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Macro fossil analysis

A deep look into the peat archive

Caroline Greiser

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Biology Education Centre and Department of Plant Ecology and Evolution, Uppsala University

Supervisor: Sebastian Sundberg

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Abstract

Over the last years several sophisticated methods have been investigated to reconstruct the history of the landscape. The peat layers of wetlands act as historical archives and by analysing the preserved plant remains, so called macro fossils, conclusions about the former local vegetation and site conditions can be drawn. The study system is boreo-nemoral rich fens, a threatened wetland type with a large floristic biodiversity. The study sites are three wetlands in the province of Uppland, where in 1950ies drainage for forestry had changed the peat and the vegetation drastically. In 2003 the sites were rewetted by ditch blocking. Older vegetation data are incomplete or not available raising the questions, how the pre-drainage conditions really have been and if the sites could be classified as rich fens. To answer this, the macro fossil assemblages of nine peat cores (three per site) were analyzed with special emphasis on mosses. To investigate the effect of drainage on the peat layer, the cores were also analyzed for degree of peat decomposition, using three different methods. The results of the decomposition analysis differed a lot among the three methods. The von Post method seemed to provide the most robust data. Drainage effect could be seen when surface peat was more decomposed than underlying layers. The macro fossil analysis resulted in a quite large number of identified species and estimations of their proportions. Several characteristic species (brown mosses, peat mosses, etc.) in the peat of all three mires indicate with high certainty that the sites have been rich fens in the past. This information can support argumentations in restoration projects. General restrictions of macro fossil analysis, the problem of aging, inhomogeneous decomposition and vegetation patchiness and future challenges are discussed.

Introduction

We can not travel back in time, but we can learn to read the landscape, that tells its own history. Over the last years several sophisticated methods have been investigated using a large variety of proxies to reconstruct the past. For example tree rings, lake varves and ice cores provided useful information for past climate reconstructions (Mann 2002). When it comes to vegetation changes during the Holocene, the time after the last glaciations in Europe, the peat layers (accumulated organic material) of wetlands act as historical archives and by analysing their features and composition, conclusions about the former local and regional vegetation can be drawn (Rydin & Jeglum 2006).

For these biostratigraphic studies, fossils of every size are analysed: from pollen grains (10-100 µm) to mammoth (several metres) – everything that is preserved in the peat. A **macro fossil** can be seen by the naked eye and ranges from 0.5 mm to 2.0 mm (median size) to large tree trunks (then termed „mega fossils“). Plant remains can be fruits, seeds, leaves, cuticles, buds, anthers, rhizomes, twigs, wood, bark but also sporangia and megaspores from lower plants as well as various animal remains (e.g. bryozoa, oribatida, chironomids) are preserved (Birks 2007).

The vegetation of a site integrates the overall conditions, like water table, nutrient status, pH and light availability, meaning that one can infer from the macro fossil assemblage more or less the former vegetation and thus the former conditions of the location. For that purpose indicator species with a small optimum range are of great help. Plant **macro fossil analysis** became, additionally to pollen (micro fossil) analysis, an important tool in paleoecological studies (Birks 2007). Kuhry *et al.* (1993) used macrofossils to reconstruct past water table and pH for boreal peatlands and to trace their developmental pathway from rich fen to poor fen to bog. Other studies included macro fossil analysis in investigating the rate and nature of carbon sequestration in peatlands (Heijmans *et al.* 2008) or to reconstruct bog surface wetness as evidence for climate change (Barber *et al.* 1998). Unlike pollen, macro remains allow often identification to the species level enabling more detailed palaeoenvironmental reconstructions (Mauquoy *et al.* 2010). Furthermore, opposed to pollen they are usually not transported away from their area of origin, which means that they represent the local vegetation, not to mention that some taxa are preserved as macro fossils, but produce no or little pollen, including cryptogams (Birks 2007).

When interpreting the data, one must be aware of the different taphonomic processes (growth reproduction, dispersal, deposition, preservation) involved in the formation of an assemblage, causing it to contain plant material from vegetation at different scales. Seeds and fruits can be dispersed far away from their origin by wind, floods, streams and animals. Some seeds are produced abundantly, but are almost never fossilized. Due to their chemical constituents, different species but also different parts of plants have different decomposition rates. In general, above-ground parts of non-woody plants are hardly preserved as fossils – except fruits and seeds (Grosse-Brauckmann 1972). Various herbs decompose and mineralize without any detectable trace, whereas seeds sometimes remain amazingly well preserved even under disturbed conditions. Moreover the degree of peat decomposition determines the quality of the fossils, and is itself a function of water level and movement, nutrient status, pH and vegetation. Another pitfall is the unbalanced identifiability. Some fossils are very distinct, while others are not. In general mosses are more easily identified in peat than vascular plants, which can lead to an overrepresentation of the former (Svensson 1986).

Peat accumulation and the **forming of macro fossils** have taken place because of inhibited decay. Oxygen poor conditions in a water-logged environment, as well as the low decomposability of the plant material are the main reasons for that (Rydin & Jeglum 2006). A wetland, where peat is being accumulated by living peat-forming plants is called a **mire**. There are different types of mires and also different ways to classify them, depending on the wetness and aeration, pH, calcium (Ca) content and base saturation (Rydin & Jeglum 2006).

The water, its chemical components and movement in the peatland plays an essential role. Therefore a widely accepted first separation of mires is made due to the origin of water, which “feeds” the mire, meaning that it not only provides humid conditions but also nutrients. If the peatland is nourished by the mineral soil water, it is called “*minerotrophic*”, if it is fed only by precipitation we call it “*ombrotrophic*”. Other terms for minerotrophic mires are “**fen**” (Swedish “kär”) or “**bog**” (Swedish “mosse”). As peat formation can start for example at the margins of a lake (terrestrialization or infilling; Rydin & Jeglum 2006), building a fen in the beginning, growing higher, losing contact to mineral soil water, becoming a bog, it is clear, that the different peat types – no matter which classification is used - are sometimes no distinct units with sharp borders, but can merge into each other.

The study system in this thesis is boreo-nemoral **rich fens**, which are characterized by high pH-values (6-8) and high mineral concentrations (Ca, Fe, Mg). The term “rich” does not refer to high nutrient contents, but to high pH, high mineral concentration and often high species richness. The latter explains them to be of high interest in biodiversity conservation issues. In general these biotopes are even nutrient poor and most of all phosphorus limited, since the calcium binds the phosphorus and makes it unavailable for plant growth (Koerselman & Verboeven 1995). Further division took place due to pH and Ca-content with *moderately* rich fens having a pH 6-7 and lower Ca-concentrations (8-30 mg/l) and *extremely* rich fens having a pH >6.8 and higher Ca-concentrations (30-100 mg/l) (Sjörs and Gunnarsson 2002).

The floristic biodiversity on rich fens is exceptional with many specialized and threatened species (Rydin & Jeglum 2006). Therefore, **indicator species** are used to classify a wetland as a moderately or extremely rich fen (Sundberg 2007). Beneath several vascular plants a number of bryophytes (brown mosses, peat mosses) are characteristic of rich fens and often well preserved as macro fossils in peat.

Peat mosses (*Sphagnum* spp.) are largely dominant in ombrotrophic bogs, but some species can even occur in minerotrophic wetlands. That is either when they prefer high pH (e.g. *S. warnstorffii*, *S. teres*, whole section Subsecunda) or when some hummocks in a mineral rich environment have grown so high that they lost the contact with the groundwater and are thus ombrotrophic “islands” (Rydin & Jeglum 2006).

Brown mosses are not a taxonomic entity, but rather an ecological group growing in rich fens (Rydin & Jeglum 2006). Historically these were species of the Amblystegiaceae and Calliergonaceae families (e.g. *Scorpidium* spp., *Calliergonella cuspidata*, *Warnstorffia* spp.), but nowadays also species from other families are factored into the ecological group (e.g. *Cinclidium stygium*) (Rydin & Jeglum 2006). For simplicity in this work the term “brown moss” refers to any moss species found in the peat, that is no *Sphagnum*. Liverworts are in this topic out of discussion, because they are rarely preserved as macrofossils (Kuhry, pers.comm.) A certain assemblage of characteristic species found preserved in the peat can indicate a mire to be or have been a rich fen.

During the last two centuries many rich fens in Sweden were **drained** for agriculture or forestry (Vasander *et al.* 2003). The lowered water table changes the chemistry and accelerates decomposition, which results in a more or less drastic vegetation change (for example invasion of dominant species; Mälson *et al.* 2008). Being biodiversity hot spots in the landscape, rich fens are interesting from a **conservation** point of view and are now on the list of threatened habitats in Sweden. This work is embedded in a larger study that evaluates different **restoration** measures of drained rich fens for effective future application (cf. Mälson *et al.* 2010).

Before drainage took place, the three peatlands under observation are thought to have been *moderately* rich fens (“Ultunaviken”, “Styggkärret”) and in case of “Severmossen” an *extremely* rich fen. But older vegetation data, especially from the period before drainage, are only sparse and not available at all for Severmossen. That raises the question, how the pre-drainage conditions really have been and if the sites could be classified as rich fens. Therefore, I used the peat layer as a historical archive by analysing the macro fossil material and examining their value for inferring former conditions in this work. I also discuss general usefulness and restrictions of macro fossil analysis. Drainage always causes severe disturbance of the peat layer: the organic material becomes aerated and decomposes faster. To investigate the effect of drainage in that sense, the peat is also analysed for its degree of decomposition.

Materials and Methods

Site Description

Peat cores were taken from three sites in the province of Uppland (boreo-nemoral vegetation zone), east central Sweden: two adjacent moderately rich fens (Styggkärret and Ultunaviken, 25km north-east of Uppsala, 59°57'N 17°18'E) and one extremely rich fen (Severmossen, 90 km north of Uppsala, 60°26'N 17°57'E, Fig.1). According to historical maps the sites were used for haymaking during the nineteenth century and drained during the 1950s for forestry (but not planted with trees). **Peat depths** range from almost 1 m at Severmossen and 1-2 m at Styggkärret, and up to 3 m at Ultunaviken (Markdagsexkursionen 2007).

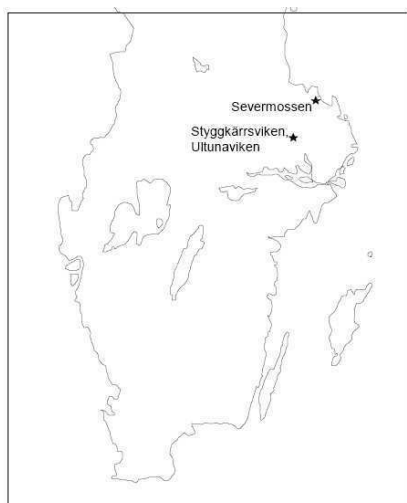


Fig. 1. Location of the study sites, from where the peat cores were taken. (Sundberg pers. comm.)

At Styggkärret, several characteristic vascular plants (such as *Eriophorum latifolium* and *Pedicularis sceptrum-carolinum*) and brown mosses (such as *Scorpidium scorpioides*, *S. cossonii* and *Campylium stellatum*) of moderately rich fens were found before drainage, with *S. scorpioides* being dominant in large parts indicating very wet conditions (von Krusenstjerna 1945; Mälson *et al.* 2010). In 2002, around 50 years after drainage, the vegetation was mainly built of *Sphagnum* spp. and *Polytrichum* spp. in the bottom layer, with only few occurring rich fen vegetation. *Betula pubescens* had colonized the site, growing rather dense and tall (ca. 12 m).

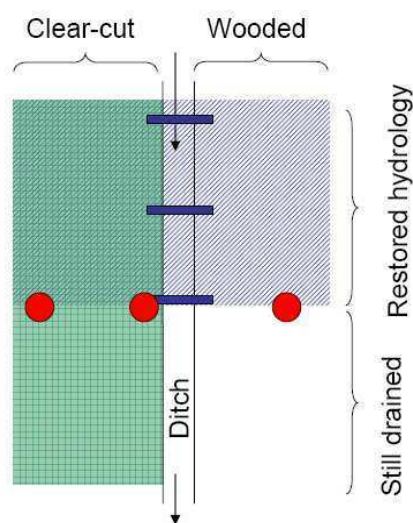


Fig. 2. Experimental design. One side of the ditch was cleared of all trees while the other side was left uncut. The dots mark the location of peat coring, which was done at the border between upstream part with restored hydrology and downstream part that was still drained (slightly changed from Mälson *et al.* 2010).

There is a lack of knowledge about the pre-drainage vegetation at Severmossen. In 2002 the site was dominated by graminoids (such as *Molinia caerulea* and *Schoenus ferrugineus* in the field layer) and *Pinus sylvestris* and *Betula pubescens* in the shrub and tree layer (6 m), although with some patches with orchids such as *Epipactis palustris* and *Ophrys insectifera*, and bryophytes such as *S. cossonii*, *Campyliadelphus elodes*, and *Preissia quadrata*, indicating (former) rich fen conditions (Mälson *et al.* 2010).

Restoration Measures and Experimental Design

In spring 2003 the main ditches were blocked to rewet the sites. After that the sites included a rewetted upstream part and a downstream part that remained drained. To recreate the light regime of an open fen, shading and evapotranspiring trees and shrubs were removed in 2002 and 2003. This took place at one side of the ditch in the rewetted and the drained part. (Fig. 2)

Peat cores

From each fen three peat cores were taken at the transition between “rewetted” and “still drained” parts 30 m apart from each other (Fig. 2): one in the nowadays open/deforested area, one close to the ditch and one in the forest area, making a total of 9 cores being analyzed. Peat cores were taken in October 2010 with a 5-cm diameter Russian peat corer reaching from the surface to 1 m below ground. The material was stored in half sections of polyvinylchloride pipes and wrapped with plastic for transport and to prevent drying. During the first three months the cores were stored in a freezer (-18°C). After that they were kept in a cooling chamber at 4°C and were only taken out into room temperature when being processed.

Lab work

One part of the lab work was done during a previous project work (von Post humification, moss decomposition, rough macro fossil analysis), while the second part (colorimetry, brown moss and *Sphagnum* identification) was done later to gain more information and data.

Humification/Decomposition

Decay and compaction of the peat makes it become more humified. Humification can be measured as degree of decomposition and can be assessed using different methods. In this work three different methods were implemented to have a backup, but also to compare the different techniques.

I) First the rather simple, but quite informative field method from **von Post** was conducted, where one squeezes a handful of peat and evaluates the water and the structure of the remaining material (von Post humification scale, Rydin & Jeglum 2006).

II) Secondly a decomposition value was assessed on the basis of **moss preservation** (modified Janssens 1983 in Kuhry *et al.* 1991). Depending on the quality of the leaves and the length of the branches the samples got a number between 1 and 4 (well – badly preserved/ low – highly decomposed).

III) During the process of decomposition humic acids (dark brown in solution) and fulvic acids (yellow to light brown in solution) are formed. Highly decomposed peat contains more humic acids. They can be extracted from peat using NaOH. With increasing amount of humic acids the percentage light absorbance rises and thus these values can be used to indicate the degree of peat humification. The **colorimetric method** was applied as a third method and required somewhat longer and more complicated sample preparation. With some changes it follows the protocol provided in Chambers *et al.* (2010). Samples of 2 cm³ were taken at three depths of each peat core, put in Petri dishes, dried at 105°C for 3 hours and ground up in an agate pestle and mortar. 100 mg of pulverised peat was diluted in 25 ml of 8% NaOH and placed in a hot water bath (95°C) for 1,5 hrs. After that the samples lost 5 ml each due to evaporation. They were then centrifuged (10 min at 4000 rpm) and filtered (Munktell 3 filter paper). Of this extract 6 ml were further diluted to 50 ml using deionised water. The absorbance was measured in a spectrophotometer (Novaspec® II, Pharmacia Biotech) at 540 nm wavelength. The plotted values are percentage absorbancy (the amount of light absorbed relative to the initial substance).

The von Post method as well as the spectrophotometry was done at three depths (20, 50 and 90 cm), whereas the moss preservation could only be implemented in the samples, prepared for macrofossil analysis, at 20 and 90 cm depth.

Pre-treatment for Macro fossil analysis

For the macro fossil analysis samples of approximately 5 cm³ were taken from the cores at two depths: 20 and 90 cm. The samples were warmed up to 60°C together with 5% aqueous KOH solution. This is done for deflocculation (dispersing agglomerates into fine particles) and to dissolve humic and fulvic acids. After that the material was disaggregated on a sieve (125 µm) keeping the residue in the sieve below the water surface in order to prevent further damage to the plant macro fossils (Mauquoy *et al.* 2010) The treated samples were stored in plastic tubes in a cooling chamber (4°C) and sieved again immediately before analysis. The analysis procedure roughly followed Kuhry *et al.* (1991) using a dissecting microscope with 6-50× magnification and a high-power microscope (40-600×) when necessary, e.g. for identification of mosses.

Identification Literature

General introduction, first rough distinction and some very detailed and nice pictures are found in Grosse-Brauckmann (1972, 1974, 1992). They show a selection ranging from monocotyledon tissues, to brown mosses, to peat mosses and also cover quite a large number of seeds. Moreover there are good plates with fossil seeds in Birks (2007) and very helpful colour picture plates in Mauquoy & van Geel (2007), even with a small selection of non-plant material from the moss fauna and fungal spores.

The determination of **mosses** is difficult at times with the standard literature (Hallingbäck & Holmåsén 1982, Nyholm 1954) because the keys require often complete fresh plants and what one finds is rather single detached, sometimes even badly preserved, leaves. However there are good drawings in Nyholm (1954) and Hedenäs (2003). Michaelis (2001) provides a useful key for the identification of single brown moss leaves. Further, a handout with microscope photographs by Hedenäs helped, as well as comparisons with moss herbaria.

For the identification of **peat mosses** the Handbook of European Sphagna (Daniels & Eddy 1985) as well as the peat moss flora published by Mossornas Vänner (2010) were used. They provide detailed drawings and measurements of the leaf anatomy (cross sections, pores, chlorocysts). They were both useful since no complete branches or even plants were preserved. In Grosse-Brauckmann (1974) one finds a selection of *Sphagnum* species represented in microscope photographs together with a rough description.

Nomenclature for mosses followed Hallingbäck *et al.* (2006) for bryophytes and Karlsson (1998) for vascular plants.

Identifiability of the material had a rather large range, so instead of counting species it was reasonable to count macro fossil types, form groups and estimate their volume percentage. Occasionally, plant remains allowed identification to the species level, e.g. the leaf tips of *Scheuchzeria palustre*, or the roots of *Carex limosa*. If possible, the brown mosses were determined to the species level. Single detached leaves of *Sphagnum* allowed at least an attribution to the section (group of closer related species), sometimes even to a species. A selection of the identified macro fossils is presented in [Appendix 1](#).

Most plant macro fossil types are estimated as **volume percentages**. This was done for inorganic matter, detritus, wood, roots, epidermal tissues, *Sphagnum* and brown mosses. Seeds, spores and *Scheuchzeria* leaf tips were simply counted and expressed as **total numbers** per sample. When analyzing and plotting the data, some categories were merged. Usually where several parts of single species occur - for example the roots and “leaves” of *Equisetum* – they should be treated as separate “pseudo-taxa”, which helps in interpreting the macro fossil diagram: roots can grow into material that is much older and seeds could originate from places far away. However, because the stratigraphic resolution in our case is so low (only 2 samples per peat core) it seemed acceptable to put *Equisetum* roots, rhizomes and leaves into one category. The following **abbreviations** for the samples are used: **UV**-Ultunaviken, **SK**-Styggkärret, **SV**-Severmossen; **O**-open/deforested area, **D**-ditch, **F**-forest; **20, 50, 90** – peat depths in cm.

Results

Humification/Decomposition

Most conspicuous, on first sight, seemed the differences in results depending on which method was applied, where von Post and Janssens showed the best agreement at least for Severmossen and Styggkärret. (Fig 3 a, b, c) Results from the spectrophotometry did not show a pattern of either agreeing or contradicting the results of the other methods, although all of them indicated a quite high decomposition at Severmossen. When taking a closer look at the decomposition rates after von Post – the most reliable data, which will be explained later – there were only two cores, where the surface peat is less decomposed than the underlying peat (UV-O and UV-D, Fig. 3 a). All the other peat cores showed a similar or even higher decomposition at the surface.

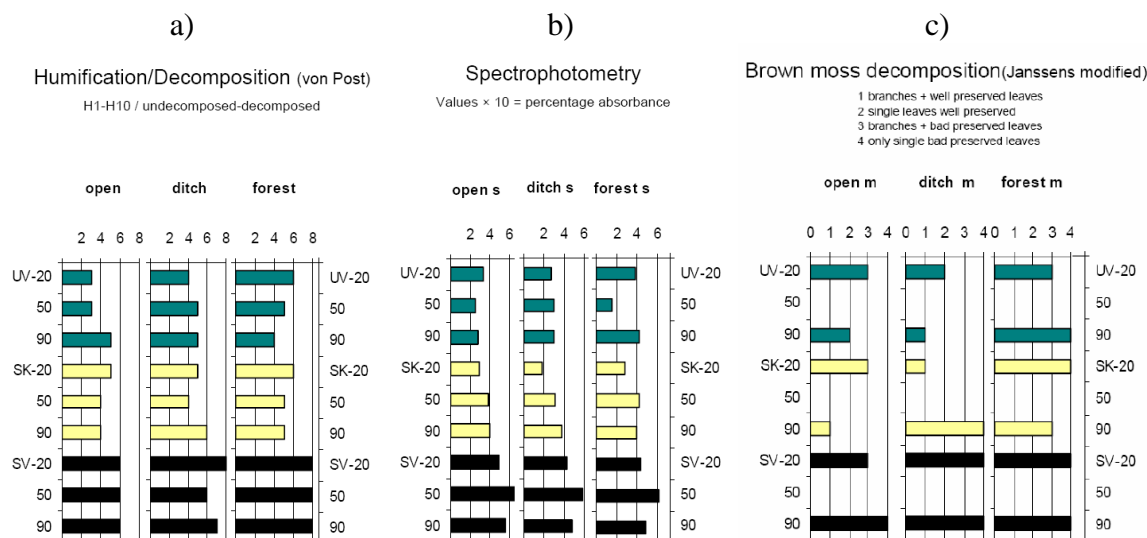


Fig. 3 a, b, c. Humification/Decomposition of peat sub-samples in three (two) different depths for all nine cores. (Numbers 20, 50 and 90 = depth in cm). Each study site is represented by one colour and its name abbreviation (UV = Ultunaviken, SK = Styggkärret, SV = Severmossen). The column headings name the location within the sites, where the peat cores were taken: O = open/deforested area, D = ditch, F = forest (see Fig. 2). Three different methods were applied: Numbers on X-axis are degree of decomposition with varying indicator: a) Humification-value H1-H10; b) Values x 10 = Percentage light absorbance; c) categories based on brown moss preservation. In all graphs higher numbers/longer panels indicate higher degree of decomposition.

Macro Fossils – Main fractions

The results are presented in two alternative plots (Fig. 4 and 5). Fig. 5 shows them in a way macro fossil results are generally shown, while Fig. 4 has the advantage of providing a faster overview of the samples' main fractions. Both will be analyzed and discussed together below.

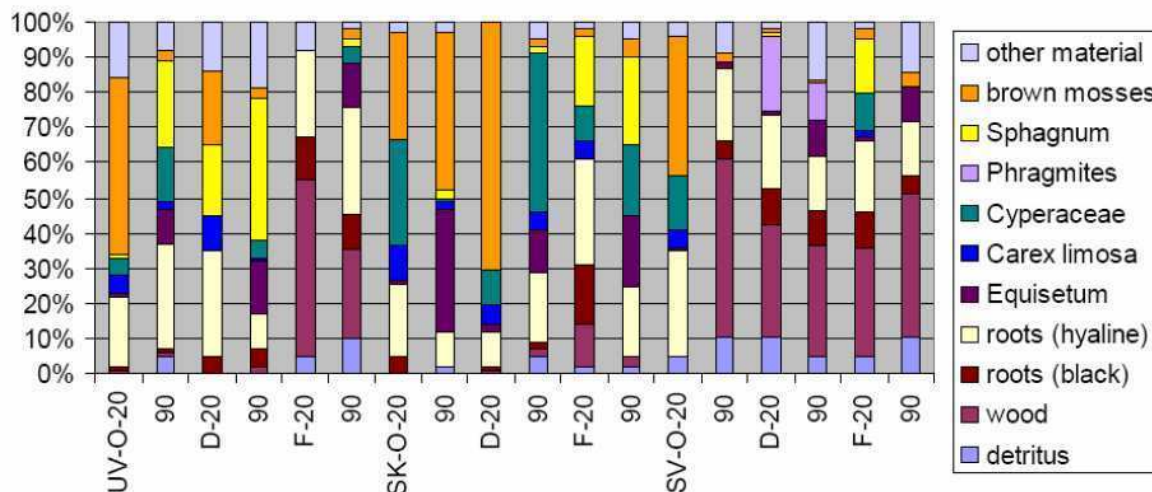


Fig. 4. Macrofossils of three former rich fens. Values are volume percentages of all macro fossil material in a sample. Abbreviations for study site, location and peat depth: UV-Ultunaviken, SK-Styggkärret, SV-Severmossen; O-open/deforested area, D-ditch, F-forest; 20, 50, 90 – peat depths in cm (see Fig. 2).

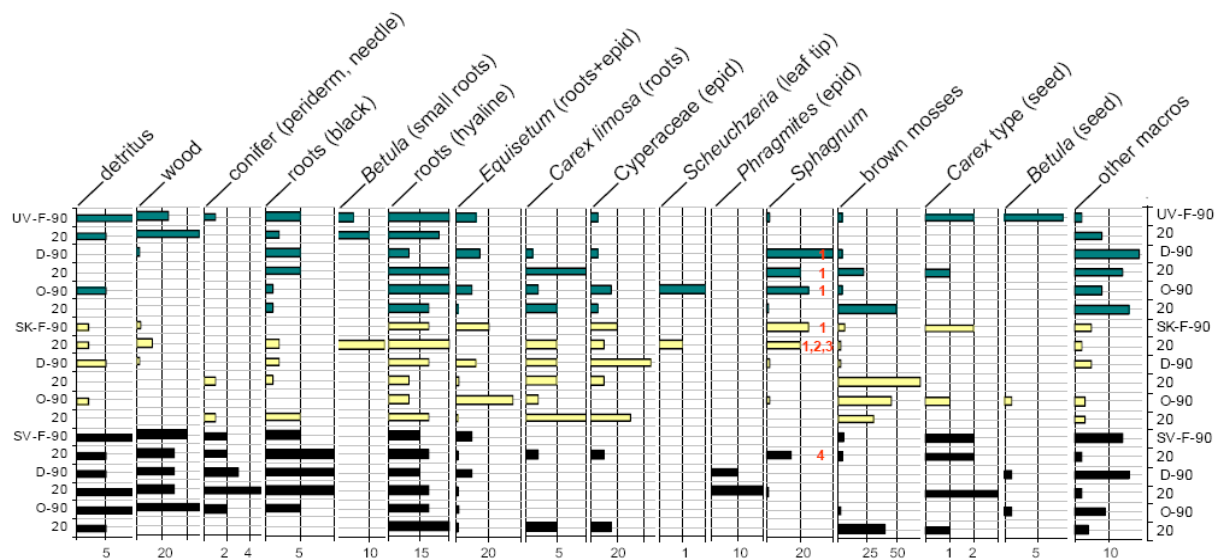


Fig. 5. Macro fossils of three former rich fens. Values are volume percentages of all macro fossil material in a sample, except total counts for: *Scheuchzeria palustris*-leaf tip, seeds (*Betula*, *Carex*), conifer periderm/needle. Red numbers (*Sphagnum*): 1 = section Subsecunda (*S. contortum*), 2 = section Acutifolia, 3 = section Sphagnum (*S. centrale*), 4 = section Squarrosa (*S. squarrosum*, *S. teres*). Abbreviations for study site, location and peat depth: UV-Ultunaviken, SK-Styggkärret, SV-Severmossen; O-open/deforested area, D-ditch, F-forest; 20, 50, 90 – peat depths in cm (see Fig. 2).

The macro fossil assemblages of the samples differed quite much from each other (Fig. 4, 5). The dissimilarity differed among sites but Severmossen's samples were quite homogeneous. Even samples from the same site and depth (but different locations) were not very similar to each other (e.g. UVO-20, UV-D-20 and UV-F-20), except all samples from Severmossen at 90 cm. In Ultunaviken the peat at the forested location differed most from the other two locations (both at 20 and 90 cm depth), mostly caused by its high wood content. In contrast, at Styggkärret the differences between samples from different locations at the same depth seemed to be similar both at 20 and 90 cm.

Wood was almost lacking in the peat at Styggkärret. It was most abundant at Severmossen, except in the sample of SV-O-20, which also differed from the others because of its remarkable brown moss fraction. The **wood type** could sometimes be inferred by using conifer needles, birch seeds or characteristic periderm of both groups as indication. However, other wood types (dwarf shrubs, *Salix*, *Alnus*, etc.) could not be clearly identified. Birch seeds and periderm was found in the forest (and wood containing) samples of Ultunaviken and Styggkärret opposed to Severmossen, where the peat contained much conifer remains. Severmossen formed an exception in many ways with in general less brown moss occurrence, but much wood and, at the ditch location, even much *Phragmites australis* remains. **Brown mosses** were most likely found at open and ditch locations rather than forest for all three sites and there rather in the 20cm-samples than in the 90cm-samples (UV-O, UV-D, SK-D). At all locations in all sites, *Equisetum fluviatile* occurred in the 90cm-samples, but almost never in the 20 cm-samples. Exceptions were SV-F, UV-O, SK-D, but there *Equisetum* made up only 1% of the material. Leaf tips from *Scheuchzeria palustris* were found in 2 samples (UV-O-90 and SK-F-20). Remains of other sedges could mostly not be identified further when only epidermal tissue was available. Exceptions were the roots of *Carex limosa*, which were very characteristic, and sometimes seeds of *Carex* spp. could be found. These three types of Cyperaceae macro fossils did not match each other in abundance, i.e. sometimes seeds were found, but no epidermis or roots (UV-F-90, SV-D-20), or *C. limosa* roots were found but no

Cyperaceae epidermis (UV-D-20, SK-O-90). The remains of *C. limosa* were also more abundant in surface samples (UV-O, UV-D, SK-O, SK-F, SV-O). *Sphagnum* abundance ranged from 0 to 40 % (UV-D-90) and was in six cases more abundant in deeper peat. Comparing all samples from one site, *Sphagnum* was best represented at the forest locations in Severmossen and Styggkärret, and at the open and ditch location in Ultunaviken. Most of the *Sphagnum* material originated from the section Subsecunda with some single leaves showing high indication for *S. contortum* (UV-D-20, UV-D-90, UV-O-90, SK-F-90). In sample SK-F-90 sections Subsecunda, Acutifolia and Sphagnum (*S. centrale*) made up the peat moss volume in a ratio of 2:2:1. The surface sample of Severmossen's forest location (SV-F-20) contained only section Squarrosa (*S. squarrosum* and *S. teres*). And finally, the older peat generally contained more **detritus**, i.e. undeterminable amorphous material.

Macro Fossils - Brown Mosses

In Fig. 6 the results for the brown mosses are presented and, as mentioned before, we included here not only the brown mosses *sensu stricto* but also other bryophytes that were not *Sphagnum*, e.g. *Aulacomnium palustre* and *Polytrichum commune*. The identification rate was rather high and in total 11 different species could be identified. The moss diversity ranged from one to four species per sample. For better display, the volume percentages were transformed into four categories. The species with highest abundance was *Scorpidium scorpioides*, which was present in almost all samples and making up most of the brown moss fraction (e.g. in SK-D-20, SK-O-90, UV-D-20), followed by *Pseudocalliergon trifarium* (that always occurred together with *S. scorpioides*), *Warnstorfia exannulata*, *W. procera* and *Scorpidium cossonii*.

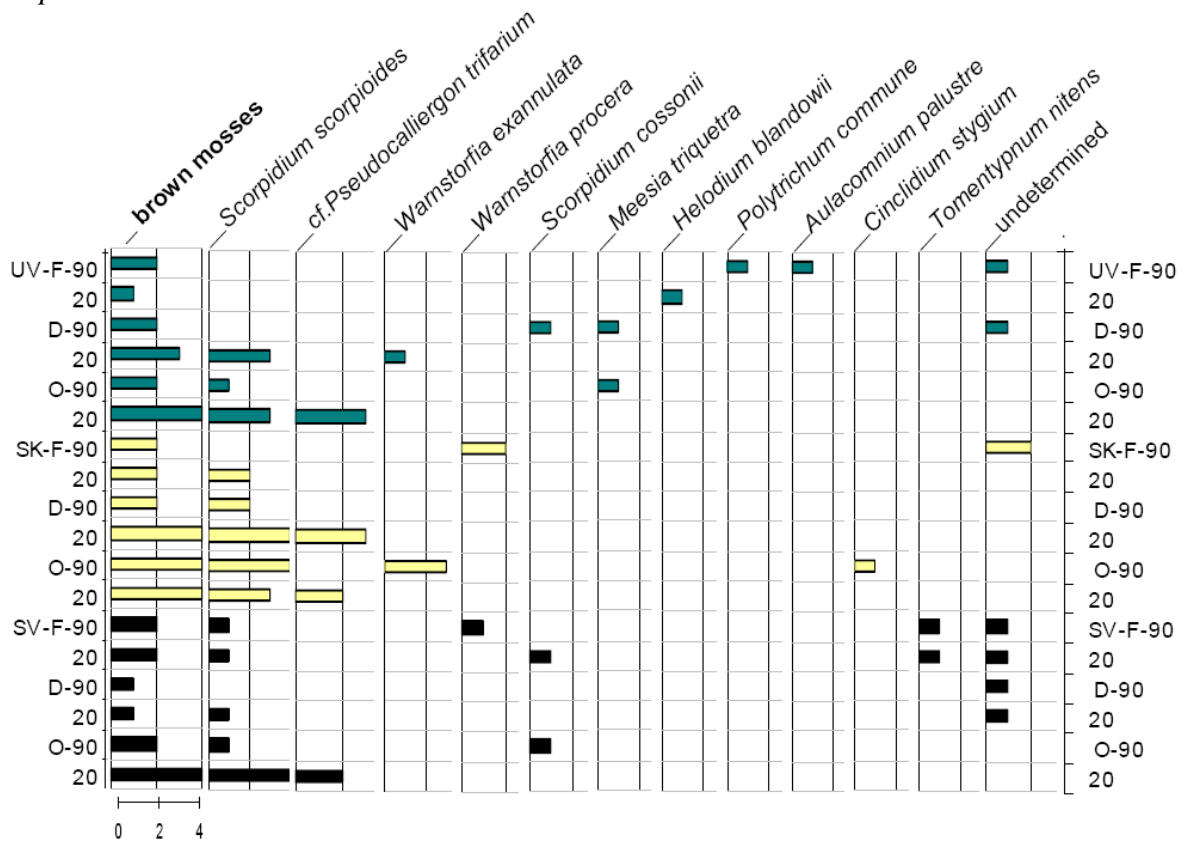


Fig. 6. Macro fossils of three former rich fens, brown mosses. Values are volume percentages of all macrofossil material per sample put in categories: 1) $\leq 1\%$; 2) 2-5%; 3) 6-25%; 4) $> 25\%$. Abbreviations for study site, location and peat depth: UV-Ultunaviken, SK-Styggkärret, SV-Severmossen; O-open/deforested area, D-ditch, F-forest; 20, 50, 90 – peat depths in cm (see Fig. 2).

Discussion

Humification/Decomposition

When using different criteria to determine the degree of peat decomposition it comes naturally that the results might not be all the same. Even though brown moss remains were found in every sample, their abundance ranged from only a few single leaves (UV-F-20) up to 70 % (SK-D-20).

The Janssens-scale was given on the basis of the best preserved mosses found in the sample. If mosses were highly abundant, the chance of finding well preserved ones is of course higher in general. Thus the numbers might be somewhat biased. Moreover, different moss species might be preserved differently, so the decomposition scale depends also on the species assemblage.

The spectrophotometry was quite complicated compared to the other methods and provided probabilities for small inexactness by the different steps that might sum up to a large effect on the results. In addition to that, the field volume samples of 2 cm³ were quite small and may not represent the peat in that layer in an appropriate way, especially when peat was very fibrous or contained larger wood pieces. For that reason the von Post method, old and simple though, seemed to provide the most robust data, because it integrates many peat decay characteristics and was therefore used for further discussion (Malterer *et al.* 1992).

Under undisturbed conditions one would expect more highly decomposed peat in deeper layers, firstly because it is older and has had more time to break down, and secondly has a heavy layer of younger peat lying on top of it, which amplifies decay. That pattern was found at two locations in Ultunaviken: at the open site and close to the ditch and is also supported by the finding of more detritus (i.e. highly degraded material) in older peat. Most of the other cores had quite highly decomposed peat at the surface layer, though, indicating a lower water table due to drainage, by which peat was aerated and broken down much faster under aerobic conditions. At Ultunaviken, the forest might accelerate the effect of drainage due to evapotranspiration. Also another species composition or overall drier conditions due to tree root penetration, could lead to more highly decomposed surface peat in the forest. At Styggkärret, the surface peat at all locations showed a higher rate of decay, meaning that drainage had a more severe effect on that site. This may be because the hydraulic conductivity of the peat was somewhat higher and allowed a more effective drainage of that mire.

Severmossen's peat was in general more decomposed than the peat at Styggkärret and Ultunaviken, which may be explained by a smaller catchment area for Severmossen (Mälson *et al.* 2010). Another reason for that could be that the peat layer is only around 1 m thick (opposed to 2-3 m at UV and SK) leading to a smaller water holding capacity. Because of that, less water is held by the underlying peat, which is not affected by drainage, and can therefore not provide humidity to the surface peat. However, then only the top surface samples would show a high decay. A high von Post value at all locations and depths at Severmossen point rather to a totally different peat type (e.g. most of the samples contained exceptionally much wood). At the ditch, water fluctuations are stronger which probably causes the surface peat at that location be more degraded than the underlying peat. In addition to that, vegetation patchiness can lead to misjudgements of decomposition (see further down).

Macro Fossil Analysis

The analysis of the peat resulted in a quite large number of identified species and estimations of their proportions. I used the modern ecological tolerances of these taxa to interpret the data by using them as indicator species. In [Table 1](#) the species are listed together with the Ellenberg values for light, moisture, reaction and nitrogen and their affinity to rich fens.

All species, whose remains were found in the peat, can grow in rich fens. There were also some **rich fen indicators**, like the often abundant brown mosses *Scorpidium scorpioides*, *S. cossonii* and *Pseudocalliergon trifarium*. Other bryophytes indicating rich fen conditions, but with sparse occurrence, were *Cinclidium stygium*, *Helodium blandowii*, *Meesia triquetra* and *Tomentypnum nitens*. The mosses *Aulacomnium palustre* and *Polytrichum commune* at UV-F-90 only indicate moist to wet conditions, but both have a rather large range of habitat requirements, regarding wetness, pH and light.

The Ellenberg values for soil reaction (R, [Table 1](#)) seem to contradict the occurrence of some species (e.g. *Polytrichum commune*, *Warnstorfia procera*, *W. exannulata*, *Sphagnum* spp., *Scheuchzeria palustris*, *Pinus sylvestris*) on less acidic and more base rich habitats. *Sphagnum centrale* is even as per Ellenberg *et al.* (1992) an indicator of extreme acidity. However, the low N-values of all these species point to a nutrient poor habitat, which a rich fen is. Also, all species can tolerate more or less calcium rich conditions. Moreover, these are the indicator values for the British flora, which might need an adjustment for Scandinavian populations (Sundberg, pers. comm.).

Table 1. List of species, that were found in the macro fossil assemblages, their indicator values for light (L), moisture (F), Reaction (R), Nitrogen (N) and their affinity to rich fens.

Species	Indicator values				Occurrence in rich fens	Sources
	L	F	R	N		
<i>Scorpidium scorpioides</i>	8	10	6	2	*	1), 2), 6)
<i>S. cossonii</i>	8	8	7	2	*	1), 2), 6)
<i>Pseudocalliergon trifarium</i>	8	9	6	2	*	1), 2), 6)
<i>Warnstorfia exannulata</i>	8	9	4	2	+	1), 2), 6)
<i>Warnstorfia procera</i>	9	8	2	-	+	1), 2), 3)
<i>Tomentypnum nitens</i>	7	9	7	2	*	2), 6)
<i>Meesia triquetra</i>	7	9	6	2	*	2), 6)
<i>Helodium blandowii</i>	7	8	6	3	*	2), 6)
<i>Cinclidium stygium</i>	7	9	6	2	*	2), 6)
<i>Polytrichum commune</i>	6	7	2	2	+	6)
<i>Aulacomnium palustre</i>	7	8	3	2	+	6)
<i>Sphagnum centrale</i>	6	7	(1)		*	2), 5), 3), 7); R-value does not apply to Sweden (Sundberg pers.comm.)
<i>Sphagnum squarrosum</i>	6	9	4	3	+	2), 6)
<i>Sphagnum teres</i>	7	9	4	2	*	2), 5), 6), 7)
<i>Sphagnum subsecundum</i>	8	9	4	2	+	2), 5), 6)
<i>Sphagnum contortum</i>	8	9	5	2	*	2), 5), 6), 7)
<i>Carex limosa</i>	8	10	4	1	+	4)
<i>Equisetum fluviatile</i>	8	10	6	4	+	4)
<i>Scheuchzeria palustris</i>	9	9	3	1	+	4)
<i>Phragmites australis</i>	7	10	7	6	+	4)
<i>Betula pubescens</i>	7	7	4	4	+	4)
<i>Pinus sylvestris</i>	7	6	2	2	+	4)

*, Rich fen indicator; +, Occurs in rich fens. 1) Hedenäs 2003; 2) Rydin *et al.* 1999; 3) Ellenberg *et al.* 1992; 4) Hill *et al.* 2004; 5) Mossornas Vänner 2010; 6) Hill *et al.* 2007; 7) Sundberg 2007.

Peat mosses were often represented by species from the section Subsecunda, namely *Sphagnum subsecundum* and *Sphagnum contortum* in UV-D, UV-O and SK-F. Both species are characteristic for mineral rich fens (Mossornas Vänner 2010). *Sphagnum contortum* is one of the few peat mosses which is able to tolerate high base status (Daniels & Eddy 1985) and prefers very wet sites (Mossornas Vänner 2010), which is also supported by the Ellenberg value for moisture (F-value 9, Table 1).

The *Sphagnum* spectrum was more various in the **surface sample of Styggkärret's forest** (SK-F-20), where three sections were represented: Subsecunda (*S. subsecundum*, *S. contortum*), Acutifolia and Sphagnum (*S. centrale*). As mentioned above the Ellenberg values might not reflect the species actual appearance in Sweden. Following Daniels & Eddy (1985) and Mossornas Vänner (2010), *S. centrale* grows on a range of mineral rich fens, being only absent from both very acid and very calcareous sites. It can also grow quite dry and is very shade-tolerant, allowing it to grow in wooded fens, which is the habitat type of the location nowadays.

In the **forest sample of Severmossen** (SV-F-20) *Sphagnum squarrosum* and *S. teres* from the section Squarrosa were detected. Both grow on minerotrophic locations in a wide range of variation in trophic status, water level and shade (Daniels & Eddy 1985). Opposed to *S. teres*, *S. squarrosum* grows more likely in wooded and rather drier areas, although Hill *et al.* (2007) classified them both as wet-site indicator (Table 1). Mälson *et al.* (2008) described *S. squarrosum* as a species that invades rich fens, when they become drier and more acid (Hedenäs & Kooijman 1996). With a lower water level, the nutrient supply increases and *S. squarrosum* is known to respond positively to that (Kooijman & Baker 1995). In addition to that, the pH range of several brown moss species (e.g. *Scorpidium scorpioides*) is the same for *S. squarrosum*, but as a peat moss the latter gradually lowers the pH of the location further (Clymo 1963, 1964) and inhibits the re-establishment of brown mosses. That can lead to problems for vegetation recovery when restoring rich fens (Mälson *et al.* 2008). The establishment of this species could have taken place after drainage, but the peat at 20 cm depth is probably older than 100 years (discussed later). More likely *Sphagnum* increased already before drainage due to general wetland succession. Peat accumulation in a fen leads after a while naturally to more ombrotrophic conditions, colonization of peat mosses and development of a bog (Rydin & Jeglum 2006).

Carex limosa, which was found mostly in surface samples, indicates, together with *Scheuchzeria palustris* (in UV-O-90 and SK-F-20), wet sites that may lack standing water for extensive periods (F-value 10, Table 1). Both can tolerate moderately high calcium content and pH, but are absent in very calcium rich sites (especially valid for *Scheuchzeria*).

Other undetermined Cyperaceae tissue and seeds cannot for sure be attributed to the former described two species. The different sedge fossil types do not show the same pattern in their presence. That is because their way of becoming a macro fossil is different, though originating from similar plants. Roots, for example can grow into older peat while seeds can be transported.

Equisetum fluviatile and *Phragmites australis* indicate the same wetness regime as the two sedges, but have slightly higher requirements for nutrients. Although *Phragmites* has a wide ecological tolerance (pH 3.6 – 7.5, Birks 2007) it may be out-competed by *Scheuchzeria palustris* and *Carex limosa* on very wet and acidic sites (Ellenberg 1988). The roots are reported to grow up to 100 cm deep (Birks 2007), which might lead to misinterpretation.

However in our case we found epidermal tissue, which gives robust information about the species presence at that location during the sampled time period, from which the surrounding peat matrix originated. The occurrence of *Phragmites* close to the ditch at Severmossen could be a result of a slightly higher nutrient supply (by floating water) or just by chance, which often shapes patchy vegetation. *Equisetum* remains in older peat layers suggest a general higher nutrient status in the earlier stages of the wetlands histories.

Historical maps from the 1860ies mark all three wetlands as areas for haymaking (i.e. open/managed), and aerial photographs from 1945 show all fens to be still open and without trees. That means that the **wood remains** in the younger peat might either originate from very small/young trees or dwarf shrubs, that cannot be detected on an aerial photograph, or from roots of larger trees, which invaded the site after drainage. The latter might be most likely for the surface samples, but not for the peat in 90 cm. Even roots from large trees of the current vegetation would not penetrate the peat deeper than 40 cm (Sundberg, pers.comm.). They would die from permanent water saturation and lack of oxygen. The roots and seeds of birch in the deeper peat of Ultunaviken/forest can be taken as a strong indication of local occurrence, although the trees might not have been very large. The birch seeds in other deep peat layers in contrast (SK-O-90, SV-D-90, SV-O-90) originated probably at the same time as the peat matrix, but might have come from adjacent forests and reached the sites via wind dispersal.

At **Severmossen**, the large **wood** fraction in almost all samples point to a history of wooded conditions. The wetland could have started as an alder carr or swamp forest, developing later into a more open fen. On the other hand it may also well be, that there have always been some trees on the site, which would in that case be classified as a wooded fen. Management in the 19th century (and earlier) led then to tree removal and opening of the site. Periderm and needles suggest that conifers (mostly *Pinus sylvestris*) had always played an important role on Severmossen, as they also do nowadays. However, as the wood fraction could not be exactly identified, other swamp forest/ wooded fen trees (e.g. *Alnus*, *Salix*) cannot be excluded to have grown there in the past.

Age of peat samples

Speaking about the “past” leads us to the question, **how old** the peat of the analyzed samples is, i.e. when the discussed plant material originated. We assume that the deeper the peat, the older it is and in doing so substitute space for time. Usually one runs radiocarbon dating for some bulk organic samples to date the peat accurately (Kuhry *et al.* 1991). This was not done in this study. The reason for that was that the time period of interest is mainly the last centuries (vegetation before drainage in the 1950ies). Radiocarbon dating cannot provide a resolution that is high enough to cover these changes. Nilsson *et al.* (2001) found that, depending on peat type and depth, the differences in calibrated ¹⁴C age within specific 2 cm thick peat samples varied between 365 and 1000 years.

Although the exact age of the macro fossil material is not known, it is possible to approach that information using the **landscape history**. First, the maximum age of the whole wetland can be inferred by calculating when peat accumulation could have started earliest. This was after the deglaciation and when the land had risen from the sea due to isostatic uplift of the Scandinavian earth crust. Ultunaviken and Styggkärret are around 50 m a.s.l., while Severmossen is about 12 m a.s.l. (Lantmäteriet 1980). Land rose much faster in the beginning after deglaciation (up to 10 cm/yr, Upplands Flora, 2010) but levelled to around 6 mm/yr at Severmossen and 4,8 mm/yr at Styggkärret and Ultunaviken (Lantmäteriet 1980). Assuming

an average post-glacial rebound of 6 mm/year at Severmossen, the land under the peatland most probably came out of the sea around 1800 yrs BP. According to the maps in Upplands Flora (2010) the land under Ultunaviken/Styggkärret came out of the sea around 7000 years ago. Doing so, one has an idea about the maximum period of peat accumulation, which could only have started land-based or in very shallow coastal waters. Assuming, that peat accumulation started immediately after marine regression the peat layers cover a time period of 1800 yrs (SV) and 7000 yrs (UV, SK) respectively. Because of longer peat accumulation time the peat layer is also much thicker at Ultunaviken and Styggkärret compared to Severmossen (2-3 m versus 1 m). When we know that the peat at Severmossen for example covers 1800 years (from start of accumulation till now) with a depth of around 1 m, we can calculate the average **accumulation rate**, which would be **0,56 mm/yr**. The peat depth in Ultunaviken and Styggkärret is between 2 and 3 m, giving an accumulation rate between **0,3** and **0,4 mm/yr**.

One might be tempted to infer the age of the peat at 20, 50 and 90 cm from that number, which would be for example for Severmossen 357, 892 and 1600 yrs. But it is not that simple, because of the different degrees of decomposition and compaction at different depths. The top layer peat is fresh and almost not compacted, while the deeper peat is more compacted due to longer time of decomposition, but also because of the weight of the above lying peat (Rydin & Jeglum 2006). In addition to that, different water levels during a wetland's lifetime (including the severe drainage) cause different decomposition rates and shrinkage of the peat body in some layers (Fig. 7).

Another approach to calculate the overall age of the peatland could be to *assume* a specific **peat accumulation rate**, but that needs to be done with cautiousness. Most studies give a general average accumulation rate of about 1 mm/yr (Rydin & Jeglum 2006), but those estimates are based on **bog peat** (Clymo 1984). It is more complicated with **fen peat** to state a general average accumulation rate.

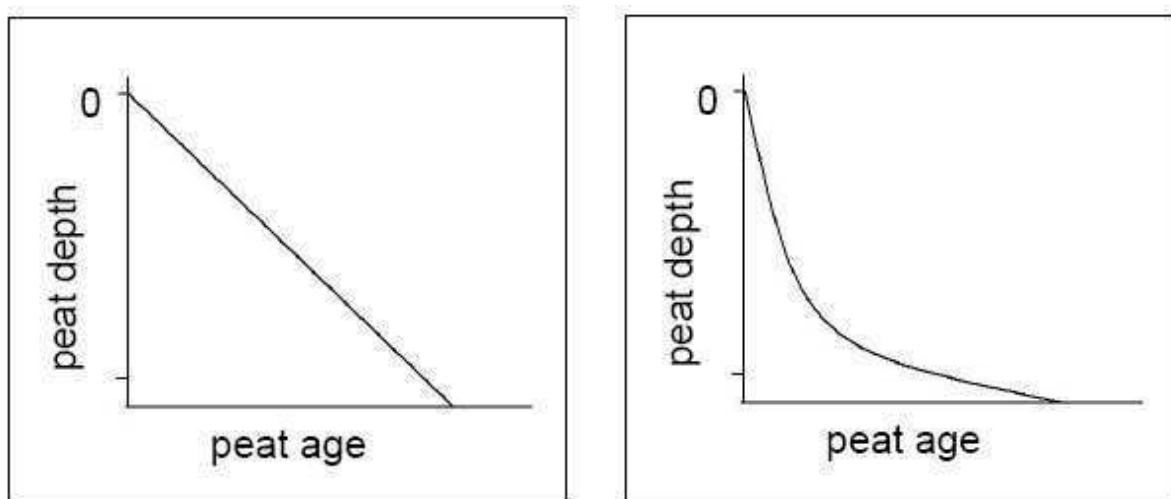


Fig. 7. Ideal (left) and most probable (right) relation between peat depth and age in undisturbed conditions for the surface peat layer (modified from Rydin & Jeglum 2006).

The three cores from each site might also represent different time periods. That is because drainage lowered the water table heterogeneously over the mire complex. Close to the ditch the draining effect was highest, while decreasing further away from it. (Fig. 8, Sandburg *et al.* 2011)

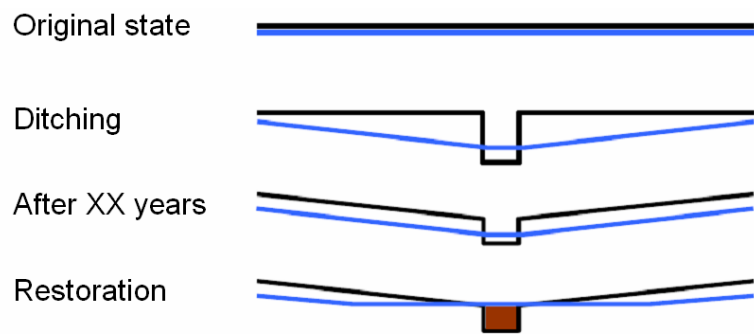


Fig. 8. Variation in surface and groundwater tables at a mire at original state, at ditching/drainage, a number of years after ditching and after restoration (modified from Sundberg *et al.* 2011).

When the water table sinks, and the peat becomes aerated, it starts to decompose and mineralize and that is followed by compaction which means, that a specific accumulation time can be represented by a thicker peat layer away from the ditch and a thinner peat layer close to the ditch. After rewetting the effect is upside down with the peat close to the ditch having a higher water table and probably lower decomposition rate. At Ultunaviken and Styggkärret, a higher *Sphagnum* growth was found close to ditch after rewetting (Sundberg, pers. comm.). Moreover different water tables favour different vegetation types, which themselves already decompose at different rates. These processes might lead to the phenomenon, that peat in the same depth can be of different age (Fig. 9) To give a rough estimate based on the accumulation rates I guess that the peat in 20 cm is around 300-400 (SV) or 500-700 (UV, SK) and in 90 cm ca. 1400-1800 (SV) and 2000-3000 (UV, SK) years old.

Assuming that the peat at the same depth has the same age, it needs to be explained why the macro fossil assemblage still differ from each other. Each of the three peat cores per site had a diameter of 5 cm. The samples taken for macro fossil analysis covered around 1-2 cm depth and therefore a longer time period in the vegetation history (30-70 years with assumed accumulation rate of 0,3mm/yr). Especially on nutrient poor and species diverse habitats the vegetation is not uniform over the whole area, but rather patchy (Schippers & Kropff 2001), meaning that a 5 cm core can of course not catch the vegetation from the whole mire. Although three cores per site were analyzed one must be aware of the, perhaps low, level of representation the cores provide.

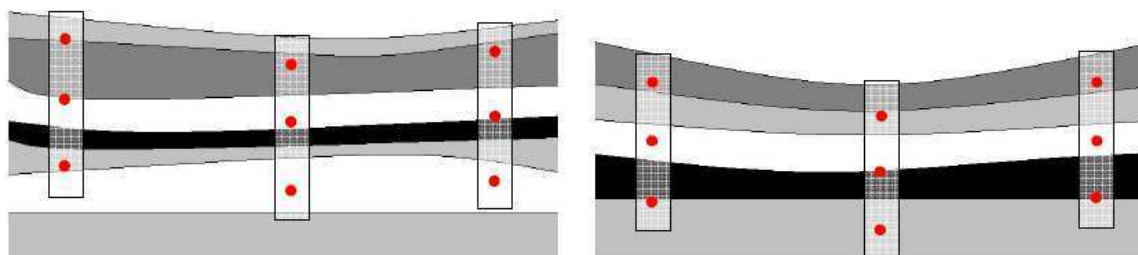


Fig. 9. Different decomposition, compaction and accumulation cause different macro fossil assemblages of the three peat cores at the same depths (same depth \neq same time). Red dots mark samples at 20, 50 and 90 cm depth.

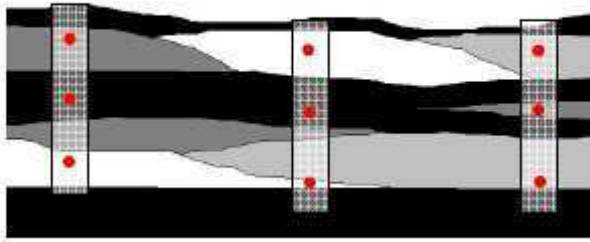


Fig. 10. Vegetation patchiness causes different macro fossil assemblage of the three peat cores in same depths (same depth = same time, but different vegetation). Red dots mark samples at 20, 50 and 90 cm depth.

In addition to that, other site factors or just chance shape a peatland vegetation more **patchy** than homogeneous. Even if accumulation and decomposition rate would be the same, it is possible to find a different macro fossil assemblage at the same depth of the three cores of one site (Fig. 10).

Greatrex (1983) compared the macro fossils (fruits, seeds) in surface samples with the contributing vegetation (local, regional) and stated that the macro fossil assemblage in a single core represents only the vegetation in the immediate vicinity. E.g. a single *Betula pubescens* tree in an otherwise open wetland adds quite a large number of achenes to the macro fossil material, whereas the number of catkin scales and other remains (twigs, roots, bark) could be better correlated with the actual presence of this species. It is thus of importance to understand all processes involved in plant fossilization (Birks 2007), and to be careful with interpretation of the data.

Conclusion

Despite all restrictions and problems the macro fossil, analysis in combination with the judgement of decomposition gave a much better picture of the vegetation history of the three sites. Several characteristic species (brown mosses, peat mosses, etc.) in the peat of all three mires indicate with high certainty that the sites have been rich fens in the past. This information can support argumentations in restoration projects, when it comes to the question, why to drown a forest or other biotopes. A higher resolution of the macro fossil profile would provide even more detailed insights into the vegetation history. Future analyses could also include better identification of wood, seed and epidermal tissue, which might offer valuable clues about former vegetation and site conditions. Brown mosses are definitely worth paying extra attention to, since they are generally well-preserved and are reliable indicators. For our questions, macro fossil analysis provided sufficient information and required no high-tech methods. In other studies, the macro fossils are often included in multiproxy analyses (pollen analysis, carbon dating, bulk density, tree rings; Birks *et al.* 2007, Kuhry *et al.* 1991) to shed light on both local and regional vegetation development, landscape history and climate change. To improve our understanding of the past, further studies should include the completion of macro fossil identification keys, how the recent vegetation contributes to the macro fossil assemblage (for different regions and wetland types) and the adjustment of indicator values for regional floras. Gathering and connecting all this information is the key to successful paleoecological research and will make our virtual journeys to the past more realistic.

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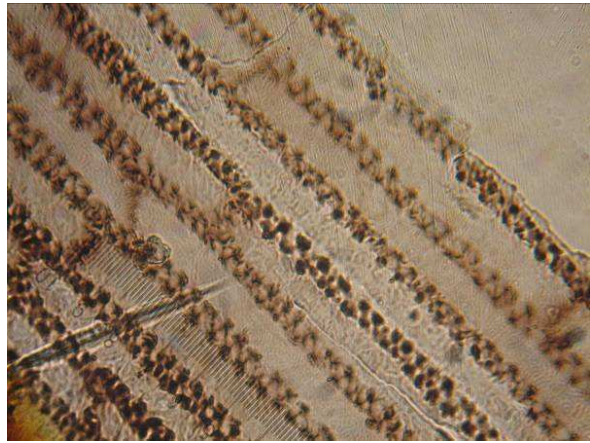
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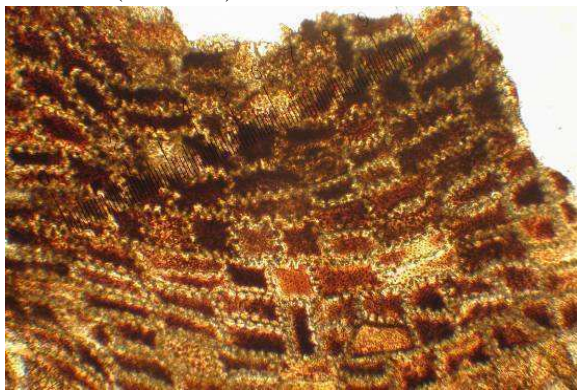
Appendix 1. Selection of macro fossil remains found in peat of three former rich fens.



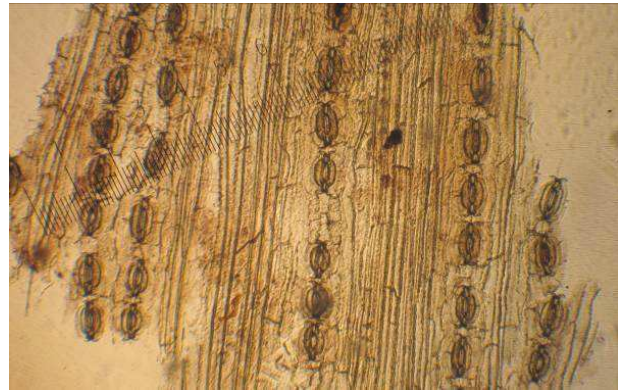
A. View on a sub-sample through a stereo-zoom microscope. Blue lines are division markings of the Petri dish (UV-O-20)



D. *Equisetum* - Epidermis 400× (SV-F-90)



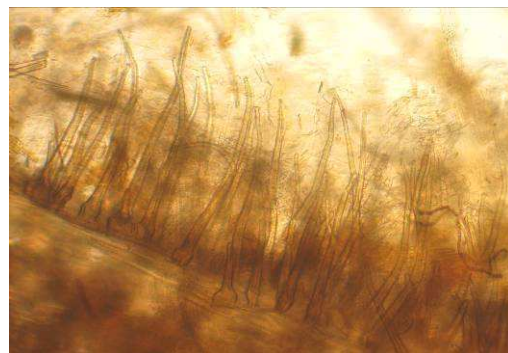
B. Conifer periderm 100× (UV-F-90)



C. Conifer needle epidermis 100× (UV-F-90)



E 1. *Carex limosa* root with dense root hairs (UV-O-20)



E 2. *Carex limosa* root hairs (UV-O-20)



F. Cyperaceae rhizome (SK-F-20)

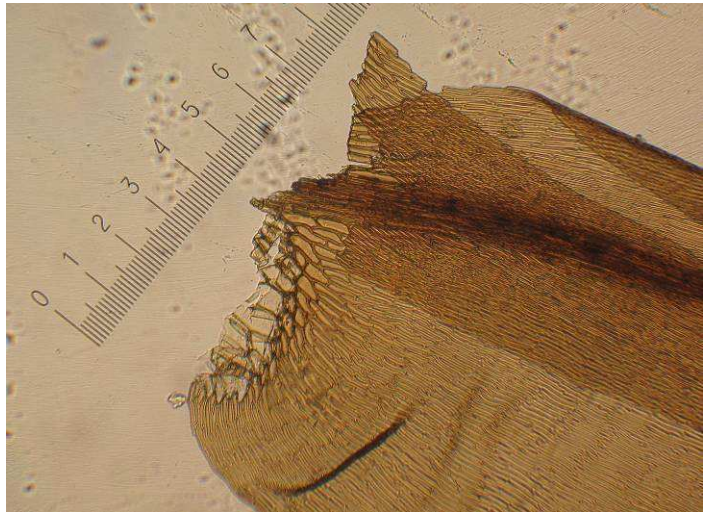


G. *Scorpidium scorpioides* (SK-D-20)

Appendix 1 (cont.) – Brown mosses



H 1. *Warnstorfia procera* (SK-F-90)



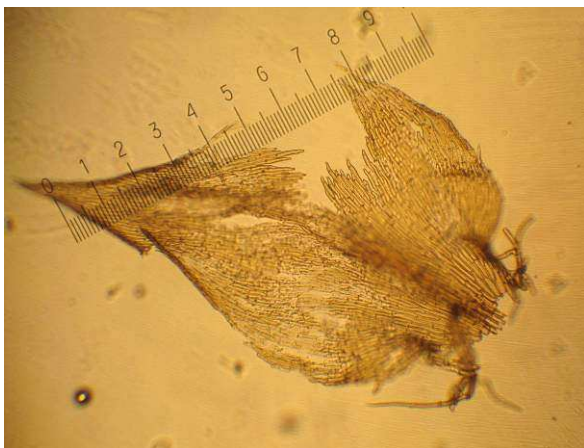
H 2. *Warnstorfia procera* 100× (SK-F-90)



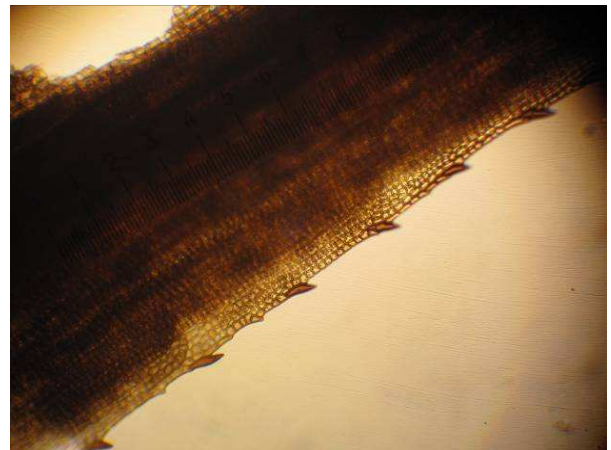
I 1. *Meesia triquetra* (UV-D-90)



I 2. *Meesia triquetra* 40× (UV-D-90)

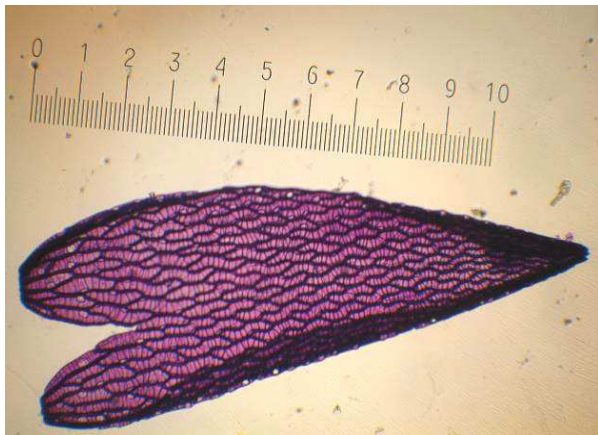


K. *Helodium blandowii* 100× (UV-F-20)

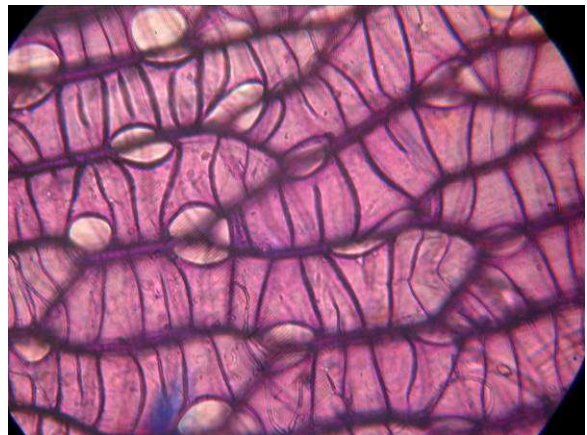


L. *Polytrichum commune* (UV-F-90)

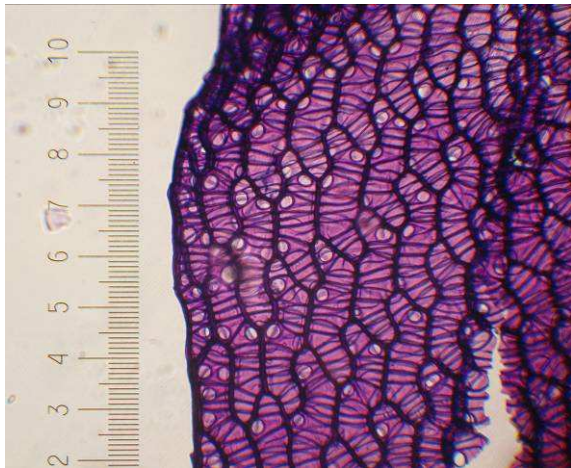
Appendix 1 (cont.) – *Sphagnum* spp. (stained with gentian violet)



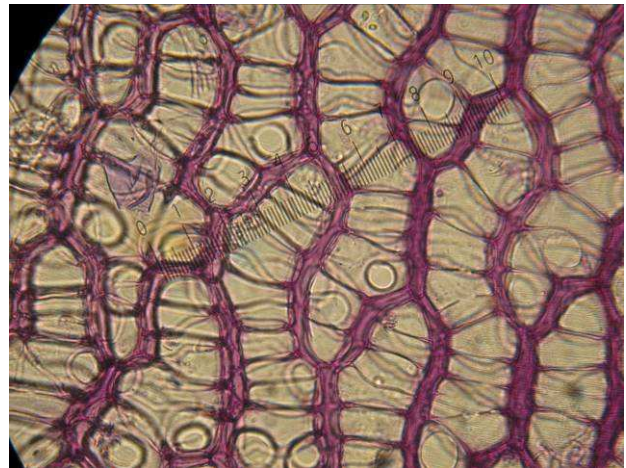
M 1. *Sphagnum* section Acutifolia 40× (SK-F-20)



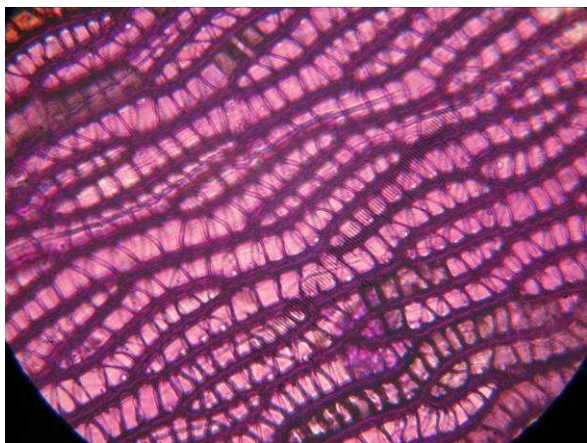
M 2. *Sphagnum* section Acutifolia 400× (SK-F-20)



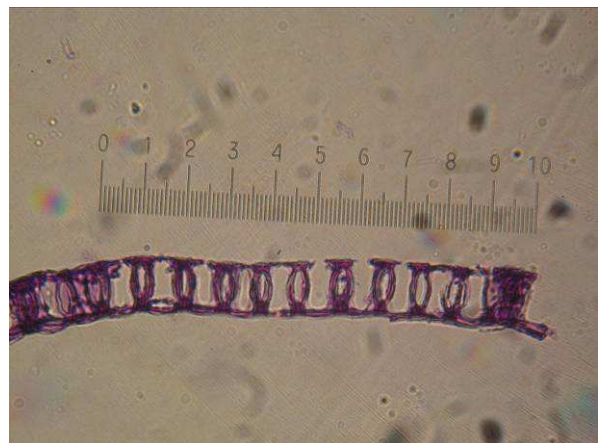
N 1. *Sphagnum centrale* 100× (SK-F-20)



N 2. *Sphagnum centrale* 400× (SK-F-20)



O 1. *Sphagnum* section Subsecunda 100× (SK-F-20)



O 2. *Sphagnum* section Subsecunda, leaf cross section 400× (UV-D-20)