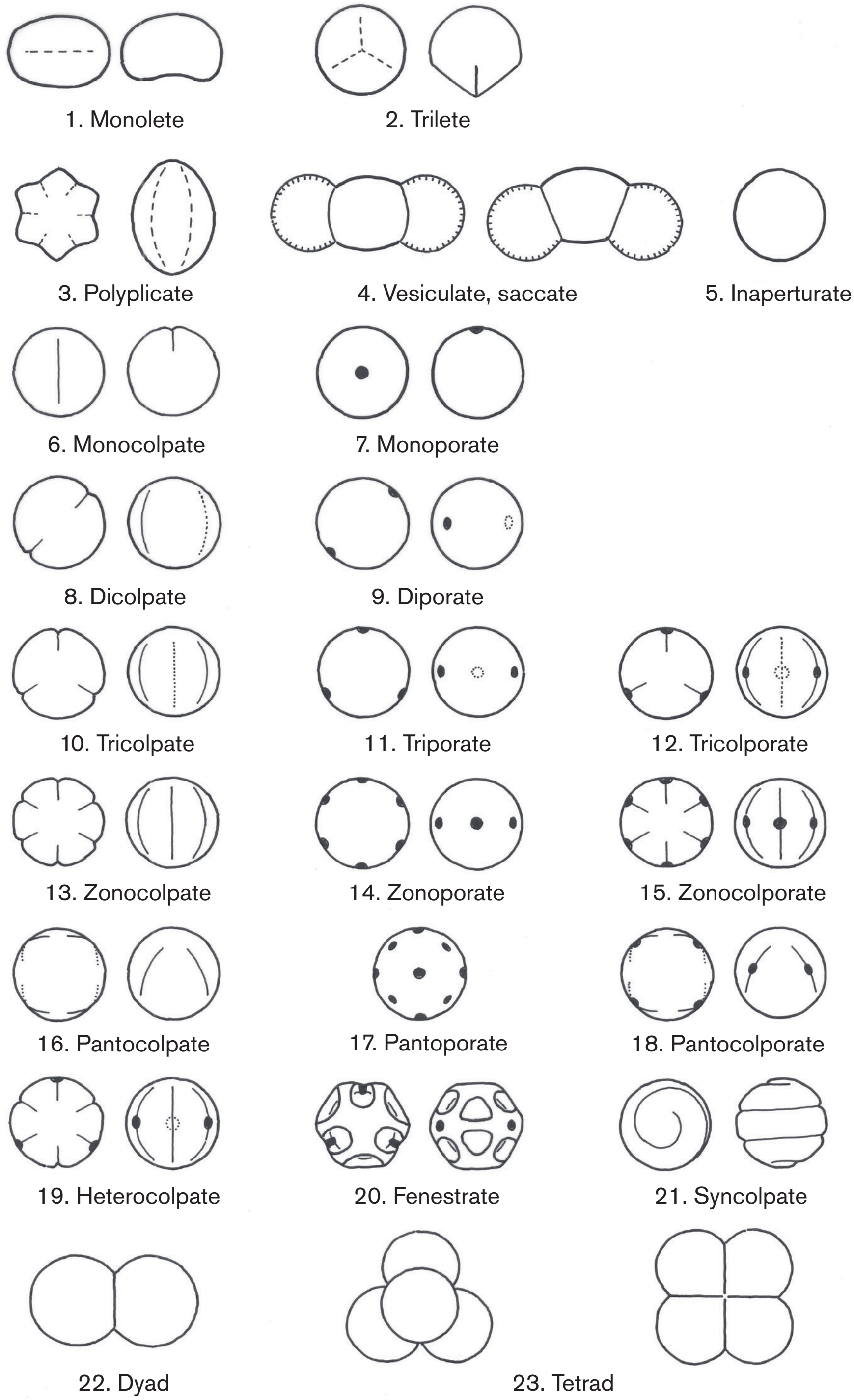

Fig. 2.3-3. Types of pollen and spores in the European flora. 1 and 2: Pteridophytes (spores). 3–5: Gymnosperms (pollen). 5–23: Angiosperms (pollen), inaperturate pollen occur both in Gymnosperms and Angiosperms. The left figures show the view from the pole; the right figures show the equatorial view, distal pole at the top, proximal pole at the bottom. Schematic, modified with additions after Iversen and Troels-Smith (1950).