

## MIRE DEVELOPMENT, POOL FORMATION AND LANDSCAPE PROCESSES ON PATTERNED FENS IN DALARNA, CENTRAL SWEDEN

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### SUMMARY

(1) Mire development and pool formation were examined stratigraphically on patterned fens in Dalarna, central Sweden. The palaeoecological study was complemented by mapping of the surface and substratum topography, description of modern landforms, analysis of the water chemistry and diatom flora, and phytosociological study of the vegetation.

(2) Forty-three relevés are organized into seven *noda*, which separate along a moisture gradient. The major landforms include mire-margin hummocks, pine islands, ridges, flarks, mud bottoms, and open-water pools.

(3) Peat cores along a 900-m transect from the base to the top of one fen slope show that the mire developed through upslope paludification. Basal radiocarbon dates decrease sequentially from  $9040 \pm 80$  years BP at the base of the slope to  $1640 \pm 50$  years BP at a point 100 m from the top of the fen. Buried forest soils and stumps of *Pinus sylvestris* at the base of the peat indicate that forest communities were replaced by sedge fen.

(4) Pools and ridges develop through gradual differentiation of the mire surface some thousands of years following mire initiation. The basal 2 m of peat beneath a flark and adjoining ridge are identical until this differentiation began.

(5) Deep pools are underlain by more than 1 m of algal gyttja, which grades downward into peat detritus, and then peat. Radiocarbon-dated profiles indicate that pools initially deepen through peat degradation before the deposition of algal sediment starts.

(6) The surface patterning is dynamic. The total pool area on the mire increases with time, and the size, shape, and orientation of individual pools may change. Pools expand through gradual submergence of marginal areas as well as through coalescence. Pool drainage may occur through coalescence of pools at different elevations, through ridge erosion, and through subsurface piping.

(7) The overall development of the mires involves progressive diversification on two scales. The regional landscape increases in complexity and landform diversity as mires form and replace forest communities. On the mires, local diversification involves the development and alteration of surface features through time.

### INTRODUCTION

This work on patterned fens (aapamires—*sensu* Cajander 1913) in central Sweden tests a hypothesis for the origins of patterns on boreal and subarctic mires (Foster *et al.* 1983, Foster 1985). We investigated two aspects of aapamire development: (i) the role of paludification in the development and expansion of the mires, and (ii) the formation of the characteristic pattern of alternating peat ridges and water-filled depressions.

Paludification was discussed as early as the 1890s by Shaler (1890, 1892) and Ganong (1897) in North America, and 1923 by Malmstrom in Sweden, and has major relevance to studies of northern ecosystem structure and function. The hypothesis of Foster *et al.*

(1983) proposes that boreal mires expand from initial sites of poor drainage through the paludification of seepage-ways and forested upland areas. This process should result in significant modification of the regional ecosystem as peatland replaces forest. Extensive mire development would alter such functional aspects of the ecosystem as the fire regime (Foster 1984), productivity (Bray & Gorham 1974), the rate and pathways of nutrient cycling (Gorham 1982, Weber & Van Cleve 1984), soil development (Rode 1955) and hydrology (Ivanov 1981), which would be recorded in lake chemistry and fossil stratigraphies (Wright 1981, Engstrom & Wright 1985, Engstrom & Hansen 1985). The extent, timing and rate at which patterned-fen formation has occurred is largely unknown and is consequently of considerable interest for understanding postglacial landscape development (Lundqvist 1951, Malmstrom 1955, Gorham 1982).

The second part of the hypothesis concerns the development of the surface pattern of ridges and hollows on boreal and subarctic mires that has long attracted the attention of ecologists and geologists, especially in Fennoscandia and the Soviet Union (Andersson & Hesselman 1907, Auer 1920, Eurola 1962, Aartolahti 1967, Washburn 1979, Backeus 1984, Seppala & Koutaniemi 1985). Foster *et al.* (1983) suggest that patterns arise secondarily on mires through a gradual differentiation of the mire surface controlled by the relative rates of plant production and decomposition. Different rates of peat accumulation (in general decreasing rates for communities at decreasing heights above the water table) lead to formation of hollows and pools, and an increase in the proportion of mire surface occupied by them.

The hypothesis also suggests that mire development during the Holocene has accentuated the diversity of the landscape, and the structural and floristic complexity of the regional vegetation (Hesselman 1970). As mires develop, the forested landscape is progressively dissected by expanding peat complexes. Subsequently, the mires themselves become more varied through pattern formation, pool expansion and coalescence, and changing mire hydrology.

This research on the Krackelbacken mires in central Sweden seeks to examine mire development in an area with different climatic conditions and flora from those of Labrador, where the hypothesis was formulated (Foster & King 1984). Although the non-vascular floras of mires in eastern North America and north-western Europe are strikingly similar, the vascular species, especially the woody plants, are quite different (Sjors 1963, Damman 1980). This dissimilarity is important for testing the universal nature of mire processes, as some studies have suggested that the branching morphology and vegetative reproduction of specific shrubs (e.g. *Calluna vulgaris*) and trees (e.g. *Picea mariana*) are essential components of hummock production and therefore pattern formation (B. Wallen & N. Malmer, unpublished data).

The specific objectives of this study include (i) determination of the pattern and timing of peatland initiation and expansion using basal dates and stratigraphies from cores taken along transects across the mire, and (ii) examination of the origin and development of peatland landforms, particularly ridges and hollows, by analysis of lithology, dating and the diatom stratigraphy of cores. Data on the modern distribution of plants within the mire are also presented to provide modern analogues for interpretation of stratigraphic data.

## STUDY AREA

The Krackelbacken mires (61°30'N, 14°13'E) are located in Dalarna province, central Sweden (Fig. 1), on Archaean granites and gneisses. The region has an annual

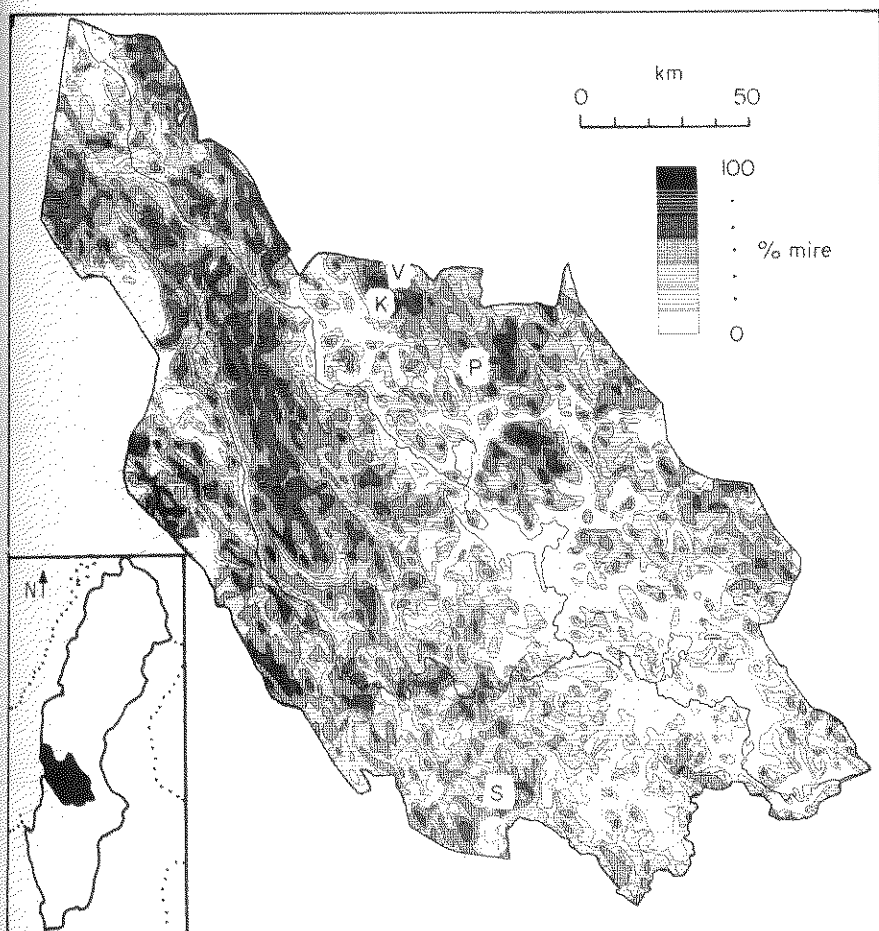


FIG 1. Location of the Kräckelbäcken mires (K) in Dalarna, central Sweden. Altitude ranges from approximately 150 m in the south-east to 1200 m in the north-west. Shading indicates the percentage of land area covered by mire. Location of mire studies referred to in the text include: S—Skattlösberg Stormosse (Sjörs 1948), P—Koppängen (Sjörs *et al.* 1973), and V—Stormyren vid Kräckelbäcken (Lundqvist 1951).

precipitation of 800 mm and mean annual temperature of approximately 0°C (Sjörs *et al.* 1973). The upland vegetation is characteristic of the northern coniferous forest (Sjörs 1965). Accounts of the mires in this region have been given by Sjörs (1948), Lundqvist (1951), Malmström (1955), and Sjörs *et al.* (1973). Altitude greatly controls the local climate and consequently governs the extent and type of mire. Kräckelbäcken mires occur in the higher northern region (600 m above sea level; Figs 1 and 2) where soligenous fens predominate over ombrotrophic bogs as a result of low temperature, high humidity and abundant snow (Sjörs 1948; Sjörs *et al.* 1973). The fens of this area are often strongly sloping, have well-developed surface patterns, extensive mud bottoms (*sensu* Sjörs 1948), and *Scirpus cespitosus* and *Molinia caerulea* lawns (Fransson 1965). In contrast, at lower elevations the extent of mires and surface patterning decreases, and in the south-east, under warmer, somewhat drier conditions, ombrotrophic bogs predominate on restricted mire areas.

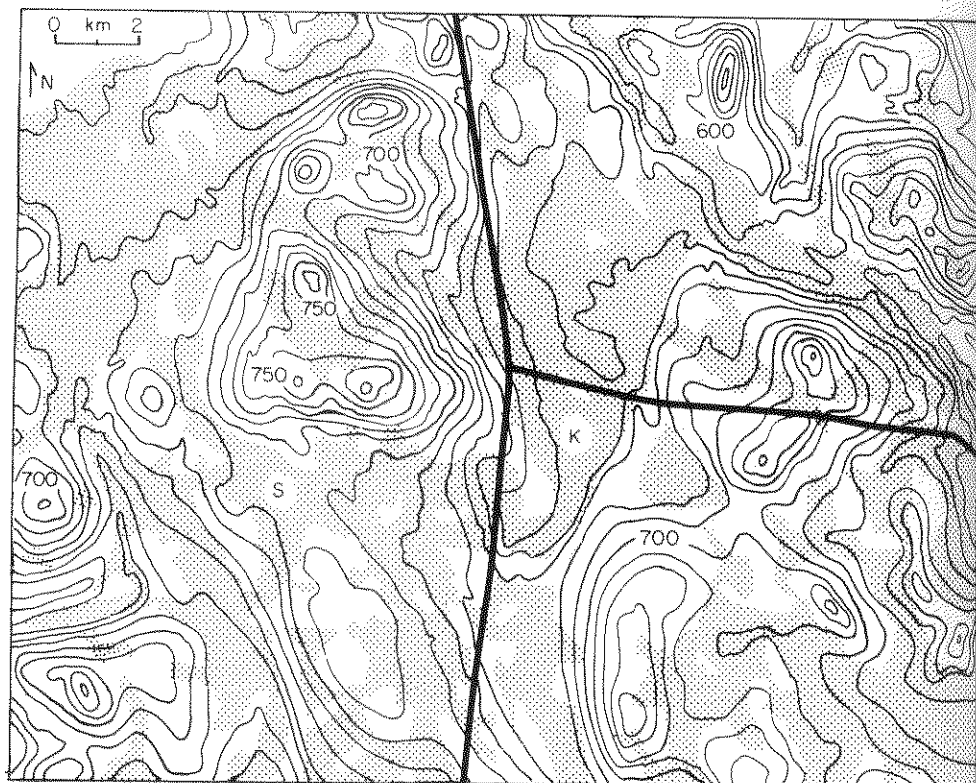


FIG. 2. Topographic map of the Kräckelbäcken area (10-m contours) showing the location of the Kräckelbäcken fen (K) and Stor Kräckelbäcken (S) mire, the distribution of mires (stippled), and local roads (black lines).

Kräckelbäcken fen contains approximately 2.0 km<sup>2</sup> of sloping fen (Fig. 3). Total rise is 31 m from the Kollan stream, which drains the mire to the east, to the western head of the mire. Much of this rise occurs in steeply sloping fens west of the strongly patterned central region. The mire is interrupted by islands of mineral soil. It contains a broad water-divide in the region of the *Carex rostrata* flark (Fig. 3) where water flows south-east into the Kollan stream and north into drainage streams. Peat depths range from <1 to 4.5 m and are largely correlated with position on the slope (see Fig. 11). Deepest peats are at the base of the slope in the heavily patterned area and beneath the *Carex rostrata* flark, whereas lesser depths occur on the steeply sloping fens. A road constructed across the western head of the mire in 1951 provides a peat exposure (Fig. 4) 80 m long.

Stor Kräckelbäcken mire is located 5 km west of Kräckelbäcken fen and consists of interconnected fens partly separated by intervening mineral uplands and covering approximately 5 km<sup>2</sup> (Fig. 5). Narrow, weakly patterned sedge fen occupies steep drainage-ways. The level confluence of the numerous fens supports deep peats, and extensive patterned areas of broad and deep pools.

## METHODS

Detailed reconstruction of the developmental history of the mires requires extensive background information on the modern environment. Consequently, stratigraphic

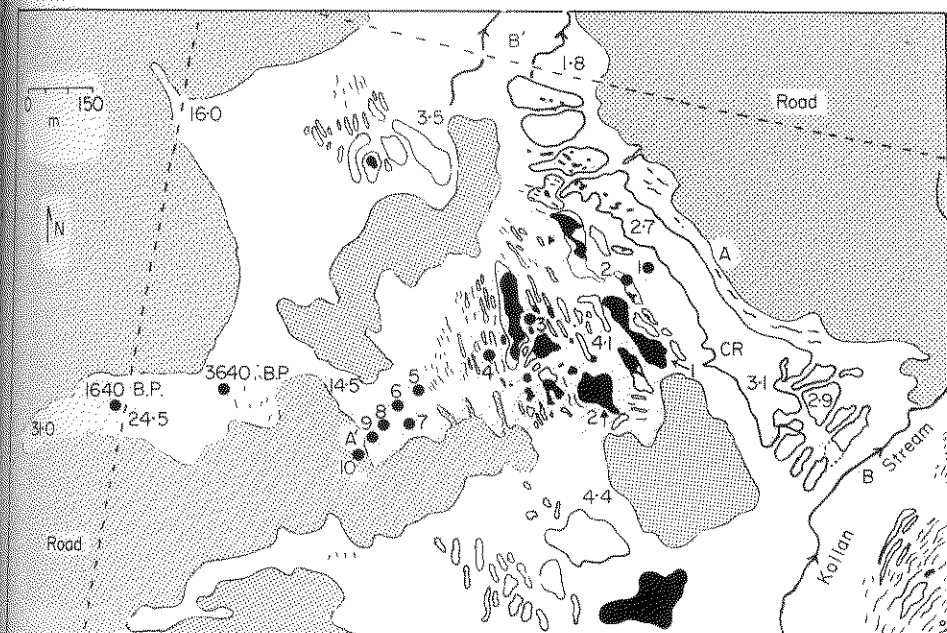


FIG. 3. Map of Kräckelbäcken fen showing the location of uplands (stippled areas), pools (black), flarks (enclosed white areas), and the *Carex rostrata* flark (CR). Transects discussed in the text (A-A', B-B') and spot elevations (in metres) above the Kollan stream are labelled. Coring sites are numbered dots, basal dates for the two eastern cores are indicated, and the locations of pools 1 and 2 are shown by arrows.

investigations were preceded by descriptions of the surface topography and peat depths, flora, microflora and water chemistry.

Base maps of the mires and surface features were drafted from enlarged aerial photographs (1:30 000; Lantmateriet, Gävle, Sweden). Surface topography of Kräckelbäcken fen was determined with a level along three transects at 20-m horizontal intervals and at spot locations. Peat depths were measured at each point along the transects with thin metal rods or a Russian peat corer.

Vegetation analysis used the sampling methods of Braun-Blanquet employed in previous studies (Foster & King 1984; Foster & Glaser 1986). Cover-abundance was estimated on the Domin scale (Birks 1973) in forty-three relevés (3 m × 3 m) taken in areas of homogeneous vegetation and site conditions. Plant names follow Lid (1974) for vascular species, Moberg & Holmasen (1982) for lichens and Nyholm (1956) for bryophytes. At each plot pH and conductivity were measured with a Radiometer pH meter and Yellow Springs conductivity meter, respectively, and depth to water table, peat depth, and site description were recorded. A phytosociological table was constructed with the FORTRAN program TWINSpan (Hill 1979b; Gauch 1982), and species and sample ordinations by reciprocal averaging were produced with ORDIFLEX (Gauch 1982).

Water samples were collected in 150-ml acid-washed polypropylene bottles from pools, carpets and mud bottoms at seven places on the mire. Analyses included pH and conductivity measured in the field and laboratory, and cation concentrations (K, Ca, Mg, Na) determined with an atomic absorption spectrophotometer at the Department of Plant Ecology, University of Lund.



FIG 4. Peat and soil profile along the road cut at Kräckelbäcken fen. The conspicuous pine stumps are overlain by very well decomposed peat or sedge peat. (Photograph by D. R. Foster.)

Surface material for diatom analysis was collected from a variety of mire habitats including pools, hollows, ridges and lawns in order to identify the composition and distribution of diatom taxa within the peatland. Site descriptions are given in Table 3 below. A phytosociological table was constructed with TWINSpan (Hill 1979b), and species and sample data were ordinated by detrended correspondence analysis with the program DECORANA (Hill 1979a).

Peat cores were taken along a transect up the central axis of the western slope at Kräckelbäcken fen (Transect A, Fig. 3) and at other selected spots. Coring was accomplished with a 10-cm diameter piston corer fitted with a serrated edge for cutting through woody or rhizomatous peat (Wright, Mann & Glaser 1984). Cores were extruded in the field and wrapped in plastic and aluminium foil. At the University of Lund the cores were cut in half lengthwise, and the bulk density was measured at 10-cm intervals. Continuous 5-cm segments were subsampled for diatom analysis and then sieved for macrofossils. Macrofossil identifications were made at magnification of  $\times 5$ – $\times 50$  under a Wild dissecting microscope. Samples were dated at the Radiocarbon Laboratory at the Department of Quaternary Geology, University of Lund.

Samples for diatom analysis were heated for 10 min in a mixture of  $\text{H}_2\text{SO}_4$  and  $\text{HNO}_3$ . Cleaned material was mounted on slides with Naphrax. Diatom valves were counted on a Leitz Ortholux microscope at a magnification of  $\times 1425$ . A minimum of 500 valves was identified in each sample.

The mineral substratum beneath Kräckelbäcken fen was examined along the road cut and in pits dug on transects across the mire and up the western axis (Transect A). Photographs were taken of all pits and exposures, the thickness of each stratigraphic unit was measured and basal wood was collected for radiocarbon dating.

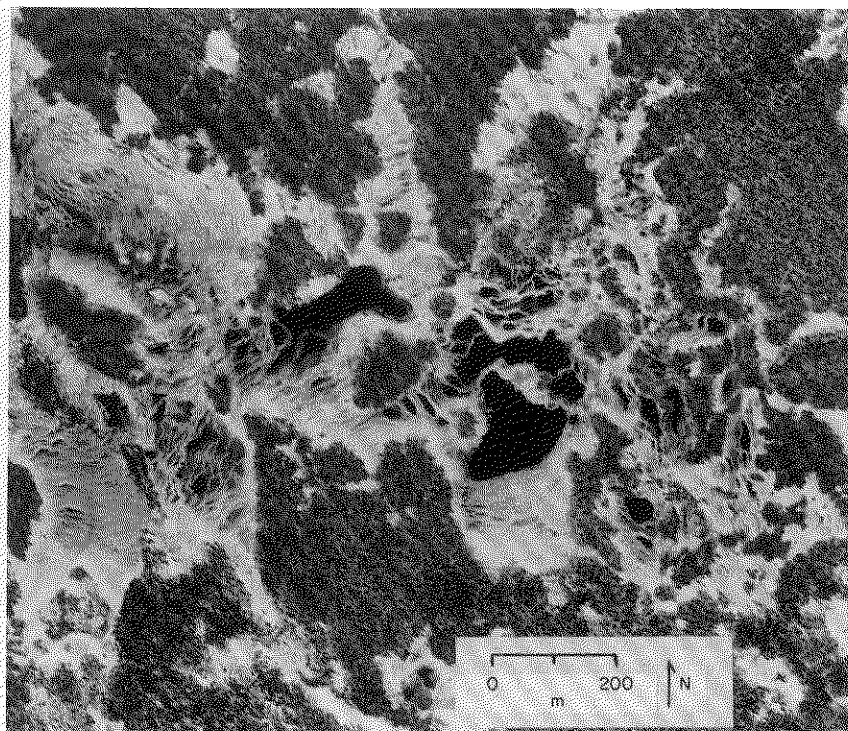


FIG. 5. Aerial photograph of the Stor Kräckelbäcken mire. *Pinus sylvestris* covers the darker uplands. Broken peat ridges and scalloped edges of pools result from peat degradation and erosion.

## RESULTS

In the following section, descriptions of the mire landforms, water chemistry, vegetation assemblages and diatom surface samples outline the modern environment and flora of the Kräckelbäcken mires. Results from the long-core stratigraphy are then presented to describe the developmental history of the mires.

### *Mire distribution and landscape features*

Discontinuous fens cover 40–60% of the land surface of the Kräckelbäcken region and form a generally interconnected drainage system on seepage-ways and low-lying surfaces (Figs 2, 3). Along streams the mires form broad margins spreading headward up side-channels, even on steep slopes exceeding 15%. Peat deposits are absent only on convex landforms, such as hill summits and water divides. Raised peat-based landforms include ridges, mire-margin hummocks, sedge lawns and pine islands. Depressed water-dominated landforms include flarks and pools. The distribution of these landforms is controlled by slope, moisture surplus and developmental history.

Ridges range in size from sinuous *Eriophorum* ridges less than 0.5 m wide to broad wooded ridges 40 cm high and several metres in breadth. The increasing height is associated with greater abundance of low shrubs (*Calluna*, *Vaccinium* spp.), oligotrophic bryophytes (*Sphagnum fuscum*, *S. nemoreum*) and lichens (*Cladonia* spp.), and decreasing





FIG. 6. Stumps jutting from the base of the peat and gravel shores beside the largest pool on Stor Kräckelbäcken mire. (Photograph by D. R. Foster.)

cover of sedges. Despite their name, mire-margin hummocks (*sensu* Sjörs 1948) may be found in central as well as peripheral areas of the mires. They are generally oval to elongate and have a surface 50–100 cm above the surrounding sedge lawns. The orientation, shape and stratigraphy suggest that many of these isolated hummocks are remnants of old degraded ridges. On sedge lawns in Kräckelbäcken mire this is especially obvious as the hummocks form irregular and discontinuous lines across the slope.

Pine islands are robust peat hummocks 20 m<sup>2</sup> or more in area and 40 cm or more in height that support tall pines (*Pinus sylvestris*) and a shrubby undergrowth of *Vaccinium* spp. and *Calluna*. Sedge lawns predominate on both mires, forming large unpatterned areas apparent on aerial photographs (Fig. 5).

Water-dominated landforms range in size and depth from shallow flarks to broad deep pools with mineral bottoms. Both flarks and pools are dammed by elongate ridges. Flarks, which are wet depressions filled with *Sphagnum* and sedge overlying loosely consolidated peat, frequently range from only one to a few metres wide and extend across the slope of the mire. An extreme example of a flark is the *Carex rostrata* flark, which is 275 m long and 50 m wide, and comprises the central part of Kräckelbäcken fen. It is dammed at both north and south ends by broad robust peat ridges.

Pools range considerably in size, shape, depth, and the nature of underlying sediments. Shallow pools less than 10 cm in depth and 5–25 m<sup>2</sup> surface area are located along the southern perimeter of Kräckelbäcken fen and up the gradual slope to the west. Broader pools 1–2 m deep and 10–40 m across are located on the roughly level plain above (west of) the *Carex rostrata* flark. The morphometry of the basins is largely controlled by the slope. On level areas, pools are subcircular, whereas on sloping surfaces the shape becomes elongate perpendicular to the slope. The largest pools occupy the central portion of Stor Kräckelbäcken mire (Fig. 5). These pools range to 200 m in length, are less than 2





FIG. 7. Large pool on Stor Kräckelbäcken mire. Expansion of the pool through erosion and degradation has left peat peninsulas, basal stumps and remnant tussock islands. (Photograph by D. R. Foster.)

TABLE 1. Water chemistry of Kräckelbäcken fen. Numbers in parentheses correspond to samples for diatom analysis taken from each site (see Table 3).

Sample location	pH (units)		Kcond ( $\mu\text{S cm}^{-1}$ at 20°C)	Na <sup>+</sup> (mg l <sup>-1</sup> )	K <sup>+</sup> (mg l <sup>-1</sup> )	Mg <sup>2+</sup> (mg l <sup>-1</sup> )	Ca <sup>2+</sup> (mg l <sup>-1</sup> )
	Field	Lab.					
Open pool (Km1)	4.2	4.3	28	0.56	<0.01	0.14	0.29
Mud bottom (Km2)	3.8	4.2	32	0.60	0.07	0.15	0.42
Open pool (Km4)	4.2	4.3	27	0.63	0.01	0.11	0.25
Drained pool (Km5)	4.1	4.3	28	0.59	0.06	0.13	0.24
<i>Sphagnum lindbergii</i> carpet (Km6)	3.8	4.5	38	0.50	0.02	0.19	0.31
<i>S. papillosum</i> carpet (Km7)	4.3	4.5	18	0.31	<0.01	0.12	0.28
<i>Carex rostrata</i> fen (Km9)	3.8	4.0	49	0.69	0.05	0.37	0.28

m deep, and have a sand and gravel floor along the southern shore and shallow peat detritus across the central basin and northern shore (Figs 6 and 7).

#### Water chemistry

The water chemistry is characteristic of poor fen conditions. The pH ranges from 3.8 to 4.3 (4.0 to 4.5 in the laboratory) and the conductivity, not adjusted for pH, from 18 to 49  $\mu\text{S cm}^{-1}$  (Table 1). Similarly low values for the cations range from 0.31–0.69 mg l<sup>-1</sup> for sodium, <0.01–0.07 mg l<sup>-1</sup> for potassium, 0.11–0.37 mg l<sup>-1</sup> for magnesium, and 0.24–0.42 mg l<sup>-1</sup> for calcium.

*Phytosociology*

The forty-three relevés are organized into seven floristic noda in the phytosociological table (Table 2). The noda separate along a moisture gradient as revealed in an ordination by reciprocal averaging (Fig. 8). Species in the phytosociological table are arranged into species groups that have similar occurrence and abundance in the noda. Species relationships were examined by principal components analysis (Fig. 9), in which the relationships of individual species and the eight species groups are graphically displayed. The resulting ordination is apparently controlled by a moisture gradient (Axis 1 in Fig. 9) and a nutrient gradient (Axis 2 in Fig. 9). Species in Groups I–IV are characteristic of dry raised sites on firm peat, Groups I and II are found along mire margins and forest borders whereas groups III and IV are found on the mire expanse, especially on raised ridges and hummocks. Species in groups V, VI and VII occur on progressively moister sites.

The noda and their distribution within the mire are described below.

*Nodum I Melampyrum—Sphagnum russowii—Eriophorum vaginatum assemblage*

This assemblage occupies the wooded margins of the fens. *Betula nana*, *Vaccinium myrtillus* and *V. uliginosum* form a discontinuous shrub layer over the herbs *Melampyrum pratense*, *Rubus chamaemorus*, *V. oxycoccus*, *Carex pauciflora* and *Eriophorum vaginatum*. The hummocky relief created by the underlying mineral soil (peat depth approximately 50 cm), by shrub growth and by *Sphagnum* hummocks presents a diverse microtopography that supports *Sphagnum russowii*, *S. magellanicum* and *S. fuscum*.

*Nodum II Calluna—Sphagnum rubellum—Eriophorum vaginatum assemblage*

On ridges 25–60 cm high *Calluna vulgaris*, *Betula nana* and *Vaccinium uliginosum* form a dense shrub layer above a discontinuous cover of *Eriophorum vaginatum*, *Andromeda polifolia*, *Rubus chamaemorus*, and *Empetrum nigrum*. The composition of the ground layer is controlled by the height above the water table, *Sphagnum* species (*S. russowii*, *S. magellanicum*, *S. rubellum*) and less mesic bryophytes (*Pleurozium schreberi* and *Polytrichum strictum*) occupy raised peat ridges, whereas lichens (*Cladonia rangiferina*, *C. mitis*, *Cetraria islandica*) occupy the hummock tops. The floristic similarities between the active ridges (relevés 22, 23, and 24) and rows of discontinuous hummocks (relevés 27 and 28) provide corroboration that the latter represent disintegrated ridges (see Discussion).

*Nodum III Sphagnum fuscum—Empetrum—Rubus chamaemorus assemblage*

This nodum is restricted to broad *Sphagnum fuscum* hummocks, 2.0–3.5 m broad, and 50–75 cm high that form a discontinuous line extending into the fen, perpendicular to the slope. *Sphagnum fuscum* predominates, with patches of *Polytrichum strictum*, *Mylia anomala* and *Cladonia rangiferina* increasing in cover towards the tops of the hummocks. Common species in the diverse lichen flora include *Cladonia mitis*, *C. chlorophaea*, *C. gracilis* and *Icmadophila ericetorum*. Peat monoliths from the upper 30 cm of the hummocks show that *Sphagnum fuscum* is succeeded by the *Cladonia* lichens, possibly as a result of changes in surface moisture (Foster 1985, Foster & Glaser 1986). *Rubus chamaemorus*, *Eriophorum vaginatum* and *Empetrum nigrum* occupy the hummock tops whereas *Molinia caerulea*, *Scirpus cespitosus* and *Betula nana* occur on the flanks. *Vaccinium oxycoccus*, *V. uliginosum*, *Andromeda polifolia*, *Drosera rotundifolia* and *Carex pauciflora* exhibit no microtopographic preference.



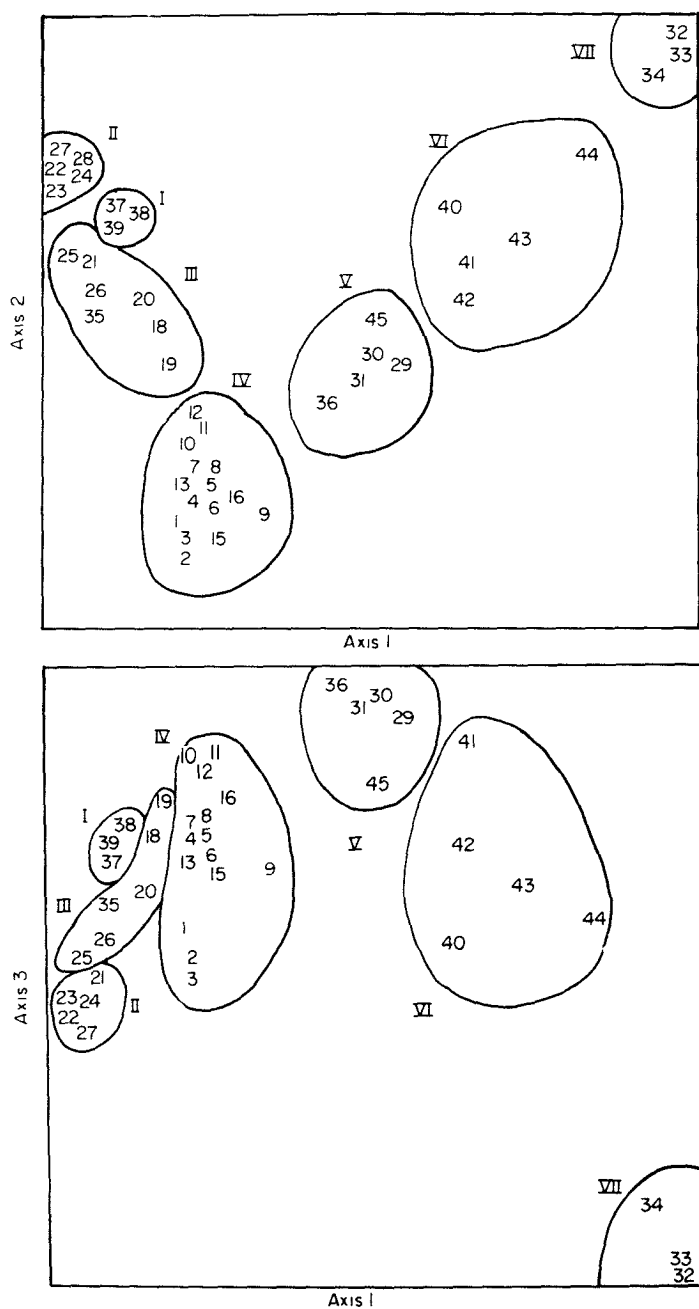


FIG 8 Ordination by reciprocal averaging of the vegetation relevés from the Krackelbacken mires along ordination axes 1, 2 and 3. Groupings designated by roman numerals correspond to the noda in the phytosociological table (Table 2)

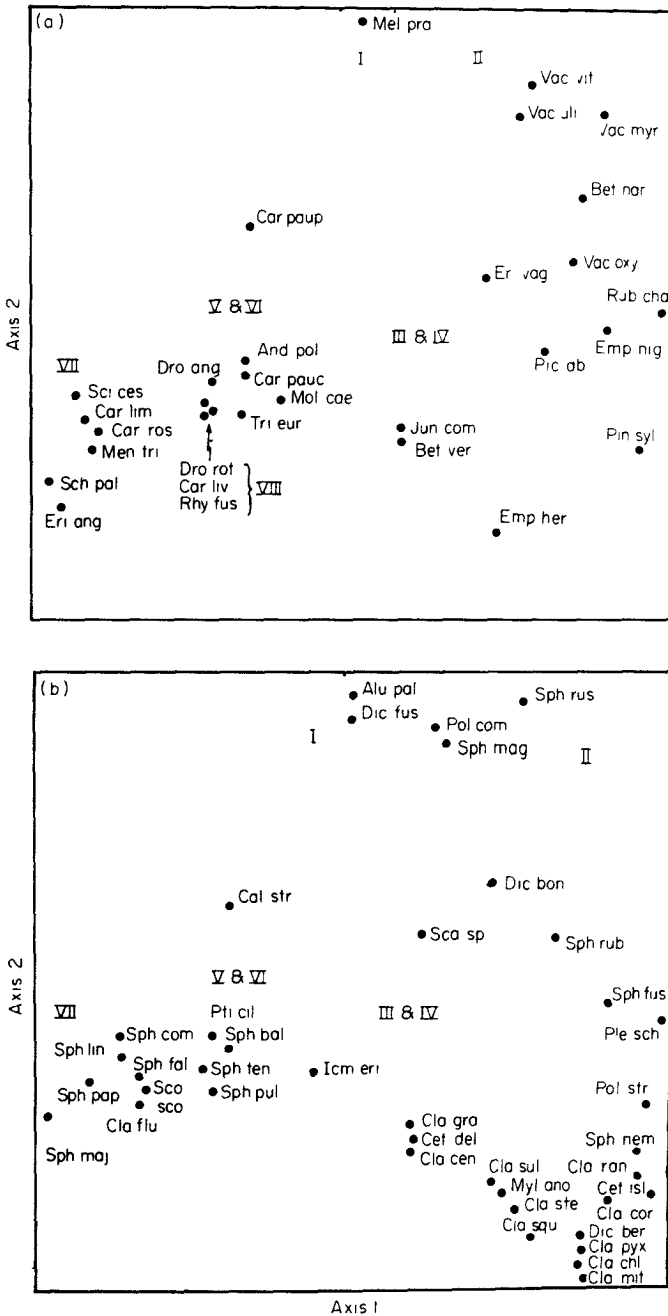


FIG 9 Ordination by principal components analysis of the species in the forty-three relevés from the Krackelbacken mires. Vascular plants are shown in 9a, cryptogams in 9b. Roman numerals refer to the species groups in the phytosociological table (Table 2). The first three letters of the genus and species are used as species abbreviations. Full names are given in Table 2.

TABLE 3 Description of surface samples from the Krackelbacken mires used in diatom analysis

Sample no	Sample description
Km1	Pool detritus on pool bottom
Km2	Flark, <i>Cladopodiella fluitans</i> mud bottom
Km3	Ridge <i>Eriophorum angustifolium</i> <i>Molinia Andromeda</i>
Km4	Pool gytja and detritus from pool bottom
Km5	Drained pool <i>Carex rostrata</i> flark
Km6	Drained pool <i>Sphagnum lindbergii</i> carpet
Km7	Drained pool <i>Sphagnum papillosum</i> — <i>S. angustifolium</i> carpet
Km8	Pool gytja and detritus from pool bottom
Km9	Flark <i>Carex rostrata</i>
Km10	Lawn <i>Scirpus cespitosus</i>

*Nodum IV Eriophorum vaginatum—Scirpus cespitosus assemblage*

This assemblage forms lawns on firm peat throughout the mire *Andromeda polifolia* *Drosera rotundifolia*, *Scirpus cespitosus*, *Eriophorum vaginatum* and *Sphagnum papillosum* occur in most releves *Molinia caerulea*, *Rubus chamaemorus*, *Sphagnum pulchrum* *Trientalis europea* and *Calluna vulgaris* are differential species (cf Mueller-Dombois & Ellenberg 1974) of a lawn community on very low ridges of sloping fens *Carex pauciflora* *Sphagnum compactum*, *Cladopodiella fluitans* and *S. majus* or *S. lindbergii* form broad lawns in unpatterned areas on fairly steep slopes

*Noda V–VII carpet assemblages*

Three carpet assemblages are separated along a moisture gradient *Sphagnum majus* and *Scheuchzeria palustris* dominate in shallow and firm flarks In moister areas, including the broad *Carex rostrata* flark, *Menyanthes trifoliata* and *Carex limosa* increase in importance In locations where the peat surface lies at the water table, *Eriophorum* spp *S. majus* and *Scorpidium scorpioides* occur In deeper water the floristic richness is reduced to four taxa—*Sphagnum majus*, *Carex rostrata*, *Menyanthes trifoliata* and *Scheuchzeria palustris*

*Diatom communities*

Diatom samples were classified with TWINSpan, which divides the samples (Table 3) into two primary groups (Table 4), one including the pools, the *Carex rostrata* flark and the *Cladopodiella fluitans* hollow, and the other containing the drained pool, the sedge lawn, and the *Eriophorum* ridge An ordination of the samples with DECORANA (Fig 10) suggests that these samples separate along a moisture gradient (Axis 1) ranging from depressed water-dominated landforms (pools, hollows) on the left of the diagram to dry, elevated landforms (ridge, sedge lawn) on the right

The species compositions of these samples are illustrated in a phytosociological table (Table 4) Species predominant in pools and hollows are shown in the upper part of the table, those in the drained pools, ridges and sedge lawns are in the lower part, and taxa without clear preferences occur in the centre

The diatom floras of the pools (samples Km1, Km4, Km8), the *Carex rostrata* flark (Km9) and the *Cladopodiella fluitans* hollow (Km2) are broadly similar and are dominated by *Eunotia denticulata* (29–70%) and *Frustulia rhomboides* var *saxonica* (19–43%) *Eunotia exigua*, *Navicula subtilissima* and *Tabellaria quadriseptata* are also abundant (3–14%) in the pools and fen samples, but are rare in the liverwort hollow

TABLE 4 Phytosociological table of Krackelbacken mire diatom taxa. Column numbers are the site codes for surface samples (Table 3). Values are for relative abundance 1,0–2%, 2,2–5%, 3,5–10%, 4,10–20%, 5, > 20%.

Sample no	I					II				
	1	4	8	9	2	5	6	7	3	10
<i>Eunotia bactriana</i> Ehr	—	—	2	2	—	—	—	—	—	—
<i>Eunotia exigua</i> (Breb.) Rabh	3	2	4	4	1	—	—	—	1	—
<i>Eunotia serra</i> Ehr	—	—	1	—	—	—	—	—	—	—
<i>Eunotia tenella</i> (Grun.) Cleve	1	1	—	—	—	—	—	—	—	—
<i>Eunotia triodon</i> Ehr	1	1	1	—	—	—	—	—	—	—
<i>Neidium bisulcatum</i> (Lagerst.) Cleve	—	—	—	1	—	—	—	—	—	—
<i>Tabellaria quadrisepitata</i> Knuds	3	1	3	3	—	—	—	—	—	—
<i>Tabellaria flocculosa</i> (Roth) Kutz	1	—	—	—	—	—	—	—	—	—
<i>Pinnularia abaujensis</i> (Pant.) Ross	1	1	1	1	—	—	—	—	—	—
<i>Pinnularia</i> sp. 11	1	—	1	1	—	—	—	—	—	—
<i>Eunotia talida</i> Hust	—	—	—	—	1	—	—	—	—	—
<i>Frustulia rhomboides</i> var saxonica (Rabh.) deToni	5	4	5	5	5	1	1	2	1	—
<i>Eunotia denticulata</i> (Breb.) Rabh	5	5	5	5	5	5	5	5	3	—
<i>Eunotia parallela</i> Ehr	1	1	1	2	1	—	—	1	1	—
<i>Natricula mediocris</i> Krasske	1	1	—	—	1	—	—	—	1	—
<i>Natricula subtilissima</i> Cleve	3	2	4	3	1	1	4	—	1	1
<i>Eunotia curvata</i> (Kutz.) Lagerst	1	—	—	—	1	—	—	1	1	—
<i>Eunotia septentrionalis</i> Østr	1	1	—	—	—	—	1	—	1	—
<i>Anomoeoneis serians</i> var brachysira (Breb.) Hust	2	1	—	—	—	—	—	—	1	1
<i>Pinnularia rupestris</i> Hantz	1	1	1	1	3	—	—	1	5	2
<i>Eunotia fallax</i> A. Cleve	—	—	—	—	—	—	—	—	2	—
<i>Eunotia lapponica</i> Grun	1	1	1	1	2	2	5	5	4	4
<i>Eunotia trimacra</i> var undulata Hust	2	—	—	1	1	1	4	5	5	5
<i>Pinnularia termitiana</i> (Ehr.) Patr	—	—	—	—	—	—	3	—	—	—

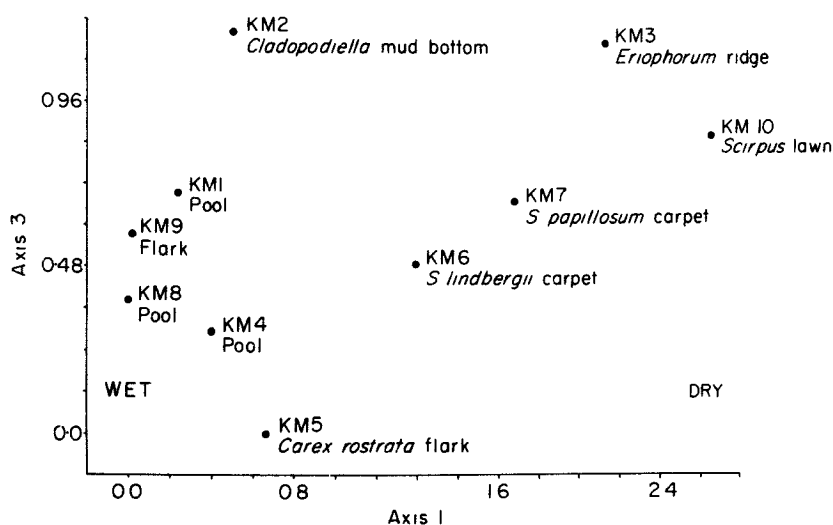


FIG 10 Ordination by detrended correspondence analysis of modern diatom samples from the Krackelbacken mires. More complete site descriptions are given in Table 3.



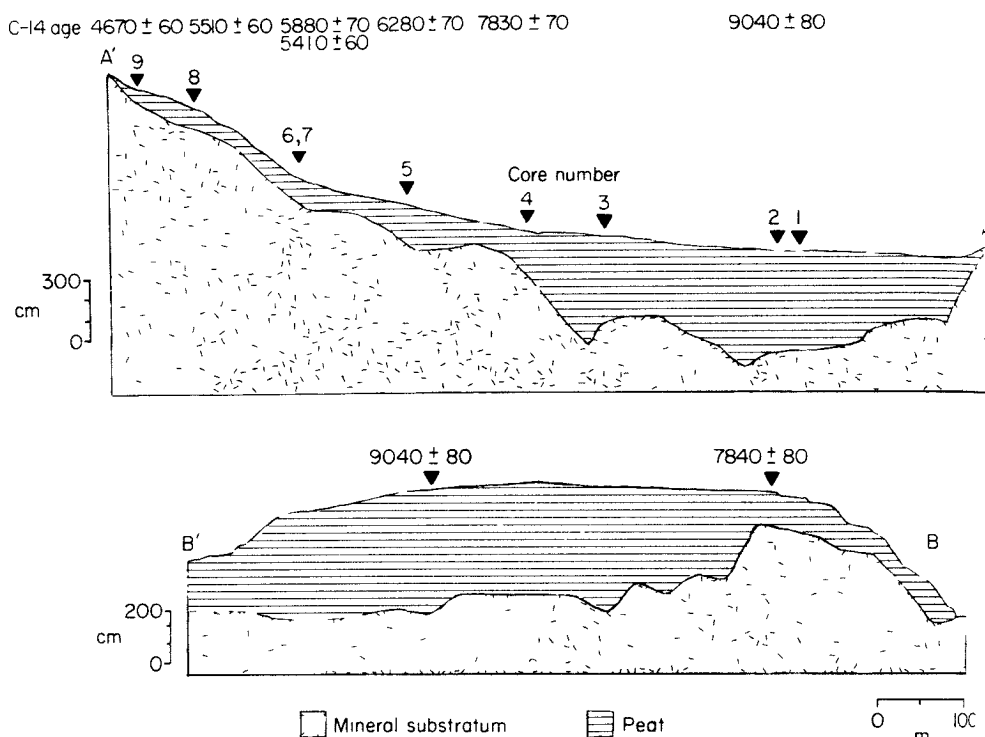


FIG 11 Cross-sections of Krackelbacken fen along transects A and B showing the coring locations and the basal radiocarbon dates

Samples from the drained pool (Km5, Km6, Km7) are also dominated by *Eunotia denticulata*, but contain much lower percentages of *Frustulia rhomboides* var *saxonica* than the pool and hollow samples. *Tabellaria quadriseptata*, *Eunotia bactriana* and *E. exigua*, which occur in moderate percentages (2–10%) in several of the pool and hollow samples, do not occur in the drained pool. Samples 6 and 7, which were taken from drier more marginal areas than sample 5, contain high percentages of *Eunotia trinacria* var *undulata* and *Eunotia lapponica*.

The *Eriophorum* ridge (Km3) and the sedge lawn (Km10), in contrast to the pools, hollows and drained pools, are dominated by *Eunotia trinacria* var *undulata*. *Eunotia lapponica* is also common (12–16%), as is *Pinnularia rupestris*. *Eunotia denticulata* is common (7%) in the ridge but is absent from the sedge lawn.

### Stratigraphy

#### Long core transect

The peat stratigraphy along the transect across the *Carex rostrata* flank and upslope to the west (Transect A, Fig 3) exhibits a distinct change where the peat thins upslope (Figs 11 and 12). All cores from that point to the head of the fen have a similar stratigraphy although they vary in depth. Charcoal was found at the base of the peat in five cores and in the monolith taken from the forest floor (Core 10, Fig 12). The lowest peats are woody and well-decomposed, twigs and larger wood fragments are embedded in a fine matrix containing few macrofossils. The woody peat is 20–60 cm thick and grades upwards into

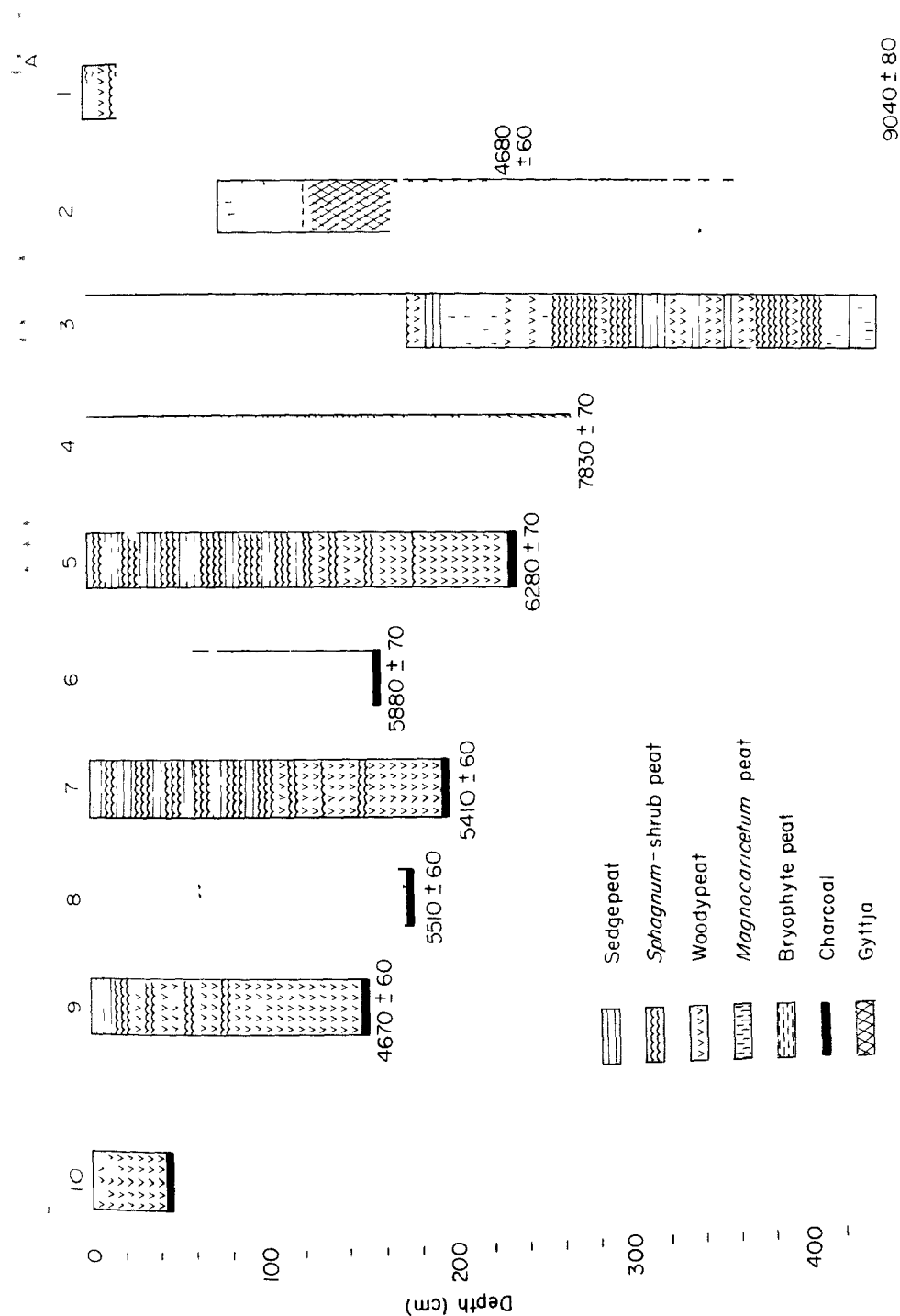


FIG 12 Stratigraphy of cores along Transect A on Krackelbacken fen. Basal radiocarbon dates are shown as well as one date for the gytija in Core 2. Core 2 (from a flask) is drawn at its actual elevation so that the stratigraphic unit may be compared with the corresponding units in the adjacent ridge (Core 1).

sedge-*Sphagnum* peat from which ligneous debris is absent except in cores 9 and 10 at the upper end of the fen. The sequence suggests that the entire upper (western) half of the mire has undergone a similar history of replacement of trees or shrubs by sedge and *Sphagnum* cover.

The lower (eastern) part of the transect is underlain by much deeper peat and has a more complex stratigraphy and vegetation history. Core 3 from a sedge lawn just below the break in the slope shows a basal peat from a *Magnocaricetum* assemblage (cf. Sjors 1948, Du Rietz 1949) containing *Carex rostrata* and *Drosera* seeds. Woody material increases above, and a sequence of *Sphagnum*-shrub peat, sedge-shrub peat, and *Sphagnum*-shrub peat continues up to 260 cm depth. *Magnocaricetum* occurs to 200 cm depth, followed by shrub peat to 80 cm and *Sphagnum* and sedge peat to the surface.

Cores 2 and 1 were taken from a flark and its damming ridge, respectively. The ridge is discontinuous with two portions that are only slightly higher than the flark. The cores were selected to examine whether the flark was a drained pool as well as to explore the general sequence of pattern development.

Both cores contain a similar stratigraphy in the lower 200 cm (Fig. 12). The basal sedge peat is overlain by bryophyte peat composed primarily of *Drepanocladus*, with abundant seeds of *Menyanthes*. At 380 cm this changes sharply to *Sphagnum* peat for 120 cm followed by a thin section of *Magnocaricetum*, 25 cm of sedge-*Sphagnum* peat, and 60 cm of *Drepanocladus* peat, which continues in the ridge core to approximately 170 cm. In the flark (core 2) a gradual transition from *Drepanocladus* peat to gyttja makes the exact point of divergence of the pool from the ridge difficult to isolate. The gyttja terminates at 110 cm depth and is overlain by 50 cm of firmer *Magnocaricetum* peat.

The sequence from *Drepanocladus* peat to gyttja to sedge peat in core 2 suggests the existence of an open-water pool that was subsequently drained and then colonized by *Carex rostrata* and *Menyanthes*. Diatom analysis of core 2 (Fig. 13) corroborates this hypothesis. The diatom assemblage in the gyttja is characteristic of pools (see Table 4) dominated by *Eunotia denticulata* and *Navicula subtilissima*, with moderate percentages of *Tabellaria quadriseptata*, *Pinnularia abaujensis* and *Eunotia bactriana*, and small percentages of *E. triodon*. The conspicuous absence of *Frustulia rhomboides* var. *saxonica*, a dominant taxon in the modern pool samples, is probably a result of dissolution of the lightly silicified valves in pore waters low in dissolved silica. The fairly sharp transition between 200 and 210 cm from a *Melosira nygaardii* Camburn assemblage in the *Drepanocladus* peat to this pool community suggests that the divergence of the pool from the present ridge may have occurred within this stratigraphic interval. The increased percentages of *Eunotia trinacria* var. *undulata* and *Eunotia lapponica* coincident with the abrupt sedimentary change from gyttja to sedge peat clearly indicates drainage of the pool, for in the modern samples these taxa are abundant only on sites without standing water.

In the ridge (Core 1) there is an abrupt transition at 160 cm from bryophyte peat below to shrub-*Sphagnum*-sedge peat, which continues to the surface. This implies that a ridge-building assemblage similar to that occupying the ridge today has consistently occupied this site since the formation of the pool upslope. The peat becomes woodier towards the surface, which suggests that the ridge has become progressively accentuated above the flark. The similarities in the lower sections of the flark and ridge cores shows that surface patterns have developed long after mire formation and are independent of the substratum underlying the peat (Seppala & Koutaniemi 1985).

Basal radiocarbon dates upslope along the central axis (E-W) of the mire yield a

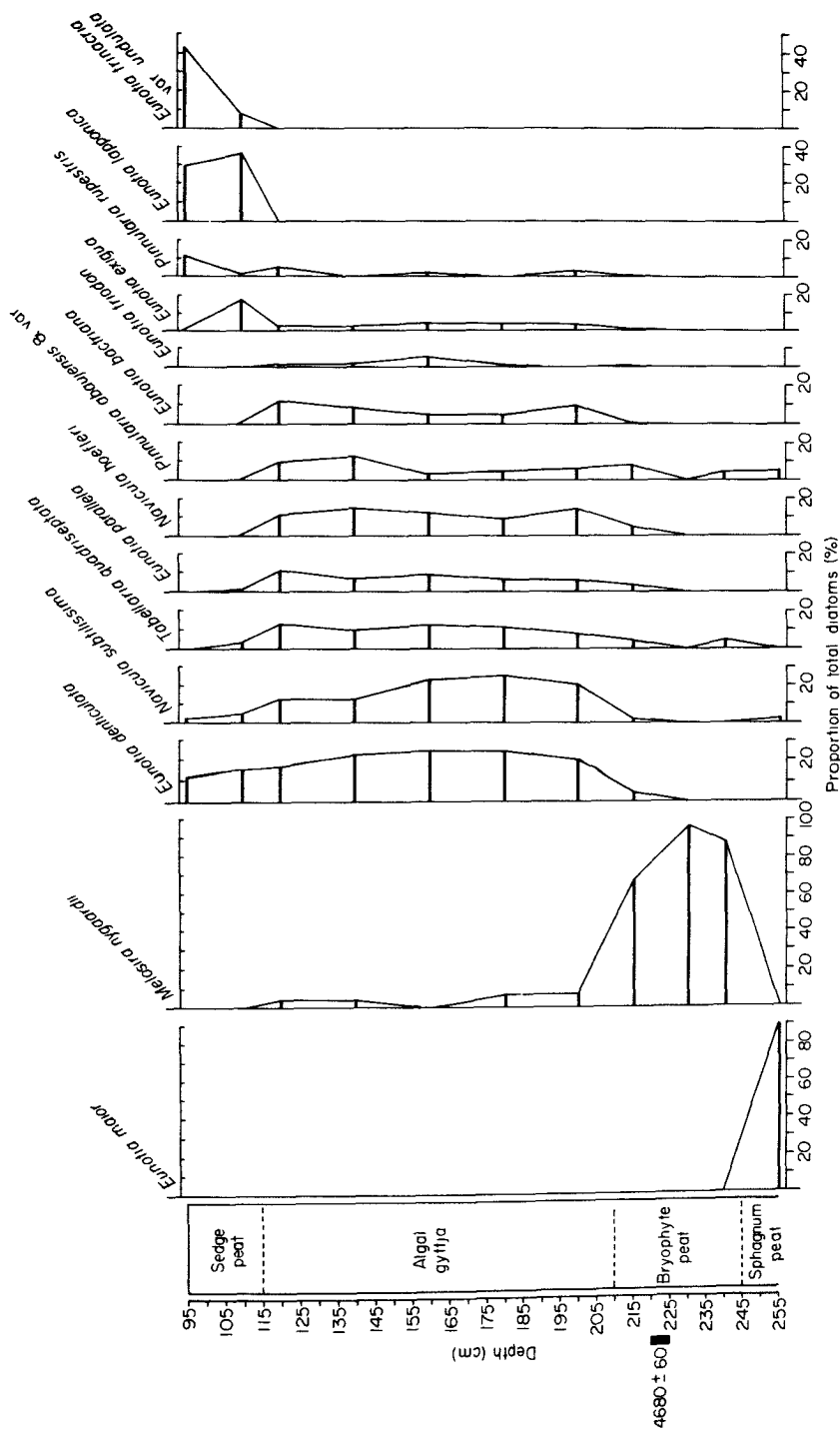


FIG 13 Stratigraphy of the most common diatom taxa in the upper portion of a core from a flark (core 2) on Kackelbacken fen. Poor diatom preservation in the *Sphagnum* peats precludes analyses below 255 cm

TABLE 5 Radiocarbon dates from the Krackelbacken mires, central Sweden

Core number or material	Laboratory number	Depth of sample (cm below water or peat surface)	Radiocarbon date (years B P)
1	Lu-2438	424-430	9040 $\pm$ 80
2	Lu-2437	220-225	4680 $\pm$ 60
4	Lu-2429	133-135	7830 $\pm$ 70
5	Lu-2430	113-115	6280 $\pm$ 70
6	Lu-2431	72-79	5880 $\pm$ 70
7	Lu-2432	98-100	5410 $\pm$ 60
8	Lu-2433	98-100	5510 $\pm$ 60
9	Lu-2434	78-80	4670 $\pm$ 60
10	Lu-2435	83-89	3640 $\pm$ 60
Pine root	Lu-2423	75	1640 $\pm$ 50
12	Lu-2439	114-120	7840 $\pm$ 80
Pool 2	Lu-2428	200-205	1370 $\pm$ 45
Pool 2	Lu-2427	235-240	3410 $\pm$ 60
Pool 1	Lu-2425	115-125	2920 $\pm$ 50
Pool 1	Lu-2426	125-135	3510 $\pm$ 60
Pine stump	Lu-2424	drained pool	3070 $\pm$ 50

sequence of progressively lesser ages (Figs 11 and 12, Table 5) ranging from  $9040 \pm 80$  years B P to  $4670 \pm 60$  years B P. Still more recent dates farther upslope are  $3640 \pm 60$  years and  $1640 \pm 50$  years B P (Fig. 3). The most recent date was obtained approximately 100 m from the head of the mire from a pine stump rooted in the substratum beneath 100 cm of peat. The position of this stump suggests that the mire is continuing to expand headward. The conversion of forested areas to sedge fen through paludification appears to have been a dominant process throughout the 9000-year history of the fen.

### *Soil profiles*

Mineral soil profiles beneath the peat were examined along the road cut towards the western head of Krackelbacken fen, along a transect from the centre to the edge of the mire 200 m downslope from the road cut, and in pits along Transect A (Fig. 3) in the lower portion of the mire. Soil pits were also dug in the forests adjacent to the mire at each of the above locations.

In all locations the buried mineral soil displays a stratigraphy characteristic of forest soils. Observations of buried pine stumps at the base of the peat in the excavations and exposures and on the bottom of drained pools on Stor Krackelbacken support the conclusion that much of what is now peatland was originally covered by forest. Along the transects the buried forest soils display better profile development towards the mire margins, and the youngest profile examined (at the road cut) is essentially identical to those found in the adjacent upland pine forest. The soil parent material is coarse sand and gravel with little silt. The upper 3-10 cm is leached to form a light grey albic horizon. Beneath is a brown argillic horizon of variable thickness that terminates below in a thin yet quite impermeable hardpan. Very loose parent material underlies the hardpan.

Changes in the soil profiles across the mire largely involve reduction in the thickness and integrity of the individual horizons. Towards the centre of the mire the albic horizon thins to a narrow, poorly leached layer darker than the corresponding zone in profiles from marginal locations. The argillic horizon exhibits a similar weakening in differentiation. The hardpan, however, is distinct in most soil pits.

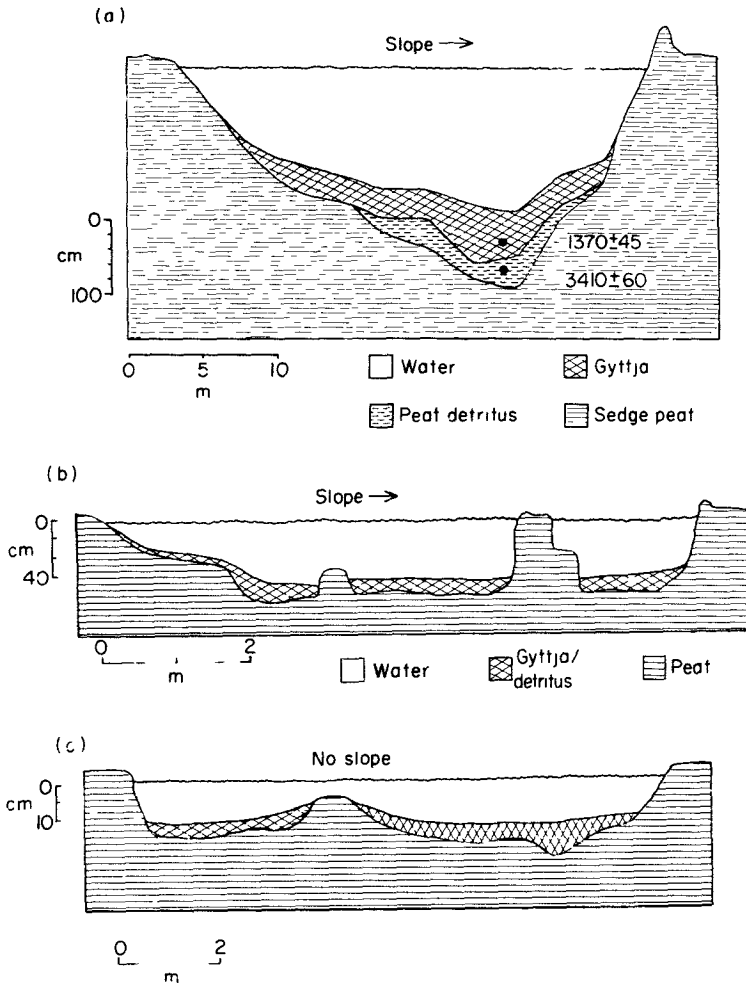


FIG 14 Cross-sections of four pools on Krackelbacken fen showing the morphometry the distribution of sediments and the mire slope. The peat depth beside each pool is approximately 3 m.

### Pools

Transects of cores were taken across four pools (Fig 14). Algal sediment has a discontinuous distribution across the irregular bottom. Small protrusions from the bottom are remnant sedge tussocks or *Sphagnum* hummocks that are relatively resistant to degradation and decomposition. These remove peat and smooth the basin floor (cf Osvald 1923, Pollard 1971, Mets 1982, Boatman 1983). In the shallow pools (Fig 14b, c) all stages of this degradative process are evident, including persistent tussock islands, dead tussocks and submerged tussock remnants. The floors of deeper basins are much smoother. The upslope margins slope gently to the bottom, which are off-centre downslope. The downslope margins are abrupt and dammed by ridges 30 cm high.

All pools contain some algal sediments which, downward, contain peat detritus (*sensu* Sernander 1905) as the sediment grades gradually into sedge, bryophyte or shrub peat, in

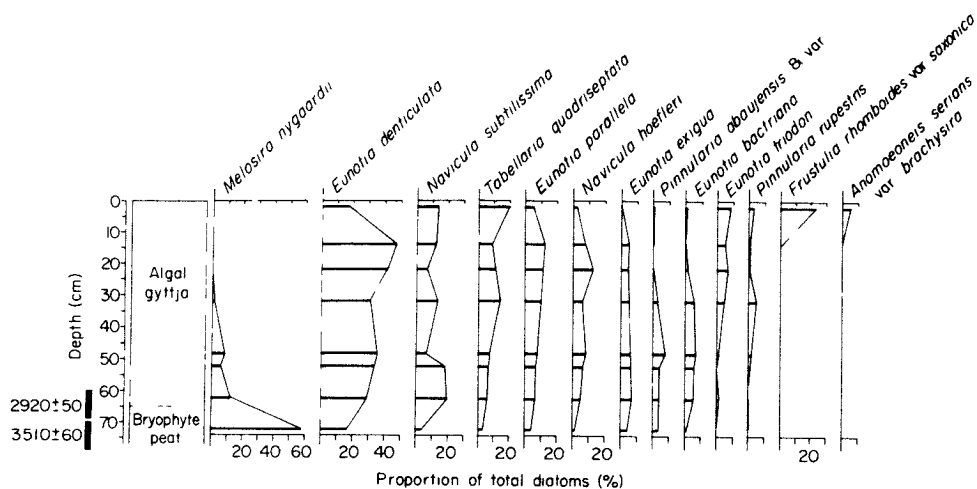


FIG. 15 Stratigraphy of the most common diatom taxa in pool 1 on Krackelbacken fen

the shallow pools. In the deeper pools the sediment is focused into the deeper downslope portion of the basin, resulting in a smoothing and levelling of the bottom (Fig. 14a). Detritus is similarly focused and is restricted to less of the basin than gyttja. Sediments are lacking from the steep walls of the pool, which are composed of flocculent and degrading sedge peat.

The stratigraphy of algal gyttja overlying peat in pool cores indicates the development of pools on areas that formerly accumulated peat. It was hoped that diatom analysis across this transition might provide some insights on the nature of this developmental sequence. A sharp shift from a diatom community in the peat dominated by *Melosira nygaardii* to one in the gyttja dominated by several *Eunotia* species, *Tabellaria quadrisepitata*, *Navicula subtilissima* and *Navicula hoefleri* Cholnoky occurs in cores taken from both a pool (Fig. 15) and a former pool (Fig. 13). The gyttja assemblages are clearly characteristic of an open-water habitat (see Table 4). *Melosira nygaardii* in the peat below, however, has only recently been described taxonomically, and consequently its ecology is poorly known. It was not found in any of the modern samples analysed from Krackelbacken mire. In the literature it has been recorded only in acid lakes (Camburn & Kingston 1986), although an undesigned *Melosira* species from shallow sedge-dominated areas of Okefenokee Swamp (Scherer 1983) is probably synonymous with *Melosira nygaardii* (J. Kingston, personal communication) and may provide the closest analogue to the Krackelbacken samples. This limited autecological information on *Melosira nygaardii* suggests that the peats preceding the algal gyttja in the Krackelbacken cores were growing in standing water, possibly in the bryophyte carpet of a flark. Given this situation, the transition to algal gyttja probably represents the development of a pool from a flark or other water-filled depression. Additional modern samples from various types of fen hollows with standing water could provide a clear analogue for the *Melosira nygaardii* community and support this hypothesis.

Radiocarbon dates from two deep pools (pools 1 and 2) suggest a discontinuity between the peat and the overlying algal sediment. Dates from pool 2 are  $3410 \pm 60$  years B.P. and  $1370 \pm 45$  years B.P. in the peat detritus and gyttja, respectively (Fig. 14a, Table 5). In pool



1 dates of  $3510 \pm 60$  years B P and  $2920 \pm 50$  years B P were obtained from the peat and peat detritus, respectively

On both Krackelbacken and Stor Krackelbacken mires drainage of pools appears to be the result of natural processes, primarily erosion, peat degradation and pool coalescence (Foster *et al* 1983, Foster & Glaser 1986) In the narrow drained pools on the steep slope at the south end of Krackelbacken fen the gyttja and peat detritus extends 20–40 cm to peat and mineral soil and is colonized by *Scirpus cespitosus* and *Eriophorum angustifolium* The sediment is very fine-grained and well decomposed and cracks into polygon shapes in dry warm weather

At Stor Krackelbacken the pools have drained as a result of ridge degradation between pools of different elevation Two of the very largest pools have been lowered nearly 1 m with the resulting exposure of much of the bottom In both situations pool sediment is discontinuous and broad areas have a mineral bottom composed of sand, gravel, and cobbles Stumps of *Pinus sylvestris* are rooted in the mineral soil and jut from the eroding peat faces that comprise the basin walls (Fig 6) The radiocarbon date of one stump is  $3070 \pm 50$  years B P (Table 5) This evidence suggests that Stor Krackelbacken also developed through a process of paludification and conversion of forest area to sedge fen

## DISCUSSION

Results from the stratigraphic studies on the Krackelbacken mires confirm the general elements of the hypothesis for patterned mire development (Foster *et al* 1983, Foster 1985) while suggesting refinements of specific details The following discussion addresses aspects of mire initiation and development, pattern formation and dynamics, and the implication of these processes in terms of landscape development and ecosystem properties

### *Mire initiation and expansion*

The stratigraphic studies suggest that the Krackelbacken fen developed initially in the area of the *Carex rostrata* flark and grew upward by peat accumulation and laterally through paludification of the surrounding uplands Complex stratigraphies involving alterations in moisture conditions as well as plant assemblages characterize the lower slopes of the fen, whereas the peats on adjacent sloping areas show a progressive change from woody to sedge communities The overall development has been complex as progressive accumulation of peat has led undoubtedly to major hydrological changes through forest swamping, increased moisture supply, and the breaching of water-divides to generate new pathways of water flow (Auer 1928)

The *Carex rostrata* flark occupies the lowest part of the mire and is underlain by the deepest peat deposits The original, peat-forming vegetation, composed of *Magnocaricetum*, dates from soon after regional deglaciation (Fries 1965, Berglund 1979), suggesting that the area was always a poorly-drained wetland The lower area receives a considerable amount of run-off, which collects on this level area before draining to the north At the time of mire initiation the original surface was several metres below the height of the southern water divide From the initial herbaceous wetland communities the vegetation underwent various changes to *Sphagnum*- and shrub-dominated assemblages and later to the sedge- and *Sphagnum*-dominated communities that still characterize this area of the mire

As the surface of the *Carex rostrata* flark rose in height through continued peat

accumulation, the water-divide at the southern end of the mire was breached. Basal radiocarbon dates suggest that this occurred approximately 7800 years B.P. The increase in moisture from water draining from the fen resulted in the initiation of peat accumulation across this southern slope. Ultimately, this drainage became a major pathway for water from the mire, leading to pattern formation and the development of robust ridges across the entire mouth of the drainage, much as is found at the northern end.

Peat gradually spread upslope from the *Carex rostrata* flark through a process of paludification, which involved the swamping and gradual conversion of forested areas to treeless sedge lawns (cf. Malmstrom 1955). The evidence for this mechanism of mire expansion is supported by the sequence of nine basal radiocarbon dates, from maps of the peat deposits, from the peat stratigraphies, and from the examination of forest soils buried beneath the peat. Large numbers of stumps rooted in the buried soils provide unequivocal evidence of forest swamping (Figs 4 & 6). A date of 1640 years B.P. from basal peats 200 m from the head of the fen suggests that mire expansion through paludification continues to the present (however, cf. Malmstrom 1923, 1955, Sjors 1983).

Evidence from the buried soil profiles supports the conclusion that marginal and upslope portions of the mire are progressively younger than the lower centre of the mire. Soil development is strongly time-dependent, and for buried podzolic profiles, the critical factor is the duration of forest occupation. More pronounced stratification and development of the soil horizons towards the upslope and marginal edges suggest a longer period of forest development and consequently younger cover of peat.

Studies of British blanket mires and south Swedish bogs suggest that stumps and other evidence of the former forest should be incorporated in the basal peats when forest is converted to mire (Osvald 1923, 1925, Moore 1973, Tallis 1975). Such evidence is apparent at Stor Krackelbacken where broad expanses of basal peat have been exposed by pool formation and drainage. At Krackelbacken fen, however, observations in the marginal forests indicate that much of the above-ground biomass, including stumps, may be thoroughly decomposed before incorporation as a fine-grained matrix in the organic layer. Peat monoliths, cores and probings in the forest organic layer reveal a surprisingly small content of wood. The presence of charcoal at the mineral soil interface and within shallow peats, suggests that repeated fires may also contribute to the breakdown of the woody material.

The lower peats in long cores from the mire slopes are similar to the well-decomposed woody material in the forest organic horizons. The content of wood, twigs and bark fragments is greatest near the base of these cores and charcoal layers are often found at these levels, implying previous forest occupation.

#### *Pool formation and development*

Stratigraphic and observational studies at the Krackelbacken mires have led to some refinements in earlier theories on pool formation and pattern development. However, the overall developmental processes appear to operate as described previously from eastern Canada (Foster *et al.* 1983, Foster & King 1984, Foster & Glaser 1986).

The major mire landforms—flarks, pools and ridges—are secondary features that develop subsequent to the accumulation of considerable peat, revealed through the similarity of the lower peat beneath a flark and adjoining ridge (cores 1 and 2, Fig. 12). Thus, landform differentiation is independent of the underlying stratigraphy and

may result from microtopographic differences that become accentuated through time (Boatman & Tomlinson 1977, Foster *et al* 1983)

Observations of the shallow flark to deep pool sequence suggest that flarks begin as local depressions that enlarge in time as the vegetation changes with gradual lowering relative to the water table. The vegetation in hollows changes to progressively more mesic assemblages, e.g. from *Scirpus-Eriophorum* lawns to firm *Sphagnum* lawns (e.g. *S. compactum*), to *Sphagnum* carpets (e.g. *S. papillosum*, *S. lindbergii*), to liverwort flarks (*Cladopodiella*, *Gymnocolea*) and eventually to mud bottoms covered with algae (Sjors 1963, Masing 1982). This is a positive feedback process in which the assemblages have progressively lower rates of peat accumulation and thereby become more depressed relative to the adjacent *Scirpus* lawns and incipient ridges (Sjors 1950, Ruuhijarvi 1960, Boatman 1972, Mets 1982). The process of hollow development proceeds unevenly across a mire slope and various stages of the 'break-up' of sedge lawns can be observed.

During the mud-bottom stage, little peat accumulates and removal of peat by decomposition and possibly by erosion might be expected (Boatman 1983). High levels of dissolved oxygen in this shallow warm water (A. Loisel, unpublished data) would favour decomposition. In pools deeper than 20 cm, however, algal production exceeds decomposition and a gyttja sediment is deposited. At first the gyttja forms a horizontally discontinuous sediment layer, but in the deepest pools investigated it exceeds 95 cm in thickness (cf. Lundqvist 1951, 1955). The rate of algal sedimentation is considerably less than that of peat accumulation in the adjacent ridge so pools deepen and enlarge (Ivanov 1981). In contrast to other descriptions (Lundqvist 1951, Sjors 1963, Foster & King 1984, Seppala & Koutaniemi 1985), once sedimentation begins in pools it continues without interruption.

Once formed, pool systems may expand, coalesce or drain—processes that have been seen or documented stratigraphically at Krackelbacken. Coupled with changes in mire hydrology and in the directions of water flow that occur with mire development (see *Landform processes and dynamics* below), these changes may result in shifting surface patterns and in multidirectional changes in the vegetation. Pools may expand through two primary mechanisms—gradual expansion as a result of differential peat growth and marginal flooding, or the coalescence of adjoining pools by the breakdown of intervening peat ridges. The latter process results in the characteristic scalloped edges and asymmetrical shape of many pools and in the narrow channels connecting pools, which are strikingly apparent on aerial photographs (Fig. 5).

Drainage or lowering of the water level may occur in a variety of ways. If pools are situated at different heights, coalescence will result in a drop in the water level of the upper pool (Auer 1933). This appears to have happened in the flark in which core 2 (Fig. 12) was taken, leading to the drainage of the pool and colonization by *Sphagnum* and sedge. Less commonly, the ridge damming the pool may break down, as has occurred on the south end of Krackelbacken fen and at several pools on Stor Krackelbacken. As the downslope ridges are generally robust, this process requires a large input of water and erosion (Ratcliffe 1964) or the physical compression of a portion of a ridge, for example, along the paths of aquatic mammals such as beavers. In many places at Krackelbacken a breakdown of a ridge is the natural consequence of pool enlargement and increased water flow (cf. Foster & Glaser 1986). When water levels are high, water seeps through low spots in the hummocky ridge and gradually erodes a narrow channel. If the water level increases as a result of increased flow or larger pool size, the channel may be deepened.

Another mechanism for drainage is subsurface piping of water between pools (Auer

1933, Fransson 1972, Foster *et al* 1983) At Stor Krackelbacken pipes 20–30 cm across and over 2 m in length connect two large pools, and the free flow of water has resulted in a 40-cm drop in the water level in the upper pool. Although not well understood, the development of subsurface pipes may be a result of hydrostatic pressure on the peat floor that follows lines of weakness in the subsurface peat.

In all cases, water-level decline can result in the exposure of broad areas of gyttja or detrital pool bottom. Rapid colonization by *Sphagnum* species and sedges produces the characteristic stratigraphy of peat–gyttja–peat observed in core 2 as well as the broad carpets and lawns on gentle slopes adjacent to pools, but within the confines of the former ridges. The lower water table may also stimulate shrub and tree growth on the hummocks and may result in an increase of oligotrophic bryophytes (e.g. *Sphagnum fuscum*, *S. nemoreum* and *Pleurozium schreberi*) as the influence of soligenous water decreases. If the ridge no longer serves as a dam and the water table is relatively flat across it, the individual hummock elements may gradually change in shape and lose distinction as part of a continuous ridge. This process may explain the enigmatic lines of large hummocks on otherwise smooth sedge fens, and the occurrence of broken ridges on the east and west flanks of the *Carex rostrata* flark that presently have no damming function.

Especially on level areas, the expanding pools can become very large and may change in their limnological characteristics. The large pools located on Stor Krackelbacken mire are approximately 150 m long and 100 m wide. On such large water bodies the wind fetch is great, whereas the water depth seldom exceeds 2 m. Consequently, wave action, mixing by wind, and possibly ice scouring disturb the sediment and promote its degradation. The sediments and peat on the bottoms of large pools are thus removed to expose the underlying mineral sediments (Fig. 6). Wave action continues to undermine the peat banks, which slump into the water and degrade as the pool expands. Consequently there is a critical point, undoubtedly dependent on the water depth, surface dimensions and exposure to the wind, at which pools revert from depositional to degradational basins (see Engstrom 1984).

#### Landform processes and dynamics

The development of patterned mires is complex and dynamic. Landform development on the mires is not simply progressive but is multidirectional and frequently asynchronous within a given fen. This results from the fact that mire development is a landscape process in which major landforms are produced that alter the prior drainage patterns and watershed hydrology (Heinselman 1970, Gorham 1982, Wright & Glaser 1983). The general process involves a gradual increase in the extent of the mire and a continual diversification and modification of the surface topography.

As the mire expands hydrological changes occur in the watershed, especially if the mire occupies forested sites (Tallis 1983). Loss of trees results in a decrease of evapotranspiration (Remezov & Pogrebynyak 1965, Bay 1966, Heikurainen & Poivanen 1970), whereas peat accumulation and the development of a hardpan in the subsoil would decrease percolation into the mineral soil (Pearsall 1950, Ivanov 1975, Ugolini & Mann 1979, Ritari & Ojanpera 1984). The resulting increase in moisture surplus would initiate or accentuate pattern formation and deliver greater moisture to the flat lower portions of the mire where it gathers in broad flarks and pools.

Once surface patterning starts, its area increases as individual hollows or pools expand and new features are continually initiated on younger peats (however, *cf* Tallis 1983). In northern areas this leads to a consistent increase in the proportion of the mire covered by

water-filled pools (Boatman 1972) Pool enlargement through coalescence and inundation inevitably leads to drainage, followed by plant colonization and stabilization of the exposed surface The re-vegetated area may be subject to renewed pattern formation and new features may develop even as the relict hummocks and pool outlines become obscured

Continual accumulation of peat results in the gradual breaching of water-divides a phenomenon observed on the south end of Krackelbacken and the north-east margin of Stor Krackelbacken As water is diverted from the original drainage-way into the newly breached watersheds, surface patterns on the mire change in orientation and accentuation Orientation is strictly controlled by the direction of water movement and as the hydrology is altered, existing flarks and pools may become realigned or new patterns may be superimposed on the old features As the degree of accentuation of surface features is controlled by the amount of moisture, flarks may dry or conversely may gradually become open-water pools with changes in drainage Breaching of the water divide on the south end of Krackelbacken led to water flow to the south and created conditions suitable for mire formation on the slope Continued water flow down the slope led to pattern development and progressively deeper pools Eventually, the quantity of water flowing down this slope overwhelmed the pool system and through erosion of the intervening ridges led to complete drainage of all pools

The overall development of the mires consequently involves continued diversification on two scales The regional landscape increases in complexity and landform diversity as mires form and replace wet forests and lowlands Within the mires there occurs local diversification as surface features develop and change with time

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