

The late-glacial (late-Devensian) and
post-glacial (Flandrian) diatom assemblages
from lochs in northern Scotland.

submitted for degree of

Ph.D.

1974

by

Elizabeth Y. Haworth

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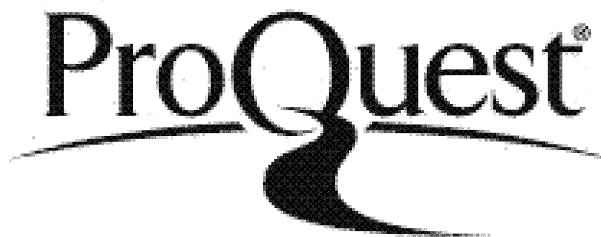
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Summary

A core from sediments of Loch Sionascaig, north-west Scotland was originally analysed to determine the changes in the late-glacial and post-glacial diatom assemblages. These indicate a trend from diatoms of alkaline assemblages in the late- and early post-glacial to those of acid and unproductive waters. This is apparently a response to changes in soils and vegetation upon the catchment area of the lake. Three diatom assemblage zones have been demonstrated within the late-glacial and zone 2 contains an unusually high proportion of planktonic Cyclotella spp.

Three other late-glacial profiles were analysed, from L. Cam and L. Borralan in the same neighbourhood, and L. Tarff in the L. Ness area, to discover 1) whether this zonation applied generally, 2) whether taxa were characteristic of certain parts of the profiles, and 3) if other profiles include a similar planktonic phase. The sites varied in size and morphometry but the three zones could always be distinguished although assemblages differed slightly; none included a high percentage of Cyclotella in zone 2. Closer interval analysis has resulted in recognition of several subzones including one that can be correlated with the Bølling-Allerød stade.

Environmental interpretation is based on comparison with modern diatom assemblages and most taxa present in the late-glacial now occur in alkaline, nutrient-rich lakes. The lack of diatom plankton in the late-glacial suggests a similarity with some alpine lakes where diatoms are predominantly benthic. This similarity may have been initially due to severe climate and low nutrient supply. Continuation of this type of assemblages throughout the interstadial and into the early post-glacial suggests that the environment depends on the type of soils, vegetation and the amount of inwash of material into the lakes, rather than on climate.

Acknowledgements

I should like to acknowledge with gratitude all the advice and assistance I have received during this study:

Access to the lochs has been by kind permission of the Nature Conservancy, the Assynt Estate and the Glendower Estate.

The present project forms a part of a larger cooperative study by the Quaternary Research Group. I have therefore been able to make many additional observations by the correlation of my analyses with those made by Mrs T. G. Tutin, Miss A. P. Bonny and Mrs J. P. Lishman. I should also like to thank the various members of the coring team for their co-operation in the field.

I have had many valuable discussions on the diatom taxonomy with J. R. Carter, R. Ross, Miss P. A. Sims, M. Möller, R. Simonsen and B. Hartley. The scanning electron microscope studies were made possible by the generosity of Dr W. Hale, Liverpool Polytechnic Biology Department, and Dr F. E. Round, Bristol University Botany Department in allowing me time on their instruments.

Reference has been made to diatom type slides at the British Museum (Natural History), London and to those loaned by the Naturhistorisches Museum, Vienna.

All personal communications have been duly acknowledged in the text.

The Royal Society granted permission for the reproduction of Figures 7 - 10 in Pennington et al 1972 (figs. S 15 and S 16).

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Table 1 Terminology used in Quaternary palaeoecology
(based on van Eysinga 1972 with reference to Sparks & West 1972)

Period	Epoch	Stage/Age (local classifications)						Pollen Zone
		N. America	Alpine	N. W. Europe	British	(casual usage)	Scandinavian	
Quaternary	Holocene			Flandrian	Flandrian	post-glacial		VIII VII VI V IV
				10 ⁴ years				
	Pleistocene	Wisconsinian	Würm	Weichselian	Devensian	late-glacial (including Interstadial)	younger dryas alleroð older dryas	III II I
					7x10 ⁴ years	full-glacial	glacial	
1.5x10 ⁶ yrs		Sangamonian	Riss-Würm Interglacial	Eemian	Ipswichian	interglacial		
	1.5x10 ⁶ yrs							

Introduction

The study of peat or lake deposits, that have accumulated in orderly succession since the last, Pleistocene, Ice Age, is directed towards the interpretation of the changes that have taken place in the environment. Several different methods of approach can be applied to this study using biological, geological or chemical methods and these can now be inter-related to provide greater definition in the interpretation of the past environments, either on a local or a regional scale.

One such approach is to study the diatom assemblages in the sediments in order to evaluate changes that have taken place in the limnological environment. This present study includes a detailed analysis of the diatom assemblages that is designed to explore the relationship of the late-glacial (Late-Devensian, table 1) diatom assemblages to the sediments in which they occur and to attempt to interpret these assemblages according to their correlation with present day diatom communities. It is recognized that the diatoms form only part of the algal community but they are the only group that, due to the siliceous nature of their cell walls, leave sufficient record in the deposits for reliable identification of practically the whole diatom assemblage. An interpretation based on these assemblages is made somewhat easier by the fact that this particular group has frequently been studied in isolation from the rest of the algal community. The remains of some of the other algal groups can also be found in lake sediments but these are never representative of a whole group and their preservation is often dependent on the type of deposits and so does not always reflect their true distribution. The only circumstances in which the diatoms may not be truly represented are in highly alkaline deposits where dissolution of the silica cell walls (frustules) may occur (Round 1963 and personal observation).

The diatom remains in geological deposits have been studied since the early nineteenth century when microscopists named and listed the taxa found in diatomaceous earths without any reference to their origin (Ehrenberg 1837, Gregory 1856). Due to the advancement of research into the sediments of the Quaternary Period (table 1) emphasis is now placed on the identification and examination of the changes in the diatom assemblages in relation to the stratigraphic sequence of the deposits in which they occur (Round 1961, Evans 1970). The present study is based on the detailed identification of as many of the taxa as possible, under the light microscope. This has necessitated reference to a wide range of taxonomic literature and to some of the original material, in the form of type slides. The scanning electron microscope has also been used to ^{explore}~~explain~~ the morphological differences between several related taxa. In this way every effort has been made to define the taxa that occur in the assemblages. This study has led me to erect several new taxa from specimens found in the sediments, as I believe that they have not previously been described (Haworth 1974).

The diatom assemblages in the sediment profiles can be defined in terms of biostratigraphic units as Diatom Assemblage Zones (DZ) in the same way that West (1970) defines Pollen Assemblage Zones. These can then be used to describe the sequence of events in the profiles through the sediments. They can also be related to similar changes in sediment composition (lithostratigraphy) or to the assemblages of other biogenic fossils present, such as pollen, seeds, ostracod, cladoceran, or other remains.

The interpretation of the past environment that is made from the composition of the diatom assemblages is based upon the known ecology of the same taxa at the present time. All the diatom taxa found in these

late-glacial (Late-Devensian) or post-glacial (Flandrian) assemblages can be found living in various parts of the world and the assumption that the ecological requirements of these taxa have not greatly changed during the last c. 14,000 years is based on the fact that this represents a relatively short period of time in the history of the group. Many of the same types can be found in deposits of Eocene age and the history of the group dates back c. 175 million years to the Jurassic. Similar assumptions are also made for terrestrial vegetation or faunal assemblages where these are used to interpret past environments (Pennington in Pennington et al.¹⁹⁷², Coope and Brophy 1972). Although something is known of the ecology of most of the dominant or ubiquitous diatom taxa and they are frequently recorded in published literature there are many taxa about which we know very little. The latter are frequently the taxa that show definite presence or absence distribution within these sediments and they could be useful as indicator taxa if their ecological preferences were better understood. There has also been a tendency for ecological studies to be concentrated on the taxa of eutrophic or alkaline waters (Jørgensen 1948, Foged 1954, 1969, Hustedt 1950) for geographical and/or practical reasons and therefore the diatoms of these waters are rather better known than those from acid or oligotrophic waters. In this project use has been made of as much ecological information as is available in the interpretation of the environmental conditions in which the diatom assemblages may have lived in lakes in northern Scotland.

The study of sediments from lakes (lochs) in northern Scotland forms a part of a programme of co-operation between members of the Quaternary Research Group of the Freshwater Biological Association in the study of the history of lakes and their catchment areas. The first part of this thesis, the diatom analysis of the sediments of Loch Sionascaig, is part of an already completed study (Pennington, Haworth, Bonny and Lishman 1972).

Prior to this profile the only other published work of this type in Scotland was Alhonen's study of Loch of Park, a drained lake basin in the lowlands in Aberdeenshire (Alhonen 1968) which was of quite different morphometry from Sionascaig. Here the diatom profile is necessarily restricted to the late-glacial and the early post-glacial in which Alhonen noted the trend from eutrophy to oligotrophy, a trend consistent with the evidence from the English Lake District (Round 1961, Haworth 1969) but apparently the reverse of that found in some of the Scandinavian lakes. The zonation in this case was based upon the pollen evidence rather than on differences in the diatom assemblages.

The choice of Loch Sionascaig as a suitable site in northern Scotland (area 1 in fig. 1) in which to study the changes in the diatom assemblages was made with the knowledge that this was one of the few of the larger British lakes in which a conformable deep-water late-glacial sequence of sediments had been found (Pennington and Lishman 1971) and where the history of the terrestrial vegetation indicated well defined environmental changes to which the diatom assemblages could be related (Pennington et al 1972). This site, and the others which are also used in this study, all lie well outside the limit of the Loch Lomond Readvance (fig. 1) which is correlated with the final cold period of the late-glacial, ie. the Younger Dryas (table 1). Sediments relating to this episode at these sites are therefore the result of solifluction of the local land surface rather than glacial inwash. Where the catchment area of a lake comes within the line of the Readvance, as at Loch Maree and Loch Clair in the vicinity of Ben Eighe, the existence of thick impenetrable mineral deposits at the base of the Flandrian organic mud suggests that there has been inwash of glacial material during this period.

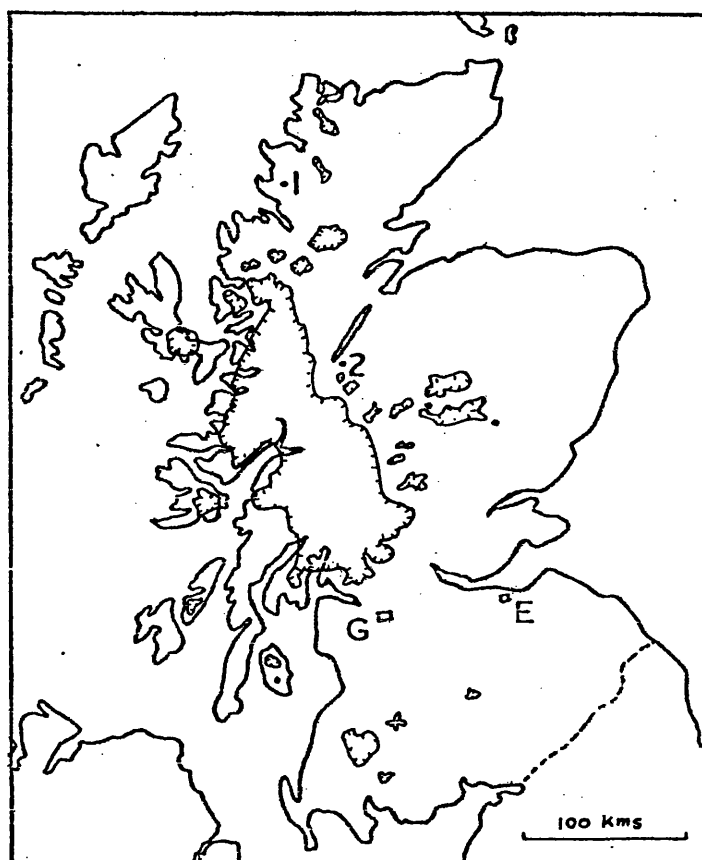



Figure 1. Location of areas 1 and 2 in Scotland and the limits of the Loch Lomond Readvance ().

From Sissons 1967.

E = Edinburgh, G = Glasgow

The sediments from Loch Sionascaig provided the opportunity for the first complete and continuous profile of the changes in the diatom assemblages from the retreat of the ice of the Devensian Stage (table 1) up to the present day, from a lake in this region. It is also the first profile from deep-water sediments from any relatively large lake in Britain. The diatom assemblages in the full profile indicate that there has been a change in the environment of this loch from eutrophy to oligotrophy of somewhat greater magnitude than the trend indicated in the sediments of the English Lake District lakes (Haworth 1969). Comparison with parallel analyses of pollen and chemistry showed that these changes can be correlated with similar changes in the soils and vegetation of the catchment area. The late-glacial and early post-glacial diatom assemblages revealed several interesting features including the unusual occurrence of a planktonic diatom phase within the late-glacial which had not previously been recorded. The length of this part of the profile and the uninterrupted stratigraphy of the late-glacial sequence also made the precise analysis of the different types of sediments within this period possible. The distribution of some of the rarer diatoms in the assemblage could also be investigated and their use as indicator taxa of either diatom zones, or environmental conditions, assessed.

In order to investigate these aspects further and to confirm that parts of the late-glacial sequence conform to a regional pattern of changes and are not merely due to circumstances prevailing at one site, three other late-glacial profiles have been analysed for comparison. Lochs Cam and Borralan both occur within the same locality as Loch Sionascaig (fig 2), and the former is comparable in size and morphometry so that it was therefore thought that the sediments might include a similar late-glacial planktonic phase, even though the local geology was

rather different (fig 3). Loch Borraran is a small shallow loch and so provided a site of contrasting size within the same area; it was also more readily accessible than other local sites. The fourth site, Loch Tarff (area 2 in fig 1) lies further to the south and further from the west coast, in a contrasting climatic region of lower rainfall and less peat. It is again a small loch, intermediate in size between Borraran and Cam (table 2) and the sediments contain a late-glacial diatom assemblage that is very similar to that found in Borraran. In the absence of other deep-water profiles the two smaller lochs also provide a more direct means of comparing the late-glacial diatom assemblages of northern Scotland with those from other sites which are of similar size in the British Isles.

As a result of the four late-glacial analyses, the theories that were originally proposed on the basis of a single analysis of the Loch Sionascaig profile have been somewhat modified. The overall division of the profile into three diatom assemblage zones (see p. 229 in Pennington et al 1972) has remained much the same but now includes several subdivisions in recognition of other changes in the assemblages that have been brought to the notice by more precise analyses.

Figure 2. Area 1, relief and drainage pattern showing Lochs Sionascaig (S); Cam (C); Borralan (B); Fionn (F); Veyatie (V); and Urigill (U), Lurgain (L).

[Scale: $\frac{5}{8}$ " = 1 mile (1 cm = 1 km); contours in feet (1000 ft = 304.8 m)]

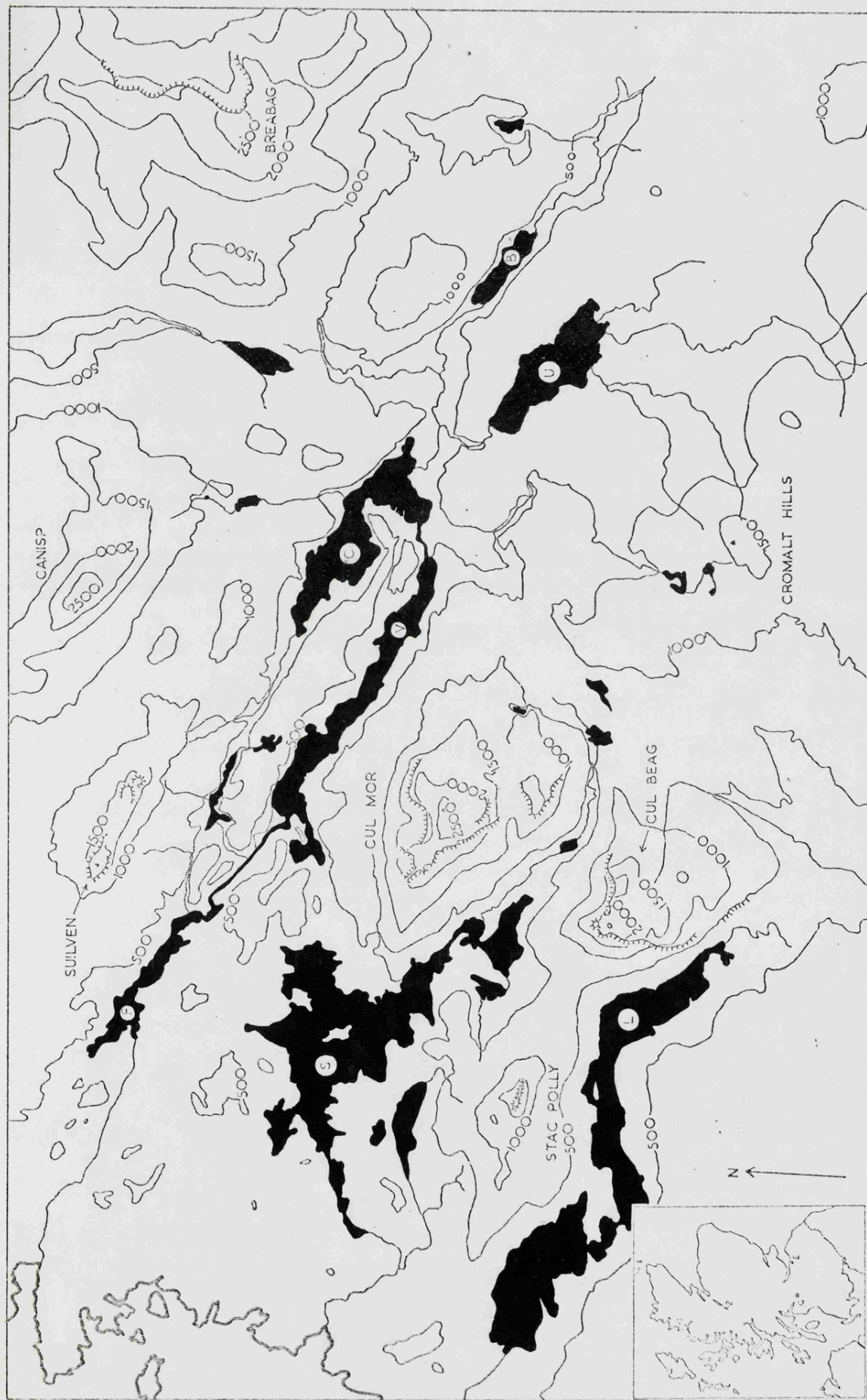


Figure 2

Location and description of the sites

Area 1. Lochs Sionascaig, Cam and Borralan are all in north-west Scotland, north of Ullapool and Loch Broom and south of Loch Assynt, the first being in the county of Ross-shire and the other two in Sutherland (fig 2). The Grid References and the dimensions of all three lochs are presented in table 2.

Loch Sionascaig forms part of the Inverpolly Nature Reserve which is leased to the Nature Conservancy. It lies on the boundary of the Lewisian gneiss of the low coastal foreland and the Torridonian sandstone mountains of Cul Mor, Cul Beag and Stack Polly (figs 2 & 3). The gneiss forms an uneven, hummocky terrain with many knobs of bare rock rising above blanket bog. There is a little remnant birch woodland on well drained slopes but the major vegetation is Calluna moor or blanket ^{bog} ~~peat~~ (Campbell 1967). Glacial drift covers the lower slopes of Cul Mor and Stack Polly and its distribution coincides with the presence of the ^{soft} bottom deposits towards the eastern, upper end of the loch (for detailed description see p. 214, Pennington, in Pennington et al 1972).

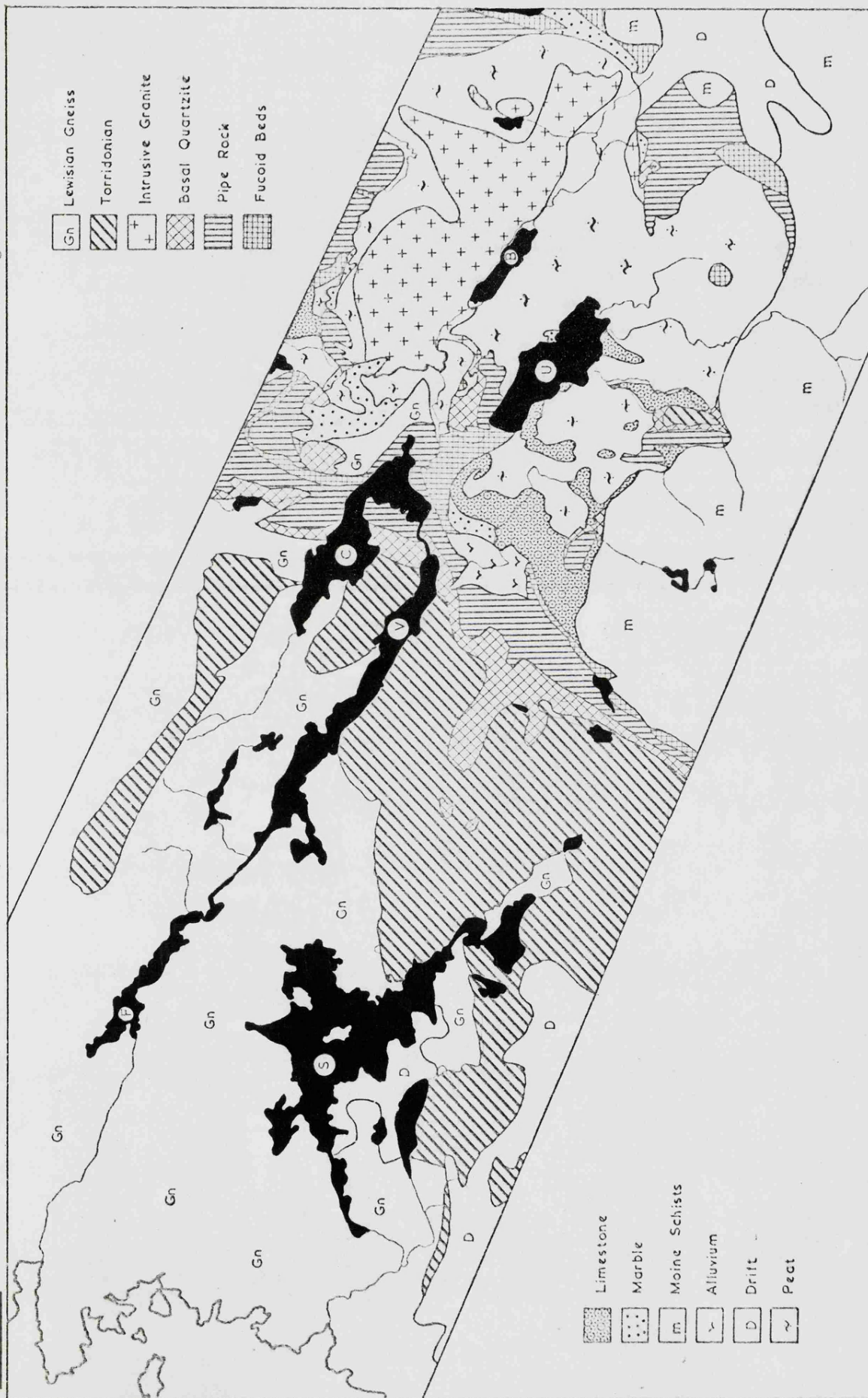
Lochs Cam and Borralan are east of Sionascaig and form part of the Fionn Loch drainage system that drains the area between Suilven, Breabag, Cul Mor and the Cromalt Hills and enters the sea via the River Kirkaig (fig 2). This area is far more complex geologically as the Ledmore basin lies across the Moine overthrust (fig 3). The west end of Cam Loch is on Lewisian gneiss but the inflow there also drains from the Torridonian slopes of Suilven. The eastern end of the loch is on sandstone and basal quartzite. There is also an outcrop of limestone to the south of the loch (fig 3). The vegetation is again heather or sphagnum bog and deer grass, with occasional

Table 2 Dimensions of the 4 sites

	Sionascaig	Cam	Borralan	Tarff
Grid Reference	NC 120140	NC 210140	NC 260110	NH 425100
Height above sea level	243 ft. 73.4 m.	405 ft. 123.5 m.	460 ft. 140 m.	956 ft. 291 m.
Length	3 miles 4.8 km.	2 $\frac{3}{4}$ miles 4.4 km.	1 mile 1.6 km.	$\frac{2}{3}$ mile 0.97 km.
Area	2 sq. miles 517 ha.	647 acres 261 ha.	118 acres 477 ha.	131 acres 52.8 ha.
Drainage area	15.5 sq. miles 4000 ha.	16 sq. miles 4140 ha.	6.5 sq. miles 1680 ha.	1 sq. miles 259 ha.
Max. depth	216 ft. 65.8 m.	122 ft. 37 m.	21 ft. 6.4 m.	89 ft. 29 m.
Mean depth	60.5 ft. 18.5 m.	38 ft. 11.6 m.	9.5 ft. 2.9 m.	24 ft. 7.3 m.
Depth of water at core sites	17 m.	14 m.	3.5 m.	11 m.

N.B. This is based on data from O.S. maps and the Bathymetric Survey by Murray and Pullar 1910 in which British Units of feet, miles and acres are used, Metric equivalents are also given.

Figure 3. Geology of area 1, based on Murray and Pullar 1910 (scales and abbreviations as in Figure 2).



birchwoods remaining in sheltered, well drained areas and on the islands in the loch. Grassland occurs on the better soils of the limestone and basal quartzite, to which fact the hamlets of Elphin and Knockan owe their existence. Part of the inflow of the River Ledbeg comes from Loch Urigill whose catchment area is part peat and part limestone; another tributary is from Loch Borralan which is in an area of glacial drift overlain by blanket peat. Borralan is the smallest and shallowest of the three lochs (table 2) and occupies a hollow in the floor of a gently undulating plain at the foot of hills of intrusive granite.

This area of Scotland now has a mild and wet climate which is influenced by the proximity to the west coast. All the sites are also at less than 500 ft (152 m) above sea level and so incur the optimal climate for that area due to their low altitude. The mean January temperatures are 4.4°C - 5.5°C while the mean July temperatures are only 12.8 - 14°C (Darling and Boyd 1964). The average rainfall of the area varies from 50" (127 cm) on the coast to 90" (229 cm) on Cul Mor, with May being the driest month and October the wettest. The area also has approximately 27 days of snowfall with snow lying on about 6 days in the year (Campbell 1967). All three lochs are affected by the east/west winds, mainly westerlies, and local information (Mr P.W. Hay, Factor of Assynt Estates - personal communication) is that the autumnal gales prevent any use of boats on Lochs Cam and Veyatie during that time; personal experience has shown that the lochs can be extremely rough, even in summer. The disturbed surface sediments of Loch Borralan show that the mud surface of this site comes within the zone of wind induced turbulence (Pennington et al 1972). Wave-cut soil and peat profiles are to be found around the shores of Sionascaig and Cam.

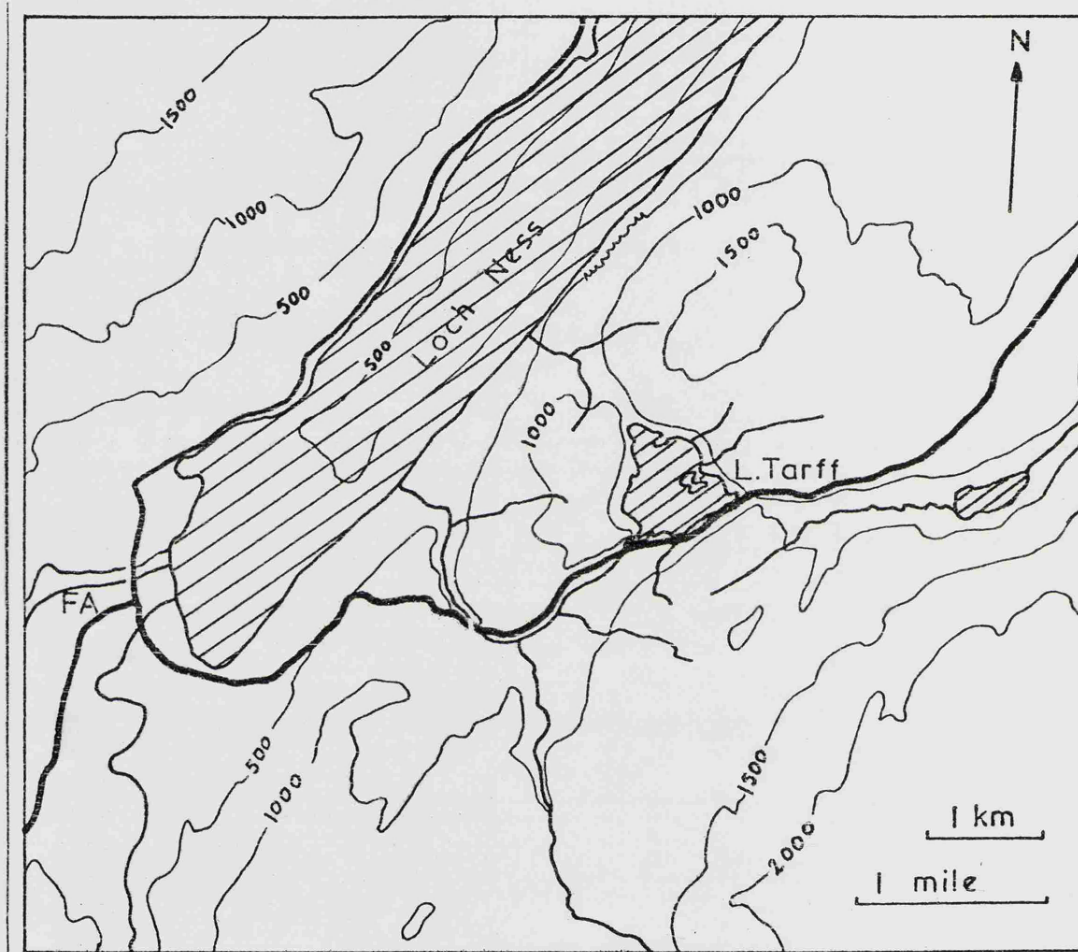


Figure 4. Area 2. Loch Tarff.

[FA = Fort Augustus; contours in feet, 1000 ft = 304.8 m]

Clearly climate and geology combine to affect the soils and the vegetation and they ultimately affect the limnology of the lochs. With the exception of the limestone outcrops, the hard rocks add little to the soils, especially in such a mild oceanic climate, and what little soil there is tends to be acid (Campbell 1967). The topography and high rainfall promote the sphagnum bog while wind, poor soils and grazing by sheep and deer exclude trees from all but the sheltered and better drained areas.

Area 2. The fourth site, Loch Tarff, is on the uplands to the east of the head of Loch Ness in the county of Inverness-shire (fig 4). The loch comes between Cam Loch and Borralan in size (table 2) and is roughly triangular in shape. The surrounding mountains of the small catchment areas rise to 1800 ft (550 m) but are only 850 ft (258 m) above the level of the loch itself. A few small streams flow into the loch and the outflow goes to Loch Ness via the Alt Doe River. The local rocks are all siliceous Moine schists (Craig 1965) and the vegetation is mainly heath and grassland on acid mor soil with a few patches of birch woodland mainly on the islands in the loch (Pennington et al 1972). The climate is perhaps slightly more extreme than that of the sites on the west coast with a mean January temperature of 3.5°C and July mean of $14 - 14.5^{\circ}\text{C}$ (Darling and Boyd 1964). The shape of the valley shelters the site from all winds except those from the south-west.

Methods

1. Fieldwork

Fieldwork expeditions to northern Scotland have been part of the programme of the Quaternary Research Group of the Freshwater Biological Association during the past 7 years, 1966 - 1973, with the object of taking cores of sediment from the various lochs in the area. The initial reason for extending quaternary studies into this area (Pennington, personal communication) was to investigate the distribution of iodine in the sediments of a lake comparable in size to Windermere in the English Lake District but within a more oceanic climate of higher precipitation-evaporation ratio (Pennington and Lishman 1971).

One of the principal factors dictating the choice of site within the area has been the accessibility for boat and coring equipment as many lochs are not even near tracks suitable for a landrover. Only in one instance was it considered feasible and practical to portage the equipment and boat overland a half-mile to reach Loch Sionascaig.

Material for this thesis has come from several expeditions even though the author was only present on those of 1969 - 1973. Some lochs have been visited several times.

- 1966 L. Ness, L. Tarff and other lochs of the Ness area.
- 1967 L. Sionascaig and Loch Borralan.
- 1969 Lochs in the Kinlochewe and Inverpolly areas (Sionascaig visited but not worked on).
- 1970 Norwegian lakes in Jostedal and Jotunheim regions (with Brathay Exploration Group expedition).

- 1971 Kinlochewe area, Loch Clair and L. Coulin.
- 1971 Lakes in south east Iceland (with Brathay Exploration Group expedition).
- 1972 L. Tarff, L. Duntelchaig and others in the Ness area; Cam Loch and L. Veyatie.
- 1973 Cam Loch, L. Veyatie, L. Stack and L. Tarff.

Cores were obtained by the use of a range of pneumatic corers designed by the late F. J. H. Mackereth to take uninterrupted cores of the lake sediments of 1 m, 4 m or 6 m in length. These corers are much used by the Quaternary Research Group of the Freshwater Biological Association and their use and operation in the field has already been fully described by Mackereth (1958, 1969), Walker (1967) and Pennington (in Pennington et al 1972). The corer is anchored to the lake bed by a drum that forms the base and the core tube is then pushed past a fixed piston into the sediments by compressed air which is fed into the space between the core tube and the outer casing. Once the corer has been brought ashore complete with its sample of sediment the core tube can be retracted by pumping water into the "annular" space behind the fixed piston. The extruded core can then be collected on wooden trays.

2. Table 3 Cores used in this study

Lake	core used for diatom analysis	other analyses, by other workers, on the same material
Sionascaig	67 - 6	pollen, chemistry, radiocarbon dating (Pennington <u>et al</u> 1972)
Borralan	67 - 1	pollen (Pennington <u>et al</u> 1972)
Tarff	66 - 1	pollen, chemistry (Pennington <u>et al</u> 1972)
Cam	72 - 7	pollen, radiocarbon dating (Pennington in press)

other cores inspected during the course of the study

Cam	72 - 9	chemistry
"	72 - 11	none
"	73 - 6	none
Veyatie	73 - 4	pollen (Pennington unpublished)
Stack	73 - 4	pollen (Pennington unpublished)
Duntelchaig	72 - 2	none
"	72 - 4	pollen (Pennington unpublished)
Windermere Low Wray Bay	73 - 2	pollen, radiocarbon dating (Pennington unpublished)
Coniston	71 - 6	pollen (Pennington unpublished)

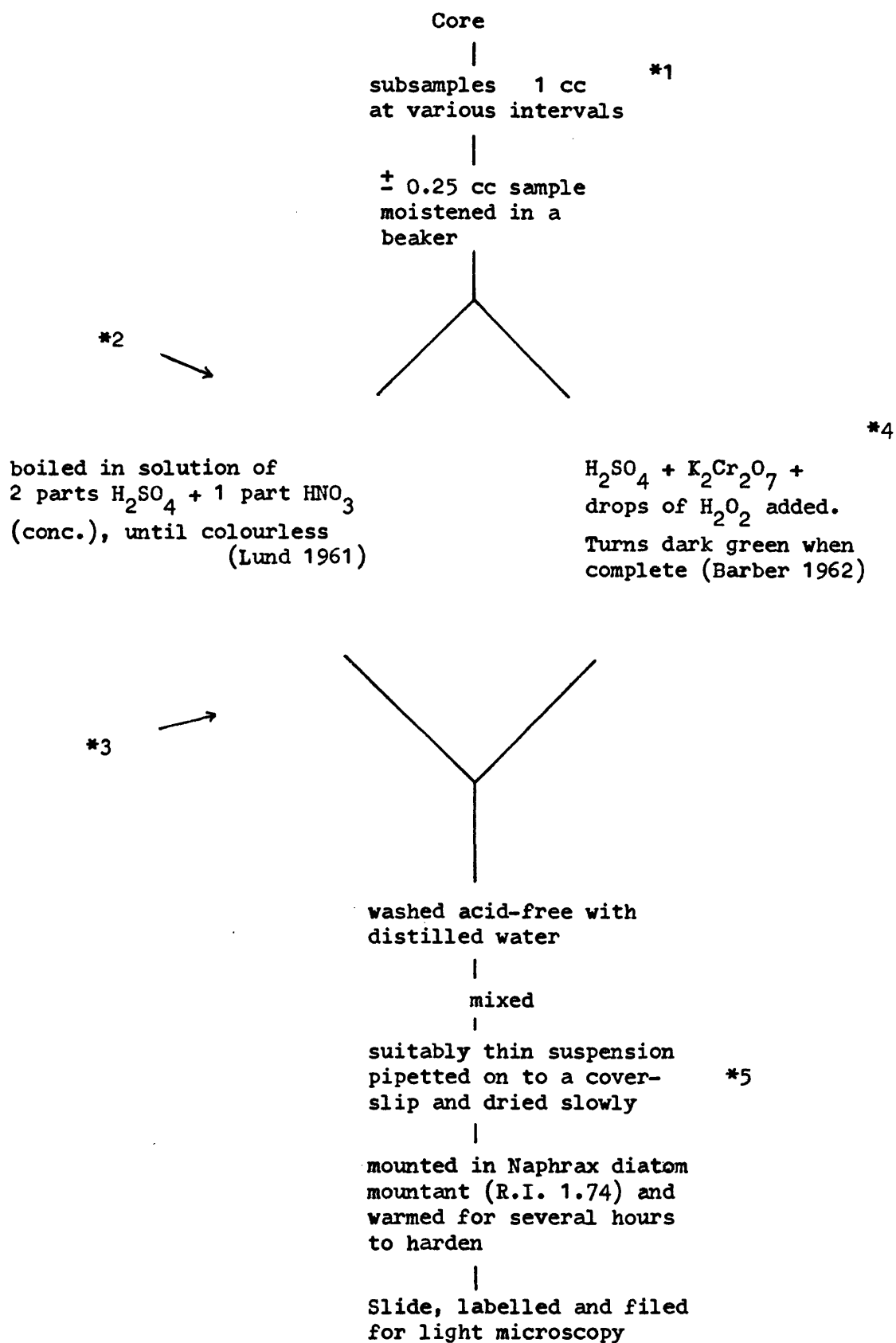
3. Laboratory Methods

The choice of the method of analysing the diatom assemblages has been guided by several circumstances concerning the sites used in this study and the part of the sediment record on which attention has been concentrated. The only previous information on the record of the diatom assemblages in the lakes in north-west Scotland was a brief list of late-glacial taxa from the site at Loch Droma, just south of Ullapool (Rev. F. Bastow, in Kirk and Godwin 1963). It was therefore desirable to study the profile from Loch Sionascaig in as much taxonomic detail as possible, in order to ascertain the changes in the diatom assemblages. Preference has been given to the use of percentage analysis as a method of assessing the whole diatom community from a large number of samples. Previous work in another region (Haworth 1969) has suggested that the diatoms which are indicative of the different phases, especially those in the late-glacial period, are often ones that are infrequent in the assemblages and that these can best be assessed at the level of 'presence and absence' as they are generally ignored by quantitative methods. As yet very little is known about the way in which these late-glacial diatom assemblages relate to a living population and to the environment that it represents. It is therefore better to seek the taxa that are indicative of certain types of environment rather than endeavour to interpret some of the complex changes in the numbers of the dominant taxa in these sediments.

An alternative approach to attempt to find a suitable method of quantitative analysis has been rejected for the present study on the grounds that there was insufficient evidence concerning the rate of accumulation of the late-glacial sediments for there to be any significant improvement

in knowledge that would offset the practical limitations. Once quantity is involved the broken fragments have also to be more carefully assessed and some account must also be taken of the large differences in the volumes of the various taxa in order to equate individual with biomass. The details of the actual numbers of individuals of different taxa have very little relevance unless they can be correlated with the annual accumulation rate of the sediment and also with the pattern of the diatom distribution over the whole basin. The calculation of the accumulation rate is dependent on the dating of discrete layers of sediment and this did not appear to be possible for the original profile from Loch Sionascaig because the late-glacial sediments contain so little carbon. It was also unlikely that this type of site could solve the problems of the lateral distribution of diatoms since the original survey of the loch (Pennington et al 1972) had already shown that the conformable sequence of sediments is not well distributed within the lake basin.

Recent studies of Cam Loch have also shown that the late-glacial sequence can only be obtained from certain parts of that loch. On the other hand it has been possible to obtain some dates for the late-glacial by radiocarbon methods (Pennington, in press and table 10), therefore the future use of quantitative methods, such as the one recently proposed by Battarbee (1973), cannot be entirely ruled out.



* see notes

a) Preparation of samples for microscopy

Subsamples from the cores, each less than 1 cc in volume, were taken at various intervals depending on the length of the profile and the lithology (see various tables and diagrams for the sites concerned). Two general methods of removing the organic matter from the sample and cleaning the diatom frustules for analysis have been used in this study. These are best explained in diagrammatic form (fig 5).

- Notes: 1. The ideal interval is based on 16 ths rather than 10 ths as this can be progressively halved by intermediate samples when closer intervals are required.
2. Some samples from Cam Loch were first heated with hydrochloric acid to remove the calcium carbonate, and samples were washed with distilled water.
3. In the upper part of the Sionascaig core samples were difficult to clean because of the nature of the sediment. The diatoms tended to matt together during the acid cleaning and this was found to be correlated with the inwash of peat from the catchment area (Pennington et al 1972) and may be due to the tendency of orthosilicate anions to aggregate into a neutral silica sol in acid water (Hutchinson 1957). This flocculation was dispersed by adding a few drops of very dilute sodium carbonate (less than 1%) to about 20 ml solution of the sample and warming for a short while. The solution was then neutralized with 2 - 3 drops of 5% hydrochloric acid. A more concentrated alkali might also have dissolved the diatoms as well so the method had to be carefully checked and microscopical observation showed that there was no detectable damage to the diatom frustule.

4. The amount of potassium dichromate picked up on a small spatula is sufficient.

5. The suspension spreads more evenly if the coverslip is first misted by breathing on it.

Some subsamples of the acid cleaned material were prepared for study under the scanning electron microscope (SEM) (see Taxonomy section part 2). The material was dried on to stubs and then coated with 10 cms of 0.25 diameter gold/palladium alloy wire at a distance of 10 cms and angle of 45° , under vacuum (R. M. Crawford, personal communication).

These samples were studied under Cambridge Scientific Instruments Mk II Stereoscans at both Liverpool Polytechnic and Bristol University Botany Department.

b) Diatom assemblage analysis

The samples for percentage analysis are simple to prepare and the concentration of material on a slide can be adjusted to make it suitable for exacting taxonomic identification at high magnification. It has therefore been possible to analyse a large number of samples from the different cores and to produce a close interval study of the relevant sections in the time available.

The diatom identification and assemblage analysis were all made under a Leitz Dialux microscope (old type) using phase contrast illumination and a X 90 objective. The taxonomic literature used in the identification is discussed in the Taxonomy section (page 30). A total of one thousand diatom valves have been counted in each sample, along a transect chosen at random, and each taxon is recorded as a percentage of the total. This total has been found to include the majority of taxa that are present on a slide as more than just isolated specimens and it is also a convenient total for percentage calculations. Duplicate counts of some of the samples

have served as a check on the distribution of the material on the slides with the re-counts falling within acceptable limits of variation.

A list has also been made of all other taxa present on the slide, the whole slide being scanned with a X 20 objective.

The broken pieces of diatom frustules (frustules are formed of two valves joined by overlapping girdle bands) that occur in the samples pose the problem in the analysis of what pieces should be included in the assemblage as representative of a diatom valve. In many cases fragments may represent material washed in from other, or previous, assemblages and may not be a part of the present assemblage at all. Some pieces are unidentifiable because they are too small and broken or because they are from a section of the frustule that cannot be identified to any specific taxon. Each case is one in which a decision must be made and familiarity plays a major role in identification as it is easier to identify smaller pieces of familiar diatoms than it is to identify the less well known ones. Some of the genera, eg. Synedra spp, are nearly always broken and difficult to identify in the sediment samples because of their long, needle-shaped frustules, if these pieces were ignored then these taxa would be under-represented or even appear to be absent from an assemblage in which, in life, they form an important part. I can only propose what, to me, seems a satisfactory philosophy. It is that any fragment greater than $\frac{1}{3}$ - $\frac{1}{2}$ of a valve should undoubtedly be treated as a single specimen. It is also more important to include the fragments of taxa that are rare in the samples or are fragile than it is to include the more abundant taxa. The latter will not increase or decrease the percentage by any great proportion whereas the former occur at presence and absence level and have a definite contribution to make to the completeness of the assemblage.

4. Use of data

a) Diatom diagrams and tables

The significant features in the basic analysis of the diatom profiles are reproduced in two ways:-

First, as diatom diagrams (figs S 15 i & ii) for the Sionascaig profile which include all those taxa that show any stratigraphic pattern within the profile. The taxa are arranged in groups according to pH preference and in order of their appearance. All other taxa that are present in consistently low percentages or occur only rarely have been omitted. The two sections of the profile constitute the early, more alkaliphilous phase (fig S 15 i) and the later, acidophilous phase (fig S 15 ii); these were divided for convenience in drafting large diagrams (Pennington et al 1972).

The second method combines a diagram for the dominant genus, Fragilaria (figs S 17, 19, 21), with tabulation of the diatom assemblage data for the Cam, Tarff and Borralan assemblages (tables S 13, S 14, S 15) with the taxa (as numbers/1000 or + = presence) arranged in ascending order of occurrence or importance in the core (but not grouped according to pH). This form of presentation avoids very long diagrams or the splitting of diagrams into confusing sections.

b) Zonation of the diatom profiles

The divisions of the profiles into diatom zones have been made by inspection of the diagrams or tables and are placed according to changes in the diatom assemblages. They are, at this point, unrelated to the lithostratigraphy or to any other analyses of the same cores. These are therefore 'diatom (assemblage) zones' (eg. SDZ 1 - Sionascaig diatom zone 1) and the zones of the different sites are initially unrelated although ultimate conclusions may prove otherwise. This is in accordance with the definition of an 'Assemblage Zone' that has been made by West (1970). The relationship of the diatomsto the lithology and the pollen zones is shown in the

tables of diatom stratigraphy for each site (tables 5 - 8).

The boundaries of the diatom zones are in actual fact arbitrary divisions made in a continually changing system for the purposes of description and have been placed at the levels where adjacent samples show the greatest differences between them. In this study the whole diatom assemblage is not shown on the diagrams and the selected taxa have also been 'arranged' to show the pattern of distribution. It is therefore convenient that a calculation based upon the whole assemblage can substantiate these boundaries in the profile of the Cam Loch assemblages (fig 13). This calculation is based upon exactly the same information as that used in visual inspection and it can therefore be said to include the same errors (that are inherent in percentage analyses) as the visual method. The percentage of similarity between samples (Southward 1966) compares two adjacent samples and sums that part that is common to both samples, ie. the lower figure in each percentage of each taxon :-

eg. If, in sample 1	and in sample 2
A = 60	20
B = 7	8
C = 10	50
D = 23	22

then the sum of similarity = $20 + 7 + 10 + 22 = 59\%$ similarity

The result is shown in fig 13 and the lowest percentages of similarity show where, overall, there is maximum change in the diatom assemblage between one sample and the next. This does not necessarily occur at the base of any increase or decrease but at the point of greatest difference between adjacent samples. The results are obviously weighted towards the dominant taxa especially, as in Loch Tarff TDZ 3, where one taxon forms a large proportion of the sample, again this can also be observed in the visual method.

c) Ecological data

The ecological preferences of many diatom taxa at the present time have been elucidated in studies by Jørgensen (1948), Foged (1953, 1954, 1964, 1968 and 1969), Round (1959), Florin (1970) and Krasske (1932). This information has been used to combine the percentage data for the taxa into various ecological groups in order to provide some indication as to the ecological conditions prevailing at the time of deposition of each of the samples. Three ecological 'spectra' have been described by Kolbe (1932) and Hustedt (1937-39) and summarized by Foged (1954) and are based on the preferences of the diatoms for water of varying salt content (Halobian spectrum), acidity (pH spectrum) and movement (Current spectrum). These categories are briefly defined in the introduction to the list of diatom taxa on page 37. The resulting diagrams of the changes in the proportions of the taxa in the various categories plotted against the depths in the cores indicate changes in the ecological preferences of the assemblages. These can sometimes be correlated with the changes in lithostratigraphy, the chemical composition or the other microfossil assemblages in the sediments.

The use of the Current spectrum (Hustedt 1937-39) has become of questionable value and it now tends to be disregarded in the literature so it is often difficult to classify the diatom taxa into the various categories. The percentage of the planktonic taxa has therefore been calculated for each sample as another method of indicating the importance of the mid-water or benthic communities. The percentages of the taxa that are frequently to be found in terrestrial habitats, the aerophilous taxa, have also been calculated. These taxa occur on wet rocks, soils and among mosses and although not all are exclusively aerial they provide evidence for the increase in inwash of terrestrial material during the periods of

increased severity in the climate. Another classification according to supposed temperature requirements is the identification of those taxa of predominantly arctic, northern alpine or 'boreal' distribution. The resulting graphs showing the proportions of boreal taxa throughout the cores (figs S 18,20,22 f) are difficult to interpret and the anomalies may well be due to the present state of knowledge concerning this group rather than to any climatic reasons.

Taxonomy

1. Identification

The essential part of a study of any diatom assemblage, be it present day or past history, is the identification of as many of the diatom taxa as possible. In the present study this has been achieved using the light microscope and it has also been possible to make use of the scanning electron microscope to clarify the taxonomic situation in one genus, Fragilaria, which will be discussed later in section 2. The case for the further interpretation of the environment in which an assemblage occurred in past history then rests on the correlation with the ecological records in the already published literature, plus any personal observations which may be relevant. It is therefore of paramount importance that the taxon identified and the taxon recorded in the literature are, in fact, one and the same.

The taxonomy of the present study therefore follows Hustedt's classification (1930, 1930-66) where possible as this is one of the standard works for northern Europe. Reference has also been made to many other authors where necessary, either, because new taxa have been identified since these works were published, eg. Achnanthes pseudoswazi (Carter 1964) or Cymbella hilliardii (Manguin 1961) or, because subsequent work has shown that it is necessary to separate some of the taxa that Hustedt previously grouped together as synonymous. Such is the nature of diatom taxonomy that opinions differ as to the grouping or separation of certain taxa; an example in the current study is the separation of Fragilaria elliptica from F. pinnata, for reasons which will be discussed later, and the distinguishing of Achnanthes minuta and A. flexella var. arctica (Cleve-Euler 1950 - 55) from A. flexella because of distinct differences in the patterns of presence or absence of these forms within the profiles of the lake sediments.

In the following taxon list the taxa have been referred to a figure, or figures, in the literature (see notes and definitions prefacing the taxon list table) in an effort to achieve some definite correlation between the taxa cited and the generally accepted taxonomy. This dispenses with the necessity of drawing every taxon listed as proof of its identity without relying on the inadequacies of written descriptions. Some of the more unusual or unidentifiable taxa are shown in figs 6 and 7 . In this way it is hoped that all the taxa cited can be related to an actual form rather than merely to one of many figured under that name such as can be found in the Fritsch collection of algal illustrations (Lund 1971).

In some cases it has been possible to check identification by reference to the actual type slide, specimen or material. Many of these are to be found in the collection held by the British Museum (Natural History) London, eg. Navicula elginensis. It has also been possible to make use of slides from the Grunow slide collection loaned by the Naturhistorisches Museum, Vienna (see part two of this section).

The authorities cited for the taxonomic names have also been checked back to their source where possible in an effort to eliminate the inaccuracies. This becomes difficult in some of the early literature where references are not always cited and the type material is not always available as the alternative method of checking.

Several of the forms found in the assemblages have not been identified to a taxon and it has seemed practical to refer to them under a code number, one that usually refers to the sample in which they were first found, and to make use of drawings, photographs and marked slides for possible identification at some future time (table 4). It would appear that several of these unidentified taxa are new to science and these have therefore been described and named in order that their position in the diatom assemblages of the lakes in this study may be discussed later (Haworth 1974).

(The relevant publication concerning the names and descriptions,
"Some problems of diatom taxonomy in Scottish lake sediments" is to be
found in the back pocket of this thesis).

Figure 6.

1. Melosira distans var. alpigena
2. Melosira tenella
3. Cyclotella comensis
4. Achnanthes levanderi (both valves)
5. Fragilaria pinnata
6. Fragilaria elliptica
7. Navicula impexa
8. Cymbella semisymmetrica
9. Navicula sp. S 340
10. Navicula sp. V
11. Navicula tenelloides
12. Amphora eximia
13. Amphora veneta var. capitata
14. Cymbella hilliardii
15. Cymbella pseudonorvegica
16. Pinnularia sp. C

Figure 6.

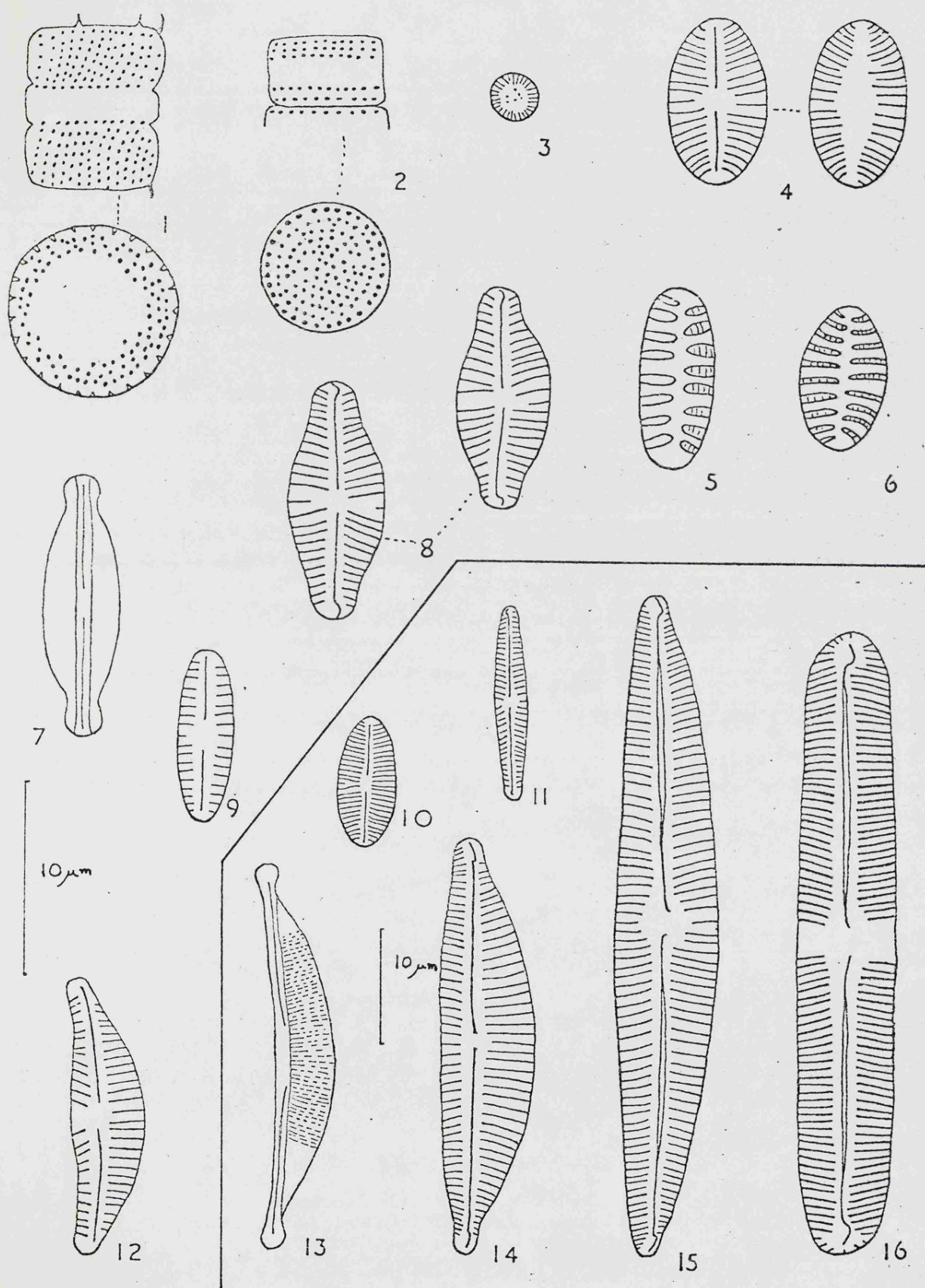


Figure 7.

17. Fragilaria sp. C 1
18. Achnanthes sp. C 546 (raphe valve)
19. Caloneis sp. C 590
20. Cymbella lacustris
21. Cymbella sp. C 546
22. Navicula subocculta
23. Navicula sp. L 100 B
24. Navicula helensis
25. Navicula interglacialis (both valves)
26. Frustulia sp. C 574 (probably F. rhomboides var. amphipleuroides)
27. Amphora sp. C 580 (probably A. ovalis)
28. Neidium sp. C 562
29. Gomphonema sp. B 168

Figure 7.

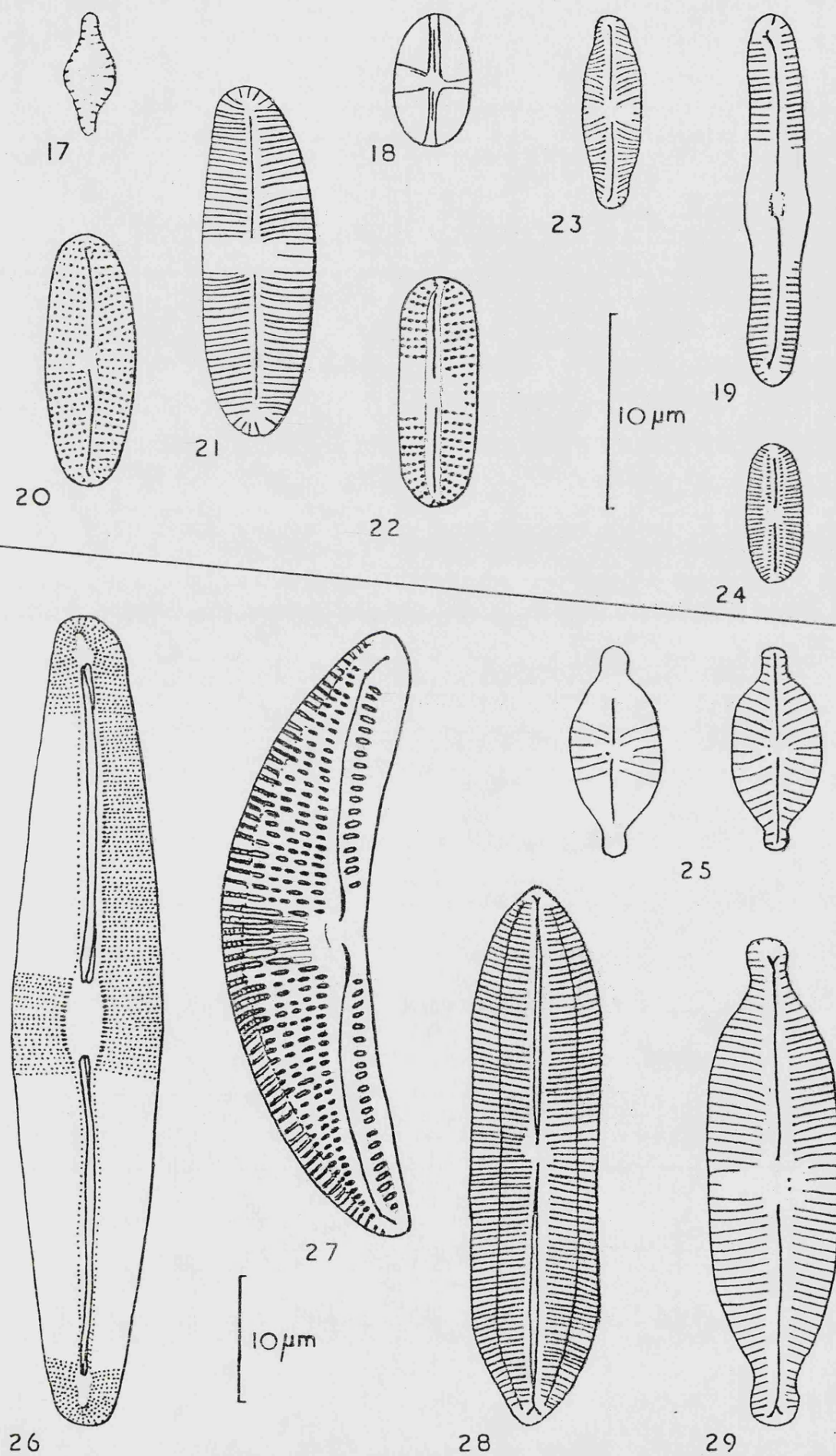


Table 4.

List of taxa found in the diatom assemblages of the
four sites.

Notes and definitions

1. Authorities and dates of publication are included where possible.
2. References: unless otherwise stated the taxa can all be referred to figures in work by Hustedt (1930, 1930 - 66). The following abbreviations have been used:-
 ACE = A. Cleve-Euler 1950 - 55. VHS = Van Heurck's Synopsis 1880 - 85.
 ASA = A. Schmidt's Atlas 1873 - 1959, * = referred to figure by original author.

Ecological notes and definitions

3. Halobion spectrum (Kolbe 1932) - the classification of diatoms according to their preference for the salt (chloride) content of the water.
 hb = halophobous - forms shunning salt and found in chloride deficient water.
 ind = indifferent - freshwater forms proper.
 hp = halophilous - forms widespread in freshwater and also thriving in slightly brackish water (less than 5% salt).
 mh = mesohalobous - forms of brackish water (5 - 20% salt).
4. pH spectrum (Hustedt 1937 - 9) - the division of diatoms according to their preference for for alkaline or acid waters.
 alb = alkalibiontic forms - living only in water with a pH above 7.
 alp = alkaliphilous forms - living mainly in water of pH 7 and above.
 ind. = indifferent forms - living in water of pH around 7.
 acp = acidophilous - living in water of pH 7 and below.
 acb = acidobiontic - living in water that has pH below 7 (except in fig 16 this group has been included in the acidophilous category).
5. Current spectrum (Hustedt 1937 - 9) - classification of diatoms according to their habitat in still-standing or flowing water.
 lp = limnophilous forms - with optimum development in standing water (these include limnobiontic (restricted) forms).
 ind = indifferent forms - widespread in flowing or standing waters.
 rp = rheophilous forms - with optimum development in flowing water (these include rheobiontic (restricted) forms).
6. pl - planktonic forms.
 ae = aerophile or terrestrial diatoms.
7. b = boreal forms - those associated with cold environments.
8. e = eutrophic; o = oligotrophic forms - those taxa associated with nutrient rich, or nutrient poor environments
9. Presence of the taxa in the four profiles:- s = Sionascaig; c = Cam; b = Borralan;
 t = Tarff. Numbers refer to columns on the respective tables, c = common, r = rare.

Taxon List

Taxon 1,2	Ecology							Loch g			
	Hal 3	pH 4	Cur 5	6	7	8	s	c	b	t	
<u>Achnanthes affinis</u> Grunow 1880		acp				o	r	c	c	r	
<u>Ac. atomus</u> Hustedt 1938							r				
<u>Ac. austriaca</u> Hustedt 1922	hb	alp			b		r	48	37		
<u>Ac. biasoletiana</u> (Kützing 1844) Grunow 1880									59		
<u>Ac. calcar</u> Cleve 1891		ind			b		2	c	54	37	
<u>Ac. clevei</u> Grunow 1880	ind	alp	lp			e	2	30	c	57	
<u>Ac. conspicua</u> Mayer 1919	hb	alp						7	117		
<u>Ac. depressa</u> (Cleve 1894) Hustedt 1933		acp					101				
<u>Ac. didyma</u> Hustedt 1933		acp					r		5		
<u>Ac. dispar</u> Cleve 1891	hp	alp						95	r		
<u>Ac. exigua</u> Grunow 1880	ind	alp			b	e		182	114	r	
<u>Ac. exigua</u> var. <u>heterovalvata</u> Krasske 1923									121		
<u>Ac. exilis</u> Kützing 1833		alp				e		55	2		
<u>Ac. flexella</u> (Kützing 1844) Brun 1880	ind	ind	lp		b		c	118	r	33	
<u>Ac. flexella</u> var. <u>alpestris</u> Brun 1880	ind	ind	lp				c		79		
<u>Ac. flexella</u> var. <u>arctica</u> (Lagerstedt 1873)	ind	ind			b			117	58		
A. Cleve 1953 *											
<u>Ac. gracillima</u> Hustedt 1926		acp					61	148	r		
<u>Ac. hauckiana</u> Grunow 1880	mh							34			
<u>Ac. holstii</u> Cleve 1882		ind					r		108	r	
<u>Ac. lanceolata</u> (Brébisson 1849) Grunow 1880	ind	alp	rb			e	r	8			
<u>Ac. lanceolata</u> v. <u>elliptica</u> Cleve 1891	ind	alp	rb				r		112		
<u>Ac. lapponica</u> v. <u>fennica</u> A. Cleve (1934) 1953 *		acp					r	64	r		
<u>Ac. laterostrata</u> Hustedt 1933	ind	ind					r	c	r	20	
<u>Ac. levanderi</u> Hustedt 1933		ind			b		49	35	49	27	
<u>Ac. linearis</u> (W. Smith 1856) Grunow 1881	ind	ind	ind		b		53	75	48	36	
<u>Ac. marginulata</u> Grunow 1880		acp					74	r	c		
<u>Ac. maxima</u> A. Cleve (1895) 1953 *										32	
<u>Ac. microcephala</u> (Kützing 1844) Grunow 1881	ind	ind	ind				57	41	c	r	
<u>Ac. minuta</u> (Cleve 1891) A. Cleve 1953 *						e		170			
<u>Ac. minutissima</u> Kützing 1833	ind	ind	ind				57	c	c	r	
<u>Ac. cf. montana</u> Krasske 1929							r				
<u>Ac. Østrupii</u> (A. Cleve 1922) Hustedt 1930	ind	ind			b		51	33	10	60	
<u>Ac. peragalli</u> Brun et Heribaud 1893		ind					r				
<u>Ac. pseudosuchlandti</u> Manguin 1961 *							83	37			
<u>Ac. pseudoswazi</u> Carter 1964 *							92				
<u>Ac. sublaevis</u> Hustedt 1937							r				
<u>Ac. suchlandti</u> Hustedt 1933	ind	ind					50	31	84	31	
<u>Ac. sp. C 546</u>								164			
<u>Ac. sp. C 562-1</u>								122			
<u>Ac. sp. C 570-1</u>								r			
<u>Ac. sp. C 570-2</u>								r			
<u>Amphipleura pellucida</u> Kützing 1833	ind	alp	lb			e	20	80	32		
<u>Amphora eximia</u> Carter, in Haworth 1974* (Am. sp.B)							78	155	c	19	
<u>Am. levenensis</u> Haworth 1974 *						e		169			
<u>Am. ovalis</u> Kützing 1844	ind	alp	ind				4	c	r	r	

Taxon	Ecology						Loch			
	Hal	pH	Cur	6	7	8	s	c	b	t
<u>Am. ovalis</u> var. <u>libyca</u> (Ehr. 1840) Cleve 1894	ind	alp	ind				4	c	27	10
<u>Am. ovalis</u> var. <u>pediculus</u> (Kützing 1844) Van Heurck 1885	ind	alp	ind				5	25	c	12
<u>Am. triundulata</u> Ross 1947 *		ind						179		
<u>Am. veneta</u> var. <u>capitata</u> Haworth 1974 *(Am. sp.A)							85	133	34	
<u>Am. sp. C 580</u>			.					c		
<u>Anomoeoneis exilis</u> (Kütz. 1844) Cleve 1891	ind	ind	ind				58	c	c	39
<u>An. exilis</u> var. <u>lanceolata</u> Mayer 1919	ind	ind	ind				59		75	
<u>An. follis</u> (Ehrenberg 1838) Cleve 1895							102			
<u>An. seriens</u> (Brébisson 1844) Cleve 1891	hb	acp					98		38	
<u>An. seriens</u> v. <u>brachysira</u> (Brébisson 1853) Cleve 1895	hb	acp					73		r	r
<u>An. zellensis</u> (Grunow 1860) Cleve 1891	hb	acp			b		68		60	46
<u>Asterionella formosa</u> Hassall 1850	ind	alp	lp	pl		e	30	50	110	
<u>Caloneis bacillum</u> (Grunow 1863) Mereschkowski 1906	ind	alp	rp				c	c	c	5
<u>Cal. fasciata</u> var. <u>fonticola</u> (Grunow 1881) Petersen 1928 *							76	c	c	c
<u>Cal. latiuscula</u> (Kützing 1844) Cleve 1894									69	
<u>Cal. cf. lepidula</u> (Grunow 1881) Cleve 1894									70	
<u>Cal. obtusa</u> (Wm. Smith 1853) Cleve 1894	ind	ind					r		65	r
<u>Cal. schroederi</u> Hustedt 1922		alp		ae					r	
<u>Cal. silicula</u> (Ehr. 1843) Cleve 1894	ind	alp	ind				10	87	c	r
<u>Cal. trochus</u> v. <u>lancettula</u> (Hustedt 1930) Mayer 1941 (ACE)		alp						6		
<u>Cal. ventricosa</u> var. <u>minuta</u> (Grunow 1881) Patrick 1966 *								94		
<u>Cal. sp. C 590</u>								1		
<u>Campylodiscus noricus</u> var. <u>hibernicus</u> (Ehrenberg 1845) Grunow 1862	ind	alb	lb			e	2	c	r	
<u>Ceratoneis arcus</u> (Ehrenberg 1838) Kützing 1844	ind	ind	rp		b		45	142	87	48
<u>Cocconeis diminuta</u> Pantocsek 1902	hb	alp	ind			e	r	103	116	18
<u>Coc. pediculus</u> Ehrenberg 1838	ind	alp	rp					79	r	
<u>Coc. placentula</u> Ehrenberg 1838	ind	alp	ind				12	45	r	
<u>Coc. placentula</u> var. <u>euglypta</u> (Ehrenberg 1854) Grunow 1884	ind	alp	ind			e	12	c	r	24
<u>Coc. placentula</u> var. <u>lineata</u> (Ehrenberg 1843) Van Heurck 1885	ind	alp	ind			e	12	29	c	22
<u>Coc. thumensis</u> Mayer 1919								12		
<u>Cyclotella antiqua</u> Wm. Smith 1853	hb	acp			b		62	81	11	44
<u>Cyc. comensis</u> Grunow 1881	ind	ind	lp	pl	b		56	141	45	c
<u>Cyc. comta</u> (Ehrenberg 1844) Kützing 1849	ind	ind	lp	pl			60	61	44	40
<u>Cyc. glomerata</u> Bachmann 1911				pl			105	158		
<u>Cyc. kützgingiana</u> Thwaites 1848	ind	ind	ind	pl			55	154	43	c
<u>Cyc. meneghiniana</u> Kützing 1844	hp	alp	ind				r	9	42	
<u>Cymatopleura elliptica</u> (Brébisson 1844) Wm. Smith 1851	ind	alp				e		38	r	
<u>Cyma. solea</u> (Brébisson 1838) Wm. Smith 1851		alp							r	
<u>Cymbella affinis</u> Kützing 1844	ind	alp	ind			e	c	c	c	r
<u>Cym. amphi-cephala</u> Naegli 1849 (in Kützing)	ind	ind						99	13	

Taxon	Ecology						Loch			
	Hal	pH	Cur	6	7	8	s	c	b	t
<u>Cym. angustata</u> (Wm. Smith 1853) Cleve 1894	ind	ind			b			138	r	
<u>Cym. aspera</u> (Ehrenberg 1839) Cleve 1894	ind	alp	ind	ae			c	100	28	35
<u>Cym. brehmii</u> Hustedt 1912				ae				65	102	
<u>Cym. caespitosa</u> var. <u>auerswaldii</u> (Rabenhorst 1853) A. Cleve 1955 *	hp	alp	lp					70	1	
<u>Cym. cesatii</u> (Rabenhorst 1853) Grunow 1881	ind	ind					c		r	
<u>Cym. cesatii</u> var. <u>capitata</u> Krieger 1933	ind	ind	ind				c	r	c	
<u>Cym. cistula</u> (Hemprich 1828) Kirchner 1878	ind	ind	lp				c	c	c	c
<u>Cym. cuspidata</u> Kützting 1844	ind	ind	ind				c	49	c	52
<u>Cym. diluviana</u> (Krasske 1932) Florin 1971 *									r	
<u>Cym. ehrenbergii</u> Kützting 1844	ind	alp						r	21	41
<u>Cym. gracilis</u> (Rabenhorst 1853) Cleve 1894	ind	ind	lp				c		r	
<u>Cym. helvetica</u> Kützting 1844	ind	alp	lb				c	115	18	r
<u>Cym. hilliardii</u> Manguin 1961 *							r	171	r	
<u>Cym. lacustris</u> (Agardh 1824) Cleve 1894 (= N. sp. C 562-2) (ASA)								126		
<u>Cym. leptoceros</u> (Ehrenberg 1843) Kützting 1844	ind	alp	lp				10	101	14	r
<u>Cym. microcephala</u> Grunow 1881	ind	alp	ind				c	c	c	r
<u>Cym. perpusilla</u> A. Cleve 1895	hb	acb					c	165	r	
<u>Cym. prostrata</u> (Berkley 1832)								185		
<u>Cym. pseudonorvegica</u> Haworth 1974* (Cym. sp. 10)							r			
<u>Cym. scotica</u> Wm. Smith 1853		acp							r	
<u>Cym. semisymmetrica</u> Haworth 1974 * (N. sp.T)							77	143	c	8
<u>Cym. sinuata</u> Gregory 1856	ind	ind	lb				39	c	83	50
<u>Cym. subaequalis</u> var. <u>oblonga</u> (Fontell 1917) Ross 1947 *	ind	ind					c	c	50	r
<u>Cym. thumensis</u> (Mayer 1919) Hustedt 1945	ind	alp						15	120	6
<u>Cym. turgida</u> Gregory 1856	ind	alp	lp				r	5	c	r
<u>Cym. ventricosa</u> Agardh 1830	ind	ind	ind				47	153	81	42
<u>Cym. sp. C 546</u>								166		
<u>Denticula tenuis</u> Kützting 1844	hb	alp					11	72	c	13
<u>Diatoma elongatum</u> (Lyngbye 1819) Agardh 1824	hp	ind		pl		e	15	71	r	
<u>Dia. vulgare</u> Bory 1828	ind	alb	rp				r	176	40	
<u>Dia. vulgare</u> var. <u>grande</u> (Wm. Smith 1856) Grunow 1862								106		
<u>Didymosphenia geminata</u> (Lyngbye 1819) Schmidt 1899	ind	ind	rp				36	69	47	r
<u>Diploneis domblittensis</u> (Grunow 1882) Cleve 1894		alp						36	7	r
<u>D. elliptica</u> (Kützting 1844) Cleve 1891	ind	ind	lp			e	37	74	r	3/4
<u>D. interrupta</u> (Kützting 1844) Cleve 1891							r			
<u>D. marginestriata</u> Hustedt 1922	ind	ind	lb				38	c	82	r
<u>D. ovalis</u> (Hilse 1861) Cleve 1891	ind	alp	ind				c	104	c	c
<u>Epithemia muelleri</u> Fricke 1904	ind	alp	lp				r	113	c	
<u>E. sorex</u> Kützting 1844	ind	alp	lb				9	18	22	
<u>E. turgida</u> (Ehrenberg 1830) Kützting 1844	ind	alb	ind				10	19	c	25
<u>E. zebra</u> (Ehrenberg 1833) Kützting 1844	ind	alb	ind				13	28	16	r
<u>Eunotia acmocephala</u> Fuscay 1953 *							70			
<u>Eu. angustata</u> (Grunow 1884) A. Berg 1939							70			
<u>Eu. arcus</u> Ehrenberg 1838	hb	ind					70	137		

Taxon	Ecology						Loch			
	Hal	pH	Cur	6	7	8	s	c	b	t
<u>Eu. arcus</u> var. <u>fallax</u> Hustedt 1930	hb	ind						184		
<u>Eu. bidentula</u> Wm. Smith 1856		acp					70			
<u>Eu. bigibba</u> var. <u>pumila</u> Grunow 1881	hb	acp					70			
<u>Eu. diodon</u> Ehrenberg 1838	hb	acp					70	181	118	
<u>Eu. elegans</u> Østrup 1910	hb	acp					70			
<u>Eu. exigua</u> (Brébisson 1849) Rabenhorst 1864		acb					70			r
<u>Eu. faba</u> (Ehrenberg 1854) Grunow 1881		acp					70			
<u>Eu. faba</u> var. <u>obtusa</u> (Grunow 1881)A.Cleve 1953		acp					70			
<u>Eu. flexuosa</u> (Brébisson 1849)Kützing 1849	ind	acp					70	174		
<u>Eu. gracilis</u> (Ehrenberg 1843) Rabenhorst 1864	hb	ind					70	r		
<u>Eu. lunaris</u> (Ehrenberg 1832) Grunow 1881	ind	ind					70	134	r	51
<u>Eu. monodon</u> Ehrenberg 1843	hb	acp	lp		b		70	136		
<u>Eu. monodon</u> var. <u>hidens</u> (Gregory 1854)	hb	acp	lp				70			
Hustedt 1932										
<u>Eu. monodon</u> var. <u>maior</u> (Wm. Smith 1856) Hustedt 1930		acp					70			
<u>Eu. pectinalis</u> var. <u>minor</u> (Kützing 1844) Rabenhorst 1864	hb	acp	ind				70		r	
<u>Eu. pectinalis</u> var. <u>minor</u> fo. <u>impressa</u> (Ehrenberg 1854) Hustedt 1930	hb	acp	ind				70		74	
<u>Eu. pectinalis</u> var. <u>ventralis</u> (Ehrenberg 1854) Hustedt 1911	hb	acp	ind				70			
<u>Eu. polyglyphis</u> Grunow 1881		acp					70			
<u>Eu. praerupta</u> Ehrenberg 1843	hb	acp	ind				70	r	r	r
<u>Eu. robusta</u> var. <u>diadema</u> (Ehr.1837)Ralfs 1861		acp					70			
<u>Eu. robusta</u> var. <u>tetradon</u> (Ehr. 1838)Ralfs 1861	hb	acp	lp				70			
<u>Eu. valida</u> Hustedt 1930	hb	acp					70			45
<u>Eu. veneris</u> (Kützing 1844) O. Müller 1898	hb	acp					70		r	
<u>Fragilaria brevistriata</u> Grunow 1881	ind	alp	ind			e	6	27	109	4
<u>F. brevistriata</u> var. <u>subcapitata</u> Grunow 1881 *						e		32	c	r
<u>F. capucina</u> var. <u>mesolepta</u> Rabenhorst (1861)1864	ind	alp	lp					135	r	
<u>F. constricta</u> Ehrenberg 1843		acp					r			
<u>F. construens</u> (Ehrenberg 1854) Grunow 1862	ind	alp	ind				7	23	25	3
<u>F. construens</u> var. <u>binodis</u> (Ehrenberg 1843) Grunow 1862	ind	alp	ind				8	102	23	11
<u>F. construens</u> var. <u>venter</u> (Ehr.1854) Grunow 1881	ind	alp						c		
<u>F. elliptica</u> Schumann 1864 (ACE)	ind	alp	ind				7	c	78	1
<u>F. cf. inflata</u> (Heiden 1900) Hustedt 1931								r		
<u>F. lapponica</u> Grunow 1881	ind		lp					r	r	
<u>F. leptostauron</u> (Ehr. 1854) Hustedt 1959	hb	alp	lp				r	178	20	r
<u>F. pinnata</u> Ehrenberg 1843	ind	alp	ind				1	26	24	2
<u>F. cf. producta</u> (Lagerstedt 1873) Grunow 1881								93		
<u>F. vaucheriae</u> (Kützing 1833) Petersen 1938	ind	alp	ind			e	27	108	56	
<u>F. virescens</u> Ralfs 1861	hb	ind	ind				54	r	68	28
<u>F. sp. C 1</u>							r	24	r	
<u>Frustulia rhomboides</u> (Ehr.1843) de Toni 1891		acp					67			r
<u>Fr. rhomboides</u> var. <u>saxonica</u> (Rabenhorst 1851) de Toni 1891	hb	acp	lp				66			

Taxon	Ecology						Loch			
	Hal	pH	Cur	6	7	8	s	c	b	t
<u>Fr. vulgaris</u> (Thwaites 1843) de Toni 1891	ind	alp	ind	ae			24	177	71	61
<u>Fr. sp. C 574</u>								62		
<u>Gomphocymbella ancyli</u> (Cleve 1902) Hustedt 1930		ind			b			105		
<u>Gomphonema abbreviatum</u> (Agardh 1830) Kütz. 1833	ind	alp	ind						r	
<u>G. acuminatum</u> Ehrenberg 1832	ind	alp	lp				r	c	19	54
<u>G. acuminatum</u> var. <u>brebissonii</u> (Kützing 1849) Grunow 1881	ind	alp	lp				r	r		
<u>G. acuminatum</u> var. <u>coronata</u> (Ehrenberg 1840) Wm. Smith 1853	ind	alp	lp				c	r	12	r
<u>G. angustatum</u> (Kützing 1844) Rabenhorst 1864	ind	alp	ind			e	c	r	c	55
<u>G. augur</u> Ehrenberg 1840	ind	alp	ind					136		
<u>G. constrictum</u> Ehrenberg 1830	ind	alp	ind			e	c	68	c	53
<u>G. gracile</u> Ehrenberg 1838	ind	alp	lp				48	111	3	
<u>G. helveticum</u> var. <u>tenuis</u> (Fricke 1902) Hustedt 1930		acp					100			
<u>G. intricatum</u> Kützing 1844	ind	alp	lb				r		r	
<u>G. intricatum</u> var. <u>dichotomum</u> fo. <u>semipura</u> Mayer 1928 (ACE)		alp					r		33	
<u>G. intricatum</u> var. <u>pulvinatum</u> (Braun, in Rabh. 1853) Grunow 1881 (ACE)							r			
<u>G. intricatum</u> var. <u>pumila</u> Grunow 1881	ind	alp	ind			e	c	42	c	26
<u>G. lanceolatum</u>	ind	alp	ind				r	90	r	
<u>G. longiceps</u> Ehrenberg 1854	ind	ind					r			
<u>G. olivaceoides</u> Hustedt 1950	ind	alp					r	132	r	
<u>G. olivaceum</u> (Horneman 1810) Brébisson 1838	ind	alb	ind				17	116	107	
<u>G. olivaceum</u> var. <u>calcareum</u> (Cleve 1868) van Heurck 1881	ind	alp	lp					183		
<u>G. parvulum</u> Kützing 1849	ind	ind	rp				r	r	94	
<u>G. subtile</u> Ehrenberg 1843	ind	ind					r		57	
<u>G. tenellum</u> Kützing 1844	ind	alp						60	r	
<u>G. ventricosum</u> Gregory 1856		ind			b		r	131		
<u>G. sp. B 168</u>									106	
<u>Gyrosigma acuminatum</u> (Kützing 1833) Rabenhorst 1853	ind	alb	rp			e	9	c	c	r
<u>Gy. attenuatum</u> (Kützing 1833) Rabenhorst 1853	ind	alb	lp					c	r	9
<u>Gy. spenceri</u> var. <u>nodifera</u> (Grunow 1881) Cleve 1894								21		
<u>Hantzschia amphioxys</u> (Ehrenberg 1843) Grunow 1880	ind	alp	ind	ae			29	167	85	
<u>Mastogloia grevillei</u> Wm. Smith, in Gregory 1856	ind	alp					r	43		
<u>M. smithii</u> var. <u>lacustris</u> Grunow 1878	hp	alp					r		55	r
<u>Melosira distans</u> (Ehrenberg 1836) Kützing 1844	hb	acp		pl			r			
<u>Mel. distans</u> var. <u>alpigena</u> Grunow 1881		acp		pl			72			
<u>Mel. islandica</u> ssp. <u>helvetica</u> O. Müller 1906	ind	alp	ind	pl		e	22	89		
<u>Mel. italica</u> (Ehrenberg 1838) Kützing 1844		ind	lp	pl			33			
<u>Mel. italica</u> ssp. <u>subarctica</u> O. Müller 1906	ind	alp	ind	pl			33		72	
<u>Mel. italica</u> var. <u>valida</u> (Grunow 1881) Hust. 1930							33			
<u>Mel. tenella</u> Nygaard 1956 *							104			
<u>Mel. teres</u> Brun 1892 (ASA)					b		75	20	c	7
<u>Meridion circulare</u> (Greville 1822) Agardh 1831	ind	alp	rb				16	57	86	
<u>Mer. circulare</u> var. <u>constrictum</u> (Ralfs 1843) Grunow 1881	ind	alp	rb				r			

Taxon	Ecology						Loch			
	Hal	pH	Cur	6	7	8	s	c	b	t
<u>Navicula avenacea</u> Brébisson ex Grunow 1878	hp	alp	rp					51		
<u>N. bacillum</u> Ehrenberg 1843	ind	ind	ind			c	25	c	c	r
<u>N. bryophila</u> Petersen 1928	ind	ind		ae			89	r	r	
<u>N. cari</u> var. <u>angusta</u> Grunow 1881	ind	ind	rb				c			r
<u>N. cincta</u> (Ehrenberg 1854) Ralfs 1861	hp	alp	rp				r	r		
<u>N. cincta</u> var. <u>heurfleri</u> Grunow (1860) 1881							r			
<u>N. clementis</u> Grunow 1882	ind	alp	ind	ae			c		r	
<u>N. cocconeiformis</u> Gregory 1856	hb	acp	rp				64	123	104	
<u>N. contenta</u> var. <u>parallela</u> Petersen 1928		alp		ae			82	140	88	49
<u>N. costulata</u> Grunow 1880	ind	alp					3	149		
<u>N. cryptocephala</u> Kützting 1844	ind	alp	ind			e	15	144	c	r
<u>N. cuspidata</u> Kützting 1844	ind	alp	ind				25	86	c	
<u>N. decussis</u> Østrup 1910	ind	alp	lb						r	
<u>N. elginensis</u> (Gregory 1856) Ralfs 1861	ind	alp					r	180		
<u>N. evanida</u> Hustedt 1942 (= <u>N. sp. C</u> 562-1)				ae				94		
<u>N. explanata</u> Hustedt 1948	ind	ind							67	15
<u>N. fossalis</u> Krasske 1929		ind						17		
<u>N. fracta</u> Hustedt 1961							79	152	100	r
<u>N. gibbula</u> Cleve 1894		ind					r	174		
<u>N. gracilis</u> Ehrenberg 1832	ind	alp						98		
<u>N. graciloides</u> Mayer 1919	ind	alb	ind			e	r	159	r	
<u>N. helensis</u> Schulz 1926								r		
<u>N. hungarica</u> Grunow 1860	hp	alp	rp					96	r	
<u>N. ignota</u> var. <u>anglica</u> Lund 1946 *		alp		ae			34		r	
<u>N. impexa</u> Hustedt 1961 (= <u>N. sp. S</u> 80)							91			
<u>N. interglacialis</u> Hustedt 1943		ind						14		
<u>N. jhrnefeltii</u> Hustedt 1936	ind	acp			b		r	120	76	21
<u>N. laevis</u> Kützting 1844	hp	alp	rb					110	15	
<u>N. lanceolata</u> (Agardh 1830) Ehrenberg 1838	ind	alp						c	c	r
<u>N. menisculus</u> Schumann 1867	ind	alp						c	80	
<u>N. minima</u> Grunow 1881	ind	alp		ae			c	c	r	59
<u>N. mutica</u> Kützting 1844	ind	ind	ind	ae			40		98	
<u>N. naumannii</u> Hustedt 1942		acp					r	56	91	
<u>N. oblonga</u> Kützting 1834	ind	alp						84	4	
<u>N. opportuna</u> Hustedt 1950	ind							83	113	
<u>N. perpusilla</u> (Kützting 1844) Grunow 1860	ind	ind		ae			41	136	95	
<u>N. petersenii</u> (Petersen 1937) Hustedt 1939	ind	ind		ae			95			
<u>N. placentula</u> var. <u>rostrata</u> Mayer 1918	ind	alp						c	6	
<u>N. platystoma</u> Ehrenberg 1838								136		
<u>N. pseudoscutiformis</u> Hustedt 1930	ind	ind	ind				c	c	89	23
<u>N. pupula</u> Kützting 1844	ind	ind	ind			e	c	c	c	r
<u>N. pupula</u> var. <u>capitata</u> Skvotzow & Meyer 1928	ind	ind	ind					r		
<u>N. pupula</u> var. <u>elliptica</u> Hustedt 1911 (sp C 590)								3		
<u>N. pupula</u> fo. <u>rectangularis</u> (Gregory 1854)	ind	ind	ind			e			c	
Hustedt 1961										
<u>N. pupula</u> fo. <u>rostrata</u> Hustedt (1911) 1961		ind						40		
<u>N. pusilla</u> Wm. Smith 1853	hp	alp	ind				r			
<u>N. radiosa</u> Kützting 1844	ind	ind	ind				c	c	c	r

Taxon	Ecology						Loch			
	Hal	pH	Cur	6	7	8	s	c	b	t
<u>N. radiosa</u> var. <u>tenella</u> (Brévisson 1849) Van Heurck 1881	ind	ind	ind				c	63	17	
<u>N. reinhardtii</u> Grunow (1860) 1880	ind	alb	ind			e	25	10		
<u>N. rhynchocephala</u> Kützing 1844	ind	alp	ind			e	26	173	r	
<u>N. rhynchocephala</u> var. <u>elongata</u> Grunow 1860 (ACE)							r			
<u>N. salinarum</u> var. <u>intermedia</u> (Grunow 1881) Cleve 1895	ind	alp						47	30	
<u>N. schmassmannii</u> Hustedt 1934					b		87	157	101	
<u>N. schönfeldtii</u> Hustedt 1930	ind	alp						r		
<u>N. scutiformis</u> Grunow 1881		ind					93			
<u>N. seminulum</u> Grunow 1860	ind	ind	ind	ae			r	125	r	
<u>N. similis</u> Krasske 1929		ind		ae				r		
<u>N. strösei</u> (Østrup 1910) Cleve-Euler 1955	ind	alb							31	
<u>N. subocculia</u> Hustedt 1930		alp						11		
<u>N. subrotundata</u> Hustedt 1945	ind	alp						13	r	
<u>N. subtilissima</u> Cleve 1891	hb	acp	lb		b		98	181	41	
<u>N. tenelloides</u> Hustedt 1938	ind	alp		ae			r	174	119	
<u>N. tuscula</u> Ehrenberg 1840	ind	alb	lb				34	82	9	r
<u>N. tuscula</u> fo. <u>minor</u> Hustedt 1930	ind	alb	lp					52		
<u>N. viridula</u> Kützing (1833) 1844	ind	alp						44		
<u>N. viridula</u> var. <u>linearis</u> Hustedt 1936 (ASA)								186	r	
<u>N. vitabunda</u> Hustedt 1930	hb	alp	lp					85	103	17
<u>N. vulpina</u> Kützing 1844	ind	alp	lp				r	112	c	
<u>N. sp. C 550-1</u>								158		
<u>N. sp. C 562-3</u>								54		
<u>N. sp. C 562-4</u>								88		
<u>N. sp. C 562-5</u>								94		
<u>N. sp. C 554</u>								136		
<u>N. sp. L 100 B</u>								78	115	
<u>N. sp. B 165</u>									r	
<u>N. sp. B 163</u>									r	
<u>N. sp. V</u>							r	147	r	
<u>N. sp. S 340</u>							r			
<u>Neidium affine</u> var. <u>amphirhynchus</u> (Ehrenberg 1843) Cleve 1894	ind	ind	lp				42	r	r	r
<u>Ne. affine</u> var. <u>undulatum</u> (Grunow 1860) Cleve 1894	hb	acp					r			
<u>Ne. bisulcatum</u> (Lagerstedt 1873) Cleve 1891	ind	ind	ind				46	172	64	r
<u>Ne. dubium</u> (Ehrenberg 1843) Cleve 1891	ind	ind	ind				42	181	52	
<u>Ne. hitchcockii</u> (Ehrenberg 1843) Cleve 1891		acp					r			
<u>Ne. iridis</u> (Ehrenberg 1843) Cleve 1894	ind	ind	lb				r		r	c
<u>Ne. iridis</u> var. <u>ampliata</u> (Ehrenberg 1862) Cleve 1894	ind	ind	lb				44		63	
<u>Ne. kozlowi</u> var. <u>elliptica</u>								91		
<u>Ne. ladogensense</u> (Cleve 1891) Foged 1952 *							r			
<u>Ne. productum</u> (Wm. Smith 1853) Cleve 1891		ind							r	r
<u>Ne. sp. C 562</u>								r		
<u>Nitzschia amphibia</u> Grunow 1862	ind	alp	ind			e	84	107	r	
<u>Ni. amphibia</u> fo. <u>abbreviata</u> Manguin 1942 *							r			

Taxon	Ecology						Loch			
	Hal	pH	Cur	6	7	8	s	c	b	t
<u>Ni. angustata</u> var. <u>acuta</u> Grunow 1880	ind	alp	lp			e	c	c	c	r
<u>Ni. communis</u> Rabenhorst 1864	ind	alp						r		
<u>Ni. denticula</u> Grunow 1880	ind	alp	ind				2	124	c	r
<u>Ni. dissipata</u> (Kützting 1844) Grunow 1880	ind	alb	rp			e	21	150	35	
<u>Ni. fonticola</u> Grunow 1881	ind	alb	ind				14	c	c	14
<u>Ni. frustulum</u> (Kützting 1844) Grunow 1880	hp	alp	lb				28	151	46	r
<u>Ni. frustulum</u> var. <u>perminuta</u> Grunow 1881 *	ind	alp					r	66	c	
<u>Ni. frustulum</u> var. <u>perpusilla</u> (Rabenhorst 1861) Grunow 1881(ACE)									r	
<u>Ni. cf. gracilis</u> Hantzsch 1860	hb	ind	ind				r		r	
<u>Ni. ignorata</u> fo. <u>longissima</u> Manguin 1950 *							90	109		
<u>Ni. kütztingiana</u> Hilse, in Rabenhorst 1861	ind	alp						r		
<u>Ni. linearis</u> (Agardh 1830) Wm. Smith 1853							r			
<u>Ni. cf. microcephala</u> Grunow 1880	ind	alp					c			
<u>Ni. palea</u> (Kützting 1844) Wm. Smith 1856	ind	ind	ind					130	r	
<u>Ni. recta</u> Hantzsch, in Rabenhorst 1861	ind	alp	rp				r	r	r	
<u>Ni. recta</u> var. <u>robusta</u> Hustedt 1950 *								58	c	
<u>Ni. sinuata</u> (Wm. Smith 1856) Grunow 1880	ind	ind					r			
<u>Ni. sinuata</u> var. <u>tabellaria</u> Grunow(1862)1881	ind	ind						181	r	
<u>Ni. sublinearis</u> Hustedt 1921							r	146	r	
<u>Ni. suchlandti</u> Hustedt 1943 *							r			
<u>Ni. thermalis</u> var. <u>minor</u> Hilse 1862 (ex Rabh.)		alp					18	136	92	
<u>Ni. tryblionella</u> var. <u>debilis</u> (Arnett & Bylander) Mayer 1913							r			
<u>Ni. cf. vivax</u> var. <u>tussei</u> A. Cleve 1952 *							r	162		
<u>Ni. sp. C 530</u>								145		
<u>Ni. sp. C 550-1</u>								158		
<u>Ni. sp. C 562-1</u>								r		
<u>Ni. sp. C 580-1</u>								77		
<u>Ni. sp. C 580-2</u>								76		
<u>Opephora martyi</u> Héribaude 1902	ind	alp	lp				r	121		
<u>Peronia heribaudi</u> Brun & Peragallo 1893		acp					96			
<u>Pinnularia acrosphaeria</u> Wm. Smith 1863		acp					r			
<u>P. alpina</u> Wm. Smith 1853		acp					99			
<u>P. balfouriana</u> Grunow, in Cleve 1894	ind	acp		ae			61	156	90	
<u>P. biceps</u> Gregory 1856	ind	ind					c	r	c	
<u>P. borealis</u> Ehrenberg 1843	ind	ind	ind	ae			r	161	96	
<u>P. braunii</u> var. <u>amphicephala</u> (Mayer 1917) Hustedt 1930	hb	ind					r			
<u>P. brebissonii</u> (Kützting 1844) Rabenhorst 1864	ind	ind	rp				r	r		
<u>P. dactylus</u> Ehrenberg 1843		ind					r			
<u>P. divergens</u> Wm. Smith 1853	hb	acp	ind				c			
<u>P. divergentissima</u> (Grunow 1881) Cleve 1891		ind		ae			r			
<u>P. episcopalis</u> Cleve 1891		ind					r			
<u>P. gentilis</u> (Donkin 1873) Cleve 1891	ind	ind	lp				r			
<u>P. gibba</u> Ehrenberg(1830) 1843 (ACE)	ind	ind					r			
<u>P. lata</u> (Brébisson 1838) Wm. Smith 1853							r			
<u>P. legumen</u> Ehrenberg 1843		ind					r			
<u>P. maior</u> (Kützting 1833) Wm. Smith 1853	ind	ind	lb				c	c	c	c

Taxon	Ecology						Loch			
	Hal	pH	Cur	6	7	8	s	c	b	t
<u>P. mesolepta</u> (Ehrenberg 1843) Wm. Smith 1853	ind	ind	ind				36	r	c	38
<u>P. microstauron</u> (Ehrenberg 1843) Cleve 1891	ind	ind	ind				c		r	
<u>P. nobilis</u> Ehrenberg (1840) 1843	hb	ind	lb				r	92	77	
<u>P. nodosa</u> (Ehrenberg 1838) Wm. Smith 1856	hb	acp	ind				43	139	99	29
<u>P. platycephala</u> (Ehrenberg 1854) Cleve 1891							88			
<u>P. semicrucata</u> (A. Schmidt 1875?) A. Cleve 1895							86	r	105	56
<u>P. silvatica</u> Petersen 1935		acp		ae			97			
<u>P. stauroptera</u> (Grunow 1860) Rabh. 1864 (ACE)							c		36	r
<u>P. stauroptera</u> var. <u>minuta</u> Mayer 1917 (ACE)							r			
<u>P. stauroptera</u> var. <u>recta</u> (Mayer 1915) Cleve-Euler 1955 *							c			
<u>P. stomatophora</u> (Grunow, in ASA 1876) Cleve 1891 (ACE)		ind					r			r
<u>P. suchlandti</u> Hustedt 1934 (ASA)							81	158	97	
<u>P. sudetica</u> Hilse 1861	ind	ind	ind				c	119	53	47
<u>P. tenuis</u> var. <u>subundata</u> Cleve-Euler 1955 *							r			
<u>P. undulata</u> Gregory 1859		acp					c			
<u>P. viridis</u> (Nitzsch 1817) Ehrenberg 1843	ind	ind	ind				c	129	r	
<u>P. sp. C</u>							r			
<u>Rhoicosphenia curvata</u> (Kützting 1834)	ind	alp	rp			e		53		
<u>Rhopalodia gibba</u> (Ehr. 1830) O. Müller 1897	ind	alp	ind			e	15	73	c	r
<u>R. gibberula</u> (Ehr. 1843) O. Müller 1899	hp	ind		ae			c			
<u>Stauroneis acuta</u> Wm. Smith 1853	hb	alp					r			
<u>Sta. anceps</u> Ehrenberg 1843	hb	ind	lb	ae			45	160	26	
<u>Sta. dilatata</u> Ehrenberg 1843									51	
<u>Sta. legumen</u> (Ehrenberg 1843) Kützting 1844	ind	ind	ind				94			
<u>Sta. phoenicenteron</u> (Nitzsch 1817) Ehr. 1843	ind	ind	ind				c	128	c	43
<u>Sta. prominula</u> (Grunow 1879) Hustedt 1959	hp	ind					r	174	r	
<u>Sta. smithii</u> Grunow 1860	ind	ind	rp				35		39	
<u>Sta. smithii</u> var. <u>borgei</u> (Manguin 1941) Hustedt 1959	ind	alp						46		
<u>Sta. smithii</u> var. <u>minima</u> Haworth 1974 *								2		
<u>Sta. thermicola</u> (Peters. 1928) Lund 1946 *		alb						r		
<u>Stenopterobia intermedia</u> (Lewis 1864) Van Heurck 1896		acp					71			
<u>Stephanodiscus astraea</u> var. <u>minutula</u> (Kützting 1844) Grunow 1881	ind	alb	ind	pl		e	19	67	73	
<u>St. hantzschii</u> Grunow 1880	ind	alp	ind	pl		e		4		
<u>Surirella angusta</u> Kützting 1844	ind	alp	rb				r		r	
<u>Su. birostrata</u> Hustedt 1912	ind	ind						114		
<u>Su. biseriata</u> var. <u>bifrons</u> (Ehrenberg 1833) Hustedt 1912	ind	alp						97		
<u>Su. biseriata</u> var. <u>bifrons</u> fo. <u>punctata</u> Meister 1912	ind	alp						c		
<u>Su. elegans</u> Ehrenberg 1843	ind	alp					52		111	58
<u>Su. gracilis</u> (Wm. Smith 1853) Grunow 1862		acp						r	r	
<u>Su. linearis</u> Wm. Smith 1853	ind	ind	ind				65	127	r	r
<u>Su. linearis</u> var. <u>constricta</u> Grunow 1862	ind	ind	ind				r		61	
<u>Su. linearis</u> var. <u>helvetica</u> (Brun 1880) Meister 1912							r			
<u>Su. ovata</u> Kützting 1844	ind	alp	rp				23	163	93	
<u>Su. ovata</u> var. <u>pinnata</u> (Wm. Smith 1853) Hustedt 1930	ind	alp	rp				23	168		

Taxon	Ecology						Loch			
	Hal	pH	Cur	6	7	8	s	c	b	t
<u>Su. robusta</u> Ehrenberg 1840	hb	ind	lb				c	59	r	
<u>Su. spiralis</u> Kützting 1844								r		
<u>Su. tenera</u> Gregory 1856	ind	alp					r			
<u>Su. tenuis</u> Mayer 1917							r			
<u>Synedra acus</u> Kützting 1844	ind	alp				e		r		
<u>Sy. amphicephala</u> Kützting 1844							r			
<u>Sy. capitata</u> Ehrenberg 1836	ind	alp	lb			e	r	16	8	
<u>Sy. nana</u> Meister 1912				pl					62	
<u>Sy. parasitica</u> (Wm, Smith 1856) Hustedt 1930	ind	alp	ind				11	22	r	16
<u>Sy. parasitica</u> var. <u>subconstricta</u> (Grunow 1881) Hustedt 1930	ind	alp	ind						66	
<u>Sy. pulchella</u> (Ralfs n.d.) Kützting 1844	mh	alp					r			
<u>Sy. radians</u> Kützting 1844	ind	alp	lb			e	31	r	c	r
<u>Sy. rumpens</u> Kützting 1844	ind	ind	lp				r			
<u>Sy. rumpens</u> var. <u>fragilaroides</u> Grunow 1881	ind	alp						94		
<u>Sy. cf. tabulata</u> var. <u>fasciculata</u> (cf. Agardh) 1830) Kützting 1844 Hustedt 1932							r			
<u>Sy. ulna</u> (Nitzsch 1817) Ehrenberg 1838	ind	alp	ind			e	32	c	c	r
<u>Sy. ulna</u> var. <u>biceps</u> (Kützting 1844) Schönfeldt 1913	ind	alp						r		
<u>Sy. ulna</u> var. <u>danica</u> (Kützting 1844) Grunow 1881	ind	alp				e		r	c	
<u>Tabellaria fenestrata</u> (Lyngbye 1819) Kütz. 1844		acp	lp	pl			69			
<u>T. flocculosa</u> (Roth. 1797) Kützting 1844	hb	acp	ind				69	175 39	29	30
<u>T. quadrisepata</u> Knudson 1952 *							69			
<u>Tetracyclus lacustris</u> Ralfs 1843		acp			b		103	r		

(As far as possible abbreviations of generic names match those on the Diatom Assemblage tables)

2. Scanning electron microscope study of some of the *Fragilaria* taxa

(The following section has already been submitted for publication as a completed manuscript).

It is not only the very small or rare diatoms that are difficult to identify correctly. This section deals with a problem of the correct identification of some of the *Fragilaria* taxa found in the late-glacial sediments and, as these are the dominant forms in many samples, their identification is of importance to the interpretation of the diatom assemblages. The author's ideas concerning some of these forms have necessarily changed somewhat as the study of the lakes profiles has progressed. In the first profile of Loch Sionascaig this genus was most simply divided into seven major taxonomic divisions. In the diatom assemblages of Lochs Cam and Borralan, which have been studied under the light microscope and the scanning electron microscope, it has become apparent that several similar forms are grouped together in some of these taxa and that they are difficult to separate especially under the light microscope. While this does not alter the conclusions drawn from the analysis in any way it must nevertheless be borne in mind that the Sionascaig profile (fig S 15) presents a more simplified version of the *Fragilaria* species complex and that Cam and Borralan represent a more advanced, but by no means complete, analysis, (figs S 17, 19). In fact the analysis of the Cam profile has been simplified by adding together the two related forms of *Fragilaria pinnata* (fig S 17) in order to make comparison of the profiles easier.

Some of the *Fragilaria* taxa are always easily identified, eg. *F. brevistriata*, *F. construens* and *F. construens* var. *binodis*, but a

problem has arisen in the separation and identification of the forms here called F. pinnata, F. elliptica and F. lapponica and the scanning electron microscope (SEM) has been used in the detailed study of these forms. The correct identification of F. construens, F. construens var. venter and F. lapponica under the light microscope has been verified by reference to the requisite slides in the Grunow slide collection.

On the respective sheets of illustrations in the Fritsch Collection of Algal Illustrations (Lund 1971) it would appear that several forms have been ascribed to the various taxa by various authors, forms that under the electron microscope can be shown to have very different structures. Reference to the original descriptions and figures does not always resolve this problem as most of these taxa were identified in the mid-nineteenth century by Ehrenberg, Grunow, Wm. Smith and others and in many cases the descriptions could fit a number of different forms and the drawings are often indeterminate. There are also usually several type sites cited and there are no designated type slides and the slides available contain several different forms, some very similar so it would be impossible to say which was used in the original description; it is quite possible that several forms have been lumped together in one taxon.

F. lapponica Grunow (fig 8 Nos 1-5). One of the major difficulties in diatom studies under the SEM is to relate the forms seen there to those seen under the light microscope but it has proved relatively easy to match the SEM study of this form to slides cited as containing F. lapponica in the Grunow Collection. Although there were no slides of any Belgian material, and none are cited in Van Heurck's Synopsis (1881), there is at least one slide from Finnish Lapland (Grunow Herbar Praparats No. 1477)

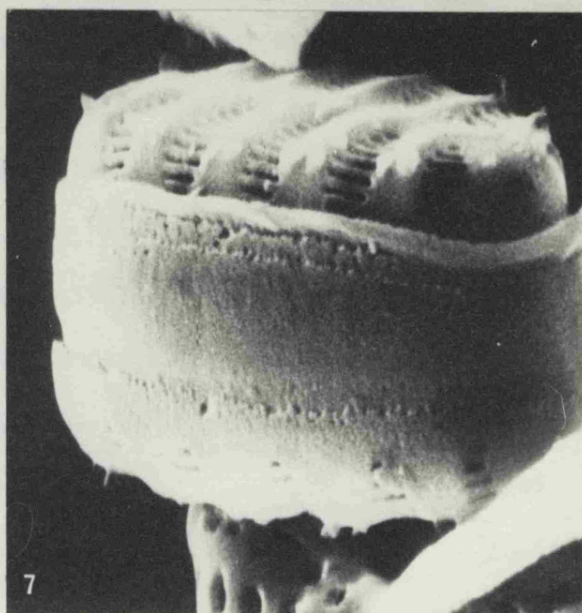
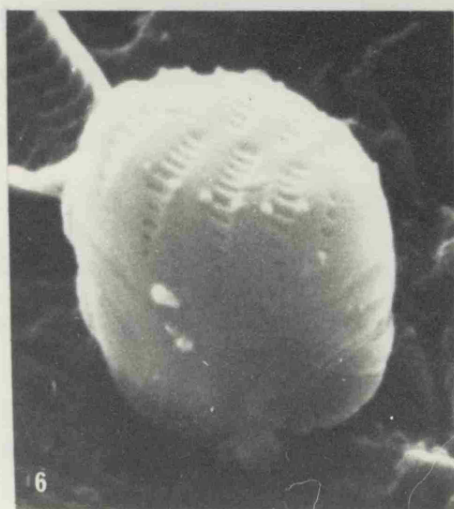
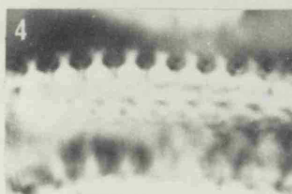
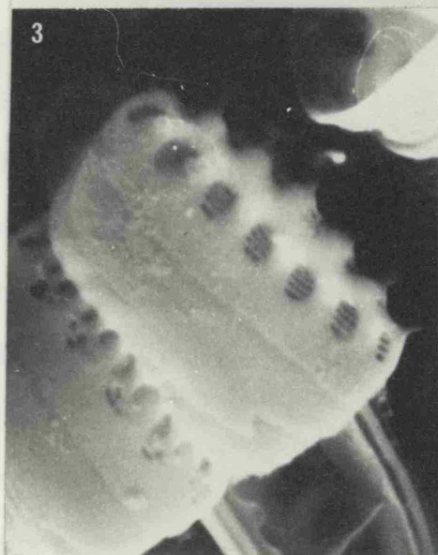
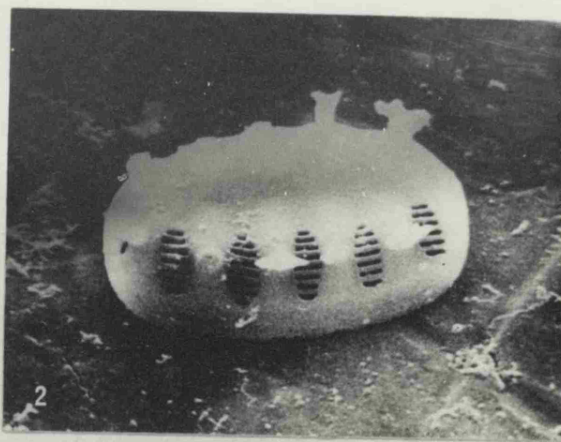
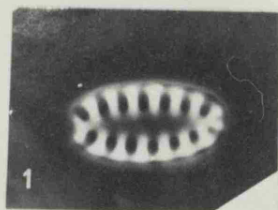
Figure 8.

Nos. 1 - 5. Fragilaria lapponica Grunow

1. Valve view of specimen on Grunow slide no. 1477; light microscopy, X 2000.
2. Valve view; SEM photograph, X 6700.
3. Girdle view of two cells; SEM, X 5500.
4. Girdle view of specimen on Grunow slide no. 2234, showing lapponica type spines; light microscopy, X 2000.
5. Detail of spines; SEM, X 29000.

Nos. 6 - 7 . Fragilaria pinnata Ehrenberg

6. Small rounded form from L. Borralan; SEM, X 13500.
7. Girdle view, form from L. Borralan; SEM, X 1400.



with which the name lapponica would appear to be connected. Hustedt (1959)* cites a Tempère & Peragallo slide (2nd edition no. 764) but no specimens relating to this form could be found on the slide at the British Museum. The forms found on Grunow's slides (Nos 1 and 4) corresponded to his figures in Van Heurck's Synopsis and had short robust striae, approx. $7 - 8/10\mu\text{m}$, which left a large elliptical central area of up to half the width of the valve. In some oblique specimens (No 4) it was possible to see the same branched spines that are so distinctive in the form studied under the SEM, which came from a fossil deposit of Loch Cuithir, Isle of Skye (Nos 2, 3 and 5).

Under the SEM the striae ~~or costae~~ appear as oval holes in the valve, crossed by bars of siliceous material (No 2). Branched spines arise between the costae at the edge of the flat part of the valve, the sides being slanted rather than vertical so that the spines form a ring inside the valve edge when viewed under the light-microscope. This would account for a significant difference in the width of the valve face as measured under the two systems. The spines of adjacent cells interlock loosely, as in other members of the genus, those of one cell overlying the costae of the other (No 5). The spines also appear hollow but this cavity does not continue through to the inside of the frustule itself. Hustedt gives the size range as $12 - 40\mu\text{m}$ long, $4 - 6\mu\text{m}$ wide and with $6 - 9$ striae in $10\mu\text{m}$; the Loch Cuithir material contained rather shorter forms but otherwise they have the same dimensions.

Both Helmcke and Krieger (1962 - 1963) and Miller (1969) call this SEM form Fragilaria pinnata but after comparison with Grunow's own material it is concluded that it is F. lapponica.

* vol. 2 of Hustedt 1930-66.

F. pinnata Ehrenberg (fig 8, Nos 6-7; fig 9, Nos 8-13). Ehrenberg's original figure of this form (1843) is very uninformative and examination of some material from one of the sites listed by him - Santafiore - failed to throw any light on actual identification.

Hustedt's description (1959) is "frustule elliptic to linear with convex, parallel or slightly concave sides and rounded ends. Striae large, rib-like, usually radially arranged towards the ends. Pseudoraphe linear or slightly lanceolate, central area absent; 3 - 35 μ m long, 2 - 6 μ m wide striae 10 - 12 in 10 μ m longitudinal lines (on striae) 20 in 10 μ m". He also describes the var. intercedens Grunow as much the same with grosser structure, striae about 6 in 10 μ m. In the taxon pinnata Hustedt also includes F. elliptica Schumann (1867) and Odontidium mutabile Wm. Smith (1856); Patrick and Reimer (1966) include the latter in var. intercedens (Grunow) Hustedt.

Smith's own slides from his sites of O. mutabile contain a mixture of types and in one case - from Raasay - the slide contained the F. lapponica form described earlier. A slide cited by Hustedt (1959) from the H.L. Smith collection (a W. Smith slide) does include a somewhat different form (No 11).

The form found in the Scottish late-glacial sediments fits Hustedt's written description but it is hard to define the separation between this and F. lapponica under the light microscope, especially in Cam Loch samples (No 10). Under the SEM a whole range of pinnata-types have been photographed (Nos 6-9) where the costae are essentially the same as in F. lapponica but are longer and tend to be pointed at the ends rather than rounded. The central area is only slightly widened and about one fifth of the valve width. The spines are variable in shape and range from simple projections

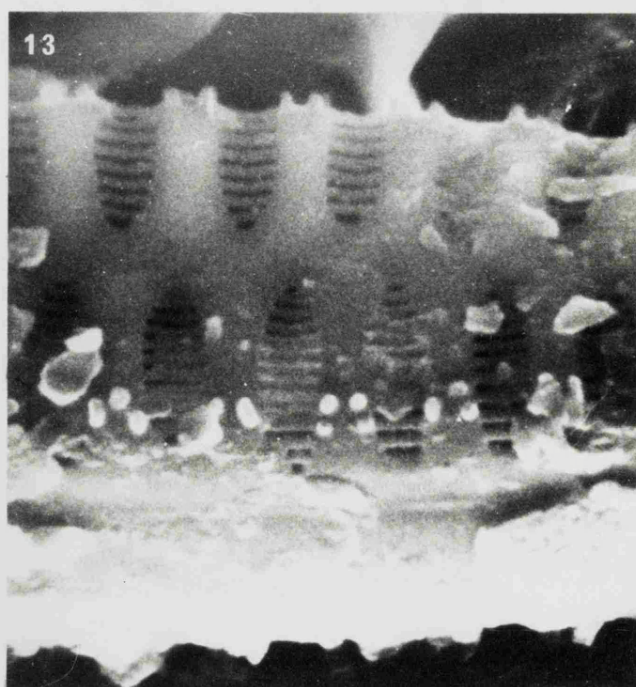
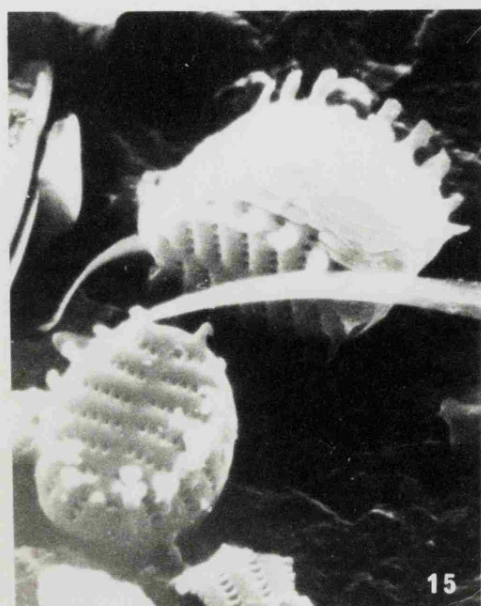
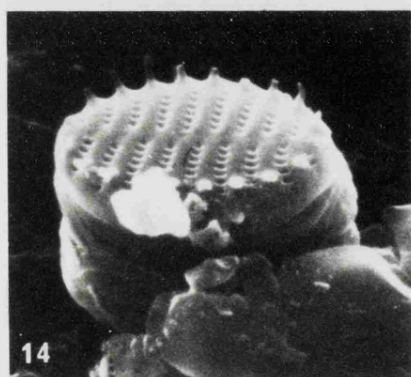
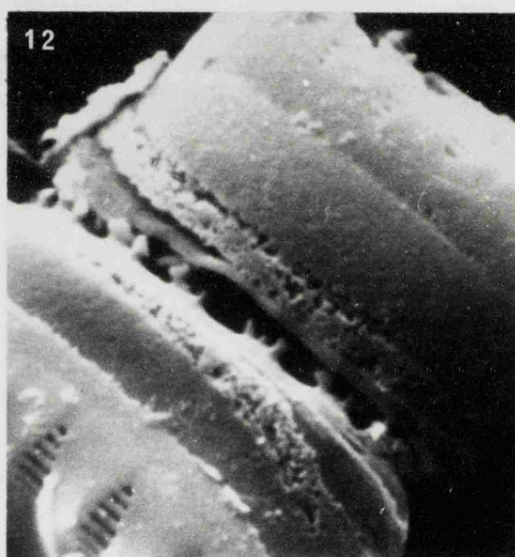
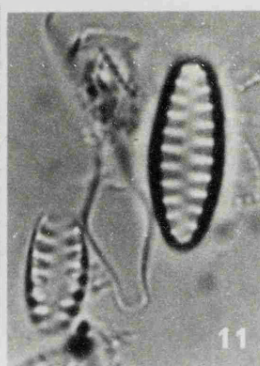
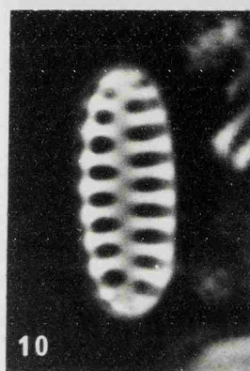
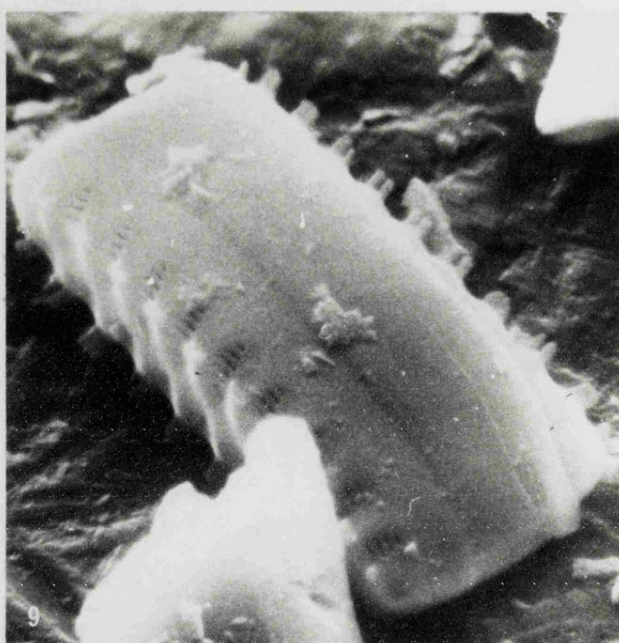
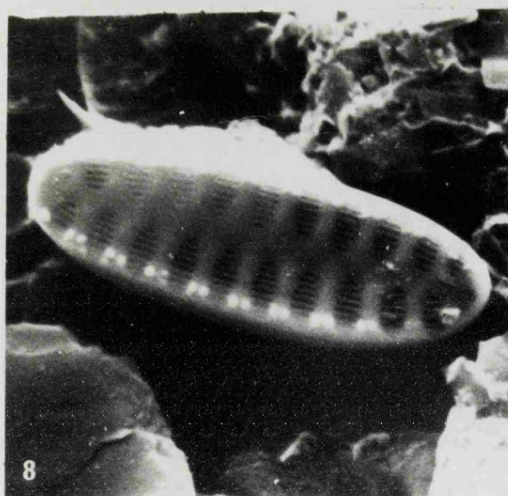
Figure 9.

Nos. 8 - 13. Fragilaria pinnata Ehrenberg

8. Valve view, showing the pairs of spines between the costae, Cam Loch material; SEM X 4900.
9. Oblique view showing spines in profile, Cam Loch material; SEM, X 7000.
10. Valve view, Cam Loch material; light microscopy, X 3000
11. Some forms of Odontidium mutabile on a Wm. Smith slide (H.L. Smith slide no. 383); light microscopy, X 2000.
12. Pair of cells with three spines between costae, Cam Loch material; SEM, X 8500.
13. Oblique view, L. Borralan material; SEM, X13500.

Nos. 14 - 15. Fragilaria elliptica Schumann

14. Single cell, L. Borralan material; SEM, X 6800.
15. Two cells showing girdle and valve views, L. Borralan material; SEM, X 6300.



placed one either side of the costae (No 6) to pairs of projections between the costae (Nos 7-9) or occasionally even three or four spines (Nos 12-13). Nothing approaching the form of the spines on F. lapponica has been seen. There is no reason to suggest that these could possibly be merely eroded spines of lapponica-type, as their point of origin is somewhat different. There is also a difference in the width of the central area, and in the number of striae (8 - 14/10 μ m) and their distance from one another. No forms of F. lapponica were found in these samples seen under the SEM. Occasionally very small forms were found with a greater number of striae, 15 - 20 in 10 μ m, and under 5 μ m long but these are very similar to the larger specimens (No 6).

It would appear there is a wide range of types in these sediments and that the range may well extend from F. pinnata var. pinnata through to pinnata var. intercedens without definable change.

F. elliptica Schumann (fig 9, Nos 14-15; fig 10, Nos 16-21). This third form was included in F. pinnata in the diatom analyses until it was realized that the striae were very much finer and looked different even under the light microscope (Nos 17-19). The samples were first put under the SEM in order to elucidate these differences. This form was then identified to F. elliptica, in accordance with Cleve Euler (fig 348 h-j 1953)*. She describes this taxon as 'small, broadly elliptical (in valve view) with narrow pseudoraphe, striae 13 - 16/10 μ m'; these striae hardly fit into the description of large and rib-like as in F. pinnata. Schumann's description (1867) is similar but his measurements are in Bavarian 'Linie' with 25 striae/100 Lin. which Mayer (1937) translates as being approximately 16/10 μ m.

* vol. 2 of Cleve Euler 1950-55.

Figure 10.

Nos. 16 - 21. Fragilaria elliptica Schumann

16. Broken specimen showing valve and overlapping spines,

L. Borralan material; SEM 13500.

17.- 19. Valve views, Cam Loch material; light microscopy, X 2000.

20. Girdle band and oblique view showing inner part of the valve;

L. Borralan material; SEM, X 14000.

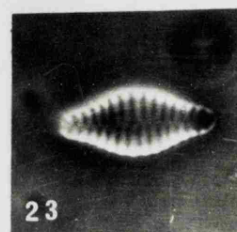
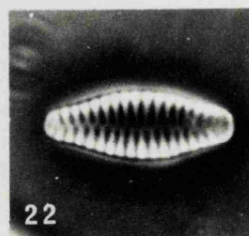
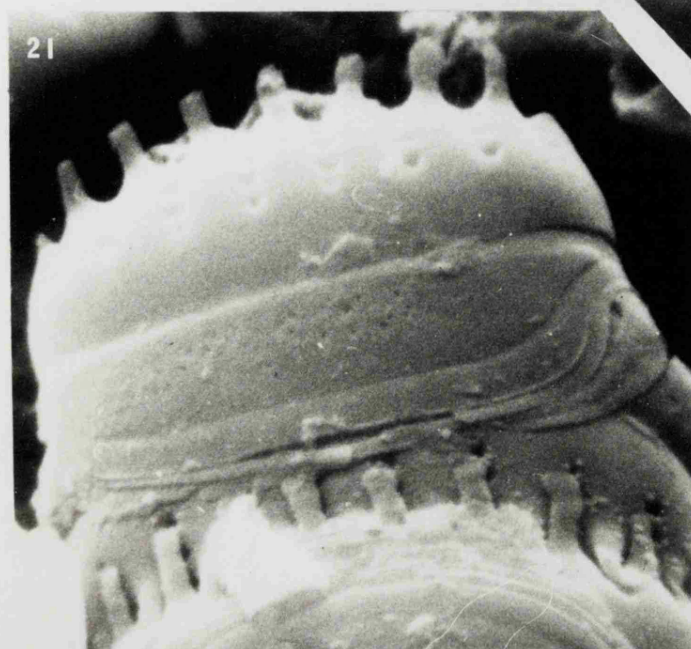
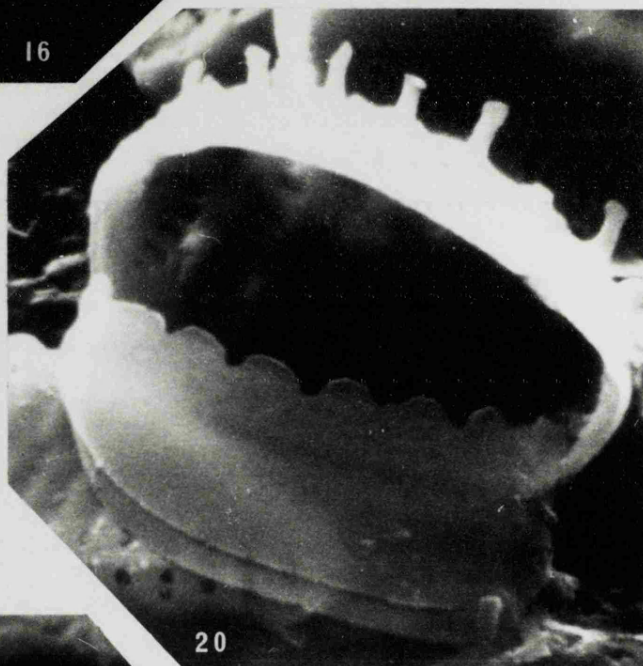
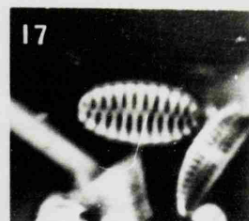
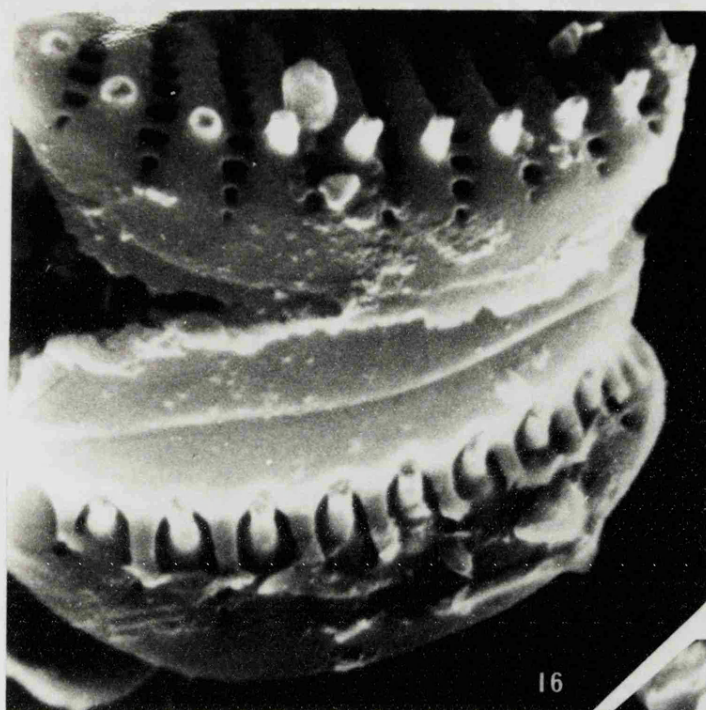
21. Side view showing arrangement of girdle bands and spines,

Cam Loch material; SEM, X 14000.

Nos. 22 - 23. Fragilaria construens var. venter (Ehr.) Grunow

22. Valve view of specimen on Grunow slide no. 1062a; light
microscopy, X 2000.

23. Valve view of specimen on Grunow slide no. 1062b; light
microscopy, X 2000.



Under the SEM the striae are resolved into a single line of pores, 16 - 20/10 μm and 4 - 6 pores/1 μm (Nos 14-16). Single horn-shaped spines arise from the edge of the valve, these are often slightly flattened or spatulate at the tips (Nos 20-21). Their point of origin seems to be variable as occasionally the spines are over a line of pores, but more frequently they arise between them. As in F. lapponica the spines appear to be hollow.

The correct taxonomic niche for this form has been more difficult to determine, there are several taxa into which it might fit according to published literature, namely, F. construens var. venter (Ehr.) Grunow; F. construens var. subsalina Hustedt or F. elliptica. Reference to the Fritsch Collection suggests that most authors place this form in F. construens var. venter although none of Grunow's drawings are of rounded forms but show that they tend to have pointed ends and inflated middle sections as in fig 10, Nos 22 and 23; this is another form which is frequent in Cam Loch sediments and has been correlated with specimens on Grunow Slides nos. 1062 a/b. As these two forms are always separable in the analyses of these sediments the rounded form is therefore referred to F. elliptica.

Table 5.

LOCH STONASCAIG DIATOM STRATIGRAPHY

Lithology (Pennington et al 1972)	Pollen Assemblage	SDZ	Core Depth (cm)	Characteristic Taxa	New Taxa	Ecological Remarks
Black organic mud rather wet	Decrease of birch	9	10-100	similar to SDZ 8		plus redeposition of late-glacial taxa, including alkali-biontic taxa
	180— Decrease of pine 2070-100 BC	8	130-260	High % of Eunotia & Cyclotella spp. Inc. of Dent. tenuis & An. exilis var. lanceolata.	N. petersenii, E. acmocerphala	Acidophilous % decreasing slightly.
	300— pino-birch-alder	7	295-340	Rise in Mel. distans v. alpigena, Eunotia spp., Cyc. kütztingiana, Fr. rhomboides v. saxonica. Dec. in Sy. acus v. radians & F. virescens.		A maximum of acidophilous taxa and slight increase in halophobous taxa.
dark brown organic mud	350— 4700-140 BC	6	360-450	Cyc. comensis dominant. Increases of Ac. minutissima Ac. microcephala, An. exilis, An. seriatus v. brachysira.	An. seriatus, An. foliis, Per. heribaudii, Ac. depressa, Mel. tenella, N. scutiformis, N4 subtilissima, P. alpina, P. silvatica, Tet. lacustris.	Acidophilous % & taxa increasing, upper limit of alkalibiontic & halophilous taxa. Alkaliphiles decreasing.
	pine-birch 5030-160 BC					
	435— birch-hazel-ferns					
light brown organic mud	495— Juniper, increasing birch	5	470-520	Fragilaria spp. decreasing. Increases of Mel. distans v. alpigena, An. exilis, Sy. acus v. radians, Ast. formosa & Tabellaria spp.	Ni. ignorata f. longissima, Ac. pseudoswazi, N. sp. S80	Decrease in alkaliphiles.
	515— Empetrum					
	528— Rumex, Lycopodium selago, sedge-willow					
pink-grey clay-mud		4	522-540	Fragilaria spp. dominant, plus other spp. that characterize SDZ 1	Mel. distans v. alpigena, Cyc. conta, Ac. pseudosuch- landti N. fracta, S. elegans.	An assemblage similar to that of SDZ 1 & high % of alkaliphiles.
pink clay		3	542-550	post-glacial late-glacial		
	Artemisia, Composite Coryophyllaceae, bryophytes			pinks of Cym. ventricosa, F. vaucheriae, F. elliptica, Am. ovalis v. libyca, Cera. arcus, Sta. auceps, N. schwaenmannii.	N. contenta v. petaliole, P. suchlandtii.	Most taxa scarce. Fewer diatoms in samples 544 & 548. Increase in aerial taxa (Fig 516a).
organic silt	B3 (juniper) B2 Empetrum (sedge) B1 (2	554-578	Increase in Cyclotella spp. Tabellaria spp. Ac. linearis, Ac. levanderi, Ac. suchlandtii, Ac. microcephala & An. exilis.	Cera. arcus, Su. ovata, Cym. sinuata, Amp. pelliculosa, Ast. formosa, Mel. islandica spp. helvetica, Ac. gracillima.	Fewer alkaliphiles due to decrease in Fragilaria spp. Halophiles present between 565-575.
moss fragments	A3 (Artemisia (bryophytes) A2 Rumex (Empetrum A1 (Lycopodium (selago	1	581-597	45% Frag. pinnata, 30% Fragilaria spp. + Epithemia spp. Sy. parasitica, D. elliptica.	Ac. calcar, Ac. clevei, Mel. teres, Cam. noricus var. hibernicus, N. costulata.	Mainly alkaliphilous taxa, almost no acidophilous (Fig 516a).
clay with silt						

Results and Discussion

1. Sionascaig: full diatom profile

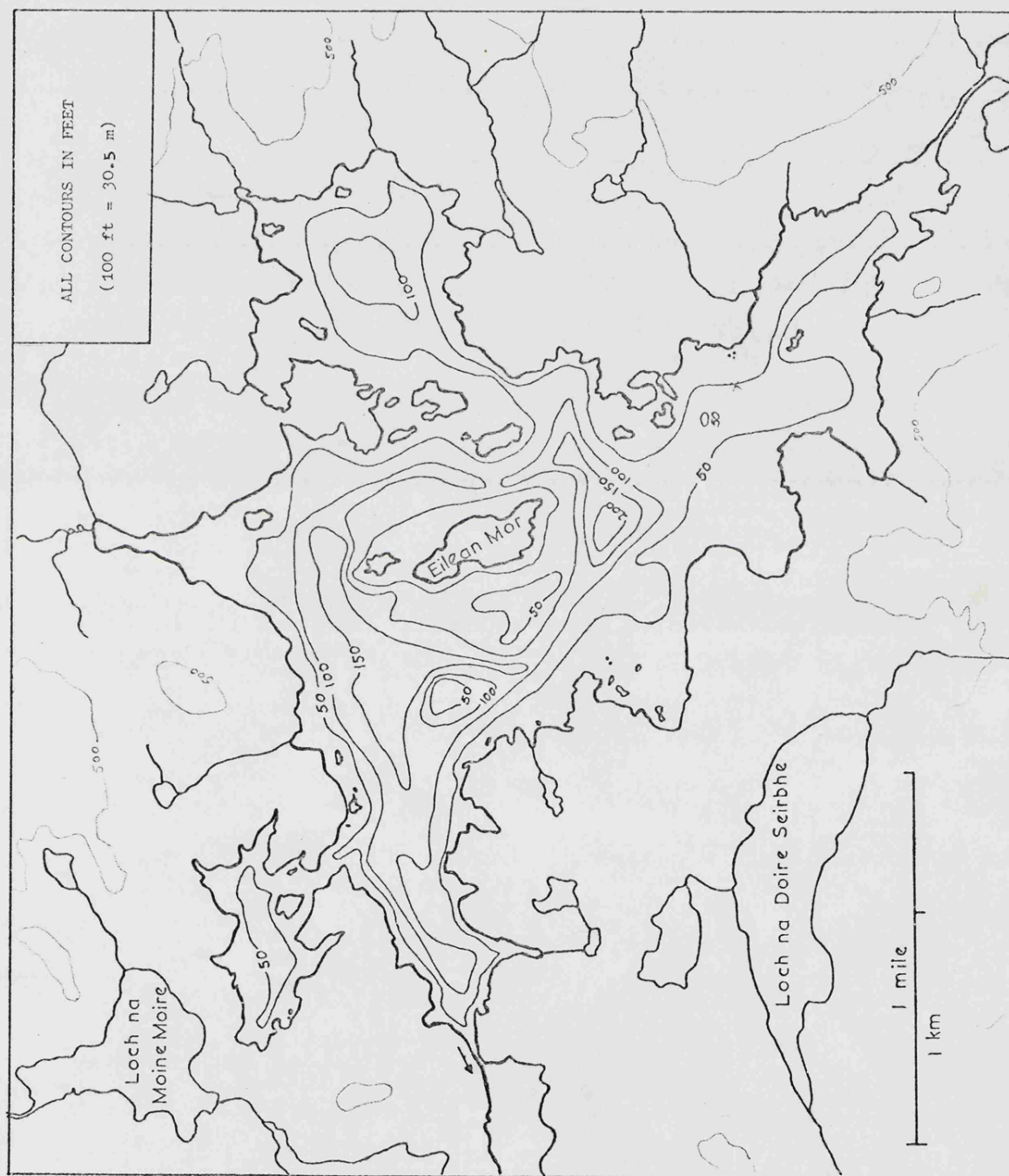
(see Table 5 and figs 11, S 15, 16)

Loch Sionascaig is an extremely irregular shaped loch (fig 11), Peach and Horne (1910) describe it as 'a rock basin in the Lewisian gneiss and Torridonian sandstone containing several minor basins'. It is roughly divided into four arms with the major inflow entering from the eastern end via Loch Doire Dhuibh; the outflow leaves from the southwest arm of the loch and flows into the River Polly. The two main basins of the loch are to northwest and southeast of the largest of the several islands, Eilean Mor, the former has a maximum depth of 184 feet (56 m) and the latter one of 218 feet (67 m). A third basin is to the northeast and has a maximum depth of 137 feet (41.5 m).

The core site of 67-6 (fig 11) is northwest of the island Eilean Dubh. In investigating the sediments of Sionascaig it was found that the only area in which there was an appreciable depth of soft deposit was in the eastern end of the loch and that this was correlated with the distribution of the glacial drift and the Torridonian sandstone (Pennington et al 1972, p. 215).

The lake is oligotrophic and a chemical analysis of the water (Heron, personal communication) shows that it is very low in total ions and has a pH of around 6.0. Its proximity to the west coast of Scotland and the effect of westerly winds is reflected by the high figures for sodium and chloride ions, 0.365 and 0.438 m-equiv./l respectively, which account for about half the ionic concentration. The water of the lake is very clear.

Figure 11. Bathymetric chart of L. Sionascaig, X = core site. From Murray and Pullar 1910.



The lake shores are covered with boulders and sand and there are thin patches of aquatic macrophytes in the littoral regions, eg. Juncus, Lobelia and Potamogeton spp. There are plenty of small streams and wet seepages where Menyanthes trifoliata, Ranunculus flammula and Potamogeton spp. grow. The diatoms found in these habitats include; Anomoeoneis exilis, A. serians var. brachysira, Tabellaria flocculosa, Frustulia rhomboides var. saxonica, Eunotia lunaris, E. pectinalis var. minor fo. impressa, E. acmocephala, Synedra ulna, S. radians, Achnanthes minutissima and Cymbella microcephala. Along the shore-line there are wave-eroded peat sections and Frustulia rhomboides var. saxonica and Pinnularia silvatica are found on the wet faces of these. All these communities explain the diatom content of the upper, recent sediments of the loch, with the exception of some redeposited material which is also included.

The changes in the diatom flora of the lake are fairly gradual ones and it is only in the late-glacial (Late Devensian) and early post-glacial (transition and early Flandrian) that these changes are great enough or rapid enough to make marked differences between one sample and another. Once the early Flandrian is past the changes are much less obvious, there are slightly fewer taxa and these show changes at different levels; there are also very few taxa which are specific to the upper zones, in contrast to the large number that are restricted to the lower ones (fig S 15).

In general the dominant taxa of any sample are those with an indifferent or wide ecological range. It is only in the lower part of the core that the dominants, ie. the Fragilaria spp, are taxa preferring an alkaline environment. Cyclotella comensis, C. kützingiana and C. comta are all widely distributed and can be found in productive Loch Leven as well as in acid, unproductive Loch Sionascaig. In contrast, most of the taxa with

more restricted ecology are scarce in the samples, sometimes only at the level of 'presence or absence', but they still suggest patterns of restriction to one zone or another. Some taxa are recorded in the literature so rarely, or in such general accounts that their ecology is virtually unknown but their presence here does suggest that they have a definite ecological niche and do not tolerate much change in their environment.

Cyclotella spp are the most abundant diatoms in nearly all the samples, especially in the upper part of the core (fig S 13). In the late-glacial and early post-glacial Fragilaria spp are also abundant and there is an interdependence between the percentages of these two genera which is due to the method of analysis. The pattern of changes in Cyclotella comensis in diatom zones 1 to 4 is therefore exaggerated as it is mainly determined by the proportions of Fragilaria spp present. These percentages are high enough for a change in one taxon to affect other taxa with high percentages but for the other genera, with low percentages, the effect is almost negligible.

One possible reason for the abundance of C. comensis in the core could be that its shape and size make it less vulnerable to damage by any movement in the sediment. Thus the size of its contribution to the diatom community may be over-emphasized although it is certainly always abundant.

The Fragilaria spp that dominate the earliest diatom zone, SDZ 1, are generally recorded from the bottom mud in the littoral or shallows of alkaline, eutrophic lakes in Europe (Hustedt 1939; Jorgensen 1948). The same taxa were also found in Iceland by Østrup (1918), Petersen (1928) and Mølder (1951) and in Greenland (Foged 1972). Mølder collected these taxa from lakes and streams at or near the margins of the glaciers along with

Tabellaria flocculosa, Melosira varians, Anomoeoneis exilis, Synedra nana,
Diatoma hiemale var. mesodon, Opehora martyii and Meridion circulare.

The other taxa present in SDZ 1 also indicate a somewhat alkaline environment in which there is a community of predominantly benthic diatoms either living in situ at the bottom of a very clear lake or being brought in from the littoral regions or streams by water movement and deposited at the core site. Many of these taxa were found in calcareous springs and streams by Round (1957a). The alkaline environment in a lake results from the inwash of inorganic material and nutrients eroded or leached from the land. The increasing percentage of planktonic taxa suggests that this zone occurred at a time of change and is perhaps merely a transitional stage between the full glacial period and SDZ 2.

In SDZ 2 Fragilaria spp all decrease in percentage and are succeeded by Cyclotella comensis and C. kützingiana, this suggests that the contribution to the sediments from the littoral zone has decreased and that the plankton community has perhaps increased (fig S 16 d). This is substantiated by the appearance of Asterionella formosa and Melosira islandica subsp. helvetica as these are planktonic and they occur in rather more alkaline and nutrient rich situations than the present-day lake provides. Melosira islandica subsp. helvetica is known as a cold water form with a temperature range of 2 to 13°C and a pH range of 6.9 to 9.8 (Rodhe 1948); this taxon and others that occur in SDZ 2 suggest that the water continues to be alkaline because of the input of inorganic nutrients, but that there is a trend towards a more acid environment in the upper limit of the zone. Achnanthes microcephala and A. minutissima are increasing and other acidophiles, eg. Frustulia rhomboides, F. rhomboides var. saxonica, Anomoeoneis seriens var. brachysira, A. zellensis, Pinnularia nodosa, Cymbella perpusilla and

Eunotia spp all appear. This trend might have continued along the lines of the eventual change in the lake that occurred in the post-glacial but for the reversion to the colder climate and the renewed input of mineral materials. SDZ 2 occupies exactly the same horizon as the Pollen Assemblage Zone B and this is cited (Pennington et al 1972, p. 225) as the time of maximum accumulation of humus in the late-glacial period; it was therefore a time of maximum soil stability when less mineral material was washed into the lake. This may explain the decrease in the percentages of Fragilaria spp, either because they are no longer being moved to the core site with eroded sediments, or because they prefer a more minerogenic environment than occurs in SDZ 2, or because other taxa become more numerous.

The change to SDZ 3 is shown by a marked decrease in many of the diatoms and sharp increases in some that have previously shown no pattern (fig S 15), including taxa which can be found on mosses or soils (fig S 16 e). This, plus an increased proportion of mineral sediment to the numbers of diatoms found on a slide, suggests that some of the diatoms have come from outside the lake, brought in by solifluction during the cold period. There is nothing to suggest that life in the lake itself ceased. Cyclotella spp are found in increasing percentages in this zone and the major taxa include C. comensis, C. kützingiana, Fragilaria brevistriata, F. elliptica, F. construens, F. virescens, Achnanthes levanderi and Navicula radiosa. The increase in F. vaucheriae is interesting because this diatom has been found in quantity among the loose particles in a stream that passes through a slate quarry and collects the dust from diamond saws (E.Y. Haworth, unpublished). Round Loch Sionascaig it may have been living on mineral particles in the local streams or in the littoral zone. It is also

frequently found in calcareous streams (Round 1957a) and is cited as being a benthic form in eutrophic lakes or ponds (Jørgensen 1948).

SDZ 4 indicates a return to the same kind of diatom assemblage as occurred in zones 1 and 2, although the sequence of events is less obvious than at the beginning of the late-glacial. A probable reason is that the diatoms of SDZ 4 were preceded by a well-established flora in SDZ 3, whereas the flora of SDZ 1 was more of a 'pioneer' one. Even so, there is some change in the assemblage between 532 and 530 cm which, coupled with a change in the lithostratigraphy from a pinkish grey clay to a light brown clay mud, suggests that this is where taxa cease to be swept in from the littoral regions and the assemblages become similar to those of SDZ 2; and this can be seen by reference to the alkaliphilous percentages (fig 5 16 a). There are also a number of taxa that appear for the first time (above 530 cm) and these differentiate SDZ 4 from SDZ 2 even though the environment in the lake must have been similar.

The general pattern of the late-glacial and early post-glacial diatoms in Loch Sionascaig appears to be governed by the type of material washed into the loch, as this is the source of inorganic and organic nutrients. An early, mainly benthic phase (SDZ 1) is followed by a planktonic phase of some apparent stability, but with signs of increasing acidity (SDZ 2). This is curtailed by the renewed cold phase and the input of freshly weathered inorganic nutrients in SDZ 3. After the cold phase the diatom community is again influenced by inorganic nutrients in SDZ 4.

This pattern in Sionascaig includes two stages that have not been apparent in other lakes studied; these are, first, the planktonic stage, SDZ 2 and secondly, the assemblage of the cold phase, SDZ 3. Diatom

profiles from other British lakes, eg. Blelham (Evans 1970), Kentmere (Round 1957b), Loch of Park (Alhonen 1968), usually show a continuation or even a climax of the Fragilaria and Epithemia assemblage in the Jessen-Godwin zone II (which is correlated with the upper part of zone B in the pollen zonation for north-west Scotland) and plankton is poorly represented. This has been thought to be typical of the late-glacial period but this may only be true for the smaller, shallower lakes. So far Loch Sionascaig is the only large, deep lake from which a 'mid-lake' diatom profile has been studied as no late-glacial profile has been found in the deep part of Cam Loch and in Windermere, Pennington (1943) described a late-glacial profile on the basis of shallow water cores only, because no deep-water facies of the interstadial is present in the north basin of this lake. There is no obvious explanation for the apparent lack of plankton during the late-glacial in lakes where plankton is present throughout the post-glacial; they are hardly likely to have been shallower than at the start of the post-glacial but the sediments at the core sites may have continued to include more material from the littoral margins or the benthos of the lakes than is found at Sionascaig. Diatom profiles have been described from lakes in Northern Europe but the only ones known to include sediments of the last interstadial of the late-Weichselian (Table 1) are from Danish sites, one of which is a dried up lake basinⁱⁿ Fünen (Foged 1965) where Mastogloia and Gomphonema spp are dominant and not Fragilaria whilst at Bølling Sø (Fjerdingstad 1954) Fragilaria spp are predominant throughout. Many of the Scandinavian lakes were originally part of the Baltic Sea and so begin with a marine phase.

In many profiles there is also an absence or scarcity of diatoms during Godwin zone III; none have the same kind of assemblage that is found in the comparable zone at Loch Sionascaig (SDZ 3), where a well-developed lake flora was present apparently without interruption. This again may be due to the size and shape of the lake and to the amount of material washed in (Pennington et al 1972, p. 239). SDZ 3 is only 12 cm thick, whereas the average thickness of zone III deposits in the other lakes cited is about 20 cm.

The changes in the Sionascaig core appear very precise with taxa being limited to certain levels, eg. Achnanthes calcar, A. pseudosuchlandti and Nitzschia denticula, but the proportions in which some of these taxa occur are so low that it will probably be necessary to find another lake profile with a similar succession to confirm that these changes have not just been caused by the chances of sampling. In this core not only do some taxa appear characteristic of 'late-glacial' conditions but, on the basis of the zonation here described, it should be possible to cite some taxa as characteristic of certain parts of the profile even though the reasons why they are so restricted are not yet clearly understood. Fragilaria spp, Epithemia spp, Achnanthes calcar, Navicula costulata, Nitzschia denticula, Campylodiscus noricus var. hibernicus and Diploneis elliptica are all characteristic of zones 1 and 4, while Cyclotella spp, Melosira islandica subsp. helvetica, Asterionella formosa, Amphipleura pellucida, Surirella ovata and Navicula perpusilla are characteristic of SDZ 2 as well as occurring in part of zone 4. In SDZ 3 Fragilaria vaucheriae, Cymbella ventricosa, Navicula contenta var. parallela and Pinnularia suchlandti are characteristic, and SDZ 4 is typified by Achnanthes pseudosuchlandti,

Navicula fracta and N. tuscula as well as those taxa previously mentioned. Further investigations are needed before it is known whether these can be generally applied to late-glacial sediments in Britain.

The most marked change in the diatom assemblage occurs between 522 and 520 cm when the diatoms cease to be of the 'late-glacial' type. Some of the alkaliphilous taxa disappear at this boundary and the rest decrease in percentage throughout SDZ 5 and 6. The halophilous taxa also disappear in SDZ 6 (fig S 16 b). These are all replaced by increased in the percentages of Achnanthes microcephala, A. minutissima, Anomoeoneis exilis and Melosira distans var. alpigena and this results in a maximum of acidophilous taxa in SDZ 7 (fig S 16 a). This is interpreted as the response to the changing chemistry and pH status of the waters of the loch caused by degradation of the local soils. This is confirmed by the chemical evidence and the fact that SDZ 7 has features related to possible redeposition, eg. many broken and eroded diatoms, appears consistent with the interpretation of increased erosion of mineral and organic soil from about 4300 B.C. (Pennington et al 1972, p. 227).

The presence of many diatoms that are typical of Sphagnum assemblages, eg. Frustulia rhomboides var. saxonica, Pinnularia spp and the increase of iron in the sediments in SDZ 7 both suggest waterlogged and therefore reducing acid soils and the build up of peat on the catchment area. The inwash of acid peat does not appear to increase the percentages of acidophilous diatoms as the highest percentages have already occurred in SDZ 7. The only characteristic separating SDZ 9 from SDZ 8 is the inclusion of taxa of 'late-glacial' type. These three diatom zones are all consistent with the onset of blanket bog in the catchment area, as demonstrated by the pollen and chemical analyses and represent the truly acid period of the loch's history spanning the last 6500 years.

The diatom profile suggests that the change early in the post-glacial, from an alkaline, slightly nutrient-rich lake to an acid, oligotrophic one has been rather more extreme in Loch Sionascaig than the same change in the other lakes cited. There is a richer assemblage of diatom taxa in the late-glacial and early post-glacial of Sionascaig than is found in other lakes and this quickly disappears to be replaced by an acidophilous assemblage which also includes many species of Eumotia and Pinnularia which are not recorded in the other profiles which have been analysed. Some of these profiles are from lakes which show evidence of cultural enrichment resulting from human settlement (eg. Windermere (Pennington 1943)) whereas Loch Sionascaig has an uninhabited catchment area.

According to the postulated time scale the change to oligotrophy took place during the first 1000 years of the post-glacial in Sionascaig (Pennington et al 1972, fig 18). This is less than a third of the length of time postulated for the similarly alkaline phase in Blea Tarn in the English Lake District which existed until the Boreal/Atlantic transition (Godwin zone VI/VII a boundary ca. 5500 B.C.) (Haworth 1969) and where the change in the diatom assemblage was not nearly so marked.

Table 6. CAM LOCH PLATEAU STRATIGRAPHY

Lithology (Pennington, personal comm.)	Pollen Assemblage (Pennington, personal comm.)	Core Depth (cm)	Characteristic Taxa	New Taxa	Ecological Remarks
grey-brown organic mud	N.S. Grass, sedge trans. Rumex zone 534-5 cm 536-7	4 526-536	F. pinnata F. brevistriata	Ac. exigua, Am. triundulata G. olivaceum v. calcarua, N. equinoneis	Inc. in alkaliphilous % dec. in indifferent % dec. in plankton, high % boreal taxa, low aerophil.
grey clay	Artemisia zone with chem. indicators of C soil erosion in the catchment area 552-3 554-5	3 538-550	peak in Cyclotella spp. N. contenta v. parallela, Ac. gracillima, N. fracta Cym. semisymmetrical, Cym. ventricosa, Cera. arcus, Su. ovata	N. graciloides, N. schmassmannii, P. borealis, P. suchlandti	Plankton inc. due to Cyc. comensis, fewer alkaliphiles, more pH indif. taxa. Greatest % boreal, aerial & rheophile taxa.
grey-brown organic silt	Empetrum, Birch B Juniper, sedges. inc. in carbon & manganese 572-3 579	2 554-580	F. spp. dominant, Ac. clevei, Ac. hauckiana, Ac. Østrupii, Amp. pollucida Am. ovalis v. pediculus, Sy. parasitica	Many taxa appear in, or are restricted to this zone inc. Ast. formosa Mel. islandica sp Helvetica, Coc. diminuta, St. astraea v. minutula	Maj. are alkaliphilous. Low % plankton but indicators present, inc. % limnophiles.
greyer with more clay	Recession. A3 dec. of Juniper inc. of Artemisia 580-1 582-3 584-5	c 582	F. constrictus, Am. ovalis v. pediculus Coc. placenta v. lineata, N. radiosa v. tenella	Cym. brehmii, Did. geminata, Dia. elongatum, N. avenacea, Ni. frustulum v. perminuta	Some aerophilous taxa present between 578-582 cm
light-brown slightly organic 582-2 584-5	Juniper, Empetrum; A2 dec. in erosion indicators 587 588-9	1 584-594 (except 590)	F. pinnata, Su. spiralis, Sta. smithii v. minima Mel. teres, Sy. parasitica (Mainly F. constrictus, inc. in Gyrogonia %)	Ac. clevei, Ac. calcar, Ac. Østrupii, Coc. thumensis, Coc. placenta v. anglypta, Ac. suchlandti, Sy. uina, Nav. helensis, Cy. elliptica (N. radiosa, N. reinhardtii, Sy. capitata)	Maj. alkaliphilous taxa, slight inc. in % pH indiffer- ent taxa. V. low plankton % low limnophiles. V. low % halophobous taxa, maj. indif.
soft grey clay v. low in organic content	Rumex, Salix herbaceous zone. v. low pollen conc. 592-2 594-5	a 596-600	F. constrictus, F. sp.1 F. elliptica Sy. parasitica Gyro. acuminatum	N. pupula v. elliptica, Cal. sp. Ø590, Su. spiralis	No planktonic taxa, low % limnophiles taxa, low % pH indifferent taxa

2. Cam Loch: late-glacial profile

(see tables 6 and S 13, figs 12, 13, S 17, S 18)

Cam is an oddly shaped loch. The main part is long and narrow and has two deep basins, both 122 ft (37 m) deep. Along the southern shore the lake widens out into a shallow bay (fig 12) and it is also wide and shallow at the eastern end where the main inflow and the outflow are both situated. Several smaller streams drain Suilven and the surrounding slopes. The bottom deposits of this east end are mainly of sand and several sand spits have accumulated by the islands.

The most orderly accumulation of sediment was found in the bay, Camas Leathan and cores 72-7 and 72-9 are both from this area, in 14 m depth of water (x on fig 12). Cores from the deep area immediately to the north of this site showed that there was a thinner deposit with an obvious discontinuity above the glacial clay, while 6-metre cores from the other deep area did not bottom the organic post-glacial deposit. A late-glacial sequence also occurs in the shallow water at the western end, where local bedrock is partly Torridonian sandstone and partly Lewisian gneiss, but micro-examination showed that this grey sandy deposit contained only weathered deposits and eroded diatoms. This site is directly in the line of greatest fetch of the waves and the deposit may well be the result of redeposition.

Cam Loch presents a more complex limnological situation than Sionascaig as the catchment area includes a range of bedrock and deposits varying from the limestone of Cnoc Breac to the peat deposits around Lochs Urigill and Borralan (fig 3); all contributing to the chemical composition of the water of the loch. Not much is known of the

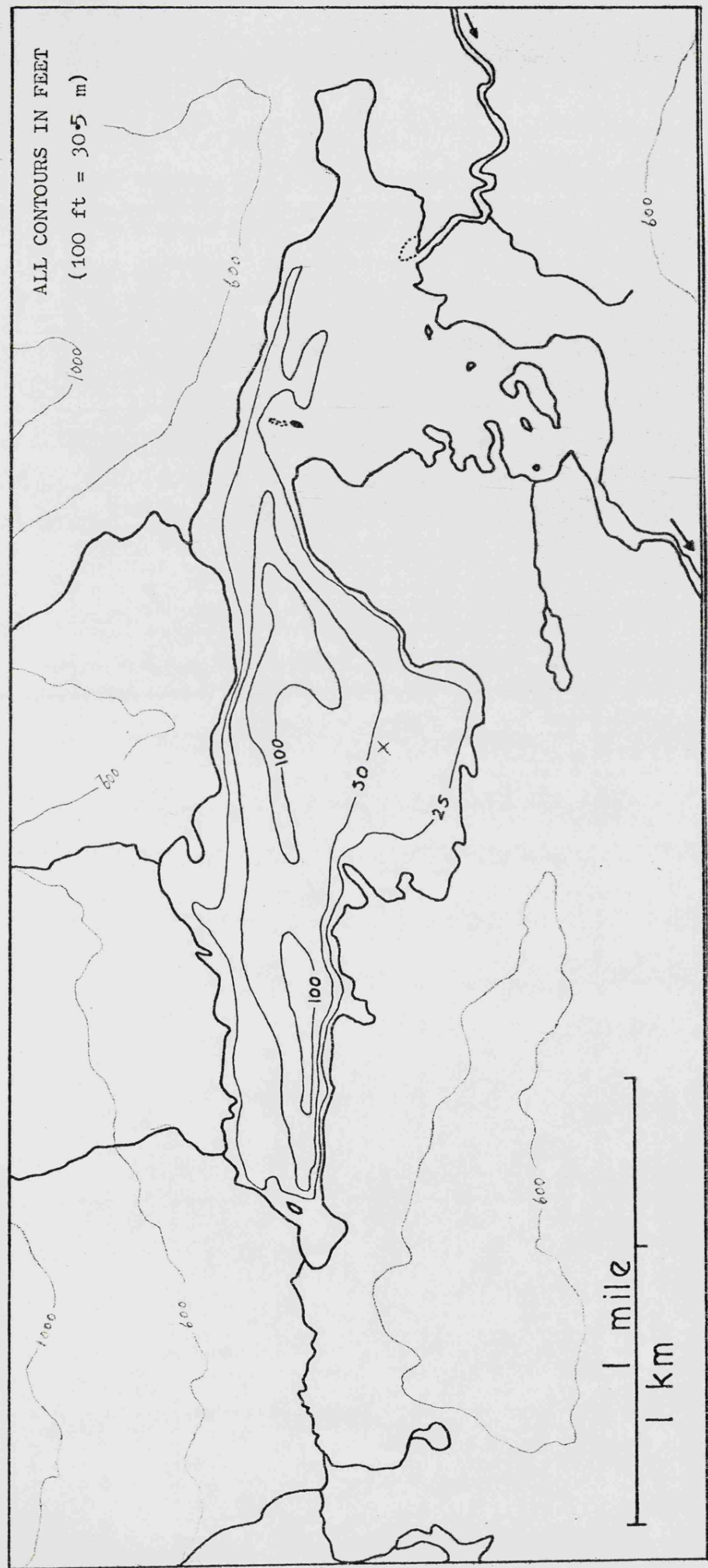


Figure 12. Bathymetric chart of Cam Loch, X = core site. From Murray and Pullar 1910.

limnology of the present loch but a pH measurement of the water in June 1972 was 6.0, on the acid side of neutral. Chemical analysis of a single water sample (Heron, personal communication) shows that calcium and sodium are the major cations present (0.260 and 0.304 m. equiv./l respectively) with carbonate and chloride the major anions (0.320 and 0.362 m.equiv./l respectively). The figures for sodium and magnesium (0.189 m.equiv./l) are probably influenced by the proximity of the loch to the sea and are only slightly lower than those for Sionascaig. The level of calcium is surprisingly low for a lake with limestone in its catchment area and is about equal to that of Windermere.

Diatom collections from around the lake shore and from the surface sediments include several of the diatoms indicative of nutrient rich or alkaline lakes eg. Cocconeis spp, Achnanthes spp, Diatoma elongatum, Asterionella formosa and also Melosira distans var. alpigena, Cymbella microcephala, Tabellaria spp, Anomoeoneis serians var. brachysira; there are fewer acid water indicators eg. Pinnularia spp. and Eunotia spp, than are found at Loch Sionascaig.

Full analysis of the post-glacial section of the profile has not yet been done and is outside the scope of the present study. It is surmised, however, that there has probably been less change in the diatom assemblage of Cam Loch than in the other lochs in the study because of the continued influx of base rich material from the calcareous rocks of the catchment area (fig 3).

Fragilaria spp. are the dominant taxa throughout the late-glacial (late-Devensian) (table 6 and fig S 17); these are all benthic or

littoral taxa of alkaline water and some taxa are also cited as being indicators of eutrophic (nutrient rich) water. The proportions of the different taxa vary through the profile (fig S 17) with F. construens always a dominant taxon except in CDZ 3, and with high percentages of F. pinnata in CDZ 1b and CDZ 4 (the early post-glacial). The zonation the Cam profile is based upon the changes in the proportions of these taxa but these are also supported by the changes in various other taxa, which can be seen in the arrangement of diatom taxa in table S 13.

Until intermediate samples were analysed the lowest diatom zone, CDZ 1, presented a confused picture with great changes in the proportions of the major taxa from sample to sample (fig S 17). Later it became apparent that the sample at 590 cm was very different from the ones adjacent to it, with fewer taxa present and in very different proportions from those of 588 and 592 cm. Furthermore, a percentage similarity diagram (see methods section 4b and fig 13) shows that if the sample 590 cm is omitted and the adjacent ones then compared with each other there is a high percentage of similarity between them, this can also be seen by visual inspection of table S 13.

If we then ignore sample 590 cm, or regard it as inwash, the lower part of the profile falls into two parts. The first, CDZ 1a, is from 600 cm to 595 cm, where fewer taxa are present and Fragilaria construens, F. elliptica and F. sp. C 1 are dominant. The analysis also indicates that the biogenic record extended below the 6 m range of the corer at this particular site but comparison with the slightly shorter profile in core 72-9 shows that the diatom assemblage was very similar to that of sample 600 cm and that barren clay is reached within approximately

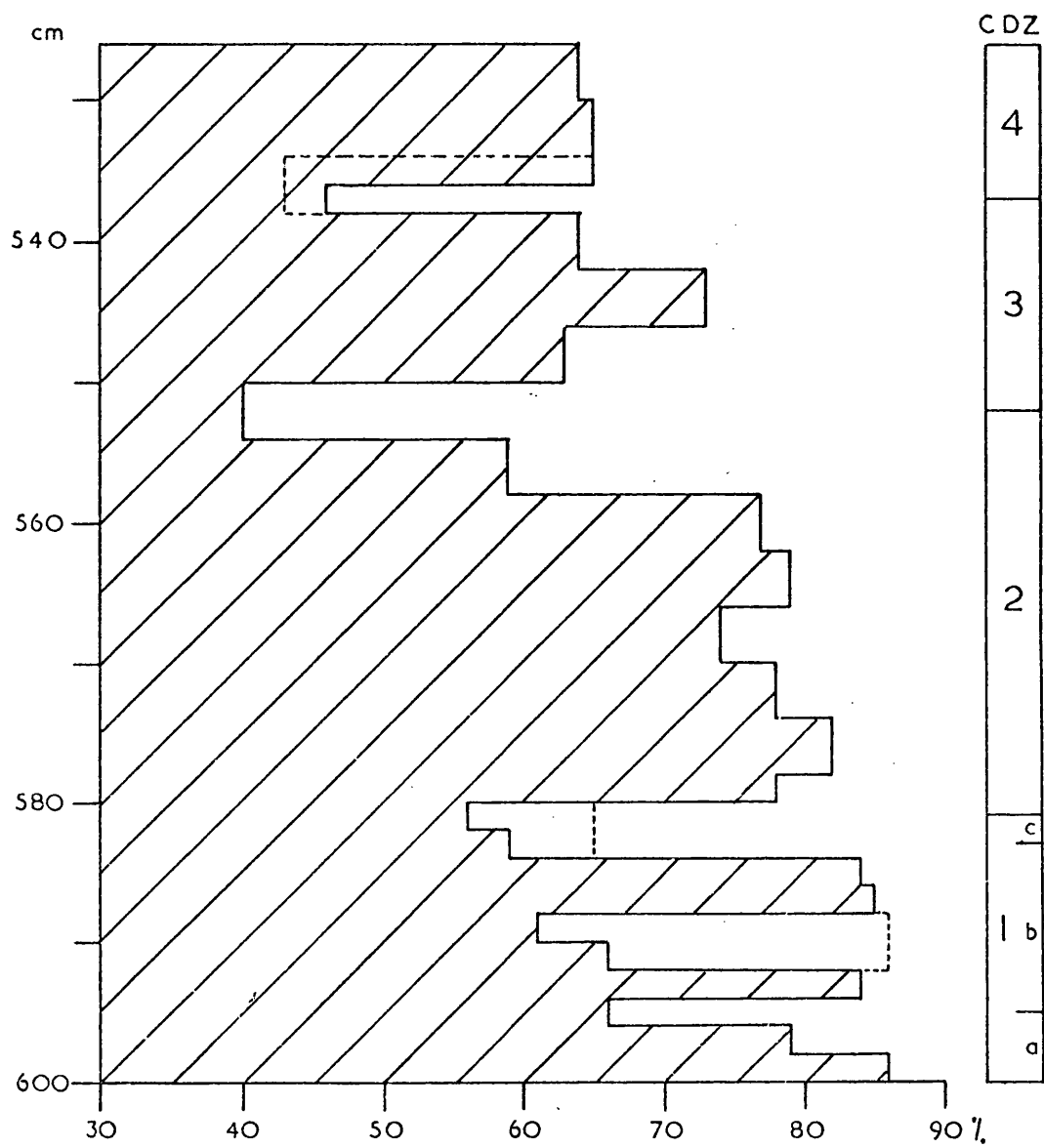


Figure 13. CAM LOCH: PERCENTAGE OF SIMILARITY IN ASSEMBLAGE OF ADJACENT SAMPLES.

Dotted lines indicate the difference between the routine and intermediate samples.

5 cm below this level. CDZ 1a is correlated with the lowest pollen assemblage zone where the pollen concentration is very low, consisting mainly of Rumex and Salix herbacea pollen and is indicative of a 'tundra biota' (Pennington, personal communication). This lower part of the pollen zone Ba presents an assemblage that is pre-Ai (table 6) and is not found at the other sites investigated. It therefore appears significant that this is the only diatom profile in which this lowest subdivision of the assemblages has also been made. The low number of taxa suggests that this diatom assemblage is a 'pioneer' one and it would appear to consist mainly of taxa that have wide tolerance of different ecological conditions rather than those that might be considered specially adapted to this particular environment. Two of the dominant taxa, Fragilaria construens and F. pinnata are also frequently found in tropical waters (Richardson 1968 and Haworth, unpublished material). Known 'boreal' or cold forms are actually rare in this lowest zone (fig. S.18 f) which could reasonably be expected to represent a period of severe climate. This suggests that there was some criterion which excluded even these forms from the initial stages of the development of the lake. The supply of nutrients may well be the decisive factor that excludes some of the taxa. The available nutrients come almost entirely from inorganic sources, from the dissolution of particles of rock flour. The amount of organic matter present is very low, as indicated by the percentage of carbon in the sediments (Pennington, in press) and it is possible that only certain taxa eg. Fragilaria spp. are able to thrive in such a minerogenic environment.

The second part of CDZ 1 is from 595 cm to 583 cm and here F. pinnata is a dominant, with corresponding decreases in the percentages of CDZ 1a dominants (table S 13). The boundary CDZ 1 a/b coincides with a change in lithology from soft grey clay to a light brown, slightly organic sediment with an increase in carbon and also with the onset of soil maturation (Pennington, personal communication). Possibly the increase in organic nutrients allows a greater diversity in the diatom assemblage in the continuum of an ever changing lake ecosystem.

A third part, CDZ 1c, consists of one sample, 582 cm, in which the assemblage is somewhat different from the previous ones (table: S 13) and where a few aerophilous taxa occur (fig S 18 e). This comes within a zone of paler grey sediment which, with such diatom taxa as Achnanthes exilis, Cymbella brehmii, Navicula bryophila, Meridion circulare and Navicula fossalis which are all moss or stream diatoms, suggests that there was increased erosion in the catchment area. The evidence is somewhat slight but Pennington also ascribes parallel changes in pollen and chemical profiles to a climatic recession corresponding to the Bølling - Allerød stade (Pennington, in press).

The planktonic element of the assemblage appears in CDZ 2 (fig S 18 d) and consists of Asterionella formosa, Stephanodiscus astra var. minutula and Cyclotella spp. This forms only a very small proportion of the assemblage and does not approach the same level of significance as the corresponding assemblage in Loch Sionascaig (fig S 16 d). The assemblage is still dominated by benthic Fragilaria spp, mainly F. construens and F. elliptica (fig S 17). There is also a greater variety of taxa than in the previous zone, on average there are 100 taxa in every

sample instead of the 50 found in CDZ 1 samples; these include taxa characteristic of this same level of the late-Devensian at other sites; eg. Amphipleura pellucida, Diatoma elongatum, Cyclotella antiqua, Melosira islandica spp. helvetica, Didymosphenia geminata, Navicula järnefeltii, Asterionella formosa and Stephanodiscus astraes var. minutula etc. The halobous, salt-hating, taxa are more frequent in the lower part of CDZ 2 (fig S 18 b) eg. Cocconeis diminuta, Amphipleura pellucida, Cyclotella antiqua, Denticula tenuis and Navicula laevissima. CDZ 2 is certainly the period in the late-glacial where the benthic taxa are most indicative of a moderately rich nutrient environment. The taxa are extremely diverse and some are also indicators of calcareous water, eg. Didymosphenia geminata. The list of taxa is very similar to that for the recent sediments of Loch Leven (Haworth 1972a), which is regarded as a eutrophic lake, and this includes some of the more unusual taxa found there eg. Achnanthes dispar, A. hauckiana, A. minuta, Amphora levenensis, Diploneis domblittensis, Navicula helensis, N. costulata, N. opportuna, N. fracta and Rhoicosphenia curvata.

Throughout the diatom profile the littoral or benthic taxa form the dominant part of the assemblage. These may be overemphasized because of the position of the core site in a bay at 14 m water depth; but the Sionascaig core site is at approximately 16.5 m depth and so the two sites are quite comparable and the latter has a high plankton percentage. The assemblage in Cam may well have been partly an 'in situ' one due to the extreme clarity of the water at that time, even in what would have been approximately 19 m water depth. The diatom floras of many present day arctic or alpine lakes also tend to be mainly benthic and any plankton is usually concentrated just above the benthos (Pechlaner,

personal communication). These lakes are very clear and light can penetrate to great depths (eg. over 15 m in Leirvatn, a lake 1600 m above sea level in south west Norway). There is also a good possibility that non-diatomaceous forms of algae may have occupied the planktonic niche in Cam Loch rather than the diatoms and this is also a feature of some of the alpine lakes (Pechlaner 1971).

Whatever the reasons for the low percentage of diatom plankton there are indications that the benthic environment of CDZ 2 was alkaline (fig S 18 a) and possibly nutrient rich. This high nutrient status can be corroborated by the work on the organic fraction of these sediments (Cranwell, personal communication) where it appears that the composition of the organic constituents in the Cam Loch late-glacial sediments are somewhat similar to those found in the recent sediments of Blelham Tarn, a small eutrophic lake in the English Lake District. In Blelham the branched chain acids are indicative of considerable bacterial contribution to the sediments under nutrient rich conditions and these acids also occur in the samples from Cam Loch. The distribution of the sterols, which is similar in both lakes, is more typical of modern productive lakes than unproductive lakes or terrestrial soils and these are thought to be of algal or protozoan origin. Only one sterol, brassica-sterol, can be identified as being associated with diatom production in particular and this is especially prominent in the pattern of the sterol component of the Cam Loch late-glacial organic fraction. One difference between the two sites is that the Blelham sediments also contain a diatom assemblage that includes a high proportion of planktonic taxa, about 50% of the assemblage, despite a very diverse flora and a maximum water depth of c. 14 m whereas the diatom plankton of the Cam Loch assemblage forms a much smaller proportion even though the lake is both larger and deeper.

In zone CDZ 3, the grey clay layer of the Younger Dryas cold period, the planktonic proportion of the diatom assemblage is higher than in the rest of the profile (fig S 18 d) because of the high percentage of Cyclotella comensis (table S 13 and fig 14^{*}) which is known as an arctic-alpine form (Hustedt 1937-39). This is an unusual feature of this profile and has not been found in the other profiles where the plankton percentage is usually lower rather than higher, or low throughout the late-glacial period as is also the case in profiles from some Lake District sites (Round 1961, Haworth 1969). Many taxa are less prominent in CDZ 3 and aerophilous taxa (fig S 18 e) are again present in the assemblage, including Hantzschia amphioxys which is a soil diatom, but they only occur in lower proportions than those found in the equivalent zone in Sionascaig. Certain of the taxa appear in their greatest proportions in this zone (table S 13) and the acidophilous and rheophilous (fig S 18 c) taxa are also best represented here, suggesting there has been some inwash of material from other environments of greater acidity than the lake itself.

Above the late-glacial/post-glacial boundary at 538 cm Fragilaria pinnata and F. brevistriata become dominant in the assemblage. Several new taxa appear, eg. Achnanthes exigua, and many taxa reappear having been absent in CDZ 3, eg. Achnanthes conspicua, A. hauckiana, Cocconeis placentula var. euglypta, Cyclotella antiqua, Cymbella leptoceros, Epithemia spp, Navicula järnefeltii, Nitzschia denticula, etc. (table S 13). Conditions would appear to revert to those of the CDZ 2 situation and possibly the climate became more temperate more quickly than in the preceding interstadial.

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Table 7. LOCH BORRALLAN DIATOM STRATIGRAPHY

Lithology (Pennington et al 1972)	Pollen Assemblage	BDZ	Core depth (cm)	Characteristic Taxa	New Taxa	Ecological Remarks
fine organic mud —160—		4	150-163	F. brevistriata, F. construens	Ac. conspicua, Ac. exigua, Ac. lanceolata v. elliptica Ast. formosa, Coc. diminuta	Higher % plankton
grey-brown silt —167—	<u>Artemisia</u> C sedges bryophytes	3	165-173	Ac. suchlandti Cym. sinuata, H. amphioxys F. elliptica, Cym. ventricosa N. contenta v. parallela	Fr. vulgaris, N. perpusilla N. fracta, P. balfouriana P. borealis, P. suchlandti	Highest % aerial taxa v. low plankton %, halophiles absent, max. % acidophiles
grey clay						
grey-brown detritus silt —182—	B3 <u>Empetrum</u> , <u>Rumex</u> —180—	2	175-205	F. construens F. virescens, Cyc. kützingiana Cyc. comta Cyc. comensis	Am. pellucida, Dia. vulgare N. salinarum v. intermedia N. jännefeltii, N. strösei N. subtilissima, Ne. dubium, Ni. dissipata Am. veneta v. capitata, Cyc. meneghiniana	Highest % limnophiles & planktonic taxa, & halophobous taxa. Inc. in acidophiles towards top. Inc. in boreal taxa at base
grey detritus silt —186—	B2 <u>Empetrum</u> , bryo- phytes, <u>Artemisia</u> —185—					
b-g det. silt —188—	B1 <u>Empetrum</u>					
grey organic clay —191—						
grey silty clay with moss threads, slightly organic	—209— <u>Rumex</u> A3 <u>Artemisia</u> bryophytes	b	208-213	F. elliptica	Ac. biasoletiana, Ac. calcar An. zellensis, F. vaucheriae M. smithii v. lacustris at 208 cm F. virescens, Mer. circulare D. marginestriata, Cera. arcus H. amphioxys, N. contenta v. parallela	lower % halophiles
		1				
grey clay mud	A2 <u>Rumex</u> , <u>Empetrum</u> —225— A1 <u>Rumex</u> , <u>Salix</u> grasses	a	215-240	F. pinnata F. construens	Ac. didyma, Cym. prostrata D. domblittensis, N. placentula v. rostrata	lower % halophobous taxa Maj. taxa are:- halobian indifferent (\pm 96%) pH alkaliphilous (\pm 92%) current indifferent (90%)

3. Borralan: late-glacial profile

(tables 7 and S 14, figs S 19, S 20)

Borralan is a small, shallow loch (table 2) in an area of glacial drift and peat bog (fig 3). The lake deposits include a good conformable late-glacial sequence but pollen analysis shows that the upper part of the post-glacial is disturbed, presumably because it came within the depth of wave action and turbulence (Pennington et al 1972).

As in Cam Loch sediments the genus Fragilaria is again dominant throughout the late-glacial profile (fig S 19). The ecological spectra are dominated by alkaliphilous, halobian-indifferent and current-indifferent taxa (fig S 20a b c) and there are very few taxa of acidophilous, rheophilous or halophobous affinities. These ecological spectra indicate that the late-glacial environment of the lake was very different to the present one, which is acid and oligotrophic (nutrient poor and with low algal productivity) and determined by the presence of blanket peat on the catchment area.

The lowest diatom zone, BDZ 1, is rather longer than the corresponding zones at the other sites, being 32 cm in depth as opposed to 19 cm in Cam, which is the next loch in the drainage system (fig 2). One may therefore assume that the rate of sedimentation may have been greater over approximately the same period in spite of the fact that its catchment area is so much smaller. This is perhaps due to the amount of easily eroded glacial debris present in the catchment area, such as can be found in recently glaciated areas of the present day. Much of the material carried by the streams would in any case have been deposited in the upper lake in the chain, ie. in Borralan rather than in Cam.

BDZ 1 contains very few acidophilous, halophobous, limnophilous or planktonic forms and it may be that the assemblage includes diatoms washed in from outside the lake, from pools and streams. The assemblage is predominantly a benthic one; no taxa appear to be restricted to this zone but fewer types of taxa are found in the lower samples (231 - 235 cm) with more taxa appearing in the next zone, BDZ 2 (table S 14). One unusual occurrence is that there are more diatom types in the lowest diatom sample at 240 cm than in succeeding samples; this is a little below the lowest sample containing pollen and so may well represent invash of some kind even though some planktonic forms are present. From rough observations of the intermediate (not analysed) samples in BDZ 1 it has been found that:-

- 241 cm - includes a few Gyrosigma spp. only
- 239 cm - is similar to sample 240 cm
- 238 - 231 cm - Fragilaria spp. predominant but fewer diatoms in proportion to mineral matter on the slides analysed than in 240 and 239 cm
- 229 - 224 cm - same as sample 225 cm
- 223 - 220 cm - fewer diatoms than previous samples and more broken specimens

The level 223 - 220 cm is tentatively correlated with the Cam Loch 590 cm layer of suggested invash material. Here there is no change in the diatom proportions, this may be because the amount of accumulation is generally greater in this zone. At neither site is there pollen or chemical evidence of any changes (Pennington, personal communication).

It is concluded that the subdivision of BDZ 1 into subzones a and b represents a simplification due to the wider sampling intervals and that a closer study could probably reveal a more complex set of diatom assemblages which might provide a better explanation of the fluctuations in this part of the profile.

Subzone BDZ 1b is based upon the sudden increase in the percentage of Fragilaria elliptica and the presence of some taxa that are also found in the upper clay zone, BDZ 3; these include Hantzschia amphioxys, Ceratoneis arcus, Meridion circulare, Achnanthes gracillima, Navicula contenta var. parallela, Amphora eximia and Diploneis marginestriata. As in Cam, the evidence for a recession is only slight but it would appear to support the pollen evidence (Pennington, personal communication).

BDZ 2 includes some of the taxa that have come to be regarded as indicators of this level in the profiles under discussion, eg. Amphora veneta var. capitata, Amphipleura pellucida, Diatoma elongatum, and Stephanodiscus astraea var. minutula but neither Asterionella formosa nor Melosira islandica ssp. helvetica have been found here and these two taxa would appear to be confined to the larger lakes of the series. In Borralan there is continued domination by Fragilaria construens and other Fragilaria spp. but about 5% of the assemblage is planktonic, mainly Cyclotella spp. (fig S 20 d and table S 14 nos 42-45). This predominance of the benthic forms is presumably due to the shallower depth of this lake, in comparison with Sionascaig and Cam, in that much of the assemblage is undoubtedly 'in situ' on the benthos at the core site. Borralan does not share the calcareous catchment area of Cam Loch and so it may be presumed that it was never as rich in algal nutrients as the latter.

The clay/cold phase, BDZ 3, is dominated by up to 60% Fragilaria elliptica (fig S 19). It would seem significant that all the specimens of this taxon found in this zone are of size and shape that would conform with what Cleve-Euler (1953)* calls the 'fae minores' which she says are characteristic planktonic forms of eutrophic waters, especially in Lappland. This suggests that the taxon not only lives on the benthos but can continue in the photic zone should this not reach the benthos because of turbidity. F. elliptica is included in the taxon F. pinnata by Hustedt (1930-66); it is not recorded in modern plankton studies, presumably because it is too small to be included in any but special studies of the nannoplankton. As a practical example, I have found specimens in the material caught in sediment traps suspended in Blelham Tarn in the English Lake District but the taxon is not recorded in the routine phytoplankton counts (Irish, personal communication). F. elliptica also occurs in the recent sediments of Loch Leven (Haworth 1972a).

Other taxa characteristic of BDZ 3 are to be found in table S 14 but Achnanthes gracillima, Ceratoneis arcus, Cymbella perpusilla, C. semisymmetrica, Pinnularia borealis and Surirella ovata must also be added to the list. A slight, but distinct, rise in the percentage of aerophilous taxa can also be discerned (fig S 20 e) and can be correlated with a maximum percentage of bryophyte spores (table 7). This zone is related to the clay layer of the post-interstadial climatic recession and becomes increasingly silty towards the upper boundary as amelioration begins (table 7).

* vol. 2 of Cleve-Euler 1950-55.

In the post-glacial, BDZ 4, Fragilaria brevistriata and F. construens are dominant and Asterionella formosa is one of the taxa to appear once the cold phase is past, a fact which raises the question of what prevented its occurrence in the lake in BDZ 2, especially as it was already present in Cam Loch at that time. Other new taxa are also indicative of renewed base richness in the environment, eg. Achnanthes exigua, A. conspicua, A. lanceolata var. elliptica and Cocconeis diminuta.

Table 8. LOCH TARFF DIATOM STRATIGRAPHY

Lithology (Pennington et al 1972)	Pollen Assemblage	TDZ	Core depth (cm)	Characteristic Taxa	New Taxa	Ecological Remarks
organic mud	<u>Empetrum</u>	4	227-229	F. pinnata F. construens N. minima	Su. elegans Ac. clevei, Ac. exigua Ac. Batrupii	Increasing plankton
clay	C <u>Artemisia</u>	3	230-234	F. elliptica Cym. ventricosa T. flocculosa Sta. phoenicenteron	A. zellensis, Cera. arcus Cym. sinuata, E. lunaris N. contenta v. parallela P. mesolepta, P. sudetica	aerial taxa represented by N. contenta v. parallela
detritus silt	B3 <u>Empetrum</u> Juniper	b	235-237	F. pinnata	Ac. calcar, Ac. levanderi Ac. suchlandti, Ac. linearis Cyc. comta, Cym. ventricosa	highest % planktonic and boreal taxa
	B2 <u>Empetrum</u> , Sedge <u>Rumex</u> , bryophytes 241	a	238-244	F. brevistriata F. construens Cym. thumensis N. vitabunda	Ac. laterostrata, Am. eximia Coc. placentula v. euglypta Cam. noricus v. hibernicus Coc. diminuta, N. järnefeltii Sy. parasitica	Majority of taxa throughout are:- Halobian indifferent pH - alkaliphilous Current indifferent
	B1 <u>Empetrum</u>	b	246-251	F. elliptica F. construens Cym. thumensis	Am. ovalis v. pediculus Am. ovalis v. libyca N. tere	
	A3 <u>Rumex</u> bryophytes 249	1	252-265	diatoms very scarce, occasional specimens at 255, 260 & 265 cm.	F. brevistriata, F. elliptica F. construens, Cyc. comensis Cal. bacillum	
unlaminated clay	A2 <u>Rumex</u> , <u>Empetrum</u> <u>Lycopodium selago</u> A1 <u>Rumex</u> , ferns <u>Lycopodium selago</u>					

4. Tarff: late-glacial profile

(see tables 8 and S 15, figs S 21, S 22)

The second of the smaller lakes, Loch Tarff, provides a diatom profile similar to that of Loch Borralan in outline although the length of the profile is very much shorter. The morphometry of the two basins is also quite different with Tarff having a very much deeper, triangular shaped basin (table 2) but the core site itself was in a shallower part of the loch near to one of the small wooded islands (fig 4), in 11 m of water (Pennington et al 1972).

Lithologically the late-glacial section is only 30 cm long, from the base of the lower unlaminate clay at 260 cm to the top of the upper clay 230 cm (table 8) but pollen analysis has shown that the pattern is consistent with other, longer profiles over this period (Pennington et al 1972). It is not really possible to give any detailed history of the diatom assemblage on the evidence of the Tarff profile alone because the profile is so short and there are fewer diatom taxa than in profiles from other sites but it provides useful evidence to support the results from the other three sites and is complementary to the analysis of Loch Borralan (table 7). In addition, the understanding of the Borralan profile makes it possible to get much more information from this profile than if it were studied in isolation.

The diatom assemblage clearly indicates that there was an alkaline environment in the late-glacial lake, which is quite different from the acidic, oligotrophic environment of today. The major points of interest in this profile are the two levels at which Fragilaria elliptica is dominant - 251 - 248 cm and 234 - 230 cm (fig S 21). These would

appear to agree with the pattern in the Borralan assemblage and to be indicative of the periods of recession in climate. They are also both correlated with the same pollen zonation (table 8). Other diatoms associated with the upper F. elliptica zone typical of zone 3 assemblages are eg. Ceratoneis arcus, Cymbella ventricosa, C. sinuata, Navicula contenta var. parallela, and Pinnularia mesolepta (table S 15).

Fragilaria construens var. binodis provides negative evidence as it shows a marked decrease within the clay zone as in the profiles of the other sites. Few of these indicators are to be found in the lower F. elliptica zone. The early part of the profile, in the lower clay layer TDZ 1a, appears not to contain the usual diatom assemblage and diatoms are rare in the samples. They only occur in some abundance within the detritus silt (table 8) with which TDZ 1b is correlated.

TDZ 2 is dominated by F. pinnata and F. construens, as in Borralan, and also by F. brevistriata. It includes a greater variety of taxa, including Achnanthes calcar, Cyclotella comta, Campylodiscus noricus var. hibernicus, Cocconeis diminuta, C. placentula var. euglypta and Synedra parasitica but does not contain any of the indicators that are usually found at this level, such as Amphipleura pellucida, Asterionella formosa and Stephanodiscus astraëa var. minutula. Perhaps the environmental conditions in Loch Tarff differed from those of the lochs in the Inverpolly area either because of its morphometry or because of some climatic aspect such as altitude or distance from the west coast, so that these forms were excluded.

There appears to be a change in the assemblage towards the top of TDZ 2 (TDZ 2b) as Achmanthes suchlandti, A. linearis, Cyclotella comta and C. comensis tend to be concentrated just below the silt/clay boundary. This subzone also contains the highest percentage of plankton and is correlated with the juniper-dominant pollen zone (table 8); this is perhaps a better equivalent of the diatom zone 2 of the other sites than the zone as a whole. The reason for this is unclear but perhaps TDZ 2b may reflect a change in environment at this site.

The diatom assemblage suggests that the late-glacial environment of Tarff was not perhaps as alkaline as that of the other sites because many of the markedly alkaline taxa are absent. In the absence of any detailed analysis of the local rocks, the Moine Schists, it is surmized that the ground up particles may not add such base-rich constituents to the water as the Torridonian sandstones or Lewisian gneiss even though the chemical analyses of the sediments of Sionascaig and Tarff are somewhat similar with respect to most of the elements analysed (Pennington et al 1972) over the interstadial section excepting that Tarff has slightly higher values for both iron and sodium.

5. Late-glacial synthesis

The purpose of this section is to correlate the analyses from the four different sites in order to establish the general sequence of diatom assemblages for the late-glacial and to attempt to make some interpretation of the environmental history of the lakes in the two regions. In consideration of each diatom zone comparison will be made with other profiles, outside the present study, and with comparable contemporary assemblages. The interpretation of these assemblages and their correlation with the evidence of other fossil assemblages in relation to climatic changes will also be discussed.

Comparison of the four profiles shows that the assemblages vary in each one and it is sometimes difficult to cite taxa as being characteristic of any given zone even though assemblages at all sites show some change in their composition at comparable levels. The advantage of comparing several sites, however, is that it becomes possible to identify what part of the diatom assemblage conforms to the general late-glacial pattern and what part is peculiar to any one site. The present analyses have also been compared with the already published studies of lake sediments from other regions, such as the English Lake District and Scandinavia (mainly Denmark), in order to see how changes in the diatom assemblages of the lakes in northern Scotland conform to any generalized pattern of diatom distribution over the period under review.

Several difficulties are encountered when correlating the events of the late-glacial from several sites and comparing them with previous

studies. There are very few studies of the diatom history of British lakes, especially of lakes that are comparable with Sionascaig and Cam, and none include the analysis of any deep-water late-glacial profile so that both these profiles are unique in that respect. The diatom profile from Windermere was described from a marginal core only, since deep-water late-glacial sediments did not contain diatoms (Pennington 1943). Kentmere (Round 1957b) was a very shallow lake, originally less than 5 m deep, which became filled in with sediment. The late-glacial profile of Blelham (Evans 1970) is based upon material from Blelham Bog, a small kettle-hole now filled in by peat. In this paper Evans did not describe a complete late-glacial profile from Blelham Tarn itself but a partial profile suggests that the sequence was similar. Loch of Park was also shallow and is now drained (Alhonen 1968) and Bølling Sø in Denmark had a similar history (Fjerdningstad 1954). Frequently diatom profiles have been analysed by different methods which also hinder comparison; Round (1957b and 1961) analysed diatoms as numbers per gram dry weight in his studies of the assemblages of Kentmere and Esthwaite. Alhonen (1968) analysed the percentage composition of the Loch of Park diatom assemblages but used a different basic sum of 150 - 200 diatoms which affects the representation of the rare taxa. Pennington (1943) also made percentage analyses but divided the assemblages into large and small sized taxa. The advantage of the present study is that all the four sites have been studied in the same manner. Even so, the progression from one site to another carries with it an increase in knowledge and understanding of the taxonomic and ecological problems (see Taxonomy section, part 2), so that there may still be differences in the resulting diatom analyses due

to the number of taxa recognized or the attention paid to the differences between samples. The Loch Sionascaig profile was analysed in what was originally considered to be 'some detail' but as a result of the closer interval analyses of the Cam and Borralan profiles, further details have been observed that can now be correlated at all sites. These details were initially overlooked or thought to be merely artifacts of the sampling technique in the Loch Sionascaig profile. A justification for the study of several sites together is that it confirms the statement in the section on Sionascaig (Haworth, in Pennington et al 1972 p. 237) that ... "another lake profile with a similar succession "may" confirm that these changes have not just been caused by the chances of sampling." Presumably closer studies of certain sections of the profiles could reveal even further patterns but until we are proficient in observing and explaining these such studies may not be worthwhile.

A third difficulty is that there are two integrated patterns present in the diatom profiles. One is a regional pattern where the diatom assemblages appear related to the lithology of the sediments and can be classified into broadly similar zones at all sites. There is a second pattern of variation within these zones because each site possesses an almost unique combination of physical factors such as morphometry, geology (fig 3), microclimate, etc. This is somewhat at variance with the situation encountered in certain other parts of the world, eg. in North America (Wright and Watts 1969) and in northern Germany (Hustedt 1950), where there are large areas of similar geology and vegetation in which many lakes of similar morphometry or trophic status occur, such as shield or kettle lakes. At some of the Scottish sites it might have

been impracticable to identify or correlate certain occurrences had there not been independent evidence from the pollen and chemical analyses to substantiate the diatom evidence as, for example, in the upper part of Diatom Zone 1. It is not easy to explain exactly what determines the differences from site to site or to decide just what importance should be attached to them. There is not yet enough information on the ecological requirements of the taxa in these diatom assemblages to allow the interpretation of the finer details of these environmental differences.

The attempted interpretation of these diatom assemblages by correlation with present day communities presents difficulties because palaeolimnological studies are based upon the small part of the algal community that is recorded in the sediments and which is mainly diatomaceous whereas studies of present day communities may be based upon the predominantly non-diatomaceous groups. The sediment assemblages also include taxa from all the ecological niches present in the catchment area but very few studies of contemporary algae cover the same range; many studies are based solely upon the phytoplankton and so comparison of the possible lake types is sometimes rather limited.

Diatom Zonation

The boundaries of the diatom assemblage zones found in each of the four profiles have been determined independently but the numbering of these is based upon the original analysis of the Loch Sionascaig profile (table 5) in order to make correlation between sites easier. The division into three zones has therefore been retained and the zones appear to represent the general pattern of the late-glacial diatom sequence and to be related to the lithology of the sediments. Diatom

Zone 1 represents the earlier part of the profile, Diatom Zone 2 occurs within the organic silt layer, and Diatom Zone 3 is related to the upper clay layer (table 9); subdivisions have been made where necessary. The relationship of this diatom zonation to the late-glacial pattern of pollen assemblages and ^{14}C dating is shown in table 9.

Diatom Zone 1

Diatom Zone 1 (DZ 1) is equated with Pollen Assemblage Zone A (table 9). This zone is subdivided into A1, A2 and A3 on pollen and chemical criteria (Pennington et al 1972) and Pennington (in press) has used the pollen data from Cam Loch to establish that there is evidence of an environmental fluctuation within PAZ A that can be correlated with the continental sequence of Bølling-Allerød Time. The ^{14}C date of the A1/A2 boundary is c. 13,000 BP and that of the A3/B boundary is c. 12,000 BP (tables 9 and 10). This latter date corresponds to the beginning of Allerød Time and PAZ A is therefore pre-Allerød in time and is correlated with Pollen Zone I of Mitchell et al (1973). PAZ A3 represents a small climatic recession comparable on ^{14}C dating with the Bølling-Allerød Stade.

Diatom subzones have also been delimited on the basis of changes in the diatom assemblages within this lowest zone and the upper subzone can be correlated with PAZ A3 at all sites.

It is suggested that local differences between the four sites were probably maximal within this zone due to the manner of the withdrawal of the ice from the area. One would expect the diatom assemblages of Cam and Borralan to be similar as they are neighbouring lochs within the same drainage system (fig 2) and some of the differences that occur may

Table 9 Correlation of late-glacial zonation

Diatom Assemblage Zones	Pollen Assemblage Zone (Pennington <u>et al</u> 1972) (Pennington 1973)	Continental sequence & ^{14}C dates (Cam Loch)	Pollen Zones (Mitchell <u>et al</u> 1973)
		<u>c.</u> 10,000 BP	
3 Aerophile taxa present, many taxa of previous zone absent	Bf C Be		III
<u>Fragilaria</u> &/or plankton dominance. 2 Increase in no. of taxa of nutrient-rich assemblages	B3 Bd B2 B1 Bc	<u>c.</u> 10,900 BP Allerød Time	II
1b Aerophile taxa present, (1c at Cam Loch)	A3 Bb	<u>c.</u> 12,000 BP	I
Alkaline benthic taxa dominant.	A2	Bølling Time	
1a Lowest no. of taxa. Pioneer community	A1 Ba	<u>c.</u> 13,000 BP	

CLAY OF FULL GLACIAL AGE

Table 10 **Radiocarbon dates from Cam Loch late-glacial;**
 core 72-7. Pennington (in press)

PAZ	Core Depth in cm	Date BP	^{14}C No. SRR
	526 - 536	10,226 \pm 190	247
C	536 - 545	10,598 \pm 450	248
	545 - 555	10,701 \pm 490	249
B	555 - 565	12,436 \pm 220	250
	565 - 575	12,764 \pm 185	251
	575 - 584	11,918 \pm 230	252
A	584 - 594	12,938 \pm 240	253

be due to the fact that Borralan lies upstream of Cam and is of different morphometry. In Cam Loch a further subdivision of DZ 1 has been made below the PAZ A3 level (CDZ 1 a/b) on the basis of a change in the dominant Fragilaria spp. Here the lowest subzone corresponds to a pre-PAZ A1 pollen zone and neither of these assemblages have been observed in other profiles (Pennington in press).

The lowest diatom remains found in the sediments are not necessarily the earliest to have grown in the area. Comparison with the area around present day glaciers in Norway and Iceland (unpublished material) suggests that diatoms may have been growing around the lakes - in water seepages, streams and pools - even while the barren clays were being added to the sediments. Any diatom remains added to the sediments would be well dispersed amongst the minerogenic contribution. This population would have provided an initial source of diatoms for the colonization of the lake and diatom remains would have begun to accumulate in the sediments once diatoms became numerous in the lake itself and when the amount of mineral sedimentation was reduced. The ease of migration of various algae, including diatoms, into new territory has been demonstrated, albeit under rather different climatic conditions, on the recently evolved volcanic island of Surtsey, off the coast of Iceland. Here Behre and Schwabe (1970) recorded that 106 algal taxa had already arrived in this new ecosystem since its evolution in 1963. The list included 71 diatom taxa, the majority of which were small benthic forms and included Fragilaria construens, F. construens var. venter and F. pinnata.

These Fragilaria taxa are also the first diatoms to occur in the late-glacial assemblages and F. construens, F. elliptica and F. pinnata are all dominants in assemblages that include Diploneis elliptica, Amphora ovalis var. pediculus, Campylodiscus noricus var. hibernicus, Cymbella ventricosa, Epithemia sorex, Gyrosigma spenceri var. nodifera and Melosira teres. The reason why these are successful pioneer forms is not altogether clear and must depend on physio-chemical conditions of the environment. As benthic taxa, living on the surface of mineral sediment, they may be better able to utilize any existing nutrients released from the ground up rock particles but this does not explain why many other inhabitants of this same ecological niche are excluded. The fact that there is a constant record of new taxa appearing in the profiles (see diatom assemblage tables) suggests that there was continuous change in environmental conditions over the period represented by this zone.

Fragilaria spp. are also found in the earliest diatom assemblages of many other sites following on the retreat of the ice, even in lakes of very different size and morphometry. Fragilaria construens and/or F. pinnata dominate the early assemblages in the Blelham kettle-hole (Evans 1970) and Kentmere (Round 1957b) in the English Lake District, and in Bølling Sø in Denmark (Fjerdingsstad 1954). The early assemblages in the marginal deposits of Windermere also include Fragilaria spp. although they are not regarded as the dominant forms (Pennington 1943). There are sites where this domination by Fragilaria spp. does not occur, as in the early sediments of Loch of Park (Alhonen 1968), where Campylodiscus noricus is dominant, and in Blea Tarn (Haworth 1969), where C. noricus and Diploneis elliptica were among the few taxa of the lowest assemblage.

The pioneer Fragilaria spp. also occur in some of the earliest assemblages in North America. The early limnic stage of Kirchmer Marsh is dominated by F. construens (Florin 1970) and both F. construens and F. pinnata are dominant at the base of the profile of Pickerel Lake sediments (Haworth 1972b) in a lake somewhat similar to Cam Loch.

Fragilaria spp. occur in the lowest samples of a short diatom profile from a small lake, Leirvatn, which is situated at 1600 m in the presently glaciated region of south-west Norway. This lake is the lowest of a chain of small lakes, the upper one of which may still receive some meltwater from the remnant ice of a retreating corrie glacier. The water of Leirvatn is very clear and there appears to be a very low rate of accumulation of the sediments, as measured by $^{137}\text{Caesium}$ (Pennington 1973). Inspection of the radiocarbon dates for Cam Loch (table 10) suggest that the rate of accumulation was similarly low during the late-glacial there too. Pennington (1973) has compared the pollen assemblage present in the surface sediment of Leirvatn with zone Ba in Blea Tarn in the English Lake District, ie. with the lowest of the pollen zones in the late-glacial sediments (table 9). One might therefore expect to find that the diatom assemblage is similar to that found in DZ 1 but it is very different in composition, being dominated by Melosira spp, of the 'distans' group and other indicators of an acid environment, such as Peronia heribaudii, Frustulia rhomboides var. saxonica, Pinnularia spp. and Eunotia spp. This indicates that there has been a change from the original alkaline environment to an acidic one. It would appear to fit the theory proposed by Ström (1958) that these Norwegian lakes have an alkaline pH only as long as there is an inflow of glacial meltwater.

Presumably this is indicative of the balance between the input of glacial debris and the development of acid humus upon the catchment area. In the Scottish lochs, and at other sites in Britain, the diatom assemblage continued to indicate an alkaline environment throughout the whole of the interstadial period and so no change in pH can have occurred when the input of glacial debris ceased in these lakes.

One site where Fragilaria pinnata is recorded as being dominant (over 90% of the assemblage) in the recent sediments, is Klareš in northern Greenland (Foged 1972). This lake is said to be alkaline in pH and to have a low nutrient level. Chemically, nitrate is undetectable and the major anions are bicarbonate and sulphate; the alkalinity being due to the local rocks which are Eocambrian sandstone and dolomite. This complete domination of the assemblage by one taxon and the paucity of other taxa is a situation very similar to that in the early part of DZ 1 and many of the types of taxa present are also similar. A ^{14}C date shows that an estimated 102 cm of sediment has been deposited in Klareš in c. 5000 years, which indicates an extremely low rate of sedimentation of 0.02 cm/year.

Having discussed the presence of late-glacial type diatom assemblages in arctic Greenland it would seem relevant to consider the supposed climate of the early part of the interstadial and whether any changes appear to be consequent upon climatic amelioration. In the absence of any direct evidence of temperature fluctuations any climatic interpretation relies heavily upon the evidence of the fossil assemblages of that period. The earliest pollen assemblages at Cam Loch (Pennington, in press) suggest that a 'tundra biota' was followed by high-alpine or

sub-alpine grass and sedge heath but it is not possible to ascertain whether this was determined solely by the low temperatures or by the state of the soils (Pennington et al 1972). Tree pollen is an accepted indication of amelioration in climate and it is known that juniper, which occurs in PAZ A2, will only flower when there is sufficient rise in temperature (Pennington, 1970). The evidence of the tree pollen distribution is that trees extended farthest northwards during Allerød Time and botanists have always supposed that this represented the warmest period of the interstadial. Coope and Brophy (1973), however, regard the Coleopteran (beetle) assemblages found in late-glacial material as being more sensitive indicators of past temperatures than plants, due to their apparently narrow ecological range and to the ease with which they can invade new territory when conditions permit. On this evidence, from a site in North Wales, they suggest that the upper part of Pollen Zone I (equated with PAZ A2, table 9) actually represents the warmest period of the whole interstadial oscillation with mean July temperatures as high as 17°C and that the rise in temperature was relatively sudden. In their opinion, the Coleoptera indicate that the climate had already begun to deteriorate and become more continental by the onset of Allerød Time (Pollen Zone II, PAZ B) and declined throughout that zone.

It would appear from the diatom zonation that there is no change in the assemblages that could be construed as being consequent upon the sudden climatic amelioration which, it is suggested, was of general occurrence in Britain during DZ 1. Although Cleve-Euler (1950-55), Hustedt (1930) and Krasske (1943) all cite certain taxa as being

characteristic of cold, boreal, alpine or arctic environments (table 4) most diatoms appear very tolerant of temperature changes and they cannot therefore be said to be good indicators of climatic changes. A feature of the distribution of reportedly boreal taxa which occur in the sediments studied is that the percentage of these forms is very low in DZ 1 and increases in DZ 2 where the species diversity is greater (figs S 18, S 20, S 22 f) ie. over the period of amelioration. It would appear that the true pioneer taxa are those which tolerate a great range of conditions rather than those which are restricted. It is, however, difficult to decide just how far this pattern reflects a true indication of diatom response to climatic change or how much this is biased by the lack of precise knowledge of the indicator taxa.

Subzone indicating recession within DZ 1

This subzone (1b at Borralan and Tarff, 1c at Cam) is correlated with pollen assemblage zone A3 (table 9) and can now be recognized at all four sites although it was originally overlooked in the Sionascaig profile due to the spacing of the samples. There it can now be identified by the changes in the percentages of several taxa, eg. the increase in Fragilaria construens and F. elliptica and the decrease in Cyclotella spp. in sample 581 cm. This is matched with the general increase in F. elliptica which occurs at the other sites over this part of the profile (fig S 15).

The evidence for change within this subzone is extremely slight, algologically; a few aerophilous taxa (figs S 16, S 18, S 20, S 22 e) indicate that there may have been some increase in the inwash of

material into the lakes, presumably as a result of erosion of less stabilized soils. This is correlated with a layer of paler grey sediment of apparently greater clay content and also with the PAZ A3 pollen evidence (Pennington et al 1972) of a decrease in Juniper pollen and the increases in Artemisia (a dominant during the DZ 3 period) and in bryophyte spores from partially stabilized soils.

Diatom zone 2

This diatom zone is equated with PAZ B and correlated with Allerød Time/Pollen Zone II on the evidence of the Cam Loch ^{14}C dates (tables 9 and 10, and Pennington, in press).

It would appear that the recession reflected in the upper subzone of DZ 1 had little effect on the environment of the lakes themselves because there is very little change in the assemblage composition, nor did it affect the overall change in environment that resulted in the diatom assemblages of DZ 2. There is an overlap of some of the characteristic taxa of the two zones, as some aerophilous taxa occur at the beginning of DZ 2 in the Cam Loch profile and a few DZ 2 taxa appear in the previous zone (table S 13).

DZ 2 assemblages differ somewhat from site to site and very few taxa characteristic of DZ 2 are actually to be found in the assemblages of all of the sites studied. This is probably due to the local environment prevailing at each site. The Cam Loch assemblage includes taxa common to the two other sites in the area as it is related to Sionascaig in size and to Borralan by the same drainage system; it also includes a greater number of alkaline and calcareous taxa because of the

proximity of the limestone outcrop, as well as several taxa which are specific to eutrophic lakes, taxa that also occur in the recent sediments of Loch Leven (Haworth 1972a).

The overall characteristics at all sites show an apparently homogeneous zone to which many diatom taxa are restricted within the late-glacial (fig S 15 and tables S 13, S 14 and S 15). Only in Loch Tarff does there appear to be any significant change within this zone and this is perhaps due to some different development of this loch because TDZ 2b appears more characteristic of the whole of DZ 2 of the other sites than is TDZ 2a even though the high percentages of Fragilaria pinnata suggest that both parts belong to the one zone (fig S 21).

Fragilaria construens is either a dominant or a characteristic taxon of the DZ 2 assemblage at all sites (figs S 15, S 17, S 19, S 21) but the actual percentages are dependent on the relative proportions of the Cyclotella spp. that are also present (fig S 15). Taxa that appear to be generally indicative of this zone include Amphipleura pellucida, Amphora veneta var. capitata, Diatoma elongatum, Fragilaria virescens, Melosira islandica ssp. helvetica, Navicula cuspidata, Stephanodiscus astra var. minutula and Cyclotella comensis (the last with the exception of Cam Loch where it is also a dominant taxon in CDZ 3, fig 14). None of these taxa are dominant forms in the assemblages and their importance is often only at the level of presence and absence. The differences that are apparent in the ecological spectra of the four sites are due to the relative proportions of Cyclotella and Fragilaria spp. because the former tend to be found in water of pH \pm 7 and the latter in alkaline waters which is why there appears to be an inverse

relationship between the planktonic and alkaline assemblages. Hustedt (1937-39) cited Cyclotella plankton as being characteristic of oligotrophic lakes of the northern subalpine and temperate zones; only in Sionascaig is the percentage of Cyclotella spp. large enough to suggest that this represents a characteristic part of the planktonic assemblage of DZ 2 and that this loch might therefore come into Hustedt's category of a Cyclotella lake, ie. oligotrophic in character. Even in this case the benthic taxa are mainly alkaline forms and only indicate a slight decline in base status of the benthos towards the SDZ 3 boundary where there is a slight increase in acidophilous percentages. The proportions of Cyclotella occurring in DZ 2 in the other three sites are small and similar proportions can be found in the recent diatom assemblages of Loch Leven (Haworth 1972a) and therefore cannot be regarded as indicative of oligotrophy in these cases.

It is not easy to compare DZ 2 of these Scottish sites with other sites that have previously been studied. Firstly, two of the sites have very different morphometry and only Borralan and Tarff can really be compared with other shallow-water sites. Secondly, division of the late-glacial profile has not always been made and in many cases the interstadial is discussed as a single unit. Fragilaria spp. are generally found to be dominant throughout the whole of the late-glacial, as in the Cam, Borralan and Tarff assemblages, and this has been regarded as indicative of the contribution of the littoral community to the sedimentary record. During Pollen Zone II (ie. Allerød Time) the diatom assemblage of Bølling S β was dominated by F. construens and var.

venter (Fjerdingstad 1954) and at Blelham F. pinnata was dominant (Evans 1970, fig 25). At Loch of Park (Alhonen 1968) and Kentmere (Round 1957b) Fragilaria and Epithemia spp. are both considered as characteristic of this zone. In every case planktonic forms are rare and this has been attributed to the size or depth of these lake basins even though, in some cases, planktonic forms occur in the post-glacial. In spite of differences at all the sites it would appear that the diatom assemblages of the interstadial are remarkably similar, though not identical, in their composition.

So far the Sionascaig DZ 2 assemblage is unique in containing a high percentage of planktonic forms (fig S 16 d) and the difficulty of finding another site containing this same late-glacial sequence has proved a major limitation to this part of the study. Moderately large lakes where it is possible to obtain a late-glacial sequence containing diatoms within the upper 6 m of deepwater sediment are infrequent, especially in an area that would be geographically and geologically similar to Sionascaig. The only other site in northern Britain where a core of late-glacial sediments has been obtained which is known to include a high proportion of plankton in a diatom assemblage of zone 2 characteristics is Loch Stack, a lake which is 256 hectares in area with a maximum depth of 33 m (108 ft), about 20 miles (32 km) north of Loch Cam. This site has not yet been fully explored (Haworth, unpublished material) but a single spot sample consisted of the following dominant diatom taxa :-

<u>Cyclotella comensis</u>	24.0%
<u>Fragilaria construens</u>	14.1%
<u>Achnanthes suchlandti</u>	6.4%
<u>Fragilaria brevistriata</u>	5.7%
<u>Cyclotella kützingiana</u>	4.6%

In Sionascaig the DZ 2 assemblage is composed of approximately 40.5% Cyclotella comensis and 10% C. kützingiana. The geology of the catchment area around Loch Stack is rather more comparable with that of Cam Loch than Sionascaig and it is not yet clear what characteristics the two sites have in common, apart from the Cyclotella percentages.

Other sites that have been explored for possible planktonic assemblages in DZ 2 include Lochs Veyatie and Duntelchaig in north-west Scotland, and Windermere and Coniston Water, in the English Lake District (table 3). Loch Veyatie lies downstream of Cam (fig 2) and has a late-glacial diatom flora similar to that found in Cam core 72-11 in containing few taxa and rather eroded specimens. The samples from Coniston (core 71-6) also contained poorly preserved material, while the marginal core from Windermere included the expected preponderance of benthic and epiphytic taxa; Pennington (1943) explored the deep-water sediments of Windermere and found no diatoms within the late-glacial profile. The late-glacial sediments from the deep-water area of Loch Duntelchaig contain a diatom assemblage similar to that of Cam Loch, the lake is also similar in size and is situated to the east of Loch Ness about 17 miles (27 km) north-east of Loch Tarff.

It is the experience of the Quaternary Research Group that fossiliferous late-glacial deposits are infrequent in the larger British

lakes and are unlikely to occur because many lakes are long, narrow valley lakes which have steeply sloping sides and a fast throughput of water. Deposits of this time from such sites often contain poorly preserved material with eroded specimens, as in Coniston. This fact severely limits the number of possible deep-water late-glacial sites in Britain.

The environmental interpretation of the DZ 2 assemblages of the four Scottish lochs is that the water tended to be slightly alkaline and that the benthos, at least, contained sufficient nutrients to allow the existence of a diatom flora similar to that occurring in some of the nutrient-rich Danish lakes (Jørgensen 1948). Only in Sionascaig does the presence of the Cyclotella spp. suggest that the mid-waters might have been circumneutral in pH and oligotrophic, while benthic taxa remain typically alkaliphilous. It is difficult to match these assemblages with any known to exist at the present time, mainly because of the absence of planktonic taxa, this parallels the fact that the pollen taxa of PAZ B "are not comparable with any known existing vegetation type" (Pennington, in Pennington et al 1972). Possibly the type of temperate climate that is postulated for this period (Coope and Brophy 1972) and discussed in the previous section (DZ 1) does not now exist in any region that would be comparable. Some diatomaceous plankton of eutrophic or oligotrophic character is usually present in lakes in a temperate climate, even where the climate is markedly continental. The diatom flora of the Danish or north German lakes (Jørgensen 1948, Hustedt 1950) shows that an alkaline benthic assemblage of the type found in the late-glacial sediments is more typically associated with the planktonic indicators of nutrient rich conditions, eg. Fragilaria crotonensis, Melosira granulata,

M. ambigua, M. islandica ssp. helvetica, Stephanodiscus dubius, S. hantzschii, S. astraea and var. minutula. The diatom flora of the nutrient poor lakes is generally different and usually includes more Eunotia, Frustulia, Pinnularia and Tabellaria spp. associated with a planktonic assemblage of Melosira distans and its varieties and Tabellaria spp. It is therefore difficult to correlate the DZ 2 assemblages with these present day assemblages because of the lack of plankton. It is assumed that this ecological niche must have been occupied by some non-diatomaceous algae, if so then the assemblage is more nearly comparable with those occurring in some of the alpine lakes where the plankton is low in biomass, consisting of nannoplanktonic forms of Chrysophyceae, Cryptophyceae and Chlorophyceae with only few diatoms occurring (Pechlaner 1971 and Brettum 1972). In these lakes the light usually penetrates to great depths and the plankton is frequently concentrated near the bottom of the lake in response to light levels and to the source of nutrients, ie. the benthos.

It is suggested that the similarity between these alpine lakes and the late-glacial lakes is not necessarily climatic but is due to the low rate of sedimentation, as measured at Leirvatn (Pennington 1973) and Cam Loch (table 10) by ^{137}Cs and ^{14}C . It is supposed that this rate represents a small influx of suspended material into the lakes. The character and amount of this material would depend on local geology, soils and the vegetation in the catchment area. One therefore presumes that if there is very little suspended matter the benthos would form the main source of nutrients. This being so the organisms best able to avail themselves of this source would be the benthic and littoral taxa and as the sediments are of an alkaline nature alkaliphilous diatoms

would occur. If nutrients are well utilized on the benthos only a small amount may be released into the mid-water to be available for planktonic organisms and a nutrient gradient would be formed which would create an ecosystem similar to that of alpine lakes. Low plankton biomass and a low amount of seston would allow deeper penetration of light through the water and increase the area of benthos coming within the photic zone. The penetration of light to depths of over 30 m have been recorded for some alpine lakes (Pechlamer 1971), if the photic zone of the Scottish lochs had extended even to c. 20 m (c. 66 ft) this would have included most of the benthos in all but Sionascaig (table 11).

It is therefore concluded that the type of diatom community present in DZ 2 assemblages must reflect the type of soils and therefore the vegetation of the catchment area rather more closely than any climatic regime.

Table 11

Present areas of the lochs between different water depths
(from Murray & Pullar 1908 - 1910)

Depths in ft	Sionascaig acres %	Cam acres %	Stack acres %	Tarff acres %	Borralan acres %
0-25	672 50.2	320 49.5	265 42	88 66	118 100
25-50		151 23.3	183 29	43 34	
50-75	422 31.7	67 10.4	146 23		
75-100		67 10.4	33 5		
100-150	171 12.7	42 6.4	5 1		
150-200	68 5.0				
200	5 .4				
Depth of late- glacial below water surface at core site	50 + 16 ft	44 + 16 ft	39 + 13 ft	33 + 7 ft	10 + 6 ft

Diatom zone 3

This zone of post-interstadial cold is probably the easiest part of the profiles to define as the diatom zones correspond to the lithological change to grey clay at all sites (tables 5 - 8). The zone is correlated with PAZ C in the pollen sequence and therefore with Pollen Zone III of Mitchell et al (table 9). There is consistent pollen and chemical evidence of colder climate and this zone is correlated with the Loch Lomond Readvance in Scotland (fig 1 and Sissons 1967).

In each of the profiles there are marked changes in the diatom assemblages at the base of DZ 3 and many taxa of the previous zone are absent from these samples, appearing again in the more organic deposits of DZ 4. Diatoms are present throughout DZ 3 at all four sites and although there may be fewer diatoms in proportion to mineral matter in the diatom slides studied they do not appear to be excluded from any part of this deposit; the same is also true of the diatom assemblage of pollen zone III at Blelham (Evans 1970) which is very similar. However, in the zone III profiles from Loch of Park (Alhonen 1968), Blea Tarn (Haworth 1969) and Kentmere (Round 1957b) there are samples of barren clay and a rather thicker clay deposit, of 20 - 30 cm, than is present at the Scottish sites. This difference is presumably due to the greater proximity of Lake District sites to the local valley glaciation of that period.

Several taxa, whilst not restricted to this zone, are either proportionately better represented or present more consistently in the samples. These include :-

<u>Achnanthes gracillima</u>	<u>Hantzschia amphioxys</u>	<u>P. borealis</u>
<u>Ceratoneis arcus</u>	<u>Meridion circulare</u>	<u>P. nodosa</u>
<u>Cymbella sinuata</u>	<u>Navicula costulata</u>	<u>P. semicruciata</u>
<u>Cy. semisymmetrica</u>	<u>N. contenta v. parallela</u>	<u>P. suchlandti</u>
<u>Cy. ventricosa</u>	<u>N. fracta</u>	<u>Stauroneis anceps</u>
<u>Fragilaria elliptica</u>	<u>N. schmassmannii</u>	<u>St. phoenicenteron</u>
<u>F. vaucheriae</u>	<u>N. sp. V</u>	<u>Surirella ovata v. pinnata</u>
<u>Gomphonema olivaceoides</u>	<u>Pinnularia balfouriana</u>	<u>Tabellaria flocculosa</u>

Not all these taxa are present at every site. Differences that are evident in the diatom assemblages may be due to the effect of the renewed cold temperature upon the different catchment areas of the lakes and also to the state to which the lake itself had evolved over the preceeding interstadial, as well as to the size and depth of the lake.

It might be supposed that diatoms that have been characterised by ecologists as boreal or cold forms would be best represented over this period. This is not so and they are generally less well represented here than in the preceeding zone (figs S 18, S 20, S 22 f). Again it is suggested that, either diatoms are insensitive as temperature indicators, or that the truly 'cold' forms have yet to properly understood and identified. The higher percentages of boreal and planktonic taxa that occur in Cam DZ 3 (fig S 18 d & f) are due to the unusual predominance of Cyclotella comensis in these sediments. In the other profiles this taxon is more generally associated with DZ 2 assemblages (fig 14) and is also partly responsible for the increase in the boreal percentages there too (figs S 18, S 20, S 22 f). The presence of this taxon in the two zones suggests that its distribution is not temperature

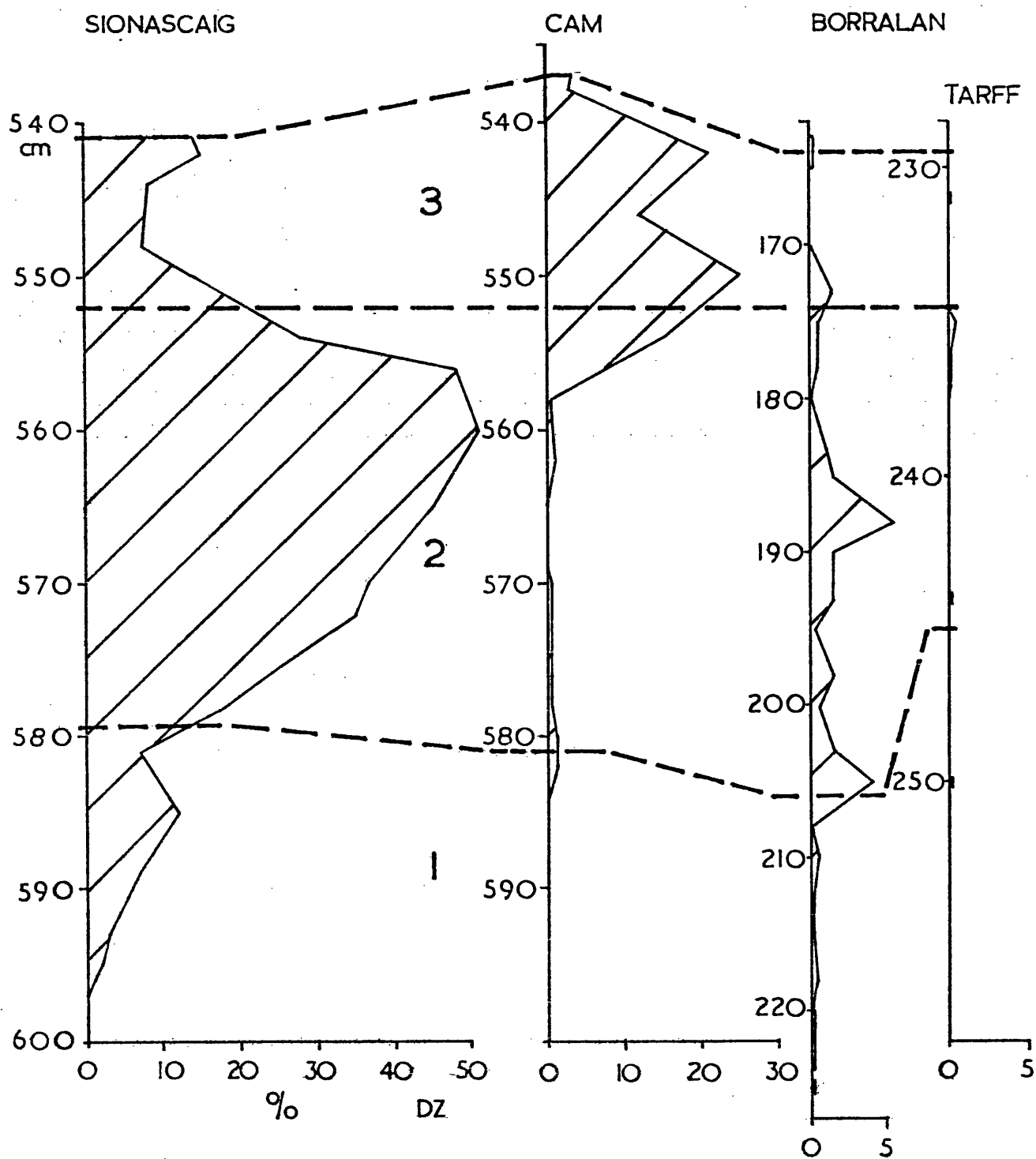


Figure 14. Percentages of *Cyclotella comensis* in the late-glacial profiles of each site.

determined even if the determining factor is, itself, temperature dependent. C. comensis is reported as characteristic of several alpine lakes (Findenegg 1971) although it is not clear why it is prominent in one small alpine lake, Gossenköllesee, and not in other similar lakes nearby (Pechlaner, personal communication).

The diatom assemblages of the sites fall into two groups based on the relative sizes of the basins; in the small lakes, Tarff and Borralan, they are dominated by Fragilaria elliptica and in the larger lakes, the Cam assemblage is dominated by F. elliptica and Cyclotella comensis (table S 13), whilst that of Sionascaig is more varied with C. kützingiana, C. comensis and F. construens being dominant. If one accepts Cleve-Euler's statement (Cleve-Euler 1958) that the small round form of F. elliptica that occurs in the DZ 3 sediments (fig 9, no 15) is a pelagic form then it would appear that the diatom plankton was possibly quite well represented during DZ 3. It would seem that the planktonic taxa of greater nutrient requirements such as Stephanodiscus astraia var. minutula, Melosira islandica ssp. helvetica and Asterionella formosa were the ones that were temporarily displaced by the decrease in temperature and the increase in mineral particles.

The diatom flora of Sionascaig DZ 3 is much more diverse than that of the other lakes which suggests a clearer lake with less severe erosion of its catchment area. Pollen and chemical evidence (Pennington et al 1972) suggests that there was inwash of interstadial soils from the catchment which is confirmed by an increase in the proportion of aerial diatom taxa (figs S 16, S 18, S 20, S 22 e), although

the rate of sedimentation remained low (table 10). All the evidence indicates that ice was absent from the catchment areas of these lakes.

Diatom zone 4

All analyses were continued into this zone, which represents the beginning of the post-glacial or Flandrian period, and they indicate the reappearance of many taxa of DZ 1 and 2 correlated with the increase in the organic content of the sediments (tables 5 - 8). Several new taxa also occur, notably Achnanthes exigua (fig S 15 and tables S 13, S 14 S 15).

For further discussion of this zone and subsequent zones of the post-glacial profile see Sionascaig section and table 5.

Studies other than those of new late-glacial profiles need to be undertaken for there to be further progress towards the interpretation of the environment of the late-glacial (late-Devensian) period in British lakes. Little is known about the autecology of many of the characteristic or rare taxa that occur in late-glacial assemblages and much of the literature currently available does not appear to provide the palaeolimnologist with suitable information on this subject. Jørgensen's study of diatoms in Danish lakes (1948) is still the most useful comprehensive study on the ecology of the different taxa but this only covers a certain range of lake types and many taxa in the late-glacial taxon list do not occur there. Possibly one should not depend on literature that concerns other aspects of algology to provide the answers on the ecological requirements of the various diatom taxa. Studies need to be specifically designed to analyse different types of sediment accumulations and to relate them to the ecosystems which they represent, studies which

combine taxonomy with precise ecological observations. Although there are numerous algal studies on lakes, many are concerned with the productivity of the phytoplankton community and it is rare that there is any information on the benthic community that can be correlated with the ecological parameters provided. Very little is known, for instance, about the ecological requirements of the benthic forms of Fragilaria, even though they occur in many diatom assemblages, whilst there are detailed studies which include the planktonic form F. crotonensis.

More information is needed concerning the ecological requirements of the benthic communities in arctic or alpine water bodies in order to interpret the early, pioneer assemblages of the late-glacial. A search into much of the literature and also in the field, in Norway and Iceland, has so far failed to reveal the exact modern counterpart of the late-glacial assemblages recognized in the present study. Such assemblages may not, in fact, exist because the climatic conditions postulated for the late-glacial, with low temperatures at low altitudes and latitudes, may not now occur in any comparable situation.

Final conclusions

The sediments of Loch Sionascaig were originally analysed to discover if the overall changes in the diatom assemblages of the lochs of north-west Scotland were similar to those found in the sediments of lakes in the English Lake District. The theories proposed as a result of this analysis of a single profile were that :-

1. There are patterns of changes in the diatom assemblages in both the late-glacial and post-glacial periods.
2. Other sites with successive diatom assemblages similar to those found in Loch Sionascaig were required for substantiation of the evidence for the zonation of the late-glacial section.
3. Certain taxa were characteristic of certain parts of the late-glacial.
4. The characteristic taxa of the late-glacial assemblages are those presently found in alkaline, somewhat nutrient rich lakes.
5. Sionascaig is unique in having a high percentage of plankton represented in the diatom zone 2 assemblage.
6. The overall trend in the environment of the lake spanning the period from the retreat of the ice up to the present day has been from an alkaline lake, where at least the benthos was rich in nutrients, to an oligotrophic, acid one. This trend in the post-glacial is correlated with the leaching of bases from the soils of the catchment area around Loch Sionascaig where pine and finally sphagnum bog became established with the consequent change in the lake to acid oligotrophy.

The subsequent analyses of the late-glacial profiles of Lochs Borralan, Tarff and Cam have shown that :-

1. Repeatable patterns do occur within the late-glacial diatom assemblages, for example, the DZ 3 assemblages of Loch Sionascaig can be easily recognized at the other three sites.
2. These further analyses have substantiated the evidence for the original zonation of the Loch Sionascaig profile and more detailed analysis of the profiles of Cam, Borralan and Tarff has indicated that there are other changes enabling more discrete zonation.
3. Although some diatom taxa show distinct patterns of presence and absence throughout the late-glacial these are not always identical at every site and the differences are probably due to local geology or the environment within the lake itself.

The taxa of DZ 1 would appear to be the most varied as, of the original list of taxa in Sionascaig DZ 1 (Pennington et al 1972) only Fragilaria spp, Epithemia spp, and Diploneis elliptica are consistently characteristic of this zone but they are not restricted to it. F. pinnata and F. construens would appear to be the pioneer taxa in the new environment of the lakes. More taxa are characteristic of DZ 2 than were originally cited for the Sionascaig profile and of that list Melosira islandica ssp. helvetica, Asterionella formosa, Cyclotella spp. and Amphipleura pellucida do generally occur in this zone. Several more taxa can also be cited after comparison of all four sites eg. Diatoma elongatum, Fragilaria virescens, Navicula cuspidata, Amphora veneta var. capitata and Stephanodiscus astraes var. minutula. The same situation is true of DZ 3 in which practically every one of the taxa originally cited from Sionascaig's DZ 3 were present at every site and several more taxa have emerged as being characteristic of the zone.

It would appear that DZ 3 is the zone that is most similar at every site and that DZ 1 is the least similar.

4. Comparison with lakes in presently glaciated regions, such as Norway, the Alps or Greenland demonstrates the early history of these late-glacial sites. There the photic zone is very deep and the diatoms almost entirely benthic. The Scottish lakes appear to have remained in this condition throughout the late-glacial period in spite of any climatic amelioration and it is suggested that there was a difference between the benthic and the planktonic environments. The planktonic environment appears to have been one of low nutrients and low biomass in which plankton may have been non-diatomaceous, except in the case of Loch Sionascaig. The benthic community existed in a more alkaline environment that appears to have had a richer supply of nutrients, mainly inorganic in nature, and presumably from the sediments. All the sediments at the core sites could have come within or near the photic zone if it extended to the depths suggested by Pechlaner (1971) during that period and therefore some of the diatom assemblage may have been formed 'in situ' during part of the late-glacial at least.

5. Factors other than size of lake or local geology would appear to be important in determining the type of plankton in the late-glacial lakes as Cyclotella spp. are only prominent, so far, in DZ 2 of Sionascaig and Loch Stack and these lakes have different morphometry and are within different types of catchment areas whilst Cam Loch, which is intermediate in size and depth, has little diatomaceous plankton in DZ 2 and C. comensis is only prominent in DZ 3.

6. The only site where the overall trend has been analysed up to the present day remains Loch Sionascaig and so there are no further conclusions to be made on post-glacial environments.

The whole history can thus be shown schematically in table 12.

Table 12 Schematic representation of the history of the lochs investigated.

DZ <u>7-9</u> (NWS 5 - present)	Maximum of acidophile diatoms in response to development of peat and decline of woodland on the catchment. Sionascaig is now an oligotrophic, acid loch showing no sign of recent enrichment due to human influence.
<u>6</u> (NWS 3-4)	Birch and pine woodlands. Increase in acidophile diatom taxa and continued decrease of alkaliphiles as water becomes more acidic.
<u>5</u> (NWS 1-2)	Sediment increasingly organic with acid humus, decrease in alkaliphile diatoms.
<u>4</u> Trans.	Retreat of the ice, cessation of solifluction, temperature amelioration. Pioneer communities and late-glacial alkaline type of diatom assemblage.
<hr/>	
post-glacial late-glacial	
<u>3</u> (PAZ C)	Climatic recession c. 500 years. Colder with solifluction of late-glacial soils and inwash into lakes. Local glaciation (Loch Lomond Readvance in west Scotland) but not within these catchment areas. No reduction in the diatom communities but some taxa excluded by the severe conditions.
<u>2</u> (PAZ B)	Clear lake with deep photic zone, some increase in the organic fraction of the sediment due to development in vegetation around the lake, low rate of sedimentation. Oligotrophic water body with mainly non-diatomaceous plankton ^{presumably} concentrated near the benthos. Benthic environment more alkaline with greater availability of nutrients and more varied diatom assemblage than in previous zone.
<u>1</u> (PAZ A)	A3. Some climatic recession with slight increase in erosion and inwash.
	Clear water lake, snowbed vegetation around the lake depositing pollen and adding carbon to sediment. Climatic amelioration in upper part of this zone, A2. Benthic diatoms in an alkaline environment which was low in suitable nutrients.
	Glacial inwash, either from melting ice or erosion of drift. Presumably diatoms in pools, streams and around the lake edge but very little deposited in the sediments.
	Retreat of active ice leaving lake into which glacial clays are deposited. No biological record.

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A core from sediments of Loch Sionascaig, north-west Scotland was originally analysed to determine the changes in the late-glacial and post-glacial diatom assemblages. These indicate a trend from diatoms of alkaline assemblages in the late- and early post-glacial to those of acid and unproductive waters. This is apparently a response to changes in soils and vegetation upon the catchment area of the lake. Three diatom assemblage zones have been demonstrated within the late-glacial and zone 2 contains an unusually high proportion of planktonic Cyclotella spp.

Three other late-glacial profiles were analysed, from L. Cam and L. Borralan in the same neighbourhood, and L. Tarff in the L. Ness area, to discover 1) whether this zonation applied generally, 2) whether taxa were characteristic of certain parts of the profiles, and 3) if other profiles include a similar planktonic phase. The sites varied in size and morphometry but the three zones could always be distinguished although assemblages differed slightly; none included a high percentage of Cyclotella in zone 2. Closer interval analysis has resulted in recognition of several subzones including one that can be correlated with the Bølling-Allerød stage.

Environmental interpretation is based on comparison with modern diatom assemblages and most taxa present in the late-glacial now occur in alkaline, nutrient-rich lakes. The lack of diatom plankton in the late-glacial suggests a similarity with some alpine lakes where diatoms are predominantly benthic. This similarity may have been initially due to severe climate and low nutrient supply. Continuation of this type of assemblages throughout the interstadial and into the early post-glacial suggests that the environment depends on the type of soils, vegetation and the amount of inwash of material into the lakes, rather than on climate.

SOME PROBLEMS OF DIATOM TAXONOMY IN SCOTTISH LAKE SEDIMENTS

By ELIZABETH Y. HAWORTH

Freshwater Biological Association, The Ferry House, Far Sawrey, Ambleside, Westmorland

The new diatom taxa *Amphora levenensis* sp. nov., *A. eximia* sp. nov. J. R. Carter, *A. veneta* Kütz. var. *capitata* var. nov., *Cymbella pseudonorvegica* sp. nov., *C. semisymmetrica* sp. nov., *Navicula stroesei* (Østrup) Cleve var. *lanceolata* var. nov. and *Stauroneis smithii* Grun. var. *minima* var. nov. are described and some problems of identification noted in the analysis of diatoms from Scottish lakes sediments.

In analysing the diatom assemblages in lake sediments I have come across several diatoms which cannot be identified from the published literature; some of these occur frequently in the samples and others only rarely and it has been my practice to assign a code name to them for the purpose of analysis in the hope that a further search will produce the correct name. Some taxa, previously published under these code names, have now been identified and I have decided that others are unpublished. The purpose of this paper is to act as a supplement and to describe some of the new species found in lake sediments from Loch Leven, Kinross (Haworth, 1972), Loch Sionascaig, Rosshire (Pennington, Haworth, Bonny & Lishman, 1972), Loch Borralan and Cam Loch, Sutherland (Haworth, unpublished). Notes on the taxonomy of some other taxa are also included.

One species, *Amphora eximia*, was first recorded by J. R. Carter of Hawick and it is his description and figure which are included here.

METHODS

All the material was acid cleaned in a mixture of sulphuric and nitric acid, washed in distilled water and mounted in Naphrax (R.I. 1.74). The identifications have been made under a Leitz Dialux microscope using phase contrast and a $\times 90$ objective. Ringed type specimens are quoted below and are deposited with the British Museum (Natural History), London (BM); the author's own slide collection (EH); and, in one case, the slide collection of Mr J. R. Carter, Hawick (JCR).

OBSERVATIONS AND DISCUSSION

AMPHORA LEVENENSIS sp. nov.

DIAGNOSIS

Frustulum ellipticum, long. 16-23 μm , lat. 11 μm , sine copulis visibilibus. Valva 4.5-4.6 μm lata, cymbelliformis, latere ventrali fere recto. Rhaphe filiformis, latus ventrale versus leviter concava. Area axialis angusta, area centralis ventraliter fasciam externe dilatata et marginem valvae attingentem formans, dorsaliter minus expansa. Striae 15-17 in 10 μm ; eae dorsales paullo radiatae, tenuiter lineolatae, linea hyalina angusta undulata in aream centralem currenti interruptae; eae ventrales centrum versus radiatae, prope apices convergentes, illae nodulum centralem maxime propinqua marginem valvae non attingentes.

Frustule elliptical, 16-23 μm long and 11 μm broad, without visible girdle bands. The valve is 4.5-4.6 μm broad, cymbelloid in shape with an almost straight ventral edge. The raphe is thread-like, gently concave to the ventral side. The axial area is narrow and the central area is a one-sided fascia, widening outwards to the ventral margin but less expanded on the dorsal side.

Striae 15–17 in 10 μm , the dorsal ones slightly radial and faintly lineolate, interrupted by a narrow, undulate longitudinal area which runs into the central area. The ventral striae are radial near the centre to convergent at the apices with the central striae not reaching to the margin of the valve.

Type slides: BM 77901; Loch Leven, 16 cm. = Holotype.

EH 318; Loch Leven, 100 cm.

This species (Figs 1, 2, 13) is seen only rarely in the recent sediments of Loch Leven (Haworth, 1972; Fig. 3 no. 9 = *Amphora* sp. L 100) and in Cam Loch. It could possibly be allied to *A. parallelistriata* Manguin (Foged, 1971, Pl. 19, no 8).

AMPHORA EXIMIA sp. nov. J. R. Carter

DIAGNOSIS

Frustulum ovale, cingulo nec lineolato nec lineis intercalaribus praebenti. Valva cymbelliformis, margine dorsali convexo, eo ventrali fere recto, interdum in centro gibboso, long. 12 μm , lat. 4–5 μm . Rraphe recta, filiformis, marginem ventralem propinqua, ad nodulum centrale non inflexa. Area axialis linearis, angusta; area centralis dorsaliter carens, ventraliter fasciam externe dilatatam et marginem valvae attingentem formans. Striae ad centrum paullo radiatae, apices versus latere dorsali radiatiores, latere ventrali convergentes, in centro c. 20 in 10 μm , apices versus crebriores ad 30 in 10 μm .

Frustule oval, connecting girdle without lineations or intercalary lines. Valves cymbelloid with convex dorsal margin and nearly straight ventral one which may, however, be slightly gibbous at the centre, about 12 μm long and 4–5 μm broad at the centre. Raphe near the ventral margin, straight and thread-like without a bend at the central nodule. Axial area very narrow, linear; central area completely absent on the dorsal side but on the ventral side a definite fascia widening outward to the margin. Striae slightly radial at the centre and more so towards the apices on the dorsal side; on the ventral side they are similarly radial at the centre but become convergent towards the apices. On both sides they are wider apart at the centre than at the apices, ranging from about 20 in 10 μm at the centre to 30 or more at the apices.

Type slides: BM 77902; Loch Leven, 20 cm. = Holotype.

JRC B.U.3; Linton Moss.

EH 565; Loch Sionascaig, 534 cm.

Present in a core of sediment from Linton Moss at a depth of about 13 m, *Amphora eximia* (Figs 3, 14) is apparently one of the first inhabitants of the lake after the melting of the ice (Ref. = L.M.B.U./3 38.OX18.1). It is also found in cores from Loch Sionascaig (Pennington *et al.*, 1972; Fig. 25, no. 12 = *Amphora* sp. B), Loch Leven and Cam Loch.

AMPHORA VENETA Kützing var. *CAPITATA* var. nov.

DIAGNOSIS

A var. *veneta* differt valvis elongatioribus, apicibus capitatis.

Frustulum anguste ellipticum, long. 20–35 μm , lat. 10 μm , aliquot copulas instructum. Valva longa, cymbelliformis, 3.5–4.5 μm lata, apicibus capitatis, latere dorsali convexo, ventrali paullo concavo. Rraphe ad marginem ventralem approximata, poris centralibus distantibus. Striae ventrales carentes, dorsales ex punctis elongatis lineas irregulares facientibus formatae, circum aream centralem quam prope apices distantiores, c. 26–30 in 10 μm .

Amphora veneta var. *capitata* differs from var. *veneta* in the elongate shape of the valve and in possessing distinctive capitate ends.

The frustule is narrowly elliptical, 20–35 μm long, 10 μm broad, with several intercalary bands. Valve long and cymbelloid, 3.5–4.5 μm broad, with capitate apices, the dorsal margin is convex while the ventral one is slightly concave. The raphe is close to the ventral margin and the central pores are distant from one another, which is a characteristic of the species. There are no striae on the ventral side and those on the dorsal consist of elongate punctae forming irregular longitudinal lines. The striae are more widely spaced around the central area than they are towards the apices, about 26–30 in 10 μm .

Type slides: BM 77901; Loch Leven, 16 cm.

BM 77902; Loch Leven 20 cm. = Holotype.

EH 546; Loch Sionascaig, 500 cm.

The designated type slide of Kützing's *A. veneta* in the British Museum does not, in fact, contain any specimens of this species at all and comparisons were made with specimens on a slide in the Van Heurck collection, BM 26321.

Var. *capitata* (Figs 6, 19) is found in the late-glacial and early post-glacial sediments of Loch Borralan and Loch Sionascaig (Pennington *et al.*, 1972; Fig. 25, no. 13 = *Amphora* sp. A); it is also present in the recent sediments of Loch Leven (Haworth, 1972; Fig. 3, no. 8). It is never found in any abundance in the samples and the species itself does not occur at all. Foged (1955) has a drawing similar to var. *capitata* (Fig. 14, no. 21) which he ascribes to the var. *veneta*, as does Mayer (1946). I also found specimens in the Comber Collection from Monnymore, Arran (BM 31860) and these were unnamed. Recently this form has been found in the collections of algal material from the Isle of Mull made by the British Museum (Miss P. Sims, personal communication).

CYMBELLA HILLIARDII Manguin

This diatom occurs in the sediments of Loch Leven and Loch Sionascaig (Pennington *et al.*, 1972, Fig. 25, no. 14 = *Cymbella* sp. L 20) but was not found in the collections of present day material. It has now been identified as *Cymbella hilliardii* Manguin (Foged, 1971; Manguin, 1961). The clearly asymmetric valve has produced and more or less acute apices and the raphe is excentric with long terminal fissures bent towards the ventral side. The specimens in the Loch Leven core are 33–40 μm long and 8–9 μm broad and the striae are 12–13 in 10 μm on the dorsal side and 14–15 in 10 μm on the ventral side, all with 22 puncta in 10 μm . *C. hilliardii* is very similar to *C. ventricosa* (Agardh) Kützing and *C. hebri-dica* (Gregory) Grunow but it differs from them in the shape of the apices and in the number and angle of the striae (Figs 4, 15).

CYMBELLA PSEUDONORVEGICA sp. nov.

DIAGNOSIS

Valva manifeste asymmetrica, margine dorsali paullo convexo, ventrali fere recto, apicibus subrostratis, long. 52–57 μm , lat. 9–11 μm . Rhaphe recta, paullo excentrica, expansa, nodulum centalem versus dorsaliter inflexa, fassis terminalibus longis et ventraliter inflexis. Area axialis angusta, area centralis manifesta rhombicaque. Striae ubique radiatae, 11–13 in 10 μm , apicibus versus crebriores, ad 18 in 10 μm , ea centralis dorsalis curtior distantiorque quam aliae, perspicue sed subtiliter punctatae.

Valve clearly asymmetrical, the dorsal margin only slightly convex and the ventral one almost straight; apices subrostrate, 52–57 μm long, 9–11 μm broad. Raphe straight and broad in the central portion, slightly excentric, bent dorsally at the central nodule and the long terminal fissures bent ventrally. Axial area narrow, central area clear and diamond shaped. Striae radial throughout, 11–13 in 10 μm , becoming closer towards the apices to 18 in 10 μm , the central stria on the dorsal side is shortened and more distant than the others; striae clearly but finely punctate.

Type slide: EH 501; Loch Sionascaig, 10 cm. = Holotype.

This species (Figs 5, 16) is similar to *C. gracilis* (Rabenh.) Cleve and to *C. norvegica* Grunow but the shape of the apices is intermediate between these two species. The central area is very similar to that of *C. norvegica*. The pattern of the striae and the central area are the distinctive features of *C. pseudonorvegica*.

The species is found in the recent sediments of Loch Sionascaig in an assemblage indicative of acidic, oligotrophic conditions (Pennington *et al.*, 1972; Fig. 25, no. 15 = *Cymbella* sp. S 10). Very rare.

CYMBELLA SEMISYMMETRICA sp. nov.

DIAGNOSIS

Valva elliptica, apicibus rostratis, paullo asymmetrica, latere dorsali leviter convexiore quam ventrali, long. 12–13.5 μm , lat. 4.5–5.5 μm . Raphe filiformis, fere semper centralis et leniter latus dorsale versus curvata, fissis terminalibus uncinatis et ambobus latus ventrale versus flexis. Area axialis angusta, linearis, ab area centrali irregulariter formata distincta. Striae 18–22 (–24) in 10 μm , distantiores circum aream centalem, subtiliter punctatae, punctis c. 36 in 10 μm ; plerumque in toto valvae radiatae, interdum prope apices perpendiculares; striae circum aream centalem longitudine et directione variantes, saepe irregulariter abbreviatae aut duae centrales vel in latere ventrali vel in lateribus ambobus fere parallelae.

Valve elliptical with rostrate apices, often slightly asymmetrical, the dorsal margin being only slightly more convex than the ventral one, 12–13.5 μm long, 4.5–5.5 μm broad. The thread-like raphe is almost always central and slightly curved towards the dorsal side, the terminal fissures are both hooked towards the ventral side of the valve. The axial area is narrow and linear, it is quite distinct from the irregularly shaped central area. The striae are 18–22 (–24) in 10 μm , wider spaced around the central area, and are finely punctate with about 36 puncta in 10 μm ; the striae are usually radial throughout the valve but sometimes appear perpendicular towards the apices. Around the central area they are variable in length and direction, often irregularly shortened or with the two central striae on the ventral side, or on both sides, almost parallel.

Type slides: BM 77899; Loch Sionascaig, 540 cm. = Holotype.

EH 570; Loch Sionascaig, 540 cm.

This species (Figs 7, 8, 17) was originally designated "*Navicula* sp. T" (Pennington *et al.*, 1972; Fig. 25, no. 8) but I have decided that it truly belongs to the genus *Cymbella* because of the asymmetry and the shape of the raphe. I have been through all the drawings of *Cymbella* species in the Fritsch Collection and find that it is similar to *C. aequalis* var. *subaequalis* (Grunow) Mayer, *C. aequalis* var. *florentina* A. Cleve, *C. diluviana* (Krasske) Florin and *C. similis* Krasske but all these species are larger in size and possess different striae numbers or patterns around the central area or apices. *C. semisymmetrica* is also similar to *Navicula absoluta* Hustedt and *N. hustedtii* var. *obtusum* Hustedt. *N. absoluta* is clearly symmetrical in outline, the axial area is narrow but widens towards the central area, which it does not do in *C. semisymmetrica*, and it has a greater number of striae, 26–28 in 10 μm , which are curved radially towards the centre but are perpendicular at the apices. Hustedt (1961) describes *N. hustedtii* var. *obtusum* as having 26–28 striae in 10 μm which are radial towards the centre and perpendicular or convergent towards the apices; he also describes a straight raphe and a clearly furrowed axial area. I am indebted to Dr M.-B. Florin and Dr R. Simonsen for their confirmation of these differences between *C. semisymmetrica*, and *C. diluviana* and *N. absoluta* respectively.

C. semisymmetrica is frequent in the late-glacial and early post-glacial sediments of Loch Sionascaig, Loch Borralan and Cam Loch and is especially to be found in the sediments of the final cold phase.

NAVICULA STROESEI (Østrup) Cleve var. *LANCEOLATA* var. nov.

DIAGNOSIS

A var. *stroesei* differt area centrali latiore, rotundatiore, circum quam striae regulariter abbreviatae sunt, valva lanceolata, non elliptico-lanceolata apicibus capitatis.

Valva lanceolata, apicibus paullo rostratis, long. 57 μm , lat. 14 μm . Raphe directa vel paululum undulata. Area axialis angusta recta, area centralis rectangularis. Striae omnino radiatae, 15 in 10 μm , clare regulariterque punctatae, punctis 18 in 10 μm , in lineis undulatis dispositis.

Var. *lanceolata* differs from var. *stroesei* in having a wider, more rounded central area around which the striae are regularly shortened, and in the outline of the valve, which is lanceolate

rather than elliptic-lanceolate with rostrate to capitate apices as described by Cleve-Euler (1953).

Valve lanceolate with only slightly rostrate apices, 57 μm long, 14 μm broad. Raphe straight or very slightly undulate. Axial area narrow and straight and central area rectangular. Striae radial throughout, 15 in 10 μm , clearly and regularly punctate with 18 puncta in 10 μm forming undulating longitudinal lines.

Type slide: EH 310; Loch Leven, Lm 80 cm. = Holotype.

Var. *lanceolata* (Figs 9, 18) is also very similar to *N. lacustris* Gregory but this has bowed axial areas and a rounded central area; also the raphe of *N. lacustris* extends into the central area, which it does not do in var. *lanceolata*.

N. stroesei var. *lanceolata* occurs rarely in the recent sediments of Loch Leven (Haworth 1972, Fig. 3, no. 26 = *Navicula* sp. Lm 80), both *N. stroesei* and *N. lacustris* also occur in the samples.

STAURONEIS SMITHII Grunow var. *MINIMA* var. nov.

DIAGNOSIS

A var. *smithii* differt ambitu valvae, quae non ad centrum inflata est, et striis crebrioribus.

Valva lanceolata, apicibus subcapitatis, long. 14–15 μm , lat. 5 μm . Pseudoseptum clare visibile. Raphe recta, filiformis. Area axialis angusta, in aream centralem paullo dilatata. Area centralem ad instar stauri angusti. Striae paullo radiatae, tenuissimae, c. 40 in 10 μm .

Differs from var. *smithii* as the valve is not inflated at the centre and has finer striae.

Valve lanceolate with subcapitate apices, 14–15 μm long, 5 μm broad. Pseudoseptum clearly visible within the apices. Raphe straight and thread-like within a narrow axial area which widens slightly at the central area. The central area is a narrow staurus reaching to the margins. The striae are slightly radial and very fine, about 40 in 10 μm near the central area becoming closer towards the apices.

Type slides: BM 77898; Cam Loch 582 cm. = Holotype.

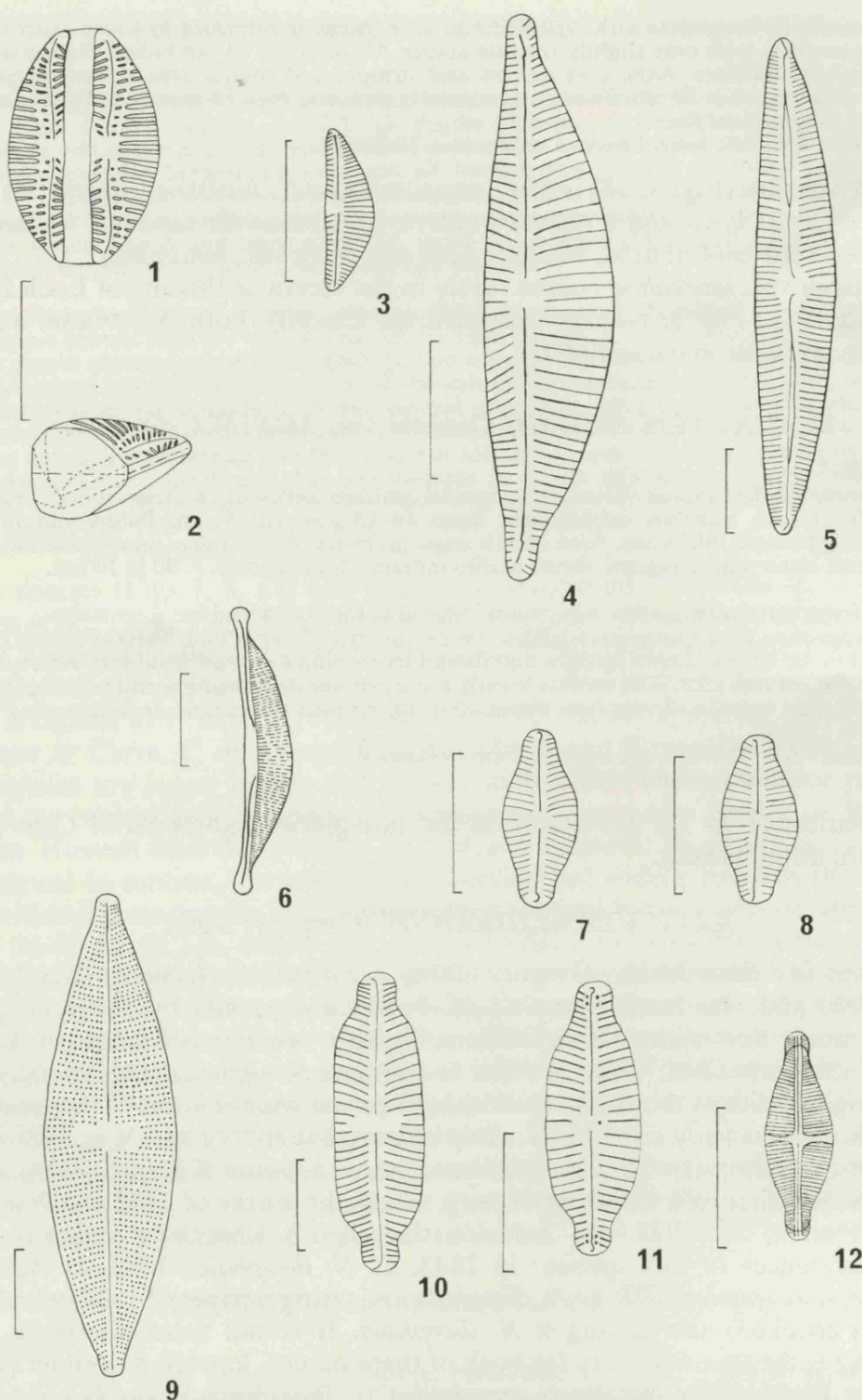
EH 855; Cam Loch 538 cm.

This variety (Figs 12, 21) occurs in the late-glacial sediments of Cam Loch (Haworth, unpublished).

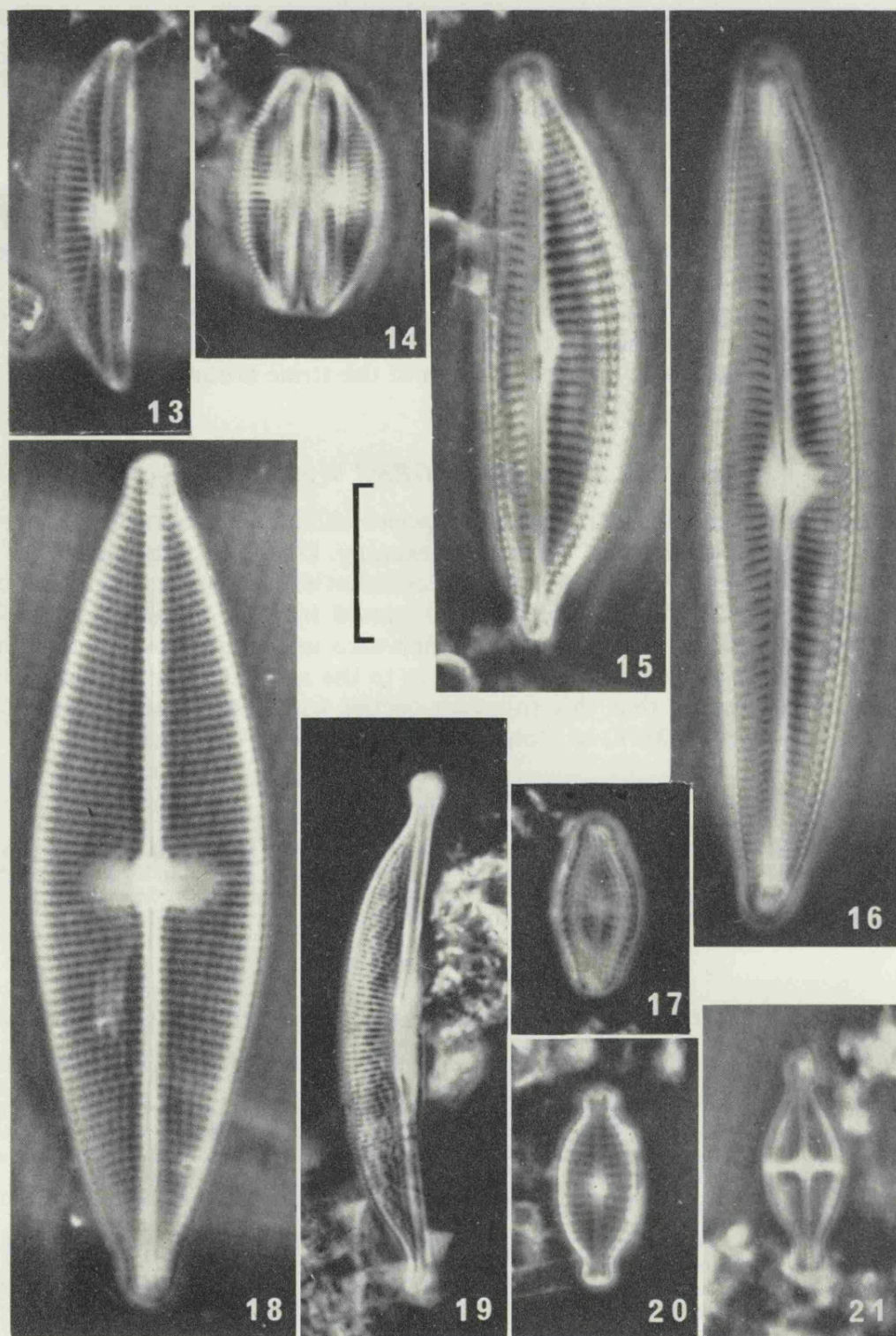
NAVICULA ELGINENSIS (Gregory) Ralfs

This was first described by Gregory (1856) as *Pinnularia elginensis* (lectotype = BM 11751) and was made a variety of *Navicula dicephala* by Cleve (1894). I recently made new slides from William Smith's original collection of Lough Mourne sediments (BM 77868) in order to compare *N. elginensis* and *N. dicephala* as the original slide is too thick to allow high power examination of the material. The authorities usually cited for *N. dicephala* are Ehrenberg and Wm. Smith but Smith, in his Synopsis of British Diatomaceae (1853) cites Kützinger (1844) as his reference. Kützinger refers it to Ehrenberg, citing the works of 1843 (on North & South America) and 1838 (the "Infusionsthierchen"). Ehrenberg makes the following references to this species: in 1843, as *N. dicephala*; 1840, as *Navicula (Pinnularia) dicephala*; 1838, as *N. dicephala* and citing a paper of 1837 (which has not been checked) also calling it *N. dicephala*. It would seem, therefore, that Ehrenberg is the true authority for both of these names. Patrick & Reimer (1966) state that Ehrenberg's specimens are similar to *Pinnularia biceps* Gregory and that this is therefore *Pinnularia dicephala* Ehrenberg. Kützinger's slides (BM 18813 – 5) also contain only *Pinnularia* specimens.

The specimens in the Lough Mourne material (Fig. 10) correspond both to the drawing in Husted's Bacillariophyta (1930, Fig. 526) and to the lectotype of *N. elginensis*. It would seem that what Wm Smith and many later authors called



FIGS 1-12. Figs 1, 2. *Amphora levenensis* sp. nov. Fig. 3. *Amphora eximia* sp. nov. Carter. Fig. 4. *Cymbella hilliardii* Manguin. Fig. 5. *Cymbella pseudonorvegica* sp. nov. Fig. 6. *Amphora veneta* var. *capitata* var. nov. Figs 7, 8. *Cymbella semisymmetrica* sp. nov. Fig. 9. *Navicula stroesei* var. *lanceolata* var. nov. Fig. 10. *Navicula elginensis* (Gregory) Ralfs. Fig. 11. *Navicula similis* Krasske. Fig. 12. *Stauroneis smithii* var. *minima* var. nov. Scales = 10 μ m.



FIGS 13–21. Fig. 13. *Amphora levenensis* sp. nov. Fig. 14. *Amphora eximia* sp. nov. Carter. Fig. 15. *Cymbella hilliardii* Manguin. Fig. 16. *Cymbella pseudonorvegica* sp. nov. Fig. 17. *Cymbella semisymmetrica* sp. nov. Fig. 18. *Navicula stroesei* var. *lanceolata* var. nov. Fig. 19. *Amphora veneta* var. *capitata* var. nov. Fig. 20. *Navicula similis* Krasske. Fig. 21. *Stauroneis smithii* var. *minima* var. nov. Scale = 10 μ m.

Navicula dicephala is *N. elginensis* and not the species of *Pinnularia* that Ehrenberg first observed.

This species occurs in the sediments of Loch Sionascaig and Loch Leven along with *N. explanata* Hustedt, with which it is sometimes confused.

NAVICULA SIMILIS Krasske

A species found in the recent sediments of Loch Leven (Haworth, 1972 Fig. 3, no. 18=*N. sp* L 20) has been identified as *N. similis* (M. Møller & N. Foged, personal communication). Contrary to the original drawing (Krasske, 1929) this species is characterised by a central punctum and punctae separated off from the two striae nearest to the apices on each side of the raphe. It is thus very similar to *N. tecta* Krasske but has a different pattern of the striae around the central area (Figs 11, 20).

PINNULARIA DIVERGENS Wm. Smith

The conventional description of this species includes a characteristic keel-shaped "Membranverdickung" or wall thickening. Under certain conditions of microscopy, i.e. under oil-immersion phase contrast at high power magnification, this is not visible and would appear to be caused by light refraction from the striae on either side of the central area when seen under low power objectives. This has, I believe, caused some confusion as to the specific limits of this species and I have determined that this situation occurs with the ringed specimen on W. Smith's slide (BM 23578) of Dolgelly Earth material.

ACKNOWLEDGEMENTS

I am very grateful to Mr J. R. Carter for permission to publish his description of *Amphora eximia* and to Mr R. Ross for writing out the Latin diagnoses. Mr R. Ross and Dr J. W. G. Lund kindly read the manuscript. I should also like to thank Dr M.-B. Florin, Miss P. Sims, Dr R. Simonsen, Mr N. Foged and Mr M. Møller for all their help and advice.

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THESIS

516328

The late-glacial (late-Devensian) and
post-glacial (Flandrian) diatom assemblages
from lochs in northern Scotland.

by

Elizabeth Y. Haworth

Figures S 15 - 22.

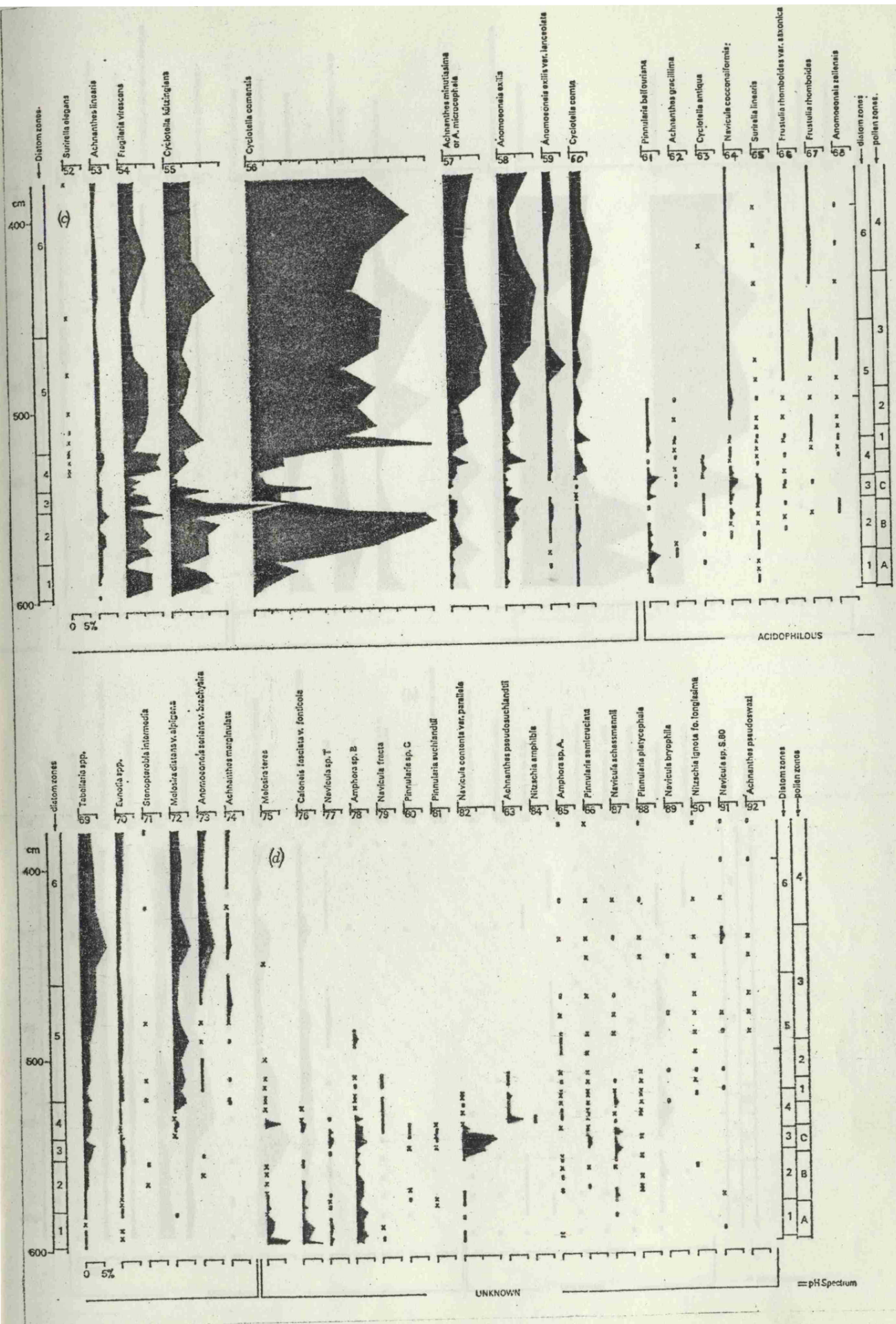
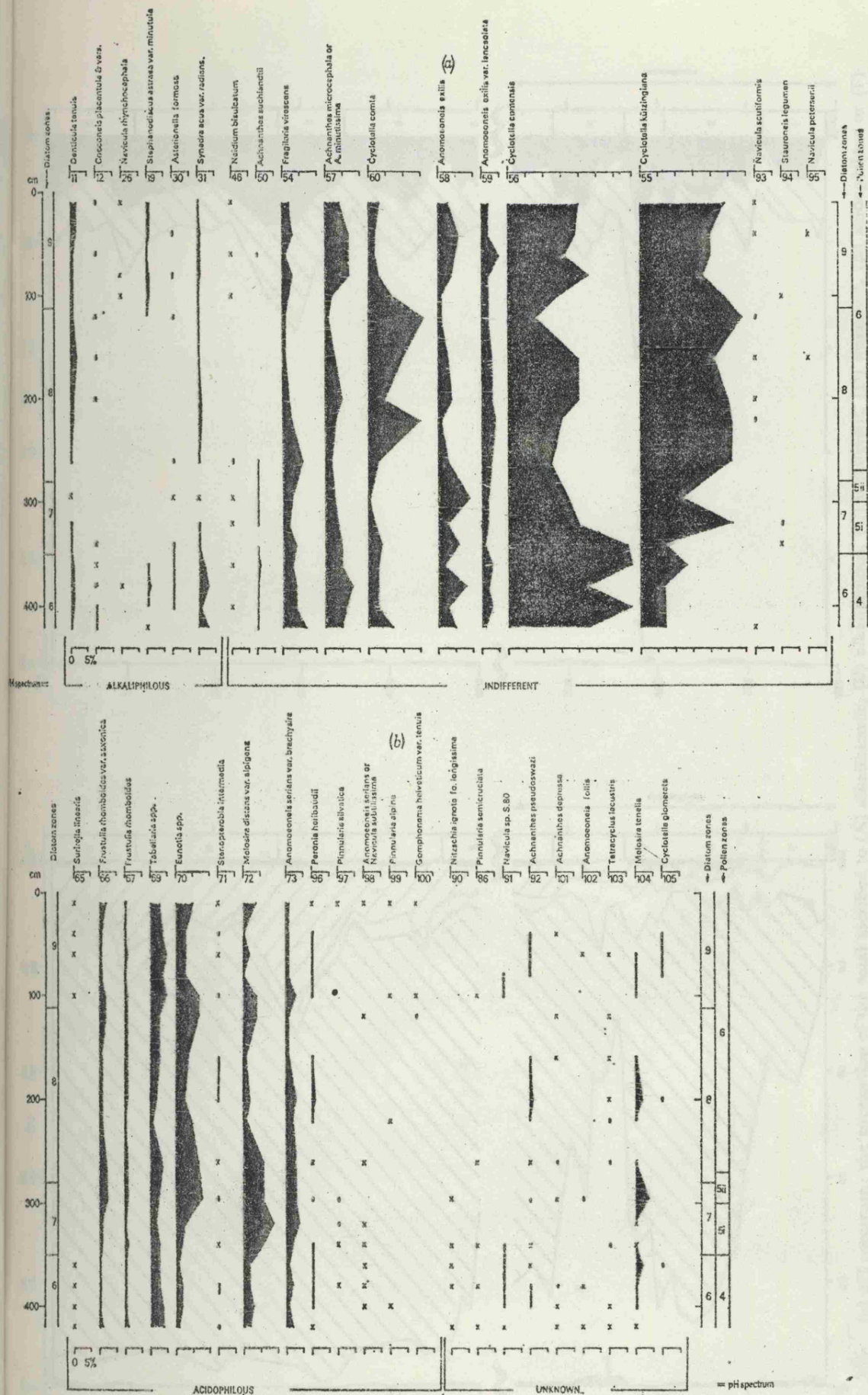


Figure S 15 i (continued). for Pinnularia zones 6 to 9.



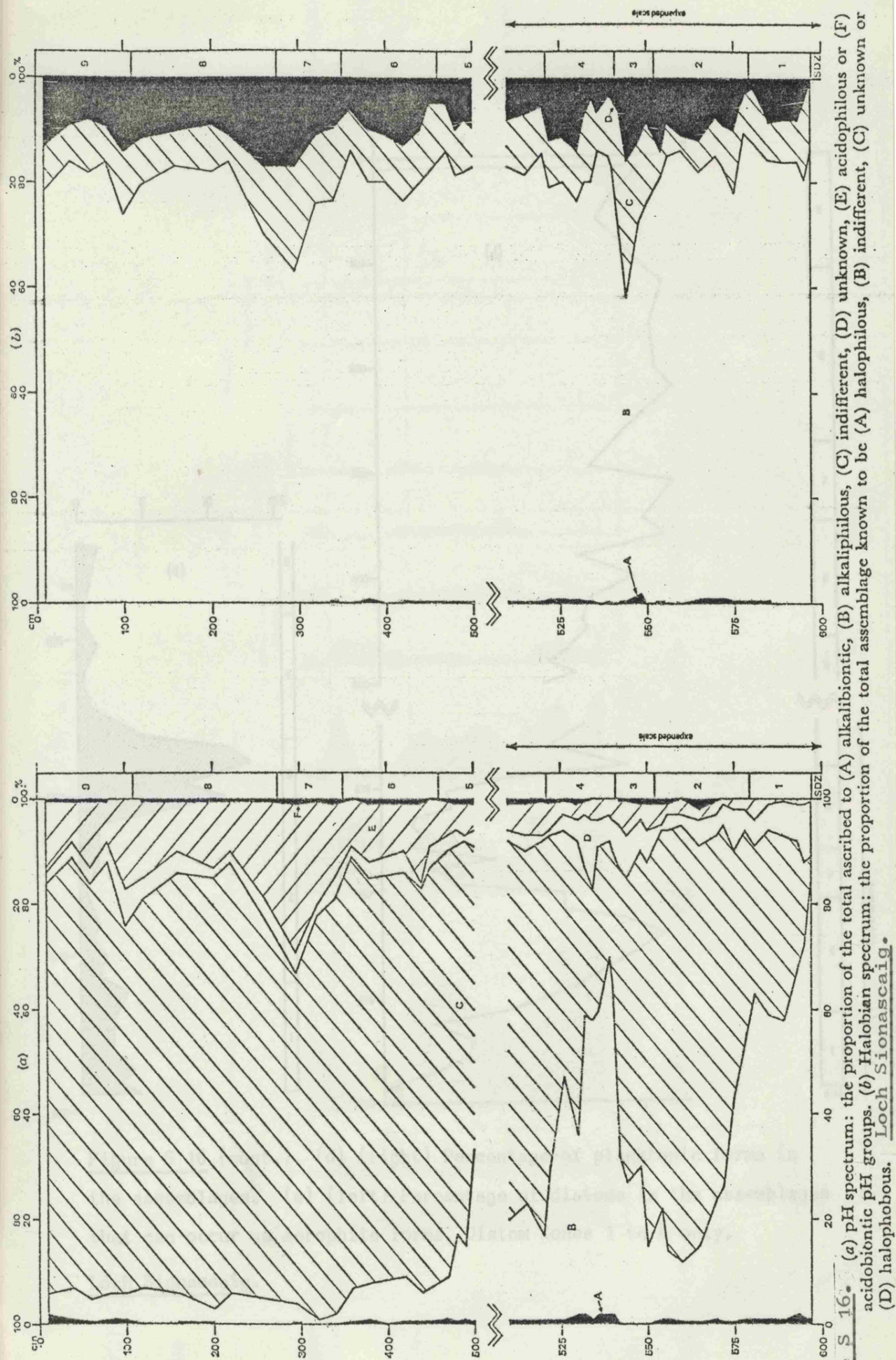


Figure S 16. (a) pH spectrum: the proportion of the total ascribed to (A) alkalibiontic, (B) alkaliphilous, (C) indifferent, (D) unknown, (E) acidophilous or (F) acidobiontic pH groups. (b) Halobian spectrum: the proportion of the total assemblage known to be (A) halophilous, (B) indifferent, (C) unknown or (D) halophobous. Loch Sionascaig.

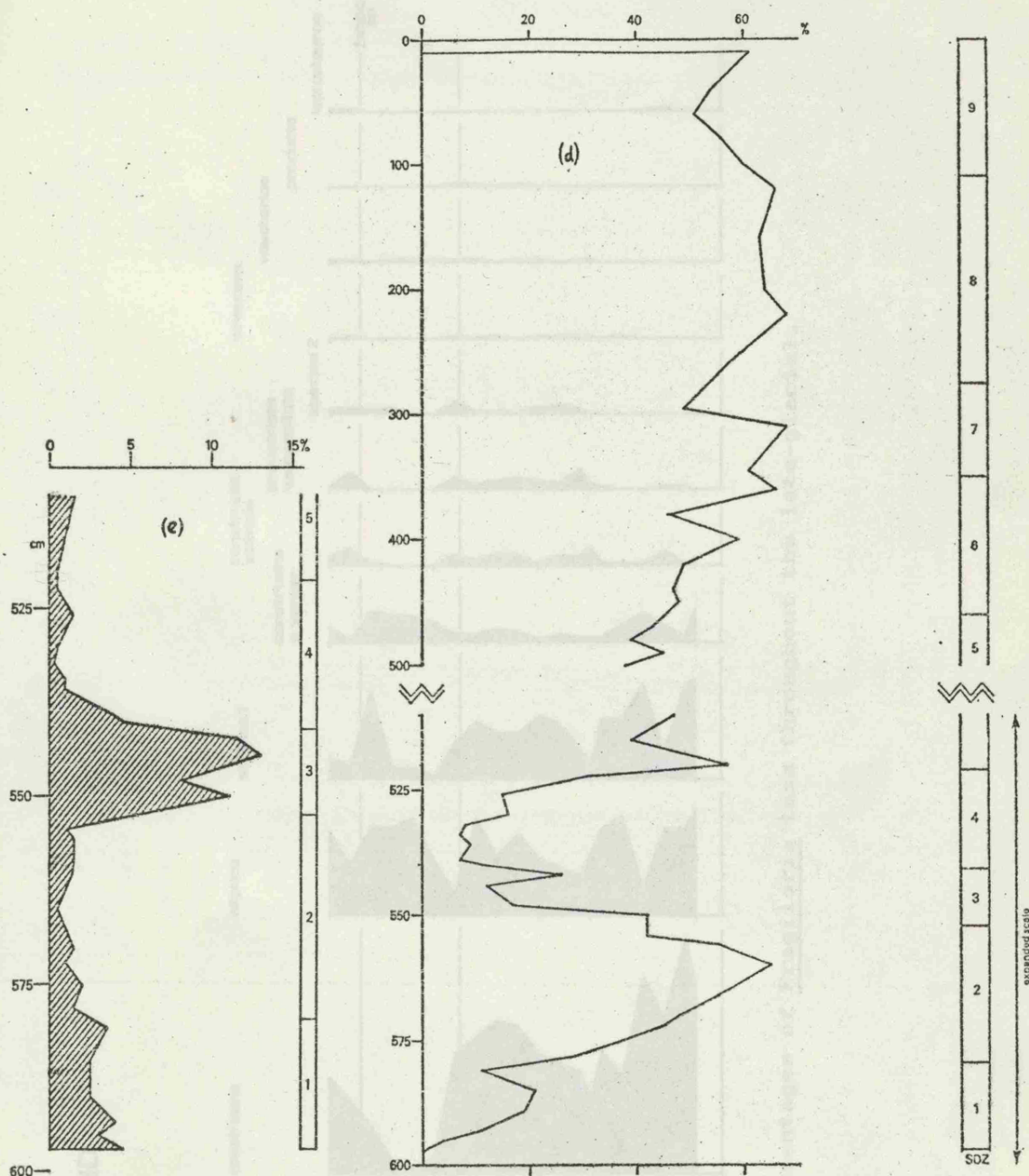


Figure S 16 (cont.) (d) (right) Percentage of planktonic forms in the assemblages. (e) (left) Percentage of diatoms in the assemblages that can occur as aerophile forms, Diatom Zones 1 to 4 only.

Loch Sionascaig.

CAM LOCH SUTHERLAND

FRAGILARIA SPP.

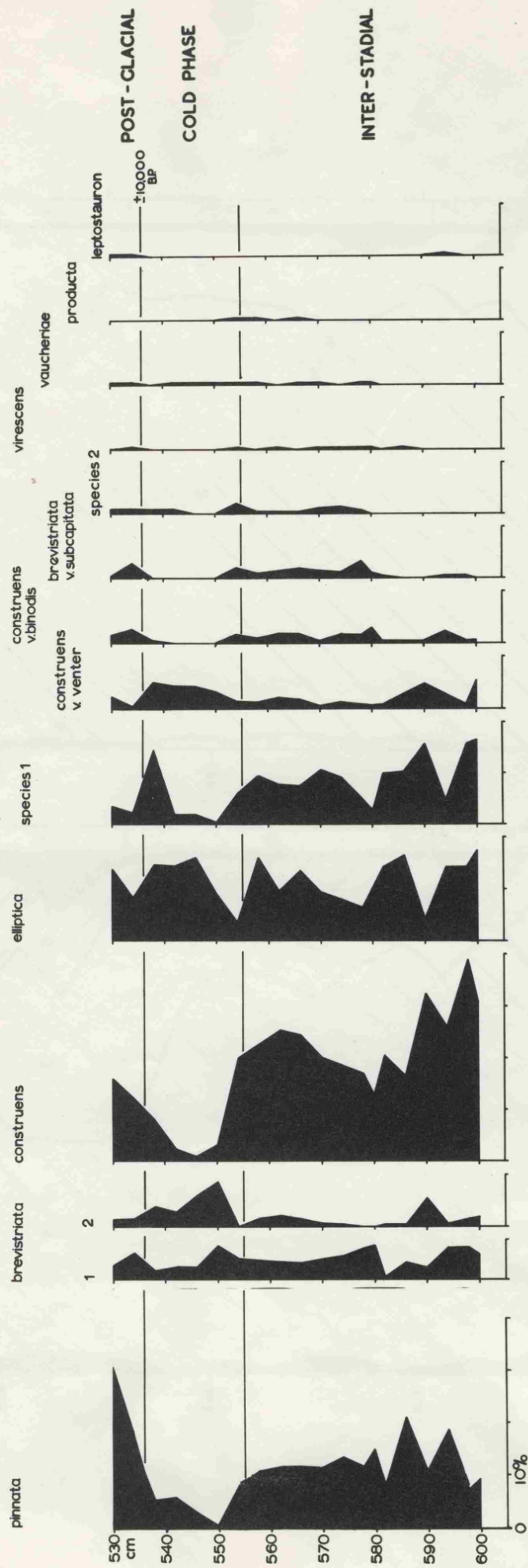


Figure S 17. Cam Loch. Percentages of *Fragilaria* taxa throughout the late-glacial.

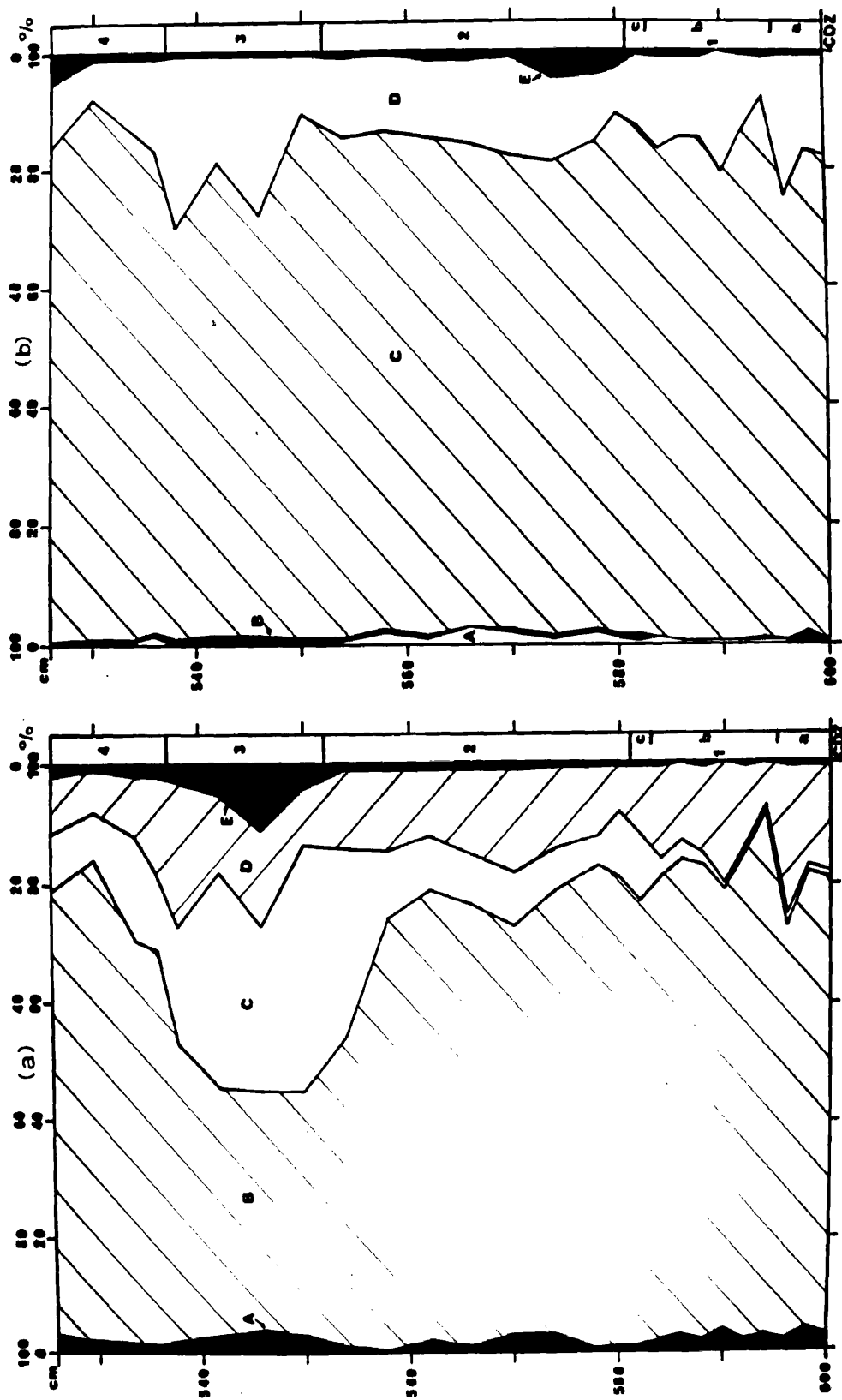


Figure S 18. Cam Loch. (a) pH spectrum: proportion of taxa that are A) alkaliphilous, B) acidophilous, C) indifferent, D) unknown, or E) acidophilous. (b) Halobian spectrum: proportion of taxa that are A) mesohalobous, B) halophobous, C) indifferent, D) unknown or E) halophilous.

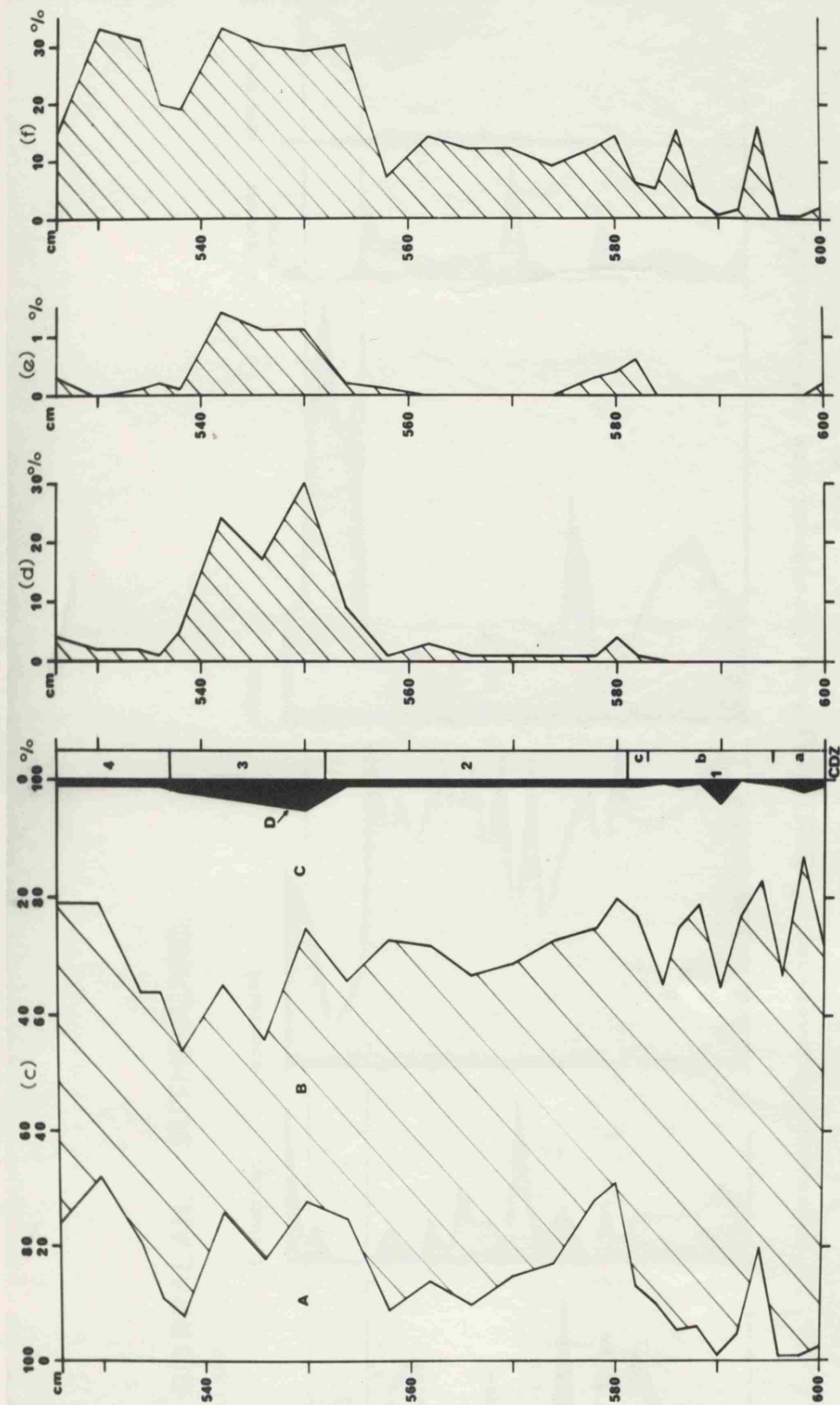


Figure S 18 cont. Cam Loch. (c) Current spectrum: proportion of taxa that are A) limnophilous, B) indifferent, C) unknown or D) rheophilous. Proportion of taxa that are: (d) planktonic, (e) aerophile and (f) boreal.

LOCH BORRALAN. SUTHERLAND.

FRAGILARIA SPP.

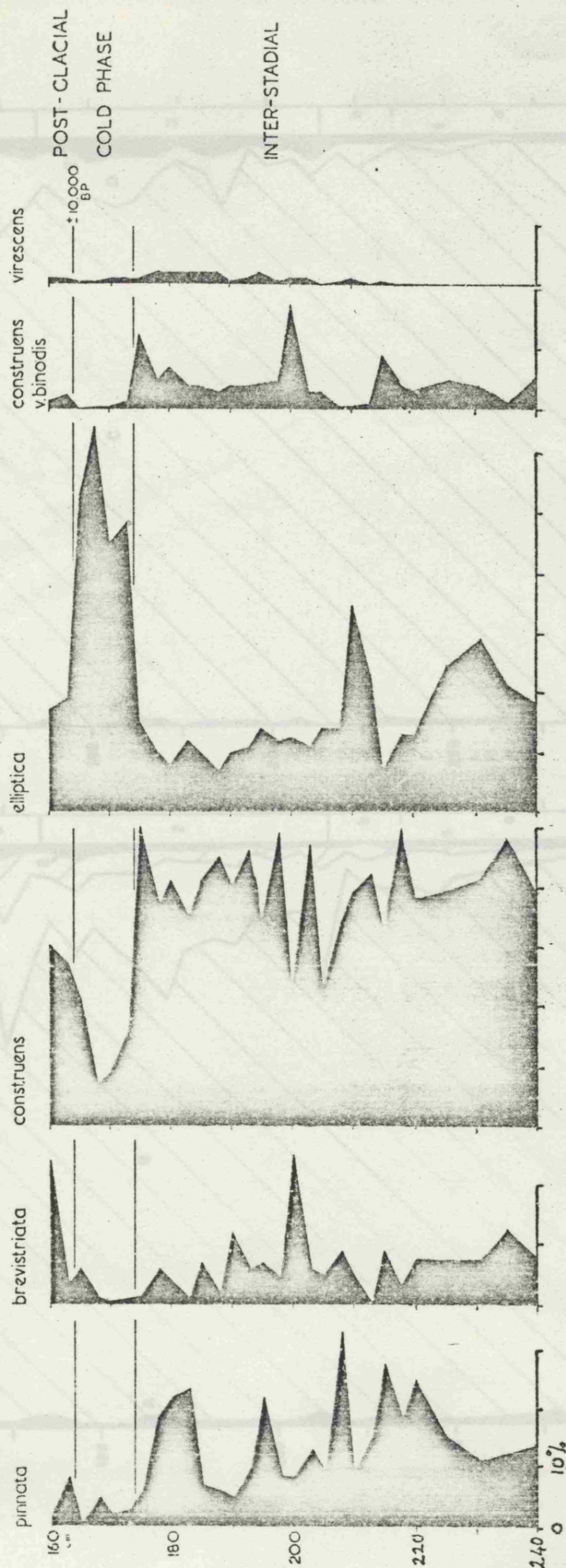


Figure S 19. L. Borralan. Percentages of *Fragilaria* taxa throughout the late-glacial.

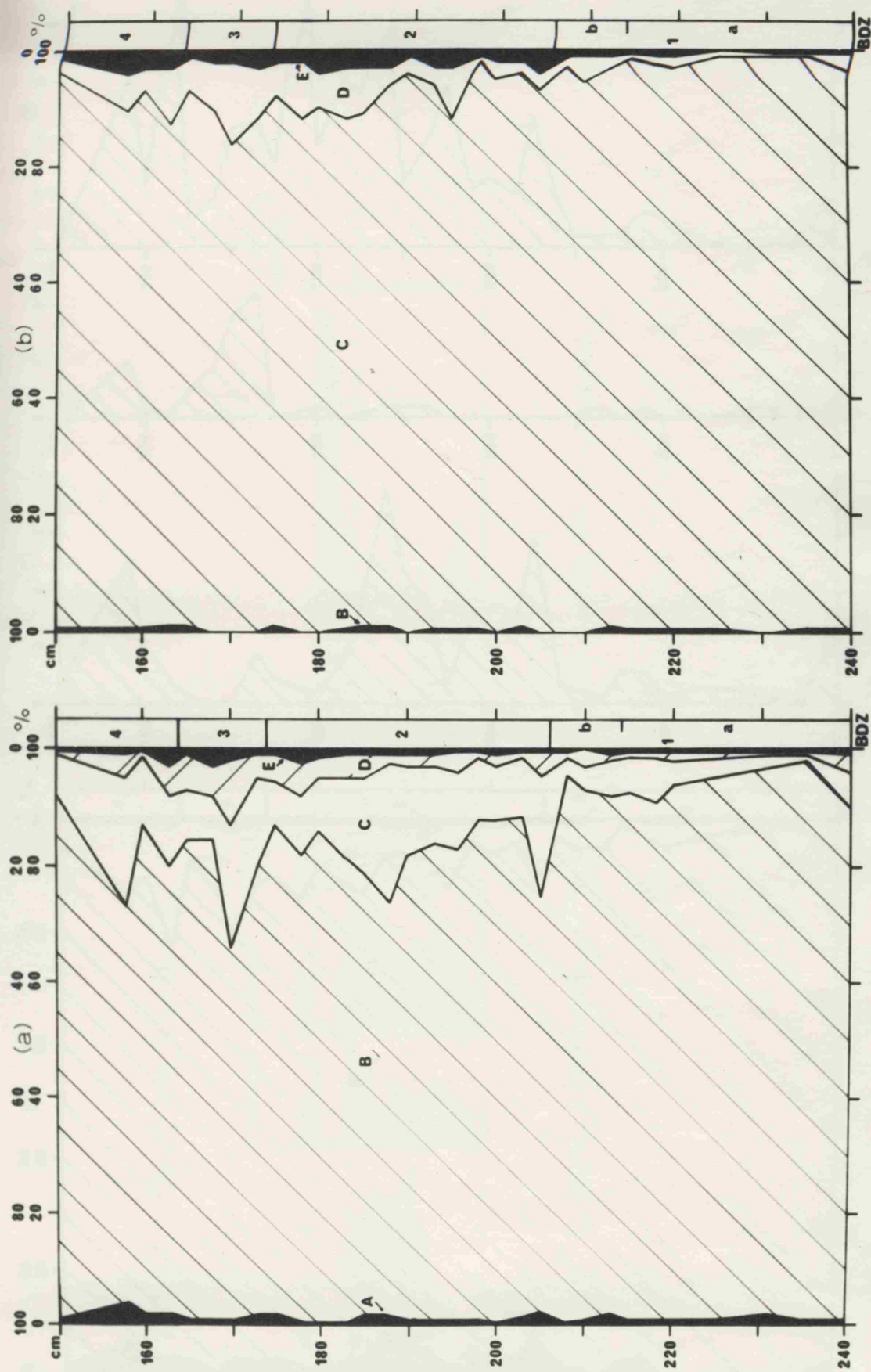


Figure S 20. Loch Borrallan. (a) pH spectrum: proportion of taxa that are A) alkaliphilous, B) alkaliphilous, C) indifferent, D) unknown or E) acidophilous. (b) Halobian spectrum: proportion of taxa that are B) halophilous, C) indifferent, D) unknown or E) halophobous.

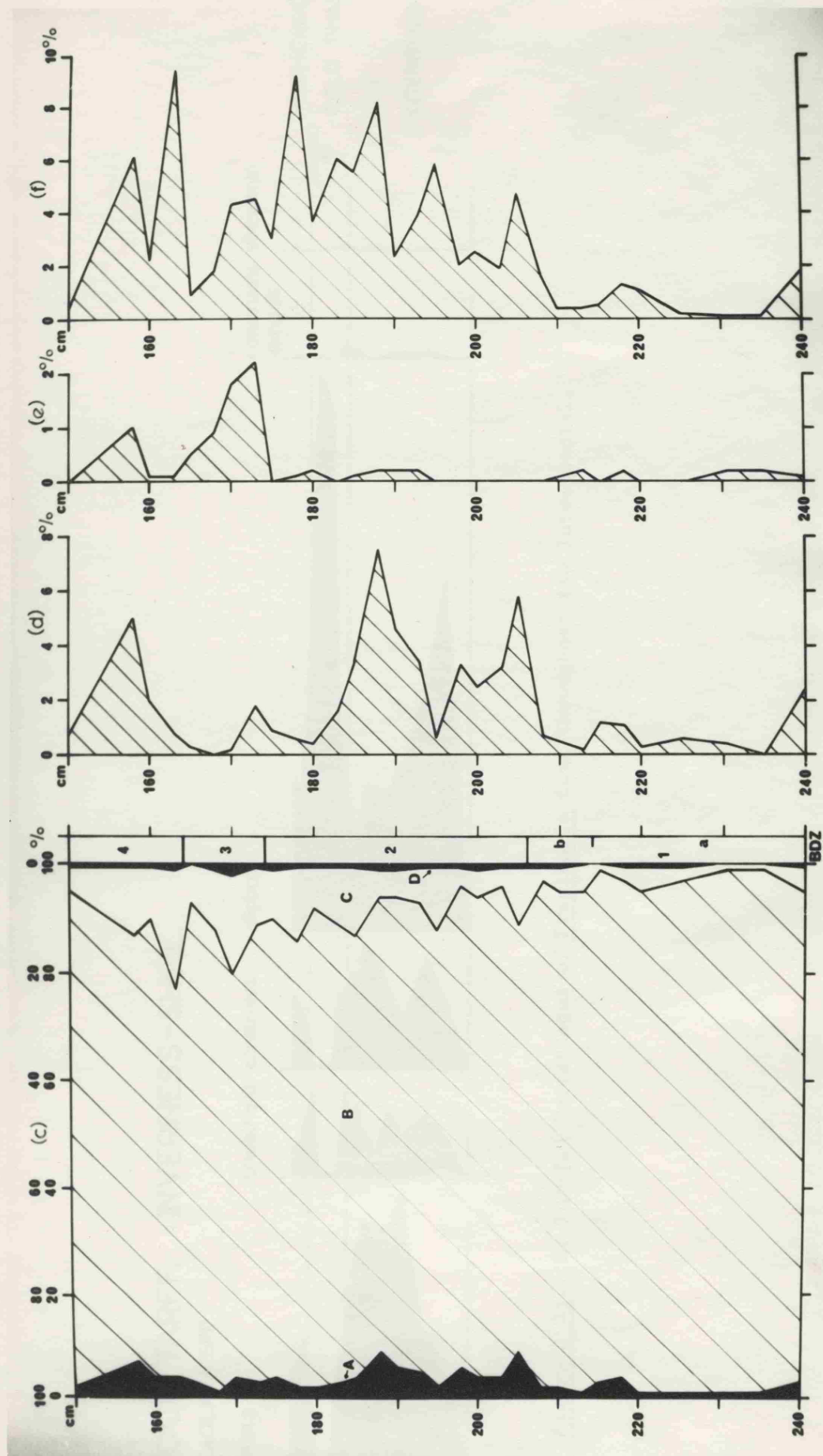


Figure S 20 cont. Loch Borrallan. (c) Current spectrum: proportion of taxa that are A) limnophilous, B) indifferent, C) unknown or D) rheophilous. Proportion of taxa that are: (d) planktonic, (e) aerophile and (f) boreal.

LOCH TARFF. INVERNESS-SHIRE.

FRAGILARIA SPP.

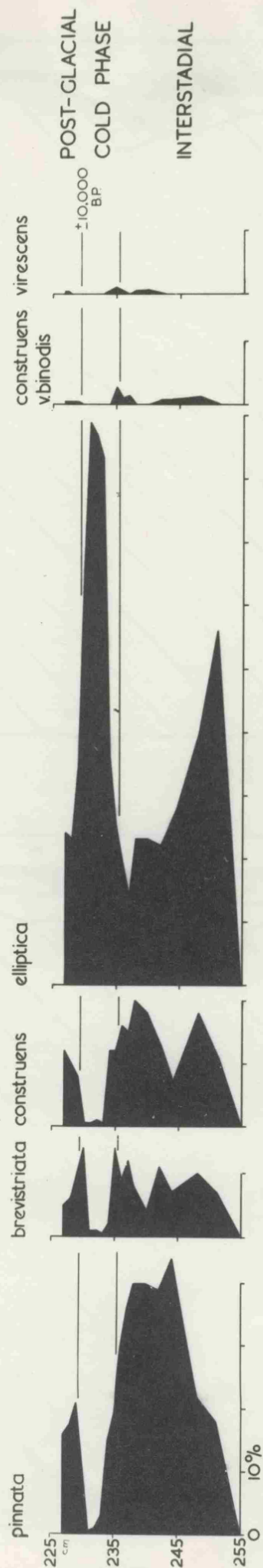
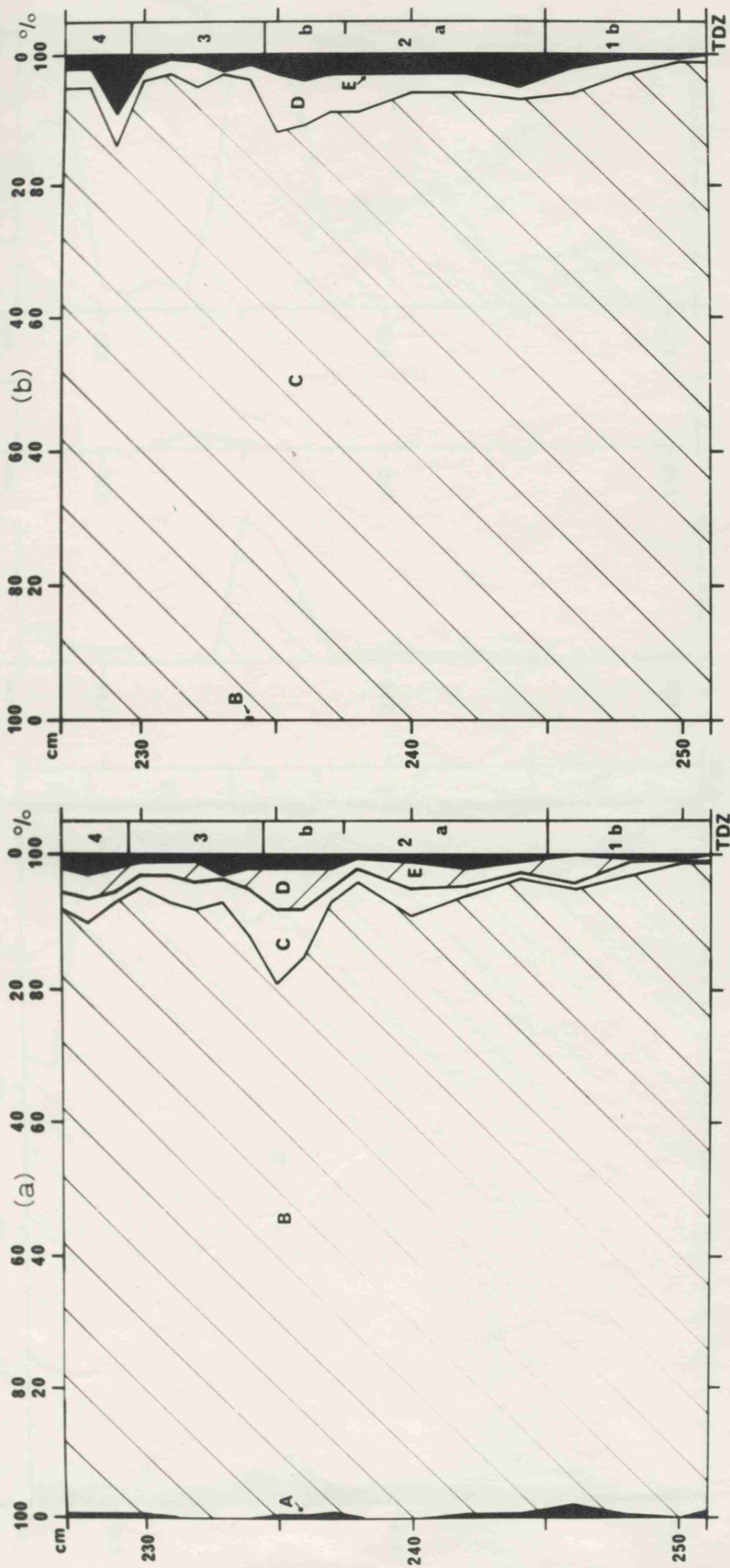


Figure S 21. L. Tarff. Percentages of Fragilaria taxa throughout the late-glacial.



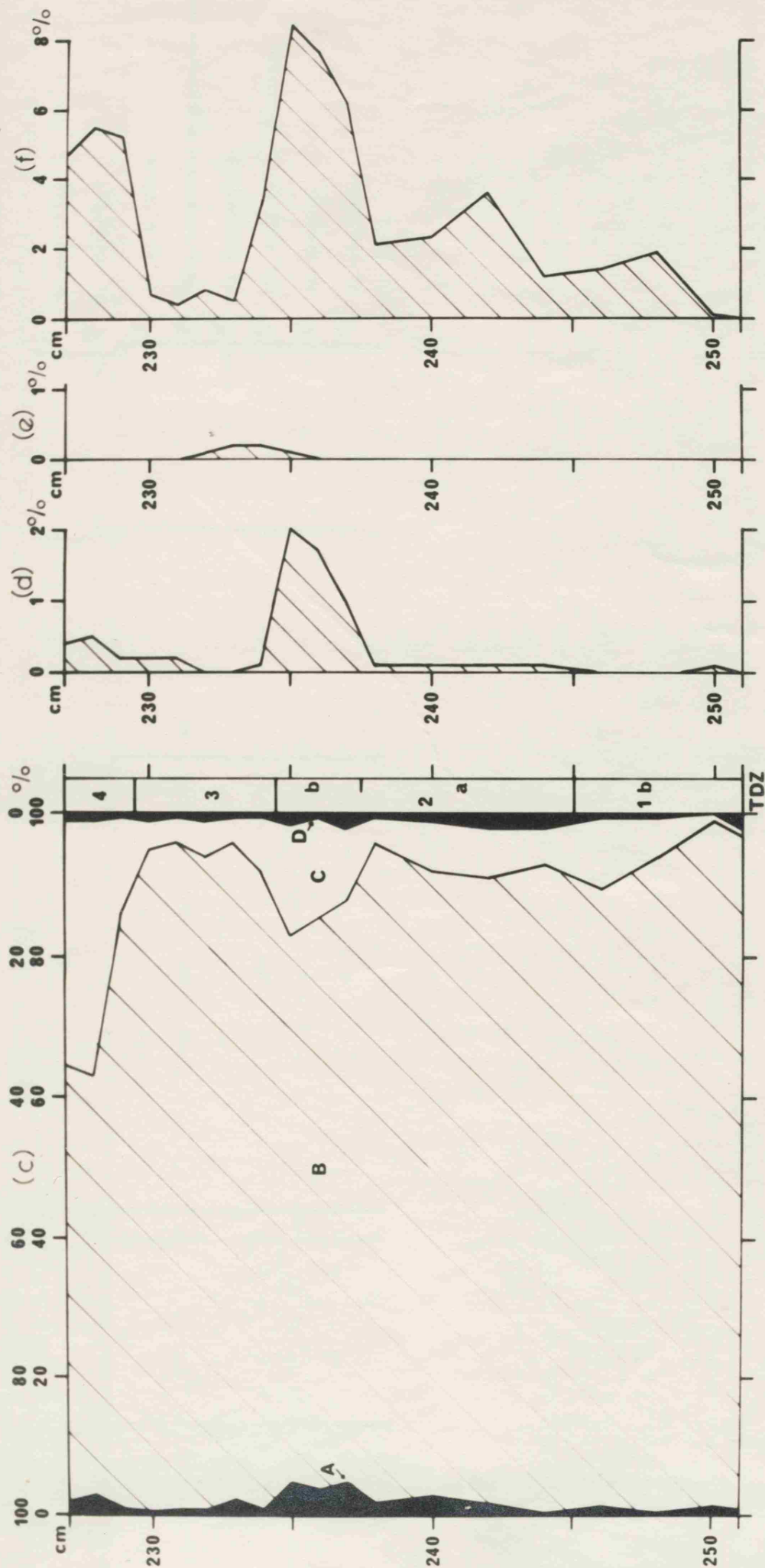


Figure S 22 cont. Loch Tarff. (c) Current spectrum: proportion of taxa that are A) limnophilous, B) indifferent, C) unknown or D) rheophilous. Proportion of taxa that are: (d) planktonic, (e) aerophile and (f) boreal.

LOCH CAM

Diatom Zones		taxa																															
core depth	cm	Cal. sp. C590	Sta. smithii v. minima	N. pupula v. elliptica	St. hantzschii	Cym. turgida	Cal. trochus v. lancettula	Ac. conspicua	Ac. lanceolata	Cyc. meneghiniana	N. reinhardtii	N. suboculta	Coc. thumensis	N. subrotundata	N. interglacialis	Cym. thumensis	Sy. capitata	N. fossalis	Epi. sores	Epi. turgida	Mel. teres	Gy. spenceri v. nodifera	Sy. parasitica	F. construens	F. sp C 1	Am. ovalis v. pediculus	F. pinnata	F. brevistriata	Epi. zebra	Coc. placentula v. lineata	Ac. clevei	Ac. suchlandtii	F. brevistriata v. subcapitata
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
4	526						6	2							+	2	+		3	4	12	1	9	68	35	47	217	121	1	8	27	4	12
	530			3	1		2	+							+		+		4	2	2	+	10	160	35	31	310	41	1	3	13	37	4
	534									1		8		5			+		7	6	15	1	14	123	22	34	189	73	+	2	20	118	28
	536	1										1		1	+				6		1	+	17	244	40	33	105	66	2		5	81	4
3	538	2																	+				5	79	145	39	54	54		3	1	22	
	542																				+			23	18	18	59	52		3		7	
	546																							9	18	6	31	83		+		14	
	550																							31	4	7	6	150	1	2			
2	554																	+	+	+	+	+	3	199	59	23	82	40	+	3	4	69	20
	558													3	2	1	+		+	+	+		9	234	94	60	108	52	+	3	12	10	10
	562									+	+	6	1	1	+				5	3	1	+	23	253	77	55	116	55	2	1	11	9	
	566							+	1			1		14			+		2	+	1		23	243	74	40	125	46	+	3	14	19	19
	570				+									5	2	+			1	+	3	+	33	200	105	80	115	45	+	3	45	13	14
	574						5		+					+	+	1		+	1	+	4	+	18	115	90	84	134	45	+	2	98	8	11
	578						9					3	6	2	+				11	+	7	+	11	168	49	77	117	60	5	10	178	9	33
	580			1			4	+							+	1		+	3	2	4	+	8	126	26	57	149	65		12	166	19	16
1c	582	+	3	+										+	+					+	2		14	204	98	171	80	3		28	39	13	2
1b	584	1					6					5	4	1	1	8			+	+	22	4	29	98	101	80	232	46	+	7	75	2	6
	586	2	4				3					6	6	4	+	8			+	1	9	2	27	164	102	88	210	38	+	2	45	5	
	588	+					2					1	6	2	+	2			+	+	18	2	17	203	90	73	231	52	+	+	41	2	6
	590	+	+	2			+				+	7			2		+		1			5	27	324	82	65	109	78	+		2	2	
1a	592		3				+	3				+	1	5		1			+	+	12	3	18	220	109	68	170	57	+	2	45	2	9
	594		2				2			1		1	9	3					1	+	16	+	14	259	46	74	187	66	+	3	68	3	+
	596	+	1	2	1		4					2		2						+	+	4	12	261	230	34	122	83	+		2		+
	598	1		4	+	+	3					4			+					+			8	15	388	157	61	76	76	+	1		1
	600	+	+				+	+				4			+	1	2		+	+	5	12	306	164	49	93	66			1			

+ = presence, nos. = per thousand

[illegible]

4	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
Ac. lapponica v. iennica																													
Cym. brehmii																													
Ni. frustulum v. perminuta			9	+	+	+	1	4	+	2	1						+		1	1	2					2			
St. astraea v. minutula				+																									
G. constrictum																													
Did. geminata																													
Cym. caespitosa v. auerswaldii																													
Dia. elongatum																													
Dent. tenuis																													
R. gibba																													
D. elliptica																													
Ac. linearis																													
Ni. sp. C 580-2																													
Ni. sp. C 580-1																													
N. sp. L 100 b																													
Coc. pediculus																													
Amp. pellucida																													
Cyc. antiqua																													
N. tuscula																													
N. opportuna																													
N. oblonga																													
N. vitabunda																													
N. cuspidata																													
Cal. silicula																													
N. sp C 562-4																													
Mel. islandica ssp. helvetica																													
G. lanceolatum																													
Ne. kozlowi v. elliptica																													
P. nobilis																													
F. producta																													

Table 13i

LOCH CAM

[illegible]

Table 13 ii

[illegible]

LOCH BORRALAN

Diatom Zones	core depth taxa																																	
cm	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32		
4	150																																	
	158		4								+	+	+	3	1		4	+			3	7	8	53	199		2	+	2			1		
	160													1			2	+	+	+	+	10	14	24	301							+		
	163															+	1		2			+	7	27	85	270		4						
3	165																+								4	214	+	3		7				
	168																+							+	53	73	+	14		13				
	170											+	+	2			4							6	10	90	4	13		10				
	173									+	1				1									16	30	158	1	3	+	4				
2	175						+	+	+			1	3		+	+		4	4	+		+	8	79	53	496	+	+		1		+	6	
	178						+	+	1	3	2	+				1	2	1					1	54	185	367		1		+		3		
	180								2		1	4		2	1	1		1			+		64	218	412	+	2	2	7			1		
	183					+	+		+		+	+		4				3			+	1	39	235	349		3	+	5					
	185				2						+					+	6						2	40	69	410		3	1	2		4		
	188			+			+	+	+		2	+	+	1		1	19	+			+	5	26	56	447	+	+	+	2	2		6		
	190		4	2							4	2		5					3			1	11	40	43	405	2	2		1		2		
	193		1	3						+	1	6	+		1	1		3	5	+		+	6	38	96	458	+	5	1	5	2		1	
	195			+	+	+	+		1	2	1	+	+	+	3	1	+	+	+		+	+	3	223	340	+	+	+	1			1		
	198			3		+			1		+	+	+	7	4	1	4	2	+		7	7	53	86	486		1	+	1					
	200			1					+		3		2	5	+		2	+					12	113	83	230		4		6	2		+	
	203			+			+	+	+		1	+	+	3	+	2	1				+	4	33	130	466	+	2	+	2			+		
	205		7	+	+		+		+		1	1	2	12		8	32	1					13	31	95	226	+	1	+	+	2	+	5	
1b	208			+		+	+		+		1	+	+	+		1	3	3		+	+	+	5	328	341	+	2	+	1			3		
	210						2						+	6	2				4		1		4	153	390	+	+		2					
	213			+		5		+	+	+	+	+				+				+			10	201	425	+	+		2		+			
1a	215	+		1			3	+		+	+		+					6	+		+	8	93	277	328	+	+		3					
	218		2	2	+			+		2	2	2		3	1	+	7	1	+		+	7	47	185	445		+	+				+		
	220			2	1				+	2	3	+		+	1		3	4	+	2	+	+	41	245	384				+					
	225				+	1	+	+	+	+		+	2	1		2	2	+	+				4	59	153	393	+	+						
	231			+				1			1	+				11							1	45	112	412								
	235	2		+												6	+	2					+	9	125	476								
	240			+							2					1	10	2						56	129	389				1				

+ = presence, nos. = per thousand

32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	6
Amp. pellucida	G. int. v. dichot. f. semipura	Am. veneta v. capitata	Ni. dissipata	P. stauroptera	Ac. austriaca	An. serians	Sta. smithii	Dia. vulgare	N. subtilissima	Cyc. meneghiniana	Cyc. kützingiana	Cyc. comta	Cyc. comensis	Ni. frustulum	Did. geminata	Ac. linearis	Ac. levanderi	Cym. subaequalis v. oblonga	Sta. dilatata	Ne. dubium	P. sudetica	Ac. calcar	Ma. smithii v. lacustris	F. vaucheriae	G. subtile	Ac. flexella v. arctica	Ac. biasoletiana	An. zellensis	Su. linearis v. constricta	Sy. nana	Ne. iridis v. ampliata	Ne. bisulcatum	Cal. obtusa	Sy. parasitica v. subconstricta	
1	+	+	+							10	12	24	2		23	26	+	+	+	+	+	+	+	1	+		8	+							
+	+									2	3	14			19	32	+		+		+	+					7	+	+	+					
											6	2	+		7	47	+	+	+	+	+	2		+			4		+						
	+									1	1	1			7	2	+	+		+	2					+									
	+								+		+		+		1	8	1	2		+	2			1	+	+						+			
										+	1	1	13		8	19	+			+	2			3											
					+					1	+	17	13		3	14	2	+			+			3				+							
6	1	1	+							2	+	4	1	6	1	1	16	+	+		+	1	+					+	+			+			
3	+										1	2	3				31		+		+	18				+	2								
1	4	2	1									4		3		1	27	+				+		2											
		+	1	+								7	8	1		1	47	1			+	+				+			+			+		1	
4	1	1									5	12	13			16	33	2							2							+			
6	3	4								1	10	6	57	10	1	5	11	+	2	+	+	1	+	2	+	+		4				+			
2	2	2					3		1		19	7	16	10		6	2	5																	
1		1								4		17	15			6	9	+	+	+	2	3			+							+			
1				1						+	1	2	2			6	52	+	+					+					+				+	+	
	+									+	10	9	14	1	+	2	3	1	+	2	+		+			2		+	3	+	+				
+	1						+	+	1	1	4	11	7			3	14	1				+	+						2						
+	1	1		1						5	8	9	13	6	+		4	2	+	+	+	+			1	+		+	+						
5	+	1		1						2	8	1	41			15	2				+	+	+	2	5	+	1								
3													1	2	+		10	+	+	+	+	4	+	+											
											+	5	1			1	4																		
											2	2	6			2	2	+	+																
										4	5	3	2	+		1	2																		
+	+	1								2	4	7				1																			
										1	1	2	1			1																			
										1	2	2	2			3																			
											3	1		+		2																			
																		1																	
										+	3	8	13	1		1								1											

64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
Ne. bisulcatum	Cal. obtusa	Sy. parasitica v. subconstricta	N. explanata	F. virescens	Cal. latiuscula	Cal. lepidula	Fr. vulgaris	Mel. italica ssp. subarctica	St. astraea v. minutula	E. pectinalis v. minor f. impressa	An. exilis var. lanceolata	N. järnefeltii	P. nobilis	F. elliptica	Ac. flexella v. alpestris	N. menisculus	Cym. ventricosa	D. marginestriata	Cym. sinuata	Ac. suchlandtii	H. amphioxys	Mer. circulare	Cera. arcus	N. contenta v. parallela	N. pseudoscutiformis	P. balfouriana	N. naumannii	Ni. thermalis v. minor	Su. ovata	G. parvulum
				2									+	130			1													
				3					1	6		+		119	1		11													
				8						+	+	2	+	167	4		6			+			+							
				6						+		25		188			6		2	1					4	1				
+				1			+	+				+		532	1	36		6	+	2		+	+	3	7	+				
				2						+		2		637		36	+	5	5				1	9	6	10				
				8			+					+		453		83	+	6	4	+		+	4	14	3	13				2
				8								+		485		58		+	11			+	+	21	6		1	+	+	+
+			+	4	+	+						7	+	154		6		+	2											
			+	18								22		90		12				3					2					
				24				+				7	+	83		6						+		+						
+		1		17							3	4		120		10			1											
				17	+		+							98		1									1					
+				18	+		+		+	+	2	2		67	+	5									+					
				5		+	+	1						98		11														
+				8	+									108		2														
	+	+	+	20										136		6		+							+					
+				1										121		11														
				10										125		2														
				7										111	+	1														
														140	+	2							2		1	+				
				13										141	+	2		+					1		2					
				5										267	+	+	4	+		+		+			+					
														231	+	+	15	+	+		2	+	+	+						
				2										68	+	4														
														125		3				3										
														123		1		+	2											
														253		3														
														288		3	+													
														208																
														182		6		1												

Table 14

[illegible]

LOCH TARFF

Diatom Zones	core depth cm	taxa																														
		F. elliptica	F. pinnata	F. construens	F. brevistriata	Cal. bacillum	Cym. thumensis	Mel. teres	Cym. semisymetrica	Gyro. attenuatum	Am. ovalis v. libyca	F. construens v. binodis	Am. ovalis v. pediculus	Dent. tenuis	Ni. fonticola	N. explanata	Sy. parasitica	N. vitabunda	Coc. diminuta	Am. eximia	Ac. laterostrata	N. jārnefeltii	Coc. placentula v. lineata	N. pseudoscutiformis	Coc. placentula v. euglypta	Epi. turgida	G. intricatum v. pumila	Ac. levanderi	F. virescens	P. nodosa	T. flocculosa	
4	227	235	155	122	52	7	2	12		1	10	4	9		1		14		17	4	2	18	1	+								
	228	225	175	102	57	9	15	10	+	+	+	2	15		1	+	2		16	10	2	26	+	5		+		1	2			
	229	338	207	87	101	3	14	29			2	2	11		4				92	4		13	1				+	1				
	230	664	108	3	135	1	3	+	5	5	2								15	5		3	1	+							3	
	231	888	4	3	8	4			3		17									6		1	4					2			3	
3	232	866	7	5	8	8		7		9									15		3	3					4			5		
	233	848	33	3	1					11			+				2	1	1		2									23		
	234	560	145	118	24	4		2	10		7	1	2					4		9	+	1					1	2	5	7		
2b	235	246	188	124	143	15	4	3	23	+	8	27	8	4				17	2	14	5	12	3	1		+	+	13	8	+	3	
	236	188	299	156	92	4	18	8	2	2	13	10	6		+	3	20	7	18	7	20	4	2	+		2	6	2	+	2		
	237	142	362	144	121	21	14	12	4	5	20	14	5		+	4	29	2		10	16	3	1	+	+	2				+		
2a	238	228	402	199	83	5		1	10	+	8	2	7				1	14		4	5	+					2		3		1	
	239																															
	240	232	395	180	44	10	1	2	13		14	1	9					16	1	5	10	7	5		2			2	6	1	2	
	241																															
	242	219	387	130	105	16	19	12	2	1	12	7	1		2	2	9	23	2	3	19	1	2	2	+	1	2	1				
	243																															
	244	277	440	68	71	21	18	7	3	+	2	6	5		3	1		2	48	2	1	3	4	2								
1b	245																															
	246	361	182	112	149	5	46	8	9	2	5	26	5		22	2	10	12	6													
	247																															
	248	399	218	183	99	5	26	18	2	1	2	13	19	1	2	+	4															
	249																															
	250	408	341	167	53		4	+			1			1																		
1a	251	575	183	110	73	21	7	+	1	9	16	2	1																			
	255	+																														
	260																															
	265	+	+	+	+		+														+											

+ = presence, nos. = per thousand

Table 15

[illegible]