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Roots, Tissues, Cells and Fragments—How to Characterize Peat from Drained and Rewetted Fens

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Abstract: We present analyses of macroscopic and microscopic remains as a tool to characterise sedge fen peats. We use it to describe peat composition and stages of peat decomposition, to assess the success of rewetting of a formerly drained fen, and to understand the workings of these novel ecosystems. We studied two percolation fen sites, one drained and one drained and rewetted 20 years ago. Years of deep drainage have resulted in a layer of strongly decomposed peat which lacks recognizable macro-remains. We could associate micro-remains with macro-remains, and thus still characterise the peat and the plants that once formed it. We show that the strongly decomposed peat is of the same origin as the slightly decomposed peat below, and that is was ploughed. We present descriptions of eight types of the main constituent of sedge peat: plant roots, including Carex rostrata type, C. lasiocarpa/rostrata type, C. limosa type, C. acutiformis type, C. echinata type, Phragmites australis type, Cladium type, Equisetum type. We describe three new non-pollen palynomorph types (microscopic remains) and five new subtypes. The rewetted fen provides insights into plant succession after rewetting and the formation of peat that predominantly consists of roots. Results indicate that leaf sheaths may be a consistent component of the peat.

Keywords: displacement peat; percolation fen; macro-remains; micro-remains; drainage; rewetting; peat degradation; non-pollen palynomorphs

1. Introduction

Peatlands cover large stretches of land in the boreal and nemoral zones of the Earth [1]. Large parts of these peatlands are fens (i.e., minerotrophic mires) that receive not only rainwater, but also water that has been in contact with the mineral soil or bedrock. Fens are commonly characterized by a dominant graminoid vegetation [2]. Their peat deposits contain, in varying proportions, mosses, roots and rhizomes of herbaceous plants and amorphous organic material or detritus. There is a fundamental difference between moss peat and peat formed by herbaceous plants. Mosses grow upward and the new material of the deposit is added at the surface. The peat of herbaceous plants consists mainly of roots and rhizomes and the new material is added at some depth in an existing, older matrix. This latter type of peat is called displacement peat [3,4]. Displacement peats are always associated with differing ages of individual components at the same depth, making them inherently more difficult to analyse and less studied than simpler moss peats.

The continued accumulation of peat in graminoid-dominated fens is not straightforward. If the peat consists of dead roots and rhizomes that grow down to displace an existing matrix of dead roots and rhizomes, how does the peat body as a whole become thicker or 'grow upward'? If mosses are present, they can provide an upward-growing matrix to be displaced by roots and rhizomes. If mosses are absent, aboveground plant litter layer could play a similar role. However, only very

little aboveground plant remains are found in these displacement peats. Degradation tests show a rapid decomposition of aboveground material of more than 90 % within a few years [5]. With a few exceptions (e.g., leaves of Ericaceae, leaf tips of *Scheuchzeria palustris*, leaf fragments of *Rhynchospora alba* and *Thelypteris palustris* [6]) and, apart from diaspores, no recognizable aboveground plant remains are known from peat formed by herbaceous plants.

If aboveground litter plays a role in peat formation it must be heavily decomposed and part of the detritus. Detritus can constitute more than half the volume of sedge peats ([7], own experience). Studies focussing on macro-remains typically discard the detritus and microscopic studies rarely try to identify material beyond pollen and spores. Yet, there is increasing interest in identification of microscopic remains other than pollen—so-called non-pollen palynomorphs (NPPs) [8]. Plenty of aboveground biomass may be part of the detritus, but it is difficult to estimate its extent. In this paper, we will describe microscopic remains from sedge peats that may be of aboveground origin.

With respect to the roots and rhizomes that constitute the peats we describe in this paper, the description and identification of remains has had a long history. In the early 20th century, a detailed characterization of botanical peat types [9,10]) was accompanied by a request for research towards a more precise identification of vegetative herbaceous plant remains in fen peats. Matjuschenko [11] developed a key for the identification of *Carex* fine roots (radicels) in peat; this key was later adapted by Bertsch [12]. In the following decades, palaeoecological research focused on refining the rapidly evolving field of pollen analysis and little attention was paid to macro-remains. Only in the 1970s did Grosse-Brauckmann [6] formulate fundamental criticism on the keys to identifying *Carex* roots, as a result of which identification to the species level was, from then on, often restricted to *Carex limosa* roots alone [13,14]. Despite some available reviews [15,16] based at least partly on the use of living plant material, recent macrofossil analyses are often limited to the identification of *Carex* sp. roots [17] or Cyperaceae roots [18–21]. Occasionally, additional root types are distinguished such as *Cladium*, *Equisetum* and *Thelypteris* roots [22] or *Phragmites* and *Scheuchzeria* roots [23].

This study aims to characterize macroscopic and microscopic remains of peat in different stages of decomposition. We analysed peat from percolation fens that have been drained and, in one case, rewetted again. We want (i) to describe different types of macro- and micro-remains that can reliably be identified, (ii) to test how analysis of micro-remains can contribute to characterize particularly decomposed peat, (iii) to characterize the material that has been deposited since the rewetting and (iv) to fill in knowledge gaps on the possible contribution of aboveground biomass in displacement peat and on the composition of the main component of displacement peat: the root mass.

2. Material and Methods

Two peat monoliths were recovered from a percolation fen complex in north-eastern Germany. Detailed descriptions of the study sites in the Recknitz valley (PD) and the Trebel valley (PW) are given in [24]. One site, PD, is drained and used for grass fodder production, the other site, PW, has been drained as well, but was rewetted in 1997. The water table has remained close to the ground surface since the rewetting [25]. The site is now under nature conservation. The first attempts at drainage of the peatland complex date back to at least 1744, but strong degradation of the peat probably only started in 1967 when deep drainage ditches of ~1.5 m deep were dug to allow for high-intensity grass cropping [26]. Peat cores of 20 cm diameter and ~50 cm length were recovered using a "Clymo corer" [27] and frozen after extraction.

Bricks of $7 \times 13 \times$ c. 50 cm were cut from the frozen monoliths and subsequently sampled into contiguous 0.5 cm thick slices using DAMOCLES [28]. Respective subsamples of these slices were analysed for macro- and micro-remains at selected depths (n = 17 for site PD and n = 26 for site PW).

2.1. Analysis of Macro-Remains

For the analysis of macro-remains, samples of 6 cm^3 ($4 \times 3 \times 0.5$ cm) were slurried with purified water and examined under an incident light microscope (10 to 40 times magnification). For tissue and

moss remains, volume percentages were estimated with reference to the total volume. Seeds, fruits, and intact mollusk shells were counted. The following literature was used in te identification of plant tissue and moss remains: [6,11–13,29], of fruits and seeds: [13,30–33], of animal remains: [34,35].

In addition, we collected fresh root material of 15 sedge species to establish a catalogue of radicel morphotypes. For AMS ^{14}C dating, 0.3 mg C (PD) and 0.7 mg C (PW) of aboveground plant material was collected (Table 1). The radiocarbon dates were calibrated to calendar years using the software CALIB v. 7.0.4. To arrive at a single point age estimate, we calculated the weighted average of the probability distribution function [36].

With respect to the question of whether the root material we found was still alive or already dead, we argued as follows: young, living or recently dead (subrecent) roots will be longer than old, dead or subfossil roots and will possess more intact branches. However, the limited sample volume and the small sample thickness (0.5 cm) made these criteria unsuitable for identification. Instead, all flattened roots were considered long-dead or (sub-)fossil and all others, i.e., with intact aerenchyma, were considered (sub-)recent. It is not possible to separate roots that died 10 or 20 years ago, and whose aerenchyma has already been completely degraded, from fossil roots of several thousand years old.

2.2. Analysis of Micro-Remains

For the analysis micro-remains, samples of 2 cm^3 (2 × 2 × 0.5 cm) were prepared. Sample preparation included treatment with HCl and KOH, sieving (125 μm), HF-treatment, acetolysis (7 min), and mounting in silicone oil [37]. Lycopodium clavatum tablets were added for the calculation of pollen concentrations [38]. Counting was done with a Zeiss Axioskop 40 light microscope with 400× magnification. The micro-remain counts are presented in concentrations of particles per volume. The following literature was used for the identification: for pollen: [39], for non-pollen palynomorphs: EMA types (Department of Peatland studies and Palaeoecology at **E**rnst-**M**oritz-**A**rndt University Greifswald) [40,41], and HdV types (**H**ugo **d**e **V**ries-Laboratory at University of Amsterdam) [42–50]. New EMA types and subtypes were identified and are first described here. In order to differentiate clearly between plant taxa and pollen types, the latter are displayed in small capitals [51].

2.3. Diagrams

The relative abundance or number of macro-remains and concentrations of micro-remains were plotted against depth using the software C2 v. 1.7.7 [52]. Zonation of the diagrams was carried out visually to distinguish zones that are a combination of informal acme zones and informal interval zones [53,54].

3. Results

3.1. Description of Macro- and Micro-Remain Morphotypes

In this section we will first present descriptions of roots of eight plants commonly occurring in percolation fens. In our descriptions of these macro-remains we will focus on features that remain identifiable even if the material is degraded. Descriptions of new EMA types of micro-remains will follow, complemented by new insights on previously described EMA types.

3.1.1. Radicel Types

Carex acutiformis type (Figure 1I–J): the colour of the radicels is whitish to slight greyish. The root hairs are often broken and only the basal part, the pustule, is left. The pustules are rather thick-walled and, when viewed from above, rectangular to trapezoid with sharp edges. The lateral walls of the pustules show a dark grey-brown colour. Pustules are often arranged in small groups. This type includes radicels of *Carex acutiformis* and *C. riparia*.
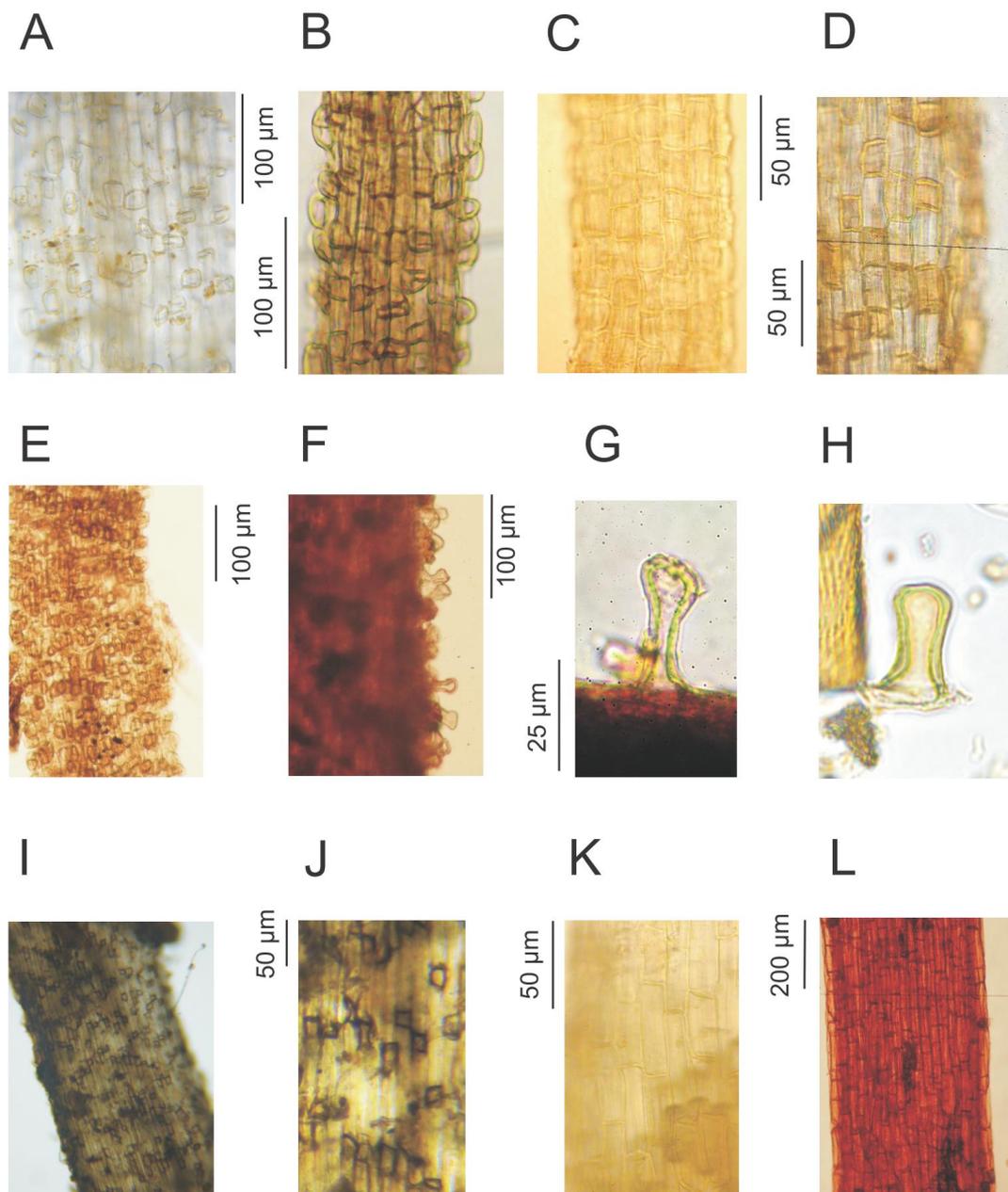
Figure 1. Radicel types: (**A**,**B**) Carex rostrata type, (**C**) Carex lasiocarpa/rostrata type, (**D**) Phragmites australis type, (**E**) Cladium type, (**F**) Carex limosa type, (**G**) pustules of Carex limosa type, (**H**) EMA-131C cf. *Carex limosa* pustules (from microscopic sample), (**I**,**J**) Carex acutiformis type, (**K**) Carex echinata type, (**L**) Equisetum type.

Carex limosa type (Figure 1F–G): the colour of the radicels is yellowish to reddish. The root hairs are more frequently preserved than in other sedges. The pustules are remarkably thick-walled and higher than they are wide. In side-view, they often show a narrowed middle section and a wider head. This type includes *Carex limosa*.

Carex rostrata type (Figure 1A–B): the colour of the radicels is whitish. The root hairs are often broken and only the pustules are left. The pustules are thick-walled and, when viewed from above, square to rectangular with rounded edges. The lateral walls of the pustules show a whitish colour. The pustules are arranged in a chessboard pattern or in small groups. This type includes *Carex rostrata* and probably its close relatives in *Carex* sect. *Vesicariae*, but not *C. vesicaria* itself with more elongated pustules [11].

Carex lasiocarpa/rostrata type (Figure 1C): the radicels of this type are very similar to the Carex rostrata type, but the pustules are less pronounced and arranged in a chessboard pattern. Single radicels can show both the somewhat more pronounced pustules of the Carex rostrata type and the less pronounced pustules of the Carex lasiocarpa type (in the sense of [11]), and therefore this type is called Carex lasiocarpa/rostrata type here. It includes *Carex lasiocarpa* and perhaps *C. rostrata*.

Carex echinata type (Figure 1K): the colour of the radicels is whitish. Root hairs are mostly not preserved; the basal part does not differentiate from the other epidermis cells, i.e., no pustules can be seen. The cells of the epidermis are approximately five times longer than they are wide.

Cladium type (Figure 1E): the radicels of this type are very similar to the Carex rostrata type, but the pustules show a light to clear brown colour. The pustules are arranged in a chessboard pattern. This type probably only includes *Cladium mariscus*.

Equisetum type (Figure 1L): radicels of this type have a reddish, reddish-brown to burgundy colour. Root hairs are occasionally preserved. Small V-shaped notches are often found at the former place of the root hairs. This type includes *Equisetum fluviatile* and probably other *Equisetum* species as well.

Phragmites australis type (Figure 1D): the colour of the radicels is whitish with a yellow touch. The elongated parts of root hairs are often broken and only the basal part, the pustule, is left. The pustules are rather thick-walled and, when viewed from above, rectangular to trapezoid with rather sharp edges. The pustules are arranged more or less in a chessboard pattern. The walls of the pustules show a yellowish colour, which gives the radicels a spotty whitish/yellowish appearance.

3.1.2. Microscopic Morphotypes

The exact origin of most of the microscopic morphotypes (NPP types, Figure 2) described here is unknown. Besides origin, taphonomic processes further determine morphotype characteristics. The depth at which a morphotype occurs and the accompanying assemblage of micro- and macro-remains provides clues to the age, origin and site conditions during and after deposition. In our descriptions of the morphotypes, we therefore refer to stratigraphic information that is presented in detail in the next section (Section 3.2, Figures 3 and 4).

EMA-1 [41]: tissue including fragments of tracheids of vascular bundles like EMA-1A and EMA-1B (see below) and EMA-68 [40]. Abundant over the entire depth of both cores, but only in very small amounts in the newly accumulated material (see Figure 3 zones PW-C2, -C3, -D). The highest amounts occur in both profiles in the upper parts of the A zone and in the lower parts of the B zone, indicating that this NPP is concentrated when the peat is slightly to moderately affected by drainage. Where drainage effects are strong, like close to the (former) soil surface, its amount is lower (in upper part of zone PD-B, Figure 4; in zones PW-B2 and PW-C1, Figure 3).

EMA-1A: separate tracheids consisting of continuous rings, type (a) in [41]. Frequent in the layers A and B, with old and degraded peat.

EMA-1B: separate tracheids with pits, type (b) in [41]. Frequent in peat layers PW-A and PW-B, but also in the newly accumulated material of radicels and leaf sheaths, where a lot of *Carex acutiformis* remains were found.

EMA-62 [40]: well-preserved to highly corroded cell infills. They are elongated and rectangular to slightly polygonal. The size of well-preserved specimen is 17.5 (20) $\times$ 120–180 μm, but frequently shorter and/or narrower particles were found, and therefore counted in classes <50 μm, 50–100 μm, <100 μm. Also smaller roundish particles with diameter $\leq$ 12–17 (23) μm were found. All are amber-like orange, psilate. Particles can include bubbles and pits of different size, shape and number; these particles were counted as corroded.
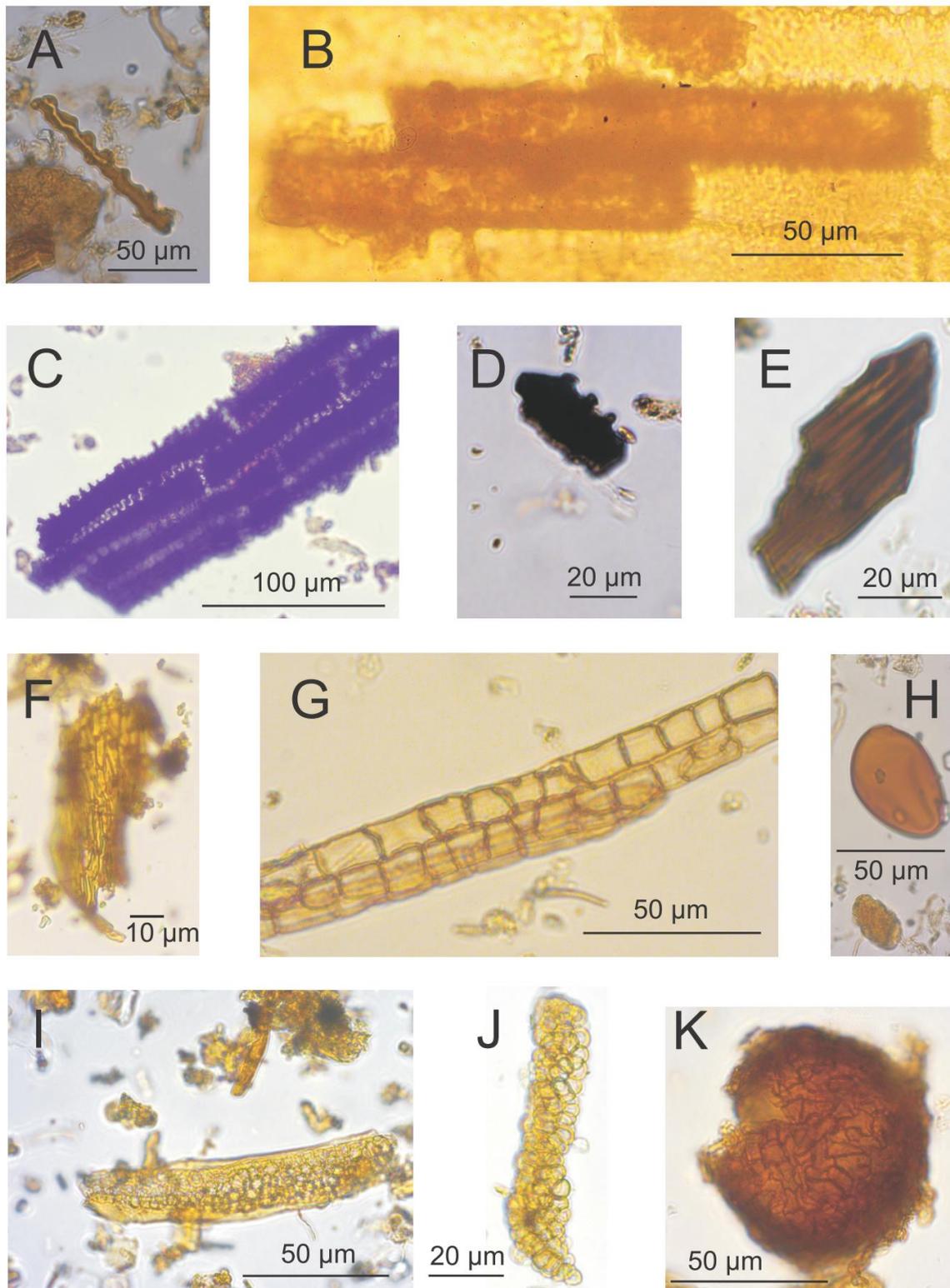
Figure 2. Microscopic remains: (**A**) EMA-62A Cell infills with undulating edges, (**B**) EMA-62A inside leaf sheath (from macroscopic sample), (**C**) EMA-132 charred: charred cell complex of Cyperaceae epidermis, (**D**) separate cells of EMA-132 charred, (**E–F**): EMA-162: moss leaf fragment with prosenchymatic cell pattern, charred (**E**) and not charred (**F**). (**G,I,J**) EMA-85: Fungal plectenchyma in shape of vascular plant cell, (**H**) EMA-160 Fungal spore, (**K**) EMA-161 Fungal fruit body.

Well-preserved particles perfectly resemble the shape of cells of Cyperaceae. In the analyses of macro-remains, cell infills of the same shape and colour were found in Cyperaceae epidermis (see also description of EMA-62A below) but also in subepidermal tissue. Such cell infills were not found in Poaceae tissue in this study and are also not known from other studies, although Poaceae cells can have the same shape and size. Cell infills were especially frequent in *Cladium* tissue: short to long (10–20 × 50–150 μm), slightly irregular rectangles or elongated polygons. In the diagram (Figure 3), the curve of EMA-62 >100 μm particles correlates very well with the presence of macroscopic Cyperaceae leaf sheaths in the zones PW-C and PW-D. Barthelmes et al. [40] assumed this NPP type to be associated with wood (decay), but our analyses of micro- and macro-remains lacks evidence for local wood presence. The material is probably a biopolymer that is incorporated in cells for stabilization and protection. Fungal decay leads to 'bubble' holes and loss of shape (see EMA-8, -9 in [41]).

All size classes occur in all states of peat indicating the local presence of Cyperaceae. Corroded particles >50 μm show the highest values in zone PW-B (Figure 3), indicating highly degraded peat. Not-corroded particles >50 μm are prominent in the old peat (zones PD-A Figure 4, PW-A Figure 3) and the newly accumulated material (PW-C3, PW-D), indicating well-preserved material.

EMA-62A (Figure 2A): cell infill of Cyperaceae epidermis. Features are as described for EMA-62, but additionally characterized by evenly undulating edges. Found in-situ in macro-remains of Cyperaceae leaf sheath (Figure 2B), but might occur in epidermis of other plant parts with regularly undulating walls as well (see EMA-132 [40]). Sporadically occurring in PD (Figure 4), and in PW in the old peat (zone A) and the newly accumulated material (zone C3 and D, Figure 3). In the diagram (Figure 3), the curve of EMA-62A runs parallel to the curve of Cyperaceae leaf sheaths. Black particles of similar shape (Figure 2D) are apparently charred EMA-62A and were separately counted. Charred particles are more frequent than non-charred ones throughout PD (Figure 4), and with low amounts but a steady occurrence characteristic for zones A and B1 in PW (Figure 3).

EMA-62A indicates the presence of Cyperaceae, especially when macroscopic remains are lost due to decomposition. Based on its origin from the leaf sheath epidermis, in our study EMA-62A indicates that material grown above the surface is incorporated into the peat.

EMA-85 [40] (Figure 2G–J): fungal plectenchyma in shape of vascular plant epidermis cells, 12–18 x 43–110 (170) μm, fungal cells round to rectangular and folded, variable, occasionally look pressed-in, 2–4 × 5.7–11 μm in diameter, yellowish to brown.

These are probably plant cells filled with fungi that consume the cell content. The plectenchyma was only once recorded with cell wall attached (Figure 2I).

We counted two variants. The variant with roundish, small cells (diameter 2–5.7 μm, Figure 2I–J) was found in the old peat in PD-A in high amounts (Figure 4). The variant with rectangular to polygonal, big cells (diameter 4–11 μm, Figure 2G) occurred in low amounts in the upper part of PD-A and in PD-B (Figure 4), indicating the former presence of plant tissue.

EMA-131 [40]: basal cells of radicel pustules, basal parts of Cyperaceae rootlets. Thick-walled cells. We separate two morphotypes described under this type number in [40] and add another one:

EMA-131A: quadrangular to rectangular radicel pustules, see pl. I Figure 131.a in [40];

EMA-131B: radicel fragment with EMA-131A type pustules, see pl. I Figure 131.a in [40];

EMA-131C (Figure 1H): cf. *Carex limosa* pustules. Single cells, thick-walled, elongated (23–27 × 10–11 μm) with constriction (5.5–7.5 μm) in the middle, one end rounded, the other end ruptured, yellow to hyaline.

Basal parts of roothairs probably of *Carex limosa* rootlets (see Figure 1G–H). Indicating local presence of Carex limosa type radicels.

EMA-132 [40] charred (Figure 2C): epidermal tissue, probably of Cyperaceae. We found black, apparently charred material that looks like a negative image of EMA-132, where walls are lacking and cell content is charred. Single charred 'cells' (Figure 2D) have the same shape as EMA-62 A and are discussed under this type (see above). Separated cells do not show the complete cell pattern of the tissue and may also derive from Poaceae, which have comparatively short cells.

EMA-160 (Figure 2H): fungal spore. Ellipsoid, 56 x 39 μm, at one end ca. 9 μm wide protruding pore, one-celled, brown. Occurring only in the newly accumulated material (zones PW-C2, -C3, -D, Figure 3), probably connected to the decomposition of fresh plant material.

EMA-161 (Figure 2K): fungal fruit body. Globose to ovoid, 70–90 × 75–100 (115) μm, ruptured, cells thick-walled, irregularly, jigsaw puzzle-like shaped, brown. Occurring in the uppermost sample of zone PW-B and in PW-C and PW-D (Figure 3), probably connected to the decomposition of recent plant material.

EMA-162 (Figure 2E–F): brown moss leaf fragments. Various shapes and sizes, prosenchymatic cell pattern, yellowish to light green (Figure 2F), when brownish to black (Figure 2E), supposed to be charred.

Yellow to green specimen very abundant in zone PW-A2 (Figure 3), together with macro-remains of brown mosses (*Drepanocladus* sp., *Calliergonella cuspidata*, *Calliergon giganteum*, *Campylium stellatum*). This type indicates the presence of brown mosses in PD where no macroscopic moss remains were found.

3.2. Diagrams

Proportions of the different macro- and micro-remains are shown in Figure 3 and 4. We distinguish four assemblage zones in PW and three in PD.

In Zone PW-A (Figure 3), we find a radicel peat which seems only slightly influenced by drainage. The proportion of radicels is higher than the proportion of fine detritus. Most of these radicels are of the Carex lasiocarpa/rostrata type. Subzone A2 contains the highest amounts of moss stems and brown moss leaf fragments of the entire profile. *Carex lasiocarpa* nutlets are present in subzone A2.

Zone PW-B is characterized by peat that is strongly modified due to agricultural drainage followed by compaction, aerobic decay and ploughing. Ploughing is evident from the disturbed pollen sequence with, e.g., Secale cereale and Centaurea cyanus pollen in the lower part of the zone B, which is normally found only in the uppermost part of pollen diagrams in the study region (Figure 3). The proportion of fine detritus is higher than the proportion of radicels. Clamydospores of the soil fungus *Glomus* cf. *fasciculatum* (HdV-207) are concentrated in this zone and microscopic fungal types in total have the highest concentrations here. Microscopic vascular tissue (EMA-1) is especially prominent in subzone B1.

Zone PW-C is somewhat heterogeneous. The line between zones B and C is drawn where the proportion of fine detritus is below 70 % and the proportion of radicels is higher than 20 %. Subzones 1 and 2 contain less than 5 % of Cyperaceae leaf sheaths, subzone 3 contains 10% to 30 %. The difference between subzone 1 and 2 is the exclusive occurrence of *Urtica dioica* nutlets in subzone 1. Fungal fruit bodies of *Tetraploa* (HdV-89) and *Microthyrium* (HdV-8b), as well as a big unknown fungal spore (EMA-160), occur only in the subzones 2–3.

Zone PW-D contains 60% to 90 % of Cyperaceae leaf sheaths and 2% to 20 % of radicels. This zone comprises the only samples in which *Typha angustifolia* fruits and *Pisidium* sp. scales have been found.

Zone PD-A (Figure 4) contains radicel peat which seems only slightly influenced by drainage. The proportion of total radicels is of the same order of magnitude as fine detritus. The major part of these radicels belongs to the Carex lasiocarpa/rostrata type. Besides this dominant radicel type, Carex limosa type and Carex echinata type radicels were found.

Zone PD-B contains strongly modified peat due to agricultural drainage followed by compaction, aerobic decay and ploughing. As in case of PW, ploughing is evident from the disturbed pollen sequence with, e.g., Secale cereale pollen in the lower part of the zone B (Figure 4). The proportion of fine detritus is higher than of radicels. Due to the strong decomposition, a significant proportion of the radicels no longer shows any epidermis cells and cannot be further identified. Microscopic remains of radicels (fragments, pustules, root break-off points) still occur in the lower part and vascular tissue (EMA-1, -1A and -1B) occurs throughout the zone. The concentration of clamydospores of the soil fungus *Glomus* cf. *fasciculatum* (HdV-207) is high. Diaspores of *Juncus* sp. and *Ranunculus* sp. show a significantly better state of preservation than the surrounding matrix material.

Zone PD-C is characterized by the remains of living grasses and ruderal mosses.

Figure 3. Selected curves of macro- and micro-remain analyses of site Trebel valley (PW). Note the scales and units of the x-axes. Curves show percentages [%] or number [N] of macro-remains as indicated, or otherwise concentrations [10^1 N cm^{-3}] of micro-remains.

Figure 4. Selected curves of macro- and micro-remain analyses of site Recknitz valley (PD). Note the scales and units of the x-axes. Curves show percentages [%] or number [N] of macro-remains as indicated, or otherwise concentrations [10^1 N cm^{-3}] of micro-remains.

3.3. Dating

The peat just below the strongly degraded agriculturally influenced layer is of considerable age in both profiles (Table 1).

Table 1. Radiocarbon dates in PW and PD.

Sample Number	Material	Lab. no	^{14}C Date	Calibrated ^{14}C-AMS-Date Weighted Average (2σ Range) [cal. BP]
PW 40 cm	*Carex lasiocarpa* nuts	Poz-107576	3365 ± 35 BP	3607 (3484–3694)
PD 26 cm	*Cladium mariscus* fruits	Poz-114673	2065 ± 35 BP	2036 (1934–2128)

The year of the rewetting of PW in 1997 can be pinpointed as well. Rewetting was carried out after the area had been abandoned and *Urtica dioica* had spread. Fruits of *U. dioica* must have fallen into cracks that had developed in the strongly degraded soil [55]. After the rapid increase in the water table upon rewetting [56], *U. dioica* died off and was replaced by *Carex* sp., as evidenced by the presence of molluscs and by aboveground remains of various *Carex* species. The year 1997 is placed at the PW-C1 to PW-C2 boundary (Figure 3).

4. Discussion

4.1. Site Development

In both cores the older, well preserved peat (zones PW-A, PD-A) shows indicators of loose, permanently water-saturated peat formed under mesotrophic nutrient conditions. The PW core contains *Meesia triquetra*, *Calliergon giganteum* and *Carex limosa* roots, the PD core *Carex limosa* roots and EMA-162 (brown moss leaf fragments), all of which are indicative of stable high-water tables relative to the surface. The remains of *Menyanthes trifoliata* and *Carex lasiocarpa* that occur simultaneously in PW support the picture of high-water tables and mesotrophic conditions, as they are typically found in sedge-dominated percolation mires [57,58]. Floating mires can have similar vegetation and they did occur in the Recknitz valley during regression phases of the Litorina Transgression in the Pomeranian Border Valley. However, they had transitioned into percolation mires more than 5000 years cal. BP ago [22].

Hardly any macro-remains that make up the original peat have remained in the layers of highly decomposed peat (PW-B, PD-B). The Carex rostrata type radicels found in PW-B may also have grown into the matrix after rewetting, as scattered *Carex rostrata* plants are found in close vicinity to the coring location. *Carex acutiformis* currently dominates the vegetation at the coring location and any radicels of Carex acutiformis type observed in PW-B2 are likely of recent origin. The fine roots without epidermis in PD-B are difficult to interpret. They may have originated during the time of drainage, but could also be younger. Certainly, the clamydospores of type HdV-207 *Glomus* cf. *fasciculatum*, a fungus that lives in aerated soils, were deposited when the site was drained. They occur in the layer of highly decomposed peat that corresponds with the formerly drained and ploughed agricultural soil. In both cores, the micro-remains EMA-162 (moss leaf fragments with prosenchymatic cell pattern), EMA-1 (vascular bundles), EMA-131 (isolated pustules and radicel fragments with pustules), microscopic radicel fragments and EMA-62 occur in both zone A and B and indicate that the peat of PW-B and PD-B originally had a similar composition to the well-preserved sedge peat immediately below.

Isolated and surprisingly well-preserved diaspores found in these layers (e.g., *Ranunculus flammula* nuts, *Juncus* sp. seeds) were probably added to the matrix when the peat was drained. Either they were mechanically worked into the soil during agricultural site preparation, or, like the *Urtica dioica* nutlets, they fell into soil cracks in the degraded peat. Although *Ranunculus flammula* is regularly found in

wet peatlands and the nuts are commonly found in peat deposits [31,56], it also grows at the drained grassland site PD.

In PW, the layer of organic material that has been deposited after rewetting does not show uniform contents over depth, but rather a development from initial pioneer vegetation (*Carex flava*-agg.) to the establishment of potentially peat-forming dominant stands of *Carex acutiformis*. In the top 6 cm of the profile, the leaf sheaths of Cyperaceae are dominant, but they are absent or very rare further down. As all *Carex* species have leaf sheaths and not only the currently dominant *Carex acutiformis*, it is most likely that they are absent from the sedge peat matrix because they are easily decomposed as part of the aboveground litter.

There are many fungi present in the upper layer, like *Tetraploa* (HdV-89), a mold on plant leaves, *Coniochaeta* cf. *lignaria* (HdV-172), an ascomycete that can decompose lignocellulosic material [59], *Microthyrium* (HdV-8b), another ascomycete, and further fungal remains (EMA-160, HdV-124). Probably, the fungi in this (periodically) oxic layer are instrumental in decomposing the aboveground litter, including leaf sheaths.

We have found cell fillings in leaf sheaths (Figure 2B) that look exactly like NPP type EMA-62 (> 100 μm). This NPP type is present over the entire depth of both profiles. Whether these cell fillings are only present in leaf sheaths, or also in other aboveground material, but not in belowground roots and rhizomes, is yet unclear. If EMA-62 were indeed of aboveground origin, it would indicate that aboveground litter could play an important role in the accumulation of sedge root displacement peat.

We find micro-remains of type EMA-62 in various sizes; we interpret the increasingly smaller remains as increasing stages of decomposition. Whether this interpretation is valid or whether there may be some other origin, particularly of the smallest EMA-62 remains, is thus far unclear.

4.2. Morphotypes

In the light of rewetting and restoration measures that have been and are carried out on the large valley mires of Central Europe, there is an interest in understanding the mechanisms of peat formation and the plant species involved. In other words, we would like to be able to identify plant remains up to the species level or at least to species groups. A large problem in the identification of fine roots is their variability depending on their state of decomposition. With very little peat decomposition, fine roots with completely preserved root hairs can occasionally be found. However, the elongated part of the root hairs often breaks off and only the basal part of the root hair (pustule) remains. If the root hair base is thicker-walled and more resistant to decay than the surrounding epidermal cells, it becomes pronounced during decomposition, resulting in the typical wavy silhouette of a pustular radicel (Figure 1B). As decomposition progresses, the pustules are often lost and only the sclerenchymatic tissue remains, which we call 'radicels without epidermis' and which look the same across all species. Grosse-Brauckmann [6] argues that the form and shape of radicels may depend on growth conditions, and that pustules may be weak or absent in species that would normally display them. Whether and how far this caveat applies remains unclear.

It is particularly difficult to identify radicels, whose root hairs are not clearly differentiated from the other epidermal cells. Matjuschenko [11] and Bertsch [12] define different root types according to the length to width ratio of the epidermal cells, but such ratios are variable depending on growth rates. For these morphotypes of Matjuschenko [11] and Bertsch [12] (e.g., Carex echinata type, Carex diandra type, and Carex appropinquata type) we deem identification to the species level to be very uncertain. The exceptions are hairless roots of *Equisetum* (reddish) and *Eriophorum vaginatum* (black-grey) which differ in colour from the mostly whitish *Carex* radicels.

Even among those radicels with more or less distinct pustules there are types that may be somewhat difficult to distinguish. Matjuschenko [11], for example, points out the great similarity of young roots of *Carex rostrata* and *Carex lasiocarpa*. In a footnote in Matjuschenko [11], Selma Ruoff (translator of the Russian original) mentions that also the fine roots of *Carex panicea* are so similar to those of *Carex rostrata* that a distinction would be hardly possible.

Phragmites fine roots are easily recognisable in the field by their yellowish colour when well-preserved, but at the cellular level they show clear similarities to *Carex* fine roots in general and to *Carex vesicaria* radicels in particular. This similarity raises two questions: How can *Phragmites* fine roots be separated from *Carex vesicaria* radicels in the event of the yellowish pustules fading, and how do palaeoecological studies, which only address Cyperaceae roots in general, exclude the possibility of including *Phragmites* radicels?

5. Conclusions

High-resolution analysis of macro-remains, even with relatively small sample volumes, is an excellent method for the investigation of fen peat. In contrast to ancient DNA, it allows for separation of vegetative and generative plant remains in peat from different times and origins. The combination of root types and diaspores can provide a detailed picture of the former vegetation of fens, especially as it also breaks down taxa that are difficult to differentiate in pollen analysis (Cyperaceae) or are lost during pollen sample preparation (*Juncus*).

In the analysis of highly decomposed peat, however, analysis of macro-remains quickly reaches its limits, while analysis of micro-remains still delivers worthwhile results. The identification of the decomposition products of sedge roots (isolated pustules, EMA-131A, -131C) and what are probably leaf sheaths (EMA-62) helps to understand the formation of fen peat also in an advanced state of decomposition.

The establishment of new deposits after rewetting of fens seems to be a complex process, which in the first years is probably only an accumulation of litter and only gradually leads to a kind of 'proto-peat'. Analysis of macro- and micro-remains shows that various degradation processes have taken place in the deposits since rewetting, making the lower part of the new layer structurally more similar to the original peat, with its high radicel and low macroscopic leaf sheath content. Together with the stratification found, the presence of young layers rich in radicels indicates that the rewetting has, thus far, successfully led to the re-establishment of an accumulating fen ecosystem.

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