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Flora, fauna and climate of Scotland during the Weichselian Middle Pleniglacial – palynological, macrofossil and coleopteran investigations

Johanna A.A. Bos[a,*], J.H. Dickson[b], G.R. Coope[c], W.G. Jardine[d]

[a] *Geobiology-Botanical Palaeoecology, Laboratory of Palaeobotany and Palynology, Utrecht University, Budapestlaan 4, NL-3584 CD Utrecht, The Netherlands*

[b] *Institute of Biomedical and Life Sciences, Division of Environmental and Evolutionary Biology, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, Scotland, UK*

[c] *Department of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK*

[d] *Department of Earth Sciences, University of Glasgow, Glasgow G12 8QQ, Scotland, UK*

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Abstract

Thin lenses of organic-rich material, on the upper surface of a layer of glacio-fluvial deposits have been studied in an open cast coal-mine near Sourlie, western Scotland. Radiocarbon dates on antler fragments, plant debris and bulk organic matter from silt, showed that the sediments accumulated between ca. 33 500 and 29 000 ^{14}C yr BP, during a period when this part of western Scotland was free of glaciers. The organic-rich sediments yielded a very rich flora and fauna and in total about 160 plant taxa and 61 coleopteran taxa were recorded together with other invertebrates. The Sourlie flora is one of the richest late Middle Weichselian floras yet studied within the British Isles. Leg bones of *Coelodonta antiquitatis* (woolly rhinoceros) and *Rangifer tarandus* (reindeer) were also found at the site. During this period, the landscape was treeless and the vegetation could be characterised as an intermediate between a low shrub tundra and sedge–grass–moss tundra. Both the flora and arthropod fauna suggest that during formation of the organic-rich layers at Sourlie, mean July temperatures were 9–10°C. The flora suggests also that at the beginning of formation of these layers, minimum mean July temperatures increased from 7 to 9–10°C, but later dropped again to 7–8°C. A possible time correlation with one of the warmer periods of the Dansgaard–Oeschger cycles in the stable oxygen isotope record of the Greenland ice cores during this period is proposed. The arthropod fauna suggests that mean January temperatures were somewhere between −34 and −11°C. Mean annual temperatures lay probably between −1 and −10°C, which implies the possible presence of discontinuous or continuous permafrost in the area. During winter, a protective snow cover of varying thickness probably enabled perennial plants, especially shrubs, to survive.

Keywords: Middle Weichselian; pollen and plant macrofossils; Vertebrates; Coleoptera; climate reconstruction; Scotland

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[*] Corresponding author. Present address: Institute for Biodiversity and Ecosystem Dynamics, Research Group Palynology and Paleo/Actuo-ecology, Faculty of Science, Universiteit van Amsterdam, Kruislaan 318, 1098 SM Amsterdam, The Netherlands. Tel.: +31-20-5257666; Fax: +31-20-5257832. *E-mail address:* jabos@science.uva.nl (J.A.A. Bos).

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1. Introduction

The occurrence of ice-free conditions in Scotland, between 35 and 26 ka BP, has frequently been questioned, mainly because reliable evidence from the Weichselian(= Devensian) Pleniglacial is strictly limited (see Edwards and Connell, 1981; Gordon and Sutherland, 1993a; Huijzer and Vandenberghe, 1998). Fossiliferous deposits that predate this period are extremely rare, probably because almost all of Scotland was overridden by Late Weichselian ice sheets. Moreover, at many Scottish Middle Weichselian sites the field evidence is uncertain and radiocarbon dates are suspect due to possible contamination (see Edwards and Connell, 1981; Gordon and Sutherland, 1993a). Probably the only previous reliable radiocarbon date comes from Tolsta Head, near the northern extremity of the Outer Hebrides, where initially a date of 27 333 ± 240 yr BP was obtained from deposits with a rather sparse flora (Von Weyman and Edwards, 1973; Birnie, 1983; Gordon and Sutherland, 1993b). However, recent reinvestigations at Tolsta Head (Whittington and Hall, 2002) demonstrated that the Tolsta Head deposits accumulated between 32 and 26 ka BP.

In 1986, in the course of open cast coal-mining operations, Middle Weichselian organic deposits were discovered interstratified with glacial and glacio-fluvial sediments at Sourlie, near Irvine, western Scotland (NS 3380 4150, Fig. 1). Preliminary laboratory investigations suggested that the organic deposits contained a rich botanical (micro- and macrofossils) and arthropod assemblage, and reindeer antler fragments, plant debris and bulk samples of organic-rich silt were dated 33 500–29 000 ^{14}C yr BP (Jardine et al., 1988). At Sourlie the stratigraphy is firmly established, relationships between individual sedimentary units are clearly recorded and both faunal and floral remains that are present have been sampled and dated by radiocarbon and amino acid techniques (Jardine et al., 1988). Since the time of excavation, backfilling and landscaping of the site has totally destroyed the original Quaternary evidence at this site.

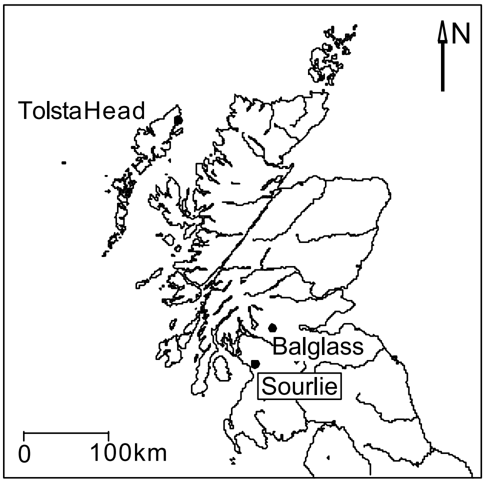


Fig. 1. Map of Scotland showing the location of the Sourlie site (western Scotland) and other Scottish locations mentioned in the text.

The evidence from Sourlie proves that ice-free interstadial conditions certainly existed in Scotland around 30 ka BP and provides information about the environment and climate at this time. Recently, another botanical and arthropod assemblage has been recovered from organic deposits at Balglass, high on the Campsie Fells (west-central Scotland), from which several radiocarbon dates around 28 000 yr BP were obtained (Brown et al., in press). The Balglass assemblages also yielded good environmental and palaeoclimatic data. Moreover, the recently re-investigated Tolsta Head site (Whittington and Hall, 2002) also provided detailed environmental and palaeoclimatic data of the period around 30 ka BP. These three sites thus have become highly significant in recording the Quaternary history of Scotland, since there can be little doubt that, at this time, much of western and central Scotland must have been ice-free.

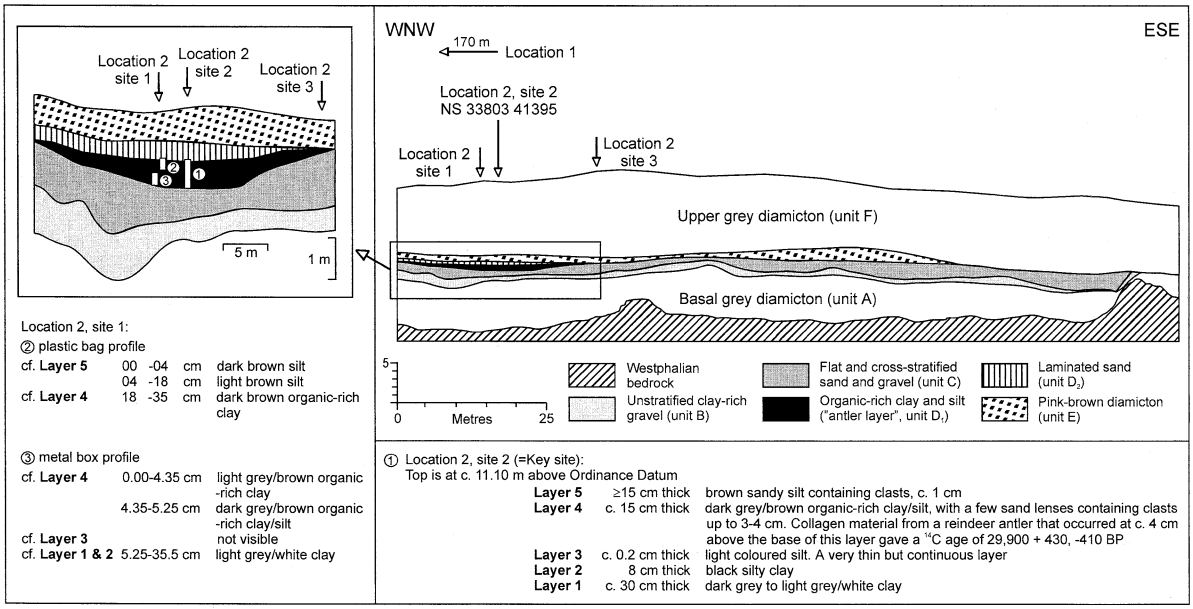
The results of detailed studies of the palaeobotanical and palaeozoological records of the Sourlie site are given below and the significance of these results as indicators of contemporaneous climatic conditions is discussed.

2. Geological setting

Prior to its excavation (Prince and McIntyre, 1990) the site at Sourlie occupied a surface area of ca. 18.8 hectares. It was located largely on the NW side of a hill (Sourlie Hill), the steeper slopes of which were to the NW and W and the gentlest slope to the SW. The hill is one of a number of drumlins, their surface deposits consisting of till, that occur to the E and SE of the town of Irvine. During the excavations, the surface till unit was found to be underlain by several Quaternary non-till sedimentary units which, in turn, were underlain by a basal till unit that rested on solid rock. The bedrock consisted mainly of Upper Carboniferous (Westphalian) sandstones and shales interstratified with several seams of coal. A dyke of basic igneous rock intersected the site. Basic igneous sills and other sheets of igneous rock occurred at short distances to the N and S of the site.

3. Lithostratigraphy

The extensive commercial coal excavations of May–September 1986 exposed thin (up to 0.6 m) lenses of organic-rich sediment (unit D_1) overlain by up to 1.0 m of laminated sand (unit D_2), preserved within pockets on the upper surface of a glacio-fluvial sedimentary unit (Fig. 2). The part of the Quaternary sedimentary complex (see Jardine et al., 1988) exposed below the organic-rich sediments comprised a grey diamicton (unit A, up to 7.5 m thick) overlain by unstratified or poorly stratified clay-rich gravel (unit B, up to 3.5 m thick) which, in turn, was overlain by a unit of stratified sand and gravel (the glacio-fluvial sediments, unit C, up to 5.5 m thick). In the parts of the complex that overlay the sporadic occurrences of organic-rich sediment (unit D_1) and thin laminated sand (unit D_2), there were two major units: a thin pink-brown shell-bearing diamicton (unit E, up to 3.5 m thick) and an overlying grey diamicton (unit F, up to 12 m thick). The shells in the pink-brown diamicton were in origin marine and amino acid racemisation suggested a Late Devensian age (Jardine et al., 1988).



Location 2, site 1:

② plastic bag profile

cf. **Layer 5**	00	-04	cm	dark brown silt
	04	-18	cm	light brown silt
cf. **Layer 4**	18	-35	cm	dark brown organic-rich clay

③ metal box profile

cf. **Layer 4**	0.00-4.35 cm	light grey/brown organic -rich clay
	4.35-5.25 cm	dark grey/brown organic -rich clay/silt
cf. **Layer 3**		not visible
cf. **Layer 1 & 2**	5.25-35.5 cm	light grey/white clay

① Location 2, site 2 (=Key site):
Top is at c. 11.10 m above Ordinance Datum

Layer 5	≥15 cm thick	brown sandy silt containing clasts, c. 1 cm
Layer 4	c. 15 cm thick	dark grey/brown organic-rich clay/silt, with a few sand lenses containing clasts up to 3-4 cm. Collagen material from a reindeer antler that occurred at c. 4 cm above the base of this layer gave a ^{14}C age of 29,900 + 430, -410 BP
Layer 3	c. 0.2 cm thick	light coloured silt. A very thin but continuous layer
Layer 2	8 cm thick	black silty clay
Layer 1	c. 30 cm thick	dark grey to light grey/white clay

Fig. 2. WNW–ESE section through the deposits at Location 2. Lithological descriptions are given for the different layers distinguished within the lower part of unit D at Location 2, site 2, the key site. The positions of the metal box and plastic bag profiles at Location 2, site 1, and the probable equivalence of the layers identified at that site to Layers 1–5 at the key site are indicated. Sediments at the key site were described in the field, those from Location 2, site 1, in the laboratory. This may explain the differences in colour of sediments from equivalent layers.

4. Methods

4.1. Locations and sites

In 1986 preliminary samples (e.g., IR1 = Rolfe sample, Table 1, Fig. 3) of organic-rich sediment were obtained from tip heaps. Later, lenses of organic-rich sediments (unit D_1, Jardine et al., 1988) were found in situ and samples were taken at three different locations: Locations 1, 2, and 3 (Figs. 2 and 3). At Location 1, samples were collected at two sites, which were at 2 m distance from each other. Location 1 was situated ca. 170 m WNW of Location 2. Location 2, site 2, where an antler of *Rangifer tarandus* was found in situ and where the sedimentary succession within unit D_1 of Jardine et al. (1988) was recorded most fully, is the key site in this study (Fig. 2). At the key site, five post-depositionally undisturbed, sometimes horizontally laminated, sedimentary layers (Layers 1–5; Fig. 2) were distinguished within the lower part of unit D of Jardine et al. (1988). Location 2, site 1 occurred 3 m WNW of Location 2, site 2 and Location 2, site 3 occurred 18 m ESE of Location 2, site 2 (Fig. 2). Layers similar to those at the key site were also found at Location 2, site 1, and at Location 1. However, it should be noted that *direct* reference to Layers 1, 2, etc. is valid only in the case of this key site. Therefore, at other sites, 'cf.' indicates probable equivalence with the relevant layer at the key site (Fig. 2). At Location 3 only a small exposure was present. The National Grid reference positions of the three main sites – Location 1, site 1 (NS 33652 41479), Location 2, site 2 (NS 33803 41395), and Location 3 (NS 33658 41432) – were obtained

Location	Site	Layer	Sediment		Code	Samples			High resolution diagram	^{14}C Dates yrs BP
						Micro-	Macrofossil	Coleoptera		
Location 1	Site 1	base of cf. Layer 4	organic silt (base)		HB1	Test	50 ml	50 ml		
					HB2	+	350 ml	—		29,290 ± 350 30,230 ± 280
					HB3	+	50 ml	50 ml	Micros + macros	
					HB4	+	350 ml	350 ml		
	Site 2	top of cf. Layer 4	organic silt (top)		HB5/ GRC1	+	350 ml	350 ml/ 0.5 kg		
		cf. Layer 4	organic silt		HB6	+	350 ml	—		
					HB14	+	300 ml	—		
					HB15	+	300 ml	—		
Location 2	Site 1	cf. Layer 4/5	(organic) clay/silt		HB7/ Plastic bag	Test	50 ml	50 ml	Micros + macros	
		cf. Layer 1-4	(organic) clay/silt		Metal box	—	—	—	Micros + macros	
	Site 2 unit D_1	Layer 4	dark/grey organic-rich clay and silt	around antler	HB29	+	—	—	Samples combined in micro- and macrofossil diagram, except for GRC2	
					HB28	+	—	—		
					HB11	+	135 ml	135 ml		
				inside antler	HB10	+	—	—		29,900 + 430 – 410
					HB24	+	200 ml	—		
					HB25	+	—	—		
		Layer 3	light coloured silt		HB26	+	—	—		
		Layer 2	black silty clay		GRC2	—	—	0.1 kg		
					HB31	+	—	—		
					HB34	+	200 ml	—		
					HB32	+	—	—		
					HB30	+	—	—		
		Layer 1	dark grey to grey/ white clay		HB33	+	—	—		
					HB27	+	—	—		
					HB9	+	450 ml	—		
	Site 3	cf. Layer 4	organic silt		GRC3	—	—	0.5 kg		
Location 3			organic silt		HB12/ GRC4	+	500 ml	500 ml/ c. 2 kg		33,270 ± 370
Unknown			organic silt		IR1	—	200 ml	200 ml		

Fig. 3. Overview of the locations and sites in the Weichselian sequence at Sourlie, western Scotland. Indicated are where samples were collected for micro-, macrofossil and coleopteran studies, and ^{14}C dating from layers of unit D of Jardine et al. (1988). The vertical order in which the code numbers of the samples are arranged is not necessarily the stratigraphical order of the samples. Sample numbers: IR = tip heap sample collected by Ian Rolfe; HB = samples processed by Hanneke Bos; GRC = samples examined by Russell Coope at a later stage.

from civil engineers employed on the excavation site. Relevant details of the sedimentary successions at Locations 1, 2 and 3 are given in Figs. 2 and 3. Samples of most of the deposits are retained in the Hunterian Museum, University of Glasgow.

4.2. Botanical analysis

At Location 2, site 2, the key site (no. 1, Fig. 2), bulk samples (often more than one) were collected from Layers 1–5. In every layer, subsamples were taken for microfossil analysis. In addition, a few larger samples were collected for macrofossil analysis (Fig. 3).

At Location 2, site 1, two ca. 35 cm long samples (i.e., plastic bag and metal box, Figs. 2 and 3) were collected for high-resolution microfossil analysis. In the sediments in the metal box (no. 3 in Fig. 2), cf. Layers 1, 2 and 4 were present; cf. Layer 3 was not visible. In the plastic bag (no. 2 in Fig. 2), cf. Layers 4 and 5 were present. From the uppermost 0–8 cm in the metal box, 14 microfossil samples and nine macrofossil samples were taken. The material between 8 and 25 cm had been disturbed during transport from the site to the laboratory, which made useful sampling impossible and the transition between Layers 1 and 2 invisible. Four microfossil samples were extracted from the sediment between 24.5 and 35.5 cm. Test samples showed a very poor macrofossil content. Therefore no macrofossil samples were collected from this part of the sedimentary profile. From the sediment in the plastic bag, four microfossil samples were extracted, at 0, 14, 22 and 30 cm. The upper part was especially poor in micro- and macrofossils. Insect remains, however, were fairly abundant.

At Location 1, site 1 (HB3, Fig. 3), the sediment consisted of dark brown organic-rich clay to silt (cf. Layer 4). The 6.5 cm thick sample of sediment showed horizontal lamination with alternating lighter and darker layers. Small clasts and small roots projecting from the sediment marked the base. The uppermost 0.8 cm was darker and more clayey than the lower part. The 6.5 cm thick sample was sliced, parallel to the lamination, into 16 0.4 cm thick successive microfossil samples. Four macrofossil samples of equal thickness were collected from the 6.5 cm thick sample (Fig. 3).

Bulk samples for micro- and macrofossil analysis were also taken from Location 1, site 2, and Location 3 and from the Rolfe sample (Fig. 3, Table 1).

Plant macrofossils were recovered by washing the sampled material over a 150 μm sieve. All material, including the left-over sediment, has been stored for future checking. Macrofossils of vascular plants were identified with a dissection microscope with a magnification of 15–45× or peripheral light and magnification of 80 and 200×.

Microfossil samples were extracted from the sediment by using a small sampler of a known volume (1–2 ml) or, where there was layering visible in the sediments, portions of sediment were cut into very thin slices. The samples were prepared according to Faegri and Iversen (1989) in addition with an overnight treatment with hydrogen fluoride (HF) to remove the clastic material, and twice (before and after HF) sodium pyrophosphate. A specific amount of *Lycopodium* spores (i.e., exotic spores) was added to each sample, to estimate microfossil concentrations. Sieving was done over a 120 μm sieve. The samples were imbedded in silicone oil. A light microscope with a 500× or 1000× magnification was used during analysis. Combined microfossil percentage and macrofossil diagrams were constructed using Tilia and Tilia.graph computer programmes (Grimm, 1992) and taxa were arranged stratigraphically in basic groups, i.e. pollen from long distance transport (trees), shrubs, herbs, pteridophytes. Although a pollen sum of 450–500 terrestrial pollen and spores was preferred, sometimes pollen sums of 100–200 had to be accepted. The pollen sum was based on pollen deposition criteria discussed by Janssen (1973, 1984). The pollen sum includes pollen from trees (*Pinus*, *Betula pubescens* type) that was transported over long distances and pollen from shrubs (*Salix*, *Betula nana* type, *Juniperus*, *Cornus suecica*), Ericales and all terrestrial herbs (including Poaceae and Cyperaceae). Other tree pollen was assumed to be reworked. A division between pollen of *B. nana*

Table 1
Botanical list of the taxa recorded at the different locations and sites at Sourlie

Location, site		Location 1, site 1				Location 1, site 2				Loc 3	
Sample code no.		HB1	HB2	HB3	HB4	HB5	HB6	HB14	HB15	HB12	IR1
Volume macro-sample (ml)		50	350	50	350	350	350	300	300	500	200
Sum pollen sample		test	505	289	515	506	539	501	523	514	-
ANGIOSPERMS:	T										
Anthemis type	p		0.2%	0.4%	0.2%	0.2%	0.6%	0.2%	0.2%	0.6%	
Anthyllis vulneraria L.	p		0.2%								
Arenaria norvegica ssp. *norvegica* Gunnerus	s					1					
Armeria maritima Willd.	p			0.7%	0.4%	0.2%	0.4%	0.6%	0.2%	1.0%	
Artemisia L.	p	+	0.4%	0.4%	8.6%	0.4%	2.4%	1.6%	5.7%	9.9%	
Asteraceae Asteroideae	p		0.2%		0.6%	0.2%	0.2%		0.6%	0.4%	
Aster type	p			0.4%				0.2%	0.2%	0.2%	
Astragalus alpinus L.	p		0.2%						0.2%		
Astragalus danicus type (cf. *Oxytropis* DC.)	p		0.2%							0.4%	
Betula L.	w						+	+			
Betula nana type	p		0.8%	0.4%	1.4%	2.6%	2.2%	0.6%	0.8%	0.6%	
Betula nana L.	fr					2					
Betula pubescens type	p			0.4%	1.6%	2.0%	1.5%	0.8%	0.8%	0.6%	
Callitriche L.	fr									1	
Callitriche hermaphroditica L.	fr										2
Callitriche cf. *palustris* L.	fr									1	
Caltha palustris L.	p										2
Campanula type	p				0.4%	0.2%	0.2%	0.4%	0.4%		
Campanula rotundifolia L.	s	2			10	9	4	7	2	4	1
Carex L. spp.	bn		4	1	7	6	2	3	1	16	2
Carex L. spp.	tn		1								
Carex acuta L.	n									4	
Carex flacca Schreb.	n		5							1	1
Carex nigra (L.) Boott	n		1			1	1			3	3
Carex sect. Acutae Fr.	n	1			1		1		1	4	
Carex recta Boott s.l.	n				2					6	
Caryophyllaceae indet.	p		0.2%		0.6%	0.4%		0.2%	0.2%	1.2%	
Cerastium arvense group	p				0.6%			0.2%		1.2%	
Cerastium fontanum type	p		0.2%				0.6%		1.1%		
cf. *Chaerophyllum temulum* L.	p						0.2%				
Chrysosplenium alterniflorum type	p			0.4%							
Cirsium Mill.	p								0.2%		
Cornus cf. *suecica* L.	p			0.4%							
Cyperaceae	p	+	15.8%	31.9%	38.4%	35.7%	27.6%	34.8%	31.5%	36.5%	
Empetrum nigrum type	p	+			0.4%	0.6%	0.7%		0.2%	0.4%	
Empetrum nigrum ssp. *nigrum* L.	s									1	
Fabaceae indet.	p		0.8%								
Gentiana nivalis L.	p		0.2%					0.2%			
Groenlandia densa (L.) Fourr.	n	2	24		1	1		1	5	4	114
Helianthemum L.	p				0.2%		0.2%	0.2%		0.2%	
Heracleum sphondylium Mill.	p					0.2%					
Herniaria glabra L.	s									1	
Hornungia type	p									0.2%	
Juncus L.	s	1	8	3	3	8	1	6		7	1
Juncus articulatus L. or *J. acutiflorus* Ehrh. ex Hoffm.	s		2			1					
Juncus balticus Willd.	s		1								
Juncus cf. *triglumis* type	s	1			1				1	1	
Koenigia islandica L.	p				0.4%					0.4%	
Leontodon autumnalis L. or *Leontodon hispidus* L.	fr									7	

Table 1 (*Continued*).

Location, site		Location 1, site 1				Location 1, site 2				Loc 3	
Sample code no.		HB1	HB2	HB3	HB4	HB5	HB6	HB14	HB15	HB12	IR1
Luzula DC.	s						1			1	
Moehringia trinervia type	p		0.4%	0.4%	0.2%	0.2%		1.0%	0.6%	1.0%	
Montia fontana ssp. *fontana* L.	s										1
Myriophyllum alterniflorum DC.	p	+	0.2%		33.0%	44.7%	40.5%	14.2%	84.1%	66.1%	
	n	5	3		43	4	161	1	63	264	
Myriophyllum spicatum L.	p	+	1.0%	10.5%	1.9%	12.8%	8.0%	8.8%	6.1%	9.8%	
	n		1		2		4	4	1	45	
Plantago maritima type	p	+	0.2%	9.8%	2.9%	6.7%	7.6%	4.2%	2.9%	1.7%	
Poaceae ($p < 35$ μm)	p	+	50.2%	20.3%	14.2%	20.1%	20.4%	23.0%	20.9%	15.2%	
Poaceae ($p > 35$ μm)	p	+	11.3%	8.8%	5.2%	10.8%	12.4%	6.4%	7.4%	6.4%	
Potamogeton L.	p	+	0.4%	16.8%	0.4%	3.7%	2.2%	4.2%	0.8%	0.8%	
	n	1									
Potamogeton filiformis Pers.	n		30	4		5		3	6	50	2
Potamogeton filiformis Pers. or **Potamogeton vaginatus* Turcz.	n		22			2		2			4
Potamogeton praelongus Wulfen	n		26	27	6	18	66	46	113	2	13
**Potamogeton vaginatus* Turcz.	n		118	6	5	7	2	6	14	1	
			cf. 61						cf. 5		
Potentilla type	p		0.2%		0.6%	0.2%	0.4%	0.6%	0.4%	0.2%	
Potentilla L.	s							1			1
Potentilla crantzii (Crantz) Beck ex Fritsch s.l.	s							1	1	3	
Quercus L.	p						0.2%				
Ranunculus L.	n									1	
Ranunculus acris group	p		0.2%		0.2%		0.2%	0.2%	0.2%	1.0%	
Ranunculus aquatilis/*glacialis* group	p	+	1.0%	2.5%	17.2%	0.8%	6.3%	3.4%	11.6%	48.0%	
Ranunculus subgen. *Batrachium* (DC.) A. Gray	n	124	294	30	961	125	658	176	418	3458	50
Rubiaceae	p		0.4%		0.2%	0.2%	0.6%	0.2%	0.2%	0.2%	
Rumex L.	p		0.2%	1.8%		1.2%	0.4%	1.2%	0.6%	0.4%	
Rumex acetosella L. (or *Oxyria* Hill)	p		9.1%	9.1%	7.6%	5.9%	7.4%	7.8%	9.9%	7.0%	
Rumex acetosella L.	n			2	1	4	1	3	2	17	
	pe							1			
Salix L.	bdc		1		1					7	
	bdf		6	1	30	1	7	6	8		
	p	+	5.5%	7.0%	3.5%	2.8%	4.0%	4.6%	4.2%	3.9%	
	w		+			+				+	
Sanguisorba officinalis L.	s		cf. 1								
Saussurea alpina (L.) DC.	p			0.4%	0.2%		0.4%	0.2%		0.2%	
Saxifraga oppositifolia type	p				0.2%					0.2%	
Saxifraga cf. *rosacea* Moench	s			1							
Saxifraga stellaris type	p				0.2%						
Schoenoplectus tabernaemontani (C.C. Gmel) Palla	n		1								
Scrophulariaceae indet.	s						1				
Silene dioica type	p		0.2%			0.6%	0.7%	0.2%		0.2%	
Silene vulgaris type	p							0.2%		0.2%	
Sinapis type	p				0.2%			0.2%			
cf. *Spergularia media* (L.) Griseb. or *Spergularia marina* (L.) C. Presl	s										3
Thalictrum L.	n									1	
Thalictrum alpinum group	p	+	1.0%	6.3%	7.6%	5.9%	5.9%	8.0%		5.2%	
Thalictrum alpinum L.	n									3	
Trifolium type	p		0.2%								
Viola palustris L.	s							1			

Table 1 (*Continued*).

Location, site		Location 1, site 1				Location 1, site 2				Loc 3	
Sample code no.		HB1	HB2	HB3	HB4	HB5	HB6	HB14	HB15	HB12	IR1
GYMNOSPERMS:											
Juniperus type	p		0.2%	0.4%			0.4%				
Pinus L.	p		0.4%		2.3%	0.6%	0.4%	0.2%	0.6%	2.0%	
PTERIDOPHYTES:											
Botrychium lunaria type	sp		0.4%	1.1%	0.2%	0.2%	0.2%	0.6%			
Diphasiastrum Holub	sp					0.2%				0.2%	
Huperzia selago (L.) Bernh. ex Schrank&C. Mart	sp		0.8%		0.2%	0.4%		0.2%		0.6%	
cf. *Lycopodium annotinum* L.	sp					0.2%					
Polypodiaceae	sp						0.2%			0.2%	
Polypodium L.	sp							0.2%			
Selaginella selaginoides (L.) P. Beauv.	mi			0.7%	1.2%	0.6%	1.7%	0.4%	1.0%	0.6%	
	me	42	51	45	231	119	197	202	134	180	3
	sa	12	4	7	24	9	34	25	18	11	
MOSSES:											
Aulacomnium palustre (Hedw.) Schwaegr.	lvst		+			+	+			+	
Aulacomnium turgidum (Hedw.) Schwaegr.	lvst		+			+	+		+	+	+
Bryum Hedw. spp.	lvst		+		+				+	+	+
Climacium dendroides (Hedw.) Web.&Mohr	lvst		+		+					+	+
Cratoneuron communtatum (Hedw.) Roth.	lvst										+
Dichodontium pellucidum (Hedw.) Schimp.	lvst									+	
Dicranum scoparium Hedw.	lvst				+	+	+			+	
Distichium Br. Eur.	lvst									+	
Drepanocladus cf. *revolvens* (Sw.) Warnst.	lvst									+	
Grimmia Hedw. s.l.	lvst						+				
Homalothecium nitens (Hedw.) Robins.	lvst				+					+	
Hylocomnium splendens (Hedw.) Br. Eur.	lvst					+	+				+
Hypnum Hedw.	lvst										+
Meesia uliginosa Hedw.	lvst					+					
Paludella squarrosa (Hedw.) Brid.	lvst					+				+	
Plagiomnium Kop. spp.	lvst		+			+					+
Pohlia Hedw. spp.	lvst									+	+
Polytrichum alpinum Hedw.	lvst									+	
Polytrichum commune Hedw.	lvst					+					
Polytrichum juniperinum Hedw. s.l.	lvst					+	+	+	+	+	
Polytrichum urnigerum (Hedw.) P. Beauv.	lvst									+	
Racomitrium lanuginosum (Hedw.) Brid.	lvst		+				+			+	+
Rhytidium rugosum (Hedw.) Kindb.	lvst				+				+	+	+
Scorpidium scorpioides (Hedw.) Limpr.	lvst										+
Scorpidium turgescens (T. Jens) Loeske	lvst						+				
Sphagnum squarrosum Crome	lvst					+					
Sphagnum L.	sp					0.4%		0.2%			
Sphagnum L. spp.	lvst	+					+			+	+
ALGAE:											
Charophytes:	o	215	161	7	448	306	498	81	217	3440	5
Chlorophytes:											
Botryococcus braunii Kütz.	c		7.9%	14%	2.5%	8.1%	11.3%	6.0%	8.4%	18.1%	
Debarya sp.	z		1.6%								
Pediastrum boryanum											
var. *cornutum* (Racib.) Sulek	c			1.1%	1.2%	0.4%	0.2%	2.0%	1.3%	3.1%	
var. *longicorne* Reinsch	c		0.4%	1.4%			1.1%	1.8%	0.4%		
Pediastrum kawraiskyi Schmidle	c		0.2%								
Pediastrum Meyen	c		7.7%	2.8%	9.2%	16.2%	13.9%	46.6%	36.3%	126%	
Tetraedon minimum (A. Br.) Hansg.	m						0.6%	1.4%	2.5%	3.5%	

Table 1 (*Continued*).

Location, site		Location 1, site 1				Location 1, site 2				Loc 3	
Sample code no.		HB1	HB2	HB3	HB4	HB5	HB6	HB14	HB15	HB12	IR1
FUNGI:											
Ascomycetae	fb		+		+					+	
Cennococcum geophilum Fr.	sc			1	98		9				
Pre-Quaternary megaspores	me									1	

Type of remains (T): bdc = budscale complete, bdf = budscale fragment, bn = bicovex nutlet, c = colony, fr = fruit, fb = fruitbody, lvst = leavy stem, m = microfossil, me = megaspore, mi = microspore, n = nutlet, o = oögonia, p = pollen, pe = perianth, s = seed, sa = sporangia, sc = sclerotia, sp = spore, tn = trigonous nutlet, w = wood, z = zygospore, * = non-British species, test = microfossil sample tested on content.

Number of remains: In general the absolute number of specimens is given, otherwise + = present; % based on a pollen sum of arboreal- and non-arboreal upland pollen inclusive Poaceae and Cyperaceae.

type and *B. pubescens* type is mainly based on differences in general morphology (see Birks, 1968; Usinger, 1977; Kolstrup, 1982; Mäkelä, 1996; Blackmore et al., 2003); since they overlap in size and shape the identification remains tentative. Furthermore, pollen of Poaceae with pollen grains > 35 and ≤ 35 μm were separated.

All micro- and macrofossils were compared with modern reference material. Pollen and spore types in general refer to Moore et al. (1991) or the Northwest European Pollen Flora 1–8 (Punt, 1976; Punt and Clarke, 1980, 1981, 1984; Punt and Blackmore, 1991; Punt et al., 1988, 1996, 2003). The names of the vascular (macrofossil) plants native to Britain follow Stace (1991, 1997) and the non-British species those of the Flora Europaea (Tutin et al., 1980, 1993). Moss nomenclature follows Smith (1980).

4.3. Zoological analysis

Invertebrates were obtained from samples collected at Locations 1, 2 and 3 (Fig. 3, Table 2). Some invertebrate remains were recovered from samples during the extraction of the macroscopic plant remains (Fig. 3; HB1, 3–5, 7, 11, 12, IR1), others were specifically analysed for arthropod fossils (Fig. 3; GRC1–4). How these samples correlate with the botanical samples can be seen in Fig. 3.

The invertebrate fossils were recovered by wet sieving the silt over 300 μm meshes and concentrating the fossils by the standard paraffin oil (kerosene) flotation technique (Coope, 1986). Almost all the fossils were of arthropods (mostly insects) though other minor groups of invertebrates were also present. The latter, such as remains of Cladocera and ephippia (resting egg capsules) of *Daphnia* were common in the samples but were not made the subject of any special investigation. Also, frail carapaces of Chydoridae were seen in the residues retained on the sieves. The fossils are preserved in tubes of alcohol to prevent fungal attack. Identifications were made by direct comparison of the fossils with well-identified modern specimens. Most recognisable fragments were of Coleoptera since they possess robust exoskeletons that are readily preserved, but many small Crustacea (chiefly Cladocera) were also seen. For the most part, these have not been identified. Nomenclature and taxonomic order follows that of the 'Katalog Die Käfer Mitteleuropas' (Lucht, 1987). However, a number of northern species do not occur in this catalogue and have been inserted in their most appropriate positions.

4.4. Radiocarbon analysis

Material was selected for conventional radiocarbon dating from the three locations (Fig. 3). At Location 1, site 1, from one sample (HB2), plant debris sieved out of the dark grey silt gave a date of 29 290 ± 350 yr BP (SRR-3146). Organic matter from a bulk sample of the same dark grey silt gave a date of 30 230 ± 280 yr BP (SRR-3147) (Jardine et al., 1988). The collagen fraction from an antler of reindeer (*Rangifer tarandus*) found

Table 2
Faunal list of the invertebrate taxa recorded at the different locations and sites at Sourlie

Location	Location 1					Location 2				Location 3		
Site	Site 1			Site 2		Site 1	Site 2		Site 3			
Sample code no.	HB1	HB3	HB4	GRC1	HB5	HB7	HB11	GRC2	GRC3	HB12	GRC4	IR1
Sample size	50 ml	50 ml	350 ml	0.5 kg	350 ml	50 ml	135 ml	0.1 kg	0.5 kg	500 ml	∼2 kg	200 ml
COLEOPTERA:												
Carabidae												
*_Diacheila arctica_ Gyll.										?	1	
*_Diacheila polita_ Fald.											1	
Notiophilus aquaticus (L.).									2		1	
Dyschirius globosus (Hbst.)				1								
Bembidion bipunctatum (L.)									1			
*_Bembidion hasti_ Sahlb.									1			
Bembidion (_Peryphus_) sp.									1			
*_Pterostichus blandulus_ Mill.					?					1	4	
Amara alpina (Payk.)				1					1			
Cymindis vaporariorum (L.)				1								
Haliplidae												
Haliplus sp.				1					2			
Dytiscidae												
Hydroporus palustris L.									1		1	
Hydroporus sp.		1		1				1	1			
Potamonectes depressus elegans (Panz.)				2		1			4			
Potamonectes griseostriatus Geer				3					3		1	
Agabus arcticus Payk.				2					3		2	
Agabus congener (Thunb.) group.								1				
Ilybius sp.									1	1		1
*_Colymbetes dolabratus_ Payk.								?	1	1	1	
Dytiscus sp.				1								
Gyrinidae												
Gyrinus opacus Sahlb.		1		1				1				
Hydraenidae												
Ochthebius sp									1			
*_Helophorus obscurellus_ Popp.									1			
*_Helophorus sibiricus_ Motsch.				1				1			2	
Helophorus grandis Illiger									1			
Helophorus aquaticus (L.)									1			
Helophorus sp.									2		1	
Hydrophilidae												
Cercyon sp.									1	1		
Hydrobius fuscipes (L.)				1				2	1			
Laccobius sp.											1	
Silphidae												
Thanatophilus sp.											1	
Staphylinidae												
Olophrum fuscum (Grav.)			1	1				1	1			
Olophrum assimile (Payk.)				1								
Eucnecosum brachypterum Grav.. and/or *_norvegicum_ Munst.		1		9	1			7	5	1	3	
*_Acidota quadrata_ Zett.				1				1			3	
Geodromicus plagiatus (F.) and/or _nigrita_ (Mull.)				2				1		2		
Geodromicus kunzei Heer									1			
*_Boreaphilus henningianus_ Sahlb.	1			2				1	2		2	

Table 2 (*Continued*).

Location	Location 1					Location 2				Location 3		
Site	Site 1			Site 2		Site 1	Site 2		Site 3			
Sample code no. Sample size	HB1 50 ml	HB3 50 ml	HB4 350 ml	GRC1 0.5 kg	HB5 350 ml	HB7 50 ml	HB11 135 ml	GRC2 0.1 kg	GRC3 0.5 kg	HB12 500 ml	GRC4 ~2 kg	IR1 200 ml
Oxytelus sp.											1	
Platystethus cornutus (Grav.)				1								
**Bledius litoralis* Heer									1			
Bledius sp.									1			
Stenus sp.				1				1	1		1	
Quedius cf *boops* (Grav.)				1					3			
Tachinus spp.		1		1	1				2		1	
Boletobiinae, Gen. et sp. indet.										1	2	
Aleocharinae, Gen. et sp. indet.				5				2	2	1	2	
Elateridae, Gen. et sp. indet				1					1			
Byrrhidae												
Simplocaria semistriata (F.)				1					4			
**Simplocaria metallica* Ström							1					
Byrrhus sp.				1					1			
**Curimopsis cyclolepidia* (Munst.)									1			
Scarabaeidae												
Aphodius sp.				1					2			
Chrysomelidae												
Galeruca tanaceti (L.)				1					1			
Mantura sp.									1			
Curculionidae												
Apion sp.				1								
Otiorhynchus dubius Ström	1										1	
**Otiorhynchus* sp.								1				
Sitona flavescens Marsh.									1			
Sitona sp.									1			
Rhynchaenus foliorum Müll. group				1		1			3			
HEMIPTERA HETEROPTERA:												
Saldidae												
Saldula sp.								+	+			
HEMIPTERA HOMOPTERA:												
Gen. et sp. indet									+			
DIPTERA:												
Chironomidae												
**Corynocera ambigua* Zett.			+	+				+	+	+	+	+
Gen. et sp. indet.	+	+	+	+		+		+	+	+	+	+
Bibionidae, *Dilophus* sp.				+				+	+			
Tipulidae, Gen. et sp. indet.				+				+	+			
TRICHOPTERA:												
Anabolia sp.					+			+	+	+	+	
Apatania sp.					+						+	
Limnephilus spp.					+		+	+	+		+	
Phrygania sp.				+						+	+	
Gen. et sp. indet.				+	+				+		+	
MEGALOPTERA:												
Sialis sp.	+	+		+	+			+	+	+	+	
HYMENOPTERA:												
Symphyta								+	+			
Parastitica				+				+	+			

Table 2 (*Continued*).

Location	Location 1					Location 2				Location 3		
Site	Site 1			Site 2		Site 1	Site 2		Site 3			
Sample code no.	HB1	HB3	HB4	GRC1	HB5	HB7	HB11	GRC2	GRC3	HB12	GRC4	IR1
Sample size	50 ml	50 ml	350 ml	0.5 kg	350 ml	50 ml	135 ml	0.1 kg	0.5 kg	500 ml	~2 kg	200 ml
CRUSTACEA:												
Daphnia sp. (ephippia)			(3)		(2)	(1)	(8)		(8)	+ (1)	+	(5)
Cladocera, Gen. et sp. indet.					+						+	
**Lepidurus arcticus* Pallas	+	+	+				+	+	+		+	
Ostracoda gen. et sp. indet.°												
ARACHNIDA:												
Spider cephalothorax										+		
Acarinae indet.	+		+	+			+	+		+	+	+
RHYNCHOBDELLAE:												
Hirudinea, *Piscicola geometra* cocoons					3						11	2
BRYOZOA:												
Plumatella sp. statoblasts					2						1	

The numbers opposite each taxon indicate the minimum numbers of individuals present in each sample and are arrived at by taking the maximum numbers of any diagnostic skeletal part of that taxon present in each sample; ° = present in other samples, * = non-British species.

in situ at Location 2, site 2, gave a date of 29 900+430, −410 yr BP (SRR-3023). A bulk sample from the organic deposits at Location 3 gave a date of 33 270 ± 370 yr BP (SRR-3148).

Radiocarbon dates from bulk material or seeds and fruits from (semi-) aquatic plants, however, can reveal ^{14}C ages which are too old due to a 'hard water effect' (Marcenko et al., 1989; Törnqvist et al., 1992). Therefore, some of the Sourlie radiocarbon samples may have revealed ^{14}C ages that are too old. However, the collagen fraction from inside the antler should give an accurate ^{14}C age. Since the ^{14}C age of this sample is comparable with the ages of the other radiocarbon samples, the series of radiocarbon dates seems rather consistent and indicates that the organic-rich sediments accumulated between ca. 33.5 and 29 ka BP (Jardine et al., 1988).

5. Palaeobotany

5.1. *Micro- and macrofossil diagrams*

The high-resolution micro- and macrofossil diagrams (Figs. 4–7) presented in this study have been divided into five regional pollen (and macrofossil) assemblage zones (PAZ), with two subzones within PAZ SO-4. The regional PAZ are defined using data from the sequences collected at Location 1, site 1, and Location 2, sites 1 and 2. The regional PAZ, their main features and their occurrences at the various locations are given in Table 3. In the micro- and macrofossil diagram of Location 2, site 2 (key site), details about a possible succession are hampered by the fact that the depth of the spectra in the different layers is not exactly known. This was taken into account while interpreting the data. However, a trend is still visible within these layers.

In the samples, relatively high microfossil values were recorded of shrubs (e.g., *Salix*), Cyperaceae, Poaceae, herbs (e.g., *Artemisia*, *Rumex acetosella*, *Plantago maritima* type, *Thalictrum alpinum* group) and Pteridophytes (e.g., *Selaginella selaginoides*, *Huperzia selago*). Macrofossils of *Salix*, Cyperaceae, *R. acetosella*, *S. selaginoides*, *Campanula rotundifolia*, *Saxifraga* spp. and mosses were dominant. However, no Poaceae caryopses were found. Furthermore, high values of aquatic micro- and macrofossil taxa (e.g., *Potamogeton* spp., *Myriophyllum* spp., *Ranunculus* subgen. *Batrachium* = *Ranunculus aquatilis* group pollen), algae (e.g., *Pediastrum* spp. and *Botryo-*

Table 3
Regional PAZ, their main features and their occurrence at the different locations and sites

Layer	Pollen diagram		Location 2, site 2	Location 2, site 1		Location 1, site 1
	Regional PAZ	Main features	Key site	Metal box	Plastic bag	HB3
5	SO-5	↓TMC very low, ↓*Salix* < 3%, ↓*Thalictrum alpinum* group, ↑NAP > 90%, ↑Poaceae total > 40%, ↑*Rumex acetosella* > 15%	–	–	0–18 cm	–
4	SO-4b	TMC high, *Salix* 5–10%, ↑*Salix* macrofossils, ↑Caryophyllaceae, ↑Compositae	+	0–3.85 cm	18–30 cm	0–3.2 cm
4	SO-4a	TMC high, *Salix* 5–10%, ↑number of taxa, ↑*Selaginella selaginoides* macrofossils	+	3.85–5.65 cm	–	3.2–6.2 cm
3	SO-3	TMC high, ↑*Salix* 10%, ↑*Thalictrum alpinum* group	+	not recognised	–	–
2	SO-2	TMC slightly higher, *Salix* 5–10%, ↑number of taxa, Poaceae total > 20%, *Rumex acetosella* > 15%	+	5.65–? cm lower boundary disturbed	–	–
1	SO-1	TMC low but increasing, *Salix* < 6%, Poaceae total > 35%, *Rumex acetosella* > 15%	+	?–35.5 cm upper boundary disturbed	–	–

coccus braunii) and Characeae were recorded. All these taxa are very common in cold stage floras (West, 2000).

5.2. The vegetation interpreted from the plant remains

Aquatic habitats are indicated by the presence of (mostly submerged) macrophytes; *Callitriche* spp., *Groenlandia densa*, *Myriophyllum* spp., *Potamogeton* spp., *Ranunculus* subgen. *Batrachium*, as well as Characeae, *Botryococcus braunii*, *Pediastrum boryanum*, *Tetraedon minimum* and *Debarya*. All taxa suggest that the pools were shallow with cool, clear water probably fed by slowly flowing streams, of which the nutrient status in general varied between eutrophic and mesotrophic.

Many of the Sourlie species grow in mires and other types of wetland. In the deposits, high values of Cyperaceae pollen (15–46.5%), and high amounts of *Carex* spp. nutlets and leavy stems of *Aulacomnium palustre* were recorded. Poor fen is indicated by *Carex nigra*, *Juncus* spp., *Parnassia palustris*, *Saxifraga hirculus*, *Viola palustris*, *Aulacomnium palustre*, *Calliergon* spp., *Campylium stellatum*, *Drepanocladus revolvens*, *Fissidens osmudoides*, *Polytrichum commune*, *Scorpidium scorpioides*, *Sphagnum squarrosum* and *Sphagnum imbricatum* (in test sample HB7). *Homalothecium nitens*, *Paludella squarrosa* and *Scorpidium turgescens* suggest the presence of intermediate to rich fens. Flushes, runnels and/or waterside habitats are indicated by *Caltha palustris*, *Carex acuta*, *Chrysosplenium*, *Koenigia islandica*, *Lysimachia*, *Montia fontana* ssp. *fontana*, *Peucedanum*, *Ranunculus hyperboreus*, *Rorippa sylvestris*, *Saxifraga stellaris* and the mosses *Climacium dendroides*, *Cratoneuron communtatum*, *Drepanocladus* and *Philonotis*. On wet rocks *Cratoneuron filicinum* and *Dichodontium pellucidum* may have been present.

Grasslands and (wet) meadows are indicated by a large number of taxa and high values of Poaceae pollen (total 20–60%). Taxa including tall herbs (often over 50 cm or more in flower) that suggest meadows are *Anthriscus sylvestris*, *Arabis hirsuta*/*scabra*, *Botrychium*, *Cardamine pratensis*, *Campanula rotundifolia*, *Chaerophyllum temulum*, *Daucus carota*, *Dianthus deltoides*, *Gentiana purpurea*, *Heracleum sphondylium*, *Leontodon hispidus/autumnalis*, *Polemonium*, *Ranunculus acris* group (≤ 2%), *Sanguisorba officinalis*, and *Thuidium abietinum*. Other taxa can be found in dry grassland or grassy plains, e.g., *Anthyllis vulneraria*, *Artemisia* (0.4–14%), *Carex flacca*, *Cerastium* (≤ 9.5%), *Gentiana nivalis*, *Helianthemum*, *Potentilla crantzii*, *Rumex acetosa*, *Saussurea alpina*, *Seseli*, *Thalictrum alpinum* (1–12.5%), and the mosses, *Aulacomnium turgidum*, *Ditrichum flexicaule*, *Eurhynchium pulchellum* and *Rhytidium rugosum*. Furthermore, Poaceae pollen grains larger than 35 μm (= *Cerealia* size) were recorded. These could have originated from wild grasses such as *Glyceria*.

The low percentages of tree pollen (< 3%) from *Pinus*, *Betula pubescens* type, *Alnus*, *Quercus* etc. and absence of any macrofossil evidence indicates that trees must have been absent from the vegetation at Sourlie. Their pollen recorded in the sediments must have been derived from long distance transport.

Local presence of *Salix* (willow) shrubs is indicated by pollen (2.5–12.5%), fragments of small twigs, substantial numbers of budscales and one badly preserved leaf of *Salix* cf. *herbacea*. From *Betula nana* (dwarf birch) two fruits, small fragments of twigs (and wood) and low amounts of pollen (≤ 3.5%) were found. Pollen of *Empetrum nigrum* type (crowberry) was recorded regularly in very low percentages (< 1%). The find of one seed confirms local presence. *Loiseleuria procumbens* (trailing azalea) and *Juniperus* (juniper) pollen were recorded occasionally and the identifications were often tentative. Modern pollen rain studies indicate that dwarf forms of juniper produce fewer pollen, while high pollen values of juniper are usually produced by tall dense scrub (Iversen, 1954; Birks, 1973a,b). Furthermore, modern surface sample studies in the (sub)Arctic suggest that *Salix* is consistently underrepresented in the pollen values, while *B. nana* has the tendency to be overrepresented (e.g., Srodon, 1960; Fredskild, 1978; Rymer, 1973). This indicates that dwarf birch and crowberry must have been scarce, while local presence of juniper remains unsure. *Salix* (*herbacea*) shrubs must have been present in higher quantities than indicated by the pollen values, forming dwarf shrub (heath) communities with some *B. nana*, *E. nigrum* and possibly *L. procumbens* and *Juniperus*. *Cornus suecica*, *Huperzia selago and Hylocomnium splendens* also may have grown in these dwarf shrub (heath) communities.

Areas with bare mineral soils (sandy, gravelly or rocky) are indicated by *Arenaria norvegica*, *Astragalus alpinus*, *Draba incana*, *Herniaria glabra*, *Lloydia serotina*, *Minuartia rubella*, *Papaver radicatum* s.l., *Plantago maritima* type (≤ 16.5%), *Polygonum aviculare*, *Rumex acetosella* (6–26%), *Sagina caespitosa*, *Saxifraga caespitosa*, *S. rosacea*, *Sedum* and the mosses *Distichium*, *Encalypta rhabtocarpa/vulgaris*, *Grimmia* s.l., *Polytrichum juniperinum* s.l., *P. urnigerum* and *Racomitrium lanuginosum*. The presence of *Cenococcum geophilum* sclerotia and high numbers of Upper Carboniferous (Westphalian) micro- and megaspores in the deposits also suggests a relatively open landscape in which soil disturbance was an important process.

No species restricted to areas of late snow-lie are recorded. However, plants that often occur in snowbed vegetation are the mosses *Conostomum tetragonum*, *Polytrichum alpinum*, *Distichium capillaceum*, the pteridophyte *Huperzia selago* and the flowering plants *Salix herbacea*, *Saxifraga oppositifolia*, *S. stellaris*, *Sagina caespitosa* and in meltwater runnels *Ranunculus hyperboreus* and *Koenigia islandica* (e.g., Böcher, 1954; Hultén, 1968; Dickson et al., 1970; Dickson, 1973; Gjærevoll, 1990; Oberdorfer, 1994). Some plants, *Betula nana*, *S. caespitosa* and *Potentilla crantzii*, grow in places where there is a good snow cover in winter. Others, *Armeria maritima* and *Astragalus alpinus*, can only tolerate a thin and transient snow cover (e.g., Iversen, 1954; Polunin, 1959; Böcher, 1977).

Two obligate halophytes are recorded, *Carex recta* s.l. and *Spergularia marina/media*, and several facultative halophyte taxa, e.g., *Armeria maritima*, Chenopodiaceae, *Juncus balticus*, *Lomatogonium rotatum* type, *Plantago maritima* type, *Parnassia palustris*, *Potamogeton filiformis*, *P. vaginatus*, *Ranunculus hyperboreus* and *Schoenoplectus tabernaemontani*. Many of the non-aquatic facultative halophytes can also occur on other places, such as cliffs, grasslands, etc. The presence of obligate halophytes, however, suggests the presence of inland brackish or saline soils or pools. Their presence in cold stage floras is common and the possible occurrence of inland saline areas during the Weichselian has been discussed elsewhere (e.g., Bell, 1970; Dickson et al., 1970; Adam, 1977; West, 2000). Formation of salt and calcrete crusts also may have been related to semi-arid or arid cold climatic conditions (Dijkmans et al., 1986).

Many plant taxa that indicate calcareous, base-rich soils were recorded at Sourlie; *Arabis hirsuta*/*scabra*, *Draba incana*, *Polemonium*, *Potentilla crantzii*, *Saxifraga oppositifolia*, *Selaginella selaginoides*, Characeae, *Thuidium abietinum*, *Cratoneuron filicinum*, *Ditrichum flexicaule*, *Encalypta rhabtocarpa*/*vulgaris* and *Rhytidium rugosum*. This is often the case in cold stage floras (West, 2000). Other taxa may prefer more acid soils: *Betula nana*, *Empetrum nigrum* ssp. *nigrum*, *Loiseleuria procumbens*, *Salix herbacea* and *Huperzia selago* and the mosses *Polytrichum commune*, *Polytrichum juniperinum* s.l., *Racomitreum lanuginosum* and *Sphagnum* spp.

5.3. Vegetation change through time

5.3.1. Xeroseral changes

During deposition of the various (organic) Layers 1–5 at Sourlie, small changes in the abundance and diversity of the flora are recorded (Figs. 4–7, Table 3). There is a trend towards the development of more diverse tundra vegetation with an increasing abundance of low (willow, dwarf birch and crowberry) shrubs, with later a return again to a shrubless vegetation and much open ground.

Layer 1 (PAZ SO-1): High values of NAP (especially Poaceae and *Rumex acetosella*) and relatively low total microfossil concentration (TMC) may suggest that the landscape was open (e.g., *R. acetosella*), with wet moorlands, patches of grassy vegetation without shrubs and bare mineral soils. Slowly, the number of *Salix* shrubs in the area started to increase (Fig. 5a).

Layer 2 (PAZ SO-2): An increase in the number of shrubs and other plant taxa, and slightly higher TMC, may indicate that the vegetation cover increased and that the flora has become more diverse. Shrubs, especially *Salix*, but also some *Empetrum nigrum* and *Betula nana*, became more abundant (Figs. 4–6).

Layer 3 (PAZ SO-3): An increase in the *Salix* pollen percentages suggests that willow shrubs became more and more abundant (Fig. 4).

Layer 4 (PAZ SO-4): The larger number of different plant taxa and high TMC suggest that the vegetation cover further increased and that a more diverse tundra vegetation developed (PAZ SO-4a; Figs. 4, 6 and 7), including low shrub heaths, grasslands and meadows, vegetation on bare mineral (sometimes slightly saline) soils and wetlands such as mires, fens and shallow pools, of which some may have been slightly brackish (see previous section). Also, the number of willow shrubs and representatives of the Caryophyllaceae and Compositae families became more abundant in the vegetation (PAZ SO-4b; Figs. 4, 5b, 6 and 7).

Layer 5 (PAZ SO-5): TMC decreases to very low values and *Salix* pollen percentages decrease again, while NAP (especially Poaceae and *Rumex acetosella*) percentages increase. This suggests that willow shrubs disappeared from the area and that rocky meadows (e.g., Poaceae) and bare mineral soils persisted (e.g., *R. acetosella*, Fig. 5b).

5.3.2. Hydroseral changes

Successions in the shallow pools at Sourlie were recorded in detail in the micro- and macrofossil diagrams of Location 2, site 1, and Location 1, site 1. At Location 2, site 1, the diagram with Layers 1–4 (Figs. 5, 6) shows that during formation of Layer 1 a shallow pond was formed in which open water taxa such as *Myriophyllum* spp., *Potamogeton* and algae such as *Pediastrum*, *Botryococcus braunii*, *Tetraedon minimum* and *Debarya* became present. *Debarya* especially develops in the initial phase of a sandy pool (van Geel et al., 1989). During formation of Layer 2 (PAZ SO-2), open water vegetation was present with *Potamogeton filiformis*, *Groenlandia densa*, *Myriophyllum alterniflorum*, *M. spicatum*, *Ranunculus* subgen. *Batrachium*, Characeae and algae.

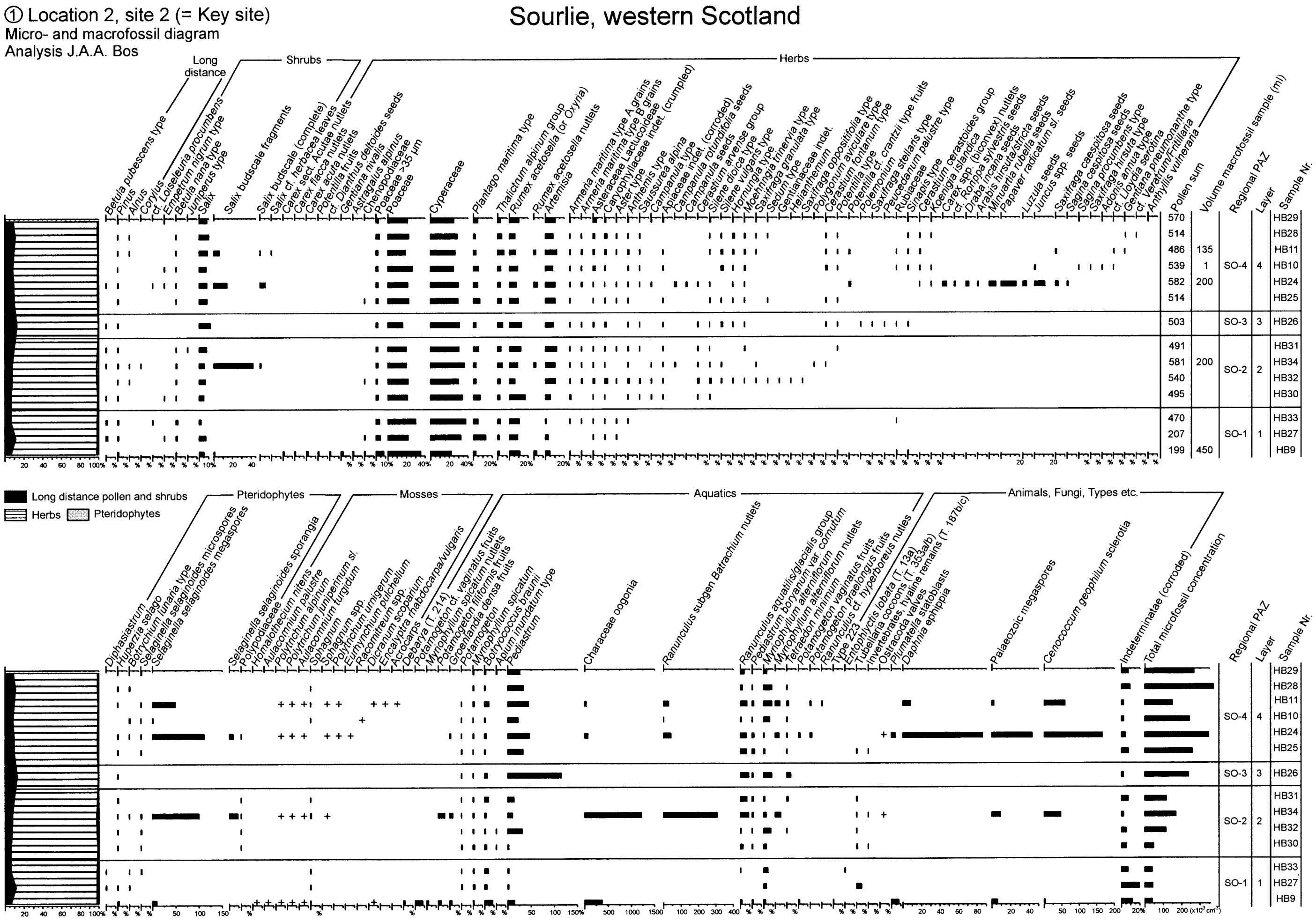


Fig. 4. Micro- and macrofossil diagram of the Layers 1–4 at Location 2, site 2. Note both micro- and macrofossils are displayed by histograms. Microfossils are given in percentages (note % at the base of the curve), macrofossils are displayed by total amounts as histograms or presence (+). No exaggeration of microfossil curves. The exact depth of the samples within the different layers is unknown, the spectra in the diagram are arranged at random to their layer of occurrence. The sample numbers indicate the order in which the samples were prepared, not a stratigraphic order.

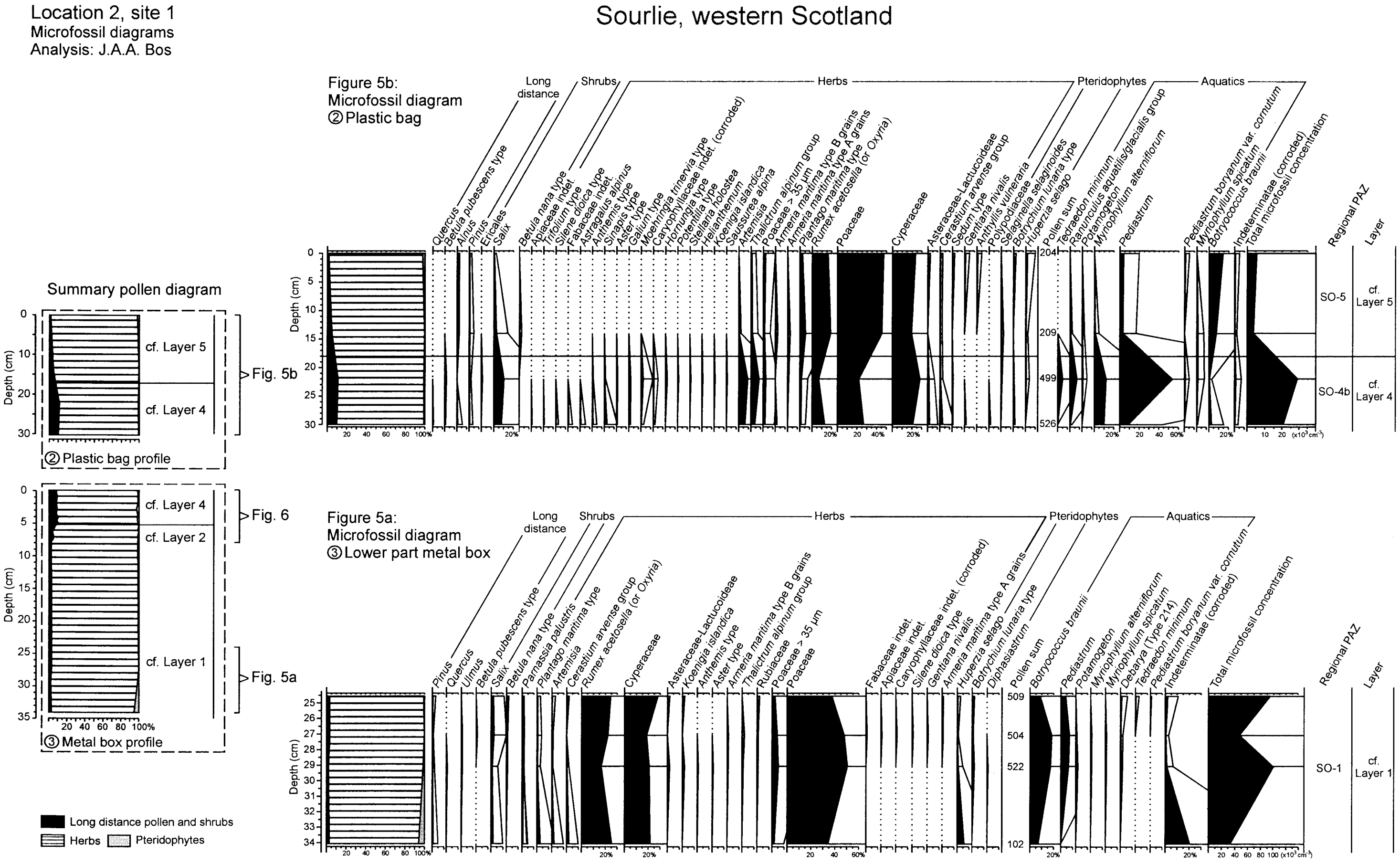


Fig. 5. Microfossil diagram of Location 2, site 1 (plastic bag, metal box), showing detailed microfossil diagrams of the lower part of the metal box (5a) and the plastic bag (5b). A detailed micro- and macrofossil diagram of the upper part of the metal box is displayed in Fig. 6. Microfossils are displayed by curves with an exaggeration of 5×.

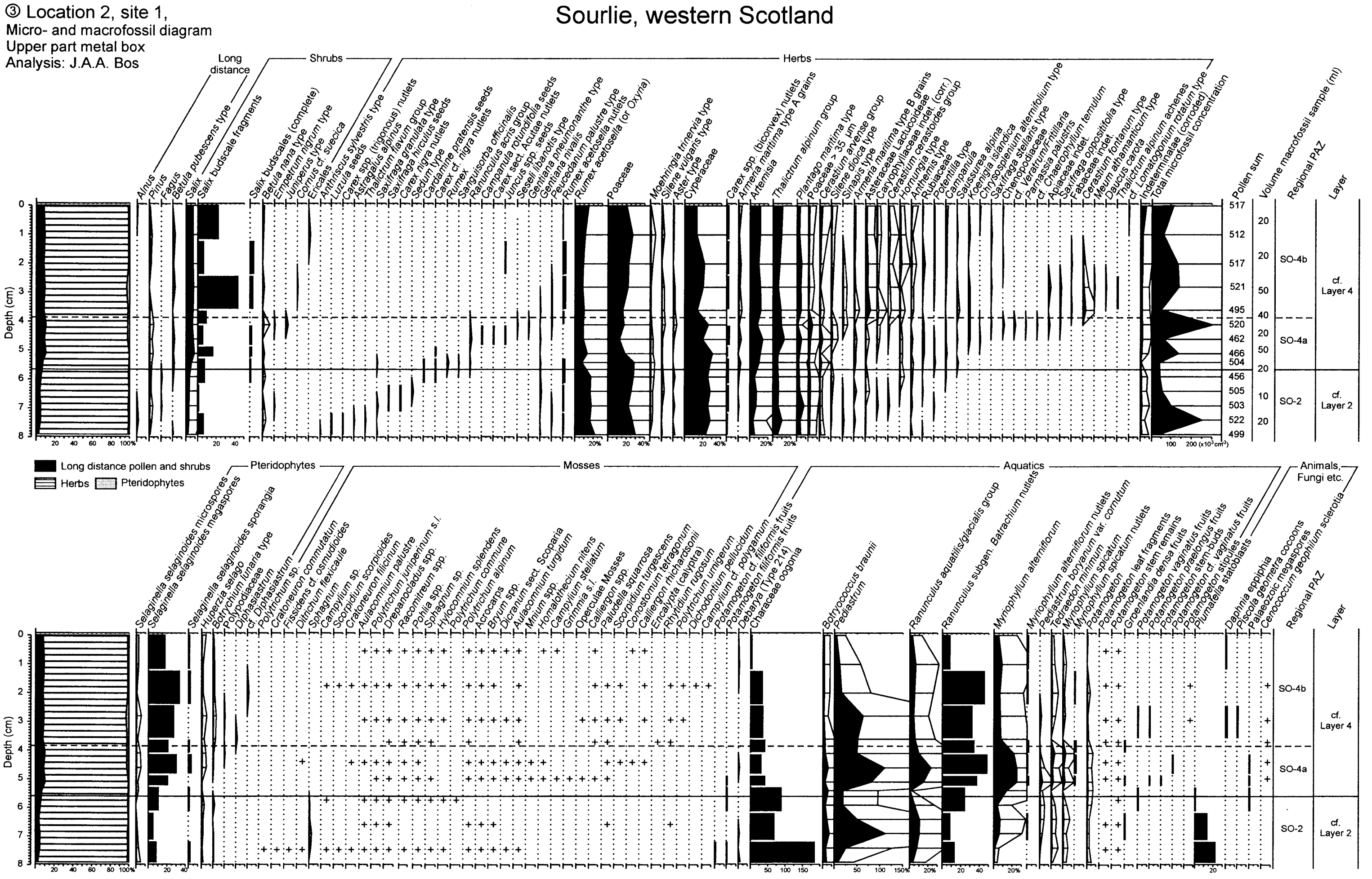


Fig. 6. Micro- and macrofossil diagram of the upper part of the metal box of Location 2, site 1. Microfossils are displayed by curves and given in percentages, macrofossils are displayed by total amounts as histograms or presence (+). Exaggeration of microfossil curves 5×.

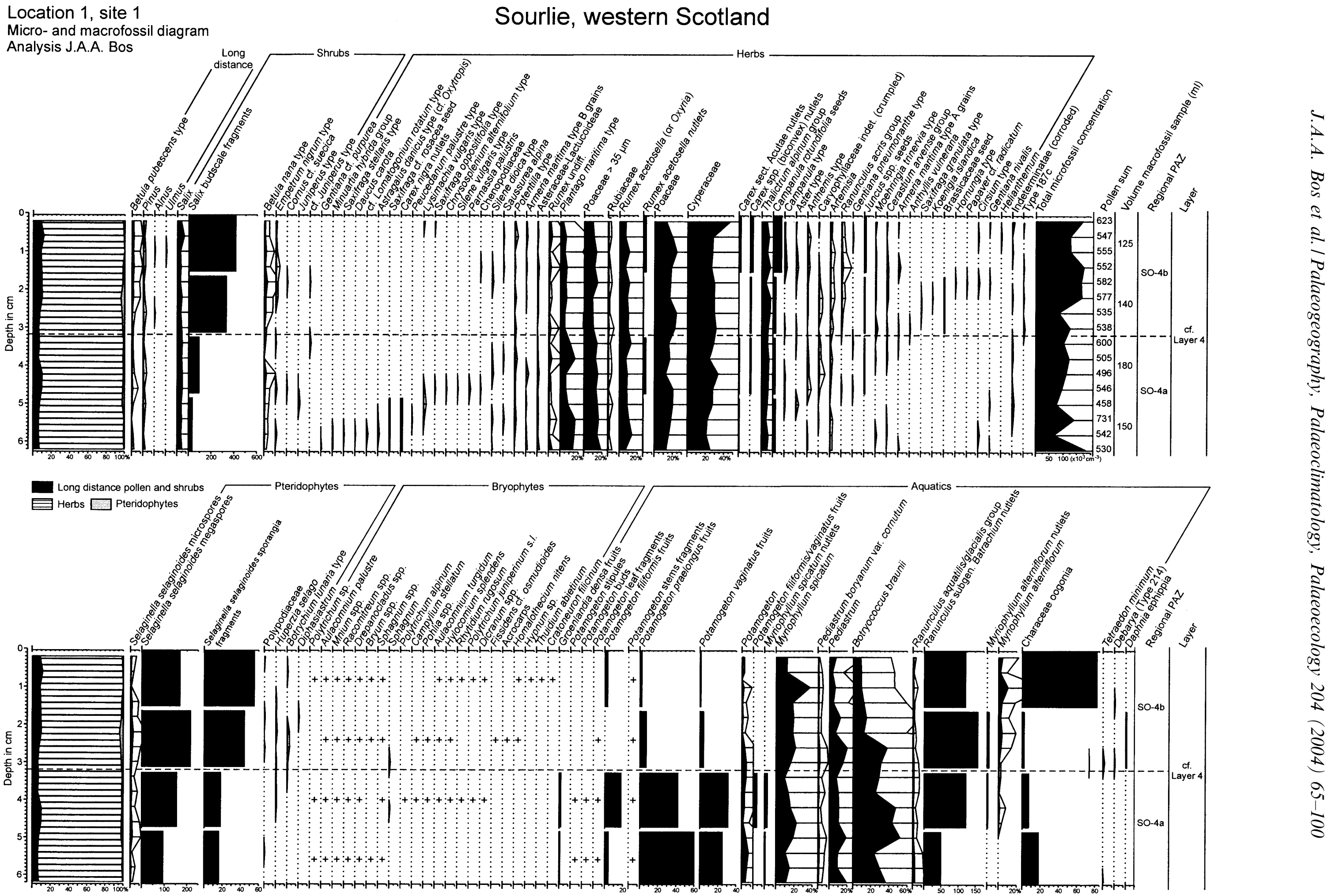


Fig. 7. Micro- and macrofossil diagram of Location 1, site 1 (HB3 profile). Microfossils are displayed by curves and given in percentages, macrofossils are displayed by total amounts as histograms or presence (+). Exaggeration of microfossil curves 5×.

Also, high numbers of Characeae oögonia and *Plumatella* statoblasts were recorded, suggesting calcareous-rich, probably flowing, fresh water. During formation of Layer 4 (PAZ SO-4a) *Potamogeton praelongus* and *Potamogeton vaginatus* appeared also, indicating clear, cool, mesotrophic water. During subzone PAZ SO-4b, *Potamogeton filiformis*, *Groenlandia densa*, *P. vaginatus* and *P. praelongus* disappeared and, together with a decline in the numbers of Characeae oögonia, this may indicate that the water had become stagnant, more shallow and less calcareous-rich. Furthermore, *Calliergon richardsonii* appeared, which probably had established itself in the shallow water. This also suggests a decrease in water depth. Synchronous fluctuations in zones PAZ SO-2, 4a and 4b (Fig. 6), in the values of aquatic microfossil taxa (see *Pediastrum*, *Tetraedon*, *Myriophyllum alterniflorum*, *M. spicatum*, *Ranunculus aquatilis* group) may suggest that fluctuations in the water level occurred. During formation of Layer 5, algae, such as *Botryococcus and Pediastrum* replaced the remaining aquatic vegetation with *Myriophyllum*, which indicates a further decrease in the water level.

At Location 1, site 1 (Fig. 7), a much shorter time interval is recorded as it only represents Layer 4 (PAZ SO-4). The aquatic taxa indicate a succession towards infilling of the pool. The presence in subzone PAZ SO-4a of *Groenlandia densa*, *Potamogeton praelongus* (often recovered with exocarps), *Potamogeton vaginatus*, *P. filiformis*, *Myriophyllum spicatum* and Characeae suggests that initially the water in the pool was cool, clear, base-rich, slightly calcareous and probably flowing. Also, water crowfoot (*Ranunculus* subgen. *Batrachium*) and algae (e.g., *Pediastrum boryanum*, *Botryococcus braunii* and *Tetraedon minimum*) were present. From subzone PAZ SO-4a to 4b, the macrofossils of *Potamogeton* spp. show a decrease with a concomitant increase in those of *Ranunculus* subgen. *Batrachium*. The presence of *Myriophyllum alterniflorum* in subzone PAZ SO-4b suggests that the water became more shallow and less nutrient- and calcareous-rich. At that time, Characeae probably could flourish near inflowing streams and at places where seepage of calcareous water occurred.

6. Palaeozoology

6.1. Vertebrate remains

At Location 2, site 2, an antler of *Rangifer tarandus* (reindeer) was found in situ in Layer 4 of unit D. Bone fragments of *Coelodonta antiquitatis* (woolly rhinoceros) and antler fragments of *R. tarandus* were found in tip heaps. The presence of large grazing herbivores is also suggested by the presence of dung beetles (*Aphodius*) in samples from Location 1, site 2 and Location 2, site 3, in layers similar to those where antler remains were found in situ.

Although no fish bones were recovered from the deposits, the presence of fish-hosted parasitic leech, *Piscicola geometra*, indicates that fish were living in ponds in which sediment accumulated at Location 1, site 2, and Location 3.

6.2. Invertebrate remains

Invertebrates were obtained from samples collected at Locations 1, 2 and 3. Though the sizes of these samples were small, they provide a fairly comprehensive view of the total fauna (Table 2). Altogether 61 coleopteran taxa were recognised of which 38 could be determined to species or species group. Of the latter, 12 species (i.e., 34%) are no longer found living in the British Isles. All species in this assemblage live today in northernmost Europe from where their ranges extend eastwards across northern Siberia. Some also occur at high altitudes in central Asia.

6.3. Local environment interpreted from the Coleoptera

Aquatic habitats are indicated by the presence of the Dytiscidae, actively swimming predatory beetles, as both larvae and adults. *Potamonectes griseostriatus*, *P. assimilis*, *Agabus arcticus* and *Colymbetes dolabratus*, all live today in ponds with a silty bottom with a fringe of sedges, rushes or mosses, in open country such as high moorland. *Hydroporus palustris* is found in rather vegetation-rich ponds. *Gyrinus opacus* is a predator that hunts the open water surface of similar boggy ponds indicating that the surface was at least in part free of floating vegetation. The habitat requirements of *Helophorus sibiricus* have been summarised by Angus (1992). Today, the species occurs on sandy banks in Finnish Lapland, where it is rare, only occurring as isolated specimens. It is not uncommon in grassy waters of the middle and lower reaches of the Lena River. Furthermore, it has been found in still waters beside meltwater streams issuing from snow patches, where the vegetation was almost entirely made up of mosses and sparse sedges, high above tree line in the mountains of southern Norway (Coope, personal observation). *Helophorus obscurellus* is not an aquatic species but is found in sandy places under stones (Angus, 1992).

Terrestrial predatory animals are also abundant in the assemblage. *Diacheila arctica* (Fig. 8) usually inhabits very marshy places overgrown by moss and especially on 'quaking ground' often formed by *Sphagnum* and *Hypnum* (Lindroth, 1992). *Diacheila polita* and *Pterostichus blandulus* (= *maeklini* Popp. and, in part, *ochoticus* Popp.) are typical species of the tundra and indicate rather less wet habitats probably further away from the immediate vicinity of the pool itself. *Notiophilus aquaticus* (in spite of its name) lives in moderately dry places and is rather eurytopic in the northern parts of its range where it lives primarily in grass-rich meadows and dwarf shrub heaths with *Empetrum*, *Betula nana* and *Cassiope tetragona*. It can even live on almost completely bare soils with little or no vegetation. *Bembidion hasti* is usually found on barren gravelly or stony sites near to the waters edge, a habitat also favoured by *Bembidion bipunctatum*.

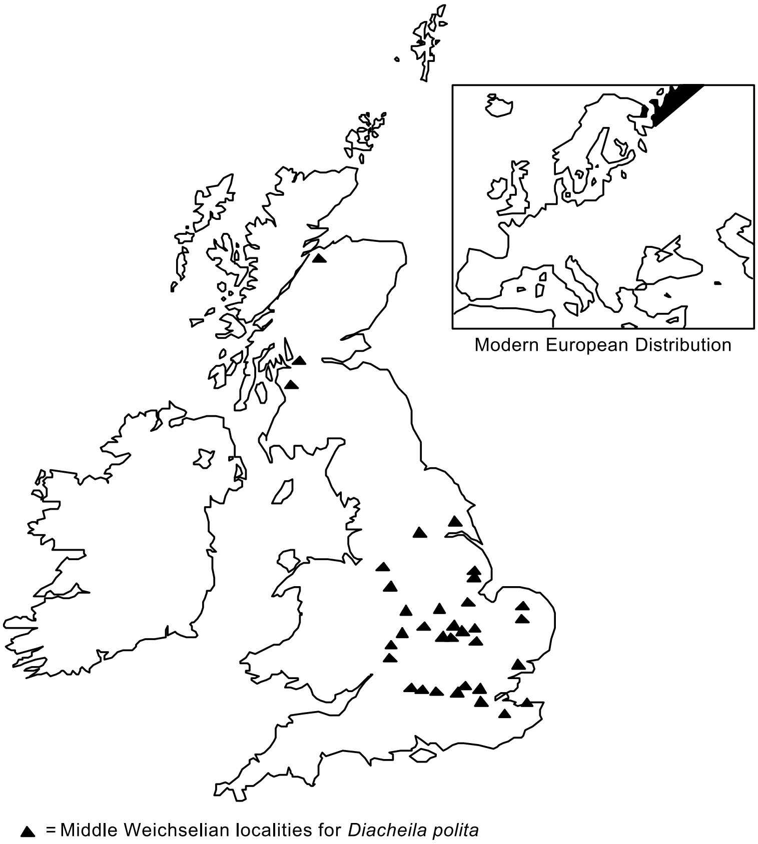


Fig. 8. Modern European distribution of *Diacheila polita* and locations of Weichselian and Late-Glacial sites in the British Isles where *D. polita* has been found as fossil (Coope, 1995a,b).

The group of staphylinid beetles in the fossil assemblage is mostly made up of moderately sized predators feeding on small soil arthropods and worms under leaf and moss litter, in moderately damp places. *Simplocaria*, *Byrrhus* and *Curimopsis cyclolepidia* feed exclusively on moss. *Rhynchaenus* of the *foliorum* group of species feed on *Salix* and were also found at levels were *Salix* is present (Tables 1 and 2). They are minute weevils and some members of the group feed on species of dwarf willows in damp places.

Amara alpina is an exclusively northern species found typically in open country above the tree line often in dwarf shrub heaths that are not too dry where the vegetation is made up of *Empetrum*, *Betula nana* and *Arctostaphylos*. *Cymindis vaporariorum* is a xerophilous species on gravely and sandy soils where the vegetation is patchy consisting of *Calluna*, *Empetrum*, *Arctostaphylos* dry grasses and *Cladonia*. In the mountains of Fennoscandia it is found with *A. alpina*. The rather cumbersome weevil *Otiorhynchus dubius* is polyphagous, feeding on a wide range of low plants including *Rumex*, *Polypodium*, *Plantago*, *Silene*, *Dryas*, *Saxifraga* and many other plants growing in open country.

6.4. Local environment interpreted from other insect groups

The larvae of Megaloptera, Trichoptera and some Diptera are almost all aquatic. The larvae of *Sialis* live on the bottoms at the margins of ponds and streams, where they are active predators on all sorts of aquatic organisms especially insects. Most of the larvae of the Trichoptera in this assemblage are characteristic of stationary water where they are also bottom dwellers. They are omnivorous, feeding on algae, fungi, detritus and often on very small invertebrates (Pennak, 1978).

The larvae of Chironomidae (non-biting midges) are also aquatic and are chiefly herbivorous feeding on algae amongst the aquatic vegetation or on the bottom. The occurrence of *Corynocera ambigua* Zett. in this fossil assemblage is of particular interest. The head capsules of its larvae are often abundant in lake and pond sediments where they are one of the earliest colonisers after deglaciation. Details of the (palaeo) ecology of this species, including its strange taxonomic history, are given in Walker and Mathewes (1989). Although normally a cold water species it can at times live in temperate water (Brodersen and Lindegaard, 1999). It was first described as a fossil in Pleistocene lake deposits, based on its distinctive larval heads only to be discovered later as a living fly emerging from a Finnish lake. From its palaeoecological history it is evident that *C. ambigua* is a very efficient pioneer species despite the fact that the adult insect is brachypterous and thus incapable of independent flight. It must be transported passively to newly available lakes and ponds either by larger animals (birds or mammals) or by convection currents or turbulent air movements. The behaviour of this species shows that being flightless is not necessarily an impediment to rapid dispersal provided that the organism is small enough to be able to ‘hitch’ a lift on some unwitting accomplice or is sufficiently light to be dispersed in the aerial plankton.

Other insects in this assemblage are terrestrial for the whole of their life cycle. Thus the parasitic Hymenoptera (ichneumon flies) are represented by adult heads and various body parts but cannot be identified further. Hymenoptera (Symphyta), the well-known ‘saw flies’ which feed on various plants, are represented by their characteristic ovipositors.

6.5. Local environment interpreted from the Crustacea

Remains of Cladocera, ephippia (resting egg capsules) of *Daphnia* and frail carapaces of Chydoridae were found. All these crustaceans are typical of ponds, which may often be temporary.

Fragments of a large notostracan crustacean *Lepidurus arcticus* Pallas (Fig. 9) were found in most of the samples. This is a species with important palaeoecological and palaeoclimatic significance. This crustacean grows to a length of about 2 cm and was represented both by its well-sclerotised jaws and the diaphanous but distinctive supra-anal segment. These pieces have such different hydrodynamic properties that had they under-

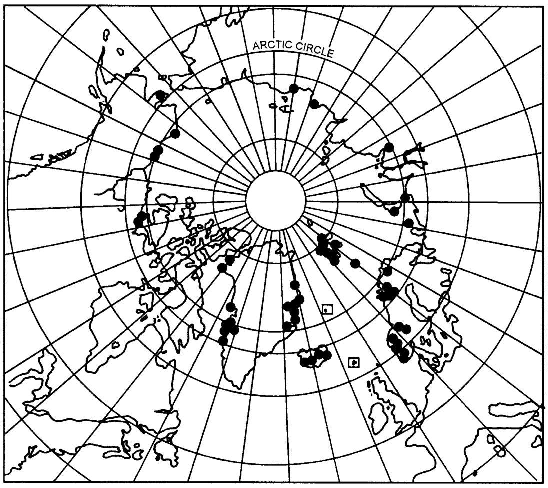


Fig. 9. Present-day distribution of *Lepidurus arcticus* (after Somme, 1934).

gone any degree of post-mortem transport, they would have become separated from one another. It is certain that *L. arcticus* must have lived in the immediate vicinity of the locality in which the fossils were found. At the present day, this species has a geographical range that lies almost entirely north of the arctic circle (Fig. 9). It lives most often in shallow water such as temporary pools or the edges of lakes, but it has been also recorded, rather enigmatically, from deep lakes in Norway. Its ability to colonise temporary bodies of water relies on the ability of its eggs to resist desiccation and freezing. In this case it is the egg that is small enough to be passively transported either by animals or in the aerial plankton.

6.6. Local environment interpreted from other invertebrate groups

Piscicola geometra is a leech of the Piscicolidae (Order Rhynchobdellae, Class Hirudinea), which at present lives in both fresh and brackish open water and is often found in vegetation with *Myriophyllum*, *Ceratophyllum* and *Chara* (Pals et al., 1980). As its name implies it is a parasite on fish. Leeches are known to be transported by fish within a single drainage system or overland to other systems by birds or mammals. Unlike many other leeches, *Piscicola* does not tolerate drying out (Pals et al., 1980), which suggests that the ponds were permanent and at least large and deep enough to prevent complete drying out during summer.

Statoblasts of the bryozoan *Plumatella* sp. (Type 390, van Geel et al., 1981) suggest shallow, fresh water that is usually stationary, though *Plumatella* can also live in turbulent water (Pennak, 1978).

7. Palaeotemperature reconstructions based on the flora and fauna

7.1. Palaeotemperature reconstructions based on the flora

Different approaches were used for making climatological reconstructions based on the Sourlie flora:

(1) A method, in which all recorded plant species are included, uses the indicator values for temperature and continentality (*T* and *K* values) of Ellenberg et al. (1991). With this method it is possible to get an indication of the palaeoclimate. The Sourlie flora (Fig. 10) shows a high number of plants, especially mosses, which indicate subcontinental conditions (*K* value: 6). Furthermore, the flora indicates cold to moderately warm conditions. However, the mosses suggest more between cold and cool conditions (*T* value: 2). Thus, the Sourlie flora indicates that around 30 ka BP the climate in western Scotland was cold and subcontinental.

(2) Palaeotemperature estimates based on the flora were also made for the different Layers 1–5 by using the climate indicator plant species method, which was introduced by Iversen (1954) and further developed by Kolstrup (1980). In this method the relationship between the geographical limit of plant distribution and temperature is used, i.e., plants require a minimum mean summer temperature to flower and reproduce. Palaeotemperature data (Table 4) were obtained from Dahl (1951), Iversen (1954), Bell (1970), Vorren (1978), Kolstrup (1979, 1980), Odgaard (1982), Brinkkemper et al. (1987) and Isarin and Bohncke (1999).

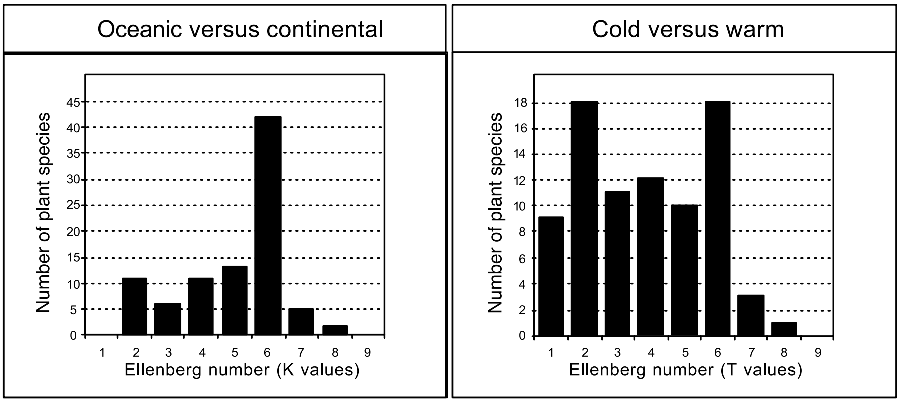


Fig. 10. Ecological indicator values for continentality (*K* values) and temperature (*T* values) of the Sourlie flora based on Ellenberg et al. (1991). *K* values: 1, euoceanic; 2, oceanic; 3, between 2 and 4; 4, suboceanic; 5, intermediate; 6, subcontinental; 7, between 6 and 8; 8, continental; 9, eucontinental. *T* values: 1, cold, alpine and nival species; 2, between 1 and 3, many alpine species; 3, cool, subalpine species; 4, between 3 and 5; 5, moderately warm, montane species; 6, between 5 and 7, submontane temperate species; 7, warm; 8, between 7 and 9, submediterranean species; 9, extremely warm, mediterranean species.

Layer 1: The botanical assemblage in the basal part of the microfossil diagram from Location 2, site 1 (PAZ SO-1, 29–34 cm; Figs. 5a, 11) shows that the landscape during this time was open with wet moorlands and patches of grassy tundra. The presence of *Parnassia palustris* may suggest that during this period minimum mean July temperatures were around 7°C. The upper three spectra (PAZ SO-1, 24–29 cm; Figs. 5a, 11) reflect the establishment of willow shrubs in the area and formation of a shallow pond in which open water taxa and algae became present. Around this time, *Koenigia islandica*, *Myriophyllum alterniflorum* and *Myriophyllum spicatum* indicate higher palaeotemperatures, 9–10°C. However, besides temperature, the absence or presence of an indicator species in the different layers also could be related to a number of other factors, e.g., precipitation (dryness), soil or succession stage. At the beginning of formation of Layer 1, pools with aquatic indicator species may have been absent because precipitation was inadequate for pools to persist. This dryness, on the other hand, also could be related with the low temperatures that characterised glacial climates during this part of the Weichselian.

Layer 2: During formation of Layers 2–4, more diverse tundra vegetation developed with an increasing abundance of low (willow, dwarf birch and crowberry) shrubs. Based on the presence at Location 2, sites 1 and 2 (PAZ SO-2; Figs. 4, 6, 11), of *Myriophyllum alterniflorum*, *M. spicatum*, *Ranunculus* subgen. *Batrachium* and *Aulacomnium turgidum*, a minimum mean July temperature of ≤ 10°C could be inferred. Although the exact depth of the different samples in Layer 2 at Location 2, site 2 is unknown, they all indicate minimum mean July temperatures of ≤ 10°C.

Layer 3: This layer was represented by only one sample in Location 2, site 2 (PAZ SO-3, Fig. 4). In this sample *Myriophyllum alterniflorum* and *M. spicatum* were recorded, which indicate minimum mean July temperatures around 9–10°C (Fig. 4).

Layer 4: At Location 1, site 1 (Fig. 7), Location 2, site 1 (Figs. 5b, 6, 11) and site 2 (Fig. 4), taxa such as *Myriophyllum alterniflorum*, *M. spicatum*, *Ranunculus* subgen. *Batrachium*, *Aulacomnium turgidum*, *Sanguisorba officinalis* and *Koenigia islandica* were recorded in most samples of Layer 4 (PAZ SO-4), indicating minimum mean July temperatures of ≤ 10°C. In the lower part of Layer 4 (and upper part of Layer 2 and in an unknown part of Layer 1) also *Groenlandia densa* nutlets were recorded. *G. densa* requires a minimum mean July temperature of 16°C (Bell, 1970), a high figure in relation to a minimum mean July temperature of ≤ 10°C suggested by the other species recorded. However, the species is often recorded in cold stage floras (Godwin, 1956; West, 2000) and is frequently found in deposits with assemblages of obligate cold-adapted insects such as those from Sourlie. Furthermore, it occurs in deposits intimately associated with ice wedge casts and evidence of intense cryoturbation. In full glacial situations it seems that *G. densa* could live in conditions far colder than its modern geographical range suggests. At Sourlie, the presence of *G. densa* was probably related to the succession stage of the vegetation in the pond rather than to temperature. However, the record of a single *Schoenoplectus tabernaemontani* nutlet (HB2, Table 1) at the base of cf. Layer 4 at Location 1, site 1, may indicate a minimum July temperature of 13°C, i.e., also rather higher than 10°C.

Layer 5: The botanical assemblage in the upper part of the microfossil diagram from Location 2, site 1 (PAZ SO-5, 0–15 cm; Figs. 5b, 11), indicates that willow shrubs disappeared from the area and that meadows and bare mineral soils persisted. Algae (*Botryococcus* and *Pediastrum*) replaced the aquatic vegetation with *Myriophyllum* spp. The presence of palaeotemperature indicator species, *Selaginella selaginoides*, *Betula nana* and *Thalictrum alpinum*, suggests a minimum mean July temperature of 7–8°C. It is possible that the disappearance of *Myriophyllum* spp. was related to the hydroseral succession process in the pond and not to a decrease in the minimum mean July temperature. However, also *Koenigia islandica* disappeared (9.1°C, Table 4), while the abundance of bare mineral soils and plant communities the species normally grows in expanded. This suggests that the climate probably became too cold and dry for specific plants to survive and ponds to persist.

Palaeotemperature reconstructions of the Layers 1–5, based on the botanical data, thus show that the vegetational development around 30 ka BP at Sourlie was related to changes in temperature (and precipitation).

Table 4

Temperature indicator plant taxa present in the Sourlie flora, their minimum mean July temperatures and reference

Minimum mean July temperature °C	Species	Reference
5.7	*Saxifraga oppositifolia*	Vorren, 1978
7	*Selaginella selaginoides*	Kolstrup, 1979, 1980
7	*Parnassia palustris*	Kolstrup, 1979, 1980
7	*Betula nana*	Brinkkemper et al., 1987; Ran, 1990
7.3	*Lycopodium alpinum/annotinum*	Vorren, 1978
7.4	*Papaver*	Vorren, 1978
7.7	*Sagina caespitosa*	Vorren, 1978
7.7	*Empetrum*	Vorren, 1978
7.7	*Thalictrum alpinum*	Vorren, 1978
8	*Potamogeton filiformis*	Kolstrup, 1979, 1980
8	*Caltha palustris*	Kolstrup, 1980
8	*Cornus suecica*	Kolstrup, 1980
8	*Ranunculus hyperboreus*	Brinkkemper et al., 1987
8	*Astragalus alpinus*	Vorren, 1978
8	*Juniperus communis*	Iversen, 1954; Isarin and Bohncke, 1999
10 (taller plants)		Kolstrup, 1980
9.1	*Koenigia islandica*	Vorren, 1978
9–10	*Myriophyllum alterniflorum*	Kolstrup, 1980; Isarin and Bohncke, 1999
9–10	*Sanguisorba officinalis*	Kolstrup, 1979, 1980
< 10	*Aulacomnium turgidum*	Odgaard, 1982
10	*Ranunculus* subgen. *Batrachium*	Brinkkemper et al., 1987
10	*Myriophyllum spicatum*	Kolstrup, 1980
13	*Schoenoplectus lacustris/tabernaemontani*	Iversen, 1954
16	*Groenlandia densa*	Bell, 1970

7.2. Palaeotemperature reconstructions based on the arthropod fauna

The arthropod fauna from Sourlie indicates arctic climatic conditions. Some of the species recorded have relatively large geographical ranges, but all the species in this assemblage can be found living today in northeastern Russia, to the east of the Kanin Peninsula. The large number of obligate cold-adapted species is especially noteworthy. Fourteen species (i.e., about 34% of the identified species) are no longer found living in Britain and have present-day geographic ranges that are restricted to high latitudes and/or high altitudes further south. These species include *Diacheila polita* whose nearest locality today is on the extreme eastern part of the Kola Peninsula. It is a common fossil in full glacial deposits in Britain (Fig. 8). The nearest modern locality for *Pterostichus blandulus* is the Kanin Peninsula and Waigatsch Island in arctic Russia. It also occurs as an isolated population at high altitudes in the High and Low Tatra mountains of eastern Europe. In Europe, *Helophorus obscurellus* is known only from the Kanin Peninsula but the species is widespread in Asia, from the Tibetan plateau to the north of Siberia (Angus, 1992). *Diacheila arctica*, *Bembidion hasti*, *Colymbetes dolabratus*, *Helophorus sibiricus*, *Acidota quadrata*, *Boreaphilus henningianus*, *Eucnecosum norvegicum*, *Simplocaria metallica* and *Curimopsis cyclolepidia* are all found today in northern Fennoscandia with ranges that extend eastwards into Siberia. The northern Chironomid fly *Corynocera ambigua* also extends as far south as Fennoscandia and Denmark. Several other species have largely boreal geographical ranges that reach as far as northern Britain. Such species include *Amara alpina*, *Agabus arcticus*, *Potamonectes griseostriatus*, *Gyrinus opacus*, *Eucnecosum brachypterum* and *Otiorhynchus dubius*. The geographical range of the crustacean *Lepidurus arcticus* (Fig. 9) is similarly confined to high latitudes. Since the Sourlie assemblage of species includes a wide spectrum of ecological types: i.e., terrestrial and aquatic species, carnivores and phytophagous species, the only common factor between them all is an adaptation to low temperatures.

Using the Mutual Climatic Range (MCR) method (Atkinson et al., 1987) it is possible to quantify these estimates of palaeotemperatures. In order to obtain palaeotemperatures that are independent of those obtained from the botanical records, only species were used in this reconstruction that are not dependent on particular host plants. Such species include carnivorous and general scavenging species. The figures (Table 5) indicate that the actual mean values probably lay somewhere between these limits and not that the temperatures ranged between them. The palaeotemperature figures reconstructed using the MCR method on the Sourlie coleopteran assemblages provide no evidence of any significant differences in thermal climat between the various sampling locations. To provide a more realistic view of the thermal climate at the time when the Sourlie fauna lived, sensitivity tests were applied to the MCR method. Corrected figures (Perry, 1986; Walkling, 1996; Coope et al., 1998) indicate that the median mean temperature of the warmest

Table 5
Estimated mean temperatures of the warmest month (= T_{max}) and coldest month (= T_{min}) based on the coleopteran taxa given for the different locations and sites

Location	Site	Sediment	Layer	Sample (no. species)	T_{max} (July) °C	T_{min} (January) °C
Location 1	site 2	top of organic silt	top cf. Layer 4	GRC1 (15 spp)	12–13	−5–−3
Location 2	site 2	black silty clay	Layer 2	GRC2 (9 spp)	9–13	−26–−3
	site 3	organic silt	cf. Layer 4	GRC3 (14 spp)	9–11	−27–−10
Location 3	–	organic silt	–	GRC4 (12 spp)	9–12	−27–−9
After correction:	Median mean temperature of the warmest month was between 6 and 9°C Median mean temperature of the coldest month was between −34 and −11°C					

Corrected figures (Perry, 1986; Walkling, 1996; Coope et al., 1998), which apply to all three locations, are given in the lowest row.

month was between 6 and 9°C and that the median mean temperature of the coldest month(s) was between −34 and −11°C.

Although not involved in the above MCR estimations, the occurrence of the crustacean *Lepidurus arcticus* with its distribution that is almost exclusively north of the arctic circle gives them added support (Fig. 9). This species has frequently been recorded as a Quaternary fossil in association with obligate cold-adapted floras and faunas from many parts of the British Isles (e.g., Mitchell, 1957; Morrison, 1959; Morgan, 1973; Taylor and Coope, 1985).

8. Synthesis

8.1. Flora and fauna

The Sourlie flora comprises a total of about 160 taxa of which more than 40 are species of mosses. Most species grow in Britain today, although seven non-British taxa were recorded. The invertebrate fauna comprises at least 61 different coleopteran taxa of which 38 could be determined to species (group). Of these species, 13 (i.e., 34%) are now extinct in Britain. One species of Chironomid fly is also now absent from the British Isles. Other insect orders include Megaloptera, Trichoptera, Diptera, Hemiptera and Hymenoptera. The arctic crustacean *Lepidurus arcticus* was present in most samples.

The flora and arthropod fauna are in very good agreement in indicating a mosaic of treeless vegetation types with bare stony ground. In open, treeless areas, such as at Sourlie around 30 ka BP, pollen, spores and small seeds may have been easily transported over long distances by wind, meltwater and streams into the shallow pool-filled depressions in spring and summer and/or wind-blown over the snow onto the frozen depressions in winter (see Glaser, 1981; Birks, 1991). The Sourlie layers exactly represent these shallow pool-filled depressions. For the other habitats indicated by the fossil flora and fauna (see below), there is no direct sedimentological evidence, but most of these vegetation types have a very low fossilisation potential (e.g., vegetation on bare mineral soils). During formation of the (organic) Layers 1–4 at Sourlie a very open landscape with patches of grassy tundra vegetation without shrubs was slowly succeeded by a more and more diverse tundra vegetation with a larger abundance of (especially *Salix*) low shrubs. This vegetational development ceased during formation of Layer 5, when shrubs disappeared from the area and only meadows and bare mineral soils persisted. As is usually the case with thin cold stage deposits such as at Sourlie (West, 2000), the precise duration of sedimentation cannot be given. However, the thinness of the layers does not have to suggest that only brief periods are represented.

Dwarf shrub heath vegetation of *Salix* (*herbacea*), *Betula nana*, *Empetrum nigrum* at Sourlie is indicated by botanical remains of *Salix*, *B. nana* and *E. nigrum* and by beetle species such as *Amara alpina* and *Cymindis vaporariorum*. The minute weevil *Rhynchaenus* of the *foliorum* species group, feeds exclusively on small species of *Salix*. The presence of *Juniperus* and *Loiseleuria procumbens* in the dwarf shrub vegetation remains unsure. *Salix herbacea* and *L. procumbens* are usually prostrate, a few cm tall. *Betula*, *Empetrum nigrum* and *Juniperus* may have been larger, up to ca. 30 cm, or also could have adopted a prostrate habitus. The vegetation at Sourlie with dwarf shrubs (*S. herbacea*, *B. nana*, *E. nigrum*), grasses and numerous sedges (*Carex* spp., *Schoenoplectus*), perennial herbs (*Draba* spp., *Saxifraga* spp., *Papaver radicatum*, *Rumex acetosella*) and mosses (*Ditrichum*, *Distichium*, *Homalothecium*, *Drepanocladus*, *Campylium*) could be characterised as an intermediate between a shrub tundra and a sedge–grass–moss tundra (sensu Bliss and Richards, 1982).

Open country and barren, rather dry places, with little or no vegetation is indicated by plants such as *Arenaria norvegica*, *Astragalus alpinus*, *Draba incana*, *Minuartia rubella*, *Papaver radicatum* s.l., *Rumex acetosella*, *Plantago*, *Sagina caespitosa*, *Saxifraga caespitosa*, *Sedum*, *Encalypta rhabtocarpa/vulgaris*, *Grimmia* s.l., *Racomitrium lanuginosum*, *Polytrichum juniperinum* s.l. and *P. urnigerum*. Weevils such as *Otiorhynchus dubius* feed on a wide range of low plants including *Ru-*

mex, *Plantago*, *Saxifraga* and many other plants growing in open country. *Notiophilus aquaticus* is chiefly a predator on *Collembola* in open apparently barren habitats whose food chains probably extend back to fungi and algae. Records of *Cenococcum geophilum* sclerotia and numerous Palaeozoic micro- and megaspores in the deposits also indicate a relatively open landscape in which soil disturbance was an important process.

Shallow fresh water and ponds with a sandy, silty bottom and a fringe of sedges, rushes or mosses is indicated by sedimentological evidence and by botanical remains of *Carex* spp., *Juncus* spp., *Luzula*, *Rorippa sylvestris*, *Caltha palustris*, *Ranunculus hyperboreus*, *R.* subgen. *Batrachium*, *Potamogeton* spp., *Myriophyllum* spp., *Callitriche* spp., and Characeae, mosses such as *Climacium dendroides*, *Cratoneuron* spp., *Drepanocladus* spp., *Philonotis* spp. and *Sphagnum squarrosum* and by beetles such as *Potamonectes griseostriatus*, *P. assimilis*, *Agabus arcticus*, *Colymbetes dolabratus* and *Hydroporus palustris*. Caddisfly larvae and those of the midge *Corynocera ambigua* also indicate shallow aquatic habitats. The Crustacea *Lepidurus arcticus* and *Daphnia* are characteristic of ponds, which may have been short lived. The leech *Piscicola geometra* lives parasitically on fish, indicating their presence here, though no bones of fish were found in the deposits. The beetles, *Diacheila arctica*, *Simplocaria*, *Byrrhus* and *Curimopsis* are typically found in mossy swamps and the last three species feed exclusively on moss. Many of the small staphylinid beetles also live under moss and leaf litter in damp places.

Brackish or saline soils or pools may have been present as is indicated by botanical remains of obligate halophytes such as *Carex recta* s.l. (*Carex palacea* group) and *Spergularia marina/media* and several facultative halophytes such as *Armeria maritima*, *Juncus balticus*, *Potamogeton filiformis*, *P. vaginatus*, *Ranunculus hyperboreus* and *Schoenocplectus tabernaemontani*.

Diacheila polita and *Pterostichus blandulus* are typical beetle species of the tundra and indicate rather less wet habitats further away from the immediate vicinity of the pools. An open sedge–grass–moss tundra vegetation is suggested by high percentages of grasses (Poaceae) and sedges (Cyperaceae) including macrofossils of *Carex flacca* and *C. nigra*, the presence of herbs such as *Anthyllis vulneraria*, *Artemisia*, *Campanula rotundifolia*, *Sanguisorba officinalis*, *Seseli*, *Thalictrum alpinum*, and mosses such as *Ditrichum flexicaule*, *Eurhynchium pulchellum*, *Thuidium abietinum* and *Rhytidium rugosum*. The presence of large grazing herbivores such as reindeer (*Rangifer tarandus*) and woolly rhinoceros (*Coelodonta antiquitatis*) is suggested also by the presence of dung beetles of *Aphodius*. The existence of large herbivores, including mammoth and woolly rhinoceros, in western central Scotland at about this time, such as those at Bishopbriggs (Rolfe, 1966) and Kilmaurs (Bishop and Coope, 1977), suggests that the vegetation must have been adequately rich and regionally extensive to support these large herbivores. However, this is not the impression that is given by the reconstructed vegetation cover. This discrepancy between vegetation and forage requirements of large herbivores, such as mammoth, has been discussed before and was called 'the productivity paradox of the Mammoth steppe' (e.g., Bliss and Richards, 1982; Guthrie, 1990; Ukraintseva, 1993; Yurtsev, 2001). The productivity paradox was explained by a much greater diversity of herbaceous plant communities (grasses, sedges and forbs) during the Pleistocene in comparison with areas today with a tundra or steppe vegetation. Also, the Sourlie flora gives the impression of representing a mosaic of rather diverse vegetation types.

8.2. Climate

Changes in temperature (and precipitation) probably determined the vegetational and faunal development at Sourlie. Palaeotemperature reconstructions based on the Sourlie high-resolution micro- and macrofossil diagrams (Figs. 4–7, 11) suggest that during the beginning of formation of Layer 1, minimum mean July temperatures increased from 7 to 9–10°C. During formation of Layers 2–4, minimum mean July temperatures were ≤ 10°C, while during formation of Layer 5 minimum mean July temperatures again dropped to 7–8°C. The coleopteran data from all three locations suggest a mean July temperature be-

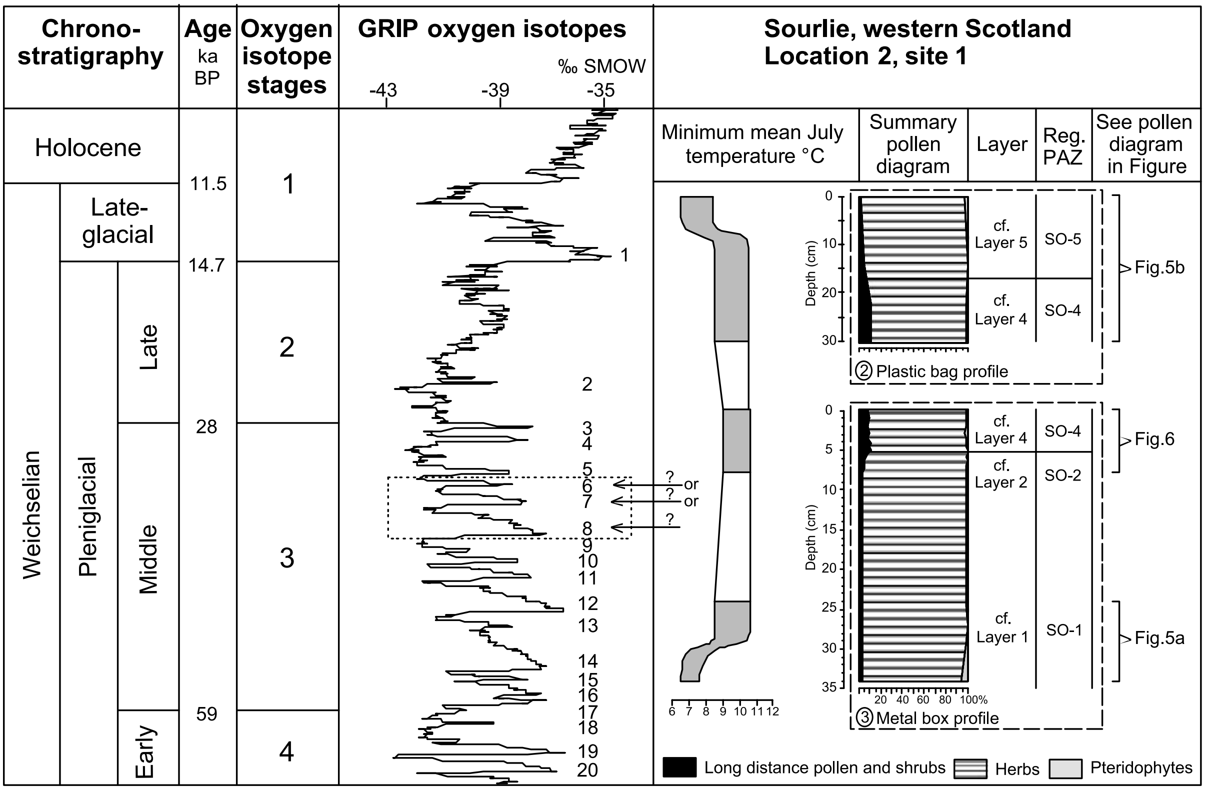


Fig. 11. Chronostratigraphy of the Weichselian, compared with the $\delta^{18}O$ record of the GRIP ice core (Johnsen et al., 1992) and the marine oxygen isotope stages (Martinson et al., 1987). Ages follow Martinson et al. (1987) and Walker et al. (1999). The (GI-)1 to 20 numbers correspond to the Dansgaard–Oeschger cycles. Regional PAZ also are indicated, and summary pollen diagrams of Location 2, site 1, are given in stratigraphical order and correlated with the layers in Location 2, site 2. The estimated minimum mean July temperatures based on the botanical evidence (micro- and macrofossils) show a shift in minimum mean July temperatures from 7 to 9–10°C and back again to 7–8°C. A possible relationship between this recorded shift in minimum mean July temperatures with one of the Dansgaard–Oeschger cycles (probably GI-8, GI-7 or GI-6) in the stable oxygen isotope record is suggested.

tween 6 and 9°C, but show no significant differences in the thermal climate. It is important to note that the palaeotemperatures from the coleopteran data are not directly comparable with those derived from the plant record. MCR figures derived from the coleopteran analysis are for *mean monthly temperatures* whilst the figures derived from the botanical analysis are for *mean monthly minimum temperatures*. The coleopteran and botanical data together provide evidence that during formation of the main organic layer(s), mean July temperatures were ca. 9–10°C.

The position of the treeline has been assumed to be related to the mean July isotherm of 10°C (van der Hammen et al., 1967). The Sourlie flora and fauna suggest that during formation of the organic layers mean July temperatures in general were 9–10°C and there is no evidence for the presence of trees. However, the absence of trees during the Middle Weichselian has been shown to be an unreliable indicator of palaeoclimates and in many cases it seemed to conflict with the temperature regime as deduced from periglacial features, pollen, macrofossils and beetles (e.g., Coope, 1975, 1977, 2000; Coope et al., 1961, 1997; West, 1977; Kolstrup, 1979, 1982, 1990; Pennington, 1986; van Geel, 1996; Ran, 1990; Bos et al., 2001). Trees were absent from much of northwestern Europe even when the climate was both temperate and oceanic. A variety of factors have been suggested, by the authors mentioned above, to explain the virtual absence or scarcity of trees in Weichselian deposits. They are: (1) the unstable environmental and climatic conditions, (2) the too dry and continental climate, (3) windy conditions, (4) heavy grazing pressure from the large mammals such as mammoth, woolly rhinoceros and bison, (5) the fact that trees need an adequate soil development, (6) the suddenness and intensity of the climatic warming, and (7) the shortness of the interstadial events that left too little time for trees to migrate from their refuges in southern Europe. Many fossil floras and faunas from the British Isles, that date from the period between 35 and 26 ka BP (such as Colhoun et al., 1972; Bryant et al., 1983; Briggs et al., 1985; Coope, 1986; Whittington and Hall, 2002) suggest cold, often very continental climatic conditions, with both minimum mean July temperatures and mean July temperatures at or just below 10°C. Under these conditions it is not surprising that trees were absent.

The Sourlie flora indicates a cold and subcontinental climate (Fig. 10), the arthropod fauna an arctic and continental climate. However, an important aspect is that the exclusively cold-adapted, eastern Asiatic species that are often in considerable abundance in many of the arthropod assemblages from English sites (e.g., Coope 1986; Briggs et al., 1985), are totally absent from Sourlie and from Balglass (Brown et al., in press). This suggests that the actual thermal climate in western and central Scotland may not have been as severely continental as it was in central England at that time. Around 30 ka BP, sea levels were much lower than today and the coastline was located slightly farther north- and westward. At that time, central England thus had a more continental environment than Scotland. Also, Huijzer and Vandenberghe (1998) showed that during the Early and Late Pleniglacial and the cold period between 41 and 38 ka BP, there was a strong north–south climatic gradient over northwestern Europe. In the time-span between 36 and 32 ka BP, evidence for a north–south gradient was slightly weaker.

The Sourlie Coleoptera fauna suggests that the mean temperature of the coldest month(s) was between −34 and −11°C. Palaeotemperature reconstructions of mean July and winter temperatures together indicate that, assuming a sinusoidal temperature curve for the seasonal variation in temperatures over the year, the mean annual temperature must have been at least as low as −1°C or even as low as −10°C, which suggests the possible presence of discontinuous or continuous permafrost (Péwé, 1966; French, 1976). At Sourlie, the organic sedimentary units were both over- and underlain by till deposits but there are no indications of freeze-thaw structures, such as cryoturbations, ice wedges or frost cracking of the organic-rich deposits. This is in contrast with similar organic deposits in central England that were so intimately involved in both cryoturbation and ice wedge formation.

Quantification of precipitation levels on the basis of the Sourlie record is difficult. Since at this time all the winter precipitation would have fallen as snow it would not have been physically available to transport sediment until the spring thaw when all the accumulated precipitation of much of the year would have suddenly become available. This seasonal process would have largely determined suitability of habitats for both plants and animals. In the tundra, snow has a protective role, especially in connection with the development of shrubs (Aleksandrova, 1988). The presence in the Sourlie flora of shrubs and herbs, such as *Betula nana*, *Salix herbacea*, *Sagina caespitosa* and *Potentilla crantzii*, suggests that, during winter, temperatures must have been sufficiently low to require a protective snow cover to moderate the ground conditions in habitats of perennial plants, especially those of shrubs. The snow cover may have varied between thick and long-lasting to thin and transient, from one place to another. Local snow patches, with taxa such as *Conostomum tetragonum*, *Polytrichum alpinum*, *Distichium capillaceum*, *S. herbacea*, *Saxifraga oppositifolia* and *Koenigia islandica*, in which snow cover was prolonged, may have been present. Furthermore, *Helophorus sibiricus* can occur in still waters beside meltwater streams issuing from snow patches where the vegetation is almost entirely made up of mosses and sparse sedges.

A certain degree of aridity of the climate may be indicated by the presence of obligate halophytes in the Sourlie flora. However, their presence also may be related to the unleached sodium-rich soils that made growth of halophytes possible (Dickson et al., 1970).

8.3. Comparison with other records

8.3.1. British Isles

The Sourlie flora (macrophyte and bryophyte) and arthropod fauna show a strong resemblance to other floras and insect faunas (for number of sites around 30 ka BP see Fig. 8) that date from the later and colder part of the Middle Weichselian (Fig. 11) in the British Isles. From Scotland, other than the Sourlie organic deposits, as yet there are only a few radiocarbon-dated deposits containing a flora and/or fauna that can lead to climatic reconstructions. Scottish late Middle Weichselian botanical sites with reliable radiocarbon dates between 35 and 26 ka BP (Fig. 1) have been recorded from Tolsta Head, located near the northern extremity of the Outer Hebrides on the Isle of Lewis (Von Weyman and Edwards, 1973; Edwards, 1979; Birnie, 1983; Gordon and Sutherland, 1993b; Whittington and Hall, 2002) and from Balglass on the Campsie Fells (Brown et al., in press.). At Tolsta Head, organic sediment buried by till deposits was analysed for pollen, macrofossils and diatoms. Recent re-investigations (Whittington and Hall, 2002) indicated that the Tolsta Head sediments and their vegetational record belong to the period around 32–26 ka BP, which means that they are of approximately the same age as the Sourlie deposits. A detailed pollen diagram (Whittington and Hall, 2002) shows high frequencies of Poaceae, Cyperaceae and *Salix* and indicates the presence of an open grassland vegetation with scattered low shrubs (*Betula nana*, *Salix herbacea*, *Juniperus* and *Empetrum nigrum*). The diatom record (Birnie, 1983) indicates fresh, alkaline, clear and still-water conditions. The Tolsta Head flora revealed a total of 64 botanical taxa and most of the taxa at Tolsta Head are also present in the Sourlie flora. Finds of *Calluna vulgaris* pollen at Tolsta Head were considered to be from an allochthonous source. So far no Coleoptera have been recovered from that site. The Sourlie site shows a strong resemblance in ^{14}C age and botanical content with the Tolsta Head site. The Sourlie and Tolsta Head deposits indicate that between 33.5 and 26 ka BP, (north)western Scotland had a cold and continental climate, but it may have been slightly less continental than in central England at that time.

The geographical distribution of Sourlie and other Scottish sites with late Middle Weichselian interstadial deposits (Fig. 1) indicates that there were both inland and coastal areas of Scotland that were ice-free during this period. Some areas, indeed, may have been ice-free until 22 ka BP (e.g., NE Scotland; Sutherland et al., 1984; Hall and Connell, 1991) – even at an altitude of 150 m above sea level (Brown et al., in press.). These results raise doubts regarding the view that the Weichselian ice sheet covered most of northern Britain at this time (Bowen et al., 2002). Given the values for the thermal climate quoted above, it seems likely that the absence of glacier ice in at least parts of Scotland at this time was due to inadequacies of precipitation rather than to the temperatures being too high. If this is so, it has widespread implications for the glacial history of the rest of the British Isles and probably for much of northwestern Europe as well.

8.3.2. Greenland ice cores

A comparison of the Sourlie minimum mean July temperature record and related vegetational development was also made with the Greenland ice core record. Investigations of the Greenland ice cores revealed many rapid oscillations (GI-1 to 20; Fig. 11) in the stable oxygen isotope record during the Weichselian Pleniglacial (e.g., Johnsen et al., 1992; Dansgaard et al., 1993). A possible time correlation between the shift in minimum mean July temperatures at Sourlie from 7 to 9–10°C (or 13°C, see Section 7.1) and back to 7–8°C, with one of these warm–cold oscillations (i.e., Dansgaard–Oeschger cycles, probably GI-8, GI-7 or GI-6) is suggested (Fig. 11). Similar trends in palaeotemperature reconstructions for Pleniglacial interstadial sequences and correlations with possible Dansgaard–Oeschger cycles have been described by Kasse et al. (1995) for thaw lake infillings in The Netherlands and by Whittington and Hall (2002) for the Tolsta Head deposits. The first showed that plant taxa in the lower part of these thaw lake infillings suggest that the climatic optimum was reached early in the sequence and was probably of short duration. In the final phase of the lake infilling a temperature drop of at least 3°C was registered. Whittington and Hall (2002) suggested that the four Dansgaard–Oeschger cycles, GI-8, GI-7, GI-6 and GI-5, could be tentatively identified within the sedimentary/palynological record of Tolsta Head.

In the Pleniglacial, the short climatic optimum during the warmer phases of the Dansgaard–Oeschger cycles was reached early in time and it is possible that during this short period mean July temperatures may well have been higher than 10°C. However, since the timescale of the Sourlie high-resolution micro- and macrofossil diagrams is unknown, this cannot be tested. Other high-resolution, radiocarbon-dated sequences are necessary to further investigate this assumption.

9. Conclusions

Detailed botanical and zoological analyses of organic layers found on the upper surface of glacio-fluvial deposits at Sourlie, provided new insights into the vegetation mosaic and climate of western Scotland during Middle Pleniglacial. Between ca. 33.5 and 29 ka BP, when this part of western Scotland was free of glaciers, an intermediate between a low shrub tundra and a sedge–grass–moss tundra was present. The vegetation must have been diverse enough and regionally extensive to support reindeer, woolly rhinoceros and mammoth. Palaeotemperature reconstructions suggest that at the beginning of formation of the organic layers minimum mean July temperatures increased from 7 to 9–10°C, but later dropped again to around 7–8°C. A possible time correlation is proposed with one of the warmer periods of the Dansgaard–Oeschger cycles, GI-8, GI-7 or GI-6, in the stable oxygen isotope record of the Greenland ice cores during the Middle Weichsellian Pleniglacial. Mean January temperatures were probably between −34 and −11°C and mean annual temperatures somewhere between −1 and −10°C. During winter, a protective snow cover of varying thickness probably enabled perennial plants, especially shrubs, to survive.

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