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Origin of string patterns in boreal peatlands

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The detailed stratigraphical analyses supported by field observations on mires in Labrador and northern Minnesota reported here provide the basis for an explanation of the development of the surface pattern of alternating peat ridges (strings) and linear depressions or pools (flarks) in boreal fens. The developmental sequence involves: drainage impediment and the concomitant initiation of peat accumulation; development of linear patterns as a result of changing hydrological conditions and differential rates of peat accumulation of hummock and hollow plant communities; and subsequent enlargement and coalescence of pools through the degradation of the underlying peat and the intervening ridges. We show here that many of the processes may be active in the development of the pool patterns on raised bogs as well as on fens.

A pattern of strings and flarks in peatlands forms one of the most distinctive landforms in boreal forests, where they were first studied in Fennoscandia, Alaska, and the Hudson Bay Lowlands[1–4]. American authors previously referred to these features as string bogs, although now it is more common to follow Scandinavian concepts that distinguish nutrient-rich fens from the nutrient-poor bogs that are fed only by atmospheric precipitation. In North America patterned fens reach their major southernmost occurrence in Minnesota[5,6], where the shallow flarks and weakly defined ridge patterns are indistinct on the ground but are easily discerned from the air. In more northerly and maritime locations such as Labrador, however, robust strings stand 15–20 cm above open-water pools, which may be more than 20 cm deep, creating ladderlike arrangements of successive pools and ridges resembling a gentle flight of terraces. The orientation of the linear patterns is invariably transverse to the direction of water flow, as controlled by the often imperceptible slope of the peat surface (Fig. 1).

The status of the problem is perhaps best summarized by Washburn[7], who lists several hypotheses. Those that depend on rifting of peat during downslope slumping[8–10] fail because of the extremely low slopes involved in most areas, the fibrous nature of the peat, and the absence of supporting stratigraphical evidence. Those that postulate a relation to permafrost processes[11,12] fail because permafrost is now absent from large areas with string patterns in eastern North America and apparently never occurred in these regions during the time of peatland development, as inferred from climatic reconstructions of pollen diagrams[13–15]. Differential heaving during annual frost may serve in some instances to accentuate the existing surface topography[16] but has not been documented in the developmental process. The hypothesis that appeals to the accumulation of plant debris in transverse riffles during spring runoff[16–18] likewise suffers from inadequate observations of the process, as does the proposal that some sedge or shrub species grow differentially across the slope to form ridges[19]. Arguments suggesting a relationship between surface patterning and substratum topography (ref. 18 and refs therein) are not supported by stratigraphical evidence, although large pools have been shown to be associated with depressions in the mineral substratum on raised bogs in Scotland[20]. Thus despite many decades of observation by peatland ecologists and geomorphologists, no consensus has emerged concerning the origin and development of the patterns, particularly the diagnostic linearity[21].

We have carried out field studies of patterned fens in southern Labrador and adjacent Nouveau Quebec[15] and in northern Minnesota[22]. The results are believed to be generally applicable to patterned fens throughout the boreal forest and may also apply to the development and particularly the enlargement of arcuate pool patterns on bogs.

The hypothesis has three elements, involving: (1) initial accumulation of peat; (2) development of linear patterns; and (3) subsequent enlargement of pools.

(1) Peat accumulation can be initiated when drainage is impeded at the base of a gentle slope. A special case involves the formation of an ice-push ridge at a lake shore. The trees that colonize such a ridge frequently serve as a snow fence against the winter winds that blow across the lake ice. Melting of the deep snow that accumulates to the lee of the fence may increase the waterlogged conditions at the base of the slope, and under a suitable climatic regime a small peatland may form. In time the peatland gradually extends upslope by continued drainage impediment. In northern Minnesota peat began to accumulate on poorly drained lake plains at the end of the mid-postglacial dry period.

(2) Accumulating peat tends to smooth out irregularities on the slope, thus converting channelled flow to sheet flow. The peat itself has low hydraulic conductivity, particularly when humified, and the surface water tends to pond on the surface in low spots. A microtopography develops as hummocks of *Carex exilis*, *Scirpus cespitosus* and *Sphagnum* grow vigorously beside hollows occupied by such weak peat producers as *Carex limosa* and *Menyanthes trifoliata*[23]. During times of high water when the hollows are inundated, plant growth along the pool margins is inhibited. As the surface rises with continued peat accumulation, adjacent pools at the same level across the slope gradually join together and remain flooded as the intervening hummock area is inundated, whereas a pool positioned upslope from another pool may simply drain downslope. Linear pools thus formed can be irregularly extended along the contours of the peatland through the gradual merging of adjoining depressions[24–26]. The explanation is equally suitable for the genesis of arcuate pools on raised bogs.

(3) Once a pool has standing water, vascular plant growth is reduced, the vegetation cover becomes sparse, and peat accumulation ceases. Degradational processes become increasingly active, and the peat on the pool floor and margins begins to break up. The process probably involves active microbial decomposition in an oxygenated environment[27,28], although various erosional processes may contribute to the degradation. Methanogenesis in the underlying peat is suggested by the escape of bubbles when the flocculent bottom is disturbed, and it may be important in the flotation of peat detritus that accumulates on the bared floor. This latter process further exposes the organic material to the oxygenated water column, thereby enhancing decomposition. Pools are thus deepened and widened by peat decomposition, and by the time the pool is 15–30 cm deep the entire floor may be bare of vegetation. As the pool sides are degraded, the intervening ridges between pools may be broken, and the pools thus coalesce preferentially along the contour. In some cases the ridges between pools are so high and are so firmly bound by shrub growth that they resist decomposition at the surface but become undermined at depth on both sides, and during times of flooding the water may siphon from one pool to the next downslope by developing a channel beneath the ridge, producing a crater in the pool bottom on each side of the ridge.

Support for this hypothesis comes from stratigraphical studies at Leech fen (53°10′ N, 58°45′ W) in southeastern Labrador[15]. The fen is located on the gentle slopes beside a shallow bay in

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0028–0836/83/460256—03$01.00

Fig. 1 Stepwise slope of a patterned fen in western Labrador exhibits closely-spaced ridges and narrow pools on steep slopes in the lower edge of the photo and anastomosing strings and broad pools on gentle slope in the centre. The fen slopes to the lake at the top of the photo where an ice-push ridge impedes drainage. Total length is ~500 m.

a lake that is fringed by a low, forested ice-push ridge. A transect of peat cores up the length of the fen indicates that an unpatterned sedge fen developed upslope from the bay, while a sedge mat was simultaneously extending across the sediments in the shallow water (Fig. 2). Gradual paludification of the upland is demonstrated by progressively younger radiocarbon dates upslope: basal peat near the lake shore yielded a radiocarbon date of 4,400 ± 60 (WIS-1355) yr BP, two-thirds of the way upslope a date of 2,900 ± 70 (WIS-1356) yr BP, and at the upslope end of the fen 760 ± 70 (WIS-1403) yr BP.

The development of a hummock/hollow topography in a vegetation of *Sphagnum*, ericaceous shrubs, and sedges is indicated in the history of Leech fen by the pollen and macrofossil evidence from peat cores and is corroborated by numerous analogues in other portions of this large mire complex. Pool deepening by decomposition is suggested by the peat stratigraphy and by comparison of pollen diagrams for cores from a pool bottom and an adjacent ridge. Radiocarbon dates of firm peat on the pool floor below the loose mat of detritus are 1,210 ± 70 (WIS-1353) and 410 ± 70 yr BP (WIS-1404) for pools on the lower and mid-slope of the fen respectively, indicating either that no deposition has occurred in several hundred years or that the pool has deepened by decomposition. Active degradational processes are demonstrated by the absence of any accumulation of pool sediment, and by the fact that the loose detritus on top of the firm peat on the pool floor consists largely of a scatter of wood fragments, representing the refractory ligneous remains of shrub peat, from which the moss and sedge components have been lost by decomposition. Lundqvist in Sweden[27] long ago attributed to decomposition the upward truncation of a pollen sequence from a pool, but the idea was never integrated into an explanation for the patterns.

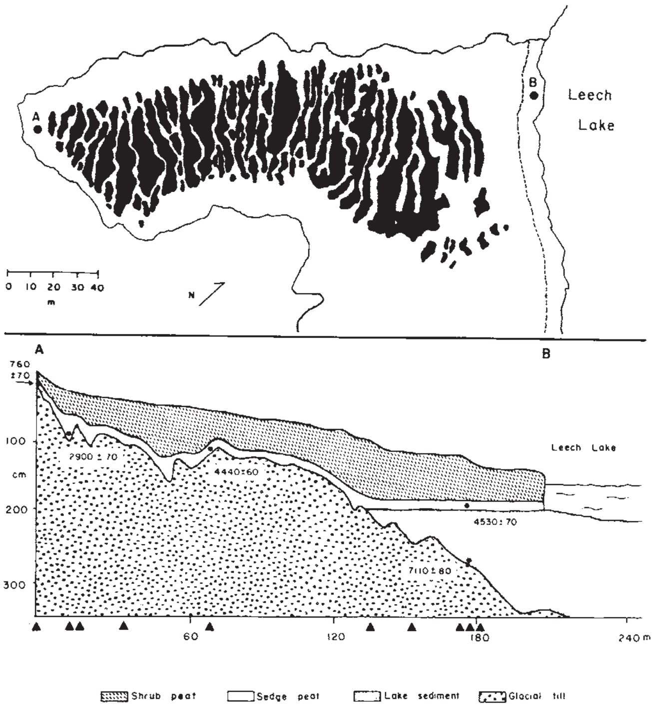

Fig. 2 Map and cross-section (along transect from points A to B) of Leech fen in southeastern Labrador. Progressively younger radiocarbon dates of basal sediments upslope indicate the gradual paludification of upland areas. Adapted from ref. 15.

Fig. 3 Disintegration and swamping of the intervening strings lead to the coalescence of flarks and formation of extensive pools on the gentle slopes of a fen in western Labrador.

Field observations of patterned fens and raised bogs elsewhere in southern Labrador and adjacent eastern Quebec indicate abundant evidence for pool enlargement and deepening by peat degradation. The largest pools (on both fens and bogs) have lost most of their peat by this process, so that the floor is the mineral substratum, perhaps with patches of peat detritus. It is probable that many of the large shallow ponds on the extensive wetlands on the flat plateau of southeastern Labrador were formed by degradation of a once more continuous peatland (Fig. 3). Conditions favourable for the aerobic decomposition of peat in pools were demonstrated in a patterned fen in western Labrador (Shovel fen, 52°41′ N, 65°55′ W), where the dissolved oxygen content was 3.7–5.3 mg L^{-1} in three small pools (100 m^2 in area and 7-cm deep) and 7.2–8.2 mg L^{-1} in six pools that were larger and deeper.

Detailed inspection and interpretation of aerial photographs of extensive regions of patterned mires in eastern Canada support the proposed method of pool enlargement. In most patterned mires, remnant hummocks occur in the middle of pools, and many ridges stretching only part way across a pool (Figs 1–3). These features result from the degradation and inundation of low points on ridges between pools, as the water table rises in the mire.

The developmental history of large peatlands may be highly complex and dynamic, for in some cases even a large pool may drain completely by decomposition of a downslope peat ridge, and the process of peat accumulation and pattern formation may start on the drained pool floor, with the formation of a *Carex limosa* lawn followed by the local hummock growth of *Scirpus cespitosus* and *Sphagnum*. The contrasting processes of peat accumulation and peat decomposition develop in a systematic way that reflects a variety of environmental controls. The result is a display of landscape patterns that are perhaps the most consistently spectacular of any to be found in the boreal forest.

Field research on wetlands in Labrador and Minnesota was supported by the Smithsonian Institution, National Geographic Society, NSF (DPP-82-05700, DEB 7922142, DEB 8109901), US Department of Energy (DE-AC02-79EV and DE-AC02-80EV10414) and the Minnesota Department of Natural Resources. Contribution no. 273, Limnological Research Center, University of Minnesota.

Received 22 July; accepted 1 September 1983.

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Ramapithecines from China: evidence from tooth dimensions

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Data obtained from ramapithecine specimens found in Asia, Africa and Europe[1–6] have suggested the existence of two major subgroups, *Ramapithecus* and *Sivapithecus*, with *Ramapithecus* having pre-human status[7,8]. Recently, however, it has been proposed that the fossils all belong to a single group, *Sivapithecus*, which is more closely related to the apes, in particular the orang-utan[9–13]. Here we analyse data from a series of similar fossils which have been found in late Miocene coalfields in Lufeng, Yunnan Province, China[14–16]. These include a number of almost complete jaws and five partial skulls which are more complete than any others so far known[17–21]. A statistical analysis of the overall dimensions of the large number of teeth included in these finds shows that the differences between the groups previously assigned to *Ramapithecus* and *Sivapithecus* are greater than those found between the sexes in the most sexually dimorphic of the living great apes. Within the groups the distribution is bimodal and we suggest each group contains sex subgroups.

The cranial fragments examined indicate that the skull of the group called *Ramapithecus* is smoother and more round and bulging than the crania of modern apes. The nuchal crest is not marked and the nuchal plane is smooth. The face is rather short and the foramen magnum situated in a much more forward position than in modern apes. The dental arch is divergent, with small vertically oriented front teeth. The canines are also small and project only slightly from the other teeth. Among the three molars the second is the biggest and all have thick enamel. The skull of the group named *Sivapithecus* contrasts considerably, having generally more ape-like configurations in each of the above features, and especially in possessing an orang-utan-like configuration of the brow ridges and concave facial profile (although both specimens seem to have these characteristics to some degree).

These new finds in China also include several hundred teeth either *in situ* in portions of jaws, or as isolated teeth. The existence of these samples of teeth, larger indeed than the entire collection of such teeth outside China, now allow new investigations of these forms.

Although much is to be learned by further detailed study of such a large assemblage of teeth, it is also possible to learn much about the general characteristics of these forms through simple quantitative studies of the overall dimensions of the teeth.

Accordingly the dimensions (length and breadth) of these teeth have been measured (by W. R.) and analysed using simple statistical methods (by C. E. O). From these studies it may be possible to understand something of the number of groups represented in the collection, their general variability and, possibly, their sexual dimorphism and socio-sexual structure.

The fossils were discovered in late Miocene aged coalfields of Lufeng (Shihuiba) in Yunnan Province. The different, but contiguous, areas of the site that were examined during each excavation, and the details of the local stratigraphy are given in the original publications[22–24].

The fossils were assigned to the genera *Sivapithecus* and *Ramapithecus* by Professor Wu on the basis of morphological examination and before the measurements were analysed. In particular these examinations were undertaken by comparing teeth (about half of the total number) that were found isolated with teeth found *in situ* in portions of upper and lower jaws, situations in which designations could be made on the basis of features of the jaws and skulls as well. Clearly, these attributions should be considered tentative because of changing views about ramapithecines; however, Professor Wu and his colleagues are extremely experienced in this general area, having examined and compared almost 1,000 ramapithecine teeth from this site alone.

The teeth are represented by every position in both upper and lower jaws. The sizes of the samples at each tooth position range from as few as 17 for the lower first incisor to as many as 44 for the lower third molar and lower canine of *Ramapithecus*. Equivalent samples for *Sivapithecus* range from as few as 16 teeth for the lower second incisor to 49 for the lower second molar. Maximum length and breadth were taken on each of a total of 934 adult, unbroken and not too badly worn teeth shared approximately equally between the two genera. In addition, in order to increase the sizes of the samples as

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0028–0836/83/460258—03$01.00