THE PHYTOPLANKTON OF A EUTROPHIC LAKE

Community Dynamics and Ultrastructural Studies

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ABSTRACT

Sawley Dene, a small secluded lake in North Yorkshire, supports large populations of diatoms in spring and blue-green algae in late summer. Characteristics of the drainage area give this shallow lake calcareous water and a long retention time; although persistent summer stratification does not occur, the summer algal populations resemble those in the epilimnion of a stratified eutrophic lake. 32 principal phytoplankton species from seven algal classes are illustrated by light micrographs and their periodicity recorded over two annual cycles; a statistical method is employed to produce graphical summaries of the patterns of species replacement. Absolute levels of algal abundance are correlated with concentrations of chlorophyll *a* and with varying Secchi disc visibility. Scale-bearing planktonic organisms from Sawley Dene were studied as whole mounts in the electron microscope and 30 taxa are distinguished, including 17 species of flagellate Chrysophyceae (*Mallomonas* and related genera). Comparative studies on samples from nearby lakes and pools show that a number of rare species occur in the Sawley area but are absent from Sawley Dene; it is suggested that Sawley Dene is too large and too calcareous to support a very diverse chrysophycean microflora. A systematic account of all the scale-bearing species found in the study area is presented and five new taxa of Chrysophyceae are distinguished, including two from Sawley Dene; these are given provisional names but will be formally described elsewhere. Mixed phytoplankton samples were embedded for electron microscopy and noteworthy features of four species were studied in detail: these include scale formation and new cytological detail in *Paraphysomonas vestita*, colony structure and scale formation in *Synura petersenii*, serial sectioning and 3-dimensional representation of the transverse flagellum of *Peridinium cinctum* and a study of the surface morphology of the scale-bearing Heliozoan *Raphidocystis tubifera*.

ACKNOWLEDGEMENTS

I should like to extend my thanks to everyone who has helped me in the course of this work. The project was made possible initially through the interest and good will of three people: the owner of Sawley Dene, Mr E.E. Binns, who volunteered his private lake as a study site together with the use of his boathouse and boats; Dr G.F. Leedale of the Dept. of Plant Sciences, Leeds University who agreed to supervise the research; and Professor H.W. Woolhouse, Head of Department, who accepted me as a research student and made available all the necessary equipment and laboratory facilities. Also within the Department, Mr A. Nichells instructed me in electron microscopy and provided technical assistance and my colleague Miss Helena Cmiech shared the field sampling trips, collaborated in making some of the measurements and gave her help and advice throughout the study.

Dr C.S. Reynolds (Freshwater Biological Association, Ambleside) has discussed freshwater algal ecology with me on numerous occasions and Dr D.J. Hibberd (Culture Centre for Algae and Protozoa, Cambridge) has advised me on aspects of algal ultrastructure. Other people who have provided information on specific points are Mr T.S. Crosby (Dept. of Plant Sciences) on the identification of flowering plants, Mr J. Palmer (Dept. of Geography) on the geological history of the area, Mr L. Bird (Meteorological Office, Harrogate) on climatic features of the region and Mr J. Heron (F.B.A., Ambleside) who provided the chemical data given in Table 1. Mr E.E. Binns kindly provided the aerial photograph reproduced in Fig. 5 and Miss H.A. Cmiech took the photographs for Figs 36 and 52 - 53. The remaining photographs and diagrams are original.

I am grateful to my supervisor, Dr G.F. Leedale for his help in carrying out the research and for his comments on the thesis in various stages of preparation, to my parents for their help and encouragement, to Mr D.J. Clark for frequent transport between home and the laboratory and to Miss Susan Miller for her skill in typing the manuscript. I also wish to thank the Yorkshire

Water Authority for permission to collect samples at Lumley Moor Reservoir and the Estate Office at Ripley Castle for permission to visit their lake. The resident farmers at Sawley Dene also deserve thanks for their helpfulness during more than seventy visits which I made to the lake over three years.

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CONTENTS

GENERAL INTRODUCTION AND LITERATURE REVIEW

Planktonic algae have attracted the attention of research workers of varied interests over a long period. Their basic diversity of cell structure and morphology, on which all investigations involving algal systematics or ecology ultimately rest, has been established principally as a result of light-microscope studies on wild populations, many of which were carried out during the last decade of the nineteenth century and the first 30 or 40 years of the present century. With the advent of electron microscopy around the early 1950s, the emphasis for cytological investigation changed from species encountered casually in the wild to those which could be cultured successfully in reasonably large numbers in the laboratory. To date, the majority of ultrastructural investigations are still carried out on the relatively small numbers of strains available from specialised sources of algal cultures.

A feature of phytoplankton growth in the wild is the capacity for a single species to form dense populations in suitable habitats at certain times of the year, only to disappear shortly afterwards to be replaced by another, temporarily dominant, species. It seemed feasible that knowledge of the nature and timing of such maxima in any site might enable ultrastructural investigations to be made on a variety of species, fixed and embedded for electron microscopy direct from the wild, and that observations on material of this nature would provide data which could be compared with results for cultured organisms; in addition, rare or unusual species might be encountered which may not previously have been studied in the electron microscope. In order to implement this approach it was decided to adopt as a field site a lake which had not hitherto received any scientific study, so that the ecological observations necessary as a foundation for any ultrastructural work might be of interest in their own right.

A provisional outline for the project was drawn up; it was envisaged that, after the initial selection of a field site, approximately equal amounts of time would be

spent on description of the phytoplankton periodicity and on laboratory cytological studies. As the project proceeded, it appeared that certain aspects of the investigation would benefit from greater emphasis than others according to the time and resources available; for example, detailed ultrastructural studies were restricted to four species in order to allocate sufficient time to each, and a preliminary EM examination of mixed plankton samples from the study site as whole mounts was expanded to provide comparative ecological and taxonomic data from neighbouring sites. Nevertheless, the present thesis retains the broad division into "ecological" and "ultrastructural" parts. The former incorporates a description of the study site in its overall context, an account of the phytoplankton populations it supports and a discussion of the trophic status of the lake, a brief description of the periodicity of each species and a taxonomic and ecological investigation into the scale-bearing planktonic organisms revealed by electron microscopy. The ultrastructural part includes studies on the cytology of four species for which new features of cell structure are described and their significance discussed.

Sawley Dene, near Fountains Abbey in North Yorkshire, is a lake which offers a number of advantages as a potential study site. It is relatively small (ca. 10 ha) and secluded so that it is largely unknown and undisturbed by public recreational use, yet it is probably of sufficient size to support planktonic algal populations such as may be characteristic of very much larger lakes. It has been known to develop summer blooms of blue-green algae for many years and would therefore be termed eutrophic; the periodicity of lakes similar to Sawley Dene in this respect has been the subject of investigations elsewhere and these suggest that relatively dense stocks of algae of other types may be anticipated to occur at various times of the year. Finally, the geographical location of Sawley Dene, in an area east of the Pennines not noted for investigations of freshwater algae since the time of West & West (1901), offers scope for augmenting distribution records for some

of the species which may be encountered and for contributing to knowledge of the freshwaters of the region.

It was therefore decided to adopt Sawley Dene as a study site and to investigate the seasonal succession of its phytoplankton, firstly to give insight into the character of the lake, secondly to describe the periodicity of the principal species and to document the occurrence of rarer forms, and thirdly to collect wild material for further study in light- and electron- microscopes. The application of electron microscopy would also be valuable for the identification of certain nanoplankton organisms based on the structure of their scales, a task which is largely impossible from light microscopy alone.

Concurrent with this study, a second project was also to be carried out at the same site wherein the seasonal development of blue-green algae was to be investigated in detail at an ultrastructural level by another worker. The cytological studies reported here were therefore to be confined to organisms outside this group.

A discussion and review of literature relevant to this study now follows in which the main areas of investigation will be kept separate, as they have to some extent been developed independently through previous eras of limnological research. The topics to be reviewed are as follows:

i) the nature of phytoplankton communities and strategies for effective sampling;

ii) the extent of investigations of phytoplankton succession elsewhere in Britain, with particular emphasis on attempts to describe the variability possible on a regional basis;

iii) progress in understanding the factors controlling the seasonal fluctuations of algal populations in natural conditions;

iv) the current level of taxonomic and other knowledge of the smallest algae that may be recognised with the electron microscope from their possession of surface scales;

v) the amount of detail with which algae of different classes have been investigated at an ultrastructural level, together with the extent to which such information has already been summarised in the literature.

i) Sampling of phytoplankton communities

Phytoplankton assemblages display many characteristics that make it difficult for effective sampling to be straightforward. The organisms show considerable quantitative and qualitative variation through time not only seasonally but also from week to week, or even on a diurnal basis. At any one time they may also be irregularly distributed in space, both horizontally and vertically. An individual species may increase in abundance over five or more orders of magnitude above the threshold of detection and discrepancies in the size of individuals of different species may be of some four orders of magnitude. Each of these variables can influence the effectiveness of a given method of sampling for phytoplankton.

Because of the magnitude of seasonal variation it is desirable to carry out sampling over as much of the year as possible if a complete picture is to be built up; indeed, it is preferable for this to be supported by observations over a longer period in order that the extent of annual reproducibility may be assessed. If only one or a few visits may be made to a particular site, it is important that the most suitable times of year are chosen for sampling in the light of what may be known about the general seasonal prevalence of the algae of interest, in the particular habitat involved. Diurnal variation may be investigated *per se*, or its effects minimised by sampling only at a certain time of the day. It is difficult to allow for horizontal variation in phytoplankton populations but careful siting of a sampling point, preferably with duplication elsewhere in the water body, is clearly important. Non-uniform vertical distribution of phytoplankton may be overcome by sampling a column of

water with a vertical tube (Lund, 1949); alternatively, its nature may be investigated by trapping limited volumes of water at selected depths.

Specific methods of sample collection have been reviewed by Lund & Talling (1957) and Vollenweider (1974). Plankton-net samples are quick and convenient to take; they may be the most feasible if sampling has to take place from the shore. They possess advantages in terms of the large quantity of material which can be collected and this may be a pre-requisite for further laboratory studies. They are also of use where the plankton is very thin or where it is desirable to detect rare species. However, they are of limited applicability for quantitative work as the actual quantity of water filtered by the net is difficult to determine and estimation of algal numbers in a known volume of water is frequently required.

Collection of a volumetric sample is usually followed by concentration of the organisms within it until sufficient density is reached for them to be counted; centrifugation, filtration or sedimentation, or a combination of these, are normally employed. Abundance may be assessed by the method of Utermohl (Lund, Kipling & LeCren, 1958) using an inverted microscope and a sedimentation chamber, or in a haemocytometer or cell of similar type. Absolute values for abundance at various times allow the growth and decline of individual species to be followed but, because of the large discrepancy in size between species, it is desirable to compensate for this before ecologically useful comparisons between species can be made and any values summated. Species may be compared on the basis of cell volume, wet or dry weight, carbon or chlorophyll content; of these, carbon and dry weight are perhaps the most stable measures but have only infrequently been determined for natural (unlike laboratory) populations. It is likewise difficult to determine average chlorophyll content per cell in the wild unless populations are particularly pure, although the chlorophyll _a_ content of a whole population is a widely used measure of standing crop. Cell volume is often used to compensate for the size difference between species; examples of measurements

are given by Findenegg (in Vollenweider, 1974), Bellinger (1974) and Willén (1976). Records of overall standing crop given in the literature may be quoted as total numbers of cells (of real value only when populations are virtually unialgal), total cell volume or dry weight, or chlorophyll a concentration. The effect of algal density on the turbidity of the water may also be assessed, as when transparency is estimated with the Secchi disc, which is discussed in a later section (p. 37).

ii) Description of phytoplankton patterns elsewhere

In Britain, phytoplankton succession has been described for a number of water bodies and a few early workers such as Griffiths (1923) examined small lakes or pools in particular. Larger lakes have been well-studied in some instances and, where efforts have been made to correlate the phytoplankton of whole areas, these results are of particular interest for comparative purposes. The major lakes of the English Lake District have all received a degree of study (see Macan, 1970; Gorham et al., 1974), as have a number of the Shropshire/Cheshire meres (Reynolds, 1976a); floristic surveys have been carried out among some Irish loughs (Round & Brook, 1959) and in a wide range of lochs in Scotland (Brook, 1964). Individual or small groups of sites have been investigated in other areas including lakes of fundamentally eutrophic type in southern England (Benson-Evans et al., 1967; Moss & Abdel Karim, 1969; Ridley, 1970; Wilson et al., 1975), eastern England (Phillips, 1977; Moss, 1977), central England (Irish, 1977), Wales (Jones & Benson-Evans, 1974; Pentecost & Happey-Wood, 1978), and Scotland (Bailey-Watts, 1974; Stewart et al., 1977). North-east England, however, is relatively little studied in this respect; Lund (1961) has described the phytoplankton of Malham Tarn but elsewhere in Yorkshire only an isolated species-list from Gormire, near Thirsk (Scott, 1948), appears to have been published since W. and G.S. West's "Alga-Flora of Yorkshire" (1901).

Comparisons with lakes outside Britain are also possible; some examples have been given in Hutchinson (1967), Round (1971) and Fogg (1975), and others continue to appear in the current periodical literature. In general, however, it is hoped to confine discussion to a regional basis as far as is practicable.

iii) Factors controlling algal growth in natural conditions

In attempting to understand the waxing and waning of phytoplankton populations, ideas have been gradually elaborated from early concepts of direct physical or chemical stimulation of growth to incorporate, in addition, complexities of species biology and behaviour; for example, such factors as relative growth rates, patterns of vertical movement and strategies for exploitation of nutrients in sub-optimal conditions may be of comparable importance to correlations with apparent temperature, pH and nutrient optima. Nevertheless, overall seasonal changes in the growth of phytoplankton are ultimately related to annual cycles of physical and chemical variables, and generalisations about the principal seasonal characteristics are possible (Lund, 1964; Hutchinson, 1967; Fogg, 1975) which in summary suggest that, for temperate eutrophic lakes in the northern hemisphere, nutrients (in particular nitrate, phosphate and silicate) are highest in winter and lowest in late summer; illumination is at its highest in mid-summer, while maximum temperatures in surface waters may occur up to one or two months after mid-summer. The interplay of these key factors gives rise to distinct seasonal phases; thus,winter is typified by chemical richness, but with algal growth limited by physical conditions; in spring, illumination increases more rapidly than temperature and algal depletion of nutrients becomes significant; summer is a period of increased temperatures and low nutrient levels; while in autumn, first illumination and then temperature declines and there may be some replenishment or increased availability of nutrients before physical conditions once again become limiting. In deeper or relatively sheltered lakes, thermal stratification may be set up over the whole summer period during which time nutrients in a poorly-illuminated

hypolimnion may be unavailable to most algae growing in the upper part of the water column.

The algae respond to these changes by producing a succession of communities, usually dominated by one or a few species, which are best adapted to exploit the prevailing ecological conditions. The shifts in dominance which result frequently conform to a generalised pattern: diatoms in the spring, often closely followed by a maximum of chrysophytes; green algae in early summer, followed by blue-green algae and/or dinoflagellates in mid- to late summer; and then a secondary diatom peak in autumn, declining over mid-winter before increasing once more in spring. Examples of lakes showing a succession of this type will be discussed in Section 2. Modifications of this pattern can sometimes be related to special conditions of lake morphometry, nutrient input or climatic influence.

The possible interpretation of such a pattern depends to a large extent on knowledge of the biology of the actual algae or algal groups concerned. Information relevant to individual species will be considered in Section 3 but certain group characteristics are also of importance. The requirement of dissolved silica for diatoms is well known (Lund, 1949 and later works) and they are also affected by changes in turbulence since they have no independent means of staying in suspension (e.g. Reynolds, 1973c). Flagellate algae, in contrast, can swim towards the surface in still water, or may take up position at particular points in the water column (e.g. Heaney, 1976). Blue-green algae can regulate their own buoyancy by the internal production of gas vacuoles (see Reynolds & Walsby, 1975) and in many cases can also utilise atmospheric nitrogen directly (see Fogg et al., 1973). It has also been suggested (Moss, 1973; Shapiro, 1973) that blue-green algae may be less dependent on dissolved CO_2 in the water than, in particular, green algae.

Other processes implicated in determining periodicity are also important and may be less consistent among the

members of a particular algal group. An example is the problem of perennation, or how algae maintain a (potential) presence in a body of water in periods when they may be undetectable in the plankton. Lund (1949, 1954) concluded that while the diatom Melosira italica subsp. subarctica perennates on the bottom mud in Lake District lakes, Asterionella formosa and other diatoms probably do not. Chrysophytes and most dinoflagellates encyst- but many green algae rarely do so. Some, but not all blue-green algae produce spores or akinetes but, in a recent study (Rother & Fay, 1977), there was little evidence to suggest that these were strictly devices for over-wintering.

Difficulties in extrapolating the results of laboratory studies to field situations have led to the experimental manipulation of natural or artificial water-bodies in an attempt to investigate particular factors underlying some aspects of phytoplankton periodicity. A promising approach is that of isolating areas of a lake in experimental enclosures, using the rest of the lake as a 'control' system (Lund, 1975, 1978). However, such experiments involve a large allocation of time and facilities for comprehensive monitoring if the results are to be meaningful and their operation is beyond the scope of all but a few specialised institutions.

iv) Electron-microscope studies of scale-bearing algae

The development of electron microscopy as a means of identifying scale-bearing organisms may be traced back to 1955, in which year Fott, Asmund, and Manton all published micrographs of algal scales; soon after, Petersen & Hansen (1956), Harris & Bradley (1957) and Takahashi (1959) made their first contributions in this field. These authors were to dominate the gradual elucidation of the taxonomy of these organisms, based on sub-light-microscopic scale characters, over the succeeding decade; Asmund and Takahashi continue to publish results from freshwaters, while more recently Peterfi (1966 onwards), Kristiansen (1969 onwards) and Wujek et al., (1972 onwards) have all carried out freshwater

investigations. Other workers (e.g. Leadbeater, 1974; Thomsen, 1975; Manton, 1977) have worked mainly on marine collections. From an initial emphasis on the study of a few species or on collections from a small area, sufficient information has gradually been accumulated to allow comprehensive treatments of whole genera to be made: for freshwaters, the significant introductions or revisions concern Synura (Petersen & Hansen, 1956, 1958; Balonov & Kuz'min, 1974); Mallomonas (Harris & Bradley, 1960; Peterfi & Momeu, 1976, 1977); Mallomonopsis (Harris, 1966); Chrysosphaerella (Asmund, 1973); Spiniferomonas (Takahashi, 1973); and Paraphysomonas in Norway (Thomsen, 1975) and in Japan (Takahashi, 1976). The preceding genera are all representatives of the class Chrysophyceae; scale-bearing members of the classes Prasinophyceae and Prymnesiophyceae (Haptophyceae) are predominantly marine and do not figure in the present study.

Investigations have to date been carried out in some 12 countries (see Takahashi, 1978, for a recent summary) but within Britain published records are largely confined to the work of K. Harris and D.E. Bradley, together and independently, over the period 1957 - 1970. Most of this work was based on collections from the Reading area, although Bradley also collected near Edinburgh (Bradley, 1966). A limited amount of other work has been carried out in Britain, concentrating on one or a few species at one time: Abdel Karim (1965) illustrated certain Mallomonas and Synura species from Abbot's Pond and Priddy Pool, near Bristol; Manton (1967) illustrated Mallomonas caudata from the Lake District; Belcher (1969) worked on two species of Mallomonas from Lancashire; and Hibberd (1973, 1978, 1979) has investigated the cytology of certain species of Synura and Paraphysomonas in collections of wild origin from a number of localities. A few species of Mallomonas and Chrysosphaerella may be reliably determined with the light microscope and so older records or those from non-electron microscope studies are available in

these cases but, for the majority of species, electron-microscopic determination is essential. There is thus still a considerable lack of knowledge of the distribution of these "nanoplankton" organisms in Britain, particularly in relation to the results of more traditional phytoplankton investigations as mentioned earlier. In addition, certain species have been found so few times throughout the world that more information concerning their morphology and range of variation is needed.

v) Cytological features of different classes of algae

Electron-microscope cytology is now recognised as a basic tool in algal systematics and modern taxonomists stress various degrees of cytological uniformity for the delimitation of algal classes and higher taxa (e.g. Dodge, 1973; Leedale, 1974a). The cell organisation in each class should therefore to a large extent display a characteristic combination of features which differs from those of all other classes and, depending on the number of cytological investigations yet carried out upon members of that class, these features may be well or little understood, while others may still await discovery. A review of the fine structure of algal cells should indicate how far studies of algae of particular types have progressed. For a study which would be based on available cultural material, a specific problem could then be selected and the relevant organisms obtained from standard sources; with a study to be based on wild material, such as the present investigation, electron-microscope preparations of a wide range of organisms might reveal features which could not have been anticipated and which may themselves prompt further study. Such an approach can only be successful if the investigator is familiar with the current level of knowledge of algal ultrastructure and can identify features revealed by the electron microscope which deserve further investigation.

Access to the research literature is available through general texts such as those of Round (1973), Sleigh (1973) and Van den Hoek (1978), together with the range

of bibliographies in Rosowski & Parker (1971); through reviews of the whole field of algal ultrastructure, such as Dodge (1973, 1974) and Leedale (1974b, 1976, 1978); and through introductions to the ultrastructure of individual algal groups, viz. Duke & Reimann (1977) on diatoms, Hibberd (1976) on chrysophytes and prymnesiophytes, Pickett-Heaps (1975) on green algae, Dodge (1971) and Sarjeant (1974) on dinoflagellates and Leedale (1967) on euglenoids. There is no comprehensive review of ultrastructure of the cryptomonads; entry to the literature is possible from the papers of Santore & Greenwood (1977), Oakley & Dodge (1976), Faust (1974) and Lucas (1970). The ultrastructure of blue-green algae is outside the scope of the present study; a separate project based on Sawley Dene will deal with the cytology of these organisms (H.A. Cmiech, thesis in preparation).

Section 5 of this thesis contains detailed observations on aspects of the ultrastructure of four species; the literature relevant to each will be reviewed at the appropriate point in that section.

SECTION 1 DESCRIPTION OF THE STUDY SITE

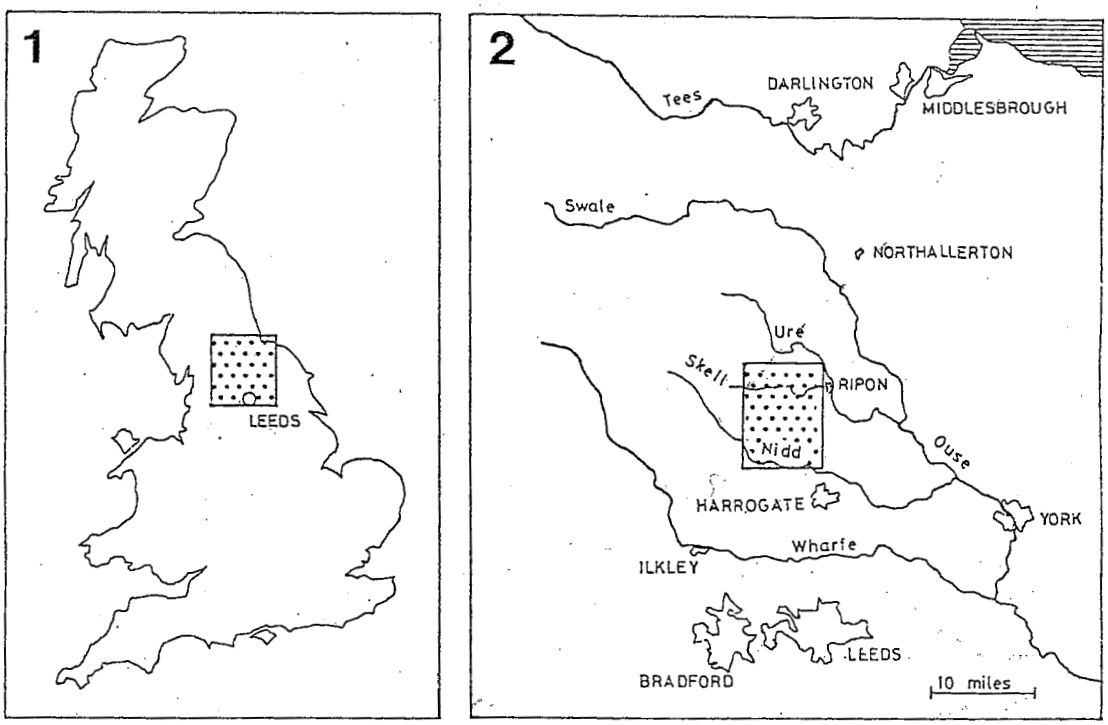
a) Location and Historical Background

Sawley Dene, Nat. Grid Ref. SE 263667, lies at an altitude of 113 m (370 ft) and is situated 7 km south-west of the city of Ripon and 1.5 km south-east of the village of Sawley in North Yorkshire, England, on the approximate boundary between the Yorkshire Dales and the Vale of York. Its general location is shown in Figs 1 and 2 and the topography of the surrounding area in Fig. 3. Sawley Dene lies a short distance from the ruined Fountains Abbey (A.D. 1132 - 1539) and the original lake on the site was constructed as a monastic fishpond associated with the Abbey, in a marshy valley on part of the Abbey estate known as Fountains Park. This name, and the course of the monastic wall, may still be traced on current maps. A sixteenth-century description of part of the Abbey lands, produced for Henry VIII following the suppression of the Abbey, has been transcribed by Walbran (1863: p. 307 et seq.) and includes the following item:

> "One greate poole or fishinge pond callyd Great deane, cont. by estimacion xvj acrez ... inclosed within the parke callyd Fontaunce park, nere unto the said late Monasterie of Fontaunce."

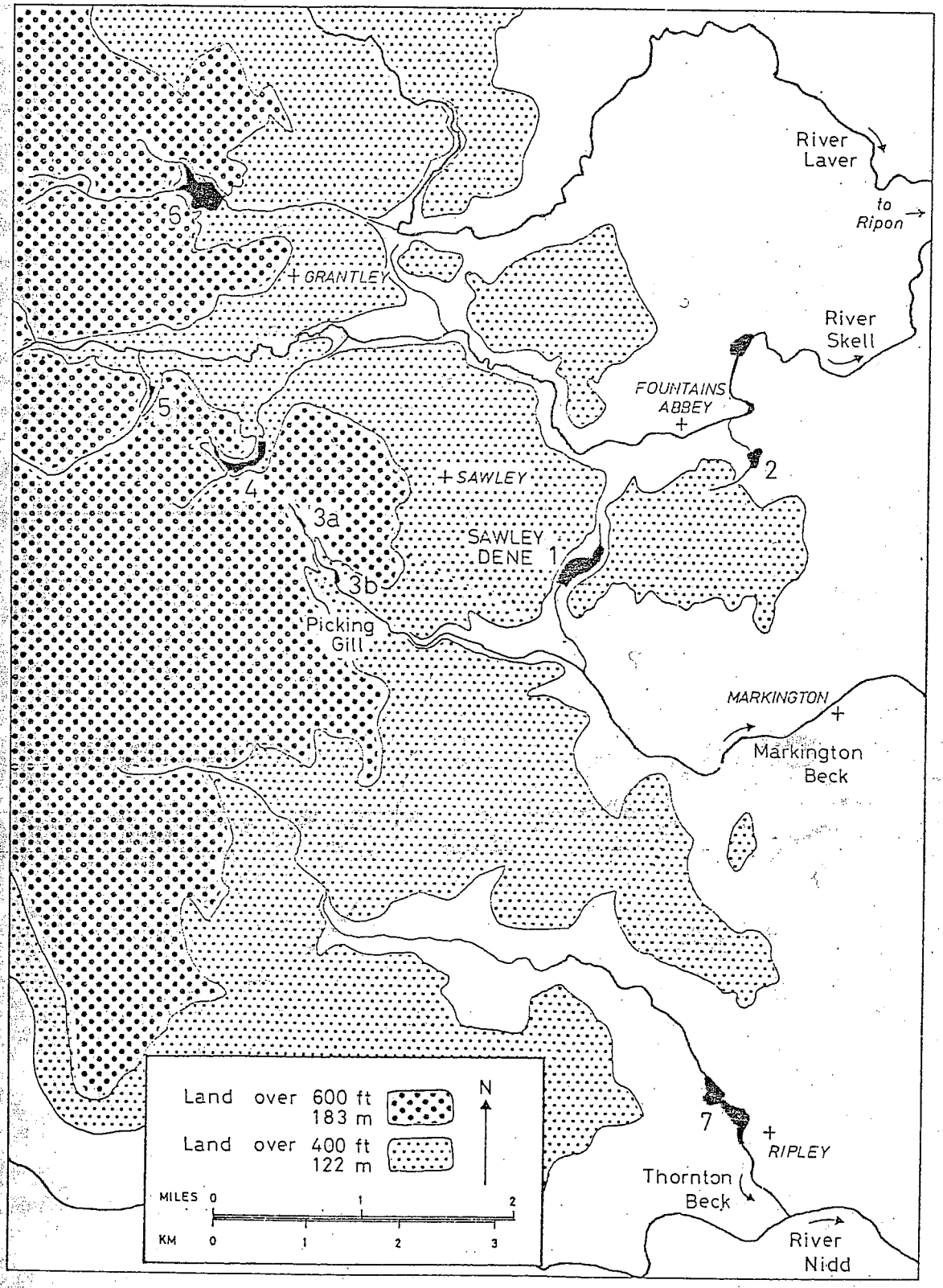
The subsequent fate of the monastic lake is obscure; the estate changed hands several times during succeeding centuries and eventually the lake was drained, for the 1st edition Ordnance Survey maps (surveyed 1848/9) show the outline of the old lake still visible but its bed occupied by three fields and drained by a small stream. The estate next passed to the future First Marquess of Ripon (d. 1909) and, on the evidence of contemporary maps, the present lake appears to have been constructed between 1896 and 1907/8. The original lake outline seems to have been followed closely, with the addition of certain features such as the causeway and foot-bridge across the north end of the lake and the small island in the north-west corner (see Fig. 4). A recent aerial photograph (Fig. 5) confirms that the features shown on the O.S. 6-inch map (1910) are essentially unchanged.

Figs 1, 2. Location of the study area.



= area shown in following Figure.

Fig. 3. Drainage and topography in the Sawley region.



Key to numbered lakes: 1 = Sawley Dene, 2 = Stanks Pond, 3a = Picking Gill Upper Pool, 3b = Picking Gill Lower Pool, 4 = Eavestone Lake, 5 = Brim Bray Pond, 6 = Lumley Moor Reservoir, 7 = Ripley Castle Lake.

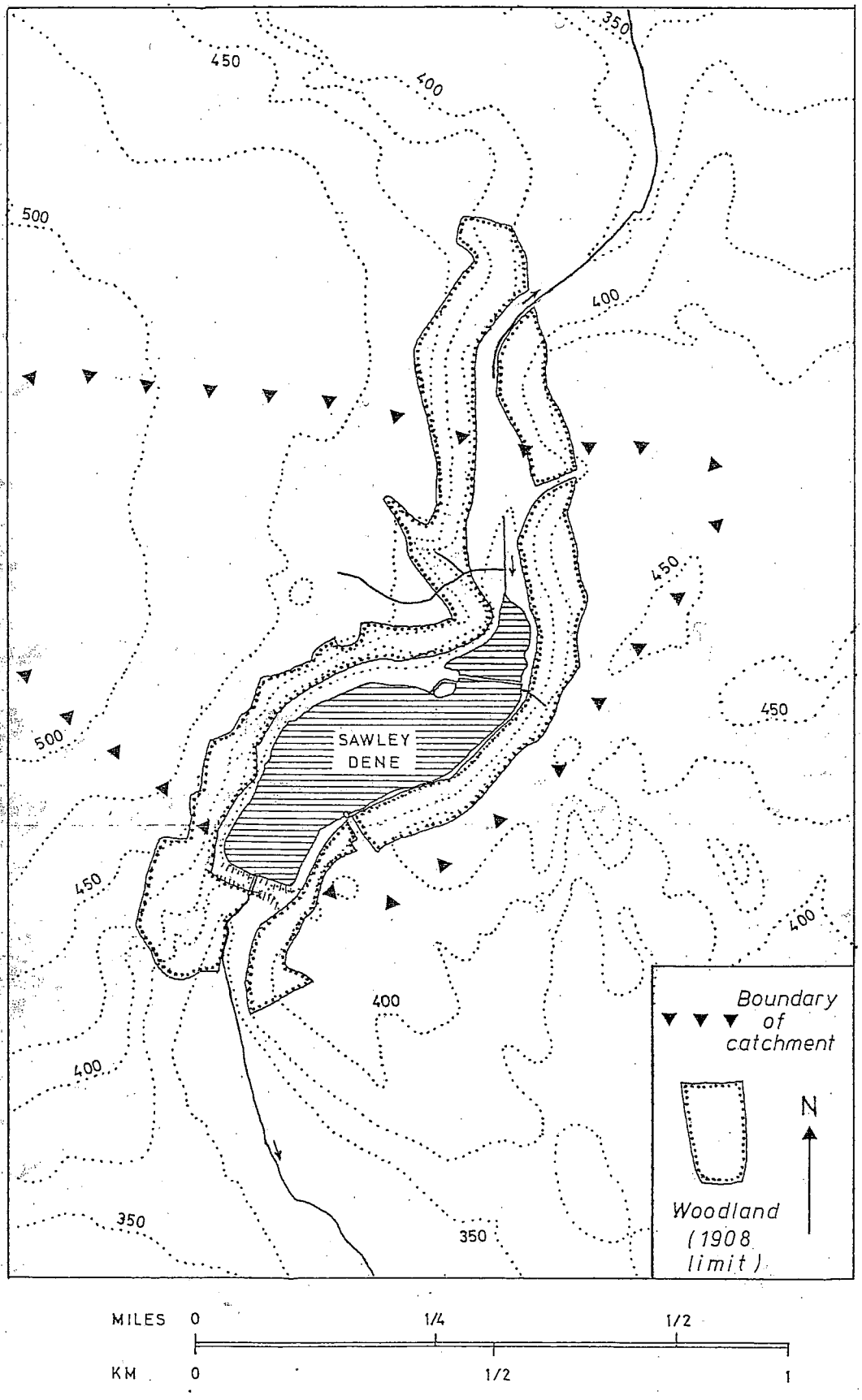
b) Drainage and Topography

The region in which Sawley Dene is situated is crossed by a number of east-flowing rivers (Figs 2, 3) which rise in the hills above the Yorkshire Dales and eventually join the south-east flowing River Ouse in the Vale of York. Sawley Dene, however, is by-passed both by the River Skell to the north and the River Nidd to the south, receiving drainage from only a small area in its immediate vicinity. In fact, the valley of The Dene would naturally support a small stream only and might even dry out completely during summer (see p. 18) were it not for the construction of the lake. Nevertheless, The Dene is a natural valley of considerable proportions and its lack of a notable stream or river requires explanation.

Examination of the valley contours (Fig. 4) reveals a second part of the valley above the head of the lake which slopes downwards towards the north, i.e. in the opposite direction to the part occupied by Sawley Dene. Together, the two parts constitute a single channel which, in effect, changes its direction of slope in mid-course. This channel is in such a position as to link the present valleys of the River Skell and Picking Gill/Markington Beck at a high level and it was suggested by Kendall & Wroot (1924) that The Dene and similar, largely dry, channels immediately to the north and south formed a route for conveying the waters from the River Ure southwards around the edge of a stationary ice-sheet in a period of the last glaciation when the lower reaches of the Skell and other river valleys were blocked by ice. In a more recent study Johnson (1969) puts forward an alternative view that the north-south route of which The Dene would be a part was followed by subglacial water during a period of general ice cover, before the formation of the present-day valleys which now contain the Rivers Laver, Skell, etc., east of this point. There is evidence that, in a pre-glacial period, each of the main rivers followed a substantially straighter course than it does today (Johnson, 1974).

It would therefore appear that The Dene was hollowed out by a large volume of water flowing southwards during the last glacial period and that this and other high-level channels were progressively abandoned as the main

Fig. 4. Principal features of Sawley Dene and catchment area.



source: O.S. 6-inch map, 1910. Contour heights in feet.

rivers in the area assumed their present-day courses. Since the River Skell, a little to the north of The Dene, is now ca. 27 m (90 ft) below the mid-point of the valley floor, this diverts almost all of the natural drainage away from Sawley Dene and leaves the valley largely dry.

The water which Sawley Dene receives is thus derived from a purely local catchment and it flows into the lake from drainage channels through the marshy area above the head of the lake and from three springs in the valley sides (Fig. 7). Water leaves the lake via an overflow channel in the dam, although during the summer months the lake level may be too low for any outflow to occur. The exit stream passes into Markington Beck (Fig. 3) which ultimately joins the River Ure south of Ripon.

c) Geology and Ionic Composition of the Water

The geology of the area is shown in the northern parts of sheets 61 and 62 of the 1-inch Geological Survey. Several important geological boundaries traverse the region in a general NNW-SSE direction, among which that between the Millstone Grit (to the west) and the Magnesian Limestone (to the east) passes 2 - 3 km east of Sawley Dene and is exposed in the valley of the River Skell at Fountains Abbey. In respect of the solid geology, the Sawley Dene catchment area overlies Millstone Grit and associated shales and might therefore be expected to display an acidic character; however, the water is moderately alkaline (see below) and this is presumed to be influenced primarily by the glacial drift which extends into the area from the east rather than by the bedrock. This drift has a significant limestone content (Edwards, 1938) and, although previously mapped as not extending as far west as Sawley Dene (Edwards, loc. cit.; Palmer, 1966), it probably continues several km further (J. Palmer, pers. comm.; see also p. 60). The relevant drift sheet of the 1-inch Geological Survey (sheet 61, drift) has not been published.

This glacial drift is known as the "newer drift" (Raistrick, 1933) and is believed to date from the last glacial re-advance in the area. Further west, remnants of an "older drift" occur which are thought to date from a

previous glacial period; these are severely dissected and decalcified (Penny, 1974) and would be expected to yield ion-poor waters similar to those of the Millstone Grit bedrock. Measurements of the pH of the Sawley Dene water give values in the range 7.6 - 8.2 (Table 6) and these contrast with values obtained from water-bodies beyond the apparent western limit of the newer drift (see p. 60).

Chemical analyses of two surface water samples from Sawley Dene have been performed by Mr. J. Heron (Freshwater Biological Association, Ambleside) and the results are given in Table 1. Also included in this Table for comparative purposes are data from the literature for some alkaline lakes elsewhere (Brook, 1964; Reynolds, 1971). The data from Brook (loc. cit.) refer to his most alkaline category which ranges from lakes of similar alkalinity to Sawley Dene to those very much more alkaline and with high ionic concentrations. From this comparison it can be seen that none of the ionic concentrations deviate unduly from "normal" values except that sulphate, not recorded by Brook, is somewhat high and rivals bicarbonate as the predominant anion, reaching a value similar to that recorded by Reynolds (1971) in Crose Mere which has a generally richer ionic concentration than Sawley Dene. The reason for the high sulphate value is undiscovered; according to Gorham (1958) the majority of sulphate in surface waters is added through rain and is of industrial origin but this would seem unlikely to apply in the present case.

Moss (1973) compares values of alkalinity and pH reported in the literature and shows that alkalinity values of 1.46 - 1.50 (as meq. l^{-1} HCO_3^-) are normally associated with pH 7.9 approx. Brook (1964) found a relationship which would suggest a slightly higher value (pH 8.2). The equilibria involving pH are discussed more fully in Hutchinson (1957).

d) Lake Morphometry and Bathymetry

Morphometric data for Sawley Dene are given in Table 2. The measurements of length and area are based on the 1:2500 O.S. map (1908/9 survey) and the data on depth derive from a bathymetric survey conducted by the author and

Table 1. Concentrations of major ions in Sawley Dene and other waters.

Ions (meq. l^{-1})	Sawley Dene, surface 30.4.76	Sawley Dene, surface 4.11.76	Range from 14 Scottish Lochs, pH >8.0 (Brook, 1964)	Crose Mere, surface May 1967 (Reynolds, 1971)
CATIONS				
Ca^{2+}	1.950	1.935	2.00 - 6.49	3.650
Mg^{2+}	0.831	0.722	0.66 - 7.32	0.773
Na^{+}	0.643	0.652	0.13 - 1.61	0.522
K^{+}	0.060	0.069	0.01 - 0.12	0.123
Total	3.484	3.378		5.068
ANIONS				
HCO_3^{-}	1.498	1.460	1.20 - 2.70	3.280
SO_4^{2-}	1.282	1.222	no data	1.207
Cl^{-}	0.765	0.753	0.92 - 1.67	0.590

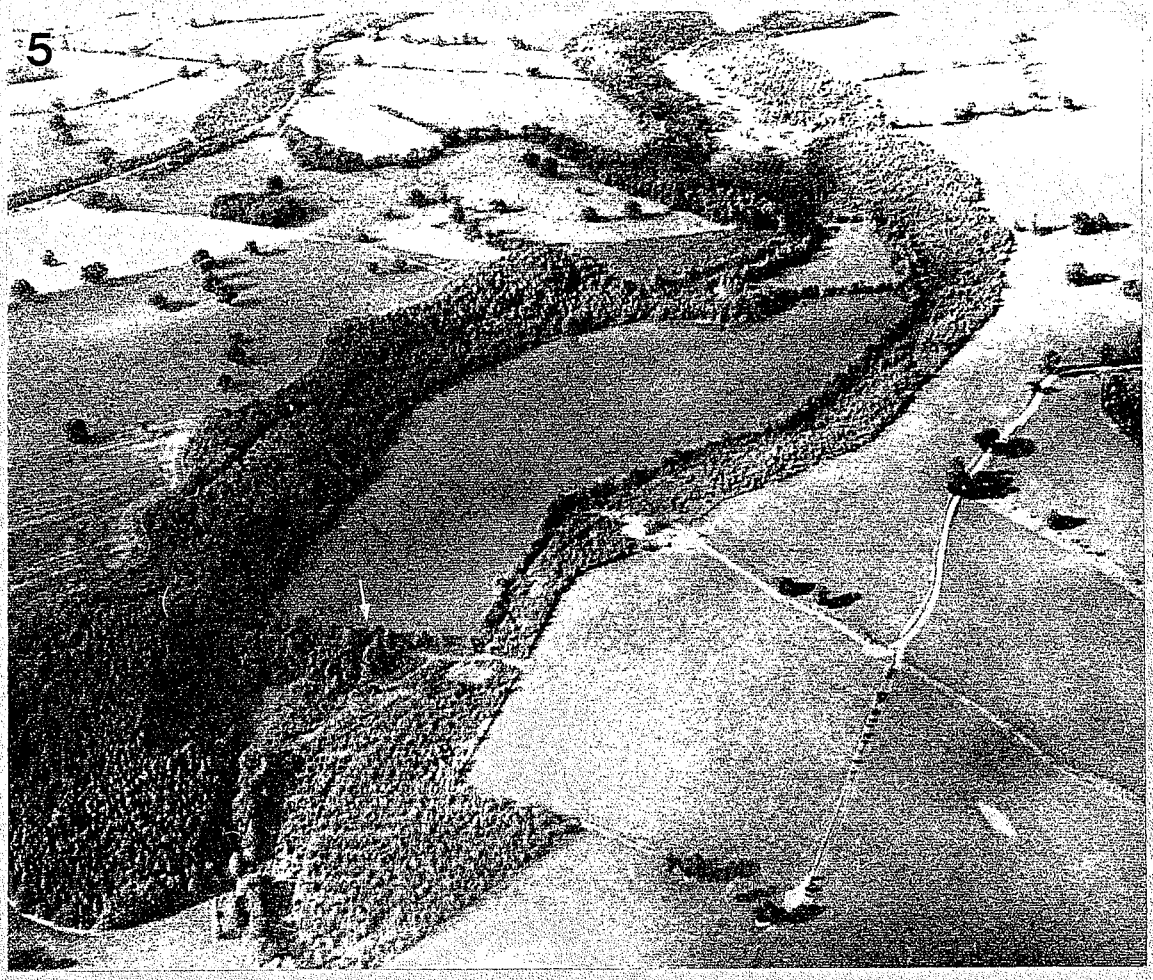
Note: data from Brook (1964) converted from p.p.m. to meq. l^{-1}.

Table 2. Morphometric data for Sawley Dene.

	Whole lake	Large basin only
Overall length (inflow - outflow)	650 m	525 m
Maximum width		195 m
Surface area	9.48 ha	8.46 ha
Lake volume	19.3×10^4 m^3	18.3×10^4 m^3
Mean depth		2.2 m
Maximum depth		4.6 m
Length of perimeter	1.91 km	1.47 km
Catchment area (including water surface)	0.784 km^2 (= 78.4 ha)	

Fig. 5 Aerial view of Sawley Dene, looking north. Arrow indicates position of outflow.

Fig. 6 View of main basin, looking south from the island towards the dam and outflow (arrow).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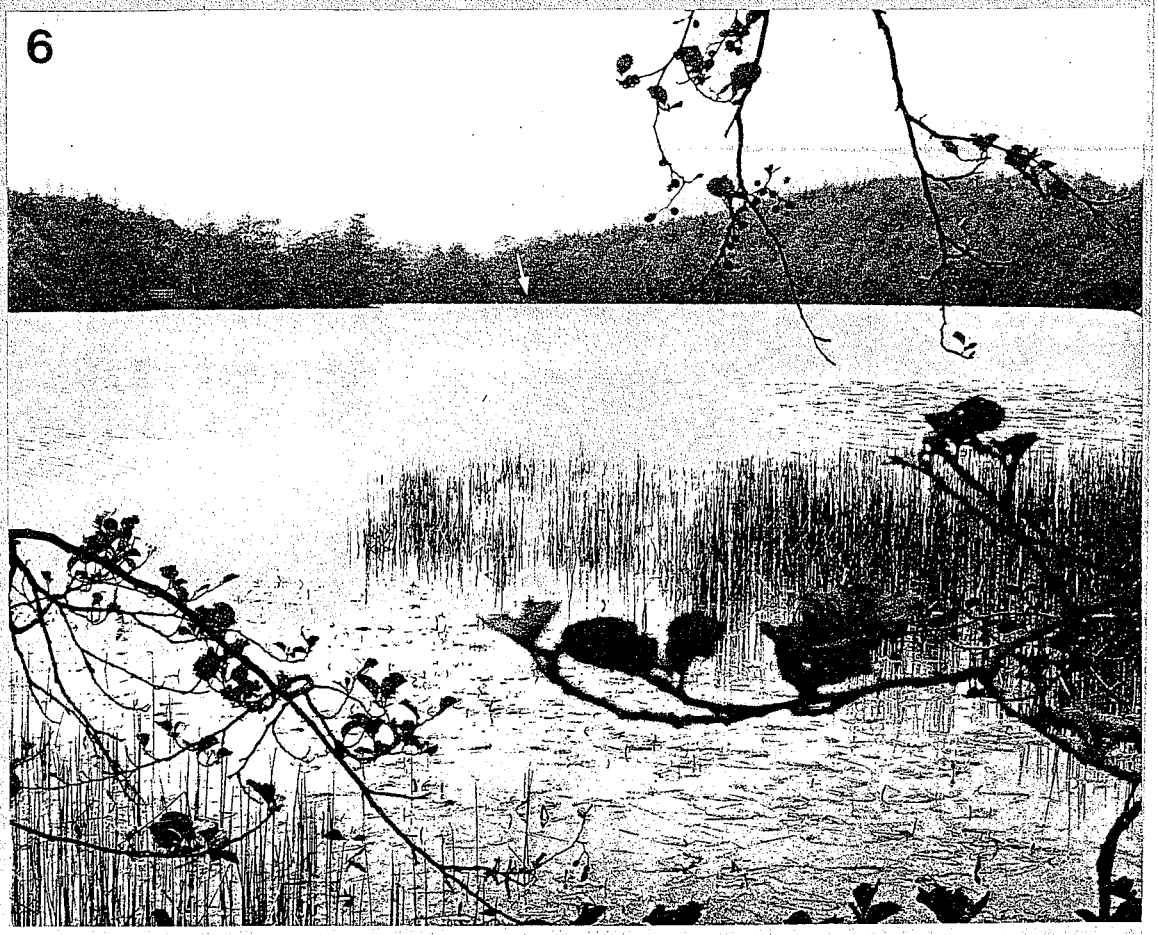
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Miss H.A. Cmiech in January - March 1976, determining depths by leadline along seven transect lines; the depth contours established are shown in Fig. 7. The approximate volume of water within each 0.5 m layer was calculated by multiplying the layer thickness by the mean area enclosed by the limiting upper and lower contours, and the values for all the layers were summated to give a figure for the volume of water in the large basin. The mean depth was calculated as the ratio of volume : surface area. The extent of the catchment area (including the lake surface) was estimated after plotting the positions of watersheds onto the 1:25,000 O.S. map.

The lake floor slopes gently from the shallow upper pool (largely 1 m in depth) to the maximum depth of 4.6 m found close to the dam. Over half of the main lake area (65%) is less than 2.5 m deep. In cross-section the lake floor appears very flat, increasing in slope only at the edges; it is therefore likely that a significant amount of silting has taken place.

Fig. 6 shows a general view of the main basin, looking south-west from the island towards the dam and outflow (arrow). The shallow area colonised by Polygonum amphibium (foreground, centre) represents one end of the small channel separating the island from the north-west corner of the basin.

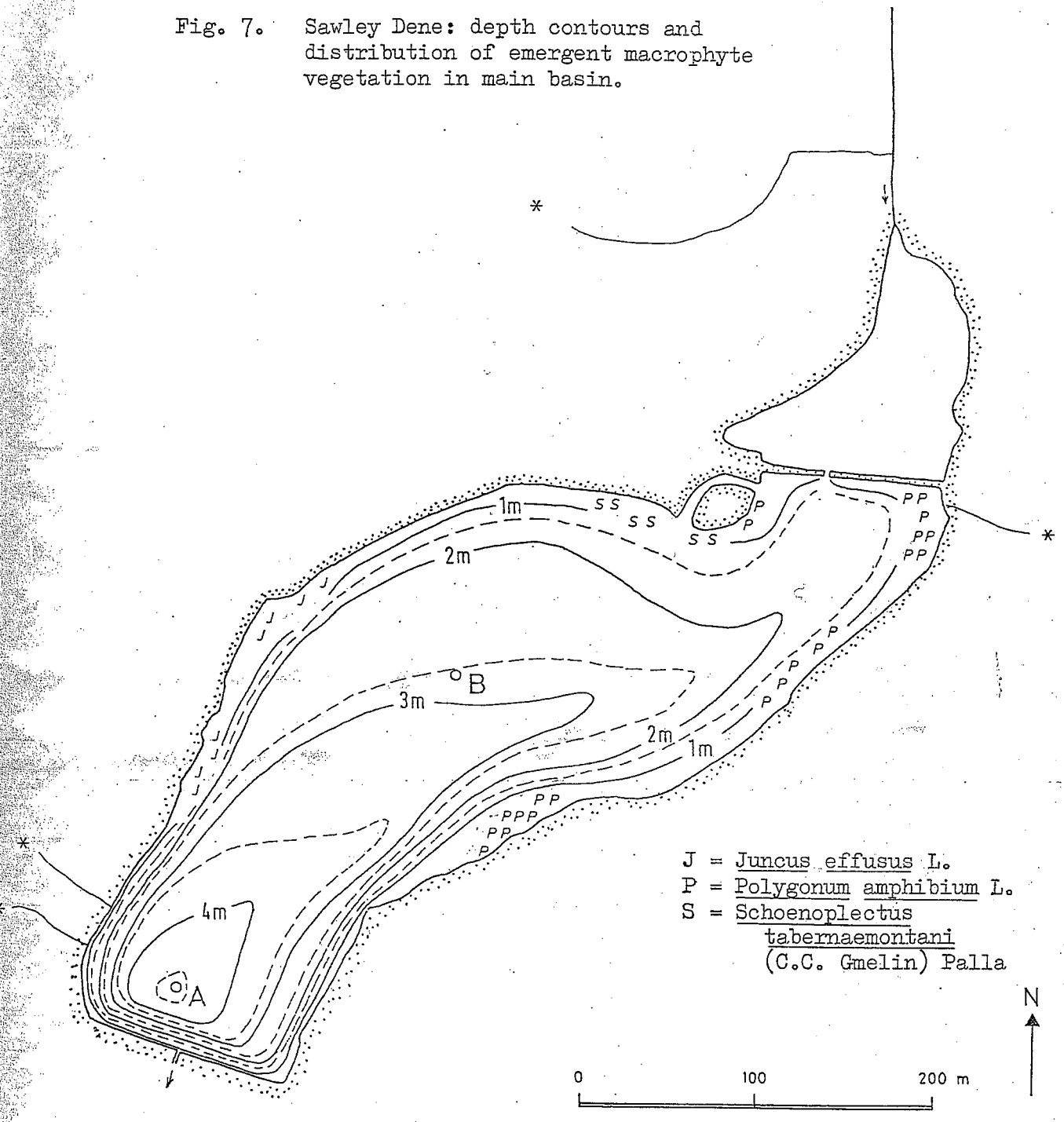
e) Climate and Hydrology

The following data (largely unpublished) are given courtesy of the Meteorological Office, Harrogate.

The climate of the region around Sawley Dene is generally moist and not prone to extremes of temperature. Annual precipitation at Sawley Dene is estimated to be ca. 825 mm (based on 1941 - 1970 averages), which may be compared with values exceeding 1100 mm over higher ground to the west and values below 675 mm in the Vale of York. At the altitude of Sawley Dene, daily mean air temperature may be estimated to average 4.0^{o}C in January and 16.8^{o}C in July (based on 1931 - 1960 average).

Monthly rainfall is typically below the annual mean value from February to June, sunshine exceeds the annual mean from April to September and mean daily air temperature

Fig. 7. Sawley Dene: depth contours and distribution of emergent macrophyte vegetation in main basin.



is above its annual mean from May to October. The lowest rainfall and highest sunshine are typically recorded for June, while the months with highest average daily maximum air temperatures are July (21.4°C) and August (20.8°C).

No single direction of prevailing wind is apparent, although W and SW winds are the most frequent in summer (data from 1932 - 1938 and 1951 - 1958). NE and E winds are the rarest in annual totals.

The availability of precipitation for a direct contribution to lake inflows depends on seasonal levels of evapotranspiration and their cumulative effect on the soil water content. Potential evapotranspiration is estimated from Penman equations involving evaporation rates, radiation, relative humidity, wind speed and air temperature but it appears to be relatively conservative over a wide area (Lockwood, 1967) although its interaction with rainfall will produce varying local patterns of soil moisture. Smith (1965: Fig. 11) compares Penman data with monthly rainfall at Harlow Hill, Harrogate (annual precipitation 803 mm) and it is apparent that potential evapotranspiration equals or exceeds rainfall during May/June/July and that the soil moisture remains below field capacity until early September. Significant run-off, and thus inflow to a lake such as Sawley Dene, must therefore be confined to the months September - April in an average year.

The theoretical annual throughput of water for Sawley Dene may be estimated from the precipitation on its catchment area and consideration of the quantities returning to the atmosphere without contributing to lake outflow. The theoretical retention time, i.e. the mean residence time of water in the lake, may then be calculated by comparing the lake volume to the mean (calculated) rate of outflow.

Values for annual precipitation, catchment area, surface area and volume of Sawley Dene have been given above (p.16 and Table 2). At sites in the Harrogate area, the annual potential evapotranspiration over turf (estimated from meteorological data by the Penman method) has been calculated as 412 mm as a long-term mean (16.22 ins: Smith, 1964) and as 371 mm, 390 mm and 410 mm for specific recent

years (Lockwood & Venkatasawmy, 1975). However, where runoff and rainfall have been measured directly over large and small catchments in the area, a difference close to 356 mm (14.0 ins) between the two annual figures is characteristically observed (Penman, 1950; Smith, 1966; Lockwood & Venkatasawmy, 1975) which is due principally to the effect of evapotranspiration. In the present calculation, therefore, the value of 356 mm will be used instead of that derived by the Penman method to represent annual evapotranspiration over that part of the catchment area not occupied by open water.

Evaporation from the water surface may also be calculated by the Penman method (Smith, 1964) but, again, observed values are slightly lower and the figure of 487 mm (19.16 ins: Smith, 1964) will be used in the calculation below. The ratio of observed values for evapotranspiration over turf : evaporation from open water is 356:487 or 0.73, which is still close to the value of 0.75 given by Penman (1948) with his original description of the method for deriving these values by calculation.

Area of catchment	78.4. ha ($m^2 \times 10^4$)		(1)
Mean annual precipitation	825 mm		(2)
Annual volume of water falling in catchment	= 64.7×10^4 m^3	(a)	= (1) x (2)
Area of catchment under vegetation	68.9 ha		(3)
Estimated annual amount of evapotranspiration	356 mm		(4)
Annual water loss through evapotranspiration	= 24.5×10^4 m^3	(b)	= (3) x (4)
Area of open water	9.5 ha		(5)
Estimated annual amount of evaporation	487 mm		(6)
Annual water loss through evaporation from open water	= 4.6×10^4 m^3	(c)	= (5) x (6)
Theoretical rate of outflow from lake (= inflow less direct evaporation)	= 35.6×10^4 $m^3 y^{-1}$	(d)	= (a) - (b) - (c), per year
Volume of lake	19.3×10^4 m^3	(e)	
Theoretical Retention Time	= 0.542 y		= (e)/(d)
	= 6.5 months approx.		

It is probable that marked deviations from this theoretical value will occur in practice with only a small variation in annual rainfall. Test calculations suggest that a 20% increase in annual rainfall, with no change in evapotranspiration rates, would result in a 25% decrease in retention time, while a 20% decrease in annual rainfall would cause the retention time to increase by 55%.

The theoretical retention time of 6.5 months calculated for Sawley Dene is unusually long for a small lake; for comparison, Blelham Tarn (area 10.2 ha) has a retention time of 1½ months* while Windermere, England's largest lake, has a retention time of ca. 9 months (Lund, 1969). Some of the Shropshire Meres, however, have very long retention times (1 - 6 years: Reynolds, 1976a).

* (Talling, 1971)

f) Natural History and Management

Biological aspects of the lake apart from the planktonic algae have not been systematically investigated; the following information is included as a preliminary account based on casual observations by the author and supplemented by information from Mr. T.S. Crosby on flowering plants and Mr. E.E. Binns on fishing and lake management.

The most frequent zooplankton organisms seen were the Cladoceran Daphnia sp. with the Rotifers Keratella cochlearis and K. quadrata. Cyclops sp. (Copepoda) was occasionally present as were a few Heliozoa, the most noticeable of which were species of Acanthocystis and Raphidocystis (see p. 54).

The lake is used principally for fishing and is stocked each spring with some 200 - 250 Brown Trout (Salmo trutta morpha fario) and a similar number of Rainbow Trout (Salmo gaidneri irideus). Apart from these fish the only species to be found in the lake is the eel, Anguilla anguilla.

A variety of water birds visit Sawley Dene but no large flocks have been seen during the present study. Species noted include Heron, Ardea cinerea; Mallard, Anas platyrhyncos; Moorhen, Gallinula chloropus; Canada Goose, Branta canadensis; and Great Crested Grebe, Podiceps cristatus.

There is no extensive development of macrophyte vegetation across the lake surface. A few well-defined stands occur at some parts of the lake margin (Fig. 7); these comprise Polygonum amphibium L. along parts of the south-east shore, Schoenoplectus tabernaemontani (C.C. Gmelin) Palla close to the southern edge of the island (visible in Fig. 6) and small quantities of Juncus effusus L. with some Sparganium erectum L. in some places near the north-west bank of the main basin. A triangular fen area occupies the south-west corner of the upper basin and contains Carex vesicaria L., Sparganium erectum, Filipendula ulmaria (L.) Maxim. and Iris pseudacorus L.

Above the head of the lake lies a region, formerly marsh, drained by the channels which enter the lake from the north. This area has been planted with widely-spaced

Populus nigra L. and some Salix spp.; the bulk of the open area contains a tall, grassy vegetation which is chiefly Calamogrostis canescens (Weber) Roth and Phalaris arundinacea L., together with Iris pseudacorus, Juncus effusus and Filipendula ulmaria. The north-west bank of the upper basin and most of the island are occupied by Rhododendron ponticum L. and the remainder of the valley sides are covered by largely coniferous woodland, with Picea spp., Larix decidua Miller, Tsuga canadensis (L.) Carr. and Pinus sylvestris L. The few broad-leaved trees include Betula pubescens Ehrh., Acer pseudoplatanus L. and Alnus glutinosa (L.) Gaertn., the latter particularly at the water edges.

The higher parts of the catchment area (Figs 4, 5) are occupied by pasture and used for grazing. There is a single human dwelling within the catchment, a cottage above the south-west bank of the main basin (visible in Fig. 5) which has no mains drainage and may thus constitute a minor source of nutrient input to the lake.

The vegetation of the region has been discussed by Lees in the classic "Flora of West Yorkshire" (1888) but, apart from some additional records in the form of a supplement (Lees, 1941), no more recent account of this aspect of the area exists.

SECTION 2 SEASONAL PATTERNS OF VARIATION WITHIN SAWLEY DENE

Introduction

This Section presents information on variation of temperature and dissolved oxygen during the study period, on changing levels of phytoplankton biomass as represented by chlorophyll a concentration and Secchi disc visibility, and on the composition of the successive phytoplankton communities. Population dynamics of individual species will be considered in detail in Section 3. The present Section is concerned with the characterisation of Sawley Dene in terms of the algal populations it supports, with comparison of phytoplankton biomass and periodicity in this and other lakes, and with a statistical analysis of community change.

Materials and Methods

(i) The Study Period

The data presented in this and the following Section were obtained during 75 visits to Sawley Dene over the period March 1976 - July 1978. Reference will be made to each sampling visit by the week in which it occurred, numbered 1-52 for each year; the years will be distinguished by designating the weeks of 1976 as 1a-52a, 1977 as 1b-52b, and 1978 as 1c-52c. A list of sampling dates, with the week to which each corresponds, is given in Appendix I.

(ii) General Sampling Procedure

Two sampling stations were established in March 1976 for routine measurements: Station A, at the deepest point in the lake (4.6m), ca. 37 m from the dam outflow; and Station B, in the centre of the main water body, ca. 97 m from the shore on each side, at a depth of 2.5 m. The positions of the sampling stations are shown on Fig. 7. Both stations were marked by anchored buoys and reached by rowing-boat. Sampling took place between 1100h and 1200h except where otherwise indicated. The following measurements/samples were taken over all or part of the study period: notes on prevailing weather conditions, water level, extent of ice cover, etc.; measurements of water

temperature and dissolved oxygen levels; estimation of Secchi disc visibility; and collection of net-tow samples and volumetric water samples for chlorophyll *a* estimation, algal identification and counts, and for providing living and fixed material for further studies (Sections 4 and 5 of this thesis).

(iii) Temperature and Dissolved Oxygen

Temperature and dissolved oxygen were measured using a Mackareth probe (combined resistance thermometer and silver/lead electrode), expressing dissolved oxygen levels as % saturation at the measured temperature using a calibration chart supplied with the instrument (Freshwater Biological Association, Windermere). The probe was lowered to selected depths from a stationary boat close to each sampling station. At Station A measurements of temperature and dissolved oxygen were taken at the water surface (i.e. within the upper 10 cm), at depths of 2 m and 4 m within the water column, and at the bottom with the probe resting on the mud surface; at Station B measurements were taken at the surface, 2 m depth and the bottom. After April 1977 measurements were taken at the surface only. From October 1977 a mercury-in-glass thermometer was used and the dissolved oxygen measurements were discontinued. The above measurements were carried out jointly by the author and Miss H.A. Cmiech.

(iv) Phytoplankton

Transparency of the water at the time of sampling was investigated with a Secchi disc of diameter 15.5 cm, which was lowered over the shaded side of the boat and its limit of visibility recorded at each sampling station. Plankton-net samples were obtained by towing a net of 10 µm nominal mesh size through the surface water in the open part of the lake. Vertical tube samples for chlorophyll *a* estimations and algal counts were taken with a length of polythene hose (internal diameter 16 mm) lowered to a depth of 4 m (Station A) or 2 m (Station B), the sample being retrieved using a string attached to the lower end of the hose as described by Lund (1949); repeated samples were bulked to give a final sample volume of at least 1.5 l. Samples were transported to the laboratory in glass or polythene containers within 1 - 2 h of collection.

The net-tow samples, concentrated by centrifugation where necessary, were examined in a Reichert Zetopan microscope for identification of the species present and for a preliminary assessment of their relative abundance. A semi-quantitative scale was adopted whereby the algae were first concentrated until an approximately consistent "dense" suspension was obtained, judged empirically, and a single drop of this was placed on a microscope slide, without a cover-slip, sufficient to cover ca. 25 fields of view at low power (x10 objective). The drop was then scanned for individuals (i.e. cells, filaments or colonies) of each species, which were recorded on the following basis: category 4 ("dominant"), more than 100 individuals per field of view at low power; category 3 ("abundant"), 10 - 100 individuals per field of view; category 2 ("common"), 1 - 10 individuals per field of view; category 1 ("sparse"), 1 individual every few fields of view, or approximately 3 - 25 individuals in the whole drop; and category "+" ("trace"), less than 3 individuals seen in the drop. This scale therefore reflects the relative abundance of organisms in an approximately logarithmic manner; the extent of its correspondence with the results of more precise counts based on the tube samples will be discussed later.

Consideration of the complete set of net-tow records enabled the constancy (average % presence over the two-year period) of each species to be calculated. However, allowance was necessary for the fact that some summer periods were particularly well-represented in the samples, while a few gaps occurred at other times. It was therefore decided to assess constancy on a fortnightly basis, all occurrences noted within any one fortnight counting as one record. Three fortnights over the two-year period were not represented by any samples; these were weeks 26a/27a, 10c/11c and 24c/25c. In these cases, suitable values were interpolated for species which could be presumed to have had an uninterrupted presence over the fortnight in question. Constancy ratings were then assigned to each species as follows: class A ("constant"), present in over

75% of records; class B ("recurrent"), present in 55 - 75% of records; class C ("intermittent"), present in 35 - 55% of records; class D ("occasional"), present in 15 - 35% of records; and class E ("infrequent"), present in less than 15% of records.

Portions of the net-tow samples were preserved by addition of Lugol's iodine (2 - 3 drops per 15 ml sample) and subsequent storage in the dark at 12°C. These samples were used to check any records where algal identity or abundance might be called into question at a later date.

Chlorophyll determinations were carried out using the method of Talling (in Vollenweider, 1974), incorporating the correction for phaeophytin. Whatmans GF/C filter paper was used to filter the organisms from a known volume of tube sample and chlorophyll was extracted using 90% acetone in the dark for 1 h at 4°C. Absorbance of the extract was measured at 750 nm and 665 nm, before and after acidification with a drop of 1N HCl, using a Unicam SP 600 spectrophotometer and glass cuvettes of path-length 1 cm. Chlorophyll a concentrations were calculated from the abbreviated formula of Talling & Driver (1963).

(v) Statistical Procedures

A statistical method was sought which would enable the changes in community structure to be displayed graphically upon axes representing the intrinsic species diversity of the phytoplankton in this system. By this means it was envisaged that detection of a seasonal pattern and of between-year variability would be more straightforward, while at the same time information on a greater number of species could be incorporated than would be possible with more traditional methods of data summary.

Appropriate statistical methods, which will produce a plot on which the distance between points (samples) reflects their degree of floristic similarity, have been reviewed recently by Whittaker (1978). For computational ease the nonparametric method of Bray & Curtis (1957) was applied to the present data; more complex analyses, e.g. principal components analysis, could also be employed, but their suggested improved "objectivity" (Anderson, 1971)

does not remove the most important limitations of the method, such as the disproportionate influence of outlying points (i.e. anomalous samples), or the probable non-linearity of axes of variation in nature. In any case, principal components analysis, when applied to phytoplankton populations, produces similar organisations of the data to those derived by simpler methods (Bartell, 1973, in Bartell et al., 1978).

Similarity coefficients between samples are required for the statistical analysis; these may be based simply on the number of species two samples have in common compared with those unique to each sample, or may incorporate some measure of abundance so that two samples with a dominant species in common are considered more similar than two samples with a rarer species in common. Such distinctions have been the subject of some dispute (Bartell et al., 1978), but were considered of sufficient value to adopt in the present procedure. The semi-quantitative scale described above (p. 25) was used as the numerical basis for the statistical analysis and similarity between any two samples (e.g. sample "M" and sample "N") was expressed using a modified Sørensen coefficient (Van der Maarel, 1969):

$$\text{coefficient of similarity, } C = \frac{2\,P_{mn}}{P_m + P_n}$$

where P_m represents the sum of species abundance values in sample M, and P_n likewise for sample N; P_{mn} represents the sum of the smaller abundance values for each species common to both samples. A specimen calculation is given in Appendix III. The abundance values are on the scale 0 - 4, with "+" transformed to 0.5 in order to include it in the calculation.

Data on eighteen species (all the "major" species less Cryptomonas and Coelosphaerium, for which complete data sets were lacking) were used as the basis for community description and the calculation of similarity coefficients (see Appendix III). The remaining species fluctuated too close to the limit of detection for the effects of sampling error to be discounted.

The construction of the ordination, by which a graphical

summary of the data is produced, was carried out according to Bray & Curtis (1957), X- and Y- values being assigned to each sample on the basis of its relative similarity to "reference sets" representing major axes of variation within the data (see Appendix III). On the resulting plots, points possessing a high degree of floristic similarity are ordinated to similar regions, while long distances separate highly dissimilar points. Insertion of a chronological axis, linking the points representing successive samples through the season, enables rates of community change to be estimated from the distances between the points; the community structure at any one time is reflected by the location of the equivalent point on the plot.

Results

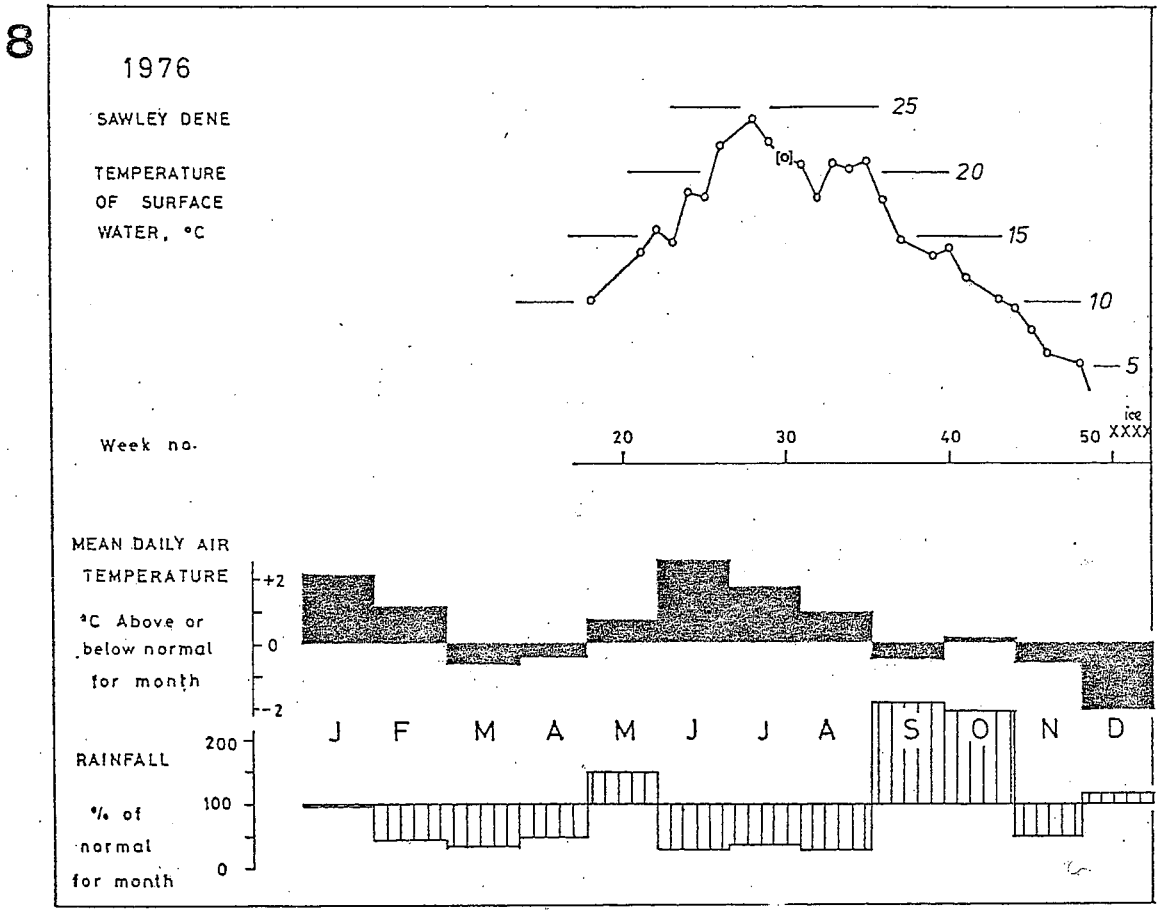
(i) Temperature and Dissolved Oxygen

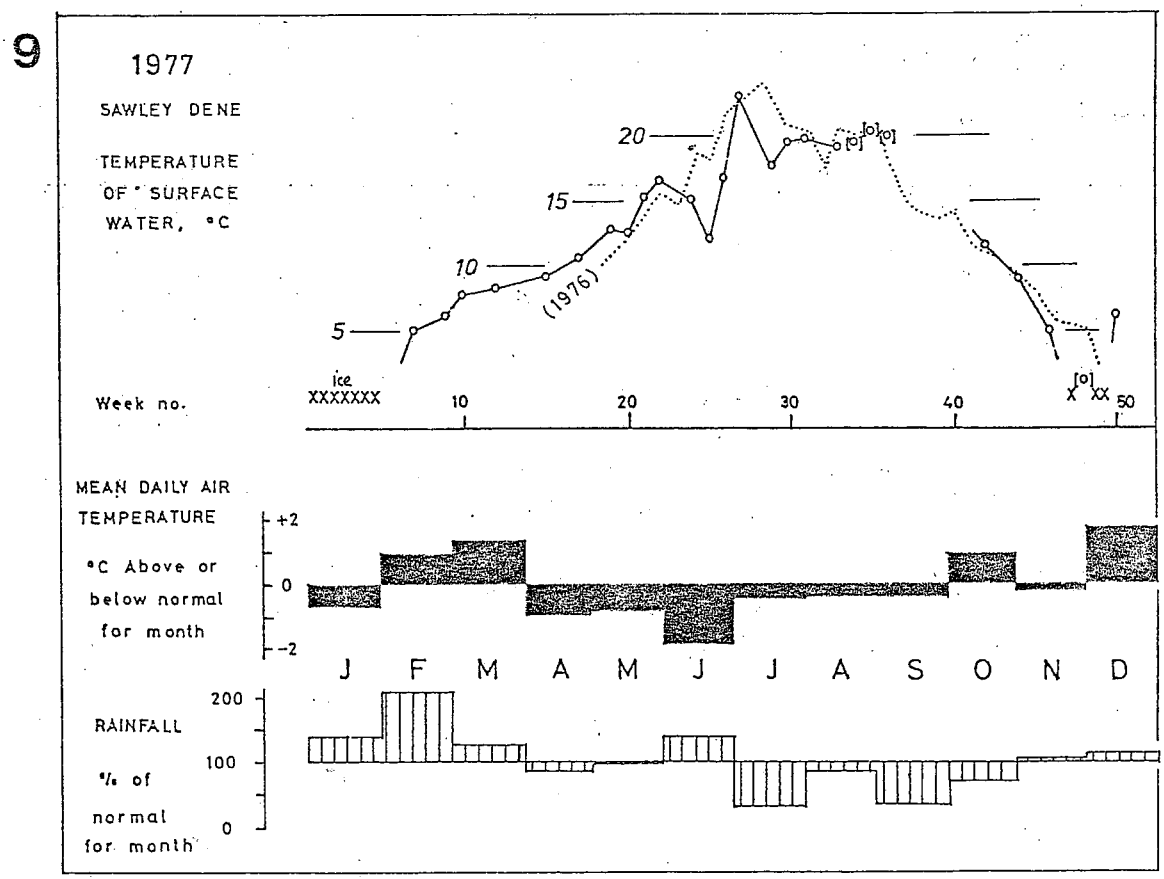
Surface water temperatures were taken before noon and thus may not represent the maximum daily values which occur, but the results from Station B (Figs 8 - 10) show an annual range from frozen conditions to values approaching 25°C. Measurements from Station A follow the Station B values so closely (within 0.3°C on most occasions, see Fig. 11) that the Station B values are representative of the pattern for each year and allow this to be compared with monthly climatic data estimated for the region as a whole, which are also included in Figs 8 - 10.

In 1976 the three months June - August had temperatures consistently above average with very low rainfall, and the extent of stratification in the water column was measured at both stations; the data from Station A, where the deepest column could be sampled, are presented in Fig. 12 as a depth-time diagram. Persistent summer stratification was found not to occur although temporary thermal gradients of up to 3°C between bottom and surface were found on two occasions following periods of rapid surface heating. The water was isothermal on many occasions in spring, summer and autumn, and temperature inversion occurred when conditions approached freezing in December. Measurements made in the shorter water column at Station B showed similar behaviour to that of the upper 2 m of the column at Station A.

Fig. 8. Water temperature and climatic data, 1976.

Fig. 9. Water temperature and climatic data, 1977.





(source of regional climate data for Figs 8 - 10: Met. Office, Monthly Weather Report, 1977 - 1979).

Fig. 10. Water temperature and climatic data, 1978.

Fig. 11. Water temperature: variation between sampling stations, 1976 - 1978.

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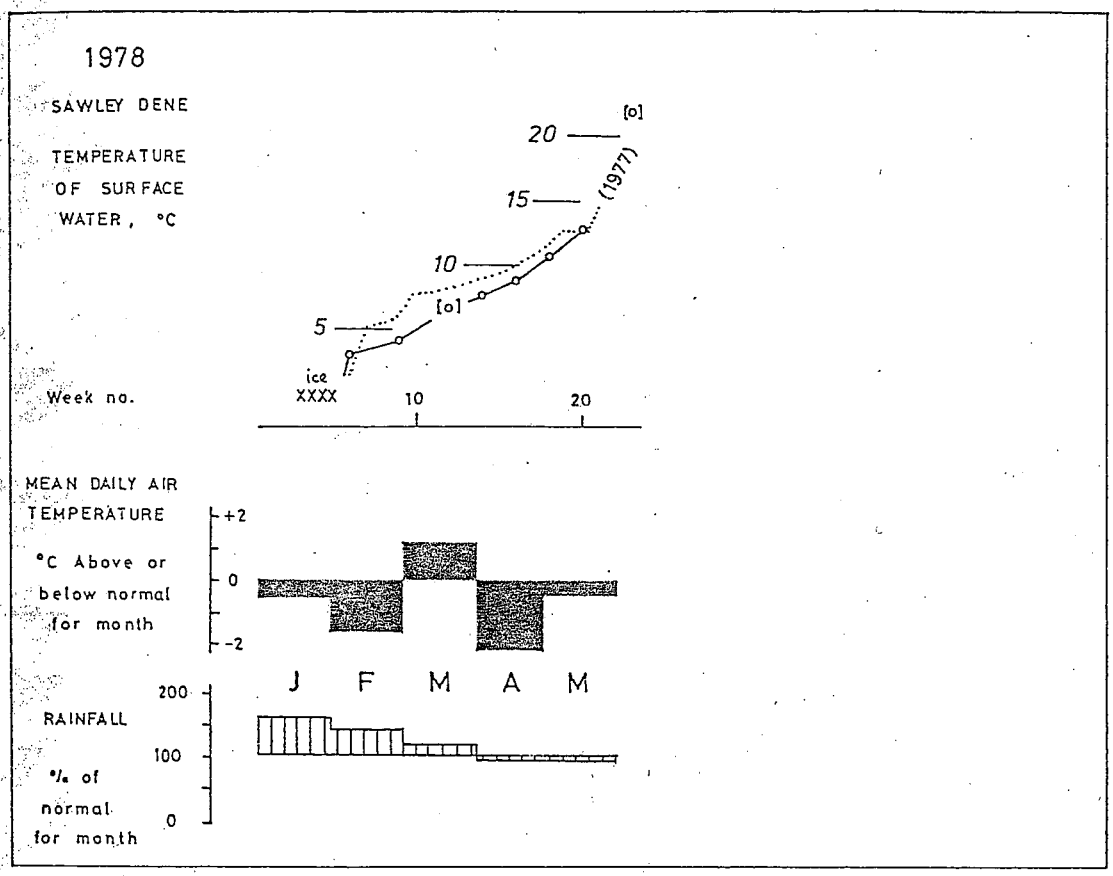

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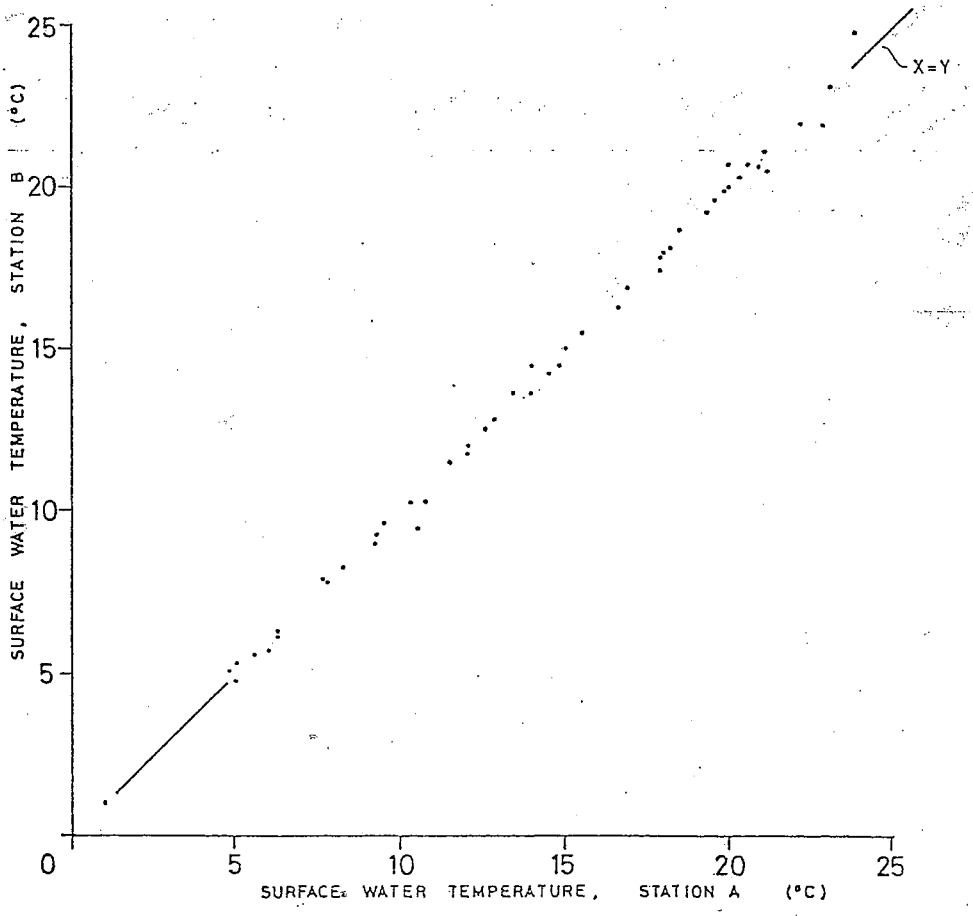
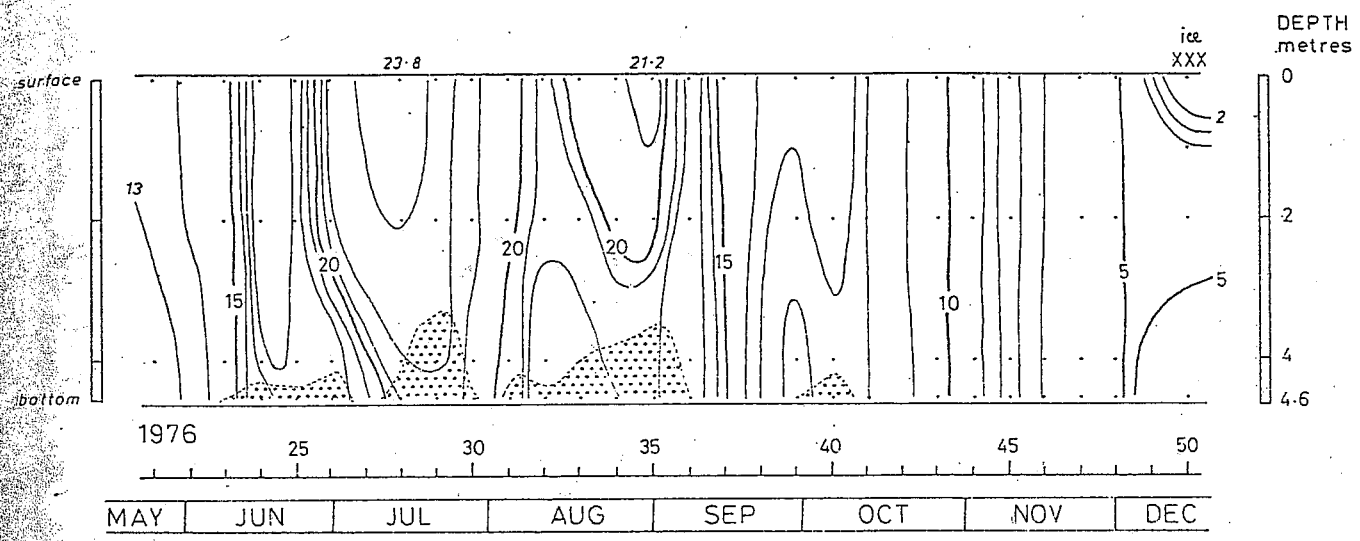


Fig. 12. Depth - time variation in water temperature, Station A, 1976. (Isotherms in °C)



= areas also showing oxygen depletion to < 20% saturation (see text).

Table 3. Dissolved oxygen levels, May - November 1976.

Sample point	Oxygen level (% saturation) mean	range	S.D.	Number of determinations
STATION A				
surface	85.9	66 - 145	18.40	22
2 m depth	75.7	51 - 113	14.11	20
4 m depth	58.5	5 - 92	25.80	21
bottom	14.9	3 - 35	8.85	18
STATION B				
surface	87.6	66 - 137	16.46	21
2 m depth	72.6	27 - 90	13.73	21
bottom	21.1	7 - 35	8.78	18

Dissolved oxygen levels were monitored at selected depths at both stations from May 1976 to April 1977 but values showed considerable week-to-week fluctuations, the only clear trend being that of declining oxygen with increasing depth (Table 3), apart from a small degree of deoxygenation in the bottom 0.5 m of water at Station A at times during the summer (Fig. 12).

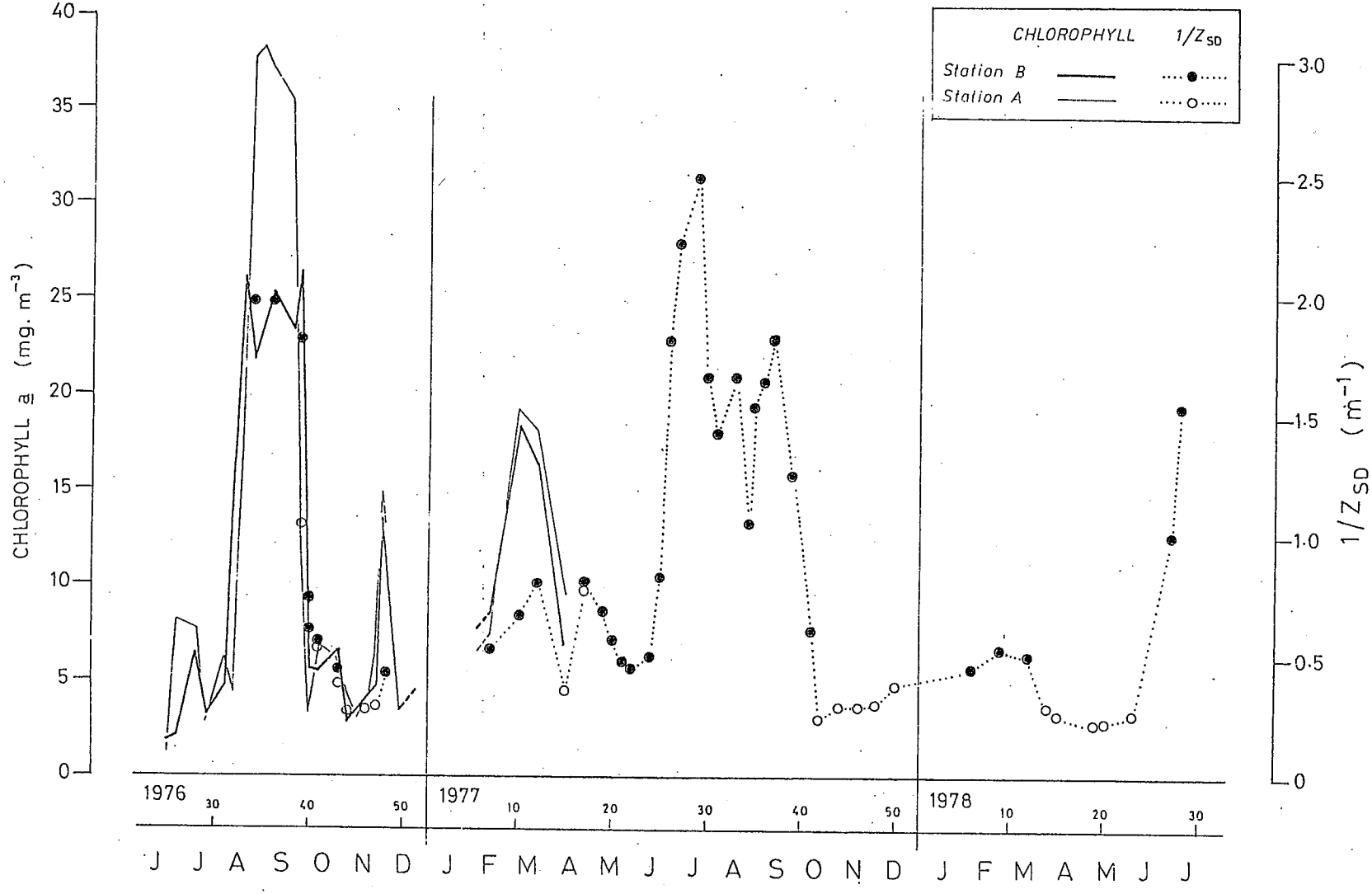
(ii) Phytoplankton

Peaks of biomass were detected by chlorophyll a analyses during 1976 and were found also to be reflected in Secchi disc readings which were continued over a longer period. Since the theoretical correlation between Secchi disc depth (Z_{SD}) and the concentration of light-scattering particles is of an inverse type (see p. 37), a plot of $1/Z_{SD}$ will show biomass peaks in a similar manner to those resulting from estimations of chlorophyll a, and the two types of data have been combined in Fig. 13 to show the seasonal distribution of biomass throughout the study period.

Fig. 13 shows the biomass peaks found by sampling at each station. In the present context the Station B values will be considered as representative of the open, moderately shallow water which makes up most of the main basin and which is the source of the net-tow samples; however, it is necessary to refer to Station A for deep-water readings of Z_{SD} in times of very low biomass.

Peak values each year occur in late summer (July - September) and in winter/spring (December - March), the latter peaks being rather lower than those of the summer. The intervening periods, centred on May and November, are typically low in phytoplankton, although a later spring peak occurred in May 1977. During the late summer peak in 1976, values of chlorophyll a reached 21.8 - 26.3 mg m^{-3} at Station B, and 35.3 - 38.0 mg m^{-3} at Station A; over the winter/spring peak in 1976/7, values at both stations reached 13.3 - 19.2 mg m^{-3} on occasions between December and March. During the late summer peaks of biomass, Z_{SD} readings in the range 0.55 - 0.4 m were obtained which may be compared with readings of 4.6 (+) - 3.0 m in periods without significant peaks (chlorophyll a below 5 mg m^{-3}).

Fig. 13. Variation in biomass over the study period.



The winter/spring peaks were reflected by decreases in transparency, Z_{SD} values of 2.25 - 1.3 m being recorded, but this decrease was less marked than that accompanying the late summer peaks.

Forty-two species of algae were identified in the net-tow collections using light microscopy; these are listed in Table 4, together with their constancy ratings (see p.25). The majority of these species are illustrated by light micrographs in Figs 14 - 58. The purpose of these illustrations is threefold: to show the range of size and form of the species represented in the plankton; to provide evidence of identity in cases of the more "critical" taxa; and to provide a sound basis for any taxonomic amendments as may become necessary at a future date. Other species, which were identified on the basis of electron-microscopic characters, are considered in Section 4. The succession of dominant species is described below and will be related to the peaks of biomass already recorded.

In spring, the diatom Asterionella formosa predominates, increasing its numbers throughout February from a relatively low mid-winter stock and producing its maximum populations in February/March (weeks 12b, 9c). As Asterionella declines in April and May, other algae may increase although the overall biomass may now be decreasing: Fragilaria capucina produced small populations in 1976 and 1978 but failed to develop in 1977; Dinobryon divergens was prominent in March 1977 and April 1978. In 1976 (28a) a brief development of Melosira italica subsp. subarctica followed that of Fragilaria.

Early summer, i.e. May/June, is still a period of comparatively low biomass and is occupied by development of further populations of chrysophytes (Dinobryon or Uroglena americana) and/or green algae (Volvox aureus, Eudorina elegans, Staurastrum cingulum, Pediastrum duplex and other species) in varying combinations in different years. Green algae were most prominent in 1976, but in 1977 and 1978 were subordinate to the chrysophytes.

Blue-green algae rapidly became dominant in late June, 1976 and 1978 (26a, 27c), while in 1977 they increased more slowly during weeks 19b - 25b. In each case Anabaena solitaria

Table 4. Species recorded in Sawley Dene net collections.

Species	Illustration	Constancy rating (see p. 25)
DIATOMS		
Asterionella formosa Hass.	Figs 14, 15	B
Fragilaria capucina Desm.	Figs 16, 17	D
Melosira italica Kutz. subsp. subarctica Mull.	Figs 18, 19	B
CHRYSOPHYTES		
Dinobryon divergens Imhof	Figs 20, 21	C
Mallomonas acaroides Perty var. striatula Asmund	Figs 24, 25	D
Mallomonas akrokomos Pascher ex Ruttner		D
Paraphysomonas vestita (Stokes) De Saedeleer	Fig. 219	E
Synura petersenii Korsh.	Figs 239, 240	E
Uroglena americana Calkins	Figs 22, 23	E
GREEN ALGAE		
Ankistrodesmus falcatus (Corda) Ralfs		E
Asterococcus superbus (Cienk.) Scherff.		D
Chlamydomonas sp(p).		E
Closterium acutum Breb. var. variabile Krieger	Fig. 27	C
Closterium cf. littorale Gay	Fig. 34	D
Coelastrum sp.		E
Dictyosphaerium pulchellum Wood	Fig. 33	E
Elakatothrix gelatinosa Wille	Fig. 31	D
Eudorina elegans Ehrenb.	Fig. 28	A
Pandorina morum Bory	Fig. 29	A
Pediastrum duplex Meyen	Fig. 32	E
Scenedesmus arcuatus Lemm.	Fig. 26	D
Staurastrum cf. cingulum (W. & G.S. West) G.M. Smith	Fig. 35	C
Volvox aureus Ehrenb.	Fig. 30	D
DINOFLAGELLATES		
Ceratium hirundinella O.F. Mull.	Fig. 36	C
Gymnodinium sp(p).		D
Peridinium cinctum Ehrenb.	Figs 260, 261	C
CRYPTOMONADS		
Cryptomonas ovata Ehrenb. (sens. lat.)	Fig. 38	C
Rhodomonas minuta Skuja	Fig. 37	C
EUGLENOIDS		
Euglena cf. velata Klebs	Fig. 41	C
Trachelomonas volvocina Ehrenb.	Fig. 39	A
Trachelomonas sp.	Fig. 40	A
BLUE-GREEN ALGAE		
Anabaena flos-aquae Breb. ex Born. et Flah.	Figs 44, 45	C
Anabaena solitaria Klebs	Figs 42, 43	C
Anabaena spiroides Klebs	Figs 46, 47	C
Aphanizomenon flos-aquae Ralfs ex Born. et Flah.	Figs 50, 51	B
Coelosphaerium naegelianum (Unger) Lemm.	Fig. 49	C
Gloeotrichia echinulata J.E. Smith	Figs 54, 55	D
Microcystis aeruginosa Kutz. emend. Elenk.	Fig. 48	B
Oscillatoria agardhii Gomont	Figs 52, 53	C
HELIOZOANS		
Acanthocystis erinaceoides Peters. et Hans.	Fig. 58	E
Acanthocystis turfacea Carter	Figs 56, 57	E
Raphidocystis tubifera Penard	Figs 286 - 294	D

FIGS 14 - 31 Light micrographs of living and fixed phytoplankton organisms from Sawley Dene, I.

Figs 14 - 19: diatoms
Figs 20 - 25: chrysophytes
Figs 26 - 31: green algae

Illumination systems on microscope: anoptral contrast (AC), bright field (BF), dark ground (DG) or phase contrast (PC).

Fig. 14: Asterionella formosa (two colonies) x 100 AC.

Fig. 15: Asterionella formosa (portion of colony), x 1,000 AC.

Fig. 16: Fragilaria capucina (filament), x 250 DG.

Fig. 17: Fragilaria capucina (portion of filament), 1,000 AC.

Fig. 18: Melosira italica subsp. subarctica (filament), x 250 BF.

Fig. 19: Melosira italica subsp. subartica (portion of filament), x 1,000 AC.

Fig. 20: Dinobryon divergens (colony), x 250 AC.

Fig. 21: Dinobryon divergens (cell), x 1,000 AC.

Fig. 22: Uroglena americana (colony), x 250 AC.

Fig. 23: Uroglena americana (portion of colony, flattened), x 1,000 AC.

Fig. 24: Mallomonas acaroides var. striatula (cell), x 500 AC.

Fig. 25: Mallomonas acaroides var. striatula (detached scales), x 1,000 AC.

Fig. 26: Scenedesmus arcuatus (coenobium), x 500 AC.

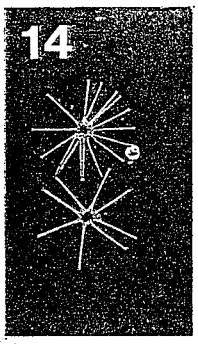
Fig. 27: Closterium acutum var. variabile (cell), x 500 AC.

Fig. 28: Eudorina elegans aff. (colony, flattened), x 500 AC.

Fig. 29: Pandorina morum (colony), x 500 AC.

Fig. 30: Volvox aureus (colony), x 250 DG.

Fig. 31: Elakatothrix gelatinosa (colony), x 500 AC.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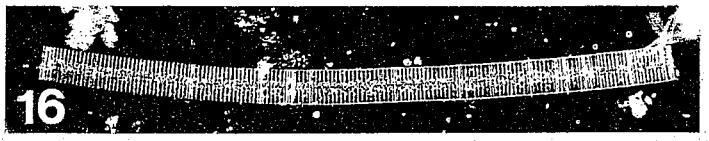
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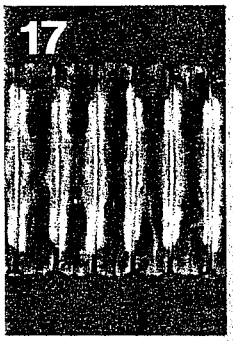
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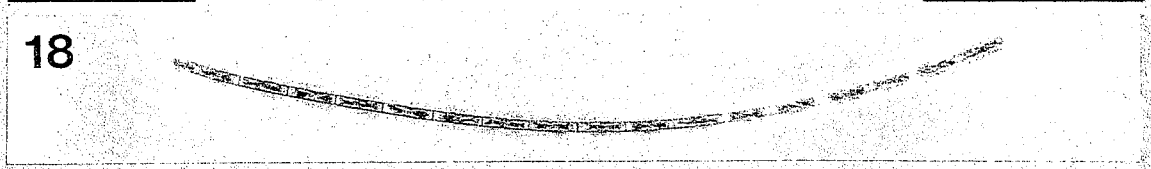
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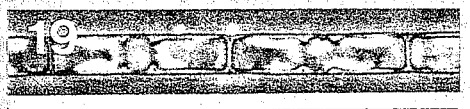
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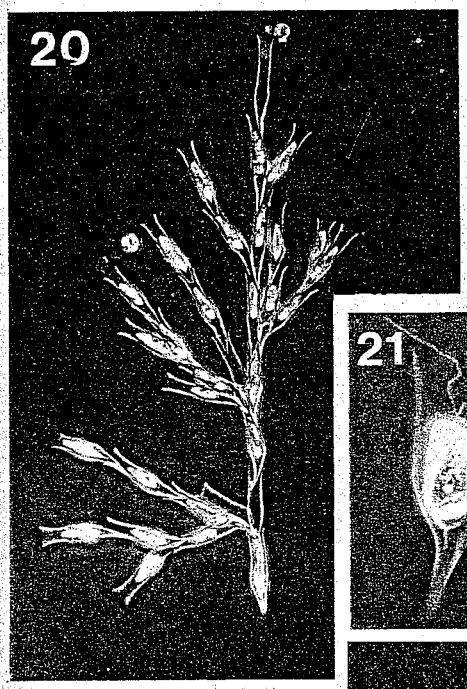
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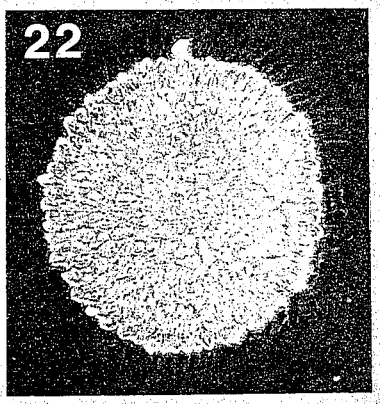
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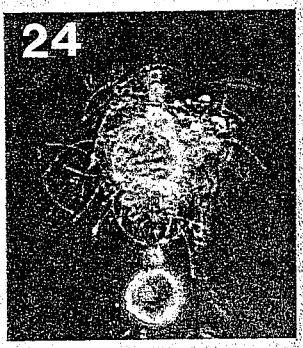
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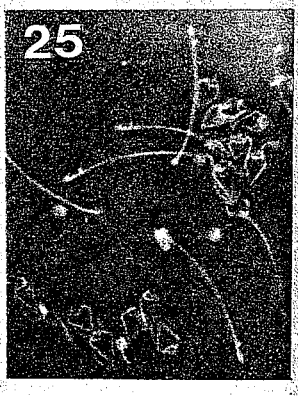
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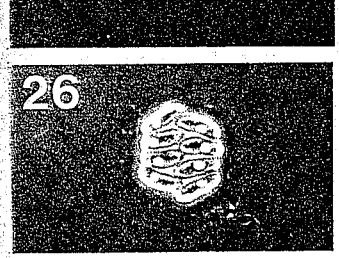
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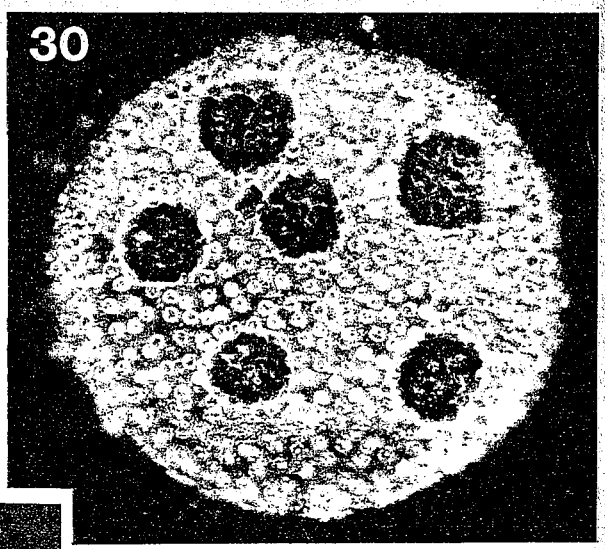
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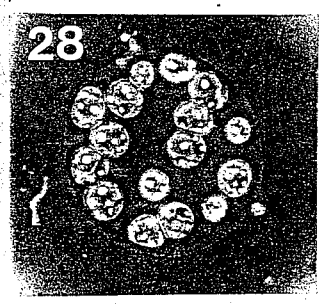
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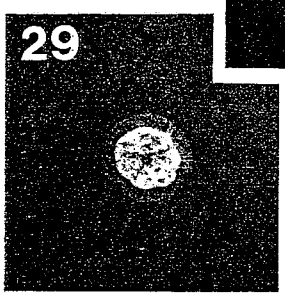
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FIGS 32 - 47 Light micrographs of living and fixed phytoplankton organisms from Sawley Dene, II.

Figs 32 - 35: green algae
Fig. 36: dinoflagellates
Figs 37 - 38: cryptomonads
Figs 39 - 41: euglenoids
Figs 42 - 47: blue-green algae

Illumination systems abbreviated as in legend to Figs 14 - 31.

Fig. 32: Pediastrum duplex (coenobium), x 500 AC

Fig. 33: Dictyosphaerium pulchellum (colony), x 500 AC.

Fig. 34: Closterium littorale (cell), x 500 AC.

Fig. 35: Staurastrum cf. cingulum (cell), x 500 AC.

Fig. 36: Ceratium hirundinella (two cells), x 250 AC.

Fig. 37: Rhodomonas lacustris*(cell), x 1,000 AC.

Fig. 38: Cryptomonas cf. ovata (cell), x 1,000 AC.

Fig. 39: Trachelomonas volvocina (two cells), x 1,000 BF.

Fig. 40: Trachelomonas sp. (cell), x 1,000 BF.

Fig. 41: Euglena cf. velata (cell), x 500 PC.

Fig. 42: Anabaena solitaria (filaments), x 100 DG.

Fig. 43: Anabaena solitaria (portion of filament), x 500 AC.

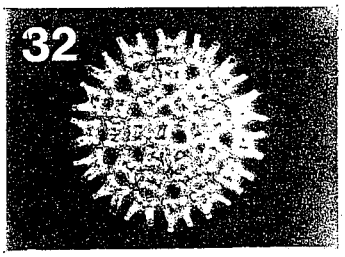
Fig. 44: Anabaena flos-aquae (filament), x 100 AC.

Fig. 45: Anabaena flos-aquae (portion of filament), x 500 AC.

Fig. 46: Anabaena spiroides (filament), x 100 DG.

Fig. 47: Anabaena spiroides (fragment of filament), x 500 AC.

* (= R. minuta in Table 4)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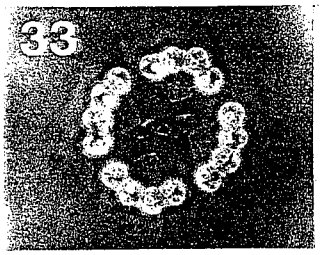
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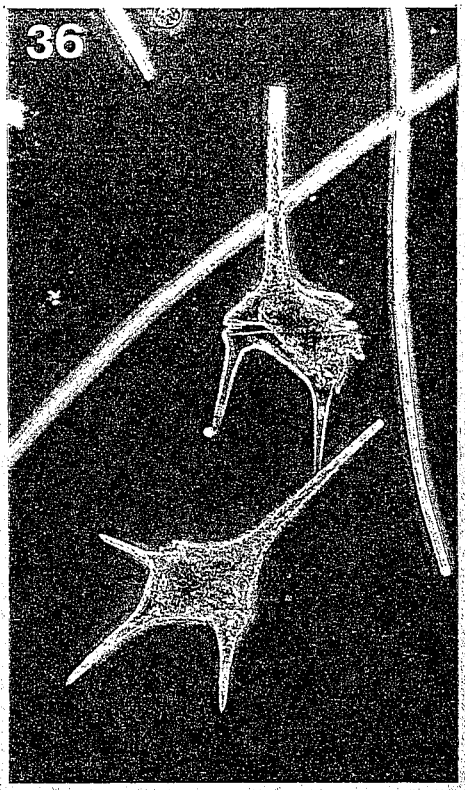
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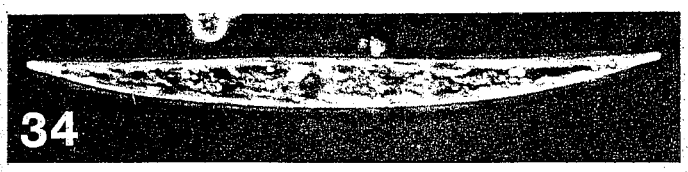
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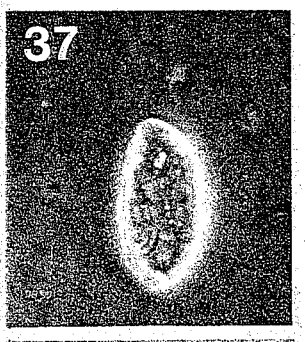
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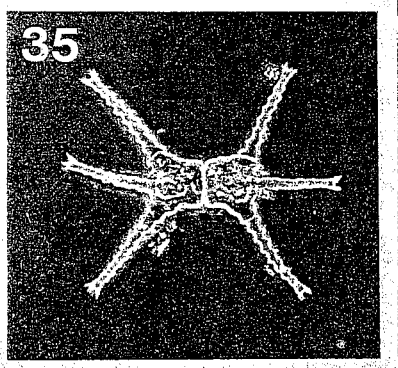
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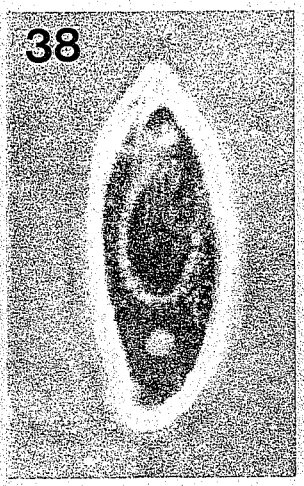
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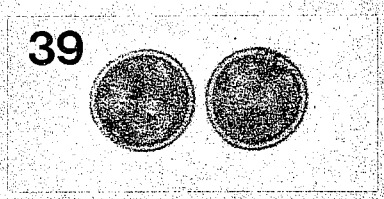
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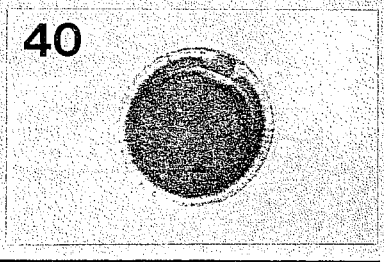
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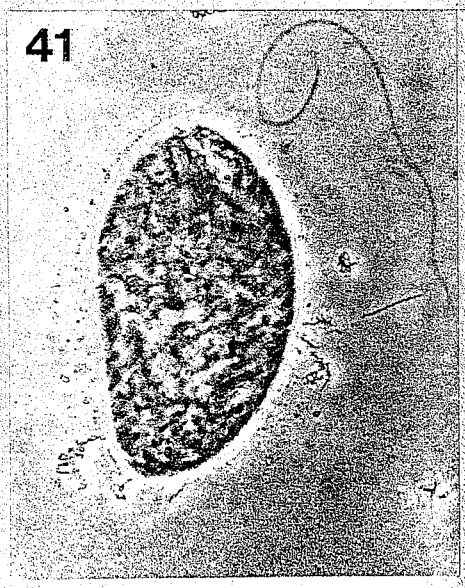
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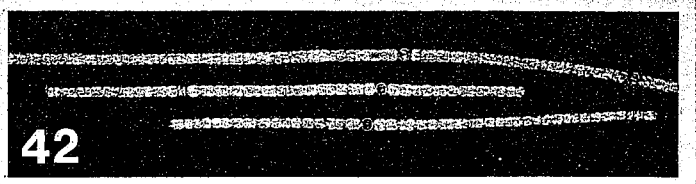
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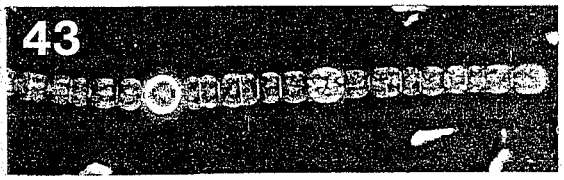
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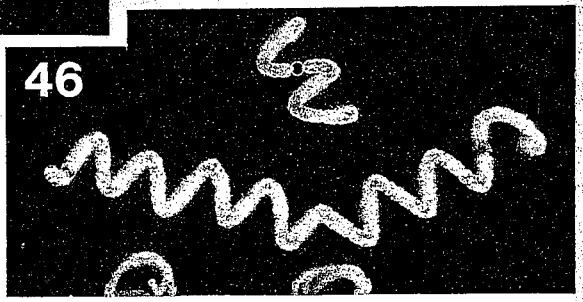
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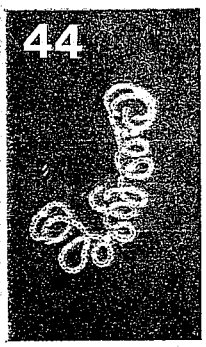
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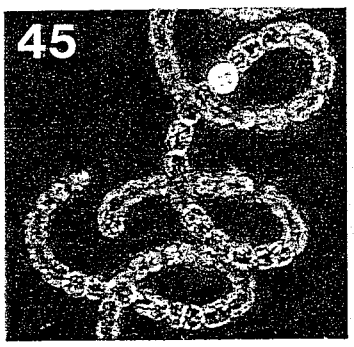
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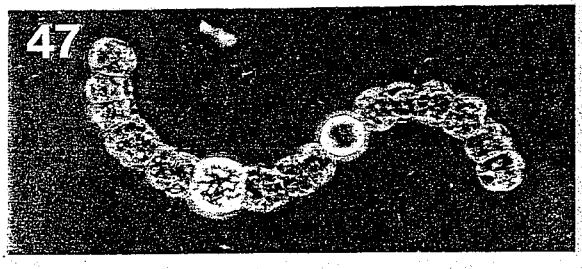
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FIGS 48 - 58 Light micrographs of living and fixed phytoplankton organisms from Sawley Dene, III.

Figs 48 - 55: blue-green algae
Figs 56 - 58: heliozoans

Illumination systems abbreviated as in legend to Figs 14 - 31.

Fig. 48: Microcystis aeruginosa (colony), x 250 AC.

Fig. 49: Coelosphaerium naegelianum (colony), x 500 BF.

Fig. 50: Aphanizomenon flos-aquae (aggregations of filaments), x 100 DG.

Fig. 51: Aphanizomenon flos-aquae (filaments), x 500 AC.

Fig. 52: Oscillatoria agardhii (filaments), x 100 DG.

Fig. 53: Oscillatoria agardhii (detail of filaments), x 500 AC.

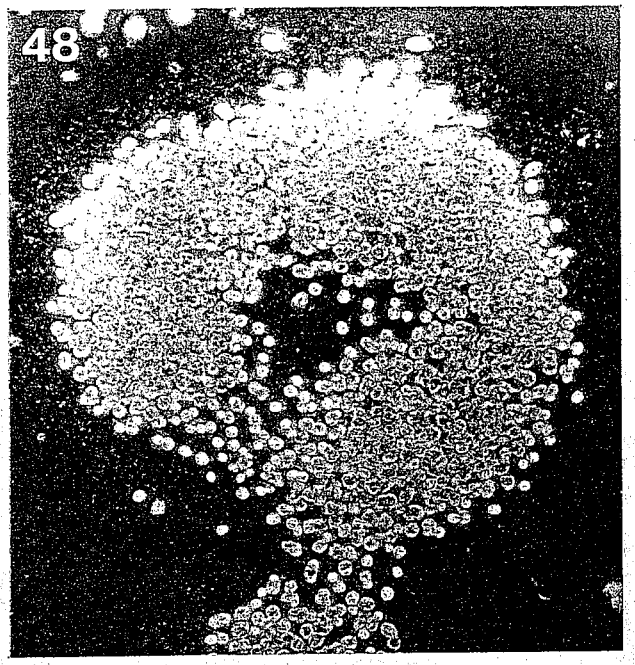
Fig. 54: Gloeotrichia echinulata (colony), x 50 DG.

Fig. 55: Gloeotrichia echinulata (central portion of colony), x 500 AC.

Fig. 56: Acanthocystis turfacea (cell), x 100 DG.

Fig. 57: Acanthocystis turfacea (detail of spines), x 1,000 AC.

Fig. 58: Acanthocystis erinaceoides (cell, flattened), x 500 AC; note detached spines (arrows).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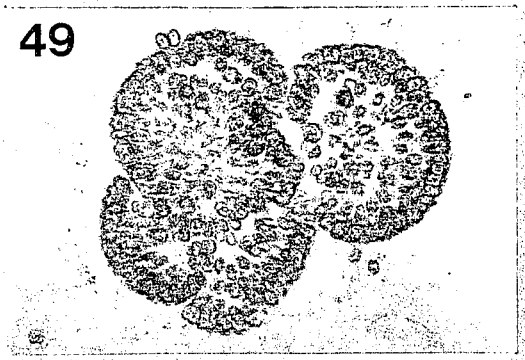
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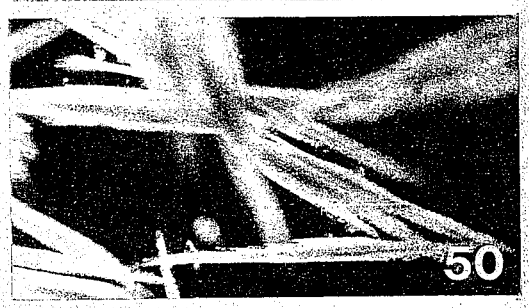
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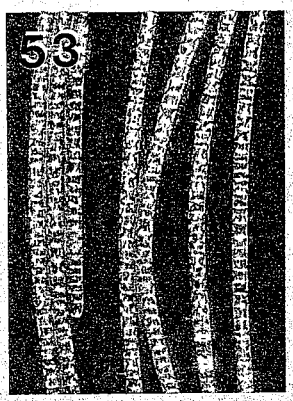
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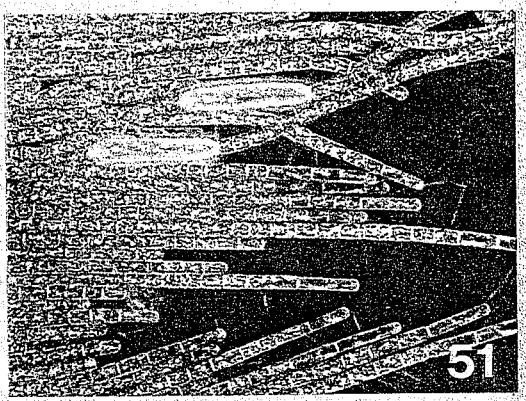
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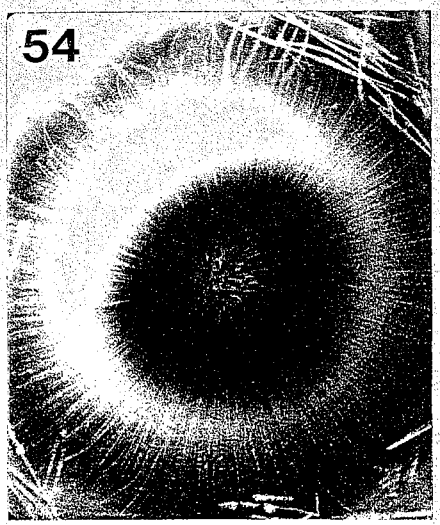
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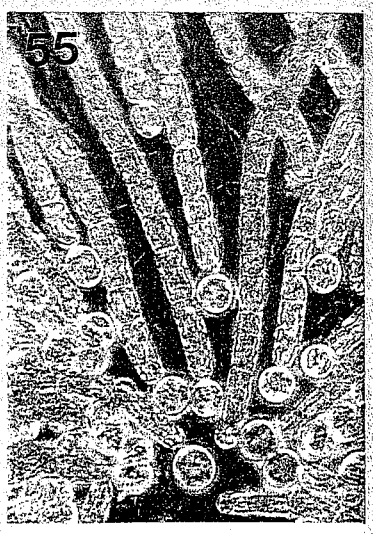
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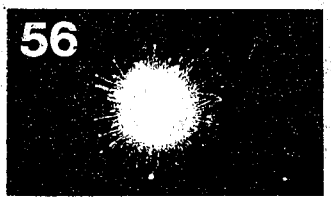
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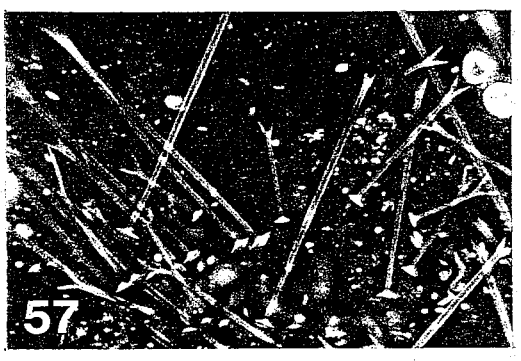
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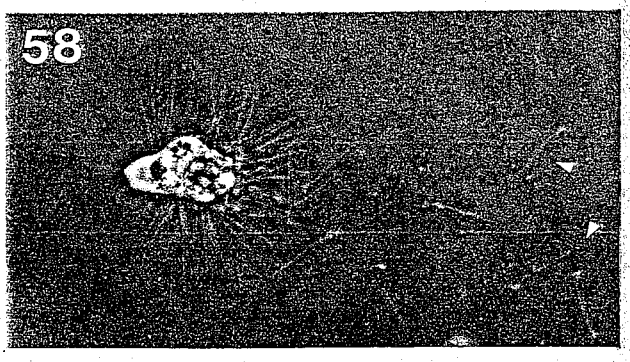

58

predominated at first, although in 1977 it was later superseded by Aphanizomenon flos-aquae and Oscillatoria agardhii. In 1976 A. solitaria remained dominant over the whole season (28a - 39a), other blue-green algae producing subsidiary peaks within this period, viz. Gloeotrichia echinulata (30a - 32a) and Aphanizomenon (40a onwards); smaller amounts of Microcystis aeruginosa, Coelosphaerium naegelianum and other Anabaena spp. were also present during the main peak period.

Significant contributions to the peak summer biomass in 1976 were provided by the large dinoflagellates Ceratium hirundinella and Peridinium cinctum, which never produced comparable populations again during the study period. After the main peak period was over, Aphanizomenon persisted in the plankton longer than the other blue-green algae, occurring through to 52a where it was found under ice cover.

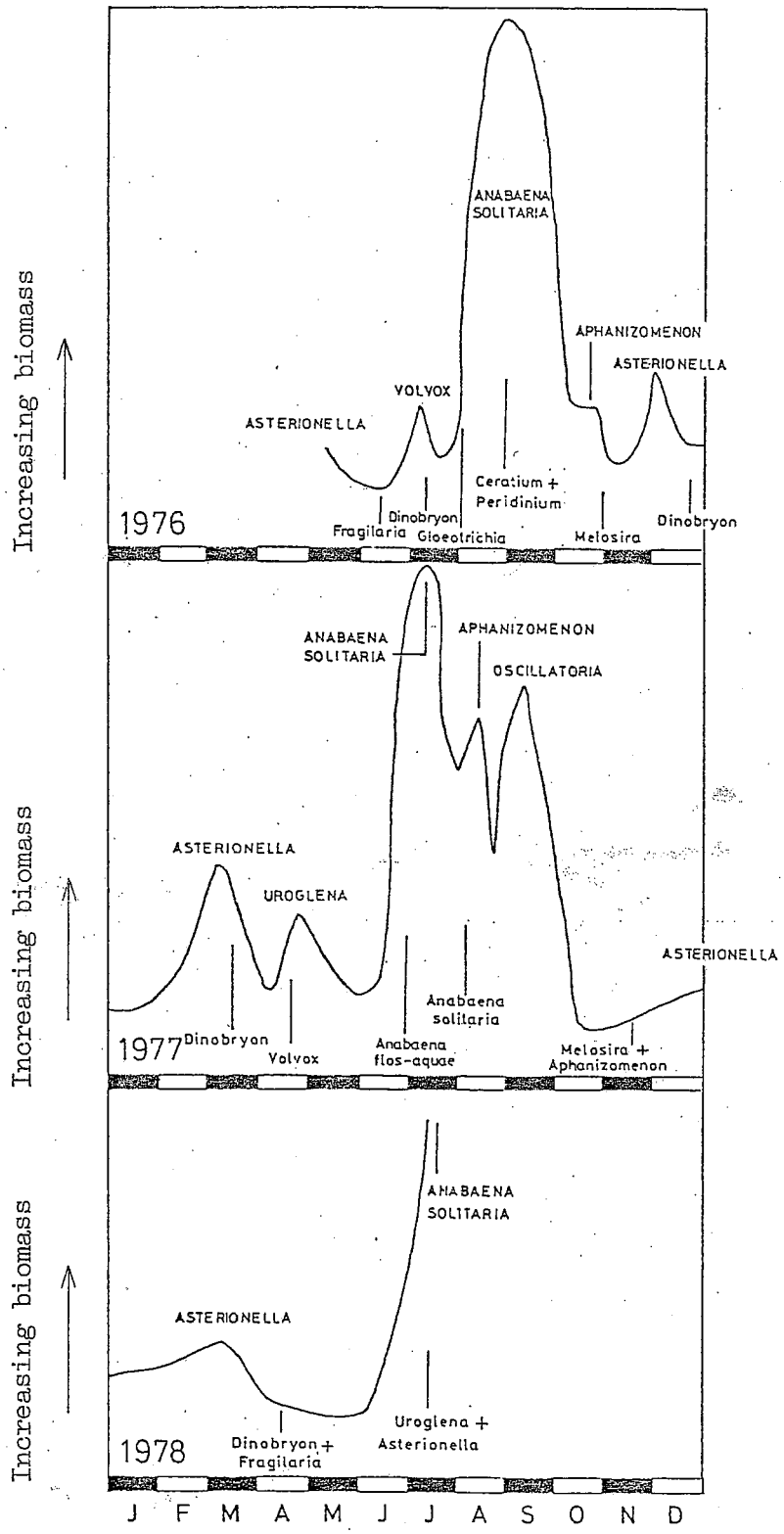
A. solitaria reached similar levels in 1977 to those of the previous year but other species of blue-greens produced larger peaks, Aphanizomenon becoming a co-dominant at about 31b, and Oscillatoria succeeding as dominant for 36b - 41b. The other blue-green species became scarce over this final period but Aphanizomenon persisted in the plankton into December as in the previous year.

Only the beginning of the 1978 summer peak fell within the study period, but this was again found to be dominated by A. solitaria.

The thin autumn plankton characteristically comprised persistent aggregations of Aphanizomenon together with the diatom Melosira italica subsp. subarctica, which tended to become more prominent about October. Trachelomonas volvocina, present all year round, was also fairly numerous at this time of year; in 1976, Mallomonas spp. (chiefly M. acaroides) and cryptomonads were also present. Asterionella reappeared in late October (43a, 44b) to produce an initial peak in November/December before a temporary mid-winter decline, usually associated with periods of ice cover. Dinobryon and Eudorina were present in winter 1976/7 but were largely absent in the succeeding winter.

Various "minor" species, notably a Euglena sp. and small Chlorococcales, appeared sporadically in the plankton

Fig. 59. Annotated annual biomass curves (diagrammatic, re-drawn from Fig. 13).



but were not regularly associated with any seasonal communities. Planktonic heliozoans (Raphidocystis and Acanthocystis spp.) were found in the summer of 1976 but were rarely seen thereafter.

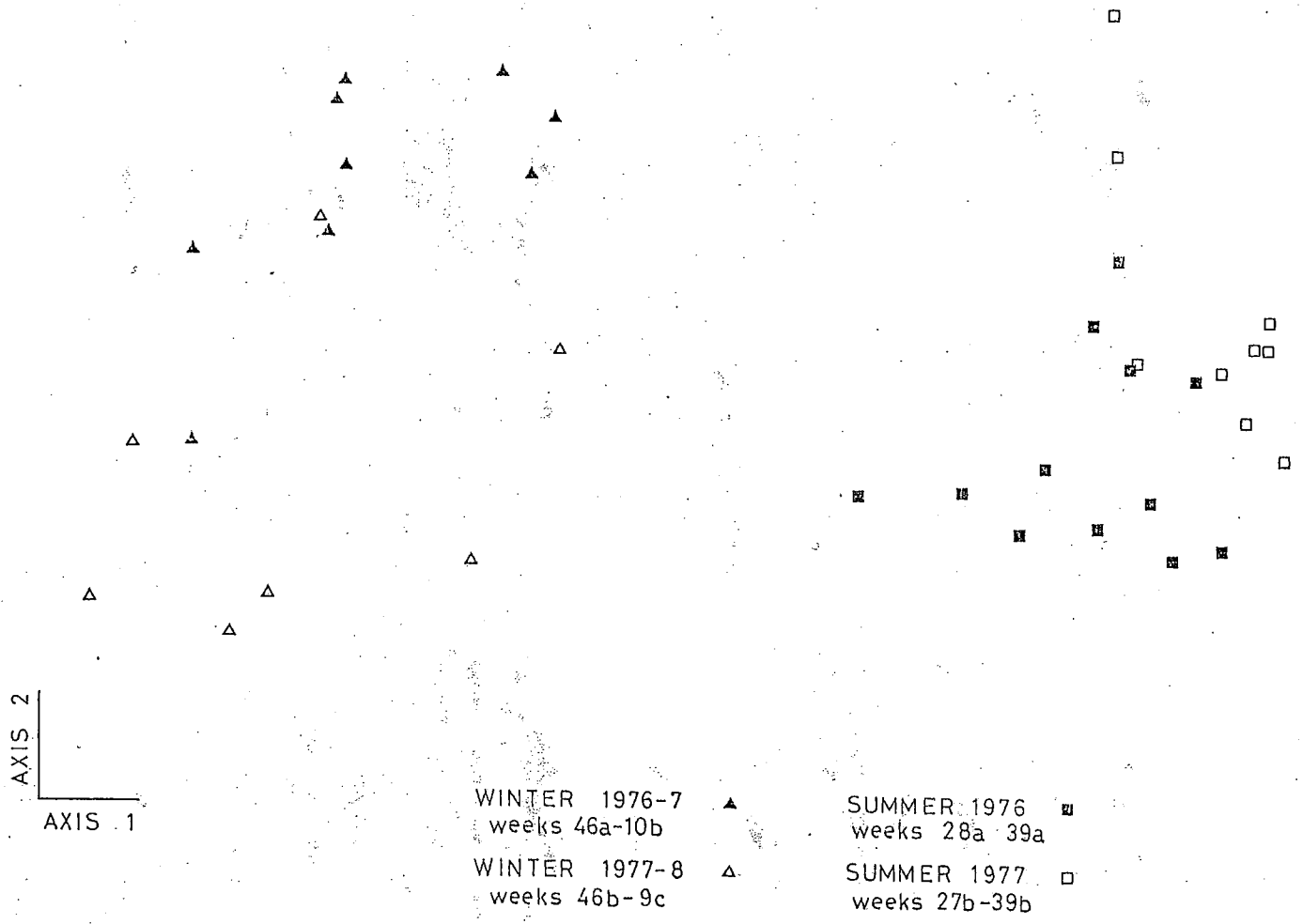
The actual net-tow records for each species are included in Section 3 where they will be discussed in more detail but certain features have been summarised in the form of a table (Appendix II) and an annotated diagram (Fig. 59), where the individual peaks seen in Fig. 13 are re-drawn and are identified according to their major constituents. Also included in this figure are the positions of seasonal maxima for species which formed important subsidiary components of the plankton but which did not contribute so strongly to the biomass peaks recorded.

(iii) Statistical Analysis

Sixty-five samples (individual net collections taken between June 1976 and July 1978) were used for the ordination, each sample providing details of the abundance, on that date, of the eighteen selected species (see p. 27). Reference sets were selected as described in Appendix III, these being samples 9b and 35b for the X-axis, and samples 28c and 43a for the Y-axis. Each of these two pairs of samples possesses a very low degree of similarity (C= 0.16 and 0.29, respectively), and they represent independent axes of variation within the data. An X- and a Y- co-ordinate could then be calculated for each sample, after comparison with the reference sets, and these were used to produce a graphical plot of the samples which, for convenience, is presented in several parts.

The first of these graphs (Fig. 60) shows the distribution of summer and winter samples during the two field seasons. Autumn and spring assemblages are omitted from this plot for purposes of clarity. The lengths of the two periods under comparison were chosen to include the main areas of stability found in the complete ordination (see below). From this graph it may be seen that, while the two years' samples return to the same general area of the plot in corresponding seasons, the sample groupings are basically distinct in the two years. With the exception

Fig. 60. Ordination of winter and summer samples, 1976 - 1978.



of the samples for winter 1977/8, the points are closely grouped which indicates stable communities without rapid rates of change.

If a chronological axis is now inserted it becomes possible to follow the changing structure of the phytoplankton community through each year; this is presented on two graphs, Figs 61 and 62. Each area of the graph corresponds to a community of a distinct type and the trace moves through these areas at a variable rate of change, suggested by the variation in distance between successive points on the plot. Because it is not possible to represent more than two independent axes of variation on a two-dimensional plot, some unrelated communities may be ordinated to a similar area of the graph although they may be separated by an unseen dimension; such superimposition can normally be detected by inspection and checked by calculation of a C-value between representatives of each community. An example of this superimposition occurs in each graph but does not complicate the interpretation unduly.

In Fig. 61 the chronological axis follows an anticlockwise path between certain periods of relative stability, within which are seen small-scale deviations or cyclic phenomena independent of the overall anticlockwise trend. The summer period of stability comprises 28a - 40a and contains small deviations centred on 29a/30a and 33a/34a. After 40a a period of rapid transition commences until by 45a the trace has entered the winter region of the plot, where it remains up to 15b although a deviation is seen during 9b - 12b. The spring transition period extends from 15b to 22b and incorporates a rapid rate of change as the community trace visits new areas of the plot before approaching the summer region again. It is noticeable that 21b/22b fit well in the basically circular pattern, while 25a the previous year occupies a different position, almost superimposed on 41a (without a high degree of similarity: C= 0.44). 25a in fact fits better with the alternative spring pattern seen in the plot for the 1978 samples, below.

Weeks 22b - 30c are shown ordinated on Fig. 62, which at first sight contrasts with the preceding picture.

Fig. 61. Path of community trace, June 1976 - May 1977 (samples identified by week number).

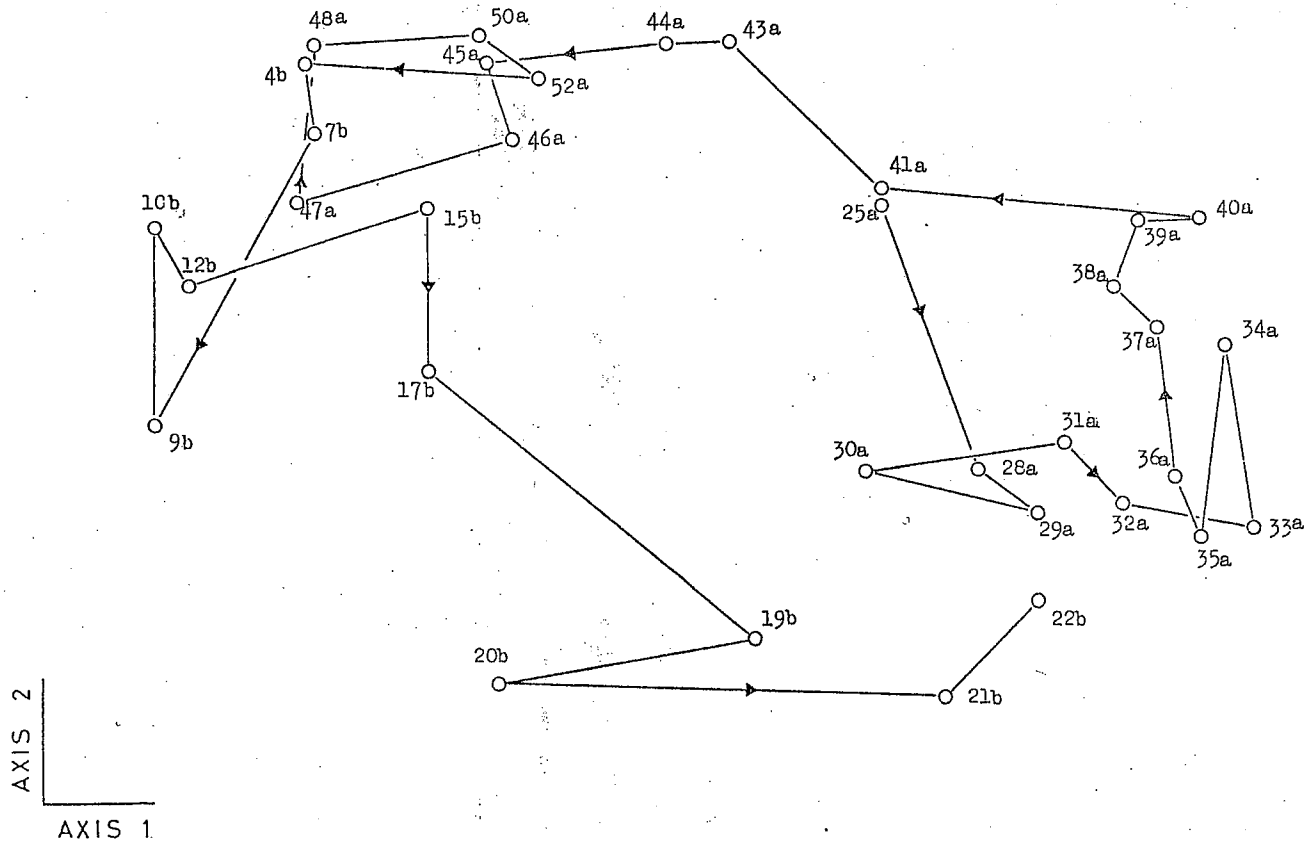
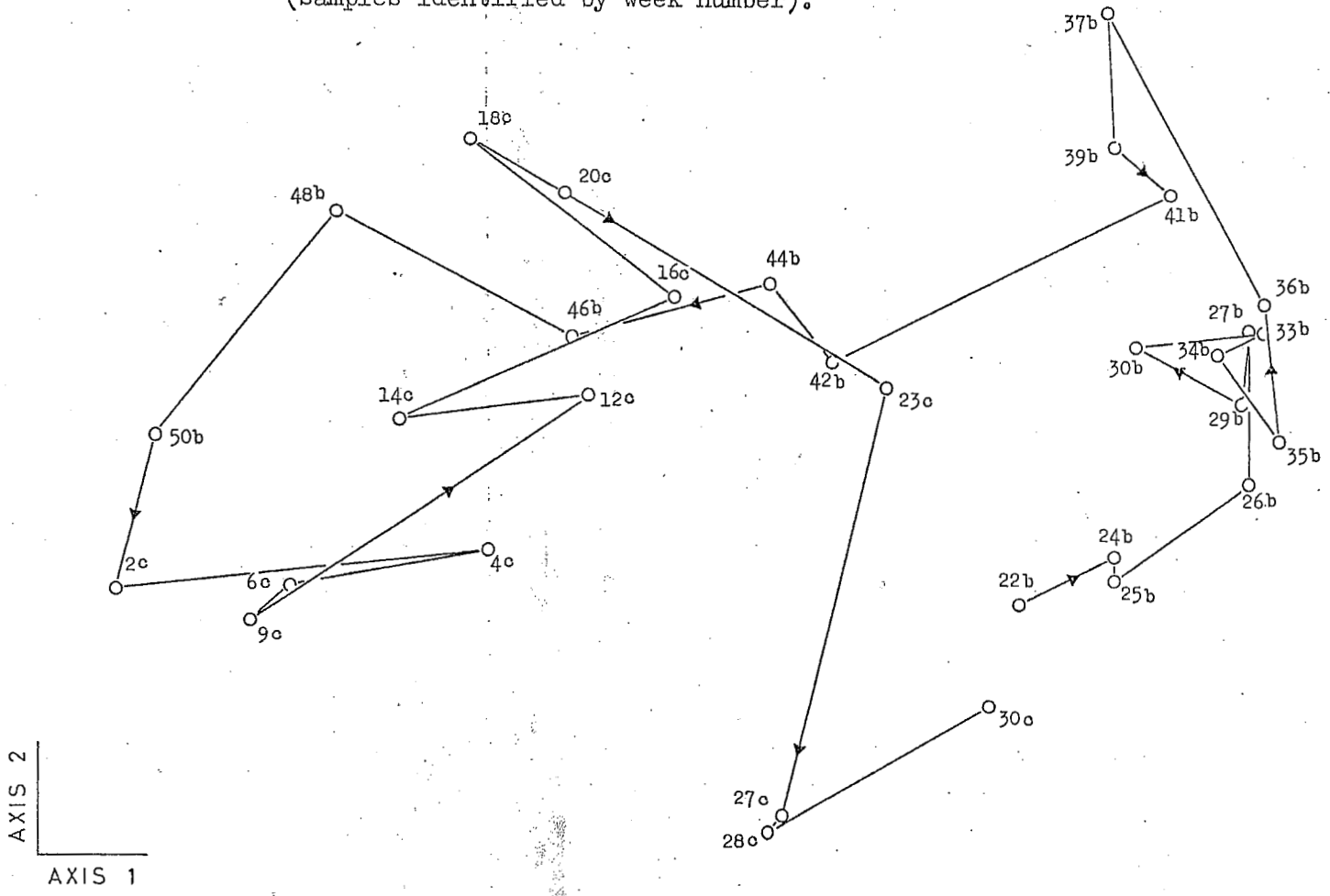


Fig. 62. Path of community trace; May 1977 - July 1978 (samples identified by week number).



This, however, is due to the superimposition of the spring and autumn portions of the trace, although these are not fundamentally similar; for example, between 46b and 16c, C= 0.40, and between 23c and 42b, C= 0.34, both of these being relatively low values. This indicates that an unrepresented dimension separates these two portions of the trace and it is likely that the path is again basically circular although on a plane inclined to that of the trace in Fig. 61.

The most stable portion of this summer period is remarkably homogeneous and lasts from 26b to 36b, after which a rapid change to a new and non-transitional community occurs (37b - 41b). Eventually the typical autumn transition is seen (42b/44b) and the winter community is established, but large excursions occur through the period to 12c which contrast with the behaviour of the previous year. 16c - 23c involve a spring trend of a new type, as explained above, but which may possess similarities with the behaviour in spring 1976, represented only by 25a on the previous plot (Fig. 61). However, a rapid change then occurs until by 27c/28c the trace is more similar to its position during 19b - 21b the previous spring, and by 30c the trace is approaching the summer communities once more.

In order to assist interpretation of these traces in the Discussion, portions of the plots have been correlated with the most important species predominating at different times of the year (see Fig.59 and Appendix II). These annotated plots are presented as Figs.63 and 64 corresponding to Figs 61 and 62, respectively.

Discussion

Certain features of the data on temperature and dissolved oxygen are of relevance to the present Section, while others will be considered in Section 3. For the purpose of characterising the lake and for investigating its annual variability, the most significant features are (i) the annual temperature regime of the surface water; (ii) the extent of summer stratification, as reflected by temperature and dissolved oxygen measurements;

Fig. 63. Annotated community trace, 1976 - 7
(see Fig. 61 for details).

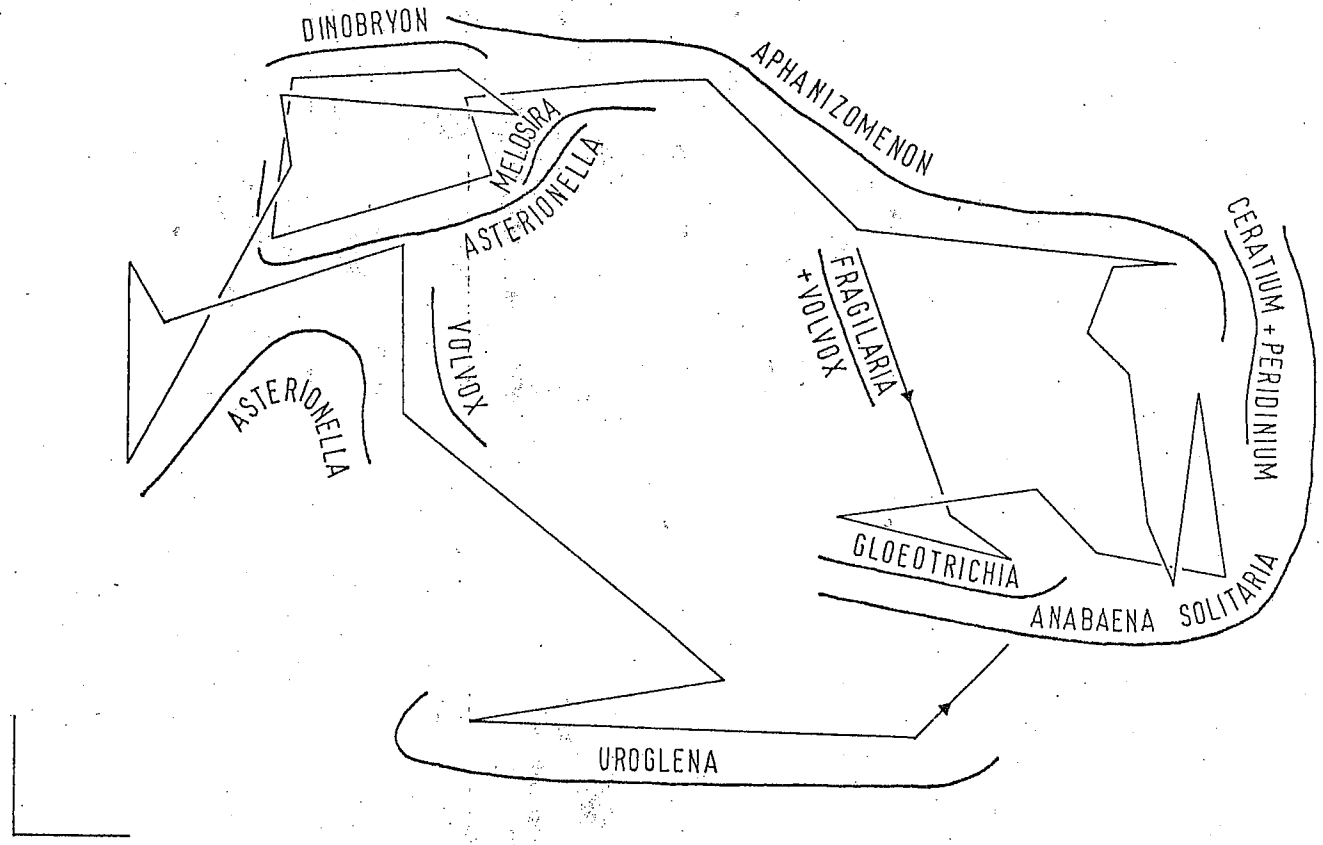
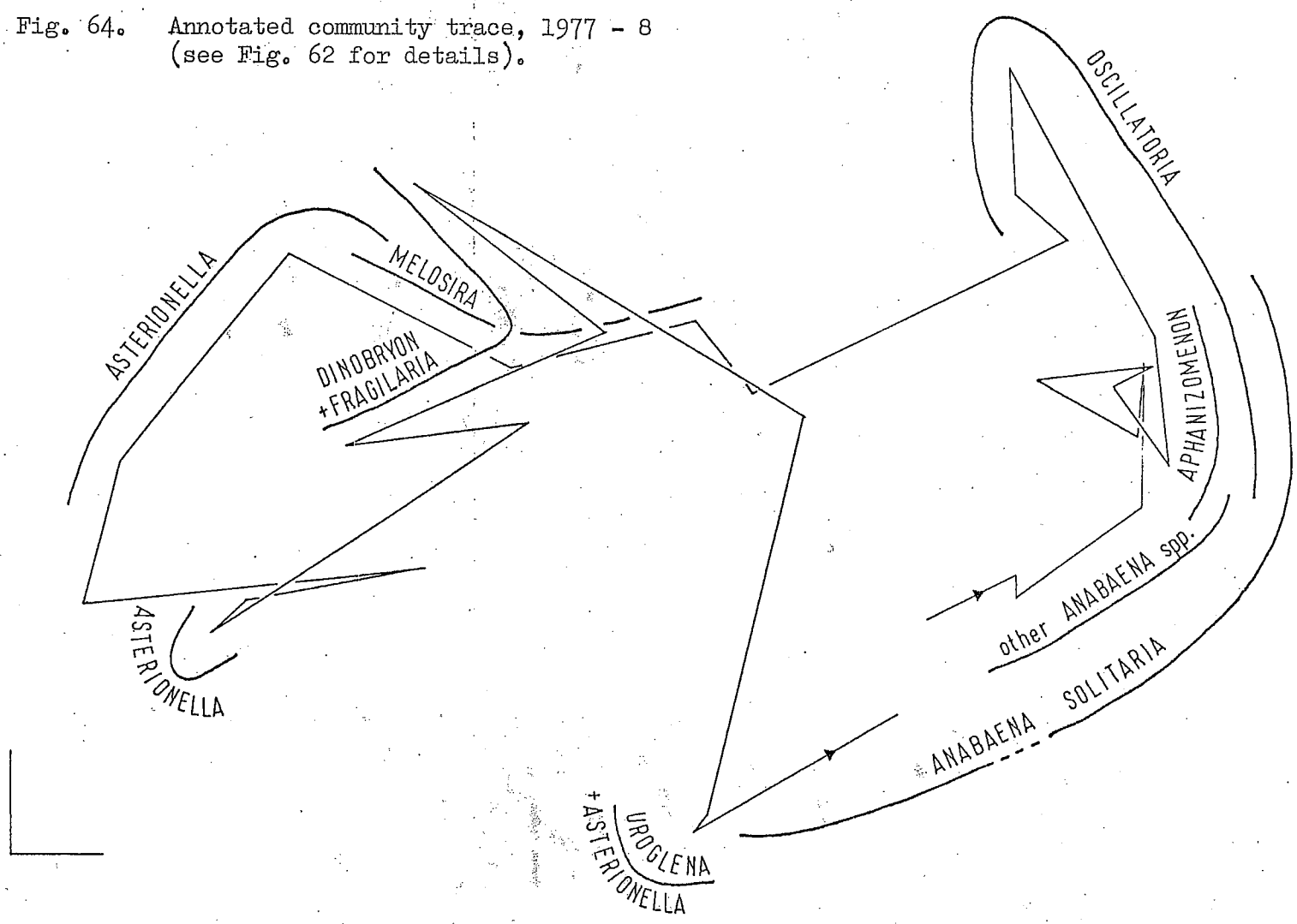


Fig. 64. Annotated community trace, 1977 - 8
(see Fig. 62 for details).



(iii) the relation between water temperature and general climatic patterns in specific years; and (iv) possible variations in temperature between the two sampling stations, in comparison with any observed differences in their phytoplankton.

The seasonal variation in temperature found in the surface water of Sawley Dene is unexceptional and does not point to an unduly exposed or sheltered situation. Its phytoplankton, therefore, might be expected to be qualitatively similar to that of many other lowland bodies of water in the British Isles of comparable nutrient status and size. Complete ice cover occurred in each winter of the study period and this would undoubtedly influence the growth and suspension of planktonic algae, in contrast to the situation in deeper lakes where ice cover is less regular or complete. The fact that persistent summer stratification was absent even in 1976, which was an exceptionally hot and dry year, suggests that the lake does not normally stratify, and this separates it from many lakes in Britain which do stratify over the summer and whose periodicity has been studied.

The differences in surface temperature for comparable times in successive years are of similar magnitude to the differences shown in the averages of daily mean air temperature over the region as a whole. It is likely that the temperatures at the time of day when visits were normally made are closer to the mean daily air temperature than to the maximum, although the diurnal fluctuation has not been investigated. From the meteorological data included on Figs 8 - 10 some noteworthy features of each year can be seen; the first eight months of 1976 were the culmination of the driest sixteen-month period on record, while September and October that year were exceptionally wet. The summer of 1976 was considerably hotter than average and that of 1977 was a little cooler. Other features of these data will be considered where appropriate later.

Differences in the maximum biomass measured at the two stations, together with other differences which will be described in Section 3, seem unlikely to be due to any difference in exposure as reflected in surface temperature,

since Fig.11 suggests that no systematic difference is detectable and that a slight scatter of points occurs only above 20°C. It will therefore be necessary to attempt to relate any algal differences found to other factors, e.g. the depth of water at each station and/or the proximity of Station A to the outflow.

The results of the phytoplankton investigations presented so far allow certain conclusions to be drawn concerning the trophic status of Sawley Dene. The lake may be said to be eutrophic on the following grounds: (i) it supports high levels of algal standing crop at certain times of the year; (ii) it displays the characteristic shift in dominance between diatoms in winter/spring and blue-green algae in late summer; and (iii) the species predominating are typical of eutrophic conditions, while species with strictly oligotrophic tendencies are absent. The degree to which each of these characteristics is developed may be seen by comparison with other eutrophic lakes.

High levels of standing crop are typical of productive situations where removal through predation or outwash is not excessive; straightforward correlations between productivity and maximum standing crop have been demonstrated by Brylinsky & Mann (1973) and Schindler (1978), and thus productive (i.e. eutrophic) lakes can be demarcated when maximum standing crop exceeds a specific level. Vollenweider (1968) suggests that the boundary between mesotrophic and eutrophic conditions occurs when maximum biomass levels of 3-5 $cm^3\ m^{-3}$ are reached, which would correspond to chlorophyll *a* concentrations of ca. 12-20 mg m^{-3} using the approximate relationship found by Lund (in Ridley, 1970). On this basis, the Lake District lakes, for example, range from Wastwater, which with a maximum chlorophyll *a* level of 1.25 mg m^{-3} is clearly oligotrophic, to Blelham Tarn and Esthwaite Water, where epilimnetic chlorophyll *a* levels may exceed 100 mg m^{-3}, well into the eutrophic range (Jones, 1972). Sawley Dene shows a maximum chlorophyll *a* level of 38 mg m^{-3} and on this basis may be classed as eutrophic, although less so than some of the other productive lakes investigated in this country (see Wilson *et al.*, 1975; Phillips, 1977).

Secchi disc transparency (Z_{SD}) readings are inversely proportional to the turbidity of the water (Tyler, 1968)* and, particularly within 5 - 7 m of the surface, this is primarily dependent upon phytoplankton density (Vollenweider, 1960, in Vollenweider, 1968). Thus clear inverse correlations between Z_{SD} and chlorophyll *a* levels can be found (Carlson, 1977), although exact correspondence is not to be expected since different forms of algae may attenuate light to different degrees and the chlorophyll *a* content of cells can vary (Eppley, 1968). Nevertheless, from the data of Carlson (*loc. cit.*), Z_{SD} levels of 1 m or less are normally associated with chlorophyll *a* values in excess of 15 mg m^{-3} and therefore probably with a eutrophic condition as suggested above. Analysis of preliminary data from Sawley Dene suggests that Z_{SD} readings of less than 1 m correspond with chlorophyll *a* values of over 13 mg m^{-3} when blue-green algae are dominant and probably at least twice this figure during maxima of *Asterionella*.

Eutrophic waters of sufficient size to be termed lakes characteristically show biomass peaks in spring and late summer (Round, 1971), dominated by diatoms and blue-green algae respectively. Sometimes *Ceratium* may be dominant with, or effectively replace, the blue-green algae (Reynolds, 1978). The two community types, which are to some extent mutually exclusive, comprise the "eutrophic diatom" and the "myxophycean" plankton types in the scheme of Hutchinson (1967). Blue-green algae (or *Ceratium*) appear to retain their ecological advantage only as far as the effects of nutrient limitation are still significant in late summer; in yet more highly eutrophic situations, or in smaller water-bodies where rates of nutrient supply per unit volume of water may be higher, green algae (especially Chlorococcales) may predominate (Reynolds, 1973a; Stoermer, 1978). Blue-green algae and *Ceratium* are markedly less abundant in waters which are not eutrophic, whereas the diatoms forming the spring peak, often with a related peak in late autumn, may still produce significant populations in less productive lakes

* TYLER, J. (1968). The Secchi Disc. Limnol. Oceanogr. 13: 1-6.

(Pearsall & Pearsall, 1925). The relative importance (as biomass) of diatom and blue-green algal peaks therefore tends to alter as a range of trophic types is traversed and thus forms an approximate index of trophic status.

In Sawley Dene, the spring diatom peaks in 1977 and 1978 were of variable intensity but were always exceeded by the late summer blue-green peaks, as recorded by chlorophyll *a* measurements and/or Z_{SD} readings, even allowing for some possible discrepancy as suggested above. Calculations of algal volumes (see p. 55) provide similar evidence. This situation is found also in the two "eutrophic" Lake District lakes, judging from cell counts of the algae concerned (Lund, 1972a, 1978) and in the most typical of the Shropshire/Cheshire meres (Reynolds, 1976a). By contrast, in the south basin of Lake Windermere, described by Lund (1973) as "neither clearly oligotrophic nor eutrophic", and with a lower maximum epilimnetic chlorophyll *a* value than that of Sawley Dene (Jones, 1972), biomass in the late summer is less than that in the spring (data of Lund, in Macan, 1970), and a similar condition is documented for other less eutrophic waters, e.g. "Stage 3" in the scheme of Stoermer (1978) for the trophic evolution of the Great Lakes. In this respect, therefore, Sawley Dene behaves like the epilimnion of a typical eutrophic lake of larger size. By comparison, Abbot's Pond, Somerset (Moss & Abdel Karim, 1969; Hickman, 1974) and Chillington Pool, Staffordshire (Irish, 1977) are examples of smaller, eutrophic water-bodies where a regular pattern of a spring diatom peak and a larger, late-summer blue-green peak is not found. Sawley Dene may be just above the threshold of size at which large ponds grade into lakes.

Scattered information upon trophic preferences of certain algae is contained in many publications; Moss (1972) consulted 70 papers for data on only some twenty species. Few papers, however, provide a comprehensive and reliable body of information concerning species of a wide range of trophic types; of these, Round & Brook (1959) and Stoermer (1978) are probably the most valuable. Collation of the results of these authors in respect of those species found during the present investigation

suggests the following groupings on the basis of trophic preference:

(i) Species common only in eutrophic waters, rare or absent elsewhere: Fragilaria capucina, Pediastrum duplex, Staurastrum cingulum*, Volvox aureus, Cryptomonas spp. (C. erosa/C. ovata), Trachelomonas volvocina, Aphanizomenon flos-aquae, Microcystis aeruginosa.

(ii) Species most common in eutrophic waters, but occurring elsewhere to a lesser extent: Melosira italica subsp. subarctica, Ankistrodesmus falcatus, Eudorina elegans, Ceratium hirundinella, Coelosphaerium naegelianum, Oscillatoria agardhii.

(iii) Species most common in oligo- or mesotrophic waters, but found elsewhere to a lesser extent: Dinobryon divergens, Mallomonas alpina, Uroglena americana.

(iv) Species common only in oligotrophic waters: None found.

(v) Species widely distributed, common in waters of varied types: Asterionella formosa, Rhodomonas minuta, Dictyosphaerium pulchellum.

Mesotrophic lakes characteristically possess elements of an oligotrophic flora in coexistence with the more eutrophic species, as may be seen in the full data of Round & Brook (1959) and Stoermer (1978). The absence of such an element from Sawley Dene clearly indicates its affinities with other truly eutrophic lakes.

The eutrophic status of Sawley Dene may be ascribed to the calcareous, moderately ion-rich water deriving from its catchment area (see p. 16) without necessarily implicating any artificial sources of enrichment. The glacial drift on which Sawley Dene is situated continues to the east, where it extends into the Vale of York; it is probable that similar, naturally eutrophic lakes might be found in this area. On the eastern margin of this glacial drift, ca. 28 km north-east of Sawley Dene, the small lake of Gormire was found to possess many eutrophic species during an isolated visit in May (Scott, 1948), among which were Ceratium hirundinella and "Anabaena sp.". However, the water of Gormire may also be influenced by the calcareous grit of Whitestone Cliff below which it stands.

*See also p. 50. Stoermer's (1978) data show a eutrophic preference for this species although Brook (1965) suggests otherwise.

To the west of Sawley, Eavestone Lake (see p. 60) is close to the western limit of the glacial drift and appears to be of similar trophic status to Sawley Dene, (see p. 85) while beyond this is an extensive acidic region of millstone grit, covered in places by a heavily leached "older drift" (Edwards, 1938) which would be ion-poor. Sawley Dene and Eavestone Lake, therefore, are probably the last eutrophic lakes which might be found for a considerable distance to the west; for example, Brim Bray Pond and Lumley Moor Reservoir (Fig. 3) are both acidic in nature. An exception is Malham Tarn, 37 km west of Sawley, which is surrounded by high-level limestone and supports a eutrophic plankton with Asterionella in spring and Anabaena flos-aquae as the dominant blue-green alga (Lund, 1961).

Elsewhere in Britain, eutrophic conditions are associated primarily with fertile lowland regions such as those surrounding the Shropshire/Cheshire Meres (Reynolds, 1973a, 1976a), parts of the Norfolk Broads (Phillips, 1977; Moss, 1977) and various lowland reservoirs (Ridley, 1970; Wilson et al., 1975). In the latter examples, chlorophyll a concentrations regularly exceed 100 mg m^{-3} and winter maximum levels of nitrogen and phosphorus may be very high (see Phillips, 1977).

Two lakes in which the seasonal succession has a strong similarity with that of Sawley Dene are Slapton Ley, Devon (Benson-Evans et al., 1967) which has a mean depth of ca. 1.5 m, and Balgavies Loch, Angus, Scotland (Brook, 1964; Stewart et al., 1977) of mean depth ca. 3 m but with a maximum depth of ca. 10 m. In Slapton Ley the succession is similar to that in Sawley except that the "spring" diatoms (Asterionella, Fragilaria capucina and Tabellaria fenestrata) tend to persist through much of the year. Dinobryon cylindricum appears in place of D. divergens in late spring, and the principal blue-green algae are Microcystis, Anabaena flos-aquae, and Gloeotrichia. Balgavies Loch has the common "spring" diatoms, Dinobryon divergens and a late-summer blue-green peak dominated by Microcystis flos-aquae but also with Aphanizomenon, Coelosphaerium, Anabaena circinalis and other Anabaena spp., and Ceratium. Examples of other

lakes where a single blue-green alga tends to predominate in summer are common, e.g. Microcystis aeruginosa in Rostherne Mere (Reynolds, 1978), Oscillatoria agardhii in some Irish loughs (Round & Brook, 1959), and Aphanizomenon in Esthwaite Water (Lund, 1972a); however, there appears to be no account in the literature of a lake regularly dominated by Anabaena solitaria. The distribution of this alga as a subsidiary component in the plankton of other lakes will be reviewed in Section 3.

Between-year variation in lakes complicates the interpretation of patterns found in any single year, a considerable body of data from other years being required before a "normal" year can be recognised with confidence (Lund, 1964; Round, 1971). The variability of the Sawley Dene phytoplankton is best shown in Fig. 59 and Figs 63 - 64; here it may be seen that winter, mid-summer and autumn patterns are more consistent than those of late spring or late summer. A notable feature is the occurrence or prominence of some species in certain years only, for example Ceratium and Gloeotrichia in 1976, Oscillatoria in 1977, and Uroglena in 1977 and 1978.

From the statistical analysis the most stable summer periods may be seen to be weeks 32a - 36a (1976) and 26b - 36b (1977), during which small-scale deviations are superimposed on the broad cyclic seasonal pattern (Figs 61, 62). These small deviations represent fluctuations in subsidiary elements of the plankton during periods of stable dominance by the major species and would perhaps be represented more accurately if daily observations were available, depending on how far the effects of sampling error could be eliminated. If their precise nature could be established it might then be possible to relate them to small-scale fluctuations in environmental factors, something which is not possible on the present data. However, the effects of diurnal variations would then be more marked and these would have to be taken into account also, complicating the picture considerably (cf. Maulood et al., 1978).

During the two winter periods the main deviations of the trace are found when Asterionella temporarily declines under ice cover leaving a thin plankton of variable composition; as Asterionella resumes its growth the trace returns to the

vicinity of its former position. The renewed growth of Asterionella in early July 1978 (27c/28c) distorts the cycle in Fig. 62. The rapid autumn transition in each year follows a very similar path and is centred on weeks 42 - 44 in each case, but the spring transition shows two distinct patterns differing in their relative proportions of Volvox, Uroglena, Dinobryon and Fragilaria. It is possible that other combinations might also be found in different years.

Since the climatic conditions in 1976 were so unusual, those of 1977 being much closer to the average, it is likely that the individual characteristics seen in the 1976 data are the more exceptional, e.g. the dominance of Anabaena solitaria over the entire blue-green peak, the early peak of Gloeotrichia and the occurrence of Ceratium and Peridinium in quantity. Spring 1977 was notable for a bloom of Uroglena which was not seen the previous year but this alga has been recorded as of sporadic appearance in different years by other authors (see p. 47). The behaviour of Asterionella in 1978 was different from that in the two previous years, forming only a small spring maximum but reappearing with the start of the blue-green algal peak. More years of records would be required before the "normal" periodicity of this alga in Sawley Dene could be established.

Much of the emphasis in studies of long-term variability in phytoplankton patterns (e.g. Lund, 1972a, 1973, 1978) has been on the detection of gradual trends of change against a background of meteorological and biological "noise". It is the nature of the latter which is of the greatest significance for a short-term study but this has received considerably less attention from researchers (Macan, 1970). It has been shown by Lund (1964) that biological factors such as fungal parastism may be important in affecting the seasonal succession in addition to the more obvious meteorological influences and, further, any interaction of such factors may produce repercussions in successive seasons by, for example, affecting pools of nutrients available for subsequent algal growth or by altering the size of "inoculum" populations. While it is clear that observations over two or three field seasons

alone cannot allow many deductions to be made about the causes of the variation observed, they do indicate the nature and extent of the variability which can occur and so suggest how much confidence can be placed in data from a single year.

SECTION 3 PERIODICITY OF THE PRINCIPAL PHYTOPLANKTON ORGANISMS

Introduction

The periodicity of phytoplankton species was followed using inverted-microscope counts over the first year of the study period and net-tow estimations over both years. Both types of records omit very small species and those which may only be identified by the use of electron microscopy (Section 4); in addition, casual species are generally omitted. A small number of non-algal species (planktonic Heliozoa) are included since these could be recognised in the samples and their occurrence is of interest with respect to other aspects of the investigation (Sections 4 and 5).

Materials and Methods

Tube samples from Stations A and B were collected over the period May 1976 - April 1977 as described earlier (Phytoplankton, p. 24). Aliquots of these samples were concentrated if necessary (e.g. by x 15 in periods of very low biomass) and one portion of each sample was placed in a sedimentation chamber (Lund et al., 1958), two drops of Lugol's iodine added and the organisms allowed to settle for a minimum of 3 h. The samples were then examined in a Prior inverted microscope and counted under a x 10 objective, enumerating 50 - 70 individuals (cells, colonies or filaments) if possible or otherwise all the individuals in the sample. The results were expressed as individuals per ml of the original (unconcentrated) sample.

In the curves as plotted here (Figs 65 - 99) the Station B values are represented by the closed circles and the continuous line while those from Station A are shown as separate open circles. Peak values indicated on the curves refer to Station B. The lower part of each graph includes the semi-quantitative estimations based on net-tow records (see p. 25) over the whole study period.

Measurements from Sawley Dene individuals were used as the basis for calculations of algal volume (Table 5),

approximating individuals to regular geometrical shapes. The accuracy of the estimations is not so great as some others in the literature (e.g. Willén, 1976) but they are believed to represent the Sawley material more closely than would data taken from other authors (see Table 5). These values were used in conjunction with the algal counts to produce a composite diagram representing the relative contributions of algae of different groups to the calculated total biomass over the first year of the study.

Results and Discussion

a) Diatoms

Asterionella formosa (Fig. 65) showed a general winter/spring periodicity, being absent over the period June - October in 1976 and 1977, although in 1978 an early summer peak occurred (27c/28c). The absence of Asterionella in summer is characteristic of the epilimnion of stratified lakes, whereas smaller lakes comparable to Sawley Dene frequently support populations of Asterionella and other "spring" diatoms throughout the year (e.g. Slapton Ley: Benson-Evans et al., 1967). The numbers of Asterionella in Sawley Dene in spring 1977 (1,200 cols. ml^{-1}, equivalent to at least 10,000 cells ml^{-1}) approach those found in nutrient-rich lakes such as Abbot's Pond (Moss, 1969), Crose Mere (Reynolds, 1973b) and Blelham Tarn (Lack & Lund, 1974), and are considerably higher than peak values of ca. 100 - 500 cells ml^{-1} typical in Malham Tarn (Lund, 1961) and Chillington Pool (Irish, 1977).

Asterionella was abundant in Sawley Dene chiefly during cold periods (measured water temperature below 12°C) but in July 1978 development occurred at over 15°C. Other instances of warm-water development have been reported elsewhere (Stoermer & Ladewski, 1976) and the decline of of this species in early summer cannot therefore be attributed to increasing water temperature. Similarly, although Asterionella declines at the onset of stratification in larger lakes (Lund, 1978) this cannot be the cause of cessation of growth in Sawley Dene; it is most likely that chemical conditions are responsible, in particular silicate depletion (cf. Lund, 1949, 1964). The secondary development of Asterionella in early summer 1978 may be

Key to symbols used in Figs 65 - 99.

Algal counts: Station B

Station A

Peak value (Station B only) ◀ 24

Levels on 0 - 4 scale of abundance (net-tow records)

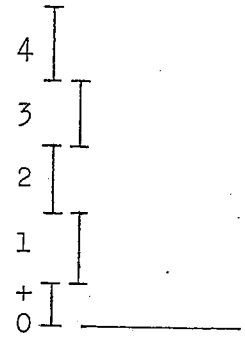
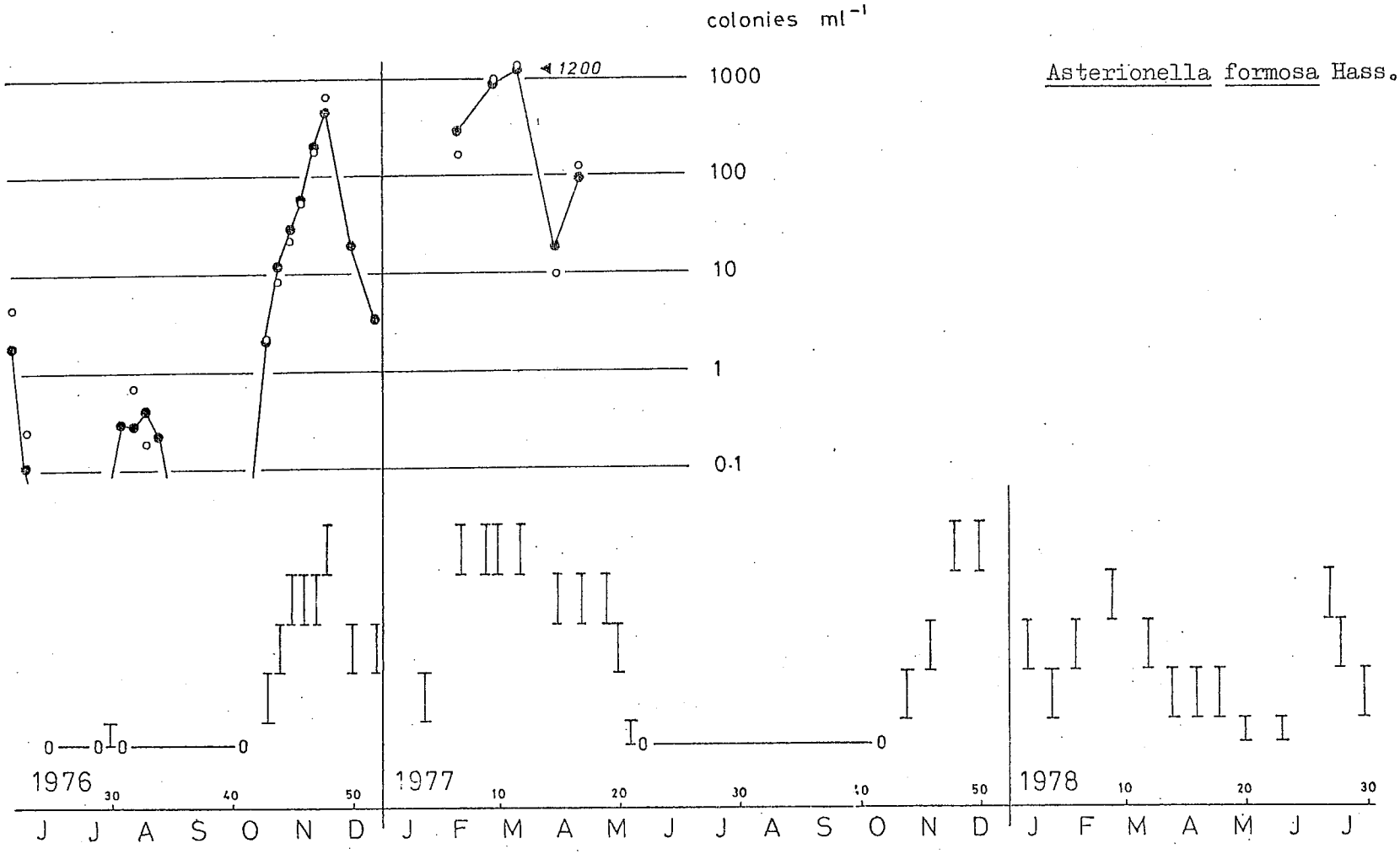


Fig. 65. Periodicity of Asterionella formosa.



related to a smaller spring population than usual, possibly limited by climatic conditions in April, which may have failed to exhaust the available silicate to the usual extent and thus permitted renewed growth of Asterionella later in the season.

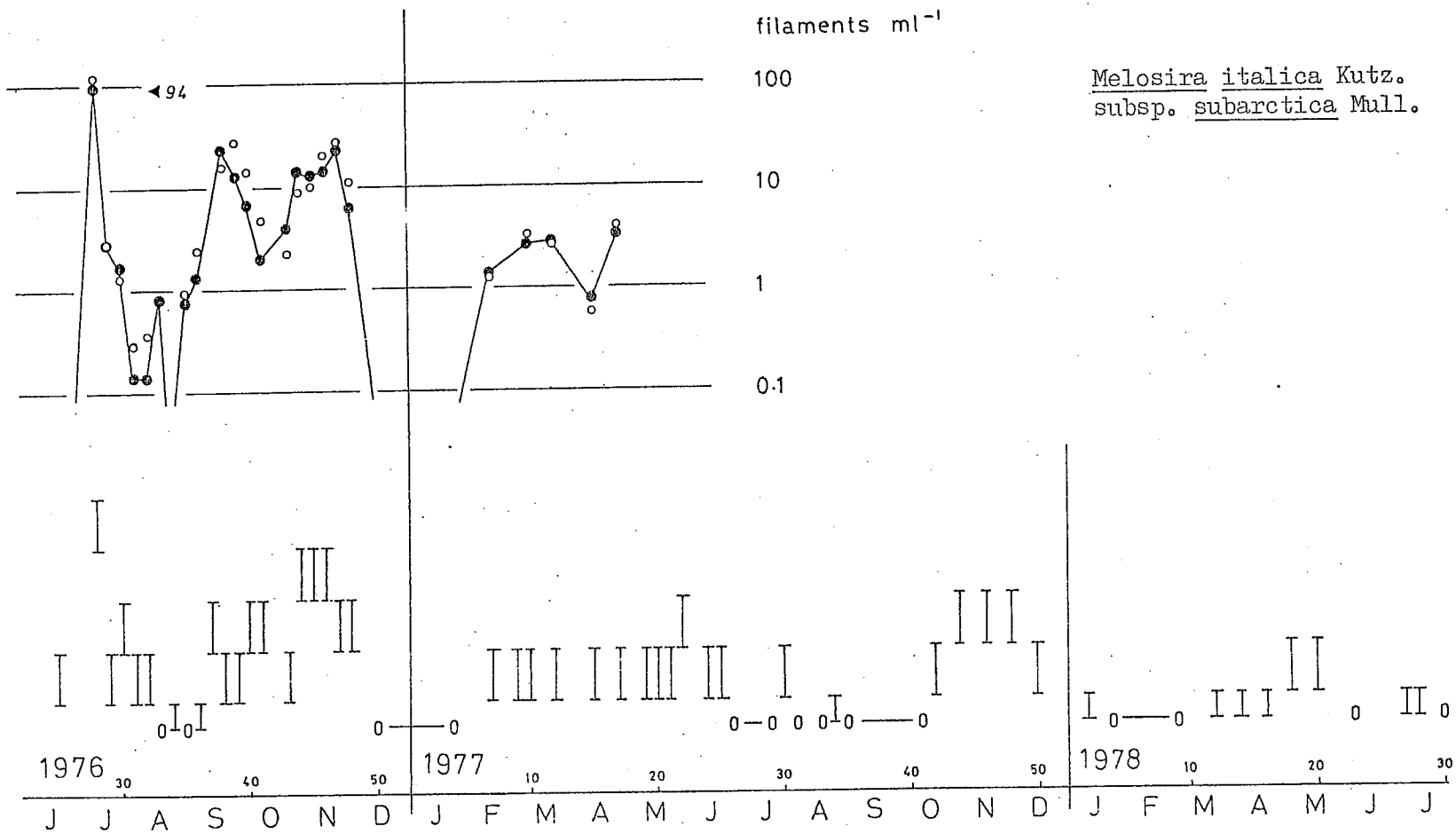
Melosira italica subsp. subarctica (Fig. 66) formed a transient large population in July 1976 (week 28a) and thereafter fluctuated erratically, being most prominent in autumn 1976 and 1977. Its rapid initial development is unexplained and does not appear to be related to sudden wind-induced mixing as has been noted elsewhere (Lund, 1954, 1971a: it occurred at the time of peak water temperature during which the lake was effectively stagnant. One feature of the Melosira trace can, however, be ascribed to the effect of turbulence, viz. the reappearance of the alga in the plankton in spring 1977 and 1978 (7b, 12c) after the breakdown of ice cover. Asterionella, by contrast, maintained a reduced population under ice each winter (Fig. 65).

With the exception of the initial peak, Melosira in Sawley Dene reached maximum levels of approx. 20 filaments ml^{-1} (ca. 300 cells ml^{-1}) which is a low value compared with those found in the eutrophic Lake District lakes (Lund, 1971a; Lack & Lund, 1974). However, there are features of the distribution of this species which are unexplained, for example its apparent absence from the Shropshire Meres (Reynolds, 1973a).

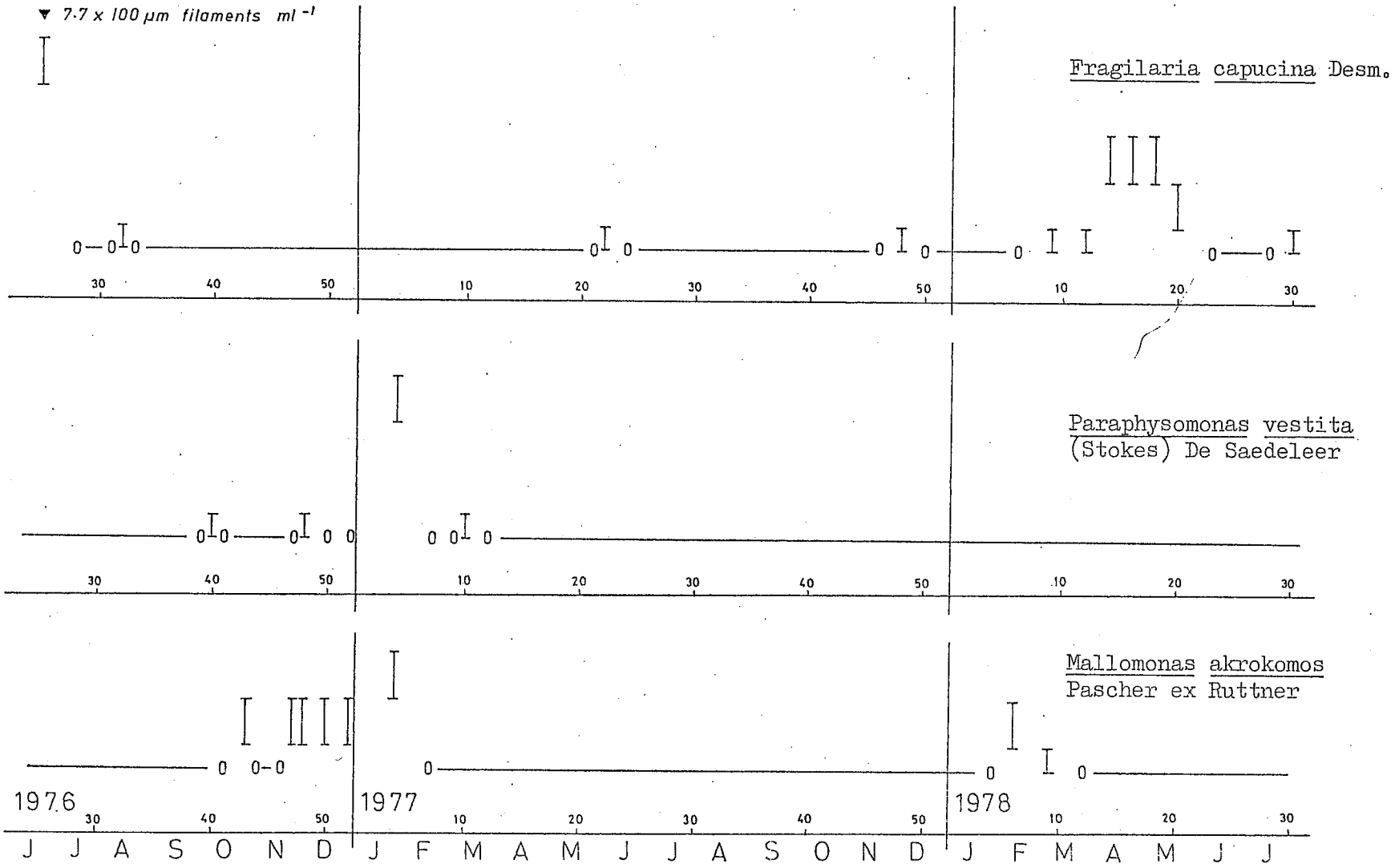
Fragilaria capucina (Fig. 67) was significant only in June 1976 and April/May 1977; the maximum Station B value in the former instance, 7.7 x 100 µm filaments ml^{-1}, corresponds to ca. 150 cells ml^{-1}. No clear pattern is shown by this alga: in 1976 it occurred during an unusually warm spell (water temperature ca. 18°C) and in 1978 it developed during a cold period (8 - 12°C), although in each case it followed a decline in the numbers of Asterionella. Its virtual absence in the intervening 21-month period suggests that this alga does not occupy a significant place in the Sawley Dene succession, in contrast to its prominent appearance in some other eutrophic lakes (Round & Brook, 1959).

Isolated cells of a number of other diatoms were found in the net collections but were not identified to species,

Fig. 66. Periodicity of Melosira italica subsp. subarctica.



Figs 67 - 69. Periodicity of Fragilaria capucina, Paraphysomonas vestita and Mallomonas akrokomos.



including members of the genera Navicula, Pinnularia, Surirella and Gyrosigma. It is likely that many of these cells originated from the bottom muds (cf. Round, 1957a) and entered the plankton through wind-induced turbulence within the relatively short, unstratified water column.

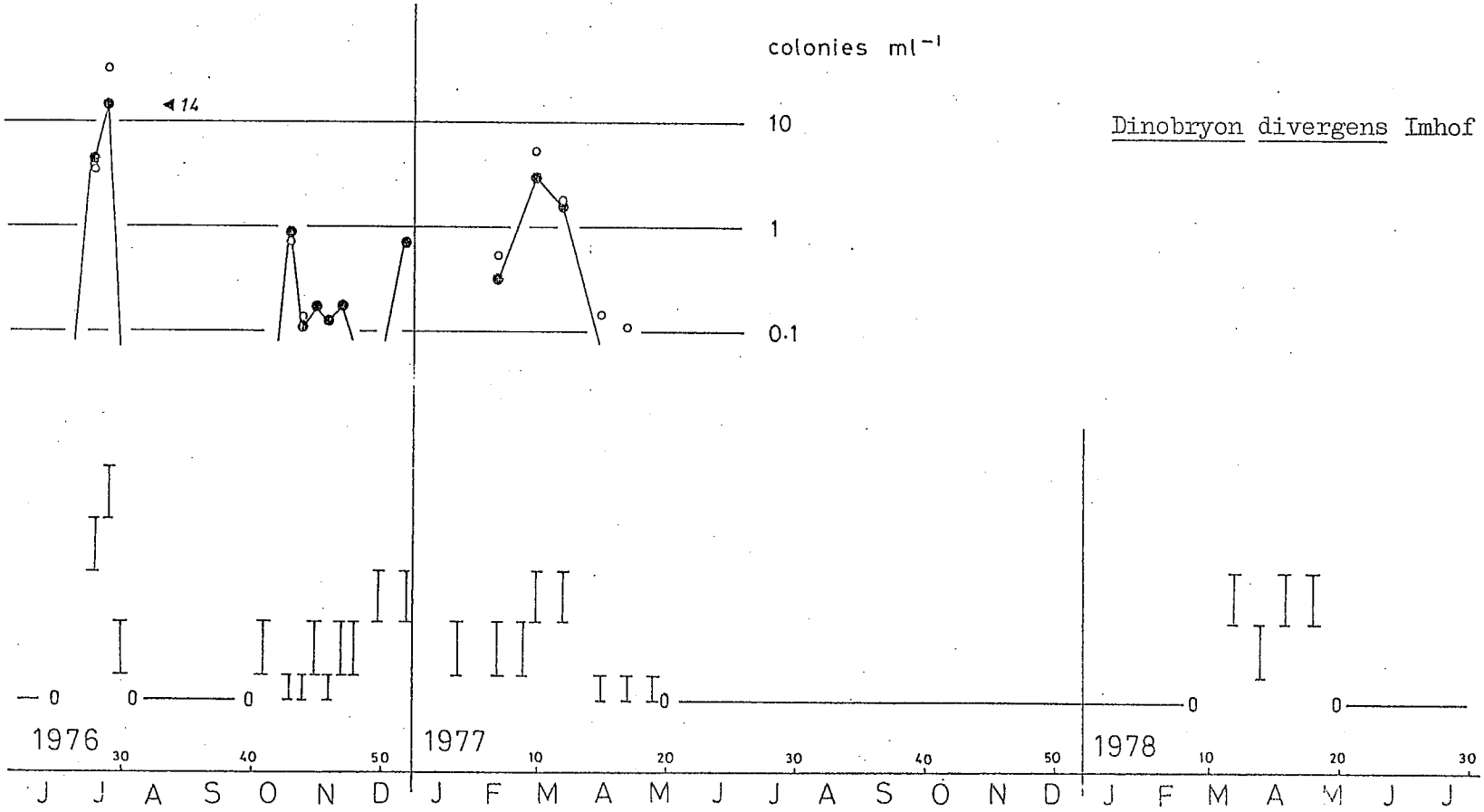
b) Chrysophytes

Dinobryon divergens (Fig. 70) tended to be a spring form in Sawley Dene but was very common only in 1976, when it peaked in July (28a/29a) after the decline of Asterionella and Fragilaria. Pearsall (1932) documented a similar tendency in the more eutrophic English Lakes; although there is some conflicting evidence, it does appear that certain Dinobryon species are adapted to exploit low phosphorus conditions such as may occur after peaks of other algae (Lehman, 1976) and are often successful in oligotrophic waters (Brook, 1964), presumably for a similar reason. The July 1976 Dinobryon peak reached 14 colonies ml^{-1}, comparable with that of 85 cells ml^{-1} recorded in Blelham Tarn after eutrophication (Lund, 1972b) but considerably less than numbers found prior to eutrophication or in the Blelham experimental tubes after reduction of nutrient supply (Lund, loc. cit.).

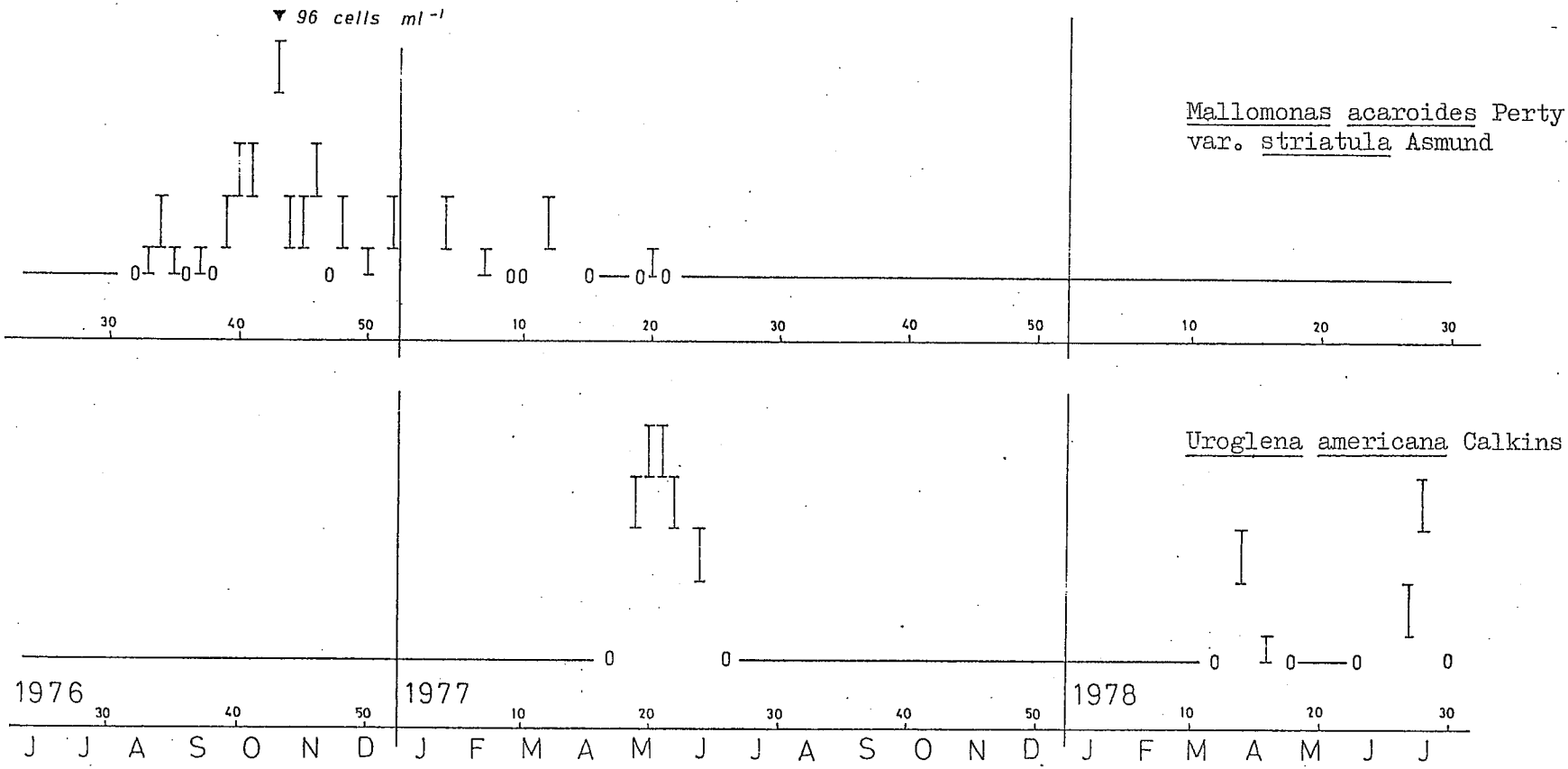
Uroglena americana (Fig. 72) was not seen in 1976 but produced occasional large populations in spring 1977 and 1978, notably at weeks 20b/21b when it was a clear dominant (ca. 60 colonies ml^{-1}). Apart from a small development in 1978 (14c) its main periods of abundance occurred during fairly warm weather (13 - 18°C), concurring with the information in Lund (1972a) and Stoermer & Ladewski (1976); the latter authors found an apparent optimum temperature of 18.5°C for this alga in Lake Michigan. It is likely that Uroglena is dependent on fairly critical weather conditions for its maximum development; in some years it has produced very large populations at certain sites (Lund, 1961; Gorham et al., 1974) while in other years its contribution has been insignificant.

Mallomonas acaroides var. striatula (Fig. 71) was prominent only in autumn and winter 1976, forming a brief peak in October (43a) after which many cells encysted. Small numbers of cells were seen through the winter, some in

Fig. 70. Periodicity of Dinobryon divergens.



Figs 71 - 72. Periodicity of Mallomonas acaroides and Uroglena americana.



collections under ice. M. acaroides is a fairly common Mallomonas species (see Section 4, p. 61) but it has rarely been recorded in LM-based surveys and its periodicity is poorly known. Asmund (1959) records it as chiefly a spring and autumn form.

Mallomonas akrokomos (Fig. 69) occurred chiefly at low temperatures (below 6°C) in Sawley Dene, in small numbers; at other sites, however, it can produce larger populations in autumn/winter (Harris, 1958; Reynolds, 1973a) and be found over much of the year except in summer. EM investigations have shown this species to be widespread (see Section 4, p. 69) and it is one of the few Mallomonas species for which reliable LM reports exist (Lund, 1942; Belcher & Storey, 1968; Irish, 1977).

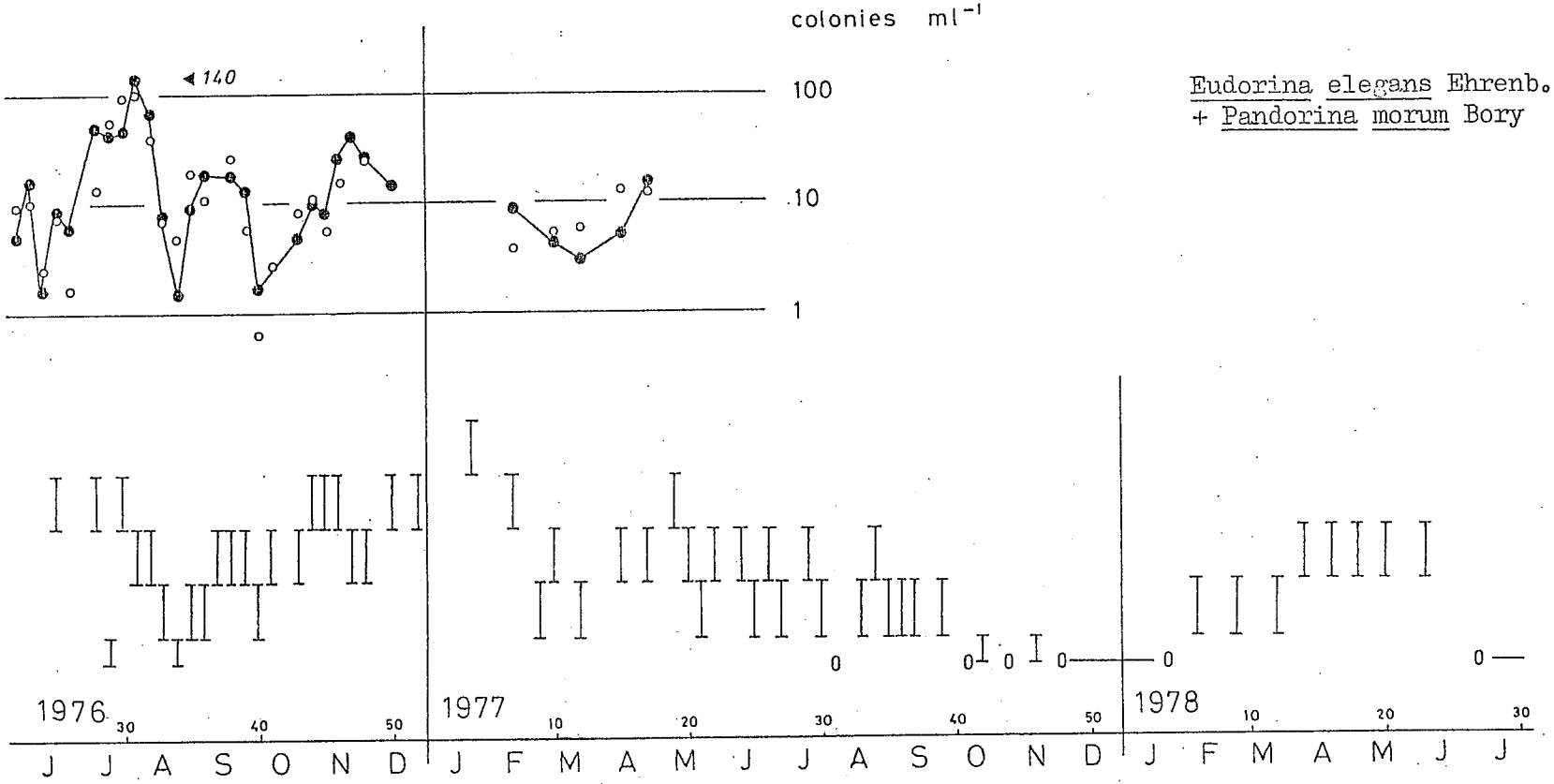
Paraphysomonas vestita (Fig. 68) was prominent on only one occasion in Sawley Dene, in a sample taken through the ice in January 1977 (4b). Its heterotrophic mode of nutrition would presumably be a competitive advantage in conditions of poor illumination. This species has rarely been recorded from freshwater but its scales are among the commonest objects seen in EM preparations (Balonov, 1972; see Section 4, p. 75). On the present evidence it would seem to favour small water-bodies and only occasionally develop truly planktonic populations.

c) Green Algae

The green algae on which data are included here belong to the genera Eudorina and Volvox of the Volvocales; Elakatothrix of the Tetrasporales; Asterococcus, Dictyosphaerium, Pediastrum and Scenedesmus of the Chlorococcales; and Closterium and Staurastrum of the Desmidiales.

Eudorina elegans (Fig. 73) was present almost continuously over the study period, a situation parallelled only by Trachelomonas volvocina (see below). Small quantities of Pandorina morum Bory were probably also present but these could not easily be distinguished from juvenile Eudorina colonies; they are included in the Eudorina counts. The numbers of Eudorina fluctuated markedly over 1976 and 1977, rising to over 100 colonies ml^{-1} in July 1976 (31a) but declining to ca. 2 colonies

Fig. 73. Periodicity of Eudorina elegans with Pandorina morum.



ml^{-1} on occasion thereafter (34a, 40a). Similar trends were seen at each sampling station and they must therefore represent a general pattern in the lake population rather than a chance sampling effect. Eudorina was plentiful under ice in winter 1976/7 but virtually absent in the corresponding period of 1977/8.

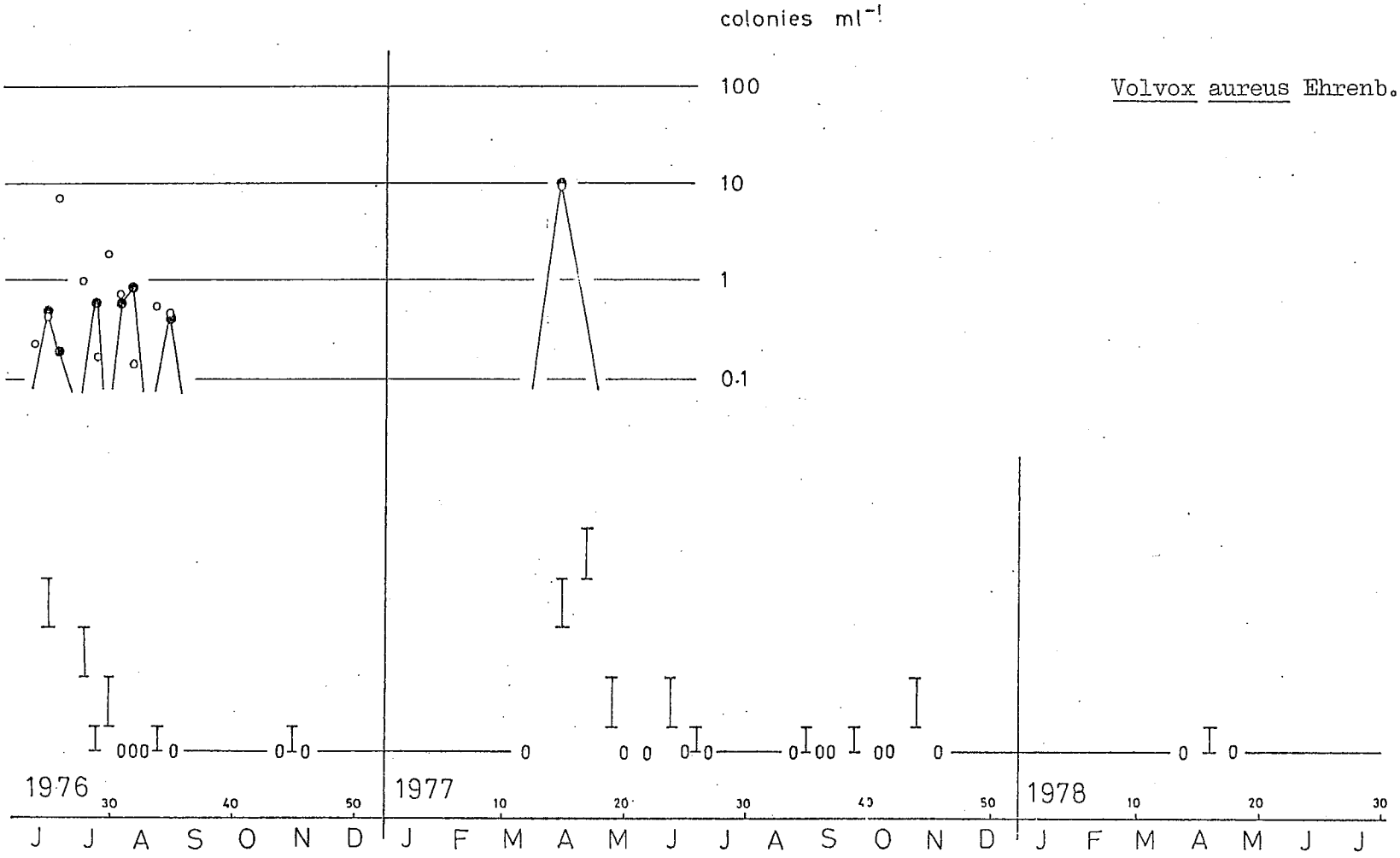
Although Eudorina (and Pandorina) is sometimes seen in mesotrophic or even oligotrophic situations (Round & Brook, 1959), its main habitat appears to be eutrophic lakes in early summer while inorganic nutrients are relatively plentiful (Hickman, 1974; Reynolds, 1976b). Thus the distribution of Eudorina in Sawley Dene might reflect the availability of nutrients, e.g. nitrogen or phosphorus, over the summer period; the two population minima in 1976 (34a, 40a) can be seen to coincide with minor "stratification" events in the water column (Fig. 12), although a previous such event (28a/29a) corresponds to only a slight decrease in Eudorina at Station B and an increase at Station A.

From October 1977 to July 1978 the numbers of Eudorina were lower than previously and on occasion it was absent altogether. The present information is insufficient to explain this apparent change in behaviour.

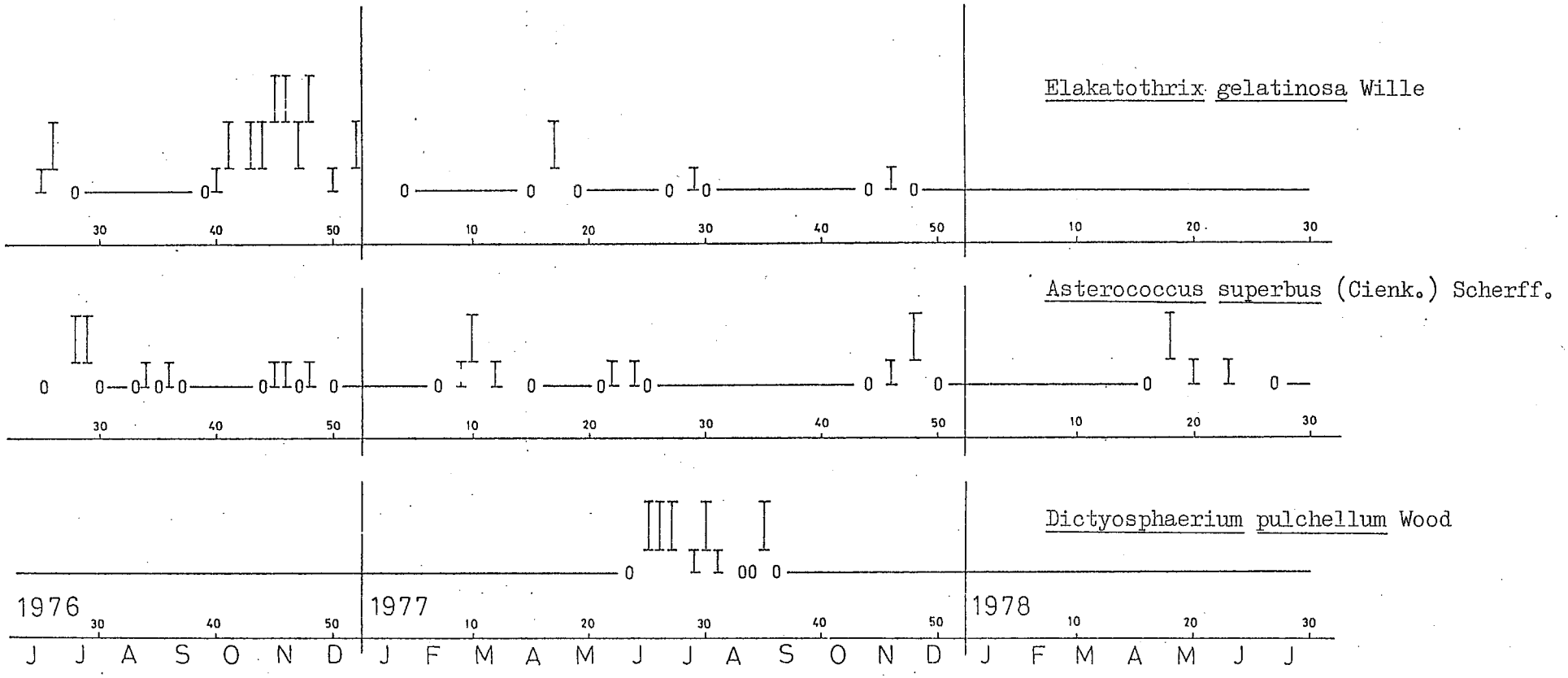
Volvox aureus (Fig. 74) contributed significantly to the early summer green algal period in 1976 although small numbers of colonies were involved. Another peak was seen in May 1977 (19b), immediately prior to a large development of Uroglena americana. V. aureus is apparently confined to eutrophic waters (Round & Brook, 1959; Brook, 1964) where it possibly shares some of the environmental requirements of Eudorina (Reynolds, 1976b), although its maxima tend to be transient (e.g. Abdel Karim, 1965). In Sawley Dene, the 1976 populations of Volvox showed the most variability of any alga between the two sampling stations.

Members of the Tetrasporales and Chlorococcales were most frequent over 1976, the periodicity involving Pediastrum duplex in June (Fig. 79) and Elakatothrix gelatinosa and Scenedesmus arcuatus in October/November (Figs 75, 78); the other species mentioned above were present only occasionally over the rest of the study period. Two species, Asterococcus superbus and Dictyosphaerium pulchellum, did slightly better than the rest in 1977 but

Fig. 74. Periodicity of Volvox aureus.



Figs 75 - 77. Periodicity of Elakatothrix gelatinosa, Asterococcus superbus and Dictyosphaerium pulchellum.



Figs 78 - 80. Periodicity of Scenedesmus arcuatus, Pediastrum duplex and Closterium cf. littorale.

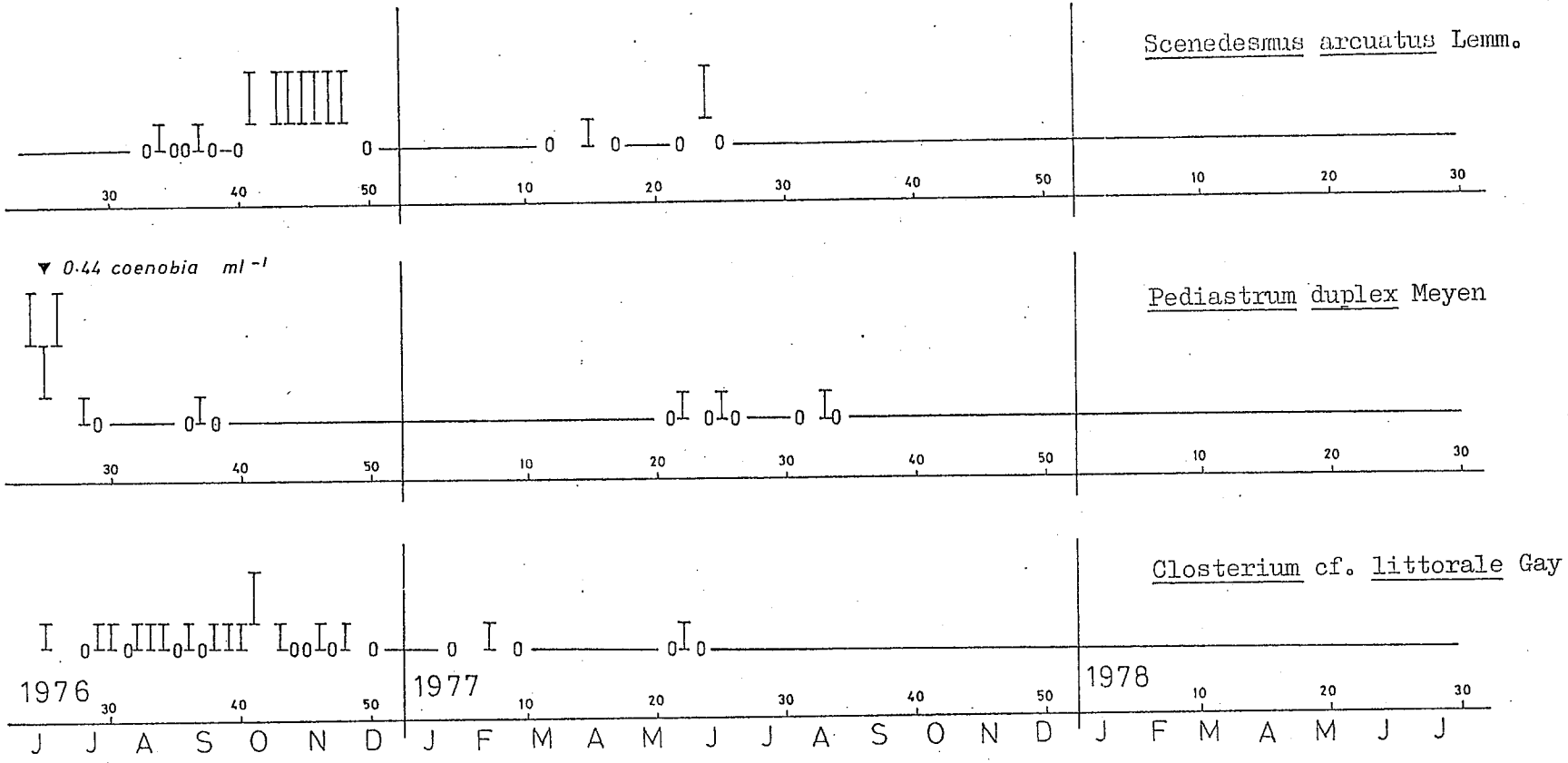


Fig. 81. Periodicity of Closterium acutum var. variabile.

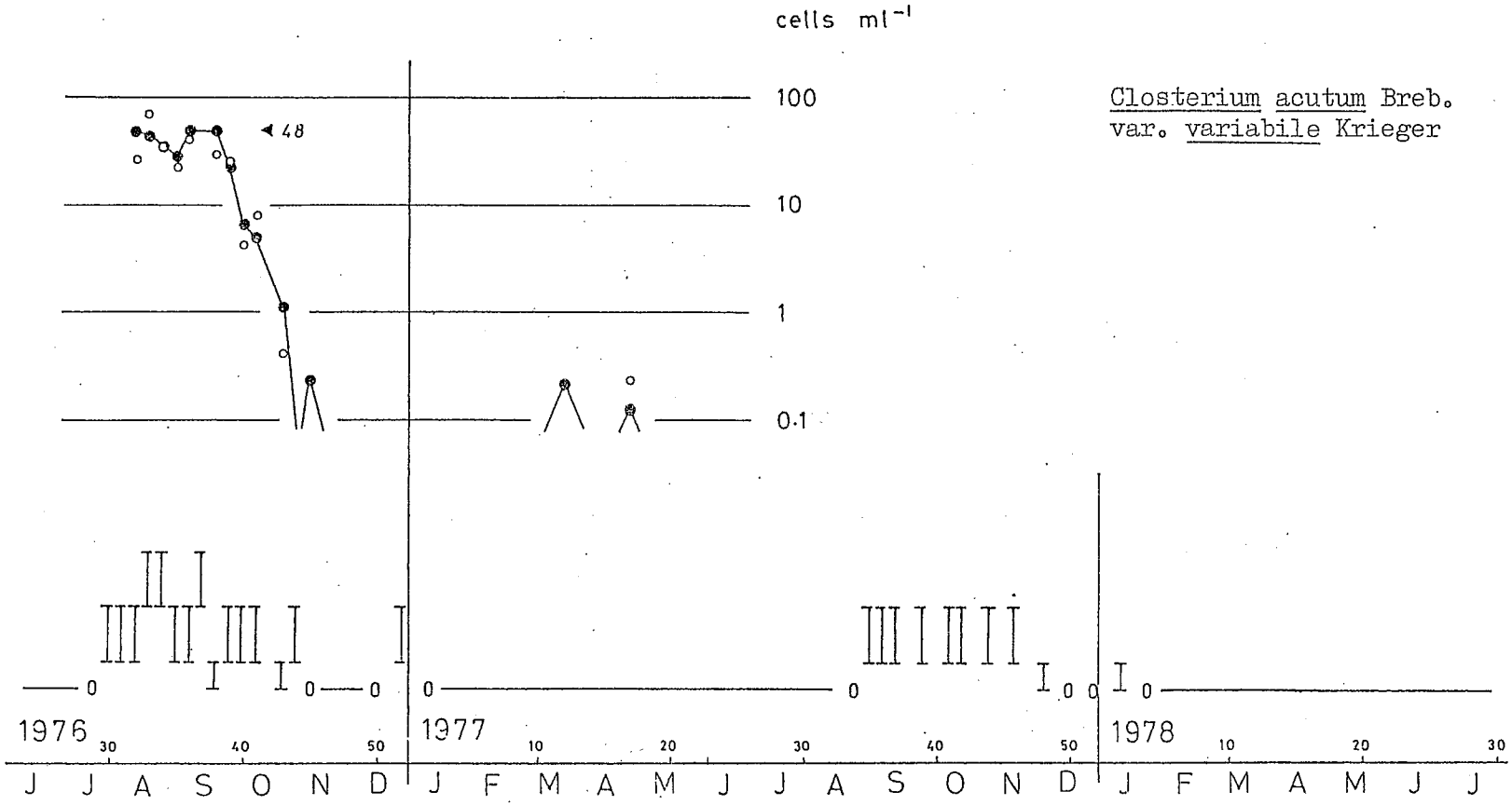
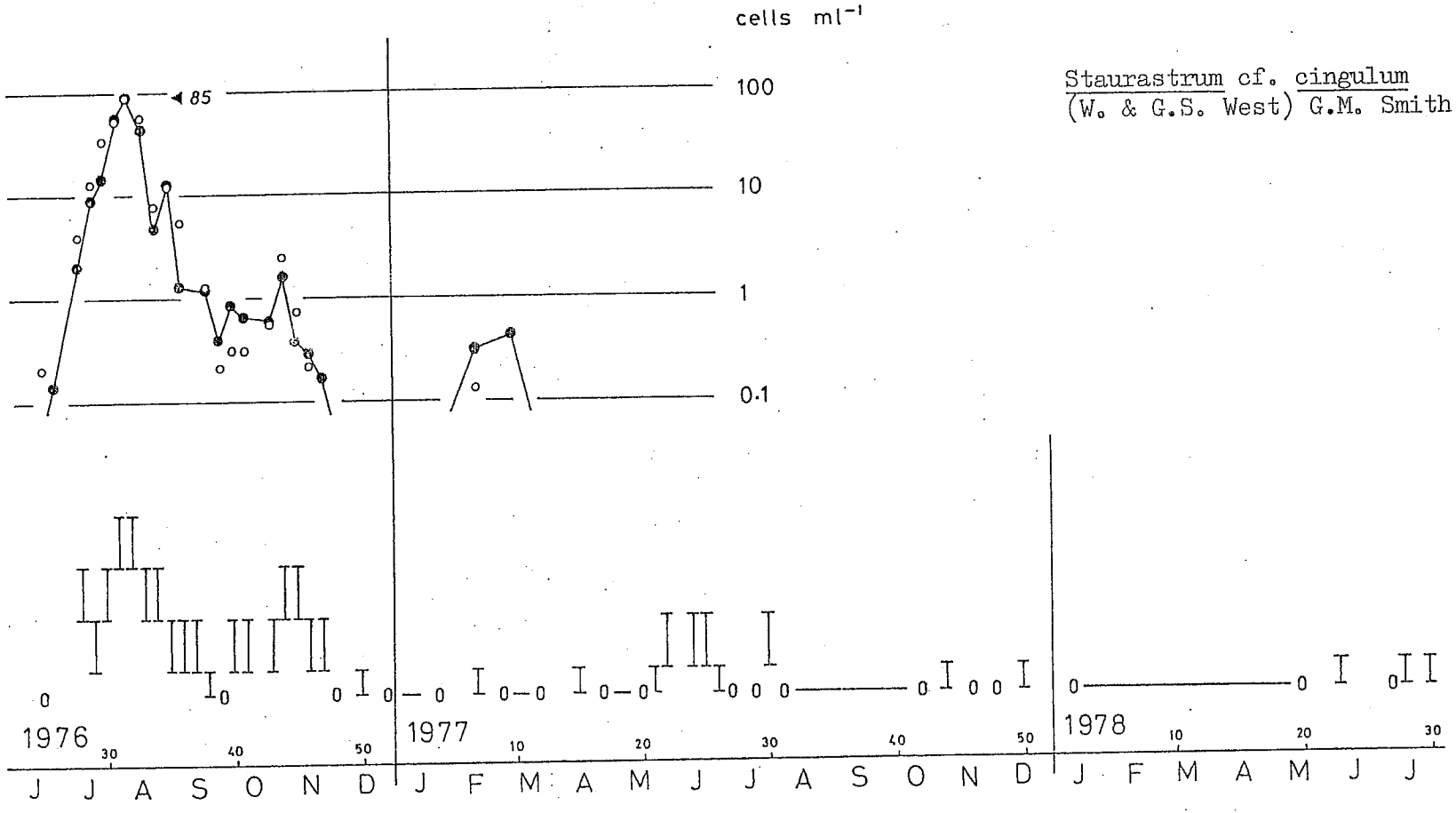


Fig. 82. Periodicity of Staurastrum cf. cingulum.



numbers were still low (Figs 76, 77).

Chlorococcales tend to favour conditions where nutrients are rarely limiting, even in summer (Stewart et al., 1977; Stoermer, 1978) and they may be common where input of organic matter is significant (Reynolds, 1973a); it has sometimes been suggested that their appearance in eutrophic lakes in summer might be related to the senescence of large populations of other algae (Reynolds, 1971). In Sawley Dene numbers were generally low and there is little evidence of a clear periodicity in successive years. Dictyosphaerium pulchellum is not restricted to eutrophic lakes (Round & Brook, 1959; Stoermer, 1978).

Three species of desmids were recorded in the Sawley Dene plankton; Closterium acutum var. variabile (Fig. 81) and Staurastrum cf. cingulum (Fig. 82) developed significant populations in summer 1976, while Closterium cf. littorale (Fig. 80) appeared sporadically in the net collections. The provisional determination of the Staurastrum species as S. cingulum was based on Brook (1959: Pl. 12, Figs 4 - 6) although S. pingue Teiling is a possible alternative identification. S. pingue has a somewhat more eutrophic distribution than S. cingulum (Brook, 1965).

Canter & Lund (1966) correlate the appearance of desmids with warm water temperatures in Windermere although the species concerned are not stated. (A later paper, Lund, 1971b, identifies only Staurastrum lunatum and two Cosmarium species in the Windermere plankton). Staurastrum "paradoxum", a name formerly applied to many forms of the S. cingulum/S. pingue type (Brook, 1959) has been found to dominate the plankton of some European lakes in summer (see Hutchinson, 1967).

d) Dinoflagellates

The two dinoflagellates Ceratium hirundinella (Fig. 83) and Peridinium cinctum (Fig. 84) were prominent during 1976 and contributed strongly to the total biomass in late summer (see Fig. 100). Both species were also seen in successive years but never developed extensive populations. Ceratium is commonly recorded in the summer plankton of eutrophic lakes, although it may also occur in waters of lower trophic status (Round & Brook, 1959); it appears

Fig. 83. Periodicity of Ceratium hirundinella.

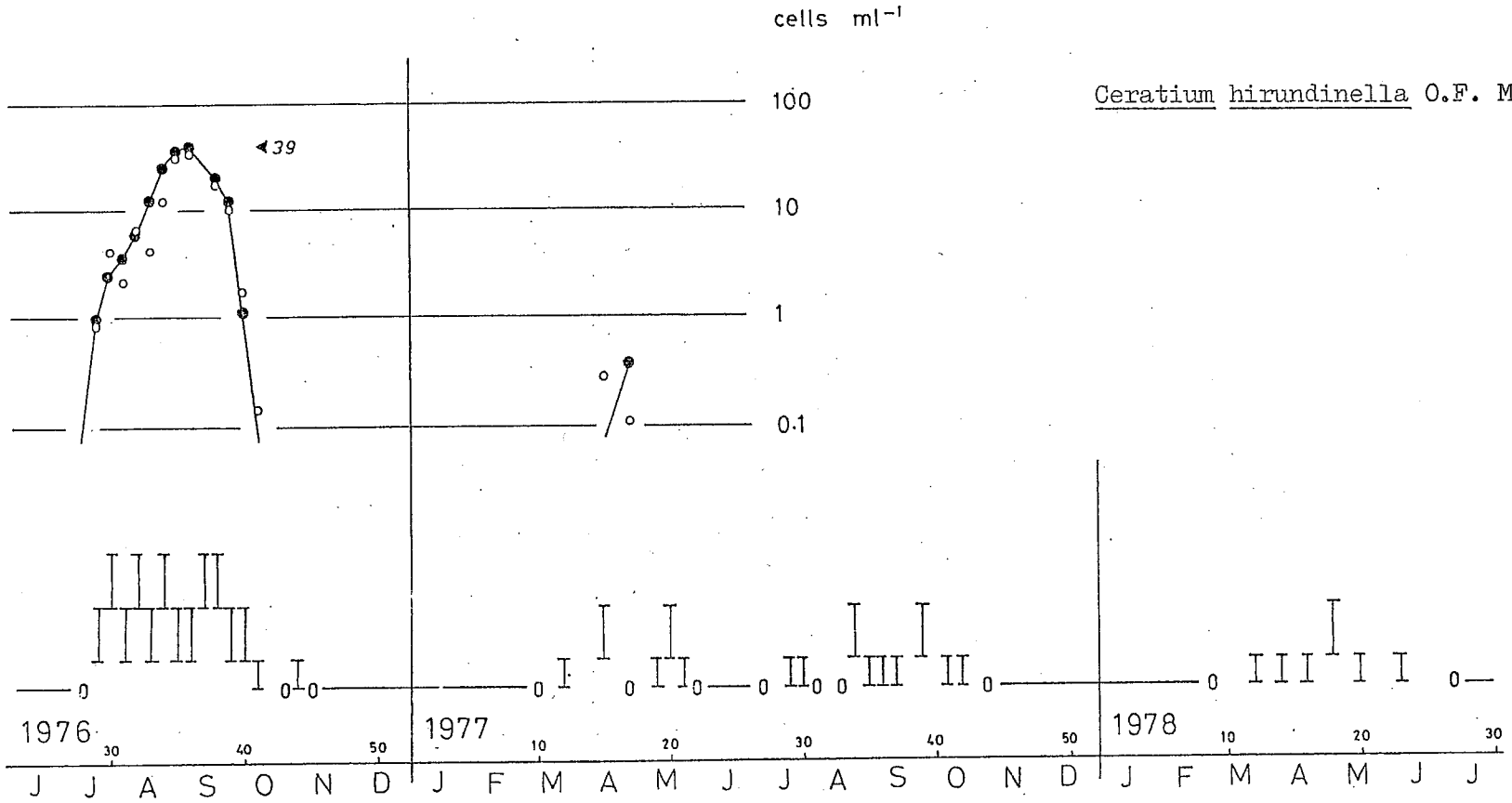
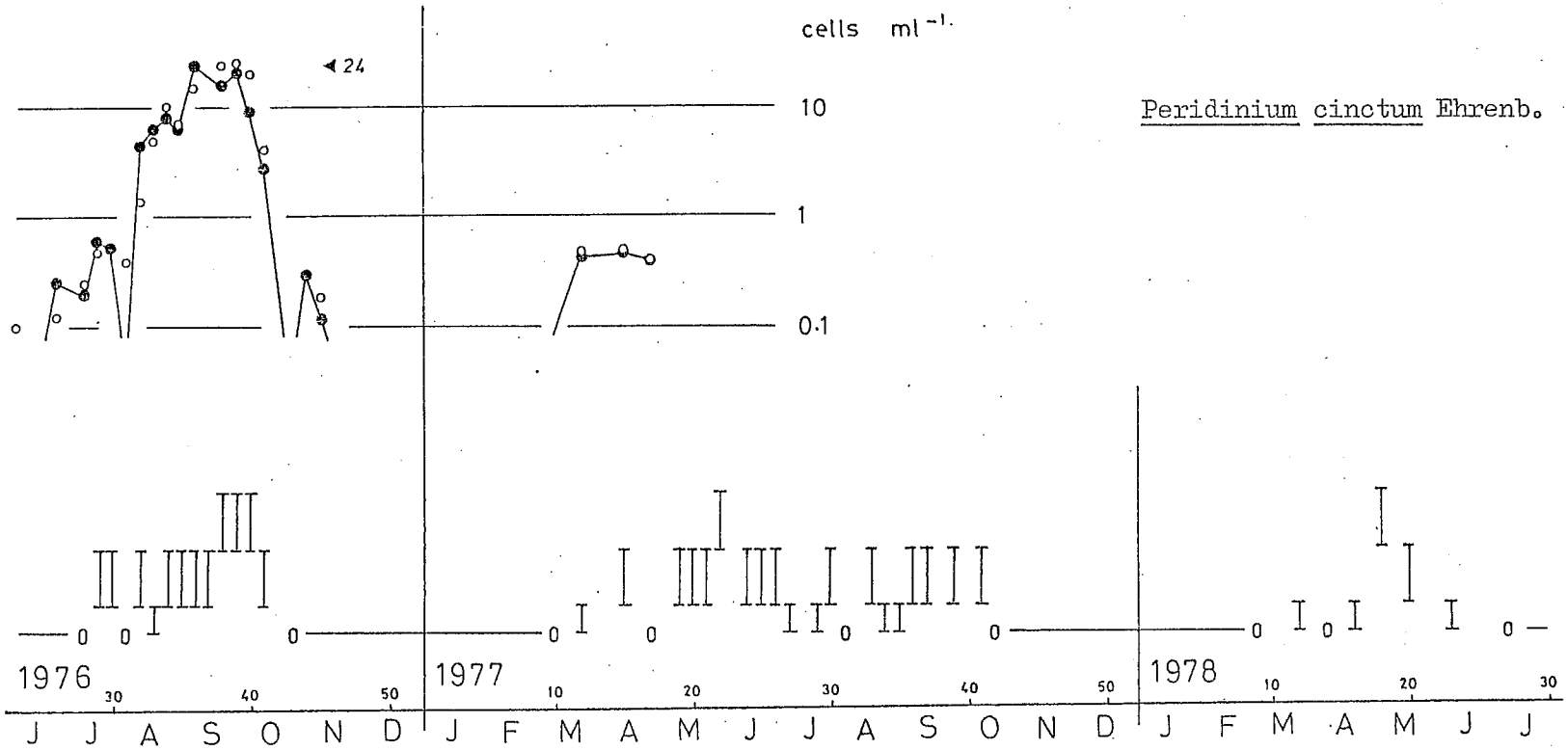


Fig. 84. Periodicity of Peridinium cinctum.



to reach its maximum abundance in relatively large water bodies (e.g. Heaney, 1976; Reynolds, 1978). The ability of Ceratium to grow in epilimnetic waters largely depleted of nutrients enables it to compete effectively with the blue-green algae, which it may eventually replace in late summer (Reynolds, 1976a). Part of the success of Ceratium under these conditions may be attributable to its capability for vertical migration on a daily basis (Talling, 1971), enabling cells to obtain nutrients from the lower layers of a stratified lake. The absence of Ceratium in quantity during 1977 and early 1978 may be the "typical" condition for Sawley Dene, which, because of its limited depth, probably does not provide the ideal situation for this alga; the 1976 population may reflect a greater degree of nutrient stress occurring in that summer and it is noteworthy that the rapid increase in Ceratium seen over weeks 31a - 33a coincides with a temporary collapse of the Eudorina population (see p. 48).

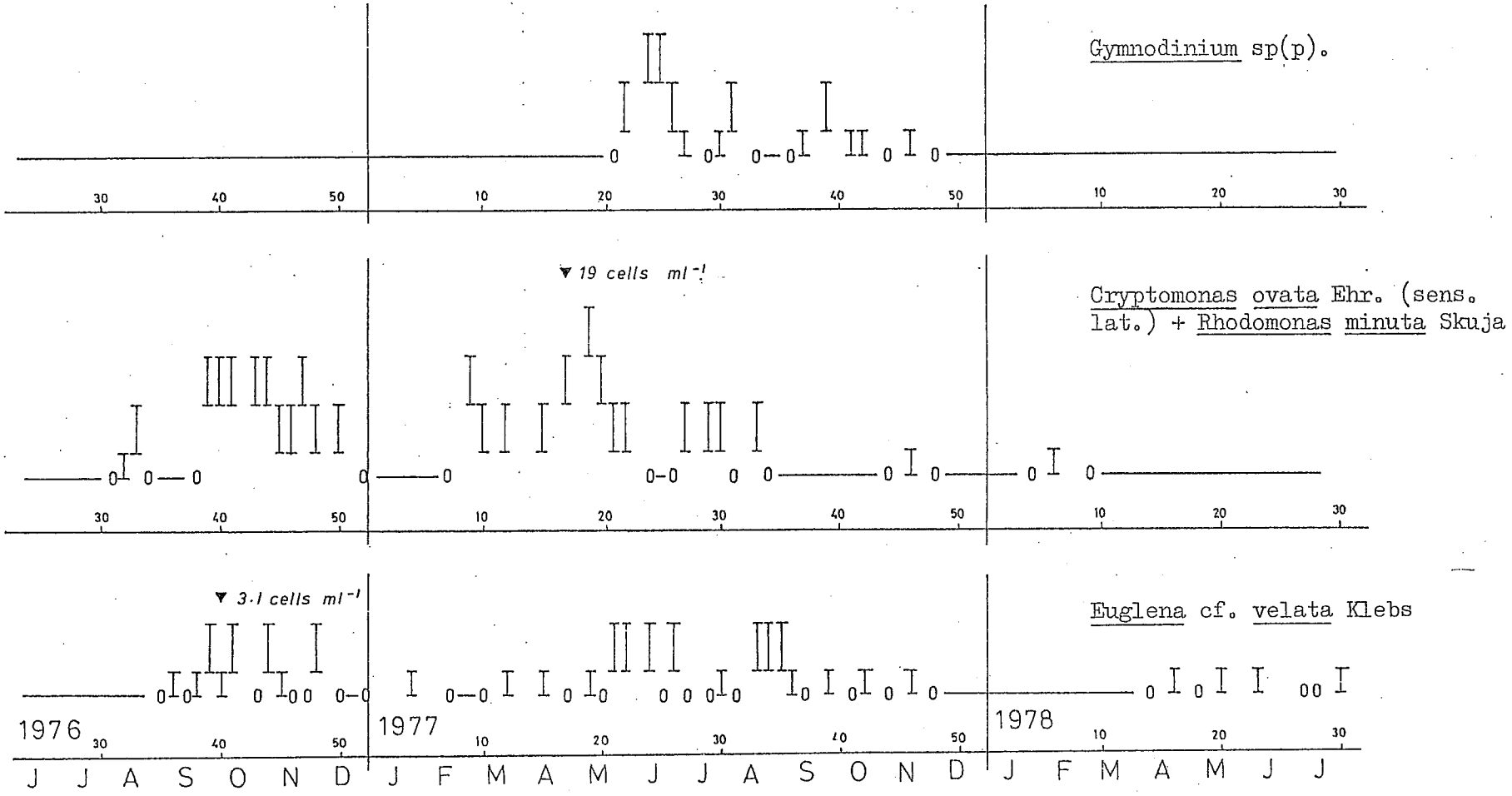
Peridinium cinctum developed in a very similar manner to Ceratium during late summer 1976, implying that the environmental requirements of the two species are probably comparable. In the succeeding seasons its periodicity was again similar to that of Ceratium although on some occasions it was present in slightly greater numbers than the latter species. In contrast to Ceratium, the genus Peridinium has a number of freshwater representatives and the summer periodicity of P. cinctum is not typical of the genus as a whole (cf. Round, 1971).

A small Gymnodinium sp. (or possibly several species) was seen for the first time in summer 1977 (Fig. 85) but the identity of the cells was not established.

e) Cryptomonads

Small cryptomonads were sometimes fairly frequent in the net collections (Fig. 86) but were only counted occasionally in the volumetric samples, e.g. on wks 18b/19b when peak levels (ca. 20 cells ml^{-1}) were encountered. Most of the cells corresponded to Rhodomonas minuta (=Rhodomonas lacustris Pascher et Ruttner in Javornicky, 1976) with occasional larger cells of the Cryptomonas ovata type (see Figs 37, 38) although exact determination was

Figs 85 - 87. Periodicity of Gymnodinium sp(p)., Cryptomonas ovata with Rhodomonas minuta and Euglena cf. velata.



usually difficult.

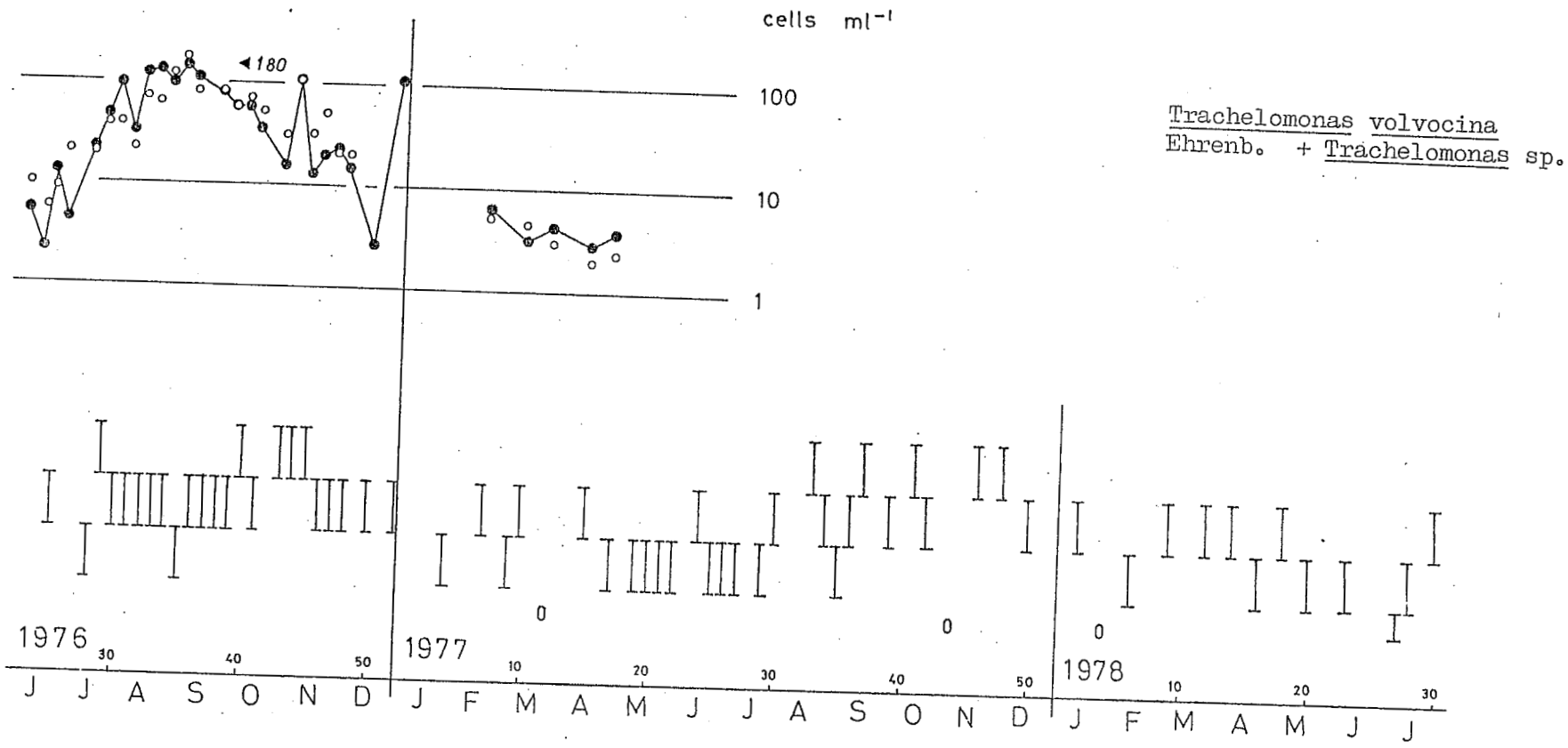
Cryptomonads are undoubtedly widely distributed (cf. Lund, 1962) but they are probably sometimes overlooked when present only in small numbers and many aspects of their ecology remain obscure. They tend to prefer eutrophic situations (Round, 1957b) where they may be frequent on the bottom muds; some of the larger species can become prominent in the plankton also, for example Cryptomonas ovata in Crose Mere (2,500 cells ml^{-1} in spring: Reynolds, 1973b) and C. erosa in Abbot's Pond (Hickman, 1974). It would therefore appear that Sawley Dene is comparatively poor in cryptomonads; this is somewhat surprising considering its eutrophic status and the generally short water column which might facilitate transfer of cells from the benthos to the plankton.

f) Euglenoids

Trachelomonas volvocina (Fig. 88) was the most constant alga recorded in this survey, occurring in 49 of the 52 fortnight-periods described on p. 25. A second Trachelomonas sp. (Fig. 40) was also present in these collections and has been included in the counts for T. volvocina, of which it typically comprised 5 - 10% of the total. Numbers of Trachelomonas showed some tendency to be highest in summer and were sufficient to make a small but detectable contribution to the summer biomass in 1976 (see Fig. 100 and p. 56). A "freak" high count of Trachelomonas was recorded from the single sample taken through the ice in wk 52a and this probably reflects local aggregation of the cells at a particular point since a similar high value was not found in the net collection from that date or under ice in the subsequent year.

Trachelomonas has been shown by Round (1957b) and Hickman (1974) to be favoured by deoxygenated, poorly illuminated conditions low in the water column and probably is at least partly heterotrophic in nutrition. Its persistence in the Sawley Dene plankton may to some extent reflect the proximity of the bottom muds to the water surface and it seems to have produced its highest populations in the hot summer of 1976 with associated temporary development of deoxygenation near the bottom muds (Fig. 12).

Fig. 88. Periodicity of Trachelomonas volvocina with Trachelomonas sp.



A Euglena species, provisionally identified as E. velata, occurred in small quantities on a number of occasions (Fig. 87). In fresh collections cells rapidly sank out and it is therefore likely that this species typically inhabits the lower part of the water column in Sawley Dene and occurs in the surface plankton only after turbulent mixing.. Round (1957b) noted a number of Euglena spp. on mud surfaces in the English Lakes, particularly in the more productive waters.

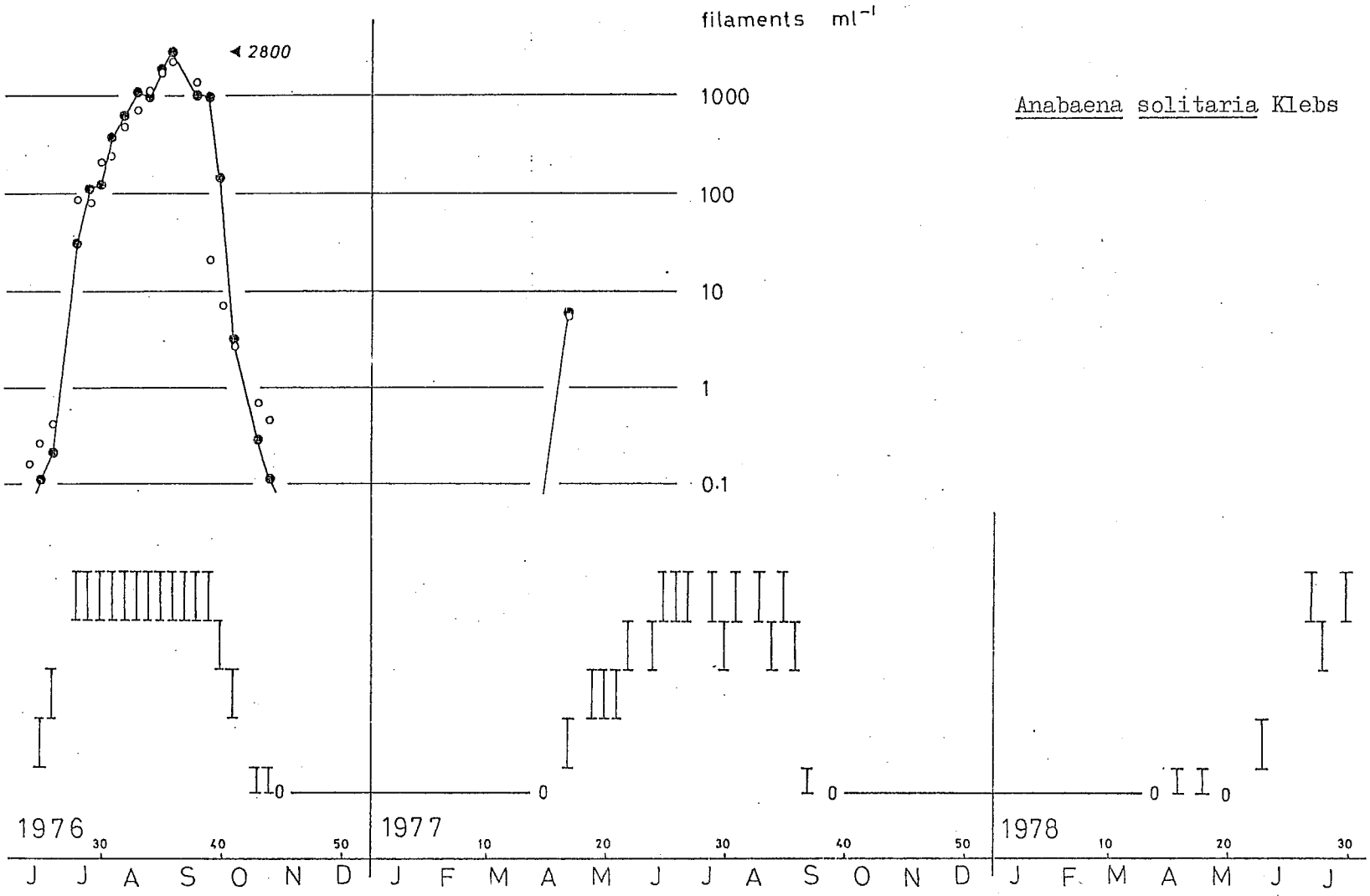
g) Blue-Green Algae

The periodicity of the blue-green algae in Sawley Dene is to be considered in detail by H.A. Cmiech (thesis in preparation) and only preliminary comments will be included here.

Anabaena solitaria (Fig. 89) reached similar, dominant levels in each year of the study period; isolated observations from 1974 and 1979 suggest that this alga is the most regular blue-green dominant in Sawley Dene, although its predominance over the whole period of peak biomass in 1976 was perhaps atypical (see previous discussion, p. 42). Aphanizomenon flos-aquae (Fig. 93) and Oscillatoria agardhii (Fig. 92) also reached dominant proportions in 1977. Of the species which produced noteworthy sub-dominant populations, Gloeotrichia echinulata (Fig. 96) formed a surface bloom early in the 1976 peak period (29a), the very large colony size (Table 5) compensating for the low numbers of colonies in the water column and producing a significant contribution to the total biomass. Anabaena flos-aquae and A. spiroides (Figs 90, 91) were more prominent in 1977 than 1976, while Microcystis aeruginosa (Fig. 94) and Coelosphaerium naegelianum (Fig. 95) remained relatively minor constituents of the blue-green algal flora each year.

The counts for Anabaena solitaria are noteworthy in that this species contributed most strongly to the 1976 peak summer biomass (see p. 56) and thus would account for much of the chlorophyll a recorded during this period (Fig. 13). The latter results show a difference between the two sampling stations, Station A displaying a shorter,

Fig. 89. Periodicity of Anabaena solitaria.



Figs 90 - 92. Periodicity of Anabaena flos-aquae, Anabaena spiroides and Oscillatoria agardhii.

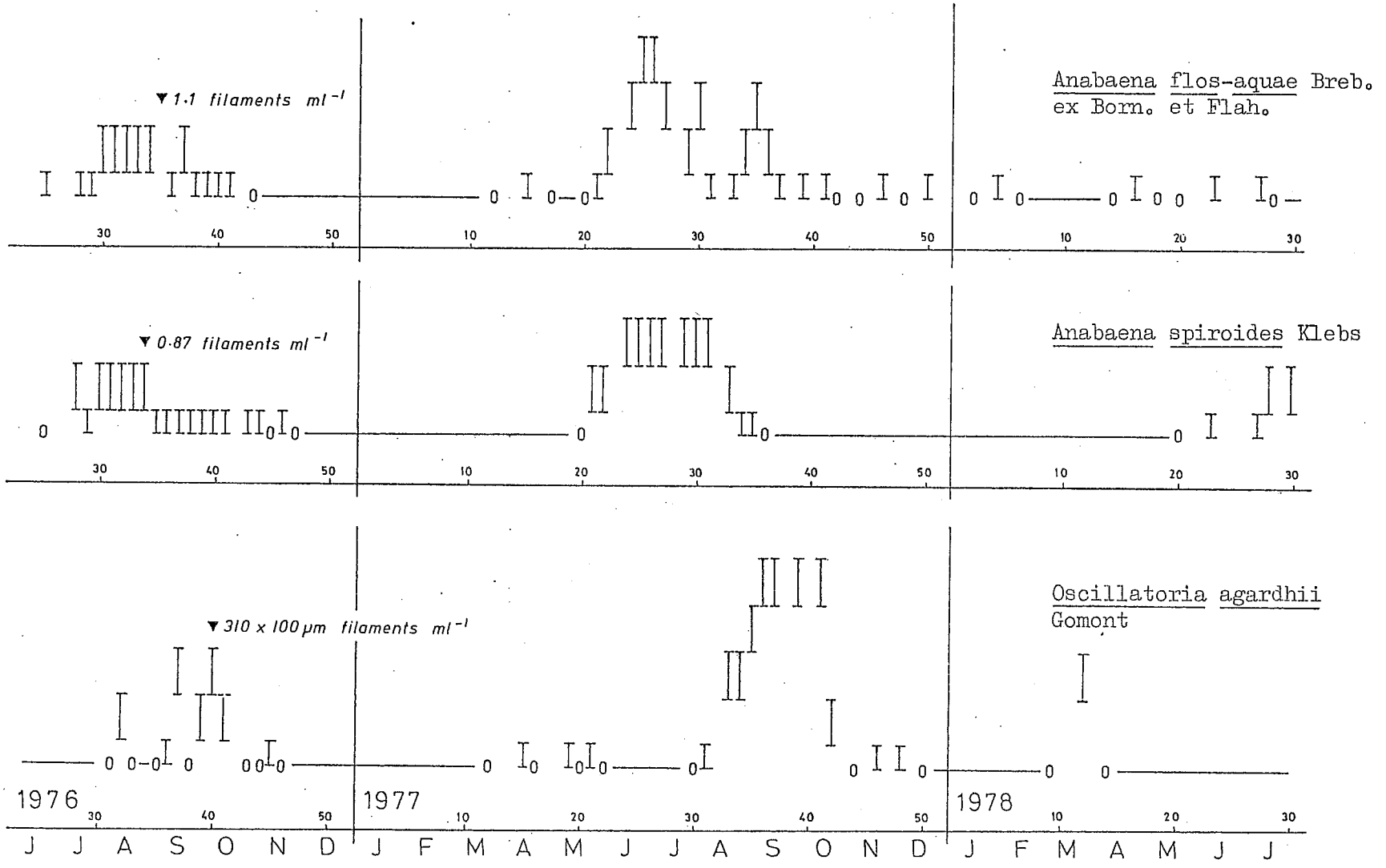


Fig. 93. Periodicity of Aphanizomenon flos-aquae.

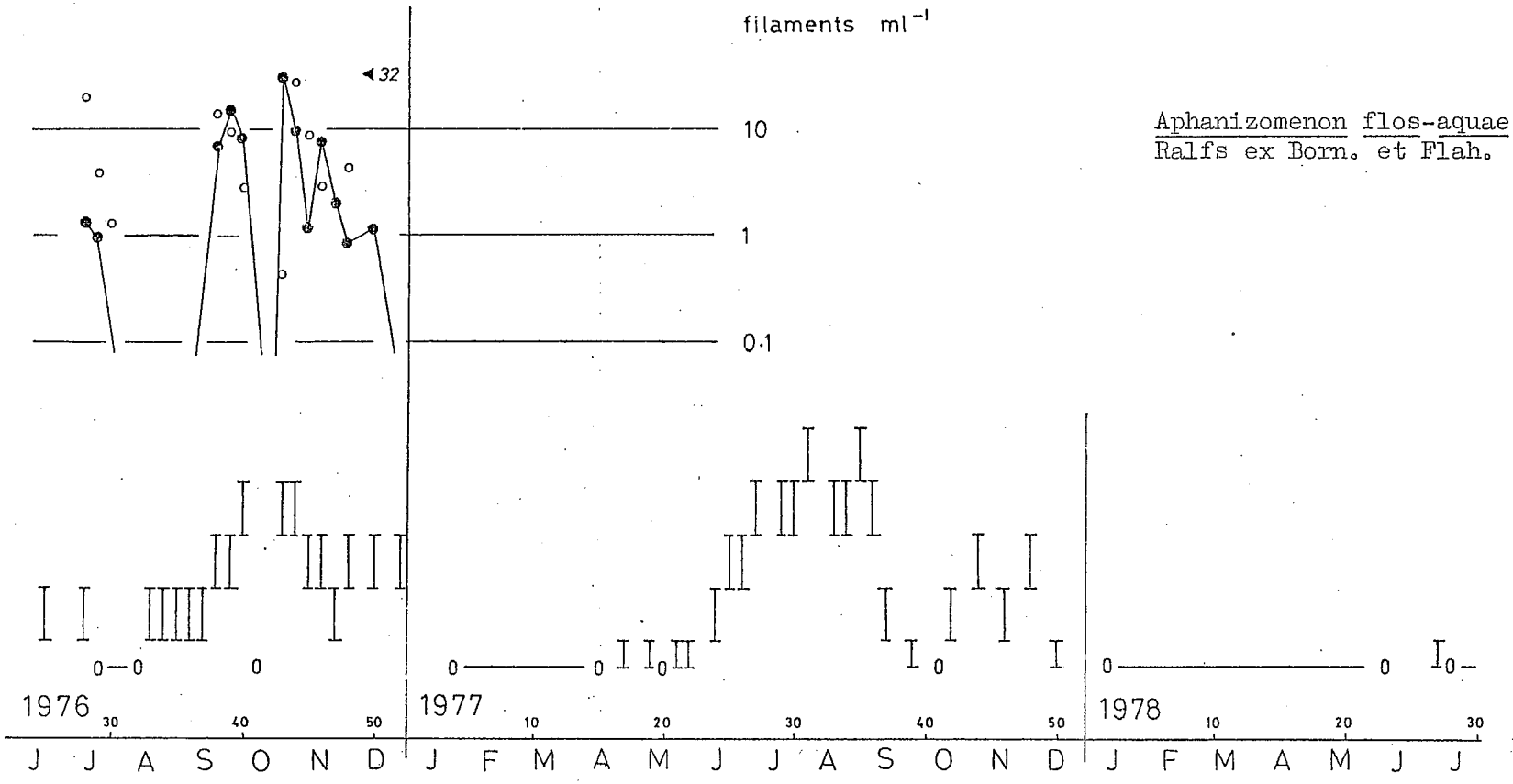


Fig. 94. Periodicity of Microcystis aeruginosa.

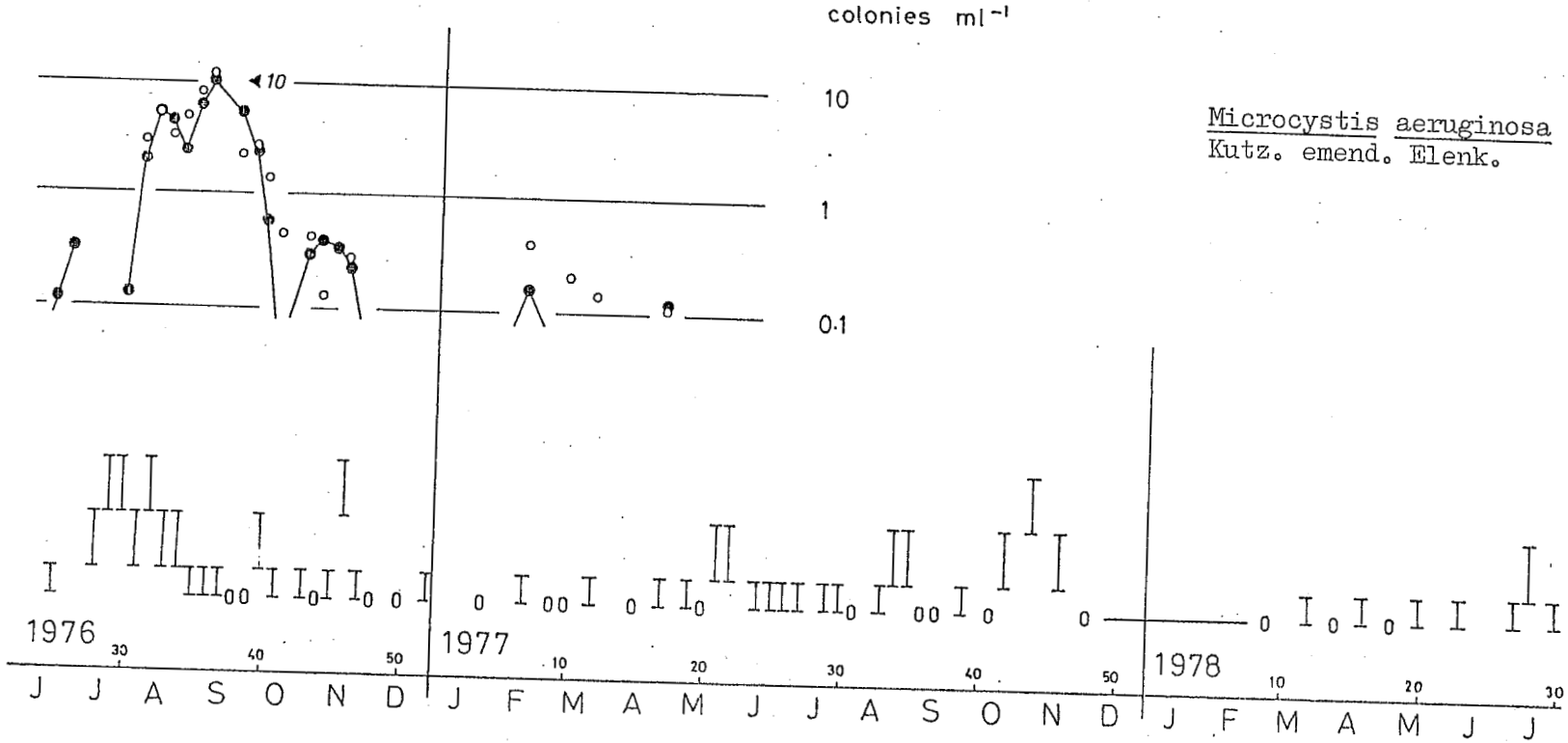


Fig. 95. Periodicity of Coelosphaerium naegelianum.

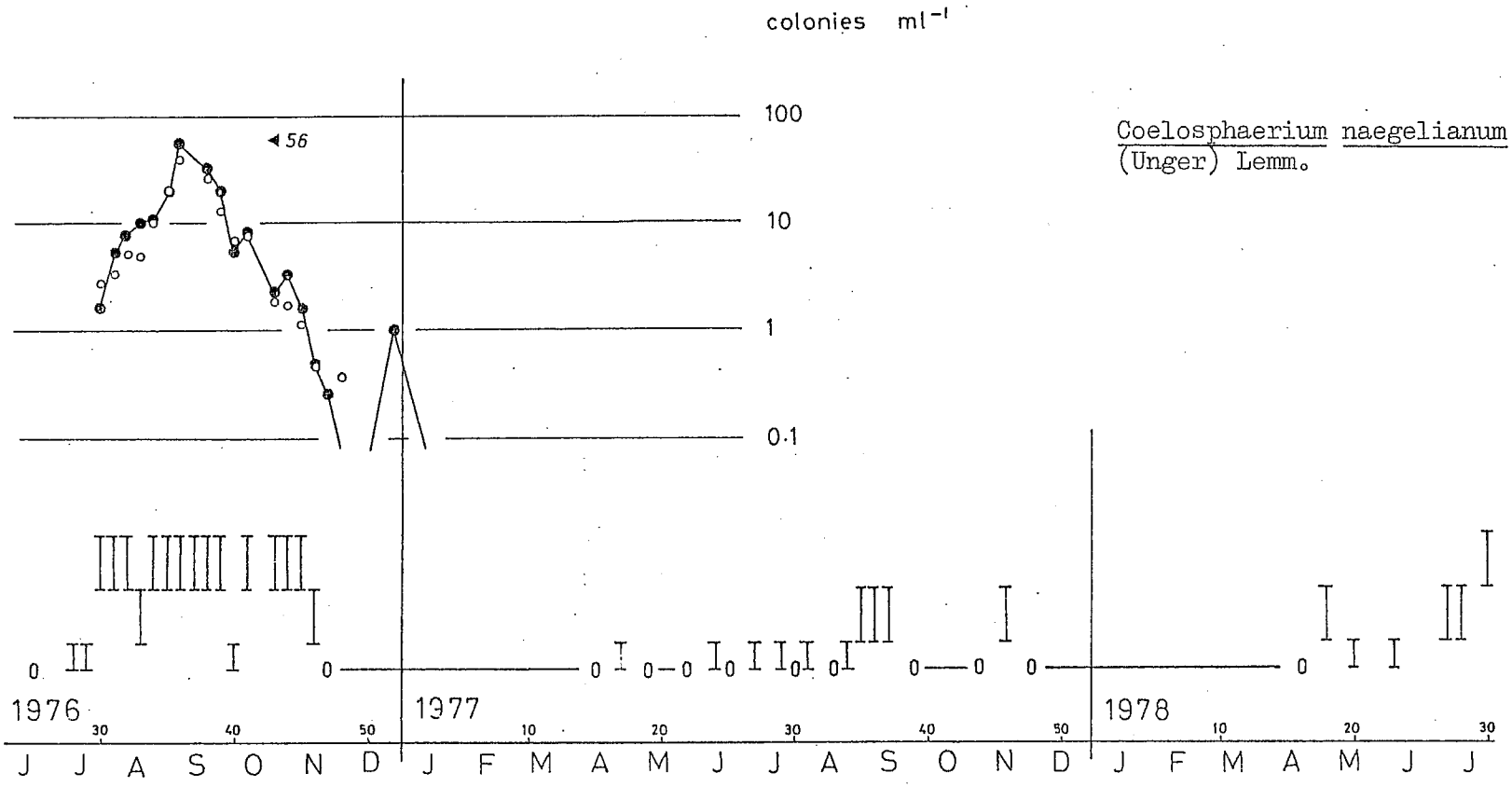
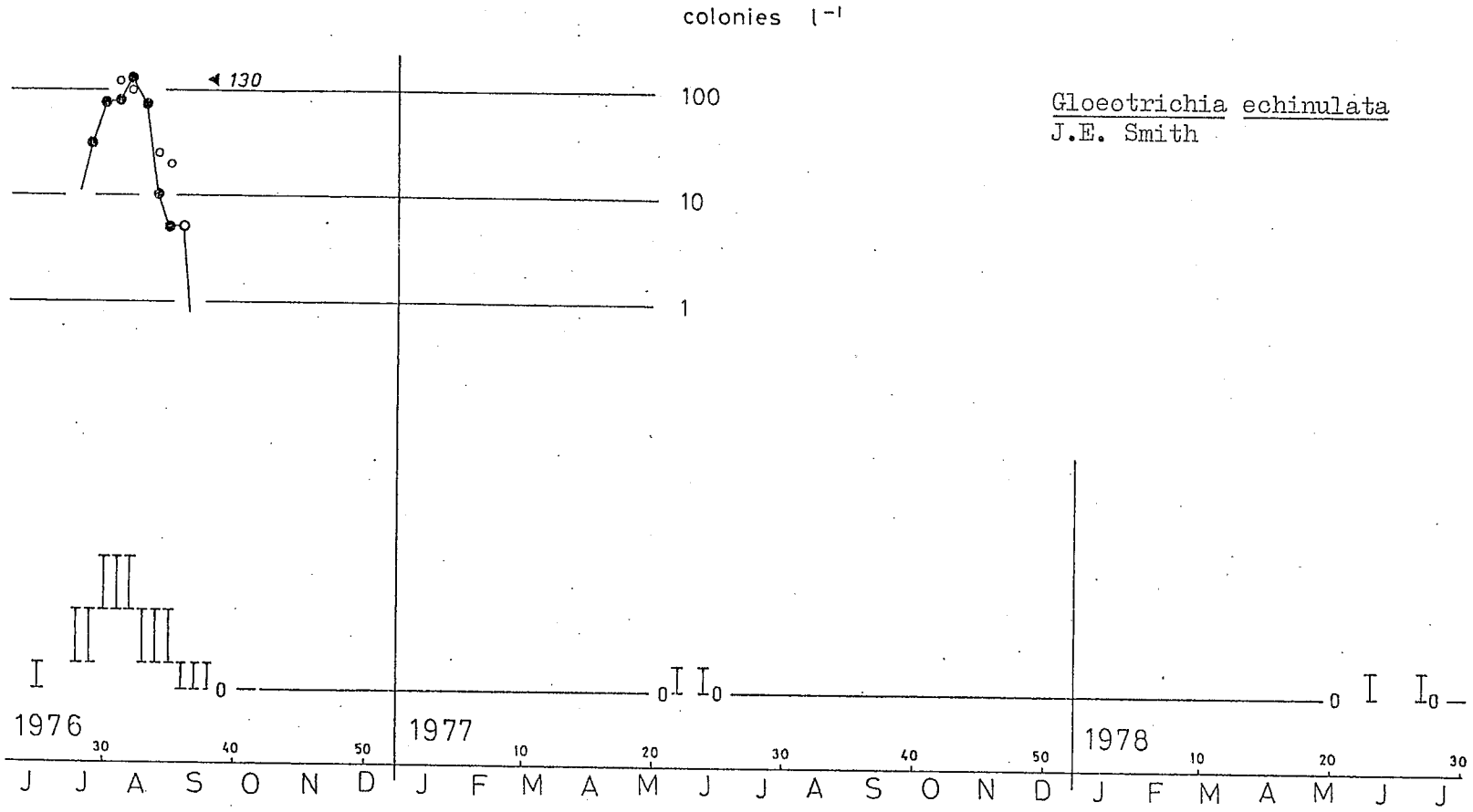


Fig. 96. Periodicity of Gloeotrichia echinulata.



more intense chlorophyll peak than Station B. By comparison, the A. solitaria counts (made on aliquots of the same samples) show no evidence of peak populations of this species being consistently higher at Station A than at Station B, although the eventual decline is more rapid at Station A as in the chlorophyll data. There would thus appear to be some limitations on the relationship between algal counts and chlorophyll a determinations; this point will be given further consideration in the General Discussion (p. 111).

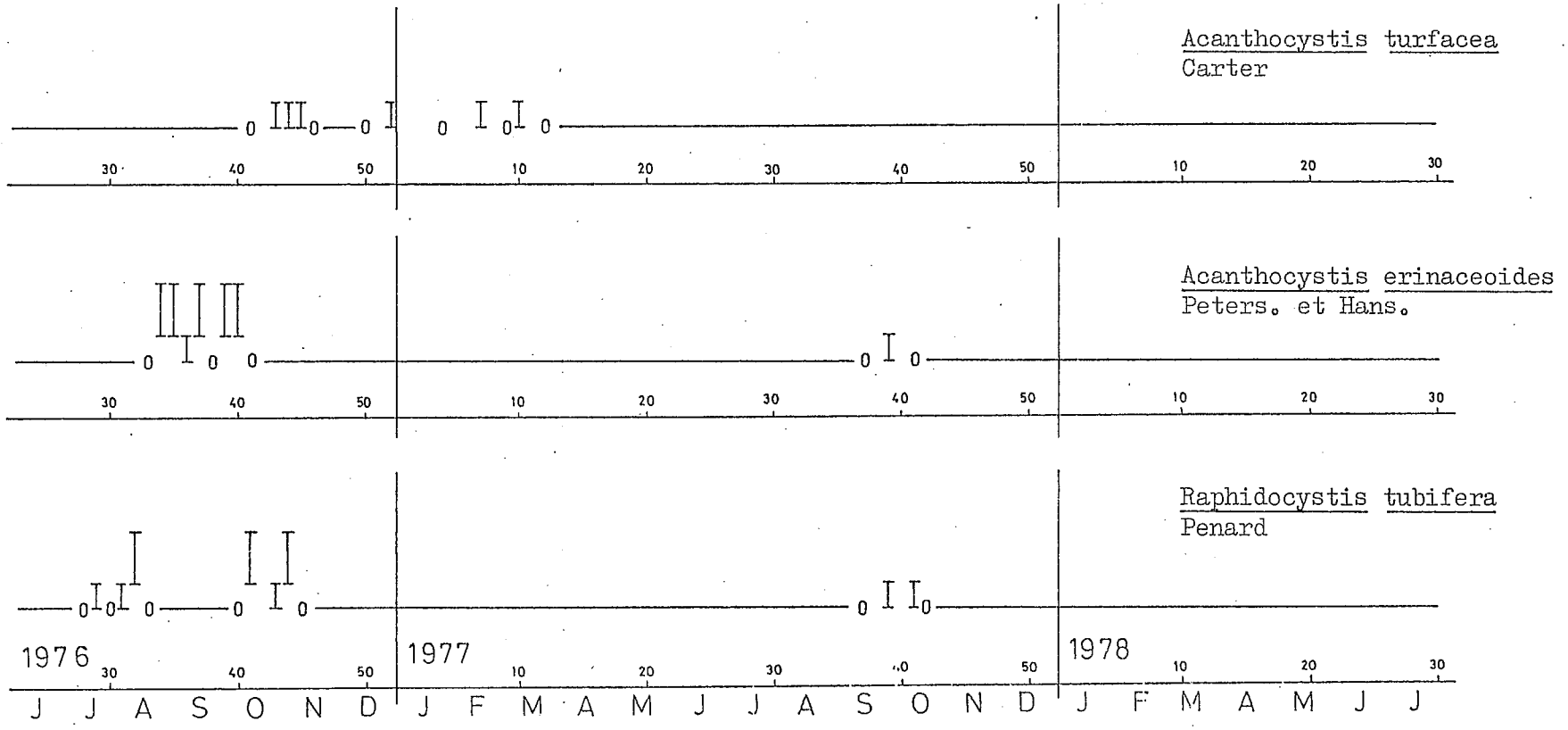
Of the other blue-green algae, the counts for Aphanizomenon show considerable fluctuations and are perhaps the least reliable, owing to the markedly non-random distribution of filaments of this alga (as aggregates or "flakes") in the samples sedimented for counting. An element of uncertainty also exists for the Microcystis determinations since a considerable variation in colony size was observed.

h) Heliozoans

The three species of Heliozoa detected with the light microscope (Acanthocystis turfacea, A. erinaceoides and Raphidocystis tubifera, Figs 97 - 99) were occasionally present in the Sawley plankton in autumn 1976 but were rarely found thereafter. It might therefore be assumed that the unusual weather conditions of 1976 could have been responsible for the appearance of these organisms in the plankton but inspection of Fig. 8 reveals that the two latter species were found both during the exceptionally dry period (July/August) and during the two months with heavy rain (September/October). A straightforward response to some climatic factor thus appears unlikely; an alternative possibility is that the appearance of these species is related to the population dynamics of some algal or protozoan food organism or of bacteria feeding on decomposing algae, but information on this point is lacking.

Acanthocystis turfacea has been recorded a number of times from Britain (Wailes 1921, including a Yorkshire record from West & West) and its preferred habitat is described as "lakes, ponds and moorland pools" (Wailes, loc. cit.). A. erinaceoides is known from its type

Figs 97 - 99. Periodicity of Acanthocystis turfacea, Acanthocystis erinaceoides and Raphidocystis tubifera.



locality in Denmark (Petersen & Hansen, 1960) and from Scotland (source of a culture deposited with C.C.A.P., Cambridge: see George, 1976). Raphidocystis tubifera is previously unrecorded for Britain; further information on this species is given in Section 5 (p. 104).

Volumetric Estimation of Biomass from Algal Counts

Estimations of the cell volumes of different species are required if the contribution of each to the total biomass is to be calculated. Values are available in the literature (See Table 5) but these show some discrepancies in individual cases even when an attempt is made by some authors to measure several hundred cells (e.g. Willén, 1976); it seems that the difference in size between the cells of different populations may render previous determinations inapplicable even if the latter were very precise. In the present investigation cell volumes were calculated according to the dimensions found here, approximating each to a sphere, cylinder or rectangular box as appropriate; some inaccuracies will inevitably have occurred owing to the approximations used or to variability in the natural populations but it is hoped that these are less serious than those which might be introduced if values were merely taken from the literature.

For colonial algae further approximations are necessary as the actual number of cells or filaments per colony sometimes cannot be estimated directly. The values adopted here are first-order approximations only and would need to be refined if more detailed quantitative studies were to be made; in that case, however, it would also be necessary to monitor changes in cell or colony size over the season and to pay more attention to the statistical reliability of the counts.

Two species of complex shape required a more involved calculation: for Staurastrum the volumes of the cell body and the protuberances were estimated separately and the values added together, while for Ceratium the calculation of Willén (1976) was followed. The counts for Trachelomonas included two species of different size; in this case the approximate ratio of their respective cell numbers was taken into account in determining a "mean" cell volume.

Table 5. Values for algal volumes used in calculation of Fig. 100.

Species	Volume per "individual" (μm^3)	Basis of estimation	Values given by other authors (μm^3)
Asterionella formosa (colony)	5,500	550 μm^3 per cell; av. 10 cells per colony	per cell: 750 (1); 700 (2); 650 (3); 800 (4); 550 (5)
Fragilaria capucina (100 µm filament)	6,800	340 μm^3 per cell; 20 cells per 100 µm	per cell: 486 (1); 200 (4)
Melosira italica subsp. *subarctica* (filament)	7,000	470 μm^3 per cell; 15 cells per filament	
Dinobryon divergens (colony)	5,500	225 μm^3 per cell; 20 cells per colony	per cell: 800 (2); 110 (5)
Mallomonas acaroides (cell)	900		
Volvox aureus (colony)	40,000	40 μm^3 per cell; 1,000 cells per colony	colony: 27,000 (1); 30,000 (4)
Eudorina elegans (colony)	2,900	180 μm^3 per cell; 16 cells per colony	13,500 (1); 4,000 (2); 3,000 (4)
Staurastrum cf. *cingulum* (cell)	7,600		*S.* "*paradoxum*": 20,000 (2)
Peridinium cinctum (cell)	45,000		*P. willei*: 40,000 (2)
Ceratium hirundinella (cell)	42,000	as in Willén (5)	70,000 (2); 41,700 (5)
Trachelomonas spp. (per cell, average)	2,100	1,530 μm^3 for small cells (ca. 90%); 5,600 μm^3 for large cells	large cells: 2,800 (5)
Anabaena solitaria (filament)	3,500	filament length 90 µm, diameter 7 µm	
Aphanizomenon flos-aquae (filament)	2,500	filament length 200 µm, diameter 4 µm	
Microcystis aeruginosa (colony)	60,000	40 μm^3 per cell; 1,500 cells per colony	per cell: 30 (1); colony: 100,000 (2); 100,000 (3)
Coelosphaerium naegelianum (colony)	15,000	30 μm^3 per cell; 500 cells per colony	per cell: 20 (5)
Gloeotrichia echinulata (colony)	14,000,000	filament length 500 µm, diameter 6 µm; 1,000 filaments per colony	

References: (1) = Bellinger (1974); (2) = Findenegg, in Vollenweider (1974); (3) = Nalewajko (1966); (4) = Nauwerck (1963); (5) = Willén (1976).

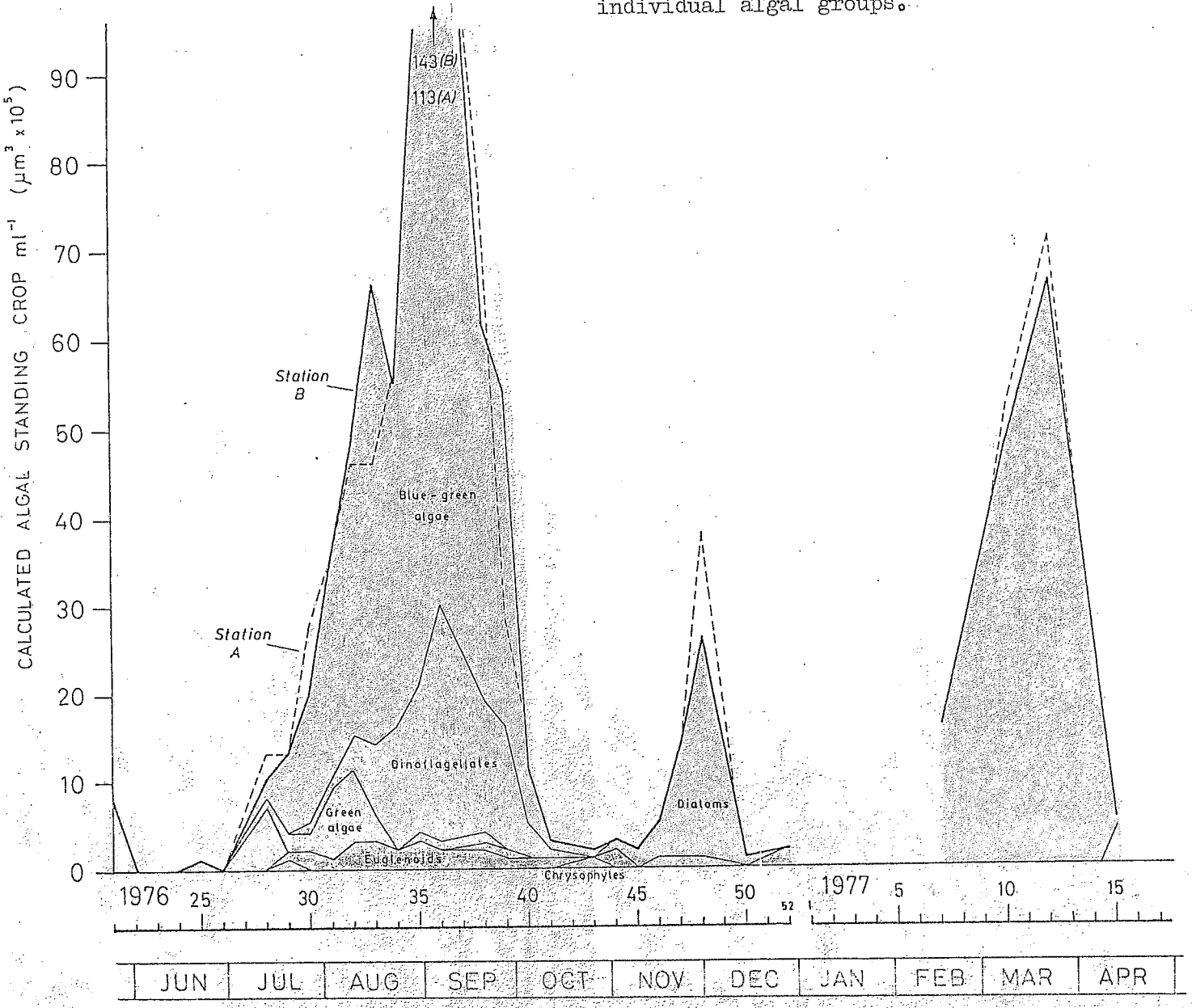
Preliminary calculations suggested that the total calculated biomass in summer 1976 would exceed 100 x 10^5 μm^3 ml^{-1}, and therefore a level of 1 x 10^5 μm^3 ml^{-1} was chosen to represent the minimum "significant" contribution by any one species. This level corresponds to 0.1 mm^3 l^{-1} or 0.1 cm^3 m^{-3} as expressed elsewhere in the literature. From the values given in Table 5 it is clear that different species would reach this level with different numbers of individuals. For example, in 1 ml, 1 x 10^5 μm^3 would be provided by approximately 110 cells of Mallomonas, 29 filaments of Anabaena solitaria, 18 colonies of Asterionella or 2.4 cells of Ceratium; the same level would be provided by 1.7 Microcystis colonies or 0.0007 of a Gloeotrichia colony. The minimum "significant" level was calculated for each species and compared with recorded values to enable periods of significant biomass to be identified, within which the volumetric contribution of each species was calculated.

Figure 100 shows the total calculated biomass for Station B and the relative contributions by algae of each class. The total biomass calculated for Station A is also shown (broken line) where this differs appreciably from that for Station B. The 1976 summer peak commencing in July is seen to be due principally to the blue-green algae although small amounts are contributed by diatoms (Melosira), green algae (chiefly Eudorina and Staurastrum) and euglenoids (Trachelomonas). From mid-August to the end of September the dinoflagellates (Peridinium and Ceratium) form an important subsidiary component of the biomass; at the peak levels recorded (wk 36a), the composition (by volume) at Station B is 79% blue-green algae (including 68.5% from Anabaena solitaria), 18.9% dinoflagellates and 2.1% from other algae.

The diatoms provide the bulk of the winter-spring crop (except under ice, when no counts were made) and all of the significant biomass is due to Asterionella. Fragilaria contributes the small peak at wk 25a, reaching only ca. 1 x 10^5 μm^3 ml^{-1}; this is also the maximum level of the chrysophytes, Dinobryon at wk 29a and Mallomonas at wk 43a.

Some discrepancies are apparent between the values from Stations A and B but in general there is good agreement,

Fig. 100. Cumulative plot of calculated algal volumes showing contributions from individual algal groups.



considering that counts of 100 organisms are subject to confidence limits of ± 20% at p = 0.05 (Lund et al., 1958) and that most of the present counts were on 50 - 70 organisms or less (see p. 44). The chief differences are seen at wks 33a and 39a and, in each case, these mainly reflect variation in the numbers of Anabaena solitaria between the two stations. The Station B trace shows a temporary setback at wk 34a which brings its total value back to the level at Station A; this was caused by an abrupt decline in numbers of Gloeotrichia coupled with a lack of increase in A. solitaria from the previous week.

The computed biomass curves are very similar to those obtained from chlorophyll a and transparency data (Fig. 13) which suggests that the use of algal volume is a sound basis for weighting the contributions of different species to a biomass total. The degree of correspondence between particular portions of the curves will be examined further in the General Discussion.

SECTION 4 ELECTRON-MICROSCOPE STUDIES ON THE DISTRIBUTION OF SCALE-BEARING PLANKTONIC ORGANISMS

Introduction

EM examination of plankton samples prepared as whole mounts allows some of the smaller organisms omitted from Section 3 to be identified from their surface scales. Such scales are found chiefly in the family Synuraceae of the Chrysophyceae but may also occur on freshwater organisms of some other groups. Typically, individual scales are highly characteristic for each species and so even isolated scales can provide a reliable indication of the presence and identity of a particular species in the body of water from which the sample was taken. Some of these species might not be detectable in any other way since their diagnostic features can be too small to recognise in the light microscope; others might be omitted from LM-based surveys if they occur only in small quantities or if their population maxima are very brief. EM study of the plankton samples aids the detection of such rare or intermittent species since large quantities of material are not essential for accurate determination to species level; in addition, traces from previous maxima may still be apparent if the scales persist longer in the plankton than do the living organisms.

A survey of some of the Sawley Dene collections with the EM would thus add to the knowledge of the algal flora of this site and might enable further comparisons to be made with lakes elsewhere. In addition, within the Sawley Dene habitat it might be possible to distinguish species of widespread or restricted distribution: the occurrence of rare species or those found only in a specific type of habitat would be of greater ecological interest than the occurrence of cosmopolitan species of wide habitat tolerance. Knowledge of the distribution of these organisms elsewhere is required before such distinctions can be made; however, examination of the literature showed that only a limited amount of data exists for other lakes. In Britain none of the major bodies of water have been surveyed at this level, with the exception of certain unpublished observations on

Abbot's Pond and Priddy Pool, Somerset (Abdel Karim, 1965). Preliminary investigations were therefore undertaken of plankton collections from a number of lakes and pools in the Sawley area in order to provide some comparative data.

Attempts to identify all the species in collections from the Sawley area met with some difficulty owing to the scattered and, in some cases, incomplete taxonomic data in the literature; without accurate identifications no meaningful ecological comments could be made. A considerable part of this Section is therefore devoted to establishing the characteristic features and systematic position of each species identified, together with its "correct" name or a provisional new name if this is necessary. An Ecological Discussion then follows in which the status of the Sawley Dene organisms and of Sawley Dene as a habitat will be compared with results from elsewhere in the study area.

In both the Taxonomic Discussion and the Ecological Discussion the Chrysophyceae are treated separately from the other organisms, since the former group have received a greater amount of attention from other workers and more information is available on their taxonomy and distribution. As many of the non-chrysophycean organisms may be protozoa rather than true algae they have usually been omitted from past surveys conducted by botanists and some are poorly known, if known at all. For these organisms, therefore, the results presented here are of a preliminary nature and fewer ecological conclusions can be drawn.

Materials and Methods

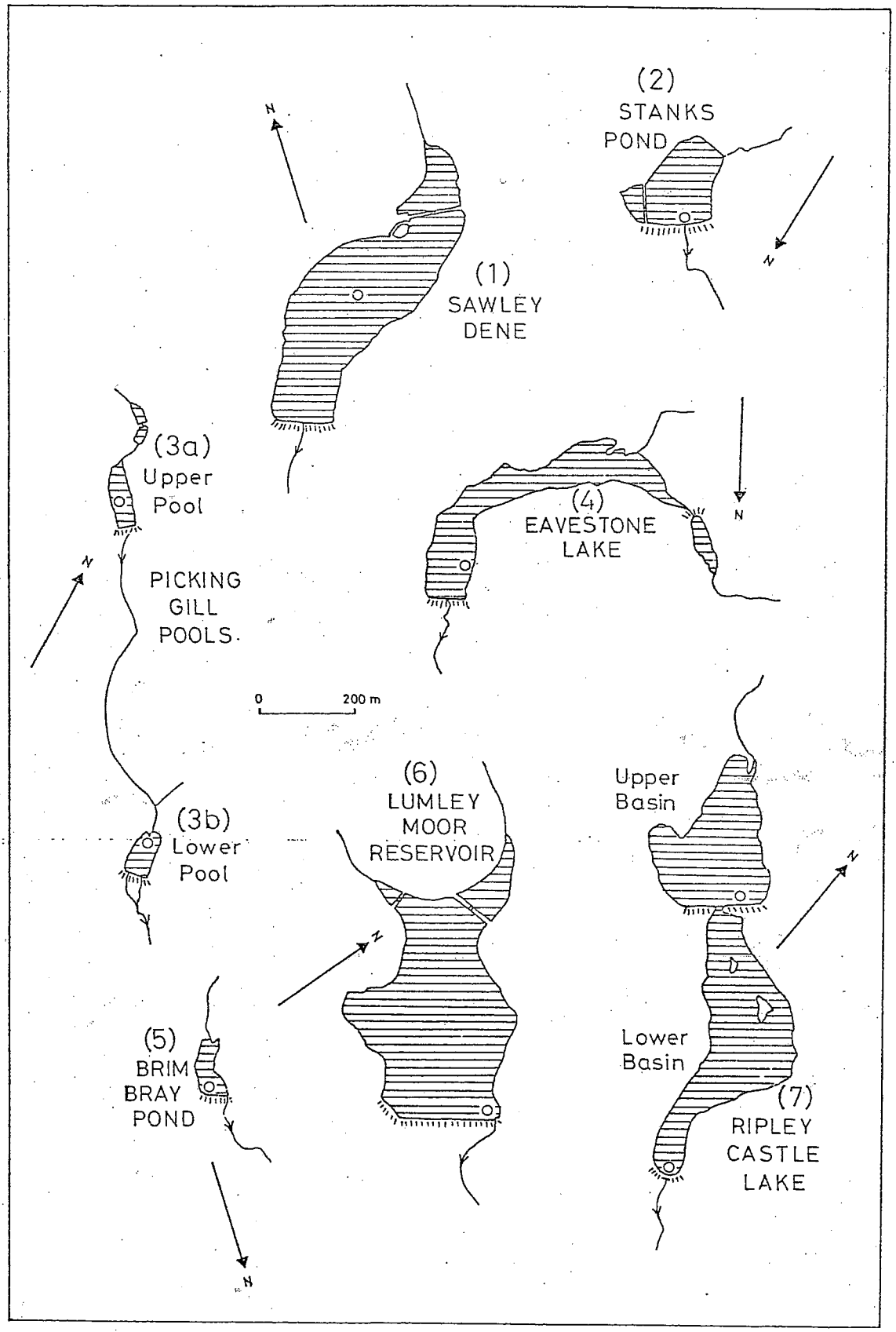
A range of living and preserved net-samples were prepared for EM examination by placing a drop of suspension containing organisms onto a formvar-coated grid, exposing to OsO_4 vapour for ½ - 1 minute to kill living cells if necessary and allowing to dry at room temperature. Dried preparations were rinsed in distilled water, dried again and coated with evaporated gold:palladium (60:40) in an NGN coating unit, using a shadowing angle of ca. 40°. Preparations were examined in Siemens Elmiskop 1A and 102 electron microscopes.

Table 6. Characteristics of lakes in Sawley area sampled for Chrysophyceae.

Lake	Grid ref.	Distance from Sawley Dene	Altitude	Surface area	Estimated max. depth	Nature of lake margins	Summer phytoplankton (if known)	pH	Date(s) of sampling
SAWLEY DENE (1)*	263667	-	113 m (370 ft)	9.5 ha	4.6 m	wooded, steep	blue-green algae	7.6 - 8.2	throughout year
STANKS POND (2)	282680	2 km	113 m (370 ft)	2.4 ha	1.5 m	farmland, gently sloping	-	8.1	28.2.78
PICKING GILL UPPER POOL (3a)	233672	3 km	195 m (640 ft)	0.48 ha	3 m	wooded, steep	-	7.6	5.4.78
PICKING GILL LOWER POOL (3b)	237666	2.5 km	149 m (490 ft)	0.43 ha	3 m	wooded, steep	-	7.6	5.4.78
EAVESTONE LAKE (4)	227678	4 km	168 m (550 ft)	4.5 ha	6 m	wooded, steep	blue-green algae	7.8	28.2.78 24.3.78 30.8.78
BRIM BRAY POND (5)	217687	5 km	170 m (560 ft)	0.51 ha	2 m	farmland/scrub, gently sloping	-	5.2	28.2.78
LUMLEY MOOR RESERVOIR (6)	223708	5.5 km	180 m (590 ft)	11.0 ha	10 m	farmland/woods, gently sloping	chrysophytes (very thin)	5.9	22.3.78 30.8.78
RIPLEY CASTLE LAKE (7)	280609	6 km	64/61 m (210/200 ft)	11.0 ha	3 m/ 4 m	farmland/park, gently sloping	chrysophytes	6.5	22.3.78 30.8.78

* numbers in brackets refer to designations on Figs 3 and 101.

Fig. 101. Lakes and ponds in Sawley region sampled for Chrysophyceae.



(deepest water towards base of each Figure; o = sampling point).

In addition to Sawley Dene samples (see Appendix I for list of samples investigated) collections from a number of other lakes and pools in the Sawley area were prepared for EM examination. The lakes were selected to represent a range of habitat types and river systems in the surrounding area; their locations are shown on Fig. 3 (Section 1) and their principal features are described in Table 6 and Fig. 101. All the lakes are artificially constructed and each has a sloping profile with a dam at the deeper end. Most of the lakes are of simple morphometry except for Ripley Castle Lake, which consists of two basins lying at different altitudes and connected by a weir, and Eavestone Lake, which has a smaller pool lying above the head of the lake and flowing into the main lake via a waterfall.

Sawley Dene, Stanks Pond, the Picking Gill Pools and Eavestone Lake represent a range of water-body types which share an alkaline nature, apparently owing to their situation on calcareous glacial drift (see p. 15). Brim Bray Pond, Lumley Moor Reservoir and Ripley Castle Lake are acidic in character and lie beyond the limit of the glacial drift, their water character being more influenced by the millstone grit bedrock.

Results and Taxonomic Discussion

PART A: CHRYSOPHYCEAE

Note: The arrangement of species in *Mallomonas*, the largest genus and that most well-represented in the study area, mainly follows Peterfi & Momeu (1976), whose scheme is derived from that of Harris & Bradley (1960); the chief departure from Peterfi & Momeu's arrangement is that *Mallomonopsis*, instead of being absorbed into *Mallomonas*, is here retained as a separate genus, following the practice of Harris (1970) and Kristiansen (1975b). *Synura* species are arranged as in Balonov & Kuz'min (1974) and species of the remaining genera (*Chrysosphaerella*, *Spiniferomonas* and *Paraphysomonas*) as in Takahashi (1978). Reference should be made to the above works for a fuller taxonomic treatment; a synopsis of the classification of *Mallomonas* and *Mallomonopsis* as adopted here is given in Appendix IV.

MALLOMONAS

Sectio Mallomonas: series acaroides

1. Mallomonas acaroides Perty emend. Iwanoff var. striatula Asmund (Figs 102 - 104).

Scales tripartite, i.e. consisting of a dome, shield and flange, the latter two areas separated by a V-rib (for further explanation see Harris & Bradley, 1960). Body of scale bearing perforations; radiating struts present on flange, extending across V-rib some distance onto shield. Bristles of two types: with unilateral serrations and a "helmet" tip (Fig. 103), and similar but without helmet tip (arrow, Fig. 102), these latter bristles being characteristic of var. striatula (Fott, 1962). This species has been illustrated earlier from the LM (Figs 24, 25).

Occurrence: Abundant in Sawley Dene, autumn/winter 1976; absent in 1977. A few scales found in Picking Gill Upper Pool and Ripley Castle Lake.

Reported Distribution: Common throughout world (usually recorded as M. acaroides). Abdel Karim (1965) found this species to be occasional in Abbot's Pond.

2. Mallomonas crassisquama (Asmund) Fott (Fig. 105)

Scales resembling those of M. acaroides but with reticulate development of thickened struts across shield. Occasional scales in a population show a lesser degree of development of this feature and can lead to confusion with M. acaroides. Uniseriate serrated bristles with and without helmet-tips present.

Occurrence: Occasional in Sawley Dene, winter 1976, with M. acaroides. Occasional in Picking Gill Upper Pool and Eavestone Lake; common in Lumley Moor Reservoir (summer sample only).

Reported Distribution: Widespread throughout world but no previous British records.

3. Mallomonas tonsurata Teiling emend. Krieger (Figs 106, 107).

Some scales tripartite, others lacking dome. Body of scale with relatively large, closely-spaced perforations. Scale rather diamond-shaped in outline, cf. M. alpina (below). Bristles of two types, neither with helmet-tip:

NOTE. In the following 18 plates (Figs 102 - 217), whole cells are illustrated at x 3,000 and individual scales at x 12,000 as far as is practicable.

FIGS 102 - 107 TEM (whole mounts) of scale-bearing Chrysophyceae, I.

Figs 102 - 104 *Mallomonas acaroides* var. *striatula*.

Fig. 102: whole cell, x 3,000; note spine without helmet tip (arrow).

Fig. 103: scale and spine, x 6,000.

Fig. 104: scale and base of spine, x 12,000.

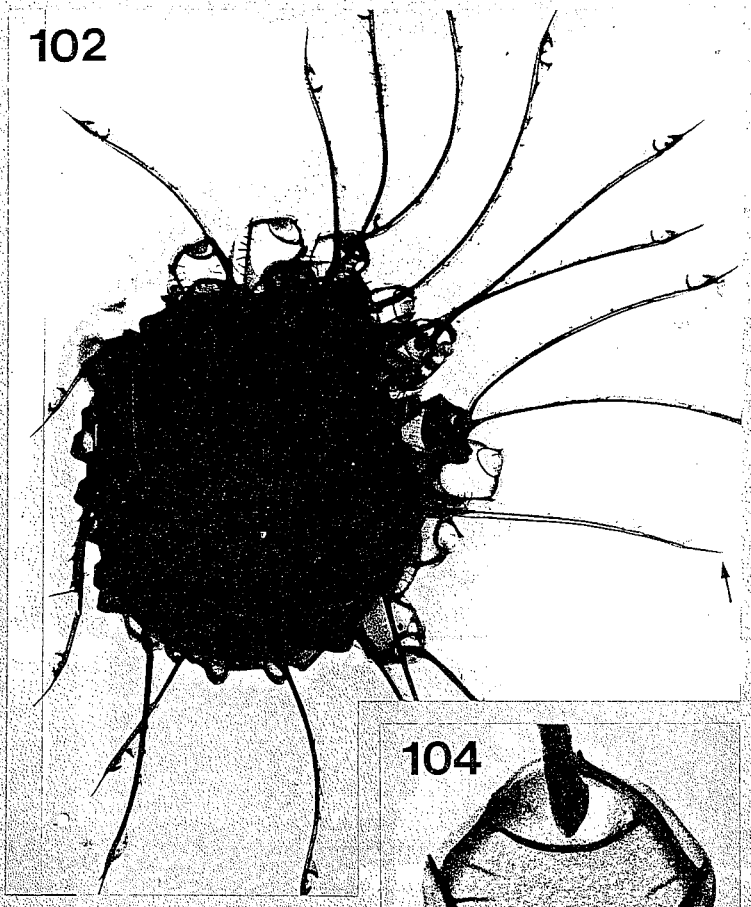
Fig. 105: *Mallomonas crassisquama*: group of scales, x 12,000.

Figs 106 - 107 *Mallomonas tonsurata*.

Fig. 106: body scale, x 12,000.

Fig. 107: domed scale and spine, x 12,000.

Source of specimens: Sawley Dene (Figs 102 - 104)
Picking Gill Upper Pool (Fig. 105)
Lumley Moor Reservoir (Figs 106 - 107).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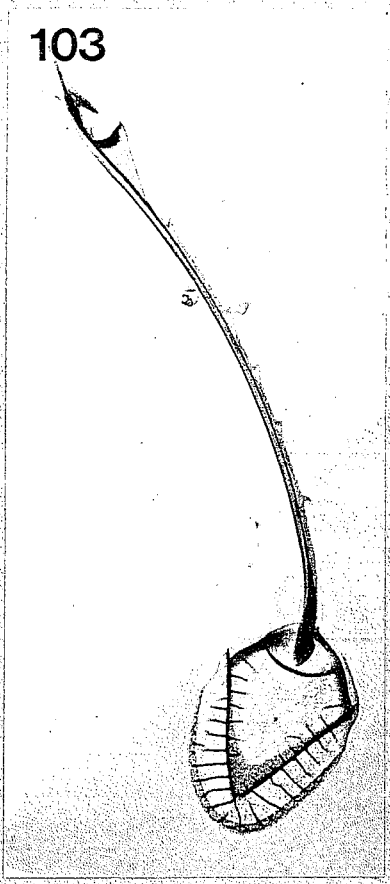
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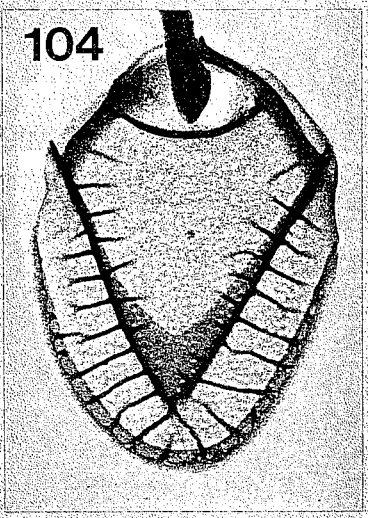
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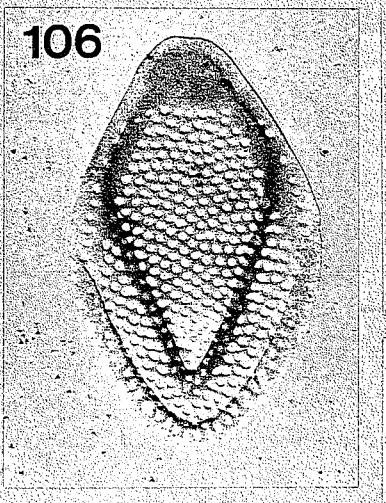
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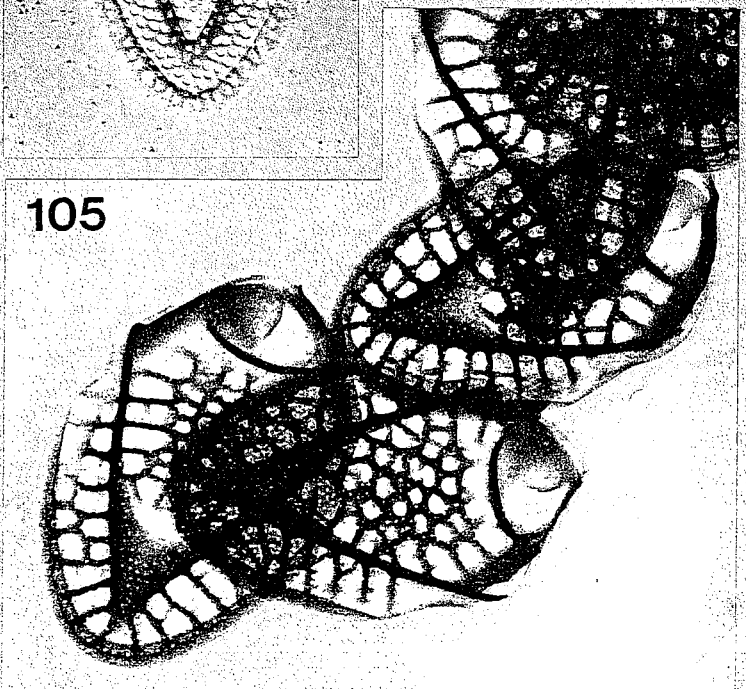
107


105

one short, broad, with prominent uniseriate serrations (Fig. 107), the other longer and smooth except for small tooth below tip (not illustrated).
Occurrence: Common, in summer samples only, from Lumley Moor Reservoir and Ripley Castle Lake.
Reported Distribution: Very common throughout world. Found by Harris & Bradley (1960) in Berkshire and Abdel Karim (1965) in Abbot's Pond. According to Asmund (1959) it is chiefly a summer form.

4. Mallomonas alpina Pascher et Ruttner (Figs 108, 109).
syn. M. tonsurata var. alpina (Pascher et Ruttner) Asmund
M. monograptus Harris et Bradley
Scales tripartite, resembling those of M. acaroides but with perforations as only ornamentation on flange and shield; differing from M. alpina in size and proportions of scale, and in density of perforations. Bristles of one type, with uniseriate serrations and pointed tip.
Occurrence: Common in Sawley Dene, spring 1978 (absent in 1977). Very common in both Picking Gill Pools. Isolated scales in Ripley Castle Lake.
Reported Distribution: Very common throughout world; according to Asmund (1959), typically a spring and autumn form. Recorded by Harris & Bradley (1960) in small pools and lakes in Berkshire.

5. Mallomonas actinoloma Asmund et Takahashi var. maramuresensis Peterfi et Momeu (Figs 110, 111).
Some scales tripartite, others (e.g. those found here) lacking a dome. Scale with characteristic lateral extension to shield, forming in effect an "anterior flange", separated from "flange" proper by a pronounced median incision. Body of scale perforated, anterior flange ornamented with short radiating struts. Var. maramuresensis is characterised by a highly developed anterior flange, sometimes with a complex pattern at the apex (arrow, Fig. 110), and by a series of parallel ribs across the shield. Bristles smooth, relatively short and slightly curved.
Occurrence: Two scales only, from Brim Bray Pond.
Reported Distribution: Known only from the type locality, an acid bog site in Romania (Peterfi & Momeu, 1976).

FIGS 108 - 112 TEM of scale-bearing Chrysophyceae, II.

Figs 108 - 109 *Mallomonas alpina*.

Fig. 108: portion of scale case, x 3,000.

Fig. 109: two scales and spines, x 12,000.

Figs 110 - 111 *Mallomonas actinoloma* var. *maramuresensis*.

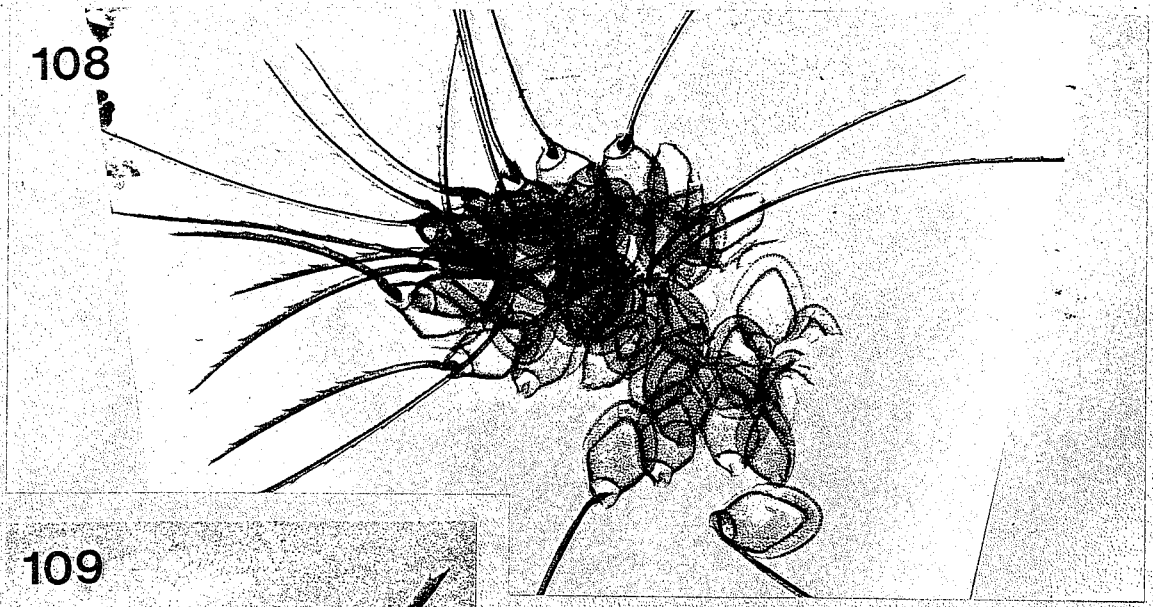
Fig. 110: domed scale, x 12,000; note markings on dome (arrow).

Fig. 111: domeless scale and spine, x 12,000.

Fig. 112: *Mallomonas striata*: whole cell, x 3,000.

Source of specimens: Sawley Dene (Figs 108 - 109, 112)
Brim Bray Pond (Figs 110 - 111).

108



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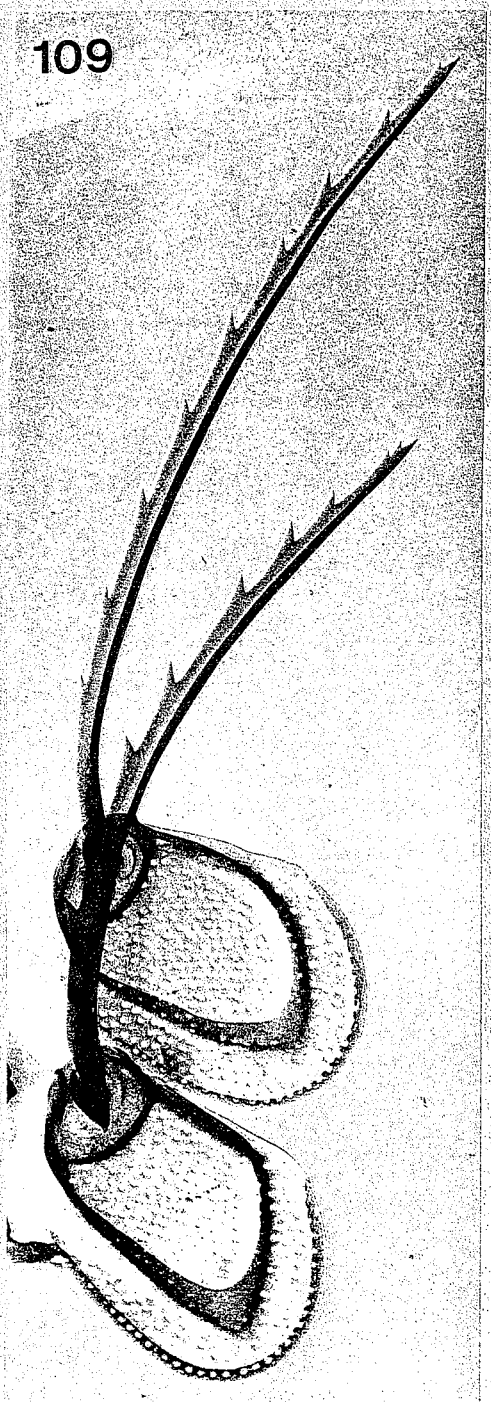

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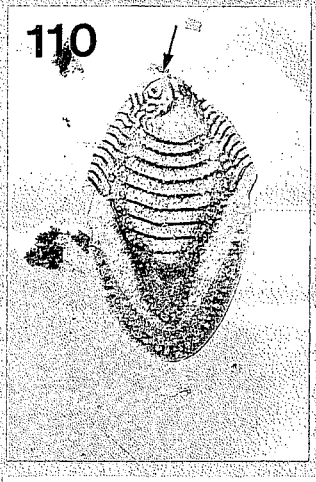


111

112

M. actinoloma var. actinoloma is also rare, recorded only from Alaska and Japan (Asmund & Takahashi, 1969), although Takahashi (1978) reports finding a variant form in Korea.

MALLOMONAS

Sectio Mallomonas (cont'd): series striatae.

6. Mallomonas striata Asmund (Figs 112, 113).
Scales tripartite, comparatively large, but with the small dome typical of the striata group (see Harris & Bradley, 1960). Body of scale with only a small group of perforations, in apex of V-rib. Shield and flange traversed by regularly-spaced ribs. Bristles (not illustrated), smooth and slightly curved.
Occurrence: Isolated scale groups in Sawley Dene, spring 1977 and 1978.
Reported Distribution: Fairly uncommon, known only from four localities throughout the world, viz. Denmark (Asmund, 1959), USSR (Balonov & Kuz'min, 1975), Scotland (Bradley, 1966) and Dove Nest in the Lake District (Asmund, 1959). It was not found by Harris & Bradley (1960), despite extensive collections in Berkshire.

7. Mallomonas striata var. serrata Harris et Bradley (Fig. 114).
Scales similar to those of the preceding taxon but smaller, without perforations in apex of V-rib, and with serrated bristles.
Occurrence: Occasional in the two Picking Gill Pools.
Reported Distribution: More widespread than M. striata but not very common. Reported by Harris & Bradley (1960) from shallow, flooded habitats in Berkshire.

8. Mallomonas flora Harris et Bradley (Figs 115 - 117).
Scales similar to those of M. striata but with characteristic pattern of pores and struts in apex of V-rib (Fig. 117). Curved ribs present on dome (cf. smooth dome of M. striata). Bristles similar to those of M. striata var. serrata.
Occurrence: Occasional cells and scales in Brim Bray Pond; isolated scales in Picking Gill Lower Pool and Lumley Moor Reservoir.
Reported Distribution: Rare throughout the world; recorded in Japan (Takahashi, 1978), USA (Wujek & Hamilton, 1972) and from the type locality, acid ponds in Berkshire (Harris & Bradley, 1960).

FIGS 113 - 117 TEM of scale-bearing Chrysophyceae, III.

Fig. 113: *Mallomonas striata*: group of scales, x 12,000.

Fig. 114: *Mallomonas striata* var. *serrata*: scale and spine, x 12,000.

Figs 115 - 117 *Mallomonas flora*.

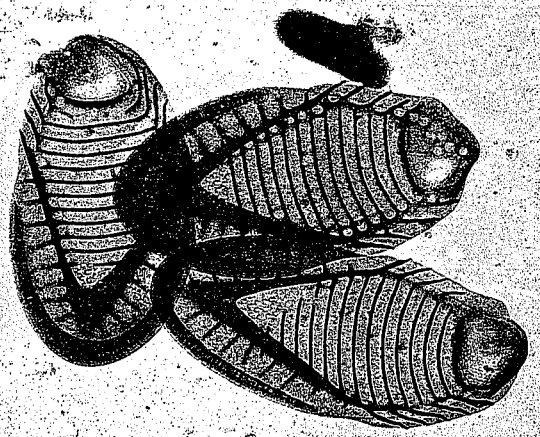
Fig. 115: whole cell, x 3,000.

Fig. 116: scale and spine, x 12,000.

Fig. 117: detail of patterning in apex of V-rib, x 24,000.

Source of specimens: Sawley Dene (Fig. 113)
Picking Gill Upper Pool (Fig. 114)
Brim Bray Pond (Figs 115 - 117).

113



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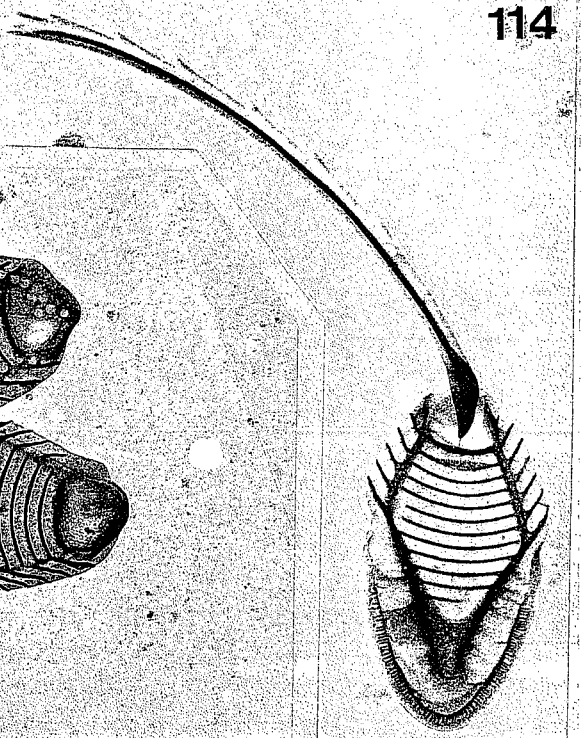

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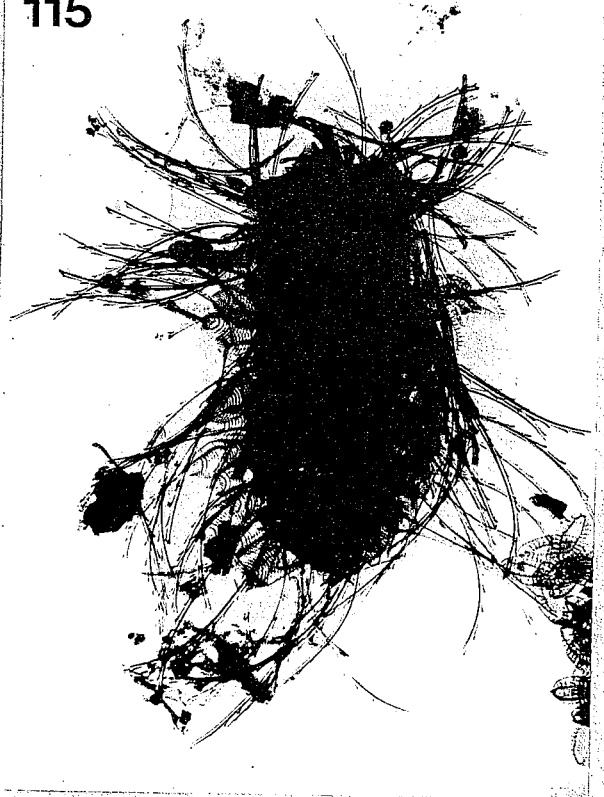

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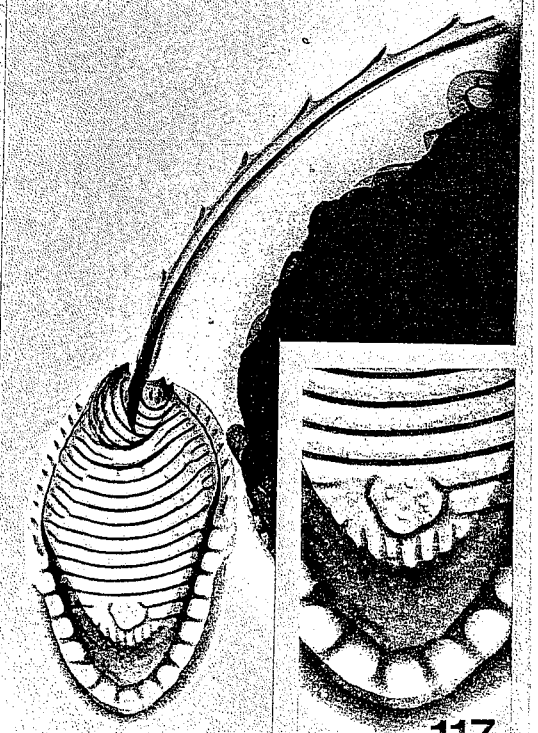


117

MALLOMONAS

Sectio Mallomonas (cont'd): series papillosae.

9. Mallomonas papillosa Harris et Bradley (Figs 118, 119).
Scales tripartite, with a small dome. Shield bears very regular pattern of papillae and is unperforated. Short radial struts extend across anterior margins of shield. Bristles short, smooth and curving.
Occurrence: A few cells in Brim Bray Pond; isolated scales in Ripley Castle Lake (spring sample).
Reported Distribution: Common throughout the world; found by Harris & Bradley (1957, 1960) in Berkshire and Belcher (1969) in Lancashire in shallow, flooded habitats.

10. Mallomonas pillula Harris (Fig. 120).
Scales similar in form to those of M. papillosa but with a hexagonal pattern of struts across the shield. On complete cells short, smooth bristles occur (Harris, 1967).
Occurrence: Picking Gill Upper Pool and Ripley Castle Lake (a single scale only from each site).
Reported Distribution: Very rare elsewhere in the world; a few scales found in Iceland (Bradley, 1964) and a specimen in Alaska (Asmund & Takahashi, 1969), in addition to the type material from a woodland lake in Berkshire (Harris, 1967).

11. Mallomonas annulata (Harris et Bradley) Harris (Figs 122 - 124).
Some scales tripartite, others diamond-shaped and lacking a dome. Body of scale with both perforations and papillae, also with rudimentary struts extending inward from the V-rib, sometimes forming a more extensive pattern (e.g. Fig. 124). Bristles short, smooth and curved.
This species has a rather confused taxonomic history: see Harris (1967).
Occurrence: Occasional scale-groups found in Sawley Dene, spring 1977 and 1978; also, in small numbers, in Picking Gill Lower Pool and Brim Bray Pond.
Reported Distribution: Fairly widespread throughout the world but often in low numbers. Recorded by Bradley (1966) from Scotland and Harris & Bradley (1960) from Berkshire.

FIGS 118 - 124 TEM of scale-bearing Chrysophyceae, IV.

Figs 118 - 119 *Mallomonas papillosa*.

Fig. 118: portion of cell, x 6,000.

Fig. 119: single scale, x 12,000.

Fig. 120: *Mallomonas pillula*: single scale, x 12,000.

Figs 121 - 124 *Mallomonas annulata*.

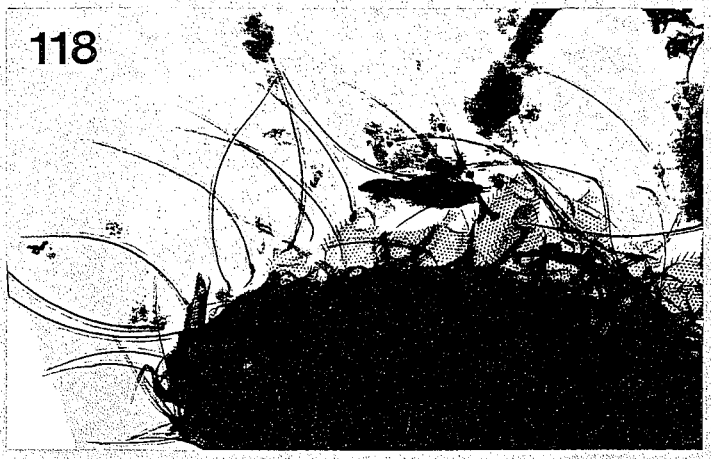
Fig. 121: whole cell, x 3,000.

Fig. 122: edge of cell, x 6,000.

Fig. 123: group of scales showing little ornamentation, x 12,000.

Fig. 124: group of scales with more marked ornamentation x 12,000.

Source of specimens: Brim Bray Pond (Figs 118 - 119, 121 - 122)
Picking Gill Upper Pool (Fig. 120)
Picking Gill Lower Pool (Fig. 123)
Sawley Dene (Fig. 124).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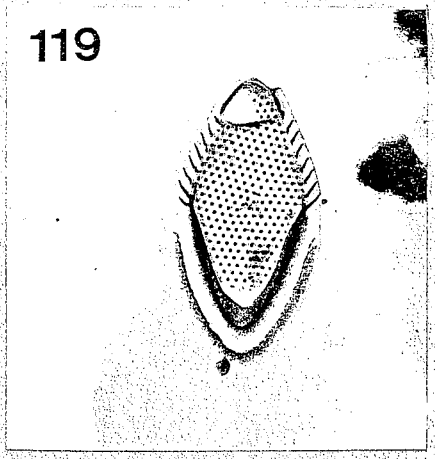
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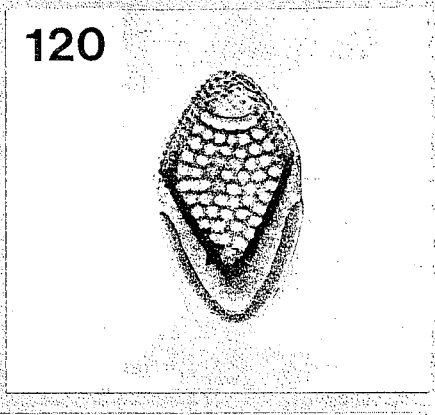
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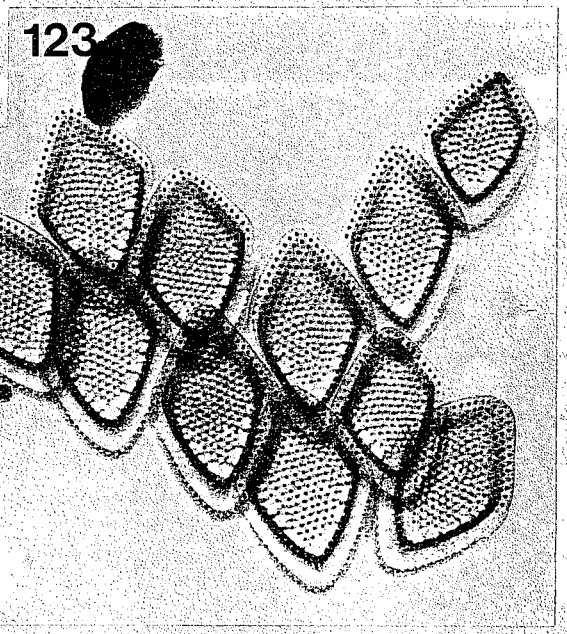
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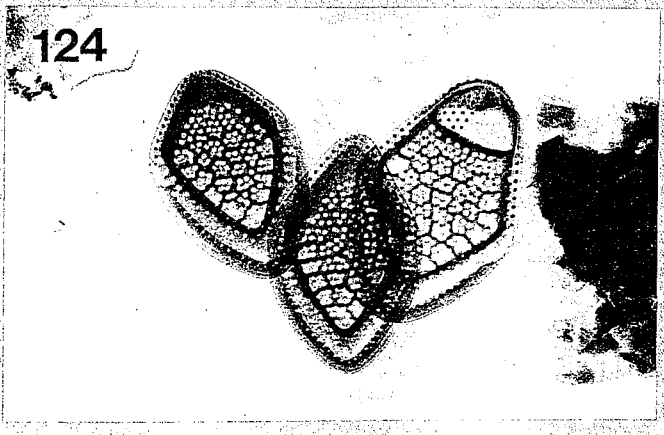

124

MALLOMONAS

Sectio Torquatae: series pumilae.

12. Mallomonas pumilio Harris et Bradley var. "perforata" var. nov. (Figs 125 - 128).

Scales of three types, characteristic of species in the Torquatae: at anterior of cell, a ring of "collar" scales asymmetric, domed and bearing bristles; diamond-shaped body scales with no dome; and diamond-shaped posterior scales bearing short spikes. Ornamentation similar on all scales, consisting of a hexagonal pattern of struts on body of scale, enclosing groups of 4 - 5 pores in "rosettes". Posterior margin of scale bears a peripheral rib and anterior margin bears double row of perforations. Bristles smooth, curving with a sharp point.

This organism resembles M. pumilio in general features and in the rosette-groupings of pores on the scale, but the ribbing is rather more delicate than in M. pumilio sens. strict. and the perforated margin is a new feature (cf. Harris & Bradley, 1960; Asmund & Hilliard, 1961; Peterfi & Momeu, 1976). These features are constant among the present population and enable this taxon to be readily distinguished from M. pumilio. The organism will therefore be treated here as a new variety of the latter species.

Occurrence: Cells fairly frequent in Brim Bray Pond, absent elsewhere.

Reported Distribution: Not found elsewhere in world. M. pumilio var. pumilio has been recorded by a number of other workers (details given above).

A detailed description of this organism is given in Appendix V.

13. Mallomonas "clavoides" sp. nov. (Figs 129, 130).

Scales of three types as in the previous species. Ornamentation on scales consisting of thick intersecting ridges which leave small depressions of irregular shape between them. Scale margins unperforated, bearing short struts resembling a row of teeth. Posterior scales with short spikes.

The ornamentation of the scales is similar to that of M. clavus Bradley, which, however, has a different cell form to the present species (see Bradley, 1964); M. clavus has long posterior spines as is typical of species in the

FIGS 125 - 130 TEM of scale-bearing Chrysophyceae, V.

Figs 125 - 128 *Mallomonas pumilio* var. "*perforata*".

Fig. 125: whole cell, x 3,000; note single flagellum.

Fig. 126: more rounded cell, x 6,000.

Fig. 127: individual body and collar scales, x 12,000.

Fig. 128: complete scale case, x 12,000; note tiny posterior spine (arrow).

Figs 129 - 130 *Mallomonas* "*clavoides*".

Fig. 129: whole cell, x 3,000.

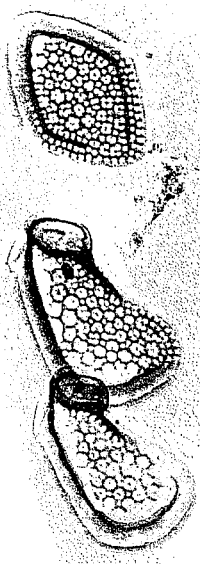
Fig. 130: another whole cell, x 12,000; note posterior spines (arrow).

Source of specimens: Brim Bray Pond (all Figures).

125

126

127



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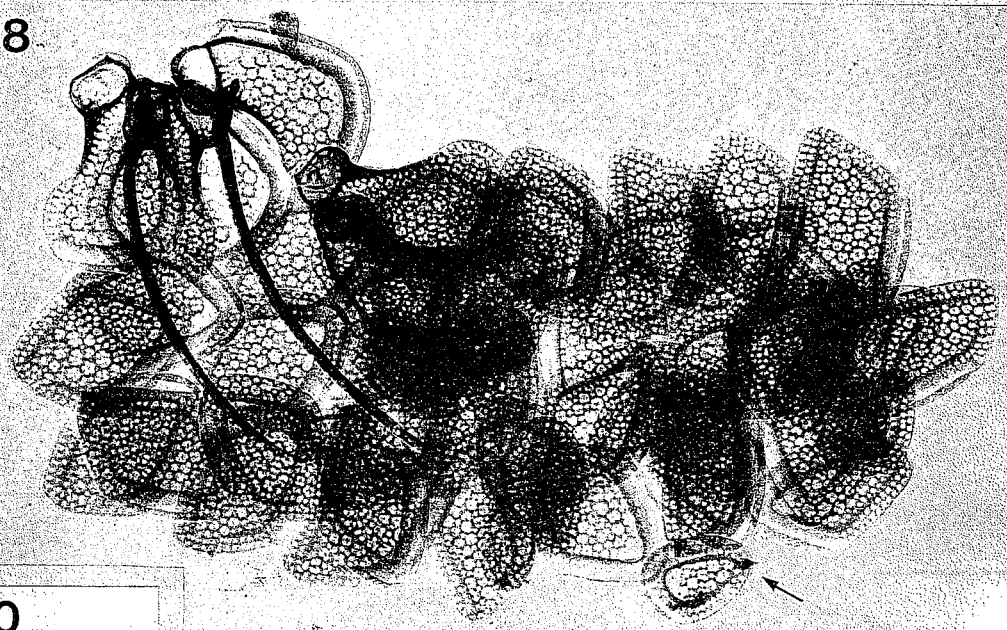

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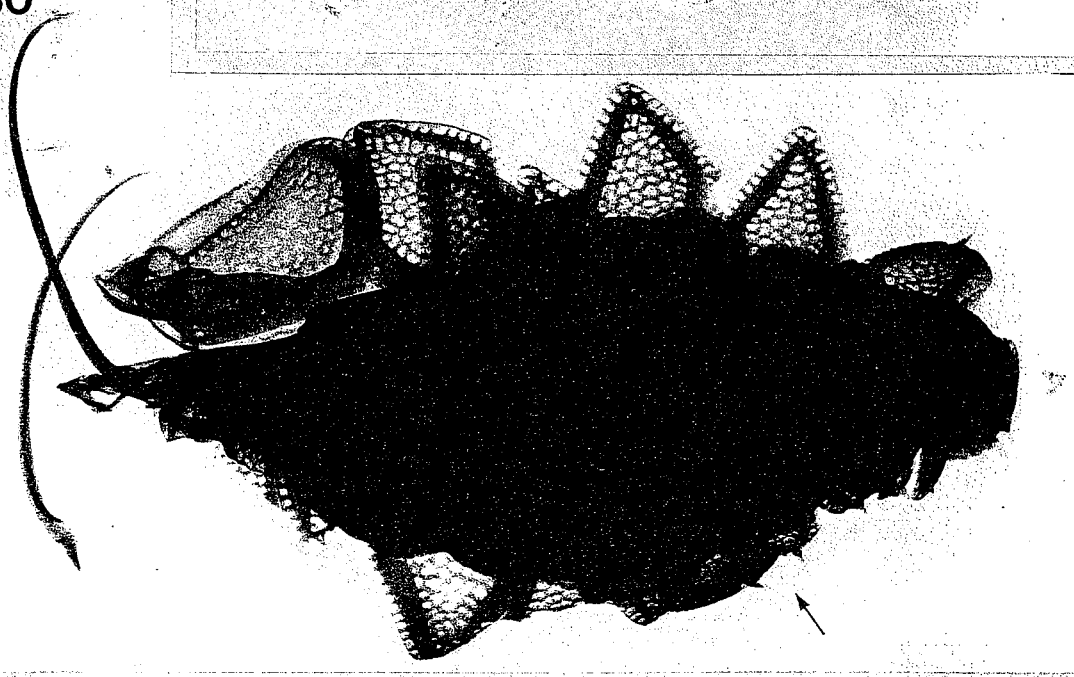


series allantoides (cf. the short posterior spikes of the present series, pumilae). No species is yet described which combines the scale type of M. clavus with the cell type of the pumilae, although one organism (identified as "M. clavus") has been illustrated which combines the scale type of M. pumilio with an allantoides cell type (Kristiansen, 1975b), which suggests that some parallel organisms may exist in each series. The present organism thus requires a new name and it is sufficiently distinct from M. pumilio, the species nearest to it in the series pumilae, to be considered a separate species.

A variety of M. pumilio, var. silvicola Harris et Bradley, is described as resembling M. pumilio but lacking the rosette structure of the pore groups (Harris & Bradley, 1960). While this description could also apply to M. "clavoides", comparison of the present organism with the micrographs of M. pumilio var. silvicola shows that the scale of M. "clavoides" is thickened much more heavily and it is easily distinguishable from the latter taxon.

M. clavus, as discussed here, does not include M. eoa Takahashi, with which it has sometimes been combined (e.g. Harris, 1970). The scales of M. eoa bear a rather different pattern of ornamentation (see Takahashi, 1963; Bradley, 1966), the ridges forming a repeating circular pattern on the scale.

Occurrence: A small number of whole cells in Brim Bray Pond; not found at the other sites studied.

Reported Distribution: No evidence of its occurrence elsewhere. A detailed description of this organism is given in Appendix V.

14. Mallomonas sp. cf. M. schwemmlei Glenk (Fig. 131). This taxon is represented by two collar scales, one with an attached bristle, indicating a position within the Torquatae. Maze-like pattern of ribbing on one of the scales reminiscent of that of M. schwemmlei (cf. Glenk & Fott, 1971), although in the latter species the ribs are rather fine and more closely-spaced. The second scale in Fig. 131 shows less ornamentation and is closer to a scale of M. "clavoides" (see above); it is therefore possible

FIGS 131 - 134 TEM of scale-bearing Chrysophyceae, VI.

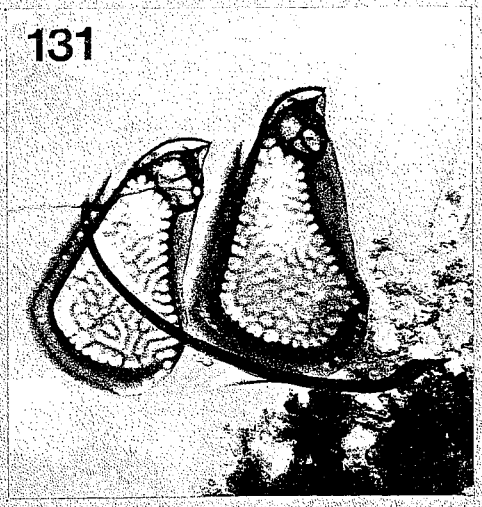
Fig. 131: Mallomonas cf. ~~doignonii~~ schwemmlei: two collar scales and spine, x 12,000.

Fig. 132: Mallomonas cf. ~~schwemmlei~~ doignonii: single collar scale, x 12,000.

Fig. 133: Mallomonas sp. (undescribed): single body scale, x 12,000.

Fig. 134: Mallomonas caudata: isolated scales and spines, x 3,000.

Source of specimens: Brim Bray Pond (Figs 131 - 133)
Lumley Moor Reservoir (Fig. 134).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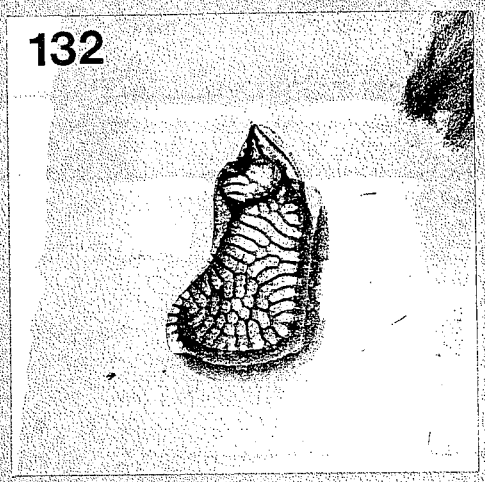
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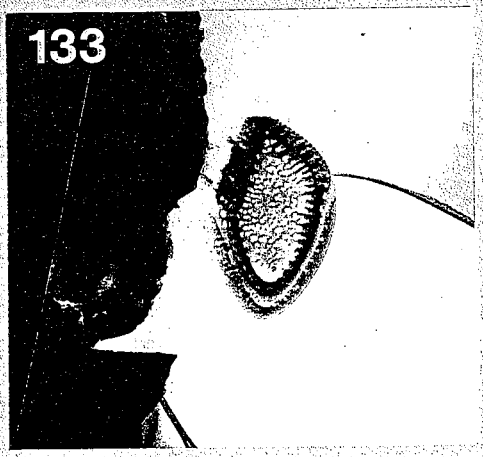
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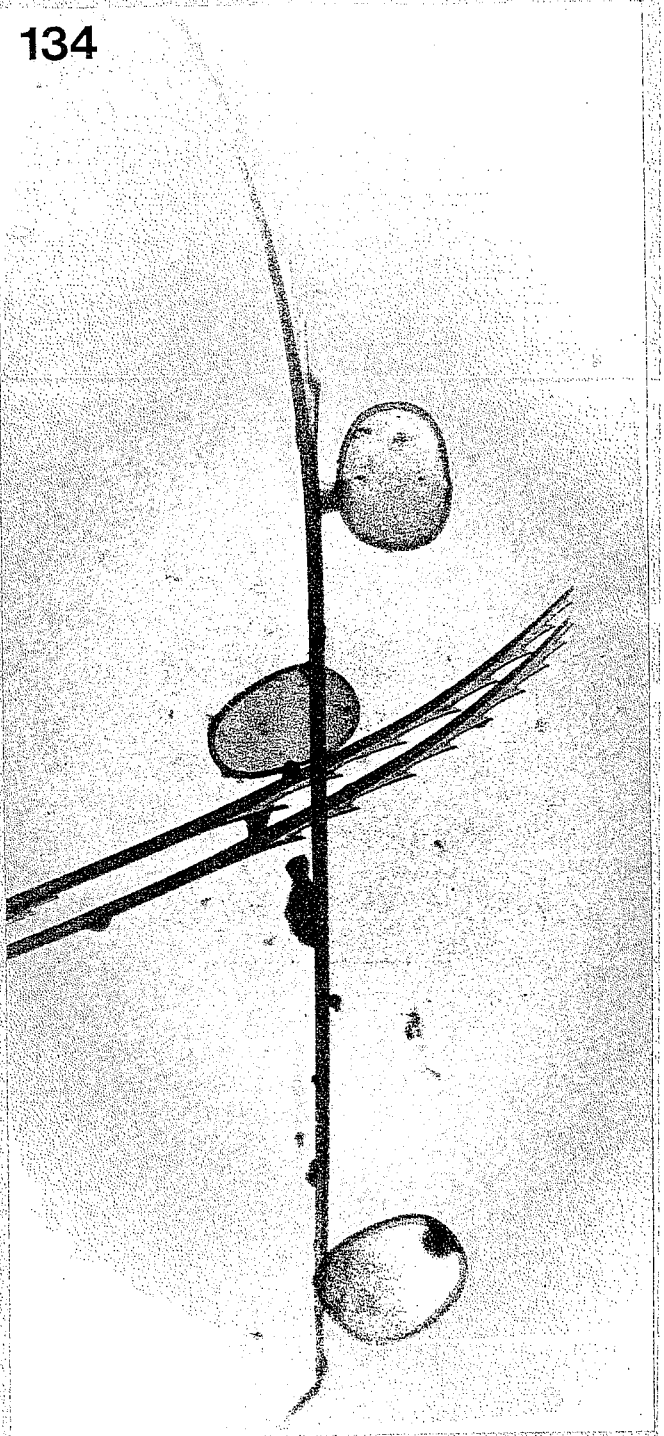

134

that these scales represent an aberrant form of that species.
Occurrence: Single record from Brim Bray Pond.
Reported Distribution: M. schwemmlei is known only from Czechoslovakia; M. "clavoides" is not known from elsewhere.

MALLOMONAS
Sectio Torquatae: series allantoides.
15. Mallomonas sp. cf. M. doignonii Bourrelly (Fig. 132).
Single collar scale, showing more pronounced maze-like pattern than seen in the preceding species, with additional double rows of pores in the spaces between the ribs. Possibly assignable to the species illustrated by Harris & Bradley (1957) as M. coronata Perm. et Vinnik., now considered to represent M. doignonii (Harris & Bradley, 1960), although some workers have suggested that the latter species is part of a range of forms which should all be referred to M. coronifera Matvienko (Glenk & Fott, 1971).
Occurrence: Single scale in Brim Bray Pond.
Reported Distribution: M. doignonii is known from Czechoslovakia, France and England (see Takahashi, 1978).

MALLOMONAS
Sectio Torquatae: series uncertain.
16. Mallomonas sp. (undescribed) (Fig. 133).
Single body scale, apparently from a species of the Torquatae, plain, irregularly perforated, with a narrow rib inside the scale perimeter from which short struts project on either side. Identical to collar and body scales illustrated by Bradley (1964: Fig. 28) from Iceland, but un-named by him owing to sparsity of material.
Occurrence: Single scale from Brim Bray Pond.
Reported Distribution: Known only from Iceland (Bradley, loc. cit.), very rare.

MALLOMONAS
Sectio Planae: series caudatae.
17. Mallomonas caudata Iwanoff emend. Krieger (Figs 134 - 136).
syn. M. fastigata Zacharias
Scales of one type only: broad, flat ovals, tending to have slightly squared corners, with a thickened margin on three sides. Body of scale perforated, but these perforations

FIGS 135 - 137 TEM of scale-bearing Chrysophyceae, VII.

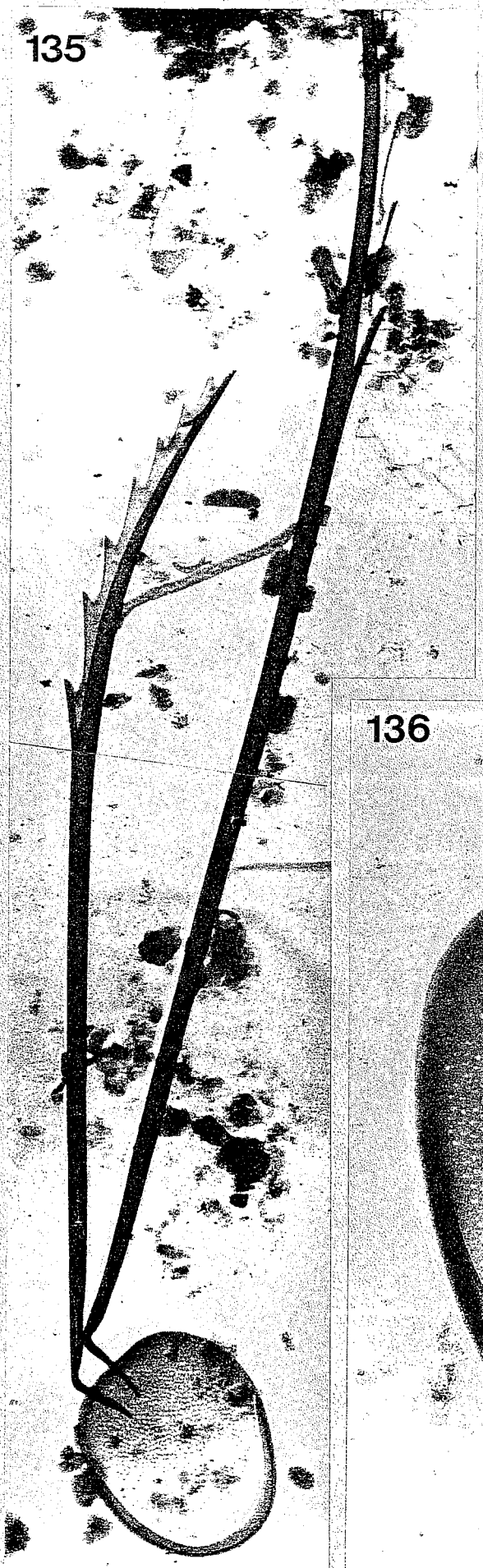
Figs 135 - 136 *Mallomonas caudata*.

Fig. 135: single scale bearing two spines, x 6,000.

Fig. 136: single scale, x 12,000; note pore in centre of posterior region of scale.

Fig. 137: *Mallomonas heterospina* (large form): scales and spanner bristles, x 6,000.

Source of specimens: Lumley Moor Reservoir (Figs 135-136)
Sawley Dene (Fig. 137).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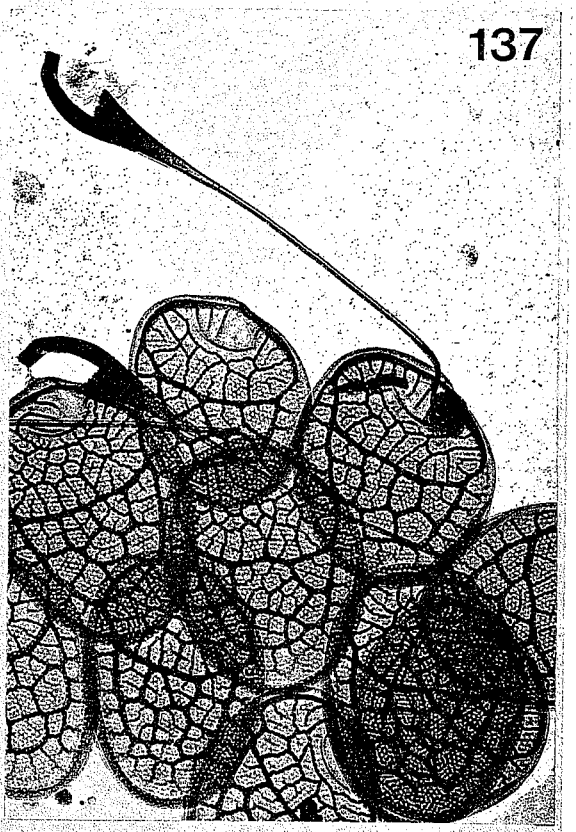
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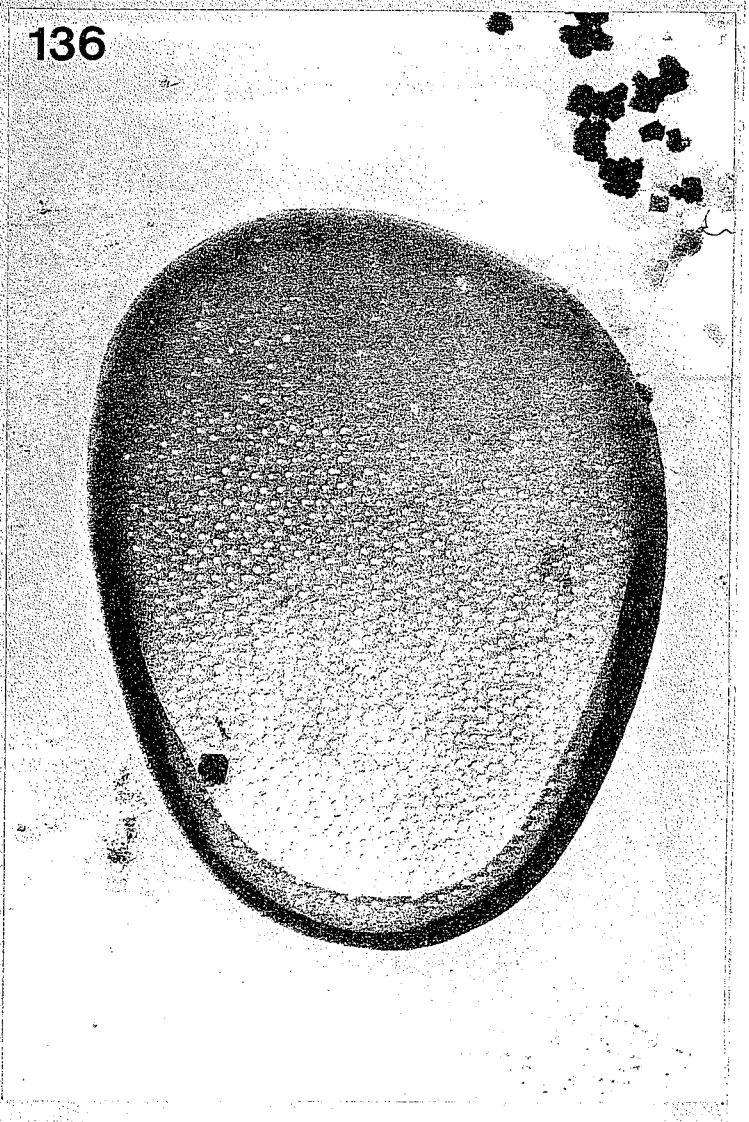

136

almost absent towards anterior edge of scale. A single large pore present in posterior region of scale (e.g. Fig. 136). Bristles of one type but varying markedly in length, unserrated for most of bristle but bearing up to 10 large barbs on one side of bristle below tip. Any single scale may bear 1 - 3 bristles (not illustrated), with no apparent specialised attachment region (cf. the dome in tripartite scales of other species). Isolated scales have similarities with those of certain Mallomonopsis species, e.g. M. elliptica (see below).

Bristles and scales of M. caudata are large and distinctive and the species is one of the few which can be reliably identified by light microscopy.
Occurrence: Fairly frequent in the summer sample from Lumley Moor Reservoir.
Reported Distribution: Widespread throughout world; often common in oligotrophic waters (see Asmund, 1959). British records include Brook (1964), Lund (1972a) and others representing a wide range of trophic types. Unpublished electron-micrographs of Manton (1967a) show this species from Windermere S. Basin and Blelham Tarn.

MALLOMONAS
Sectio Heterospinae.
18. Mallomonas heterospina Lund (Figs 137 - 142).
Scales of one type, flat, perforated and with complex pattern of ribs. A rudimentary dome normally present but no strict V-rib. Bristles of two types: straight spines with an angled basal portion, and short, slender bristles with distinctive spanner-shaped tips. Reports of other authors (e.g. Asmund, 1956) describe cells bearing bristles of both types together, but some dimorphism seen in the present material: scales from Sawley Dene (Figs 137 - 139) are large (ca. 3.5 x 5 µm), with the principal transverse rib dividing the scale into approximately equal halves, and bear spanner bristles only; scales from Lumley Moor Reservoir (Figs 140 - 142) are smaller (ca. 2 x 3 µm), with the main transverse rib closer to the dome, and bear straight spines only. Although other species close to M. heterospina are known, e.g. M. multiunca

FIGS 138 - 142 TEM of scale-bearing Chrysophyceae, VIII.

Figs 138 - 139 *Mallomonas heterospina* (Large form).

Fig. 138: group of scales, x 3,000.

Fig. 139: individual scales, x 12,000.

Figs 140 - 142 *Mallomonas heterospina* (small form).

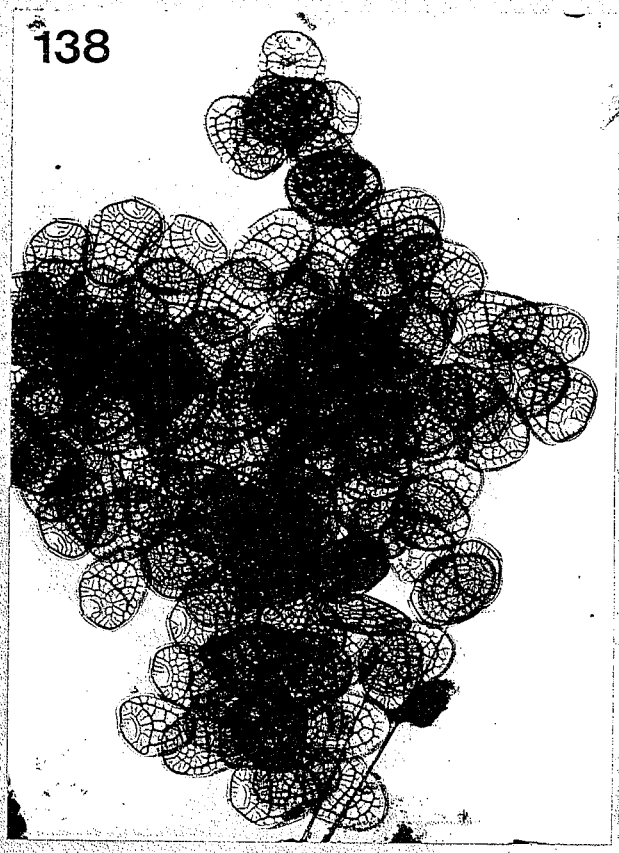
Fig. 140: scale and straight spine, x 12,000.

Fig. 141: whole cell, x 3,000.

Fig. 142: group of scales, x 12,000; note one simpler scale present.

Source of specimens: Sawley Dene (Figs 138-139)
Lumley Moor Reservoir (Figs 140 - 142).

138



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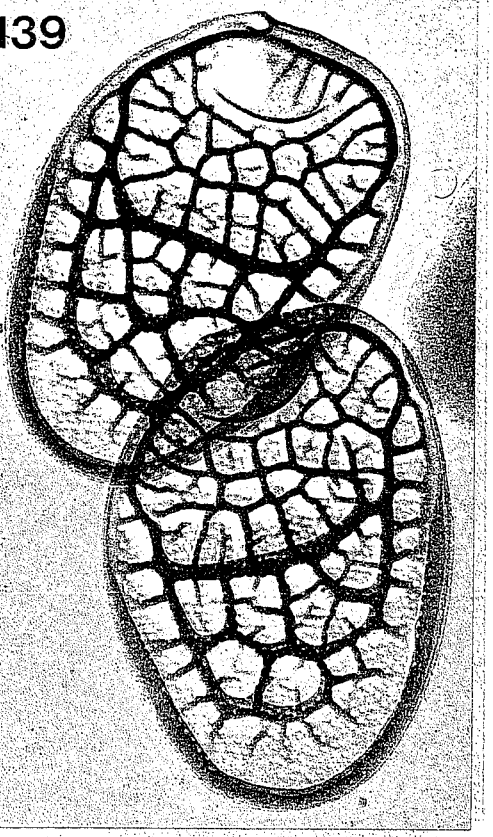

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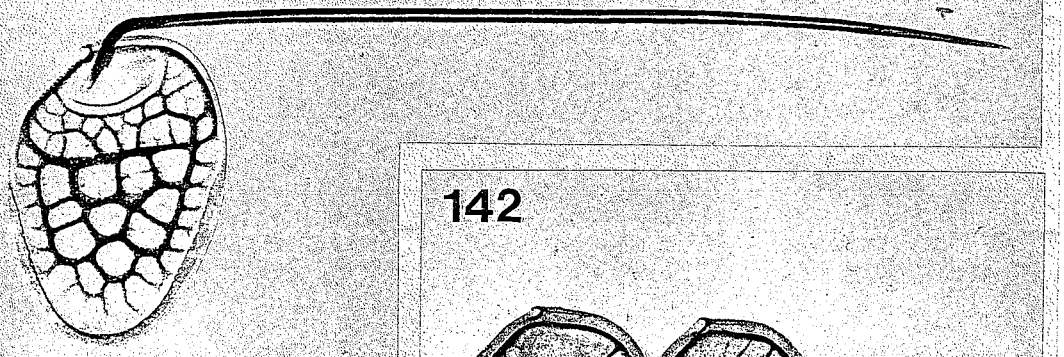

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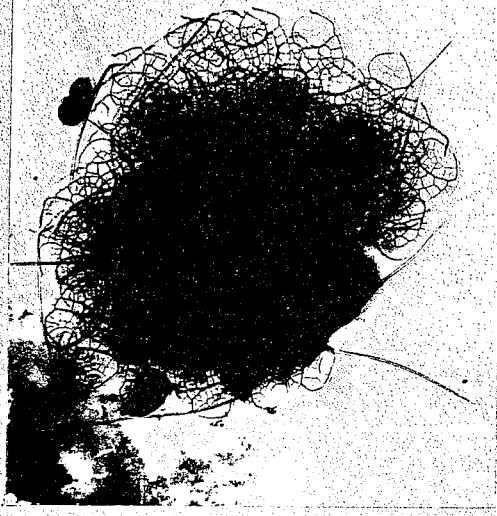

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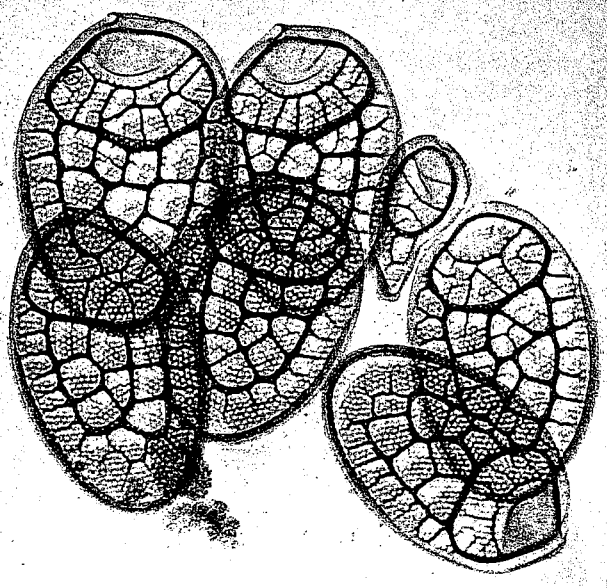


Asmund, it appears that, despite the variation seen in the present material, it should nevertheless all be assigned to M. heterospina (cf. Asmund, 1956; Harris, 1970; Peterfi & Momeu, 1977).
Occurrence: Sawley Dene, occasional in spring 1977 (large form); common in Lumley Moor Reservoir, spring sample (small form); occasional scales in Picking Gill Upper Pool, Eavestone Lake, Brim Bray Pond, Ripley Castle Lake.
Reported Distribution: Common throughout world. English records include Lund (1942) from Surrey and Harris & Bradley (1957) from Berkshire.

19. Mallomonas hamata Asmund (Figs 143 - 146).
Most body scales oval but somewhat pointed at anterior end; smooth, regularly perforated, with thickened rim at posterior end and rudimentary unperforated dome fringed with tiny teeth. Small group of long, smooth spines at anterior end; some scales also bearing short spanner bristles similar to those of M. heterospina. Some body scales rather reduced, especially towards posterior end (e.g. Fig. 146). This species has large cells which are distinctive in the light microscope (Asmund, 1959) but appears to be very rare.
Occurrence: A few scale groups in Lumley Moor Reservoir, summer sample only.
Reported Distribution: Known only from the type locality in Denmark (Asmund, loc. cit.), although Asmund refers to its unpublished occurrence in Berkshire also. In the Danish locality it was found in an oligotrophic lake in spring - summer.

MALLOMONAS
Isolated species.
20. Mallomonas akrokomos Pascher ex Ruttner (Figs 147 - 151).
Cell of very distinctive shape, bearing scales of a number of different types. Domed collar scales form a ring at anterior end (Fig. 150) and bear long, segmented bristles (Figs 147, 148). Body scales are small, basically oval in shape but with pointed ends and show a small perforated area in the posterior region of the scale,

FIGS 143 - 146 TEM of scale-bearing Chrysophyceae, IX.

Figs 143 - 146 *Mallomonas hamata*.

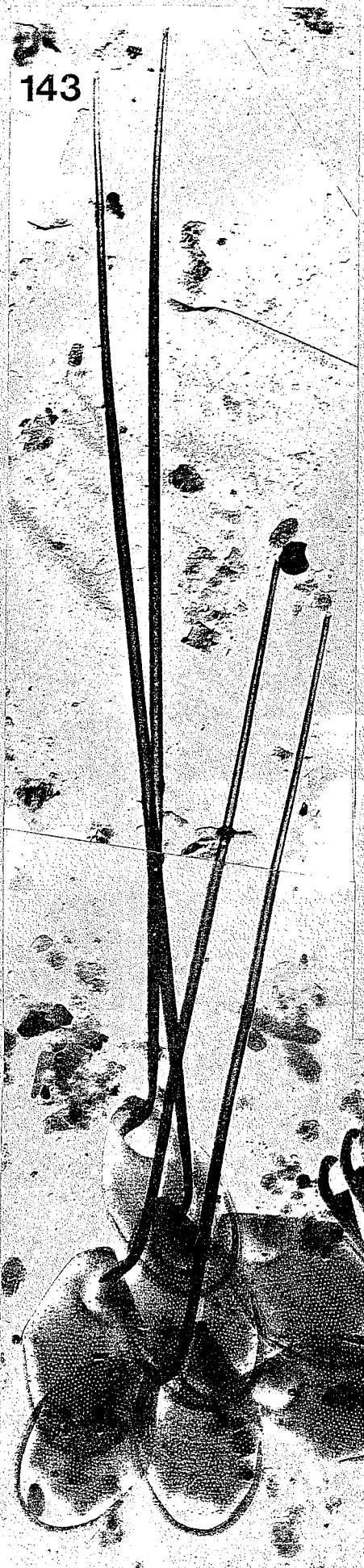
Fig. 143: group of scales, spanner bristles and spines, x 6,000.

Fig. 144: scales and spanner bristles, x 12,000; note fringe of teeth at anterior of scale (arrow).

Fig. 145: fragment of scale case, x 6,000.

Fig. 146: small posterior scale, x 12,000.

Source of specimens: Lumley Moor Reservoir (all Figures).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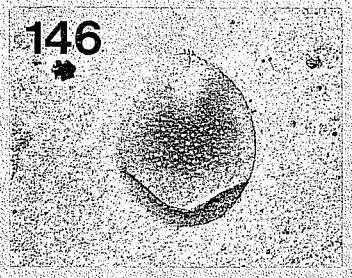
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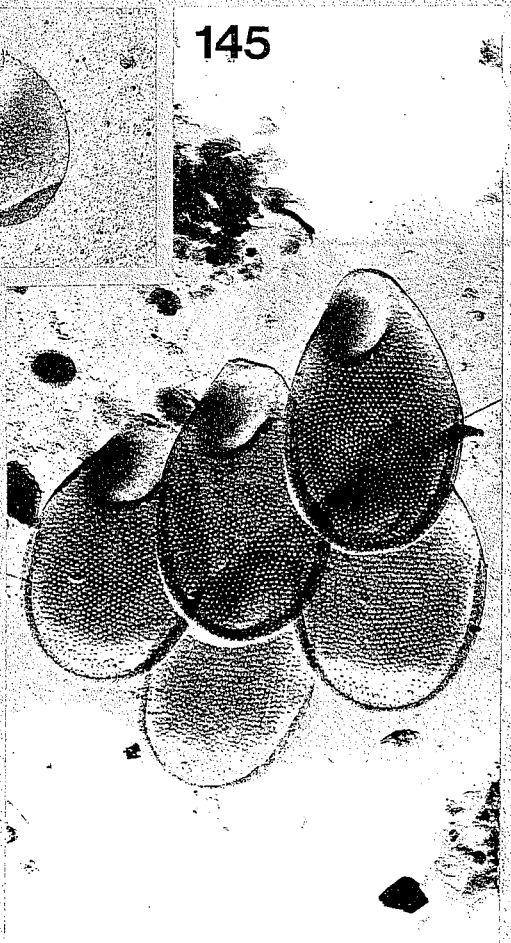
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FIGS 147 - 152 TEM of scale-bearing Chrysophyceae, X.

Figs 147 - 151 *Mallomonas akrokomos*.

Fig. 147: whole cell, x 3,000; note flagellum and apical spines.

Fig. 148: collar scale with base of spine, x 12,000.

Fig. 149: body scale, x 12,000.

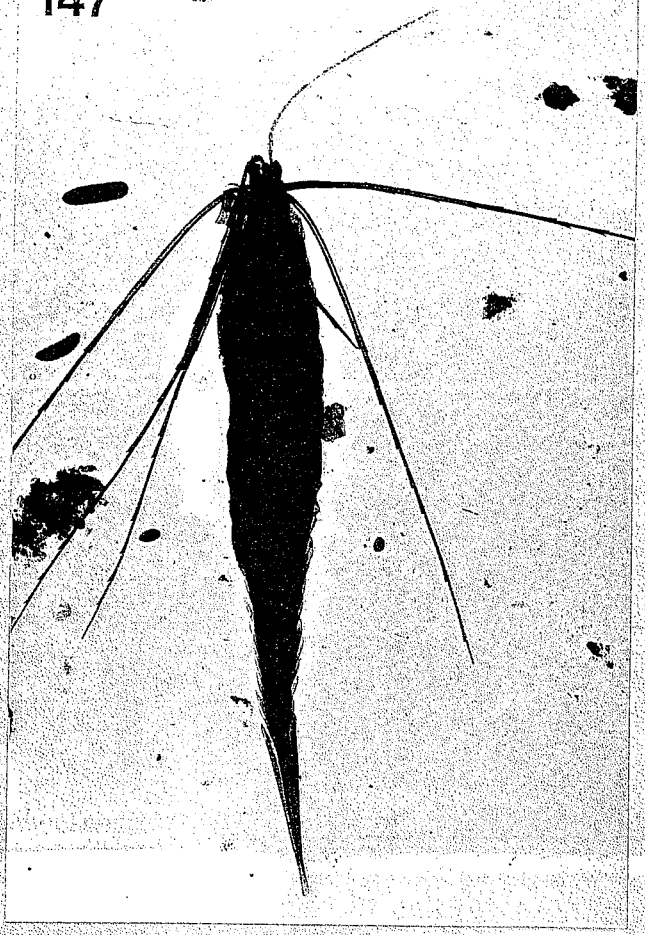
Fig. 150: body scales and anterior portion of "tail", x 12,000.

Fig. 151: anterior of cell showing ring of collar scales, x 12,000.

Fig. 152: *Mallomonas insignis*: single body scale, x 12,000.

Source of specimens: Sawley Dene (Figs 147 - 151)
Picking Gill Lower Pool (Fig. 152).

147



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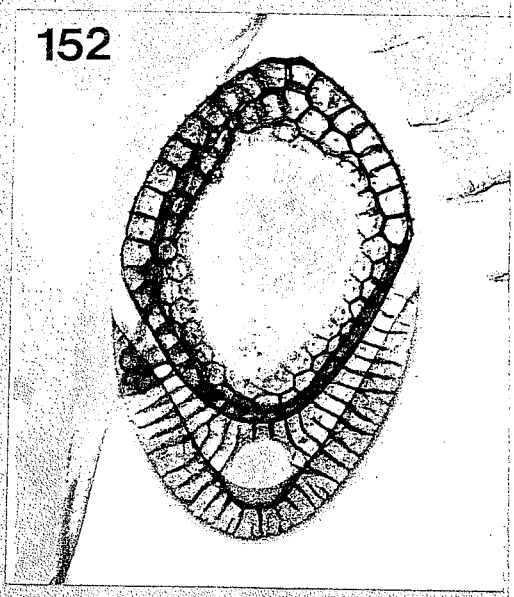

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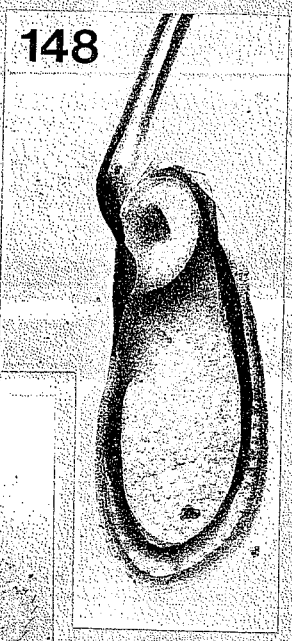

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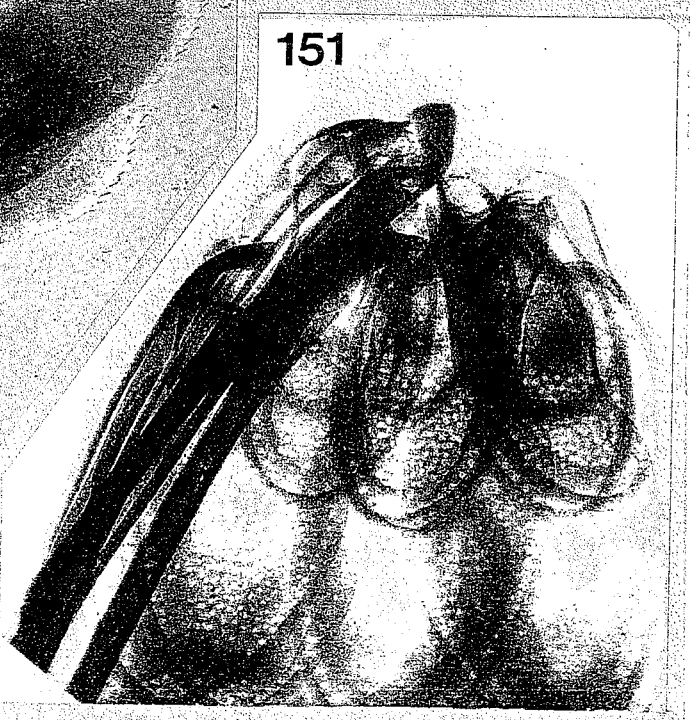


surrounded by a row of larger pores and a peripheral rib (Figs 149, 151). Posterior of cell consists of a unique "tail" region formed by specialised Y-shaped scales and terminating in a single spike. The affinities of this species are unclear; it possesses features reminiscent of the Torquatae, others similar to certain Heterospinae (e.g. M. hamata), as well as some features not known in any other species.
Occurrence: Occasional in many samples from Sawley Dene, common in January 1978; see p. 48 for LM records.
Fairly frequent in most of the other sites, viz. Stanks Pond, Picking Gill Upper Pool, Eavestone Lake, Brim Bray Pond and Ripley Castle Lake.
Reported Distribution: Very common throughout the world. English examples studied by Harris (1958).

MALLOMONAS
Isolated species.
21. Mallomonas insignis Penard (Fig. 152).
Scales of several types, including spined scales at both ends of cell (see Harris, 1958). Individual body scales (e.g. Fig. 152) without spine or dome but with shield region and complex flange. Shield bears honeycomb pattern which was shown by Harris (loc. cit.) to be an internal feature not visible on surface replicas. Scales very distinctive and unlike those of any other Mallomonas species, more similar to those of some Synura species, e.g. S. curtispina (Figs 165, 167). The cell of M. insignis also resembles one cell of a Synura colony in having a cytoplasmic "tail" covered in scales (cf. Synura petersenii, p. 95).
Occurrence: A few single scales in Picking Gill Lower Pool.
Reported Distribution: Relatively uncommon, although recognisable by light microscopy; known from Switzerland, France and England. Harris (1958) found it to be sometimes common in temporary, flooded habitats in Berkshire.

MALLOMONOPSIS
Sectio Mallomonopsis.
1. Mallomonopsis elliptica Matvienko (Figs 153 - 156).
Oval scales of one type, perforated with fairly large,

FIGS 153 - 161 TEM of scale-bearing Chrysophyceae, XI.

Figs 153 - 156 *Mallomonopsis elliptica*.

Fig. 153: single scale, x 12,000.

Fig. 154: detail of pore in posterior region of scale, x 24,000.

Fig. 155: single spine, x 12,000; note angled, flattened foot and blunt tip.

Fig. 156: group of scales, x 3,000.

Figs 157 - 158 *Mallomonopsis calceolus*.

Fig. 157: single scale and base of spine, x 12,000.

Fig. 158: group of scales and spines, x 6,000.

Figs 159 - 161 *Mallomonopsis* "*minuta*".

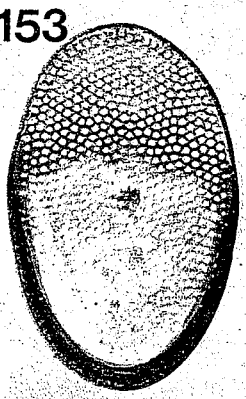
Fig. 159: whole cell, x 12,000.

Fig. 160: single scale and spine, x 24,000.

Fig. 161: whole cell, x 3,000; note small size relative to other *Mallomonas*/*Mallomonopsis* spp.

Source of specimens: Brim Bray Pond (all Figures).

153



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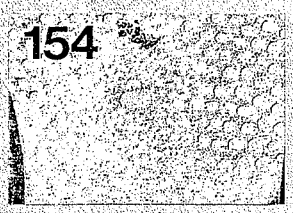

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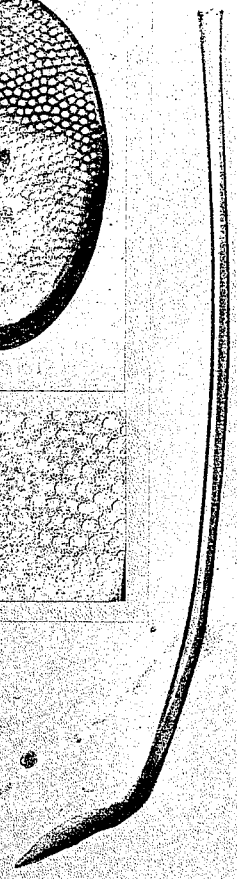

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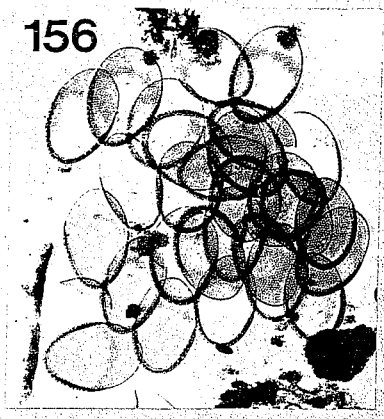

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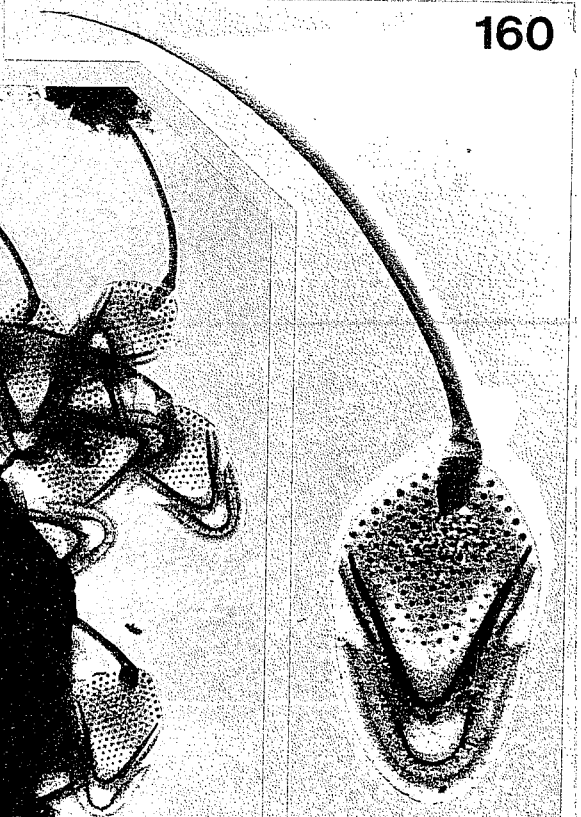

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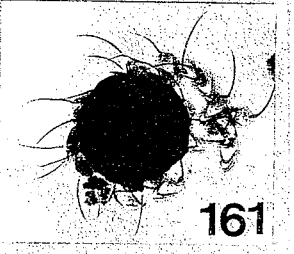


161

closely-spaced pores; a thickened rim surrounding the posterior half of the scale, in the centre of which is one large pore (Fig. 154). Scales reminiscent of those of Mallomonas caudata but smaller and more truly oval. Bristles of stout appearance, squared at tip, with an angled, flattened foot. Some other varieties of this species have recently been raised to specific level by Kristiansen (1975b).

Occurrence: A few scales seen in Sawley Dene, spring 1978; occasional scale groups in Picking Gill Lower Pool and Brim Bray Pond.

Reported Distribution: A limited number of records in the world but probably fairly widespread. Recorded in England by Lund (1942: as "Ochromallomonas pelophila") and Harris (1966); appears to be sometimes common in humus-rich environments.

MALLOMONOPSIS

Sectio Paxillatae.

2. Mallomonopsis calceolus (Bradley) comb. nov. (Figs 157, 158).

Basionym: Mallomonas calceolus Bradley

Scales tripartite, with weakly defined dome. Shield unperforated, bearing a limited number of regularly-spaced papillae; flange unornamented. Bristles short, slightly curved, smooth but with an asymmetrically biforked tip.

The form of the bristle is characteristic of this section of Mallomonopsis but, when originally described (Bradley, 1964), this species was considered to be a Mallomonas, as only a single flagellum was reported. Subsequently Belcher (1969) demonstrated the presence of a second flagellum although the transfer to Mallomonopsis was not made since this author advocated the suppression of Mallomonopsis as a genus. If Mallomonopsis is to be retained, as favoured by the present treatment, the change in nomenclature above becomes necessary.

Occurrence: Occasional scale groups in Brim Bray Pond.

Reported Distribution: Rather rare throughout world; recorded by Wujek & Van der Veer (1976) from the Netherlands, otherwise only by Bradley (1964, 1966) from Iceland and Scotland; Belcher (loc. cit.) from Lancashire.

3. Mallomonopsis "minuta" sp. nov. (Figs 159 - 161). Scales lacking a dome but divided by a V-rib into shield and flange. Shield unperforated, bearing a hexagonal array of papillae over whole surface; flange unornamented except for a marginal thickening resembling a second V-rib. Bristles short, curved, with a single sub-apical tooth; attached to scale by a flattened foot set at a slight angle to the rest of the bristle.

This organism does not correspond to any described species although isolated scales similar to those seen here have been figured by other authors (see below). The form of the scale and the bristle is consistent with a position in the genus Mallomonopsis close to M. calceolus and M. paxillata Bradley (see Bradley, 1964); the only similarities with any Mallomonas species are with the domeless body scales of M. mangofera Harris et Bradley but the latter organism is clearly a member of the Torquatae (see Harris & Bradley, 1960), while the present species displays none of the characteristics of that group.

At present, species are assigned to Mallomonopsis primarily if they show two emergent flagella. This feature has not yet been demonstrated for M. "minuta".

Occurrence: Occasional cells and scales found in Brim Bray Pond.

Reported Distribution: As unidentified scales, by Bradley (1966: Figs 40, 42) from Scotland, and a variant form with a more markedly toothed bristle in Japan by Takahashi (1959; in Takahashi, 1978: Figs 64, 65). Scales of M. "minuta" have also been found by the present author in samples from an oligotrophic lake near Leeds, November 1978. A detailed description of this organism is given in Appendix V.

SYNURA

Sectio Petersenia.

1. Synura petersenii Korshikov (Figs 162 - 164). Scales oval, base-plate perforated and bearing radial struts; perforated, raised cylindrical structure running down centre of scale, sometimes bearing an apical tooth. Posterior margin of scale reflexed and extending ca. half-way around sides. Scales borne on posterior region of cell are smaller

FIGS 162 - 169 TEM of scale-bearing Chrysophyceae, XII.

Figs 162 - 164 *Synura petersenii*.

Fig. 162: single cell (detached from colony), x 3,000; note two emergent flagella.

Fig. 163: portion of scale case, x 8,000.

Fig. 164: single scale, 12,000.

Figs 165 - 166 *Synura curtispina*.

Fig. 165: group of scales, x 6,000; note small posterior scale (arrow).

Fig. 166: single scale, x 12,000.

Figs 167 - 168 *Synura echinulata*.

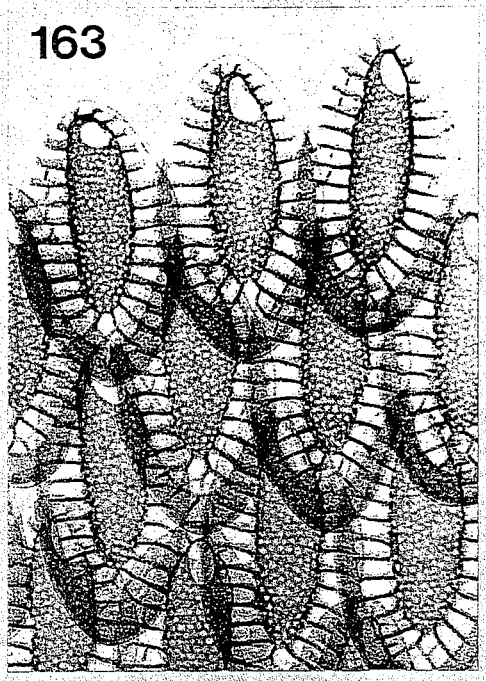
Fig. 167: single cell (detached from colony), x 6,000; note small posterior scales (arrow).

Fig. 168: group of scales, x 12,000.

Fig. 169: *Synura sphagnicola*: single scale (part of spine missing), x 12,000.

Source of specimens: Brim Bray Pond (Figs 162 - 163, 167 - 169)
Sawley Dene (Figs 164 - 165).
Ripley Castle Lake (Fig. 166).


162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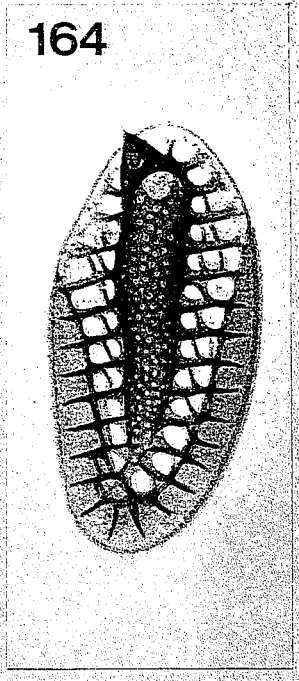
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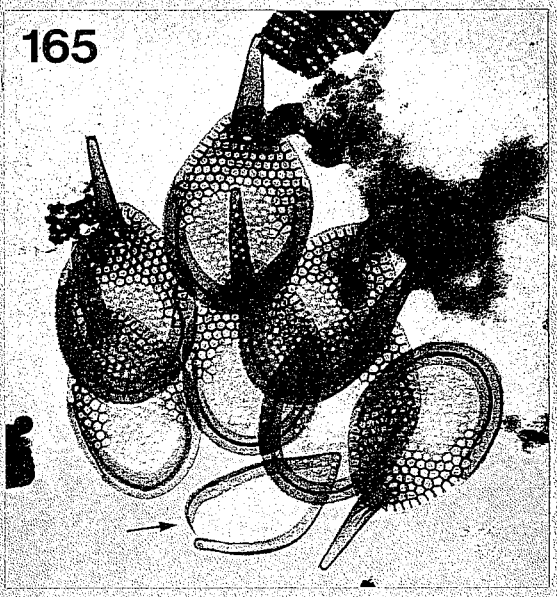
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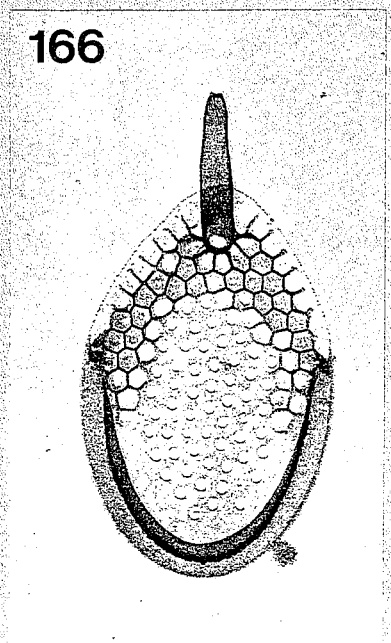
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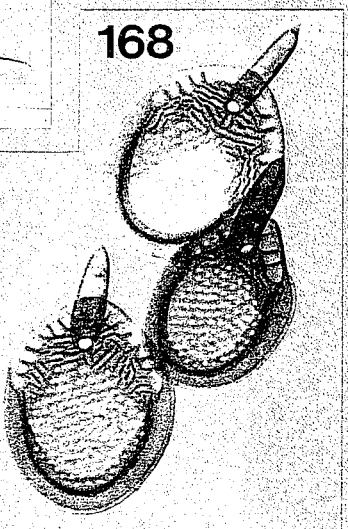

168

and may lack some of these features (not illustrated).
Occurrence: Small quantities seen in Sawley Dene, spring 1977 and 1978; common in Stanks Pond; occasional in Picking Gill Lower Pool, Eavestone Lake, Lumley Moor Reservoir (spring sample) and Ripley Castle Lake.
Reported Distribution: Very common throughout world, in habitats of varied types. Recent British material figured by Hibberd (1973). Additional information on this species is given in Section 5 (p. 95).

SYNURA
Sectio Synura.

2. Synura curtispina (Petersen et Hansen) Asmund (Figs 165, 166).

Flat oval scales, somewhat pointed at anterior end, with large perforations in posterior and central area of scale and honeycomb-like pattern covering approx. 1/3 of scale area towards apex. Stout, slightly tapering spine borne at apex of scale, terminating in 2 - 3 small teeth. Posterior margin reflexed and extending around posterior half of scale. Scales from rear portion of cell may be simpler and lack some of these features (Fig. 165).
Occurrence: A few scales in Sawley Dene, winter 1976; trace amounts also in Picking Gill Upper Pool, Eavestone Lake, Lumley Moor Reservoir and Ripley Castle Lake.
Reported Distribution: Widespread throughout world but less common than S. petersenii. Apparently unrecorded for Britain.

3. Synura echinulata Korshikov (Figs 167, 168).

Scales similar to those of S. curtispina but smaller, with characteristic zigzag ribbing on anterior portion of scale. Apical spine of variable length and may be pointed or rather blunt. Simple posterior scales again present (Fig. 167).
Occurrence: Fairly frequent in Brim Bray Pond.
Reported Distribution: Widespread throughout world, fairly common in a range of habitat types. Recorded in England by Abdel Karim (1965) from Priddy Pool and by Hibberd (1973).

4. Synura sphagnicola (Korshikov) Korshikov (Fig. 169).
Scales simple, covered with perforations, with a thinly reflexed margin extending most of the way around the scale and a slender apical spine (cf. Hibberd, 1978).
Occurrence: A single, incomplete scale found in Brim Bray Pond.
Reported Distribution: Widespread but apparently restricted to acid localities. Recorded from Britain by Harris & Bradley (1958) and Hibberd (loc. cit.).

CHRYSOSPHAERELLA

1. Chrysosphaerella brevispina Korshikov emend. Harris et Bradley (Figs 170 - 172).
Scales oval, with characteristic ring of fluted ornamentation around central area; spines stout, with biforked tip and complex bobbin-shaped basal region, the three dimensional structure of which has been recently illustrated by Takahashi (1978).
Occurrence: A few scale groups found in Picking Gill Pools (Upper and Lower) and in Ripley Castle Lake.
Reported Distribution: Widespread in world but fairly uncommon. British examples studied by Harris & Bradley (1958).

SPINIFEROMONAS

1. Spiniferomonas bourrellii Takahashi (Figs 173 - 175).
Scales oval, plain except for faint oval outline to central portion. Each cell with 3 - 5 long spines, tapering towards tip and flaring near cell to form a conical basal region.

One scale seen (arrow, Fig. 175) bears double central marking not previously figured for this species and reminiscent of S. bilacunosa (see Takahashi, 1973).
Occurrence: Small numbers in Sawley Dene, January 1978; also occasional in Picking Gill Pools (Upper and Lower) and Eavestone Lake.
Reported Distribution: Previously known only from type locality, mountain ponds in Japan (Takahashi, loc. cit.).

2. Spiniferomonas bourrellii var. "simplex" var. nov. (Fig. 176).
Cell and scale details as for S. bourrellii, but oval scales

FIGS 170 - 176 TEM of scale-bearing Chrysophyceae, XIII.

Figs 170 - 172 *Chrysosphaerella brevispina*.

Fig. 170: single spine, x 12,000; note complex basal portion.

Fig. 171: group of spines and oval scales, x 3,000.

Fig. 172: isolated oval scales, x 12,000.

Figs 173 - 175 *Spiniferomonas bourrellii*.

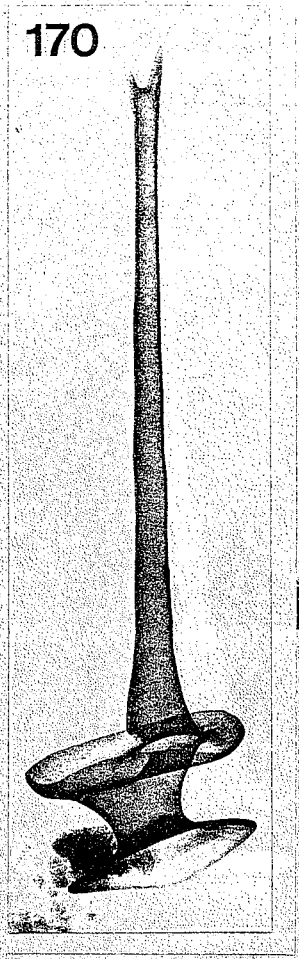
Fig. 173: whole cell, epiphytic on *Asterionella*, x 3,000; note two flagella present.

Fig. 174: another whole cell, x 6,000; parts of flagella visible at lower right.

Fig. 175: isolated spines and oval scales, x 12,000; one scale (arrow) has double central marking.

Fig. 176: *Spiniferomonas bourrellii* var. "*simplex*": oval scales and part of spine, x 12,000.

Source of specimens: Ripley Castle Lake (Figs 170 - 172)
Sawley Dene (Figs 173 - 176).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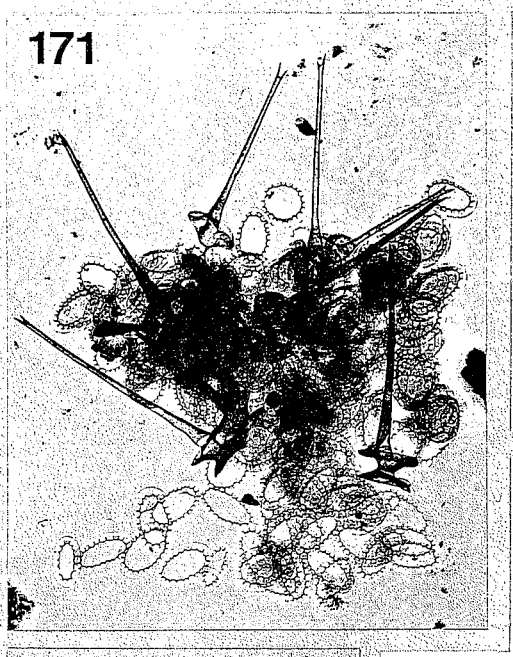
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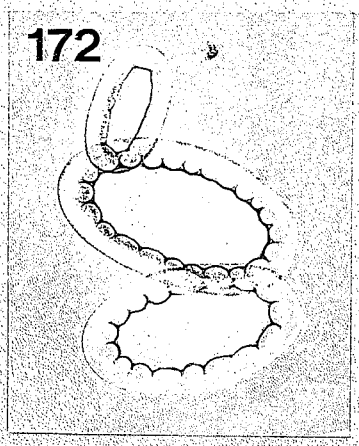
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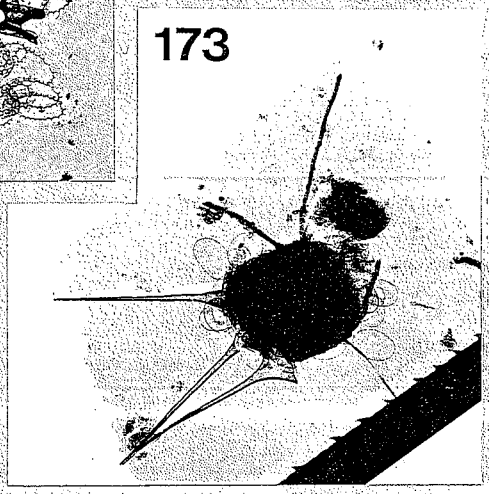
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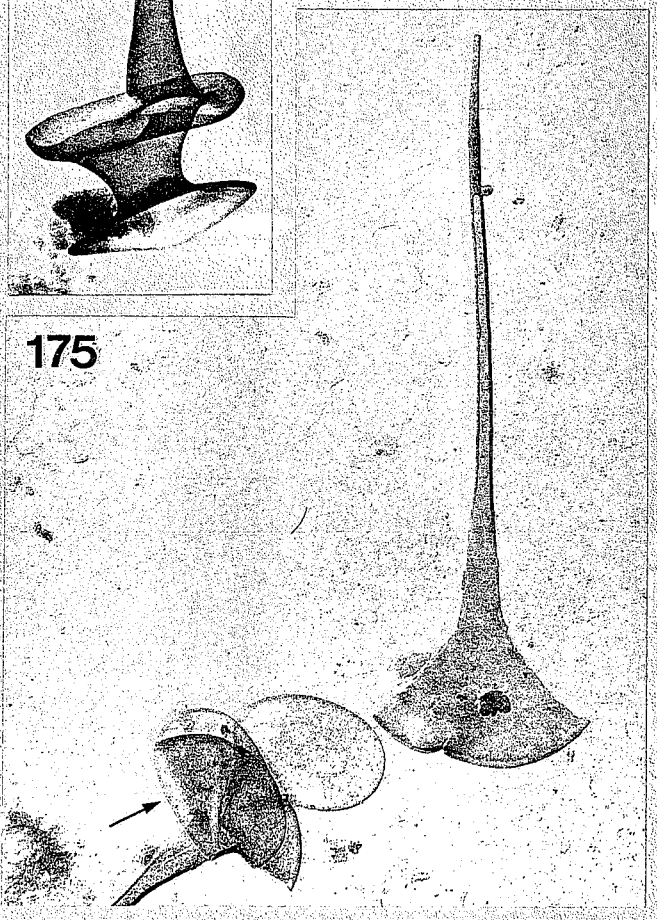
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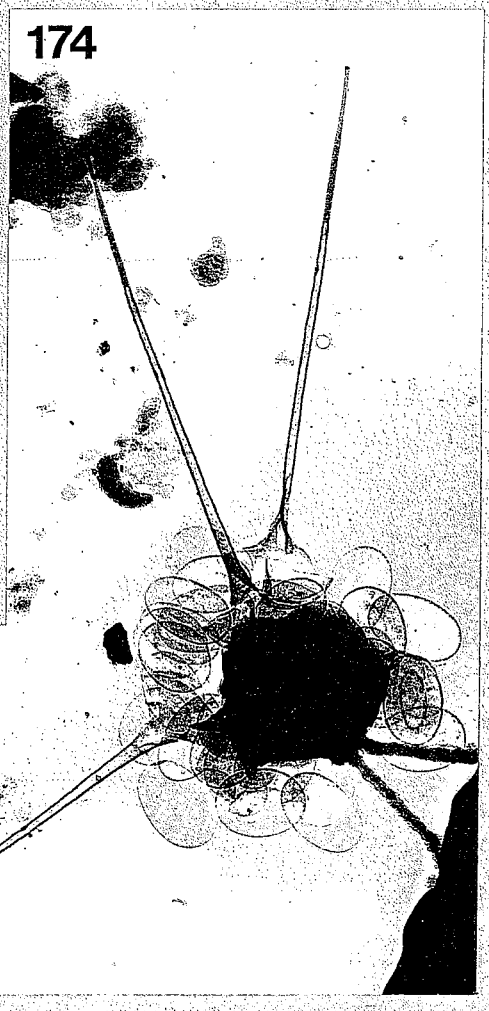
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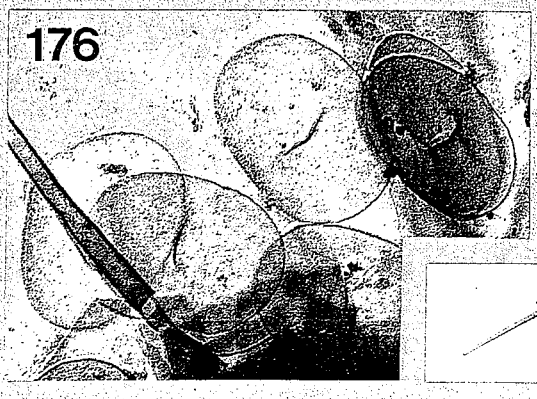
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lacking delineated central region, ornamented only by a short transverse strut. Scales of this type have not been described previously for Spiniferomonas, although somewhat similar plate scales are borne by the marine (?chrysophyte) organism Meringosphaera mediterranea Lohmann (see Leadbeater, 1974: Plate lV, F). The appearance of the whole cell (not illustrated) and the spines are otherwise typical of S. bourrellii.
Occurrence: A single cell found in Sawley Dene, January 1978.
Reported Distribution: Not previously found.
A description of this variety is given in Appendix V.

3. Spiniferomonas trioralis Takahashi (Figs 177, 178).
Scales oval, with conspicuously thickened inner ring surrounding the central region. Spines numerous on one cell, showing two or three flanges extending from a longitudinal rib; pointed at apex, flaring slightly to basal "foot" at right angles to long axis of spine.
Occurrence: Scales very common (whole cells rare) in Stanks Pond and Picking Gill Pools. Isolated scales (perhaps by contamination) in Ripley Castle Lake sample.
Reported Distribution: Species only recently described (Takahashi, 1973) but apparently widespread (Kristiansen, 1975a, b; Stoermer & Sicko-Goad, 1977; Takahashi, 1978; and other records). Not previously reported from Britain.

4. Spiniferomonas crucigera Takahashi (Figs 179 - 181).
Cell bearing scales of several types: small oval scales most common, open in centre but with complex H-shaped projections bridging central gap; small number of larger, oval scales with open centres; and, in addition, a few short spear-shaped spines reminiscent of those of S. trioralis but broader and flatter.
Occurrence: Single cell and isolated scale-groups found in Lumley Moor Reservoir (summer sample only).
Reported Distribution: Previously known only from type locality in a mountain pond in Japan (Takahashi, 1973).

PARAPHYSOMONAS

1. Paraphysomonas vestita (Stokes) De Saedeleer (Figs 182, 184).
Scales the largest in the genus, consisting of a plain

FIGS 177 - 182 TEM of scale-bearing Chrysophyceae, XIV.

Figs 177 - 178 *Spiniferomonas trioralis*.

Fig. 177: whole cell among *Asterionella* frustules, x 3,000 (flagella not visible).

Fig. 178: isolated spines and oval scales, x 12,000.

Figs 179 - 181 *Spiniferomonas crucigera*.

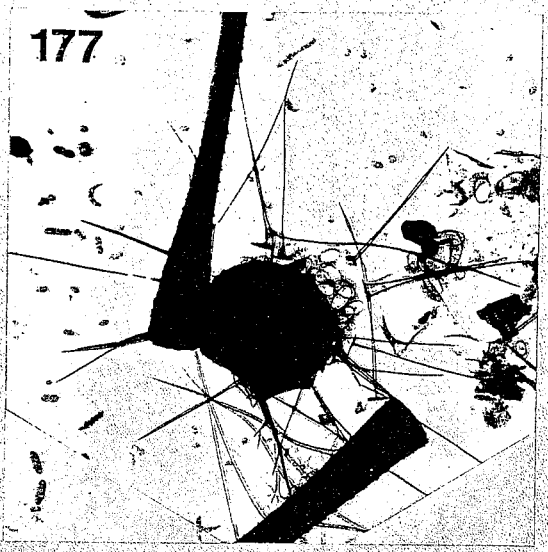
Fig. 179: whole cell, x 3,000; two flagella visible.

Fig. 180: detail of cell body, x 12,000; arrow indicates short flagellum. Note variety of scale types.

Fig. 181: isolated scales, x 24,000, showing two of the scale types.

Fig. 182: *Paraphysomonas vestita*: whole cell, x 3,000; scales and two flagella visible.

Source of specimens: Picking Gill Upper Pool (Figs 177 - 178)
Lumley Moor Reservoir (Figs 179 - 181)
Sawley Dene (Fig. 182).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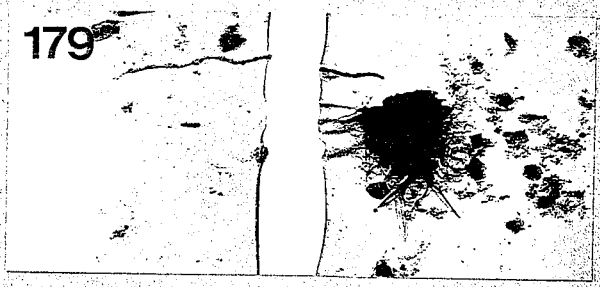
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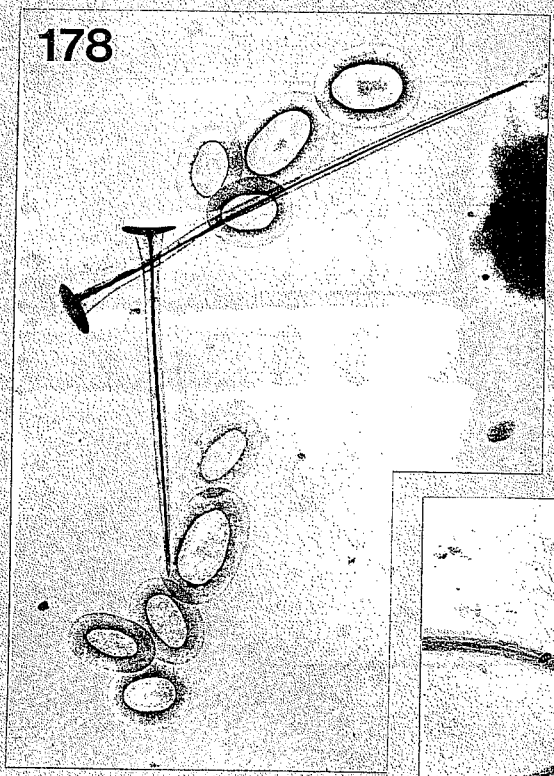
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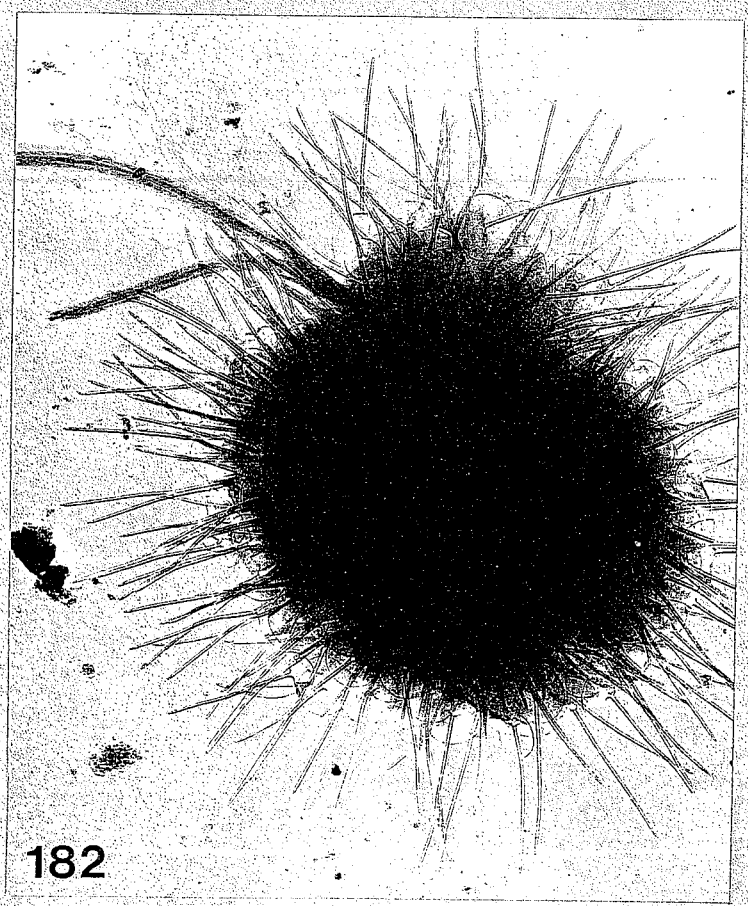

182

circular base-plate with a thickened rim and a slightly tapering spine arising from the centre of the scale-base.
Occurrence: Abundant in Sawley Dene, January 1977, occasional in spring 1978; fairly common in Stanks Pond, Picking Gill Pools and Eavestone Lake; a few scales in Ripley Castle Lake.
Reported Distribution: Very common throughout the world, possibly the most common chrysophycean species in freshwater; also found in salt water (Thomsen, 1975; Lee, 1978). Rarest in acid conditions (Takahashi, 1978).
See p. 48 and p. 89 for more information on this species.

2. Paraphysomonas imperforata Lucas (Figs 183, 184).
Scales of same basic form as those of P. vestita but less than half the size and lacking thickened rim. Cell very much smaller than that of P. vestita (compare Figs 183 and 182).
Occurrence: Present in small numbers throughout spring 1978 in Sawley Dene; fairly common in Stanks Pond.
Reported Distribution: Recorded several times from salt or brackish water throughout the world, including English sites (Lucas, 1967; Hibberd, 1979); Takahashi (1976) illustrates some slightly variant scales from freshwater in Japan.

3. Paraphysomonas foraminifera Lucas var. "trifida" var. nov. (Figs 185, 186).
Scales a little larger than those of P. imperforata, comprising a meshwork base-plate from which arises a central tapering spine, branched into three near its base. Some scales apparently lacking such a spine.

This taxon is close to P. foraminifera (see Lucas, 1967) but in the latter species the base-plate of the scale is clearly formed from an amorphous matrix which is perforated, rather than from a meshwork of narrow struts as seen in this taxon and some other Paraphysomonas species (see Rees et al., 1974). In addition, each scale of P. foraminifera sens. strict. bears a single slender spine arising from the centre of the base-plate, without a branched base. The present taxon is considered here as an undescribed variety

FIGS 183 - 191 TEM of scale-bearing Chrysophyceae, XV.

Figs 183 - 184 *Paraphysomonas imperforata*.

Fig. 183: whole cell, x 3,000, showing scales and two flagella.

Fig. 184: detached scales, x 12,000, with scale of *P. vestita* to show comparative size.

Figs 185 - 186 *Paraphysomonas foraminifera* var. "*trifida*".

Fig. 185: two scales, x 12,000.

Fig. 186: group of scales, x 6,000; some scales lack central spine.

Figs 187 - 190 *Paraphysomonas bandaiensis*.

Fig. 187: whole cell, x 3,000, showing two flagella.

Fig. 188: scale complement from a single cell, x 6,000.

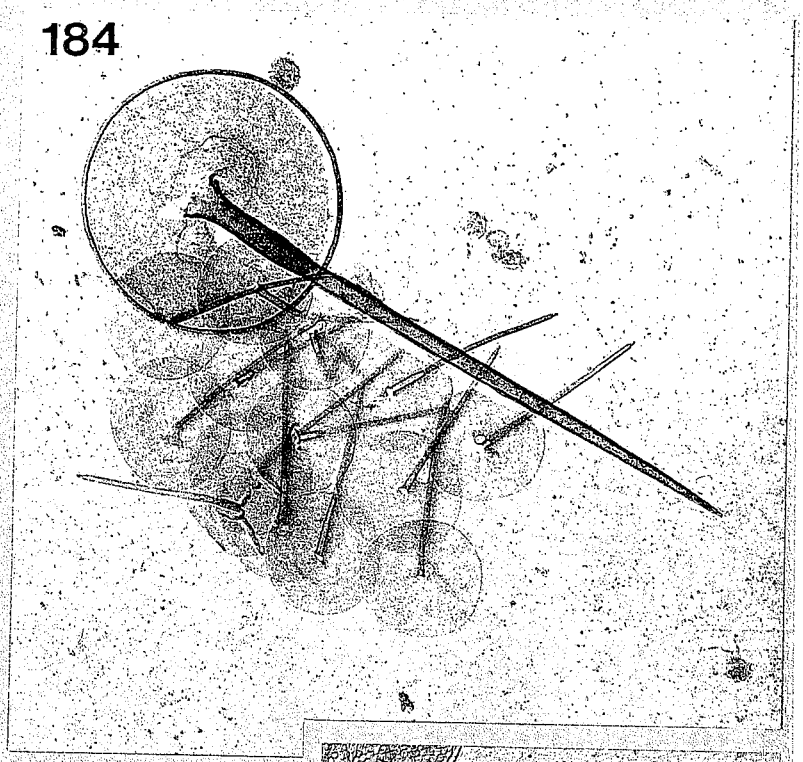
Fig. 189: group of scales, x 12,000.

Fig. 190: detail of individual scales, x 24,000.

Fig. 191: *Paraphysomonas butcheri*: single plate scale, x 24,000.

Source of specimens: Sawley Dene (all Figures).


183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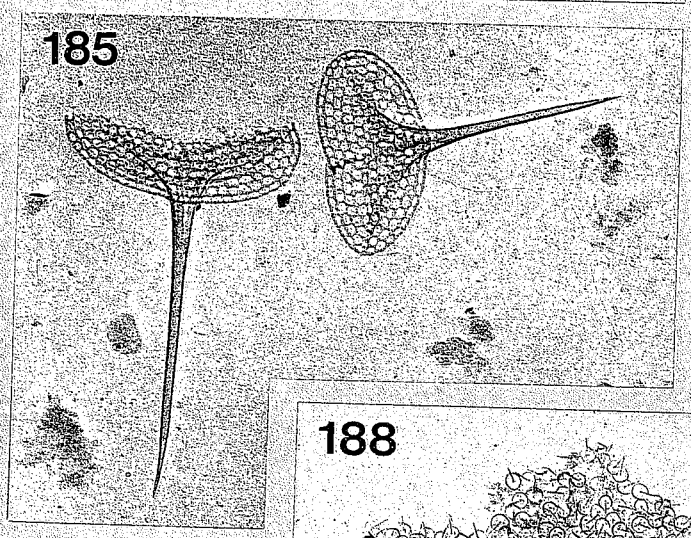
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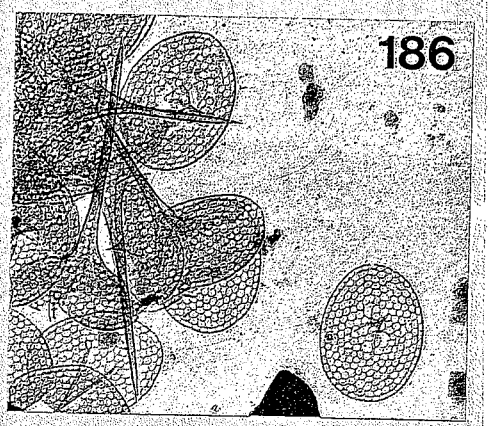
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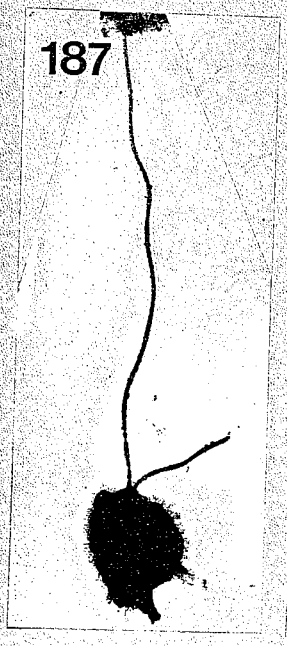
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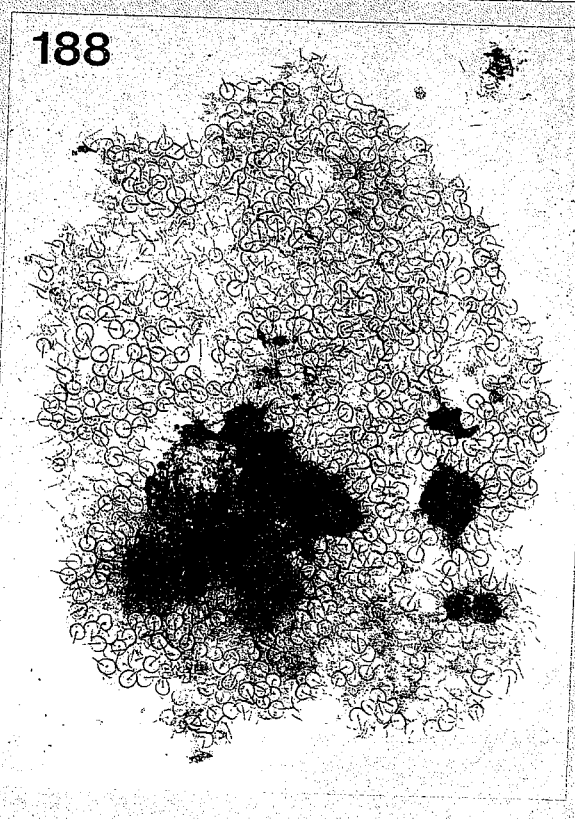
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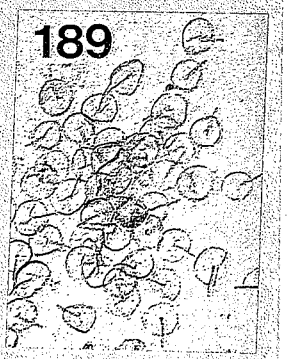
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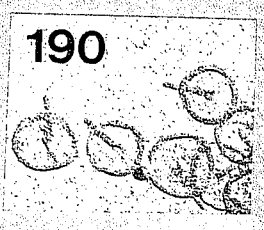
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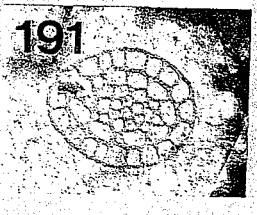

191

of P. foraminifera but its affinities with the other, meshwork-scaled species might justify its raising to specific level on the study of more material.
Occurrence: Isolated scales in Sawley Dene, spring 1978; also in Picking Gill Upper Pool and Lumley Moor Reservoir.
Reported Distribution: Similar scales figured by Takahashi (1976) from freshwater in Japan. Other English specimens (Hibberd, 1979) from Dorset are referable to P. foraminifera sens. strict.
A description of this variety is given in Appendix V.

4. Paraphysomonas bandaiensis Takahashi (Figs 187 - 190). Minute scales of same basic form as in P. vestita but covering cell in very large numbers. Each scale has marginal rib and short central spine, both of similar thickness.
Occurrence: Occasional in Sawley Dene, spring 1977 and 1978, usually epiphytic on Asterionella and attached to the diatom wall with a short stalk. Fairly frequent in Picking Gill Upper Pool.
Reported Distribution: Recorded infrequently in freshwater only (Takahashi, 1976; Hibberd, 1979, from the English Lake District).

5. Paraphysomonas butcheri Pennick et Clarke (Fig. 191). Meshwork scales of two types (see Pennick & Clarke, 1972): raised "crown" scales and flat "plate" scales. Plate scales oval, very small, composed of a meshwork of struts leaving rings of approximately concentric spaces, less regular in the centre. Somewhat similar plate scales are borne by other Paraphysomonas species (see Thomsen, 1975; Takahashi, 1976).
Occurrence: A very few plate scales seen in Sawley Dene, January 1978, but easily overlooked at low magnifications and probably under-recorded.
Reported Distribution: Known from marine and a few freshwater sites (e.g. Wujek & Van der Veer, 1976). Not previously reported from freshwater in Britain.

Results and Taxonomic Discussion

PART B: NON-CHRYSOPHYCEAN ORGANISMS

Note: Species which may be positively determined as Heliozoa are arranged as in Rainer (1968). Undetermined species of the heliozoan genus Acanthocystis are included with the named species. The genus Gyromitus is at present unclassifiable (see Swale & Belcher, 1974). Scales of undescribed organisms are placed last.

Heliozoa: Centrohelidia

ACANTHOCYSTIS

1. Acanthocystis turfacea Carter (Fig. 192).
syn. A. chaetophora (Schrank)

Biforked spines of two lengths (cf. Fig. 57) together with oval plate scales. Scale in Fig. 192 is 7.3 µm long and corresponds to the smallest type visible in Fig. 57.
Occurrence: A few spines in Sawley Dene, January 1978 (see p. 54 for LM observations).
Reported Distribution: One of the commoner freshwater heliozoans (Wailes, 1921) but few modern records.

2. Acanthocystis erinaceoides Petersen et Hansen (Figs 193, 194).
Spines slender, virtually straight with blunt tip and distinctive paddle-shaped projections at base (Fig. 194; cf. Fig. 58) terminating in a reflexed semi-circular "lip" (A. Rees, unpublished SEM observations). Oval plate scales also present, with thickened, slightly irregular margin. Fig. 58 shows the appearance of this species in the LM.
Occurrence: Small numbers of cells in Sawley Dene, March - May 1977 (see p. 55 for LM records). Cells also in Ripley Castle Lake.
Reported Distribution: Known from Denmark and Scotland (see p. 55).

3. Acanthocystis "sp. 1" (undescribed) (Figs 195, 196).
Spines with biforked tips but smaller than those of A. turfacea and of two characteristic types: one 3.5 - 5.5 µm long, biforked close to scale tip and with serrations on inner margins; the other 1.5 - 2.0 µm long, dividing

FIGS 192 - 201 TEM of non-chrysophycean scale-bearing organisms, I.

Fig. 192: Acanthocystis turfacea: single spine, x 12,000.

Figs 193 - 194 Acanthocystis erinaceoides.

Fig. 193: whole cell, x 3,000.

Fig. 194: two oval scales and base of spine, x 12,000.

Figs 195 - 196 Acanthocystis "sp. 1".

Fig. 195: group of spines, x 12,000; note serrations inside biforked spine tip (arrow).

Fig. 196: single scale with 4-branched tip, x 12,000.

Fig. 197: Acanthocystis cf. echinata: single spine, x 12,000.

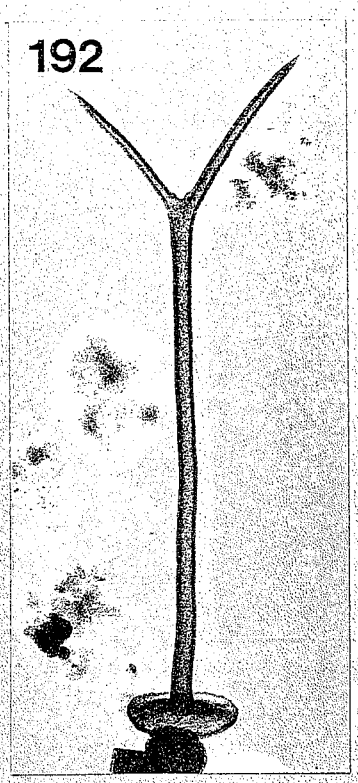
Fig. 198: Acanthocystis "sp. 2": single spine and oval scale, x 12,000; note teeth at apex of spine (arrow).

Fig. 199: Acanthocystis cf. perpusilla: single spine, x 12,000.

Fig. 200: Acanthocystis "sp. 3": single spine, x 12,000.

Fig. 201: Acanthocystis "sp. 4": single spine, x 12,000.

Source of specimens: Sawley Dene (Figs 192 - 194, 196 - 197, 199 - 201)
Ripley Castle Lake (Fig. 195)
Brim Bray Pond (Fig. 198).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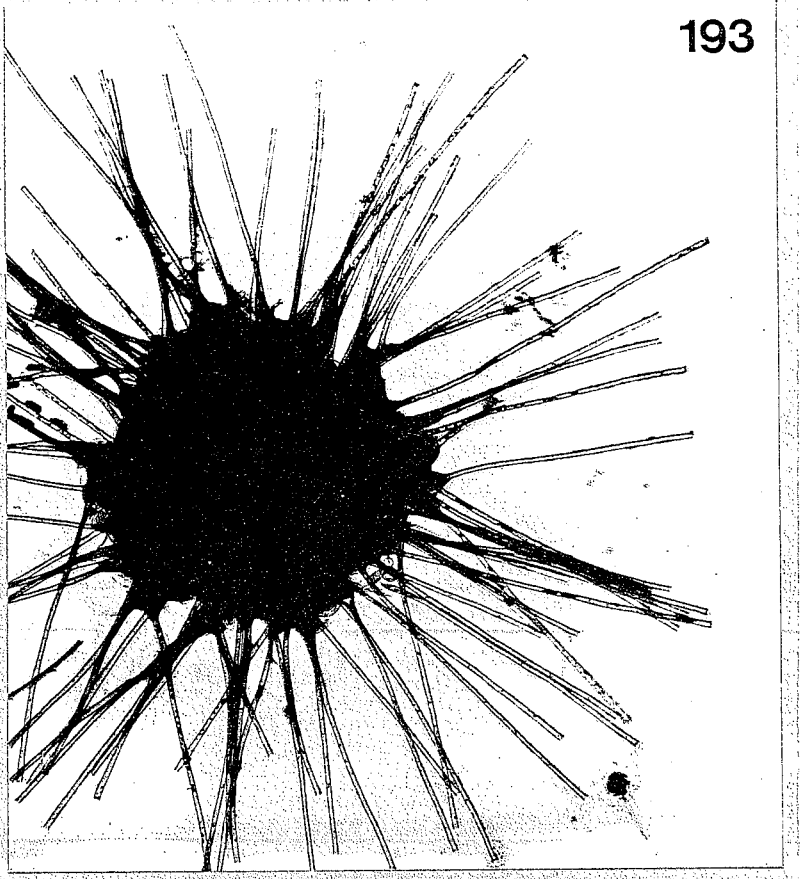
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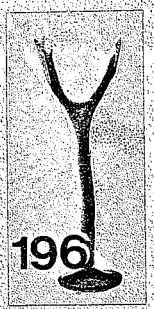
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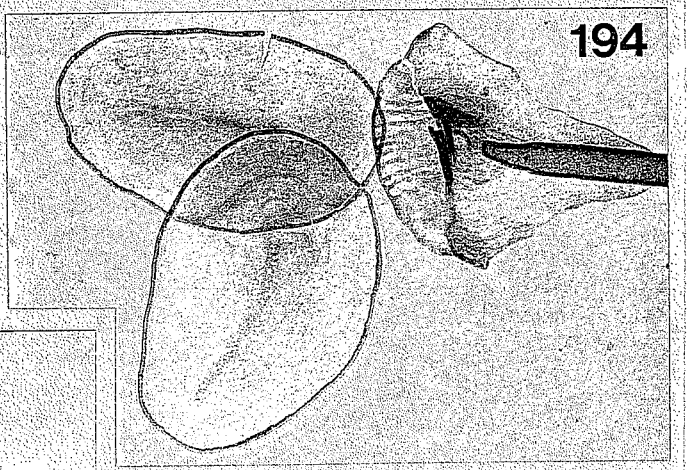
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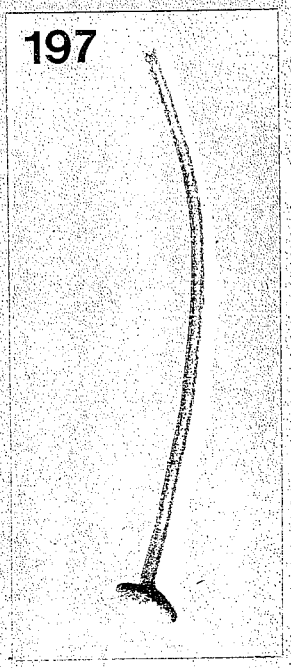
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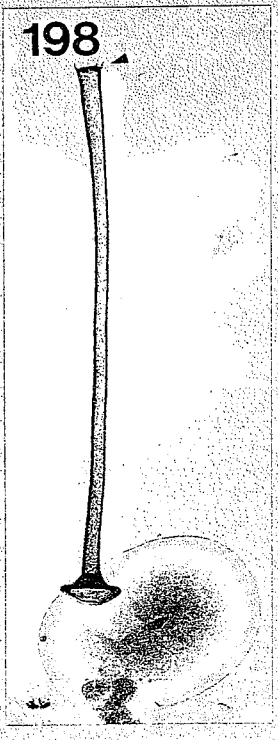
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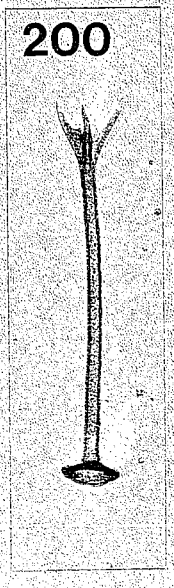
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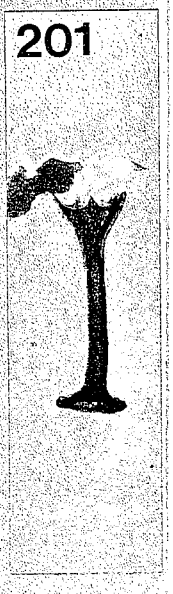

201

into two parts about halfway along scale and subsequently dividing again to produce four projections, the tip of each often ending in two teeth (Fig. 196). Oval plate scales also present (not visible in Fig. 195), ca. 1.5 x 1.0 µm.
Occurrence: Single cell in Ripley Castle Lake; isolated scale from Sawley Dene, January 1978.
Reported Distribution: Not known.

4. Acanthocystis sp. cf. A. echinata Rainer (Fig. 197).
Spines slender, curving, blunt-tipped; length ca. 6 µm. Comparison with drawings based on light microscopy in Rainer (1968) suggests the above identity but several other described species have somewhat similar spines (A. penardi Wailes, A. spinifera Greeff).
Occurrence: Sawley Dene, January 1978; also a whole cell, possibly the same species, in Lumley Moor Reservoir.
Reported Distribution: Known only from Rainer's description, from freshwater in Germany.

5. Acanthocystis "sp. 2" (undescribed) (Fig. 198).
Spines basically straight, with small base-plate, flaring somewhat towards tip, and crowned with ring of tiny teeth. Oval plate scales also present. Length of spines 3 - 7 µm; ovals ca. 2.5 x 2.0 µm. Not identical to spines described elsewhere.
Occurrence: A small number of spines and plates in Brim Bray Pond.
Reported Distribution: Not known.

6. Acanthocystis sp. cf. A. perpusilla Petersen et Hansen (Fig. 199).
Spine relatively thick, rather irregular, with large, asymmetrically placed base-plate. Tip of spine blunt; spine length 5 µm. Comparison with electron micrographs of Petersen & Hansen (1960) suggests that this is a scale of A. perpusilla but more material would be required for a definite identification.
Occurrence: Single scale in Sawley Dene, January 1978.
Reported Distribution: One slightly acid freshwater locality in Denmark (Petersen & Hansen, loc. cit.).

7. Acanthocystis "sp. 3" (undescribed) (Fig. 200).
Spine 4 μm long, fairly slender, with small base-plate and triple branching at tip to produce three projecting points. No named species with similar spines but scales seen in Japan (Takahashi, 1959).
Occurrence: Single scale in Sawley Dene, January 1978.
Reported Distribution: As "microplankton sp. 7", from a paddy-field in Japan (Takahashi, loc. cit.: spines and oval plates shown).

8. Acanthocystis "sp. 4" (undescribed) (Fig. 201).
Spine 2.3 μm long, with fairly small base-plate and distinctive tip which is flared outwards and terminates in five points. This scale is again of a new type; it has some resemblance to Acanthocystis "sp. 3" but is probably a separate taxon.
Occurrence: Single scale in Sawley Dene, February 1978.
Reported Distribution: Not previously found.

RAPHIDOCYSTIS
1. Raphidocystis tubifera Penard (Section 5, Figs 286 - 310).
Scales of three types: oval plates and small bell-shaped scales, both of meshwork-type construction, and long amorphous tubular spines with flared, open ends. A detailed description of this species is given in Section 5 (p. 104).
Occurrence: Sawley Dene, small numbers of cells in summer/autumn 1976 and 1977 (see p. 54). Not found at any other sites.
Reported Distribution: See p. 104.

Genus of Uncertain Taxonomic Position
GYROMITUS
1. Gyromitus disomatus Skuja (Figs 202 - 204).
Scales of one type only: short, oval cylinders with thickened rims, each wall perforated, with thin base-plate closing one end (see Swale & Belcher, 1974). The whole cell of this organism, studied with sections by Swale & Belcher, is colourless, with two equal, smooth flagella and is unique (except for another species of Gyromitus) in forming scales in vesicles associated with the mitochondrion.

FIGS 202 - 208 TEM of non-chrysophycean scale-bearing organisms, II.

Figs 202 - 204 *Gyromitus disomatus*.

Fig. 202: group of scales, x 6,000.

Fig. 203: portion of scale group, x 12,000.

Fig. 204: individual scales, x 24,000.

Figs 205 - 206 Unknown species A.

Fig. 205: whole cell and scales, x 12,000; note parts of two flagella at top of Figure.

Fig. 206: isolated scales, x 12,000.

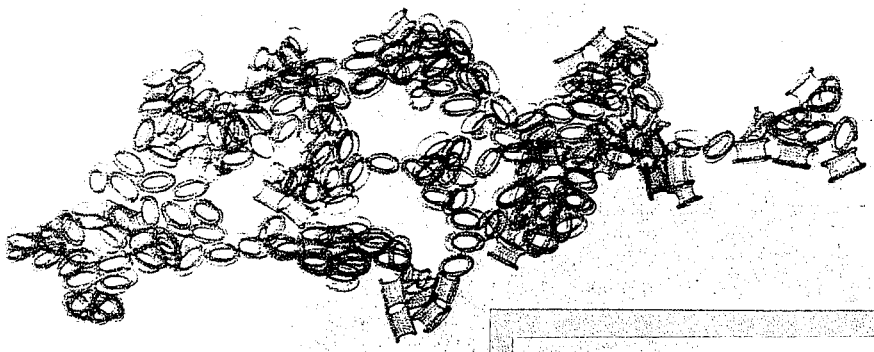
Figs 207 - 208 Unknown species B.

Fig. 207: group of spines and oval scales, x 12,000.

Fig. 208: detail of single spine and oval scales, x 24,000.

Source of specimens: Sawley Dene (all Figures).

202



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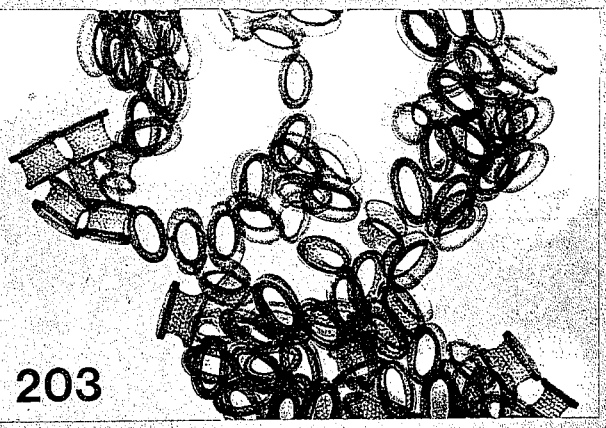

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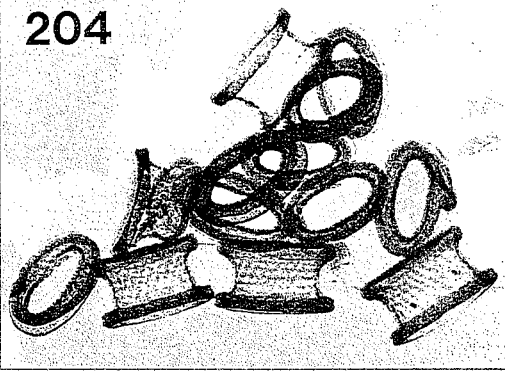

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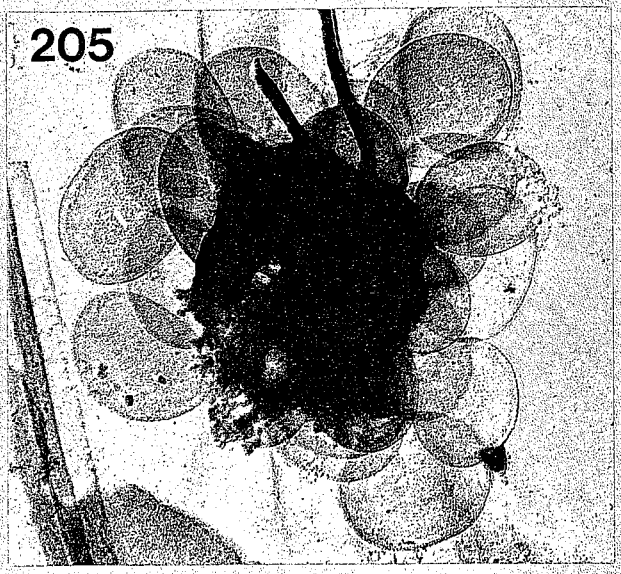

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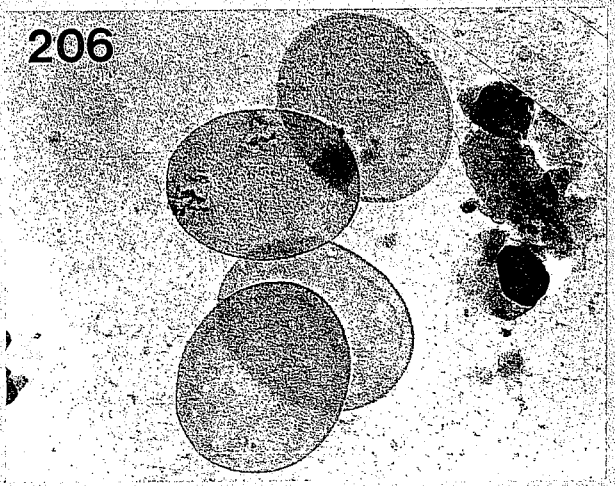

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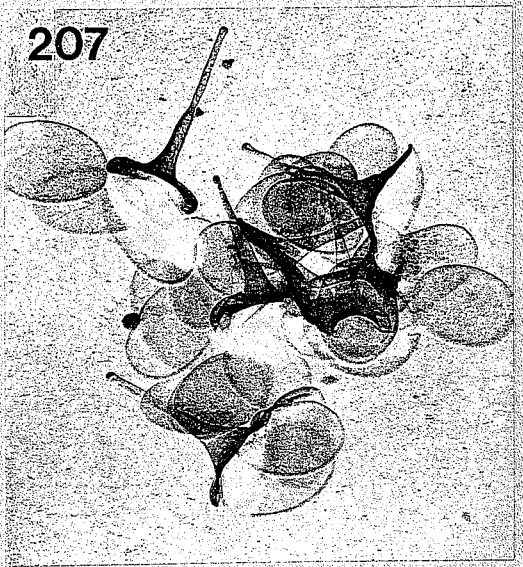

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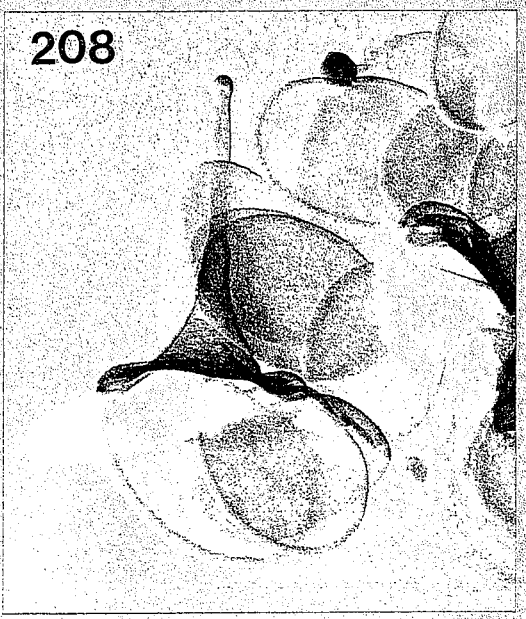


This suggests a rather isolated taxonomic position for the genus.
Occurrence: Single scale-group in Sawley Dene, February 1978.
Reported Distribution: Known only from freshwater in Europe and England (see Swale & Belcher, loc. cit.).

Species with Scales of Undescribed Types

Unknown species A (Figs 205, 206).
Scales of a single type: round or sub-oval plates, 1.5 - 2.2 µm x 1.2 - 1.8 µm, flat and unornamented except for a faint thickening around the scale margin. Cell (Fig. 205) ca. 3.5 µm in diameter, with heterokont flagella and bearing ca. 20 scales. The scales of this organism are reminiscent of the plate scales of certain Spiniferomonas species, e.g. S. bourrellii (Figs 173 - 175), but it appears to lack the spines typical of a Spiniferomonas although its flagella would be consistent with a taxonomic position within the Chrysophyceae.
Occurrence: Sawley Dene, isolated cell and scales, August 1976 and January 1978.
Reported Distribution: Not previously found.

Unknown species B (Figs 207, 208).
Scales of two types: flat ovals with a distinctly thickened rim, 1.0 - 1.3 µm x 0.7 - 0.85 µm, and short bell-shaped scales with an extended tubular tip, 1.5 - 2.0 µm long and 1.2 µm in diameter at the flared end. Scales, particularly the latter type, unlike those known for any other species with the possible exception of Raphidocystis tubifera (e.g. Fig. 301) which has bell-shaped scales composed of a meshwork material.
Occurrence: Single scale group in Sawley Dene, January 1978.
Reported Distribution: Not previously found.

Unknown species C (Figs 209, 210).
Scales of two basic types: round or sub-oval plates 2.3 - 3.0 µm in diameter and flattened spines 4.5 - 8.0 µm long. Each plate scale with ornamentation of distinctive type (Fig. 210): outer 2/3 of scale thick, with closely-spaced

FIGS 209 - 217 TEM of non-chrysophycean scale-bearing organisms, III.

Figs 209 - 210 Unknown species C.

Fig. 209: group of spines and plates, x 6,000; note spines with both pointed and squared tips.

Fig. 210: single plate scale, x 12,000.

Fig. 211: Unknown species D: single plate scale, x 12,000.

Figs 212 - 213 Unknown species E.

Fig. 212: group of scales, x 6,000.

Fig. 213: single scale, x 12,000.

Fig. 214: Unknown species F: single scale, x 12,000.

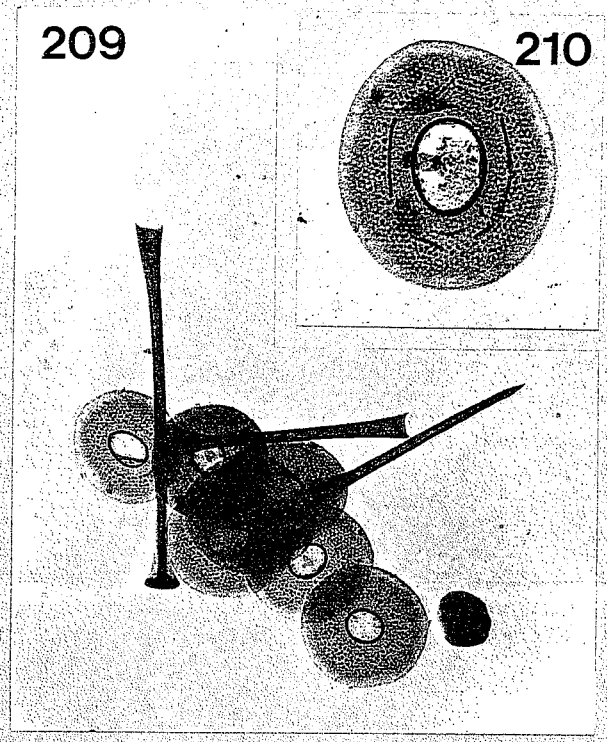
Figs 215 - 216 Unknown species G.

Fig. 215: group of scales, x 6,000.

Fig. 216: single scale, x 12,000.

Fig. 217: Unknown species H: single scale, x 12,000.

Source of specimens: Sawley Dene (Figs. 209 - 211)
Brim Bray Pond (Figs 212 - 213, 215 - 217)
Lumley Moor Reservoir (Fig. 214).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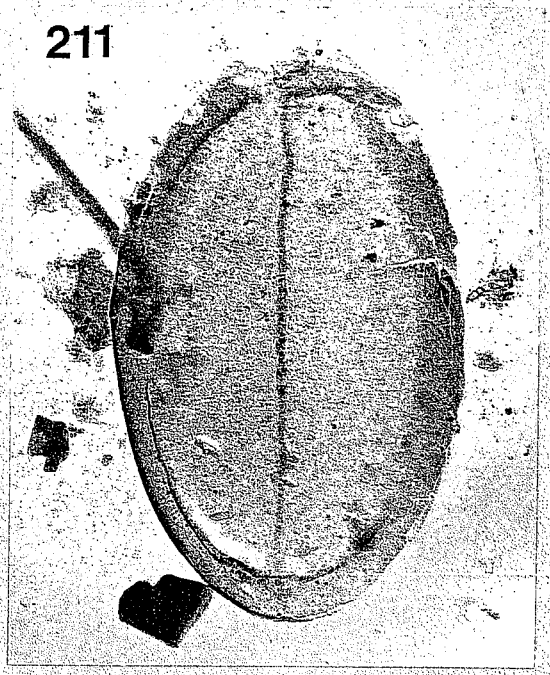
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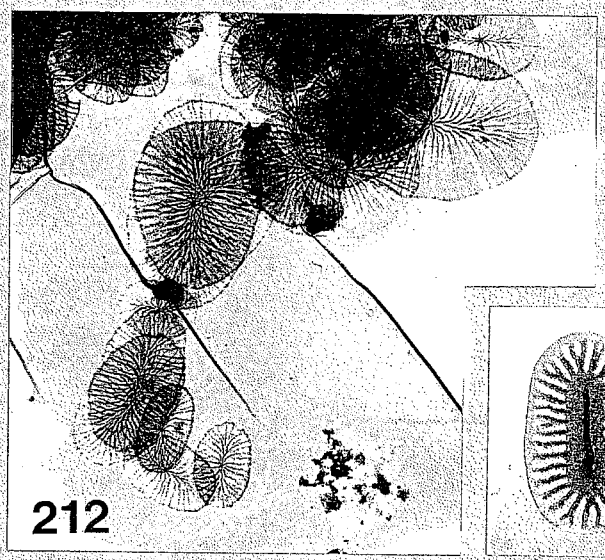
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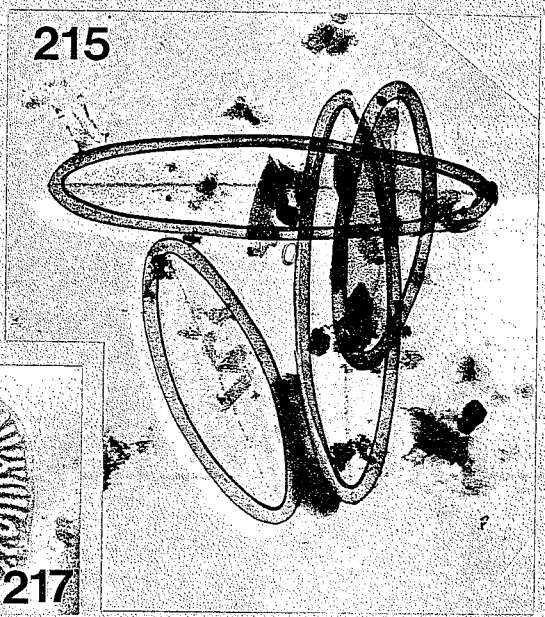
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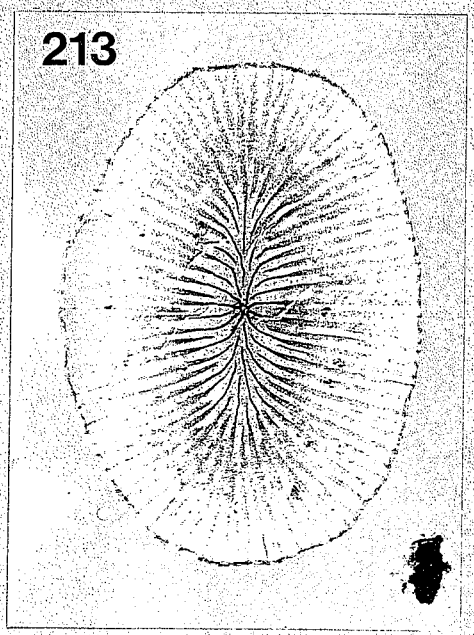
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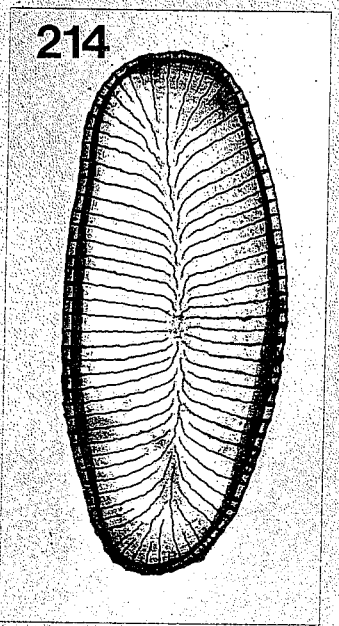
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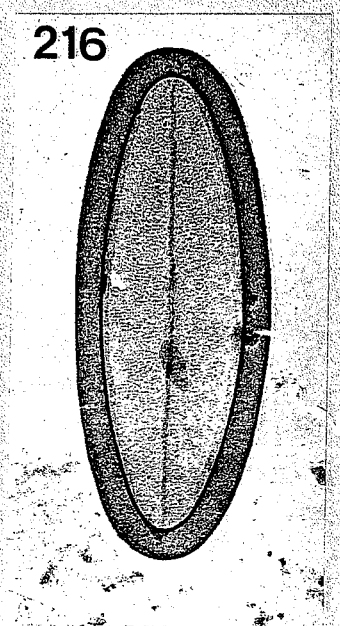
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perforations except at scale rim; oval inner region thin, with similar but more clearly visibly perforations. Spines with triangular base-plate, the long axis of spine bearing central or marginal ribs, terminating in a pointed or squared, slightly biforked tip.

These scales do not closely resemble any previously recorded types, with the possible exception of some plate scales ascribed to Potamodiscus (Gaarder et al., 1976: Figs 15 - 16) but not belonging to the single known species P. kalbei Gerloff. The latter species is in fact a late synonym for the heliozoan organism Pinaciophora fluviatilis Greeff, the scales of which have recently been examined by electron microscopy (Belcher & Swale, 1978). It is therefore possible that the present organism is a heliozoan close to Pinaciophora, although in the latter genus spine scales are unknown.

Occurrence: A few scales in Sawley Dene on two occasions, January 1978.

Reported Distribution: Not previously found but further examples collected in a small oligotrophic lake near Leeds (A. Rees, unpublished).

Unknown species D (Fig. 211).

A single oval scale found, amorphous but with faint suggestion of meshwork structure, dimensions 4.0 x 6.0 µm. Distinctive thickened margin, 0.4 - 0.5 µm wide, and narrow mid-rib along long axis of scale. This scale appears to be of similar type to the oval scales of the heliozoan Raphidocystis tubifera (see p. 106) and may belong to an undetermined member of that genus. Alternatively, oval scales have been seen by light microscopy in related genera, e.g. Raphidiophrys (Penard, 1904; Rainer, 1968).

Occurrence: Single scale in Sawley Dene, January 1978.

Reported Distribution: Not known.

Unknown species E (Figs 212, 213).

Thin oval scales bearing ribbed thickenings radiating in a clearly-defined pattern from the central area of the scale (Fig. 213); scales varying in size from 1.2 x 2.0 µm to 4.0 x 5.5 µm. Margin slightly thickened but rather

delicate in appearance (cf. Unknown species F, below). The affinities of these scales are obscure, although they are possibly heliozoan in origin (see remarks on species F).
Occurrence: Isolated scales and scale-groups in Brim Bray Pond.
Reported Distribution: Not known.

Unknown species F (Fig. 214).
A single oval scale, 2.5 x 6.0 µm, resembling a scale of species E but distinguished by a thickened margin, ca. 0.25 µm wide, and a more strongly parallel pattern of ribs arising from an extended central region. This last feature is reminiscent of the mid-rib seen in the oval scales of Raphidocystis (see p. 107 and species G, below), suggesting that the organism concerned may be another heliozoan.
Occurrence: Lumley Moor Reservoir (one scale only).
Reported Distribution: Very similar scales illustrated by Takahashi (1959: Fig. 53) from a Japanese lake.

Unknown species G (Figs 215, 216).
Scales oval, 2.3 x 6.0 µm to 2.5 x 10.0 µm, identical to oval scales of Raphidocystis tubifera (see Fig. 302) except for more elongated shape. This species is clearly a close relative of R. tubifera, possibly a variant form of the same species.
Occurrence: Isolated scales and scale groups in Brim Bray Pond only (R. tubifera found only in Sawley Dene).
Reported Distribution: Not known.

Unknown species H (Fig. 217).
Single scale found, 1.3 x 2.2 µm, with thickened central region and short mid-rib, and strongly ribbed outer region. Appearance unlike that of any other scales in this survey or reported in the literature, except possibly scales from the auxospore wall of certain diatoms (Crawford, 1974).
Occurrence: Brim Bray Pond
Reported Distribution: Not known.

Ecological Discussion

PART A: CHRYSOPHYCEAE

Tables 7 - 8 and Fig. 218 summarise this part of the investigation, showing how the same data may be used to indicate both the distribution patterns of individual species and the relative species richness of the sites visited. In Table 7 the species have been arranged into three groups according to how widely they occur outside Sawley Dene in the study area; from this table it might be concluded that within the Sawley Dene plankton a group of cosmopolitan, pH-indifferent species (group a) is distinguishable from a group of apparently "alkaline" species (group b) and another group with an alkaline preference but a more restricted occurrence (group c). Further consideration of the data, however, suggests that such a distinction on the basis of pH-preference may be artificial: Takahashi (1978: Fig. 304) indicates that few species of the Synuraceae are found solely in alkaline habitats, and reference to the distribution records already noted shows that, by contrast to the group a species, those in groups b and c have rarely been recorded and their true habitat preferences may not be properly known. It is therefore possible that the species in the latter groups are simply uncommon, their distribution being limited by factors which may or may not include pH.

Table 8 shows the species which are absent from Sawley Dene but occur elsewhere in the study area and thus presumably would grow in Sawley Dene if conditions were more suitable. In these cases it would appear that many of the species are excluded from Sawley Dene because of narrow pH tolerance: of the 21 species listed in the Table, 15 were found locally in no other alkaline lakes and in at least some instances (Mallomonas actinoloma var. maramuresensis, M. papillosa, M. hamata, Synura sphagnicola) a similar preference has been noted elsewhere (see Takahashi, 1978, and references previously cited). Nevertheless, some caution is still required before extrapolating from limited data; for example, Takahashi gives an acidic habitat range for Chrysosphaerella brevispina and Spiniferomonas trioralis, while on the present evidence

Table 7. Distribution of scale-bearing Chrysophyceae: organisms found in Sawley Dene.

Collecting sites abbreviated as follows: BB = Brim Bray Pond; Ea = Eavestone Lake; LM = Lumley Moor Reservoir; PG/i = Picking Gill Upper Pool; PG/ii = Picking Gill Lower Pool; Sa = Sawley Dene; St = Stanks Pond.

(a)	Species occurring locally in lakes of varied types		
	Mallomonas	1. M. acaroides var. striatula	Sa, PG/i, RC
		2. M. crassisquama	Sa, PG/i, Ea, LM
		4. M. alpina	Sa, PG/i, PG/ii, RC
		11. M. annulata	Sa, PG/ii, BB
		18. M. heterospina	Sa, PG/i, Ea, BB, LM
		20. M. akrokomos	Sa, St, PG/i, Ea, BB, RC
	Mallomonopsis	1. M. elliptica	Sa, PG/ii, BB
	Synura	1. S. petersenii	Sa, St, PG/i, Ea, LM, RC
		2. S. curtispina	Sa, PG/i, Ea, LM, RC
	Paraphysomonas	1. P. vestita	Sa, St, PG/i, PG/ii, Ea, RC
		3. P. foraminifera var. "trifida"	Sa, PG/i, LM
(b)	Species occurring locally in alkaline lakes only		
	Spiniferomonas	1. S. bourrellii	Sa, PG/i, PG/ii, Ea
	Paraphysomonas	2. P. imperforata	Sa, St
		4. P. bandaiensis	Sa, PG/i
(c)	Species found locally in Sawley Dene only		
	Mallomonas	6. M. striata	Sa
	Spiniferomonas	2. S. bourrellii var. "simplex"	Sa
	Paraphysomonas	5. P. butcheri	Sa

Table 8. Distribution of scale-bearing Chrysophyceae: organisms absent from Sawley Dene but found in other local collections.

Collecting sites abbreviated as in Table 7.

Mallomonas	3. M. tonsurata	LM, RC
	5. M. actinoloma var. maramuresensis	BB
	7. M. striata var. serrata	PG/i, PG/ii
	8. M. flora	PG/ii, BB, LM
	9. M. papillosa	BB, RC
	10. M. pillula	PG/i, RC
	12. M. pumilio var. "perforata"	BB
	13. M. "clavoides"	BB
	14. M. cf. schwemmlei	BB
	15. M. cf. doignonii	BB
	16. M. sp. (undescribed)	BB
	17. M. caudata	LM
	19. M. hamata	LM
	21. M. insignis	PG/ii
Mallomonopsis	2. M. calceolus	BB
	3. M. "minuta"	BB
Synura	3. S. echinulata	BB
	4. S. sphagnicola	BB
Chrysosphaerella	1. C. brevispina	PG/i, PG/ii, RC
Spiniferomonas	3. S. trioralis	St, PG/i, PG/ii, (?)RC
	4. S. crucigera	LM

these species may also occur in alkaline sites such as the Picking Gill Pools and Stanks Pond.

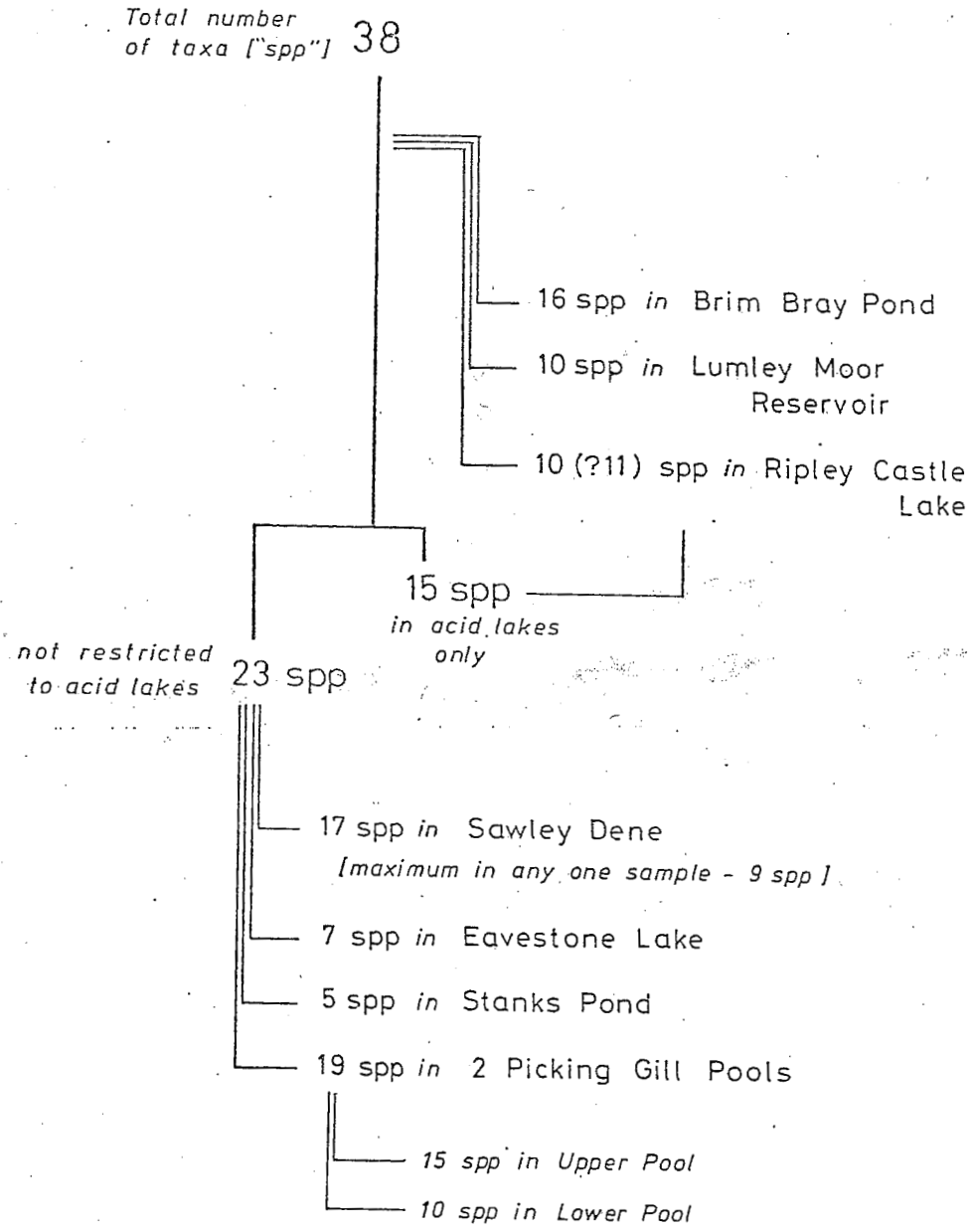
Figure 218 enables the number of species found in Sawley Dene to be compared with those found in the other sites. It should be emphasised that Sawley Dene is much more "completely" studied than the other lakes and has, accordingly, provided evidence of a disproportionately large number of species. Any single collection from Sawley Dene never contained more than 9 species and it is this figure which is perhaps the most appropriate for the present comparison.

Among the sites studied it is clear than the"large" lakes are in general inferior to the smaller lakes or pools in terms of species diversity, although at times they may support one or a few species of Chrysophyceae in considerable numbers. The diversity of species found in single collections from Brim Bray Pond and the Picking Gill Pools compares with that found in Sawley Dene over a much longer period of sampling. Stanks Pond, however, which is also relatively small, is anomalous in that, while it was dominated by Chrysophyceae at the time of sampling, only a few species were present.

The apparent difference between the complements of Sawley Dene and Eavestone Lake, which are of comparable size, setting and trophic status, seems to be due almost entirely to the difference in sampling frequency in the present study; all of the 7 species collected from Eavestone Lake were also found in Sawley Dene at some time and it is probable that more of the Sawley taxa would also be seen in Eavestone Lake with more extensive sampling.

Despite the general affinities of large or small, alkaline or acid lakes on the basis of species diversity, as shown in Fig. 218, many of the sites produced examples of species found nowhere else in the study area. In Sawley Dene these comprised Mallomonas striata, Spiniferomonas bourrellii var. "simplex", and Paraphysomonas butcheri; in the Picking Gill Pools, Mallomonas striata var. serrata and M. insignis; in Lumley Moor Reservoir, Mallomonas caudata, M. hamata and Spiniferomonas crucigera; and in Brim Bray Pond, an astonishing ten species. It is clear that this

Fig. 218. Numbers of scale-bearing chrysophyte species found at individual sites.



latter site, in particular, would repay further study. While these apparent degrees of distinctiveness might be lessened with more intensive sampling, it is nevertheless noticeable that lakes where generally similar ecological conditions should prevail can still support rather different algal populations.

PART B: NON-CHRYSOPHYCEAN ORGANISMS

Of the 18 taxa treated under this heading, 13 were found in Sawley Dene (Table 9) although in some cases only a single scale or scale-group was seen, even during the most thoroughly sampled period (January/February 1978). Whole cells were encountered in relatively few cases (Acanthocystis turfacea, A. erinaceoides, Raphidocystis tubifera, Unknown sp. A) and in general these organisms were much rarer than the chrysophyte species and never showed a tendency to form large populations at any time of year, such as is found for some Chrysophyceae in spring (see Section 2).

The overall rarity of this element of the plankton, together with its exclusion from strict phytoplankton surveys, has resulted in a paucity of ecological information in the literature; likewise, the fragmentary distribution records from the present survey add little habitat information, in contrast to the chrysophycean records. It is possible that the open water of lakes and large pools, as investigated in this survey, are not the best sites for collection of these organisms: Wailes (1921) suggests that Heliozoa should be sought among aquatic vegetation and in boggy sites. The development of any planktonic populations, such as those of Raphidocystis tubifera in Sawley Dene in autumn 1976, might therefore be a comparatively rare occurrence.

For those species about which some information does exist, a wide variety of possible habitats is revealed. Penard (1904) and Wailes (1921) collected Heliozoa from freshwater, but Acanthocystis cf. turfacea has been found in the sea (Leadbeater, 1974: as "Aurosphaera sp."), as have various species of Pinaciophora (Gaarder et al., 1976: as "Potamodiscus spp."). Gyromitus disomatus was found in a ditch near Cambridge (Swale & Belcher, 1974) and some Heliozoa

Table 9. Distribution of non-chrysophycean scale-bearing organisms.

Collecting sites abbreviated as in Table 7.

I.	Organisms found in Sawley Dene		
	Acanthocystis	A. turfacea	Sa
		A. erinaceoides	Sa, RC
		A. "sp. 1"	Sa, RC
		A. cf. echinata	Sa, LM
		A. cf. perpusilla	Sa
		A. "sp. 3"	Sa
		A. "sp. 4"	Sa
	Raphidocystis	R. tubifera	Sa
	Gyromitus	G. disomatus	Sa
	Unknown sp. A		Sa
	Unknown sp. B		Sa
	Unknown sp. C		Sa
	Unknown sp. D		Sa
II.	Organisms found at other sites only		
	Acanthocystis	A. "sp. 2"	BB
	Unknown sp. E		BB
	Unknown sp. F		LM
	Unknown sp. G		BB
	Unknown sp. H		BB

are frequent in Sphagnum bogs (Wailes, 1921). It would therefore appear that many of the organisms described in this category are rather less habitat-specific than the Chrysophyceae and, accordingly, they may in future be found by other workers collecting from waters of diverse types.

SECTION 5 LIGHT- AND ELECTRON- MICROSCOPE OBSERVATIONS ON SELECTED SPECIES

Introduction

One of the main objectives of the present study was to investigate the ultrastructure of species found in the wild collections. It was decided to carry out routine EM fixations of wild material and undertake preliminary sectioning of a wide range of species, selecting a small number for detailed study on the basis of success in fixation, embedding and sectioning and on the potential scientific value of the ultrastructural observations on each species. Thus well-studied species were in general avoided and, of the others, the selection was to some extent directed by the ease with which a desired organism could be located in the blocks of fixed material, together with the technical quality of the preparations finally obtained. The results reported in the main part of this Section (pp. 89 - 108) concern four species on which the observations were considered to be of particular value, both within and beyond the context of the present study. Observations made with light- and scanning electron-microscopes are included where appropriate.

Materials and Methods

EM fixations were carried out on ca. 40 samples of wild material from the net-tow collections (see p. 24 for sampling details), with the aim of incorporating a wide range of species at their periods of relative abundance. In specific cases the samples were manipulated to obtain the maximum yield of the desired species, e.g. by allowing the samples to stand for several hours and exploiting the tendency of diatoms to sink to the bottom, of blue-green algae to accumulate at the surface, or of some pigmented flagellates to display positive phototaxis. Filtration of samples through nylon mesh of known pore-size was also employed to obtain sub-samples relatively rich in algae of a distinct size-category.

Material for fixation was concentrated by centrifugation

and fixed at 4°C for 2h in 2% OsO_4 mixed 1:1 with 5% glutaraldehyde immediately prior to addition to the sample, both fixatives being made up in phosphate buffer at pH7. Fixed samples were rinsed in buffer (3 x 30 min washes), dehydrated in an ethanol series (20 min in each of 6 steps) and embedded in Spurr's resin. Sections were cut with glass knives on a Reichert OmU2 ultramicrotome, stained with 1% aqueous uranyl acetate (30 - 60 min) and Reynolds' lead citrate (15 - 30 min) and examined in Siemens Elmiskop 1A and 102 electron microscopes.

For scanning electron microscopy, fresh samples were dried onto formvar-coated grids as previously described for preparation of whole mounts for the TEM (p. 59) or onto glass cover-slips in a similar manner. After rinsing with distilled water, samples were cemented onto aluminium stubs, coated with gold at 1.2 kv in a Solatron sputter-coater and examined in a Cambridge S600 Stereoscan.

Details of light microscopy and TEM examination of whole mounts have been given previously (pp. 25, 59).

Results and Discussion

(i) Preliminary Investigations

A number of species were sectioned for EM examination in order to test for adequate fixation and to assess their suitability for further study. Species investigated included *Asterionella formosa*, *Uroglena americana*, *Mallomonas akrokomos*, *Paraphysomonas vestita*, *Closterium littorale*, *Volvox aureus*, *Pediastrum duplex*, *Trachelomonas volvocina*, *Euglena* cf. *velata*, *Ceratium hirundinella* and *Peridinium cinctum*. Sections of a number of unidentified flagellates were also encountered, as were species of blue-green algae which are to be reported on separately (H.A. Cmiech, thesis in preparation). *Paraphysomonas* and *Peridinium* were eventually selected for detailed study, to which were added *Synura petersenii* and *Raphidocystis tubifera*, species for which a special search was made since their ultrastructure was anticipated to be of interest (see pp. 95, 104).

(ii) Detailed Study of Organisms

(a) *Paraphysomonas vestita* (Chrysophyceae)

Paraphysomonas cells were abundant on only one occasion in Sawley Dene, this being a sample taken through the ice

(wk 4b). Living cells were occasionally noted at other times (see p.48) and it is likely that the species was present on additional occasions but was overlooked since the cells are colourless and the characteristic scales are clearly visible only with phase optics. Scales of P. vestita were regularly found in EM preparations during winter/spring 1977 and 1978 (wks 4b, 10b, 19b, 2c - 9c, 14c) and the species is widely distributed elsewhere in the Sawley area (see p. 76).

Paraphysomonas is a genus of colourless flagellates classified in the Chrysophyceae (see Hibberd, 1976, 1979) and the structure of P. vestita, the largest and most well-recorded species, was described in an early EM study by Manton & Leedale (1961), who found that an organelle previously observed with LM, near the flagellar bases, was an unusually large Golgi body and that the mineralised scales covering the cell originated in vesicles within the cytoplasm. At that time the organisms now separated as the class Prymnesiophyceae were still grouped within the Chrysophyceae and it was suggested that the scale-forming process in Paraphysomonas resembled that in the prymnesiophyte Chrysochromulina; subsequent work on prymnesiophyte genera (e.g. Manton, 1966) has shown that in this class scales are formed in Golgi vesicles, while in other (pigmented) chrysophyte genera scale vesicles are typically associated with a sheath of chloroplast ER (Belcher, 1969; Schnepf & Deichgraber, 1969). Recently Hibberd (pers. comm. and Hibberd, 1979) has found scale vesicles associated with free ER in another species of Paraphysomonas, P. bandaiensis, and thus a re-examination of P. vestita for more scale details seemed desirable. In addition, some cell features were either imperfectly preserved or not sectioned in the study of Manton & Leedale (1961) and it was hoped that additional new observations could be made.

Subsequent to the completion of this work the report of Lee (1978) was published in which further details of scale-formation in P. vestita were described and the occurrence of tubular mastigonemes in Golgi vesicles was noted. Some of the observations presented here are therefore no longer original and their correspondence with the results of Lee

(1978) will be indicated where appropriate. Lee's EM observations were limited to these two points, however, and certain aspects of the cell structure still remain to be properly described.

A living cell of P. vestita is shown in Fig. 219, flattened under cover-slip pressure to display the cell contents. The principal features are clearly visible, viz. the external scale case, two unequal flagella, the parabasal nucleus and a large posterior food vacuole. Also visible are the Golgi body in its characteristic position adjacent to the nucleus and the flagellar bases, the contractile vacuole, other vacuoles and granular inclusions in the cytoplasm, at least some of which are probably ingested food particles. The cell in Fig. 219 corresponds closely with the cells illustrated by Manton & Leedale (1961: Figs 1 - 7) except that, in the latter material, food particles were regularly spherical and very prominent in the cytoplasm.

Fig. 220 shows a cell in transverse section; the plane of this section is very similar to that of Fig. 12 in Manton & Leedale (loc. cit.). The cell appears slightly contracted within its scale case and displays the nucleus, Golgi body, mitochondria, membraneous inclusions, scale-forming vesicles in the cytoplasm (arrows) and a large food vacuole of irregular shape, containing mature scales in addition to bacteria and other debris. This vacuole is of similar appearance to other vacuoles which contain recognisably extraneous organisms (see below) and is clearly the result of phagotrophy; the suggestion of Manton & Leedale (1961) that similar vacuoles might represent the last stage in the process of scale formation and release seems to be incorrect. Scales may continue to be released through that part of the plasmalemma which delimits a newly-formed food vacuole but they are typically released directly to the cell surface. This process is shown in Figs 221 - 224 where the profile of a scale may be traced in successive sections at the point when its scale vesicle has fused with the plasmalemma and the contents are being discharged to the outside.

The micrographs of Manton & Leedale (1961) show that many mature scales may be found within slightly dilated

FIGS 219 - 230 *Paraphysomonas vestita*, I.

Fig. 219: LM of living cell viewed with anoptral contrast, x 1,000; note two flagella, scales (s), nucleus (n) with nucleolus, Golgi body (g) and food vacuole(fv).

Figs 220 - 230 TEM of sectioned material.

Fig. 220: median section of cell, x 6,500 , showing features indicated in Fig. 219 and, in addition, scale vesicles within cytoplasm (arrows).

Fig. 221 - 224: serial sections through scale vesicle (sv) containing scale (s), after fusion with plasmalemma (pm), x 15,000.

Fig. 225: two scale vesicles within cytoplasm, x 20,000; each scale vesicle (sv) associated with an ER cisterna (er). Arrows show small vesicles, possibly fusing with scale vesicle.

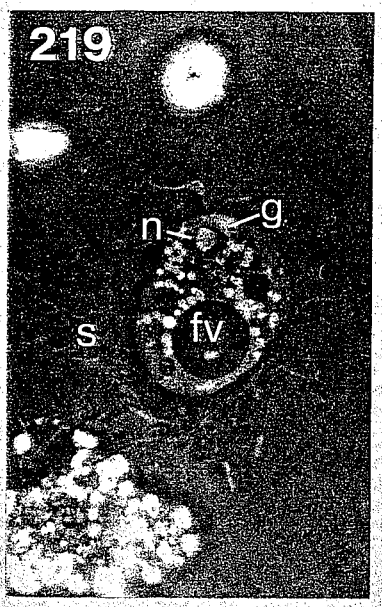
Fig. 226: adjacent serial section to Fig. 225, x 20,000, showing limits of scale vesicles more clearly.

Fig. 227: detail of membranes in vicinity of scale vesicle, x 100,000; sv = scale vesicle, er = ER cisterna.

Fig. 228: explanatory diagram showing identity of membranes visible in Fig. 227.

Fig. 229: peripheral region of cell, x 20,000, showing contractile vacuole (cv) and plasmalemma (pm).

Fig. 230: vesicles within cytoplasm, x 40,000, containing mastigonemes (m) in oblique and transverse section.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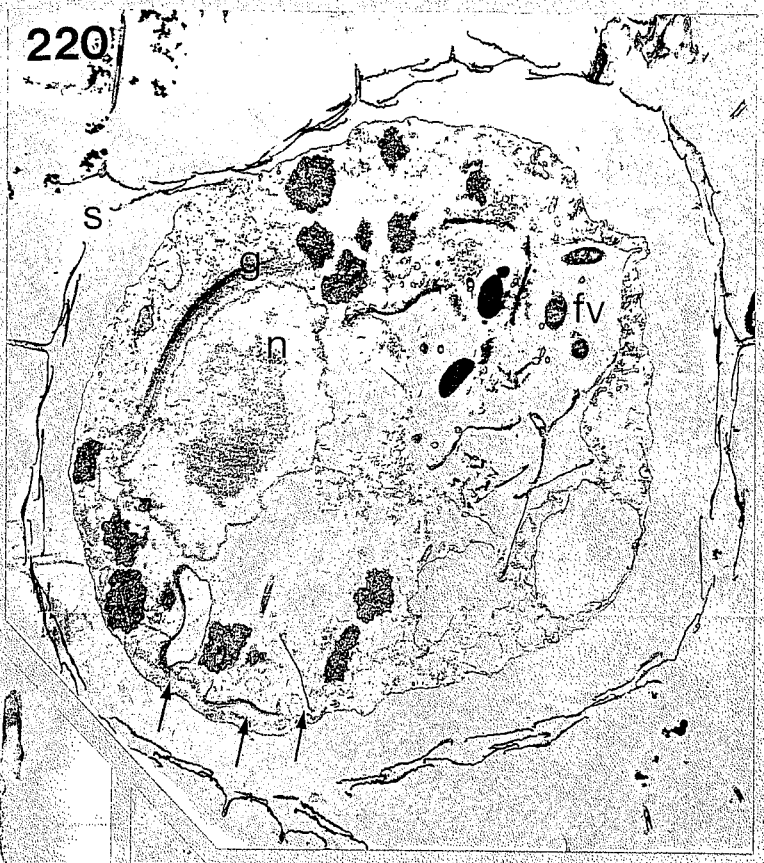
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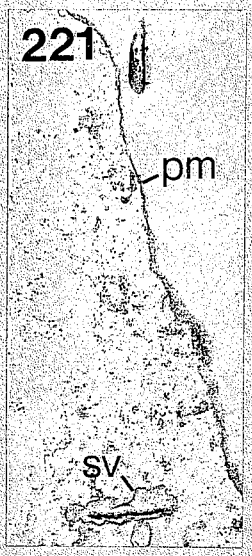
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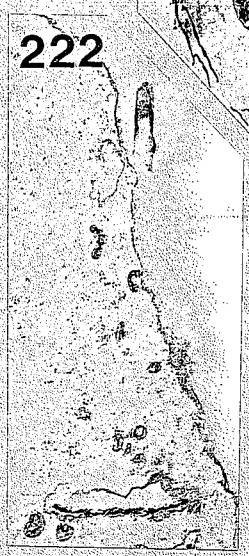
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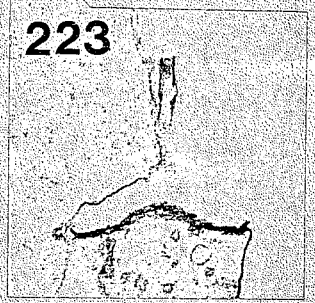
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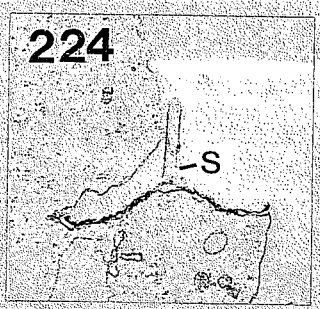
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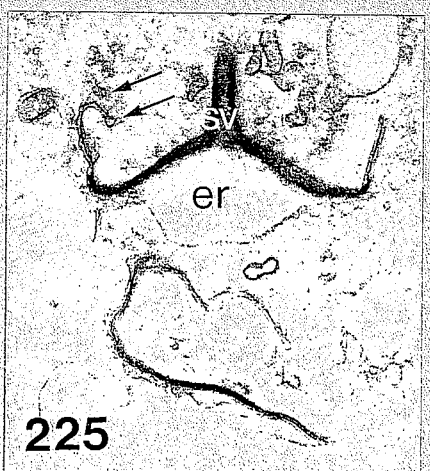
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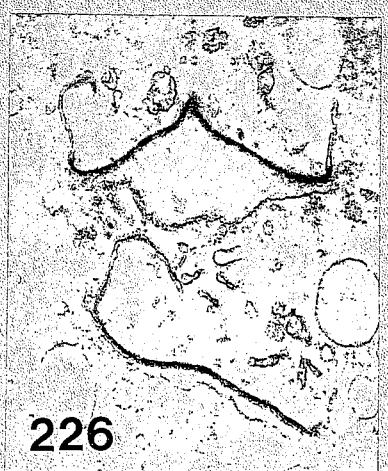
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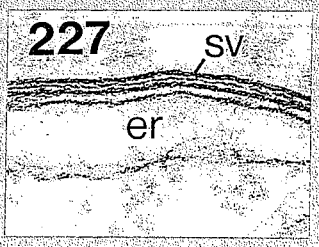
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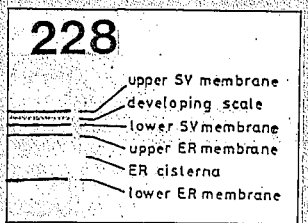
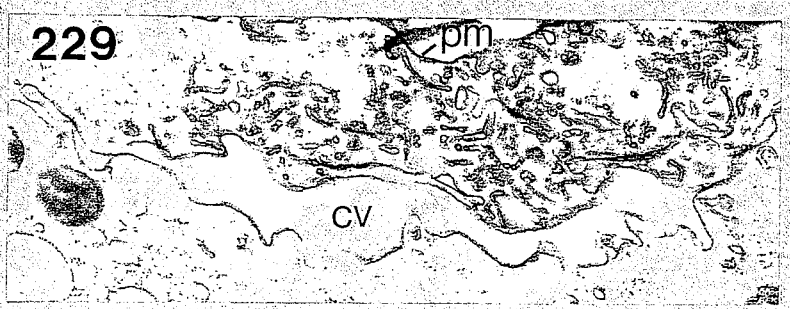
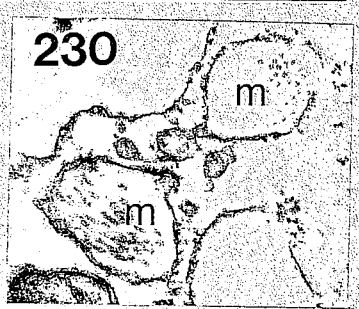

228
upper SV membrane
developing scale
lower SV membrane
upper ER membrane
ER cisterna
lower ER membrane


229
pm
cv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m
m

vesicles in the cytoplasm but their sections give no indication of how such scales and vesicles form. Early stages in scale-formation are included in Fig. 220 and similar stages are shown at higher magnification in Figs 225 and 226. Fig. 225 shows the basal part of a mineralised scale within a closely adpressed vesicle which continues upwards for a short distance beyond the scale margin on either side. Immediately beneath the scale-containing portion of this vesicle lies a dilated ER cisterna, the upper membrane of which closely follows the contour of the lower edge of the scale vesicle. The arrangement of membranes in this area is shown more clearly in an adjacent serial section (Fig. 226) and in a more highly magnified detail (Fig. 227). Fig. 228 is a diagrammatic interpretation of the membrane profiles seen in the latter micrograph; the scale is represented by a thinly mineralised layer within the scale vesicle. The origin of the scale material has not been established but possible fusion of small globular vesicles with the scale vesicle may be seen in Fig. 225 (arrows).

The occurrence of ER cisternae directly beneath scale vesicles has now also been shown by Lee (1978) for P. vestita and in certain of his micrographs (e.g. his Figs 5, 6) the scale vesicle is dilated in the region above the scale. This condition possibly represents a later stage in scale-formation than that shown in Figs 225/226, prior to retraction of the upper ER membrane (shown by Lee to pass up inside the hollow spine) and separation of the scale vesicle for transport to the cell surface. A similar process is apparent in Synura petersenii (see p. 98).

The structure of most of the cell components has been described by Manton & Leedale (1961) but two features seen in the present sections and not described in that study are the contractile vacuole (Fig. 229) and small vesicles containing mastigonemes (Fig. 230). The latter have now also been reported by Lee (1978). The region between the contractile vacuole and the plasmalemma is occupied by elongated "alveolate vesicles" whose structure is of typical chrysophycean type (Wessel & Robinson, 1979) in contrast to the more spherical vesicles associated

with the contractile vacuole in some other algal groups. The mastigonemes (eventually transported to the long flagellum: cf. Fig. 182) are 10 - 12 nm in diameter and are similar in appearance to those described by Leedale et al. (1970) in other species of Chrysophyceae and Xanthophyceae. From Lee (1978) it is clear that these mastigoneme-containing vesicles originate in the Golgi body.

The flagella of P. vestita were seen in some sections by Manton & Leedale (1961) but their detailed structure was not investigated. Since the "heterokont" flagella of this species are one of the main reasons for its classification in the Chrysophyceae it was considered desirable to examine the transition region for typical chrysophyte features, in particular the "transitional helix" (Hibberd, 1976) which Hibberd (unpubl., in Hibberd, 1979) has reported as present in Paraphysomonas bandaiensis. It is possible to view Paraphysomonas as representing a reduced condition from a basic Ochromonas type (Hibberd, 1976); according to this interpretation a species such as P. vestita would have lost its chloroplast and eyespot and probably also the associated swelling on the short flagellum (cf. Synura petersenii, Figs 243/244, which lacks an eyespot but retains the flagellar swelling).

No flagellar swelling is visible in whole mounts (e.g. Fig. 182) or in section and it is therefore presumed to be absent. This condition does not allow the long and the short flagellum to be distinguished in section (cf. Synura, Figs 243/244). A glancing section of the anterior of the cell is shown in Fig. 231 and includes sections of the two flagella within the scale case. A detail of this section is shown in Fig. 232 and the flagellum designated f_1 may be seen to display the 9+2 sub-structure typical of the free part of the flagellum, while in flagellum f_2 a transitional helix is apparent (arrow) forming a ring around the central tubule pair of the axoneme. Fig. 233 shows a section slightly below this level; in flagellum f_2 the central pair are no longer visible and the outer nine doublets are surrounded by additional radiating fibres characteristic of the "transverse

FIGS 231 - 238 *Paraphysomonas vestita*, II; TEM of sectioned material.

Fig. 231: transverse section near cell apex, x 6,000, showing two flagella (f_1, f_2) inside scale case at this level.

Fig. 232: detail of flagella from Fig. 231, x 20,000, showing transitional helix (arrow) within axoneme of flagellum f_2.

Fig. 233: detail of flagella at a lower level, x 20,000, showing transverse partition in flagellum f_2.

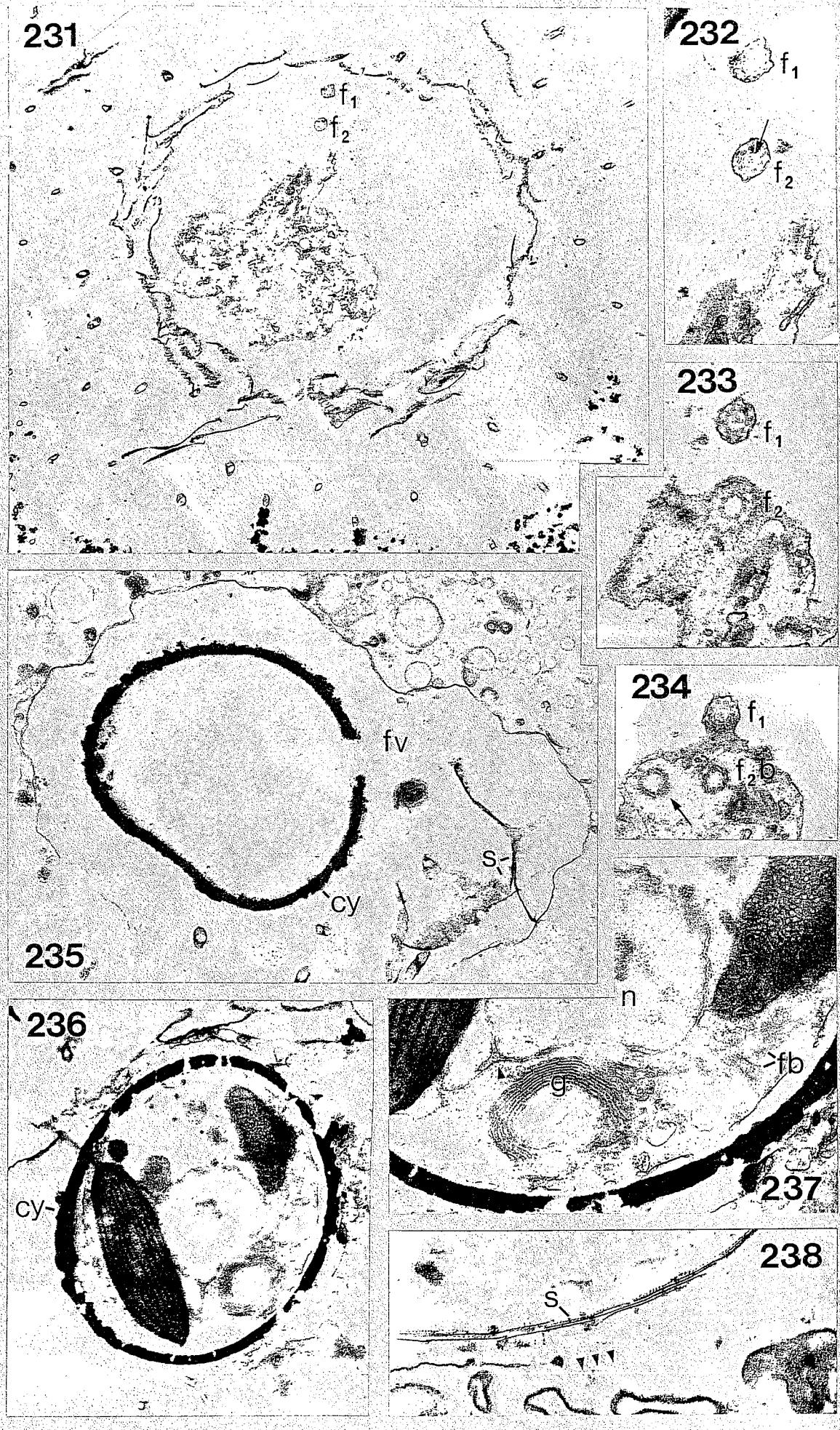
Fig. 234: detail of flagella at a lower level, x 20,000, showing f_2 flagellar base (f_2b), transitional helix in flagellum f_1 and additional basal body (arrow).

Fig. 235: section of food vacuole (fv), x 10,000, containing ingested scales (s) and empty cyst (cy).

Fig. 236: section of another ingested cyst (cy), x 10,000, retaining contents intact.

Fig. 237: detail of cyst shown in Fig. 236, x 20,000, showing internal organelles: nucleus (n), Golgi body (g), mitochondrion and flagellar bases (fb). Arrow indicates continuity between nuclear membrane and chloroplast ER.

Fig. 238: edge of another cell within *Paraphysomonas* cytoplasm, x 20,000, displaying multiple layer of scales (s). Arrows indicate boundary of *Paraphysomonas* cytoplasm (lower part of Figure).


231
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f2
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f1
f2
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cy
n
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fb
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s

partition" (Hibberd, 1976). By the level of Fig. 234 the basal body of flagellum f_2 appears in transverse section while flagellum f_1 now displays a transitional helix. A separate basal body visible in Fig. 234 (arrow) cannot be connected to flagellum f_1 or f_2 and would appear to represent the result of duplication of the f_2 flagellar base prior to cell division.

The final observations on Paraphysomonas presented here concern extraneous objects found within some cells in this population. Paraphysomonas is a phagotroph and food vacuoles are typically present; these may contain undigested food organisms in addition to the mineral parts of previously ingested objects and numbers of Paraphysomonas scales which are presumably engulfed accidentally (Figs 220, 235). Fig. 235 shows a mineralised cyst, from which the contents have been removed, within a food vacuole; another cyst with its contents intact is shown in Fig. 236 (and detail, Fig. 237). From the array of cytoplasmic features that this displays (chloroplast and nucleus with associated ER continuity; Golgi body associated with the nucleus; mitochondrion and flagellar bases) the ingested organism would appear to be an encysted pigmented flagellate alga which is not forming scales and which is a member of the "heterokont" groups (viz. Chrysophyceae, Xanthophyceae or Bacillariophyceae). The most likely identity would therefore be an Ochromonas or Dinobryon species, possibly Dinobryon divergens which was noted in the plankton during the preceding weeks (see p. 47). Cysts of Ochromonas tuberculatus, investigated by Hibberd (1977), show a general similarity to the object shown in Figs 236 - 237.

Fig. 238 shows the edge of a cell of a different kind within the cytoplasm of a P. vestita cell; unfortunately, no more micrographs of this object are available since the preparation was lost before it could be re-examined. The "inclusion" cell bears thin unmineralised scales, each with delicate ribbed markings, arranged in several layers which strongly suggests that it is a prymnesiophyte similar to Chrysochromulina (cf. Manton, 1967b: Figs 2, 5). It would therefore appear that this Paraphysomonas cell has ingested a previously undetected prymnesiophyte from the

Sawley Dene plankton. A more remote possibility is that the prymnesiophyte cell could be living symbiotically within the Paraphysomonas cytoplasm in a manner similar to that described by Febvre & Febvre-Chevalier (1979) for the zooxanthellae of certain protozoans, which also appear to be cells of a Chrysochromulina type.

(b) Synura petersennii (Chrysophyceae)

Scales of S. petersenii were found on several occasions in Sawley Dene during spring 1977 and 1978 (weeks 7b, 9c and 14c). In view of the observations on Paraphysomonas already obtained (p. 89), it was decided that sections of Synura would be desirable so that the ultrastructure of a pigmented and a colourless chrysophycean flagellate could be compared. Whole cells of S. petersenii were seen in Sawley Dene in only one collection (50b), in quantities too small for successful EM fixation, but since this species was more abundant at some of the other sites visited in spring 1978 (see p. 73) fixations were made of material from these collections also. The sample from Stanks Pond (Fig. 101, Table 6) yielded a number of Synura colonies and it was on this material that the following observations were made.

The structure of S. petersenii has been investigated previously and some of its features are well understood. Manton (1955) examined cultured material attributed to Synura caroliniana Whitford (now considered to be conspecific with S. petersenii), illustrating body scales and flagella from whole mounts and certain features of the cell structure, although much of the intracellular detail was lost on fixation. Schnepf and Deichgraber (1969), in a detailed study of S. petersenii, clarified many points including the organisation of the principal cell components, the fine structure of the flagellar appendages and the first details of scale formation. They showed that the large body scales were formed in vesicles associated with the chloroplast ER, a site which has since been found to be normal for pigmented chrysophytes (see below), in contrast to the formation of scales in vesicles of the Golgi apparatus as is found in the prymnesiophytes (see Manton, 1966, and other papers). Hibberd (1973) examined the tiny flagellar scales of various species of Synura and included one micrograph showing

a possible flagellar scale reservoir in the anterior of a cell of S. petersenii. He has since worked on Synura sphagnicola (Hibberd, 1978), a species which shows several points of difference from S. petersenii.

The present account deals only briefly with ultrastructural features which conform to previous descriptions, concentrating on areas where new observations have been made. These include a description of the central region of the colony, where the "tail" portions of the cells converge, and an account of the later stages of scale-formation.

Colonies of S. petersenii consist of upwards of 16 biflagellate, golden-brown cells joined by posterior cytoplasmic "tails" (Fig. 239). Each cell is covered with silicified body-scales (see p. 72 and Figs 162 - 164) and a very uniform layout of internal organelles is visible in both light- and electron- microscopes (Figs 240 - 242). Two chloroplasts are located along parallel sides of the cell and between them may be seen an approximately central nucleus and a large, slightly posterior vacuole which probably contains the characteristic chrysophyte liquid storage material, leucosin or chrysolaminarin (see Hibberd, 1976). Cell components visible only with the electron microscope include a single anterior Golgi body associated with one face of the nucleus, mitochondria dispersed through the cytoplasm and scale vesicles associated with the outer margins of the chloroplasts (Figs 241, 242). The two subequal flagella (see Fig. 162), inserted at the anterior of the cell, show standard "chrysophyte" features (cf. Hibberd, 1976) including a 9 + 2 pattern of microtubular fibrils, a dense structureless swelling near the base of one flagellum and an association between the flagellar bases and the anterior end of the nucleus (Figs 243, 244). In some cells the flagella are clearly inserted in an apical depression (Fig. 245).

The three-dimensional form of the central region of the colony may be visualised by examining the sequence of micrographs in Figs 246 - 248. Figure 246 represents a plane of section some distance above the centre. Oblique longitudinal sections of eight cells are visible around the edge of the field of view; these are the cells which are

FIGS 239 - 245 *Synura petersenii*, I.

Figs 239 - 240 LM of living colony viewed with anoptral contrast.

Fig. 239: whole colony, x 500; flagella not visible.

Fig. 240: portion of flattened colony, x 1,000; note scales (s), position of chloroplasts (c) and leucosin vacuole (l).

Figs 241 - 244 TEM of sectioned material.

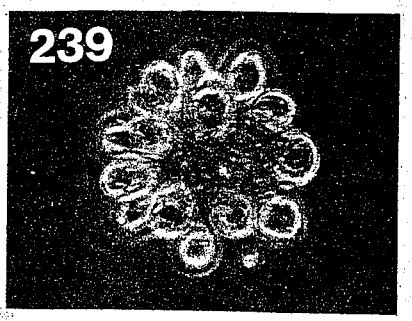
Fig. 241: median section through colony, x 2,000.

Fig. 242: single cell in L.S., x 5,000, showing scales (s), chloroplasts (c), nucleus (n) with nucleolus, leucosin vacuole (l) and scale vesicles external to the chloroplast (arrow).

Fig. 243: L.S. showing anterior end of cell, x 18,000; note position of flagellar insertion relative to nucleus (n) and Golgi body (g). sw = flagellar swelling; f_2b = base of flagellum f_2.

Fig. 244: T.S. across anterior end of cell, x 15,000 (cf. Fig. 243), showing two flagella (f_1, f_2) within a depression of the cell surface. Flagellar swelling (sw) visible on flagellum f_2.

Fig. 245: T.S. showing a level below that of Fig. 244, x 15,000, showing extent of invagination into cell around the two flagella. pm = plasmalemma.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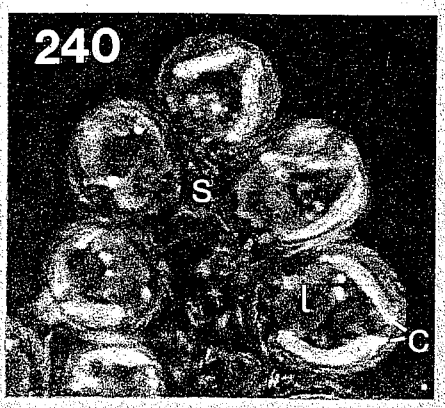
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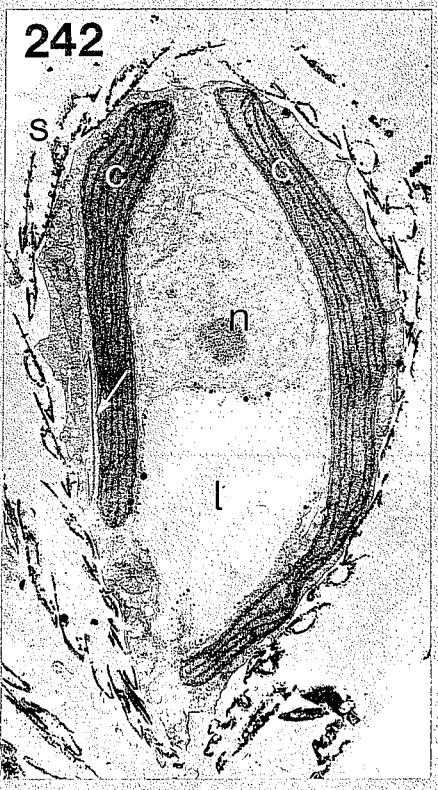
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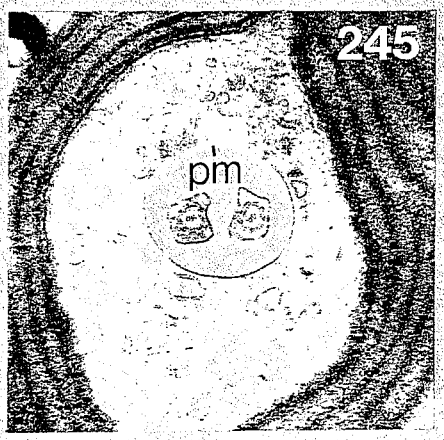
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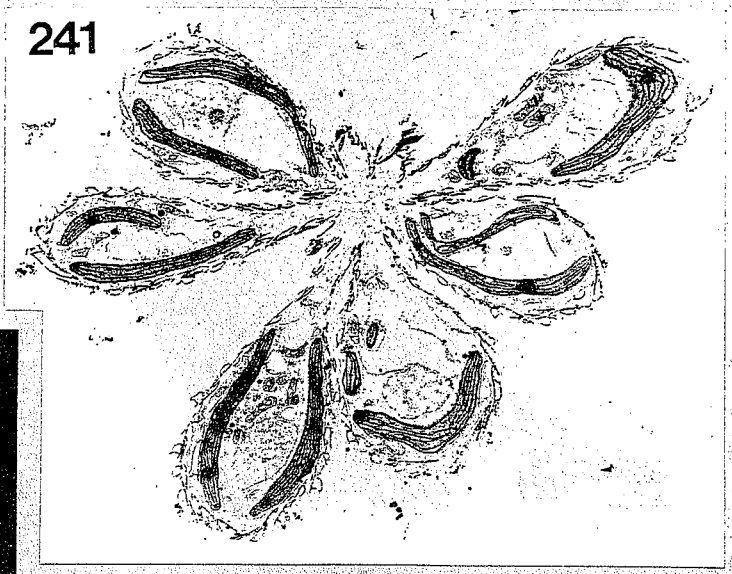
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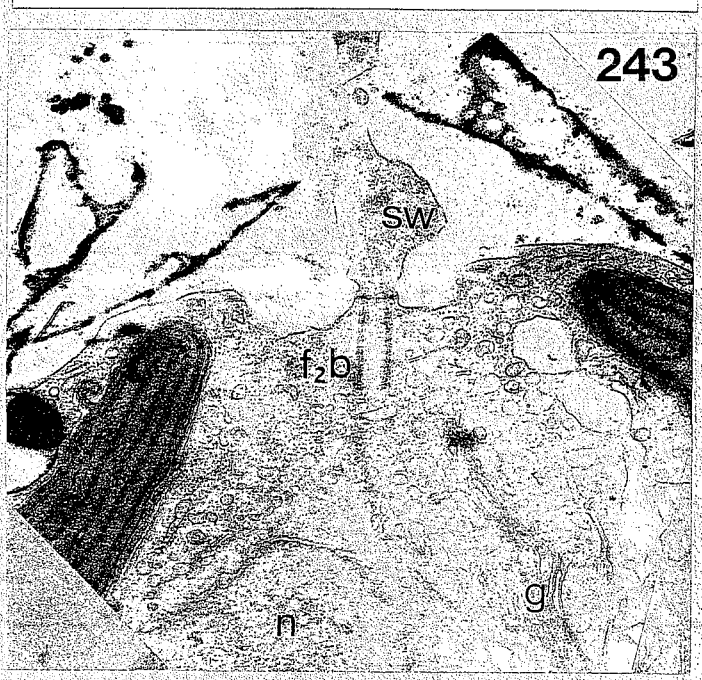
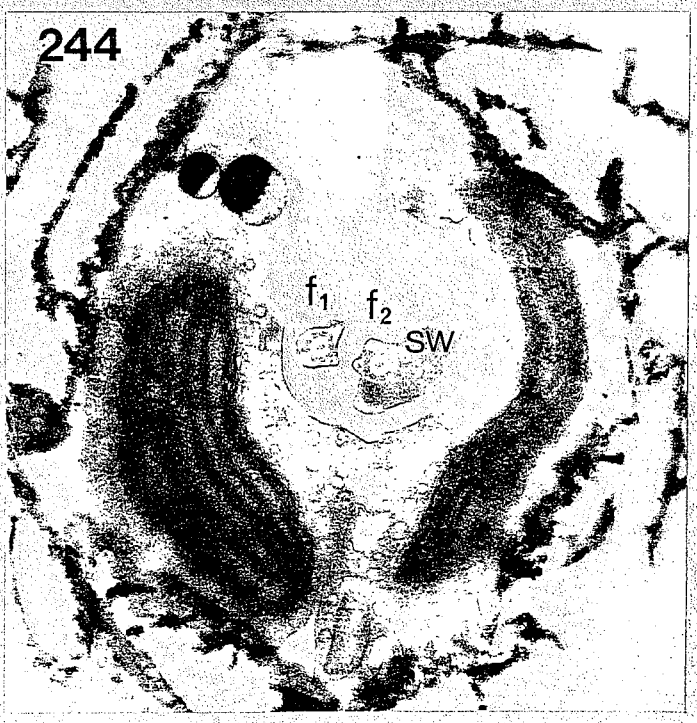

243
sw
f2b
n
g


244
f1
f2
sw

seen in true L.S. in Fig. 248. Transverse sections through the "tails" of four cells which lie beyond the plane of section appear in the centre of the micrograph. Each "tail" is completely surrounded by scales, although there is no indication of how these maintain their position since they appear to be some distance from the cytoplasm in each case.

Figure 247 shows a section taken nearer to the centre of the colony. The "tails", while still distinct, are packed more closely into the central region, but it is clear that even at this stage each "tail" still possesses its own scale case, although in some instances the scales from adjacent cells may be more closely associated with each other than the scales of any one cell with its own plasmalemma.

The exact centre of the colony is shown in Fig. 248, where parts of some 16 cells must be adjoining although it is not possible to distinguish all of these. The ultimate tips are devoid of scales, enabling the plasmalemma of each cell to be in close contact with that of others, although actual fusion of membranes does not occur. The integrity of the colony is apparently maintained by the complex interdigitation of parts of all the cells, there being no evidence for an extracellular adhesive substance of the type suggested by Hibberd (1978) as possibly present in colonies of Synura sphagnicola.

A single "tail" in longitudinal section (Fig. 249) appears to consist of unspecialised cytoplasm, with normal inclusions such as mitochondria visible. However, the chloroplasts and their associated ER do not extend into the "tail" region and so, since these are the sites of scale formation (see below), some process of transport of scales to the outside of the "tail" must be envisaged.

Longitudinal sections of cells (e.g. Fig. 242) typically include profiles of several scale-forming vesicles along the outer margins of the chloroplasts (arrow); other vesicles containing mature scales occur between the chloroplasts and the plasmalemma. A scheme for scale formation was presented in Schnepf & Deichgraber (1969: Fig. 40), representing vesicle development as seen in T.S.;

FIGS 246 - 253 — *Synura petersenii*, III; TEM of sectioned material.

Figs 246 - 248 — Sections in parallel planes approaching centre of colony; note "tail" regions of cells and surface scales.

Fig. 246: x 3,000.

Fig. 247: x 5,000.

Fig. 248: x 8,000, showing interdigitation of membranes from separate cells.

Fig. 249: detail of "tail" region of one cell, x 16,000, with part of the centre of the colony.

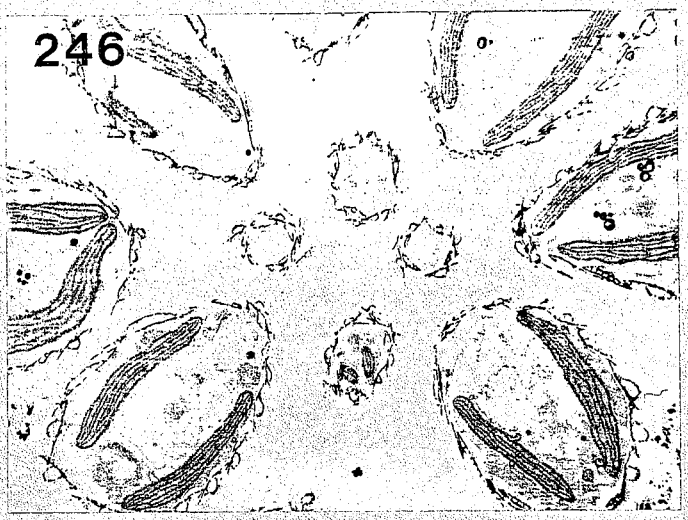
Figs 250 - 253 — Stages in scale formation, i - vi; see text and Fig. 254 for further details.

Fig. 250: an early stage in scale formation, x 12,000; scale vesicle (sv) overlies chloroplast ER (cer) around chloroplast (c).

Fig. 251: further early stages in scale formation, x 12,000.

Fig. 252: later stages in scale formation, x 12,000.

Fig. 253: detail of last stages in scale formation and mature scales outside cell, x 18,000; pm = plasmalemma.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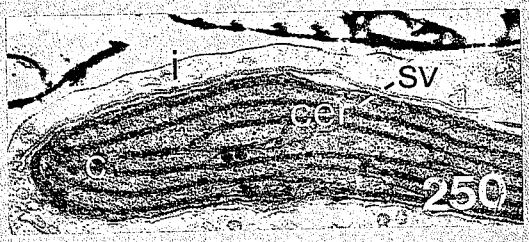
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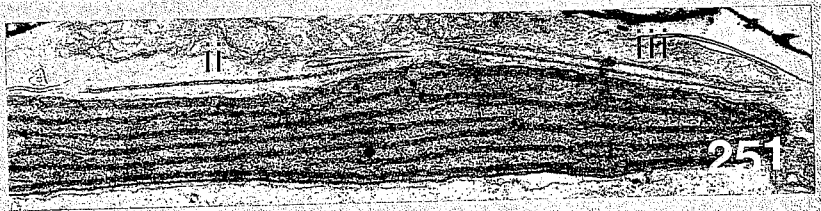
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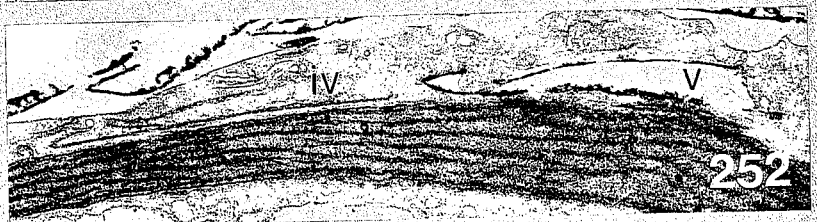
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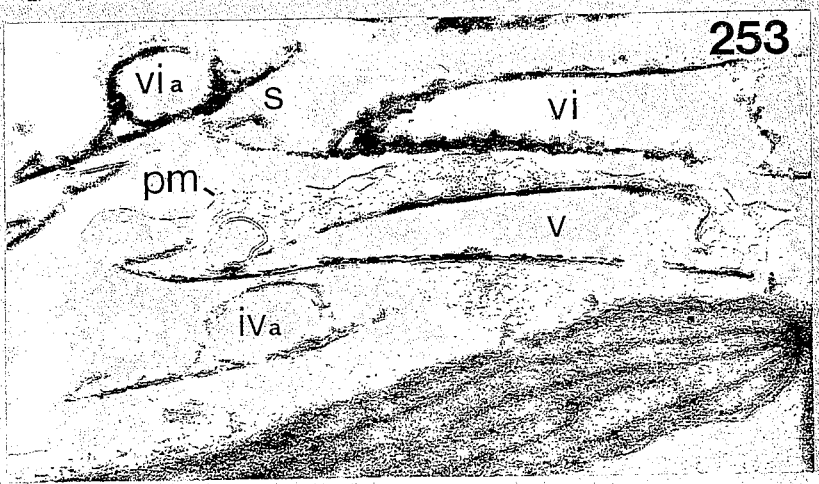
253
VIa
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VI
pm
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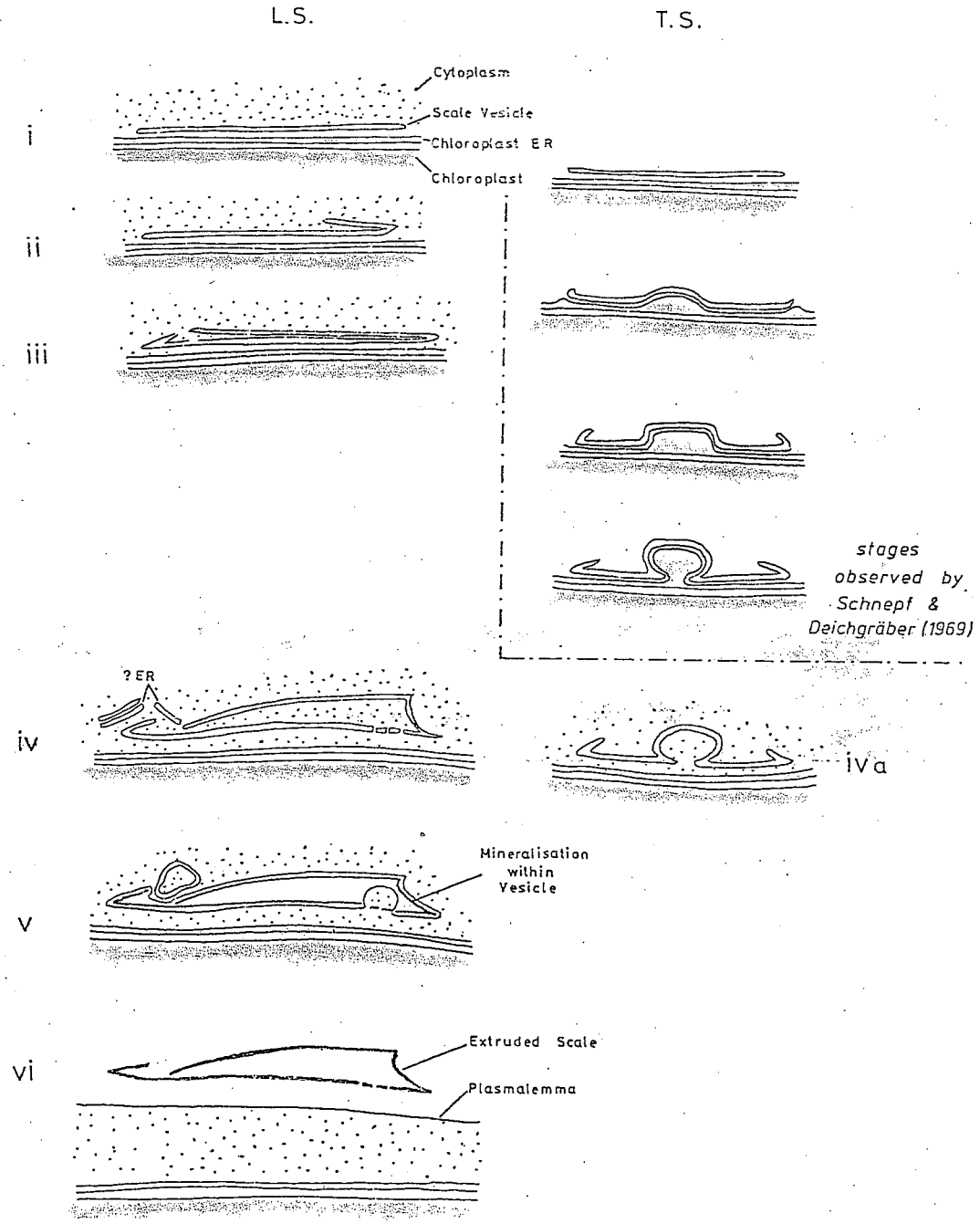
IVa

their micrographs show the outer of the two chloroplast ER membranes becoming convoluted and acting as a template for shaping the underside of the scale vesicle. However, in the micrographs presented here the areas within and beneath the maturing scale vesicles appear to be filled with cytoplasm (Figs 252, 253) and so it is suggested that the phase of direct chloroplast ER involvement observed by Schnepf & Deichgraber does not persist through the whole process of scale formation.

These later stages are seen in Figs 252 and 253 and the process is shown diagrammatically in Fig. 254; some early stages (stages i - iii, Figs 250, 251) are also included but they do not show the features observed by Schnepf & Deichgraber, possibly because the plane of section does not pass through the central, hollow portion of the scale outline. By stage iv the shape of the scale vesicle corresponds very closely with that of a completed scale, although in some areas additional membraneous material is present which may be of ER derivation. In both L.S. (Fig. 252, iv) and T.S. (Fig. 253, iva) the vesicle at this stage is narrow and appears to delineate regions where mineralisation will occur; the central area within the scale profile is occupied by cytoplasm. As mineralisation proceeds and the scale is being formed, this cytoplasmic filling retracts through an upper gap and a lower pore in the scale, the actual nature of which may be seen in direct electron-micrographs (e.g. Fig. 164). This is represented by stage v of the scheme. When this process is complete the newly-formed scale will lie in an otherwise "empty" vesicle, which can release its contents to the cell exterior by fusion of its membrane with the plasmalemma. Mature scales in situ outside the cell are shown in stage vi/via (Fig. 253).

The scheme suggested above thus extends the observations of Schnepf & Deichgraber (1969) and allows more of the entire sequence to be followed. Information is still lacking on some points, however, notably the extent of chloroplast ER involvement in "moulding" all of the scale vesicle, the source of material for mineralisation of the scale, and the origin of the scale vesicle itself. Some of these aspects will be considered further in the General Discussion.

Fig. 254. Stages of scale development in Synura petersenii (see text for details).



(c) Peridinium cinctum (Dinophyceae)

The periodicity of P. cinctum in Sawley Dene has been described earlier (p. 51). Its interest from an ultrastructural viewpoint lay in the satisfactory preservation of many of the cell components in the fixed material, including such details as flagella in situ which are easily lost on fixation (J.D. Dodge, pers. comm.). The material used for the present study was collected from Sawley Dene in June 1977 (24b) and fixed within 1 h of collection; cells of Peridinium could be recognised in the EM blocks under the light microscope and selected individually for sectioning. Light microscopy of fresh and iodine-fixed material allowed the organism to be identified on the basis of spreads of its thecal plates (Figs 255 - 258, 259); the complement 4', 3a, 7", 5"' and 2"", together with the size and shape of certain plates (e.g. plates 1' and 3') are typical of P. cinctum (cf. Schiller, 1937; Boltovskoy, 1975).

A number of workers have studied the thecal plates and the general ultrastructure of P. cinctum. Early EM observations of the theca were made by Venkataraman & Mehta (1960) and more details from sections and whole mounts were added by Dodge & Crawford (1970a). The appearance of the cell exterior in the SEM has been illustrated by Dodge (1971, and in Round, 1973) and Boltovskoy (1975) has used LM and SEM as the basis for a complete redescription of the thecal complement including the plates in the previously little-known sulcal region. Berdach (1977) showed additional SEM pictures which included views of the transverse flagellum which apparently contradicted the accepted concept of the organisation of this organelle (see below). The ultrastructure of Peridinium westii Lemmm., now considered to be a form of P. cinctum (see Schiller, 1937), has been comprehensively described by Messer & Ben-Shaul (1969), who have subsequently studied the processes of trichocyst development and chloroplast senescence (Messer & Ben-Shaul, 1971, 1972). The emphasis in the present account will therefore be upon the principal new observations made, which concern the appearance of the transverse flagellum within the cingulum, particularly as revealed by serial sectioning.

FIGS 255 - 259 *Peridinium cinctum*, I. Tabulation of thecal plates.

Figs 255 - 258 LM of detached plates from a single cell, viewed with anoptral contrast, x 1,000; additional filamentous objects are cells of *Anabaena solitaria*. Plates are numbered in the system of Kofoid, following Dickensheets & Cox (1971).

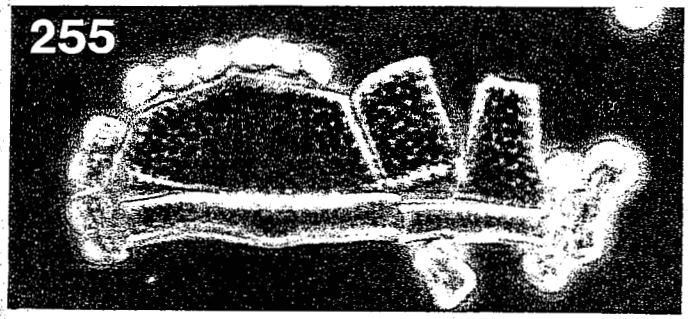
Fig. 255: plates $4''$ - $6''$ and parts of cingulum.

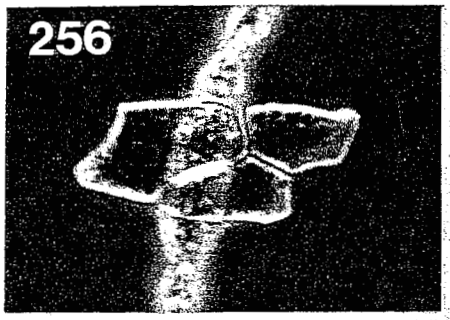
Fig. 256: plates 2a - 3a and plate $3'$.

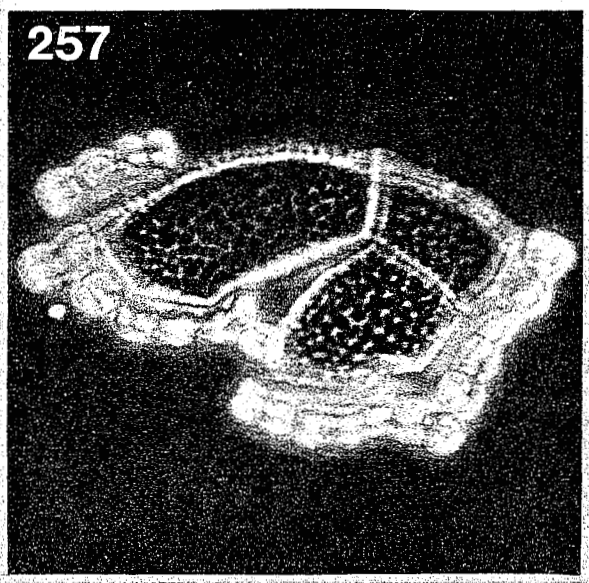
Fig. 257: plates $3'''$ - $4'''$ and plate $2''''$.

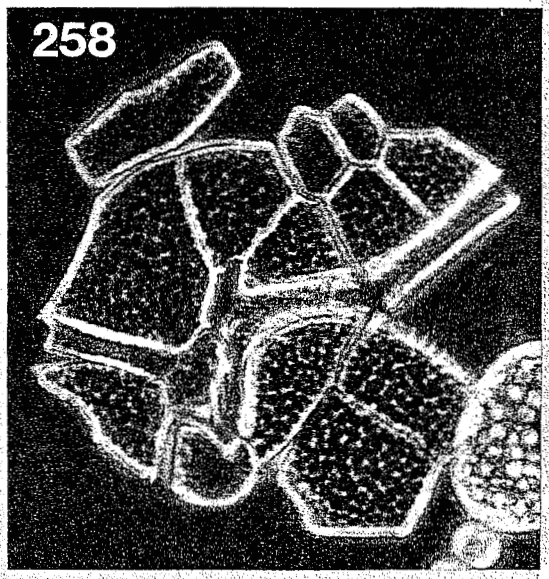
Fig. 258: remainder of the thecal complement including plates of the ventral surface.

Fig. 259: diagram showing full thecal complement as seen in Figs 255 - 258, identified and set out to show arrangement on cell surface.

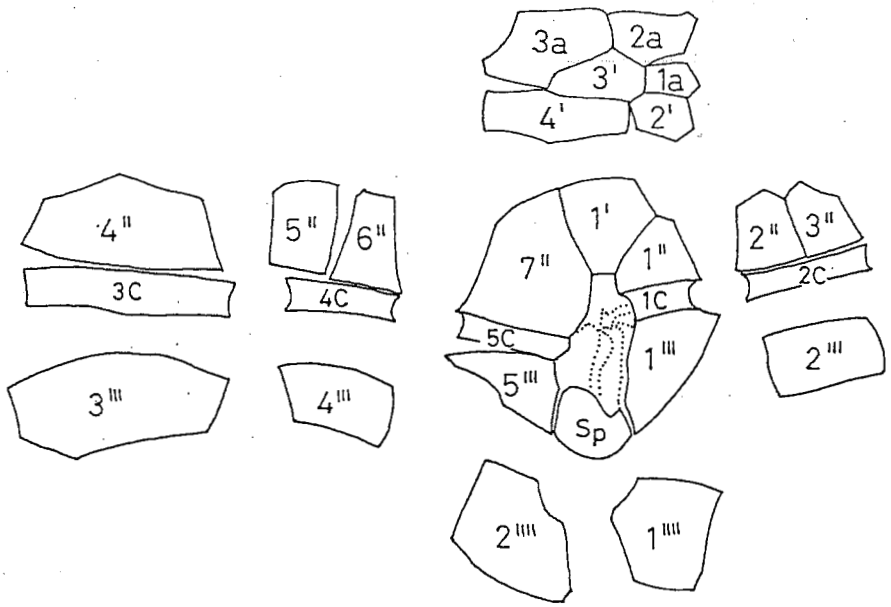








259



In the light microscope cells of P. cinctum are roughly circular in face view (Fig. 260) and kidney-shaped in apical view (Fig. 261), the ventral face appearing as a concave surface. The posterior portion of the ventral face is occupied by the sulcus, a depression in which the longitudinal (trailing) flagellum arises; a second depression, the cingulum, runs at right angles to the sulcus around the equator of the cell (Fig. 260) and contains the tethered transverse flagellum which beats within it. Portions of this flagellum, displaced from the cingulum, are shown in Figs 261 - 262.

General features of the cell in L.S. (i.e. sectioned parallel to the ventral face) are shown in Fig. 263, where the extent of the sulcal depression can be seen as can the equatorial position of the cingulum. The distribution of the principal organelles, excepting the nucleus, is also shown; the latter occupies a position nearer the centre of the cell and is shown in Fig. 264. Details of characteristic dinophycean organelles are illustrated in Figs 265 - 267; these include chloroplasts with individual lamellae comprising 3 - 4 thylakoids, permanently condensed chromosomes in the nucleus and undischarged trichocysts within their sacs, all of which have been described by other workers (Messer & Ben-Shaul, 1969) and are similar to those of other armoured dinoflagellates, e.g. Ceratium hirundinella (Dodge & Crawford, 1970b).

As mentioned above, the principal feature of interest in these sections is the preservation of the transverse flagellum in situ. For convenience, the micrographs which follow have been oriented so that this flagellum appears to stand upright within the cingulum, which may thus be said to have a "base" and a "top" (cf. the appearance of the cingulum in Figs 263, 264). From its appearance in the light microscope (Fig. 262) it may be seen that the transverse flagellum is a specialised structure with at least two components, a convoluted axoneme and a straight accessory strand. An early description of the flagellum by Kofoid & Swezy (1921: p.11) is remarkably detailed and accurate and is of sufficient interest to be quoted in full:

FIGS 260 - 264 *Peridinium cinctum*, II.

Figs 260 - 262 LM of intact cells viewed with anoptral contrast.

Fig. 260: appearance of cell viewed from ventral side, x 750; note cingulum (ci) and sulcus (su).

Fig. 261: apical view of cell, x 750, showing part of transverse flagellum (tf) displaced from cingulum.

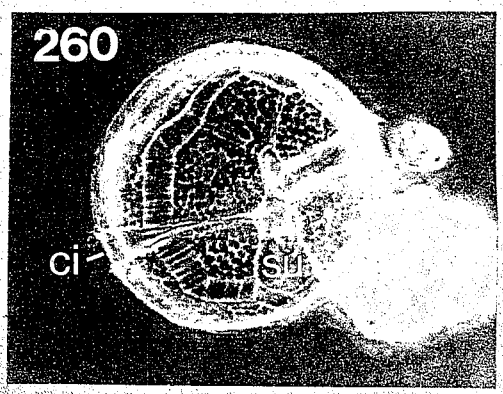
Fig. 262: detail of displaced transverse flagellum, x 1,500, showing straight flagellar strand (st) and coiled axoneme (a).*

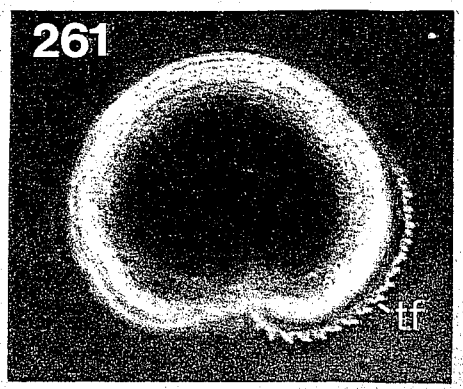
Figs 263 - 264 TEM of sectioned material.

Fig. 263: general view of cell in L.S., x 3,000, showing thecal plates (tp), cingulum (ci), sulcus (su) with longitudinal flagellar canal (lfc) and distribution of organelles within cytoplasm.

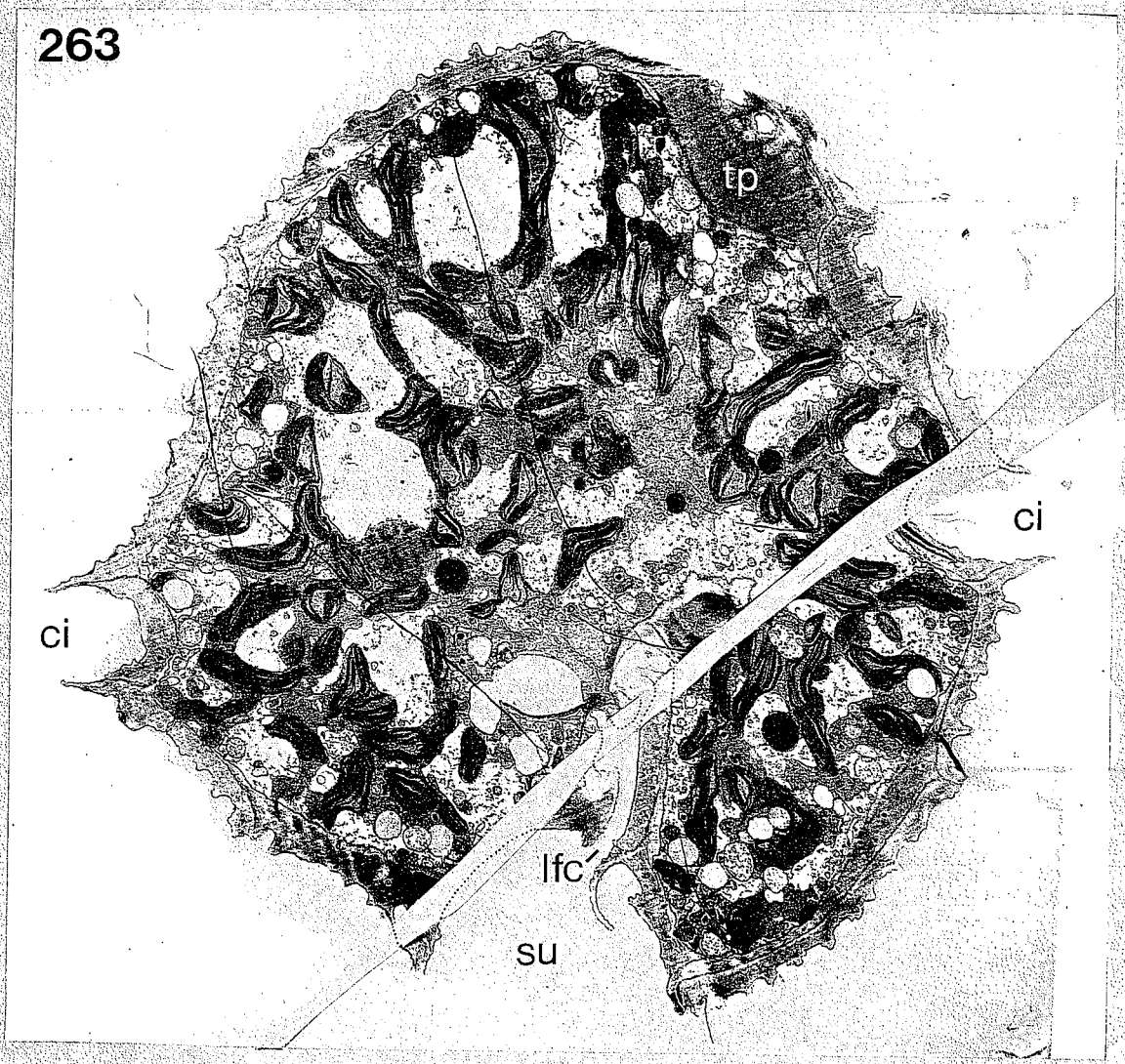
Fig. 264: portion of median L.S., x 2,750, showing elongated profile of nucleus (n) with nucleolus (no); transverse flagellum (tf) visible within cingulum.

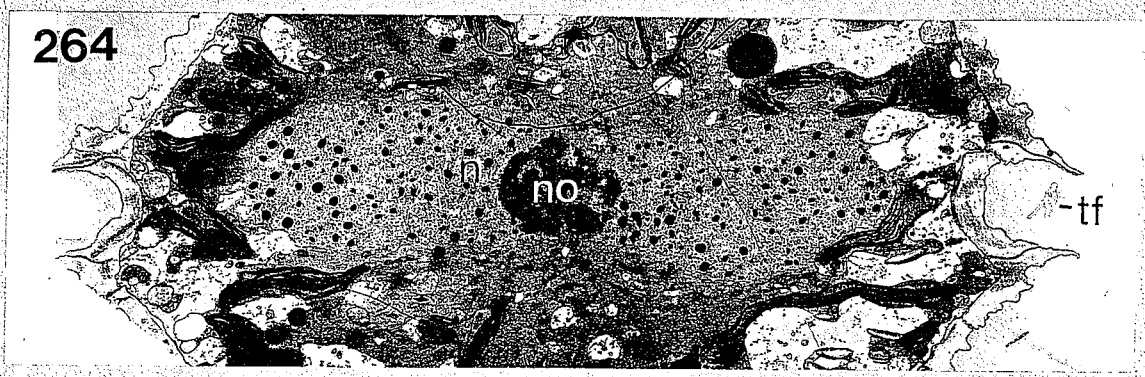
* In this figure the positions of the abbreviations "a" and "st" have been reversed.


260
ci
su


261
tf


262
a
st


263
tp
ci
ci
lfc
su


264
n
no
tf

FIGS 265 - 269 *Peridinium cinctum*, III; TEM of sectioned material.

Fig. 265: single chloroplast (c), x 20,000, displaying amorphous stroma and thylakoids (th) arranged in lamellae.

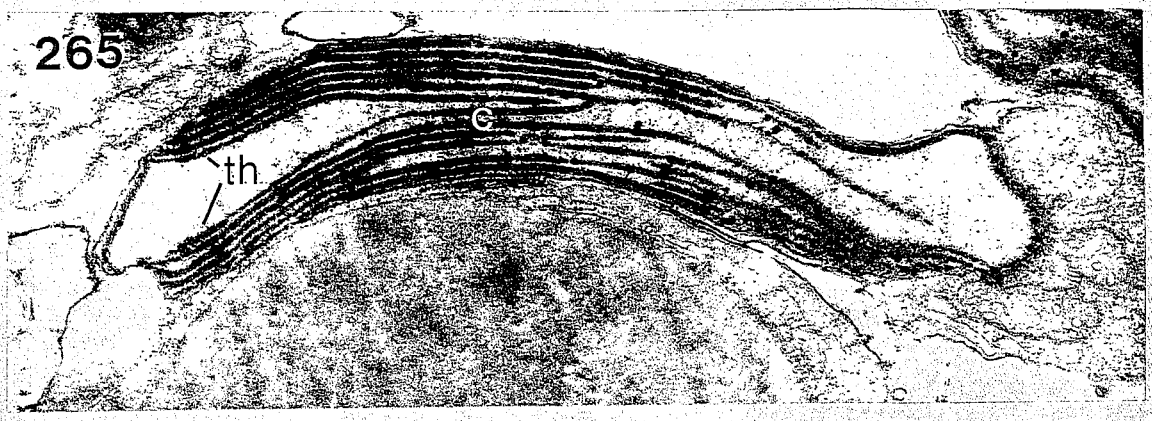
Fig. 266: part of nucleus (n) containing chromosomes (ch), x 9,000; cytoplasm in lower part of Figure contains elongated mitochondrial profiles and numerous small vacuoles.

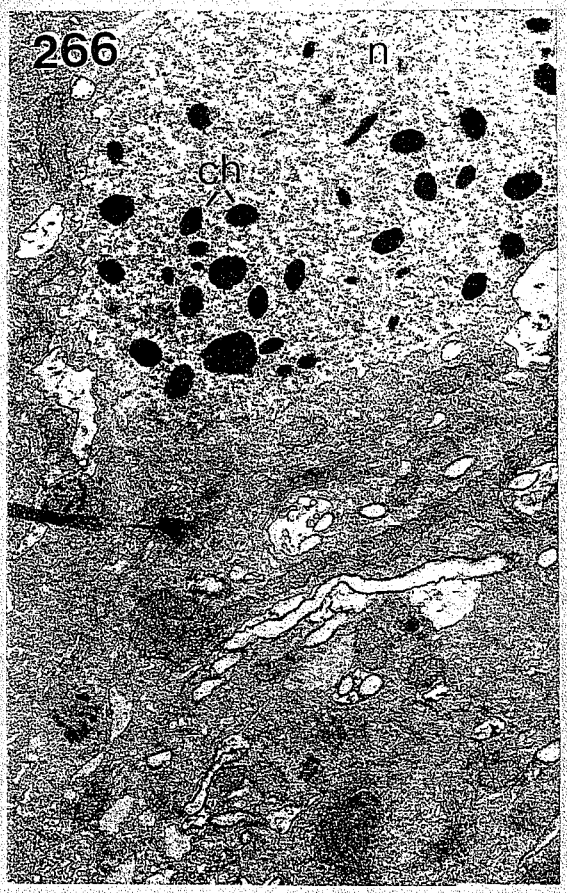
Fig. 267: section close to edge of cell, x 45,000, showing trichocysts (t) within trichocyst sacs, part of a chloroplast (c) and fibrous bodies of unknown nature.

Figs 268 - 269 Radial sections of transverse flagellum (tf) within cingulum (ci); note absence of connection between flagellum and base of cingulum.

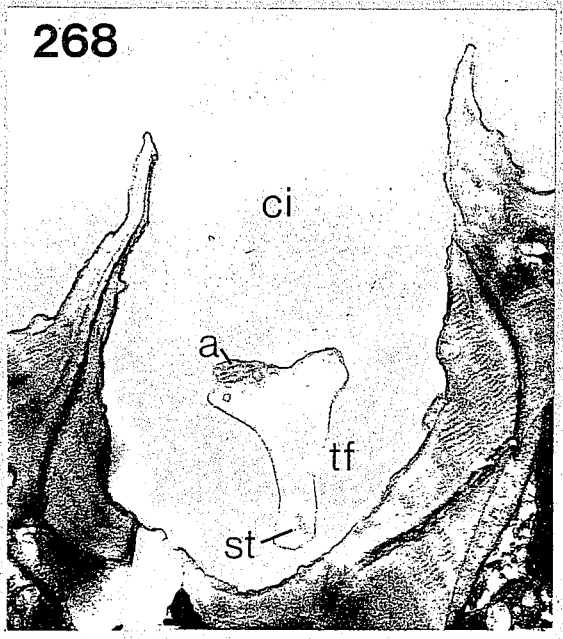
Fig. 268: section of flagellum showing triangular profile, x 10,000, including flagellar strand (st) and axoneme (a) within flagellar membrane.

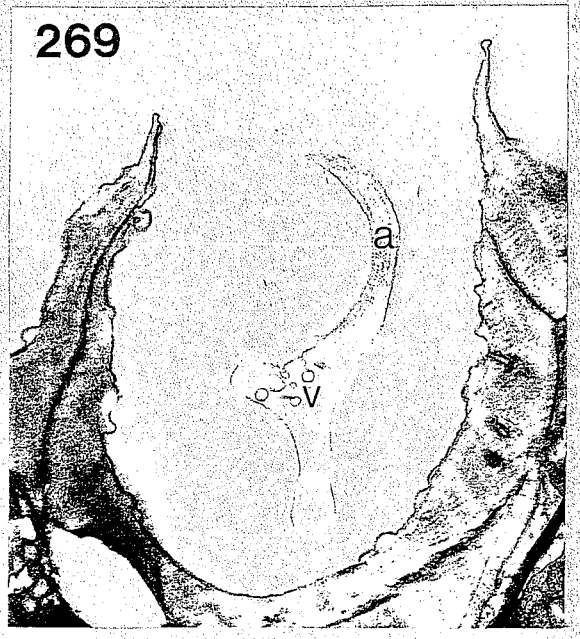
Fig. 269: section of flagellum showing extended profile surrounding axoneme (a), x 10,000; vesicles (v) visible within expanded portion of flagellar sheath.


265
c
th


266
n
ch


c
267


268
ci
a
tf
st


269
a
V

> "The transverse flagellum itself consists of a deeply staining thread or stout fibril, bordered on one side by a comparatively wide, finlike sheet of transparent protoplasm or membrane, somewhat greater in length than itself, and thrown into ripples or folds of wider amplitude than the fibril. This is in constant, wavelike motion from the proximal end distally. Reversals in direction have occasionally been noted."

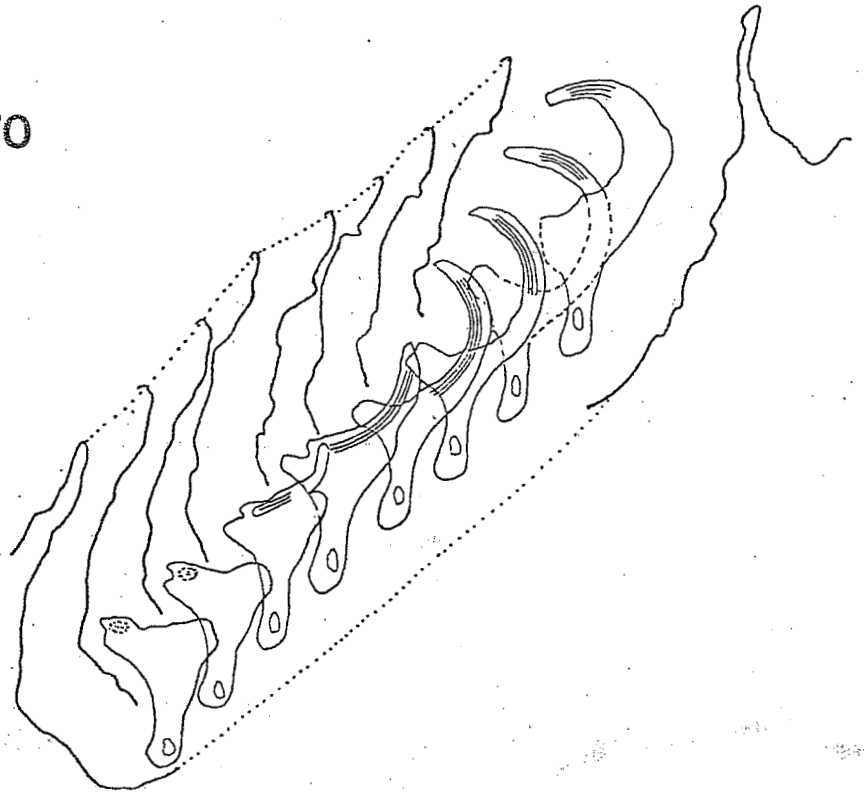
Leadbeater & Dodge (1967a, b) studied the flagella of Woloszynskia micra in section and as whole mounts in the TEM and concluded that the axoneme followed a spiral path around the accessory strand, although an alternative conclusion may also be drawn from their micrographs (see below). Subsequently Taylor (1975) showed that in SEM preparations of several species the accessory strand could be seen to be separate from the axoneme; Leblond & Taylor (1976) re-interpret the micrographs of Leadbeater & Dodge (loc. cit.) in accordance with this finding. In the three-dimensional form proposed by Taylor (1975) and subsequently supported by Leblond & Taylor (1976) and Herman & Sweeney (1977), the flagellum resembles a ruffle, the outer edge of which is delimited by the axoneme following a "hemi-helical" path back and forth above the strand. Leblond & Taylor (1976) examine the possible locomotory efficiency of such a structure with respect to its apparent manner of beating.

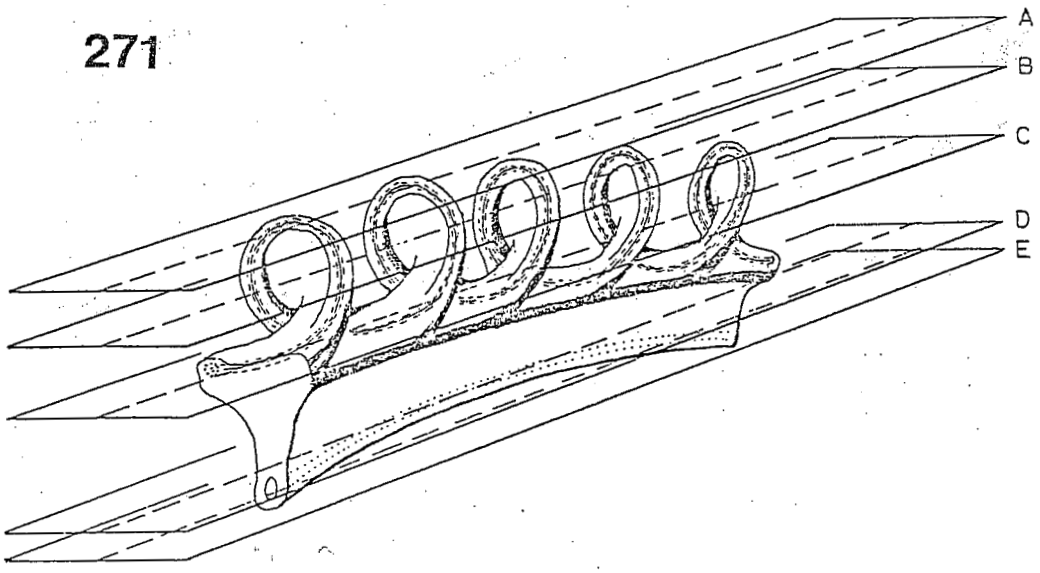
Berdach (1977) illustrated flagella of Peridinium cinctum with SEM and suggested that the "hemi-helical" model was not applicable in this species and that the axoneme was in fact coiled like a screw above the accessory strand. The preservation of the transverse flagellum of P. cinctum in the present material offered the opportunity to test Berdach's conclusion and to speculate on its possible significance.

Fig. 268 shows a radial section in which the flagellum appears as a triangular structure apparently freely suspended within the cingulum. The area within the profile represents the expanded flagellar sheath, surrounded by a single membrane, containing the dense accessory strand towards the bottom and a transverse section of the axoneme at one side of its upper portion. This type of profile is that most frequently found in sections but at

Fig. 270. Peridinium cinctum, IV(a). Profiles of transverse flagellum from consecutive radial sections, x 7,500.

Fig. 271. Peridinium cinctum, IV(b). Reconstruction of flagellar form based on Figs 262 and 270.





intervals the position of the axoneme changes and it curves upwards, e.g. as seen in Fig. 269, where the axoneme now appears in oblique L.S. A sequence of tracings from eight consecutive micrographs is represented in Fig. 270, where the axoneme, together with an extension of the flagellar sheath, traces part of a helical path, the completion of which would bring the axoneme back to its position at the start of the sequence. A diagrammatic reconstruction of such a three-dimensional form, incorporating the repeating structure visible in light micrographs (e.g. Fig. 262), is shown in Fig. 271, with the cingulum walls omitted for clarity.

The accuracy of this reconstruction can be tested by examining sections taken in a tangential plane, i.e. parallel to the planes A - E indicated on the drawing (Fig. 271). Parts of a series of 24 such sections, passing through the flagellar apparatus from top to bottom, are presented in Figs 272 - 277.

Fig. 272 shows a level close to the top of the cingulum and the flagellum, corresponding approximately to plane A in the diagram (Fig. 271). The plane of section passes through the tops of two axoneme loops which are seen between the walls of the cingulum (cf. the upper portion of Fig. 269). Fig. 273 illustrates a level close to plane B in the diagram; the expanded flagellar sheath forms a membraneous "wing" bounded on each side by axoneme, while the top of an adjacent axoneme loop appears at the left (arrow). These three loops are linked at a lower level by the remaining portions of axoneme (Fig. 274 and plane C in the diagram), whose position corresponds to the top of the flattened region of the flagellar sheath visible in Fig. 268. Immediately below each of these linking portions of axoneme are located rows of vesicles within the flagellar sheath (Fig. 275), some of which may also be seen in the radial sections, e.g. Fig. 269.

At lower levels than that in Fig. 275, the flagellar sheath becomes narrower and eventually profiles of the accessory strand are encountered. In Fig. 276, corresponding to plane D in the diagram, the strand is sectioned twice as it arcs through the plane of section. At the lowest levels

FIGS 272 - 281 — *Peridinium cinctum*, V. Details of transverse flagellum; TEM of sectioned material.

Figs 272 - 277 — Tangential sections of transverse flagellum (tf) within cingulum (ci): parts of a series passing through flagellar apparatus towards base of cingulum.

Fig. 272: glancing section of flagellum, x 4,000, showing tops of two axoneme loops.

Fig. 273: section of a lower level, x 4,000, showing median sections of these two axoneme loops (axoneme, a, seen at each side of profile) and top of next loop to the left (arrow).

Fig. 274: section at bottom of axoneme coil, x 4,000, showing linking portions of axoneme and top of next loop to the right (arrow). tp = thecal plates.

Fig. 275: section of expanded portion of flagellar sheath beneath axoneme (cf. Figs 268/269), x 4,000; note arrays of vesicles (v) beneath path of axoneme.

Fig. 276: basal parts of flagellum, x 4,000, showing two oblique sections of the flagellar strand (st) within narrow part of profile.

Fig. 277: section passing beneath flagellum in centre of Figure (arrows), x 4,000. Axoneme (a) at left is close to point of emergence from thecal flagellar pore; relationship of cingulum with sulcus (su) is visible.

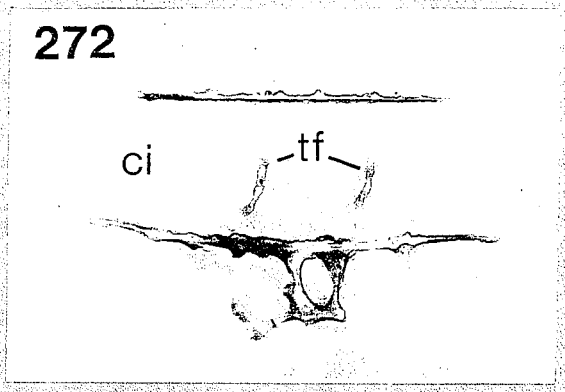
Figs 278 - 281 — High-power details of features visible in tangential sections.

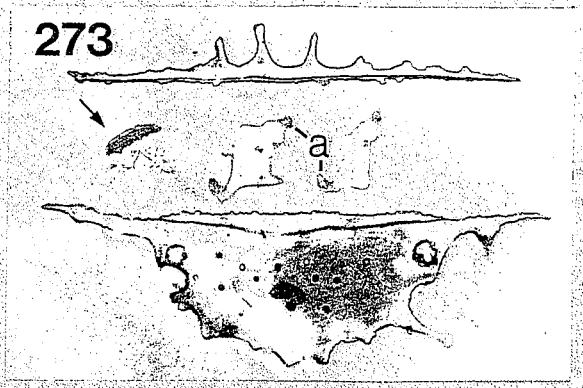
Fig. 278: median section of vesicles (v) within flagellar sheath, x 20,000.

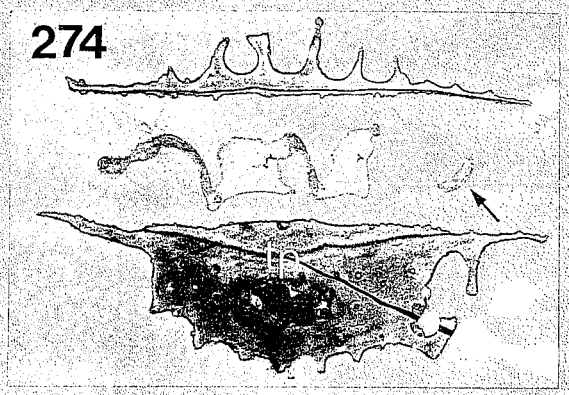
Fig. 279: glacing section of the same vesicle group, x 20,000; note continuity of vesicles with flagellar membrane (arrow).

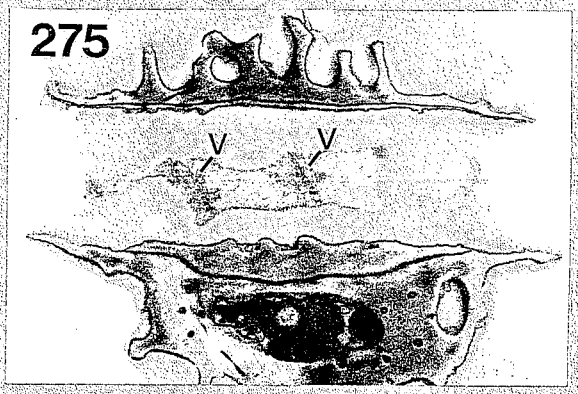
Fig. 280: part of flagellum showing axoneme (a) in L.S., x 20,000; note two types of flagellar hairs (h) present.

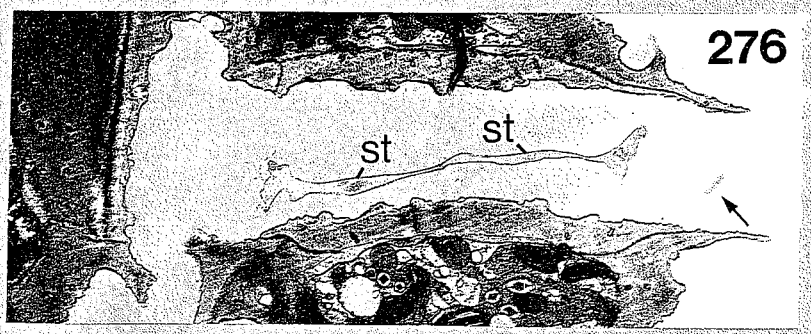
Fig. 281: part of flagellum showing axoneme (a) in T.S., x 20,000; note flagellar hairs and appearance of strand (st). tp = thecal plates (part of cingulum).


272
ci
tf

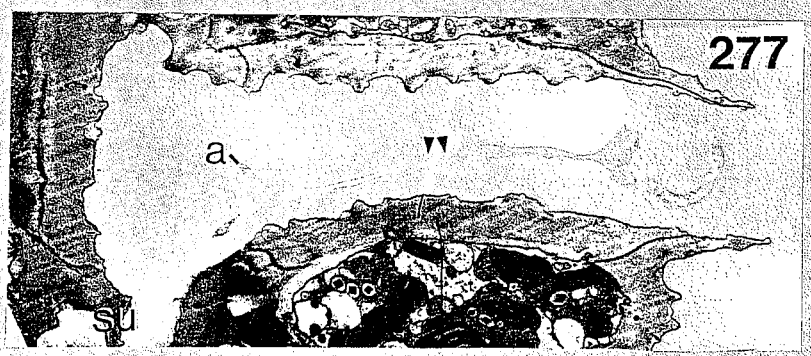

273
a

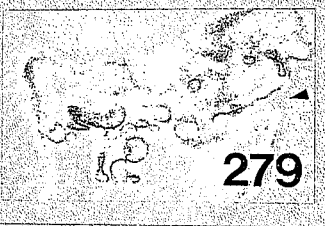

274
lp

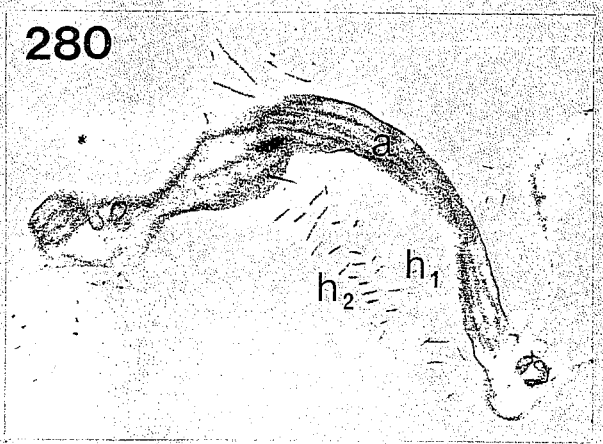

275
v
v

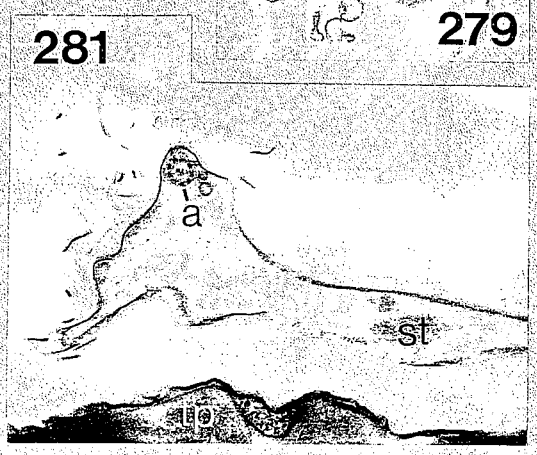

276
st
st


a
v
278


277
a
stl


279


280
a
h2
h1


281
a
st

in the sequence (e.g. Fig. 277 and plane E) a gap appears in the centre of the micrographs as the plane of section passes into the space between the lower edge of the flagellum and the base of the cingulum. By these levels, sufficient of the surrounding cell area is visible to enable the location of the sectioned area to be seen with respect to the sulcus and the edge of the cell (cf. Figs 258, 260).

Selected details from micrographs in this sequence are presented in Figs. 278 - 281, showing the appearance of the flagellar sheath vesicles at higher magnification and at two levels (Figs 278, 279), flagellar hairs of two distinct types (Fig. 280), and transverse sections of the axoneme and the accessory strand (Fig. 281). Some of the vesicles appear to be in continuity with the flagellar membrane (arrow, Fig. 279) and they perhaps represent a complex series of infoldings into the sheath. The axoneme has the "normal" 9 + 2 configuration of sub-units; the accessory strand shows no periodic structure, in contrast to that seen in the "striated strand" of other dinoflagellates (Leadbeater & Dodge, 1967b; Lee, 1977).

Recovery of the complete sequence of 24 tangential sections allowed a model to be constructed to represent the three-dimensional structure indicated in the micrographs. The profile from each level was traced onto glass, the dense areas blocked in with coloured transparent film and the sheets of glass stacked in their correct vertical sequence. Stereo-pair photographs of this model are shown in Figs 282 - 285 and allow the vertical relationships between the flagellar components to be seen if used in conjunction with an appropriate stereo viewer. The model is first shown in three parts, representing the upper ten levels (Fig 282), the central three levels (Fig. 283) and the lower eleven levels (Fig. 284); the final stereo pair (Fig. 285) shows the complete model produced by stacking the three parts. In the model the helical path of the axoneme can be clearly seen, as can the curving accessory strand beneath.

These results indicate that a previous account of a helically-coiled axoneme in P. cinctum, based on SEM

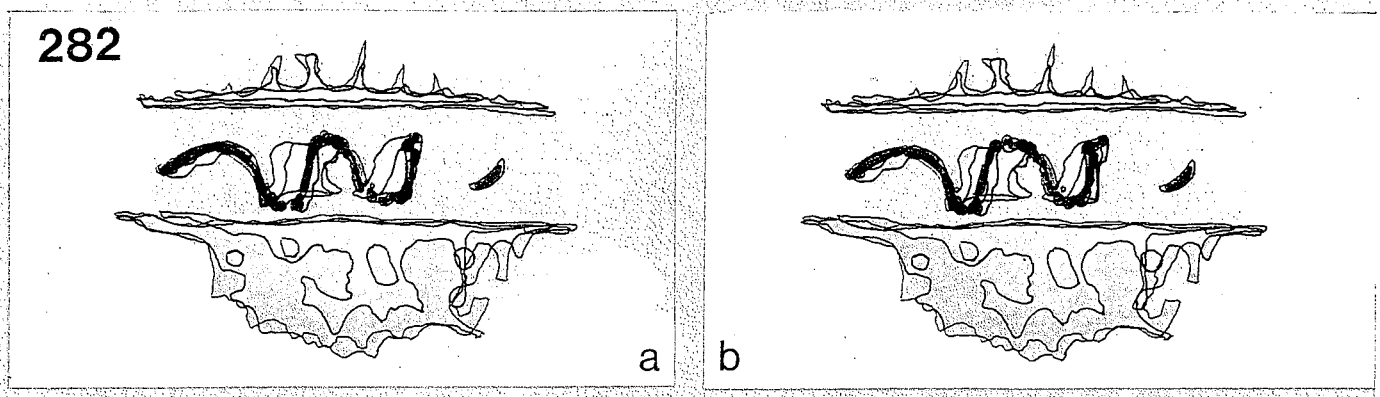
FIGS 282 - 285 *Peridinium cinctum*, VI. Stereo-pair photographs of 3-dimensional model of transverse flagellum, based on series of tangential sections. Some membrane and thecal profiles omitted for clarity. All figures x 2,900.

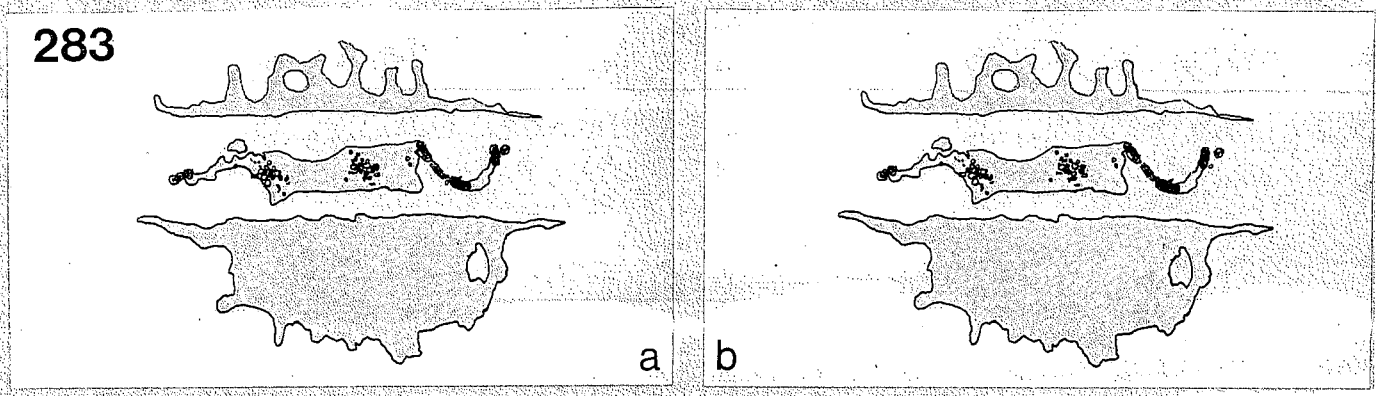
Fig. 282: upper 10 levels of tangential series, showing axoneme and expanded flagellar sheath within cingulum.

Fig. 283: central 3 levels of series, showing flattened region of sheath containing vesicles.

Fig. 284: lower 11 levels of series, showing lowest portion of flagellum enclosing flagellar strand.

Fig. 285: view of complete model (24 levels).


282
a
b


283
a
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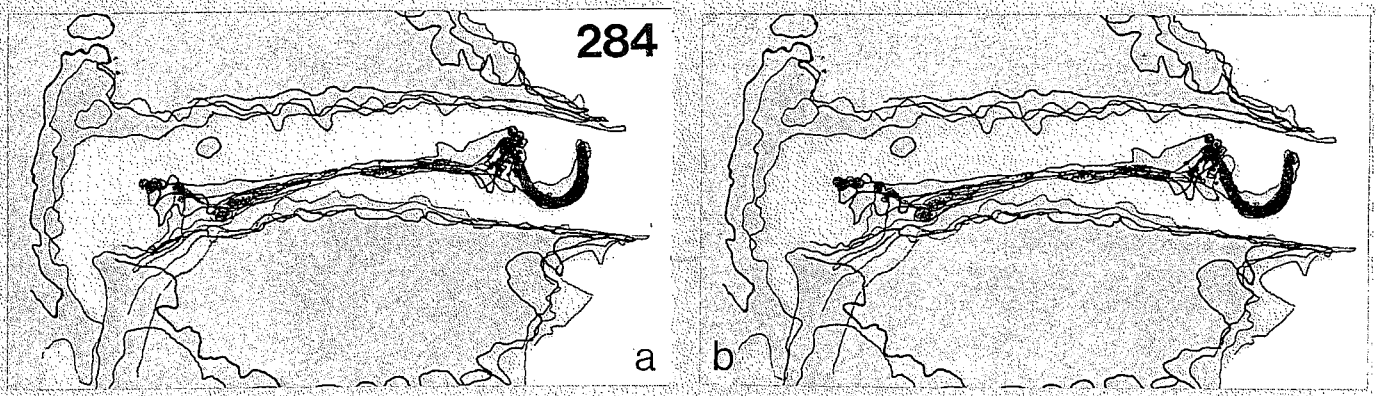
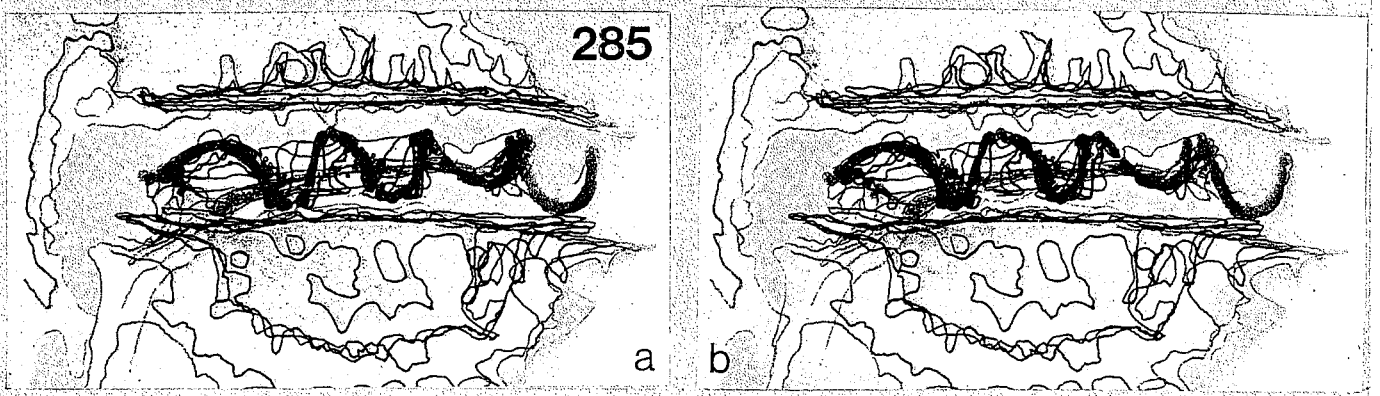

284
a
b


285
a
b

observations (Berdach, 1977) is essentially correct, and that the "hemi-helical" configuration proposed by Taylor (1975) cannot apply in this case. In addition, features such as the flagellar hairs and the vesicles within the flagellar sheath are of interest, as is the form of the lower part of the flagellum, since these could not be observed with the SEM. In the General Discussion the significance of the above observations will be discussed in a wider context; further aspects are also considered by Rees & Leedale (in press).

(d) Raphidocystis tubifera (Heliozoa : Centrohelidia)

This organism was present on isolated occasions in the plankton of Sawley Dene (see p. 54). Although a heliozoan, and therefore not an alga, it nevertheless represents a type of protistan organisation with some parallels to that of certain unicellular algae; in particular, in its possession of silicified scales it is reminiscent of certain genera of the Chrysophyceae. EM studies reported in Section 4 include scales of a variety of organisms, among which may be algae, protozoa and currently unclassifiable protists; others are more clearly heliozoan and may belong to organisms very close to Raphidocystis. An electron-microscope study of R. tubifera might aid the identification of non-algal scales in the plankton collections and possibly shed light on differences or affinities between these organisms and true algae. It is clear from earlier reports (see p. 86) that scales and whole cells of similar organisms have on occasion been determined as algae by other workers.

The original light-microscope description of R. tubifera was given by Penard (1904), based on material from four French sites. Subsequently, the species appears to have gone unrecorded except by Rainer (1968) who found R. tubifera associated with Sphagnum. Certain heliozoans have been receiving attention from electron microscopists but among these only Heterophrys marina belongs to the same sub-order as Raphidocystis and should therefore show many similarities in cell organisation. H. marina bears chitinous needles which are formed in a specialised organelle beneath the plasma membrane (Bardele, 1975). Scales of the freshwater

heliozoan Pinaciophora fluviatilis have recently been examined in the LM and as whole mounts in the TEM (Gaarder et al, 1976, as Potamodiscus kalbei; Belcher & Swale, 1978).

In fresh collections cells of R. tubifera appear as free-floating, generally colourless spheres surrounded by radiating axopodia (Fig. 286) and the species may be recognised from the form of its surface scales which are visible at a higher magnification (Fig. 290). Cells retract their axopodia on disturbance, e.g. on addition of a cover-slip to a fresh preparation, and thus axopodia are not visible in the micrographs which follow.

The cell organisation is displayed in the sequence of micrographs showing a cell progressively flattening under cover-slip pressure (Figs 287 - 290). The general appearance of the cell and its scales corresponds closely with the illustration of Penard (1904) but the use of phase optics here allows additional features to be recognised. The nucleus (Fig. 288) contains a prominent nucleolus and occupies a peripheral position in the cell; the centre of the cell contains a small refractive body, the centriaster, which under optimum optical conditions appears faintly stellate (Fig. 291). This organelle is characteristic of heliozoans in the sub-class Centrohelidia (Bardele, 1975) and forms the centre of the radiating microtubule system which extends into the axopodia. The cytoplasm of the cell contains small vacuoles which swell and contract irregularly, various granular inclusions and liquid droplets of unknown nature (Figs 289, 290). Chloroplasts and eyespot are absent, as are any flagella or other locomotory structures.

On one occasion a cell was found to have encysted within its scale case (Fig. 292); the cyst is granular but displays no specific external ornamentation. Some cells from the final collection to include this organism (see p. 54) appeared green due to the presence of unicellular algae in the cytoplasm (Fig. 293). Such algal cells have been found to be present in other heliozoans (Wailes, 1921) and they are believed to be symbionts. The fine structure of similar "zoochlorellae" or "zooxanthellae" has been investigated in a related group, Acantharia (Febvre & Febvre-Chevalier, 1979).

FIGS 286 - 294 *Raphidocystis tubifera*, I. LM of living cells and scales, viewed with anoptral contrast (AC), dark ground (DG) or phase contrast (PC) illumination.

Fig. 286: undisturbed living cell, x 200 DG (no coverslip on slide); note numerous fine radiating axopodia (ax).

Figs 287 - 290 Sequence showing a single cell flattening under coverslip pressure, x 500 AC; axopodia not visible.

Fig. 287: cell before flattening, showing appearance of scale case (s).

Fig. 288: partially flattened cell.

Fig. 289: flattened cell showing nucleus (n) with prominent nucleolus and centriaster (ca) in central position.

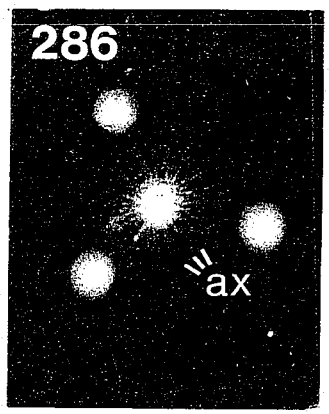
Fig. 290: flattened cell escaping from scale case; note size and complexity of scale case.

Fig. 291: detail of centriaster (ca) in a living cell, x 1,500 AC.

Fig. 292: encysted cell (cy) within scale case, x 700 PC.

Fig. 293: living cell containing numerous green zoochlorellae (z) within peripheral region of cytoplasm, x1,000 AC. n = nucleus.

Fig. 294: detail of individual scales, x 1,500 AC, showing appearance of the three types: trumpet-shaped scales (s_1), bell-shaped scales (s_2) and oval scales (s_3).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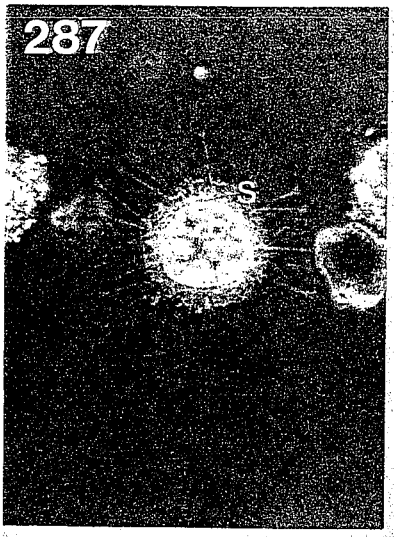
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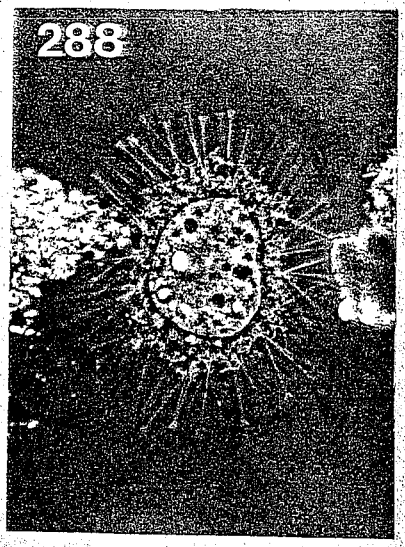
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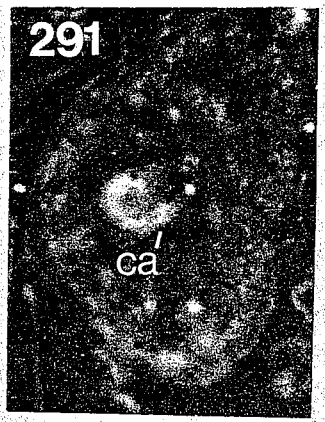
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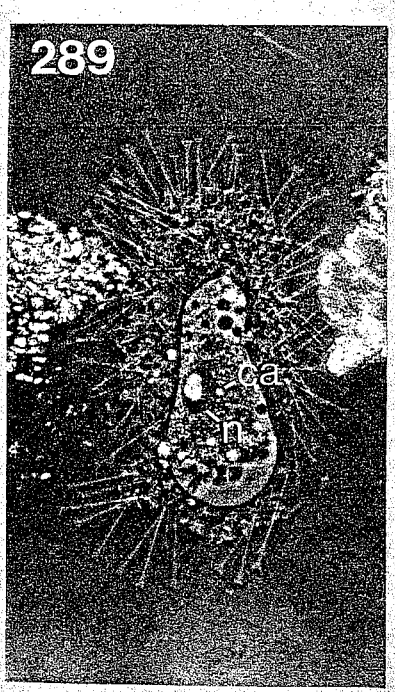
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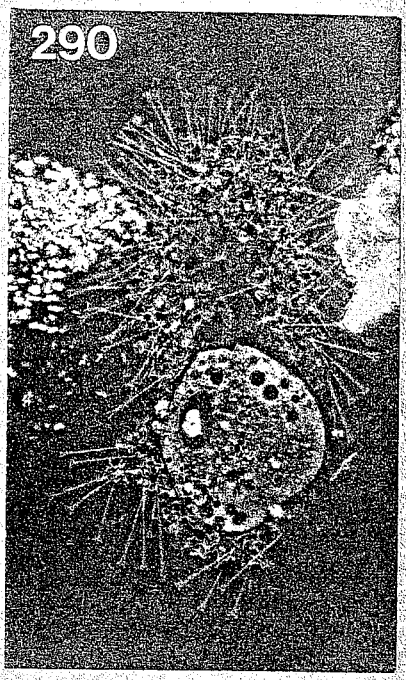
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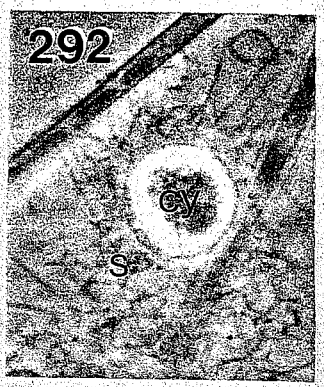
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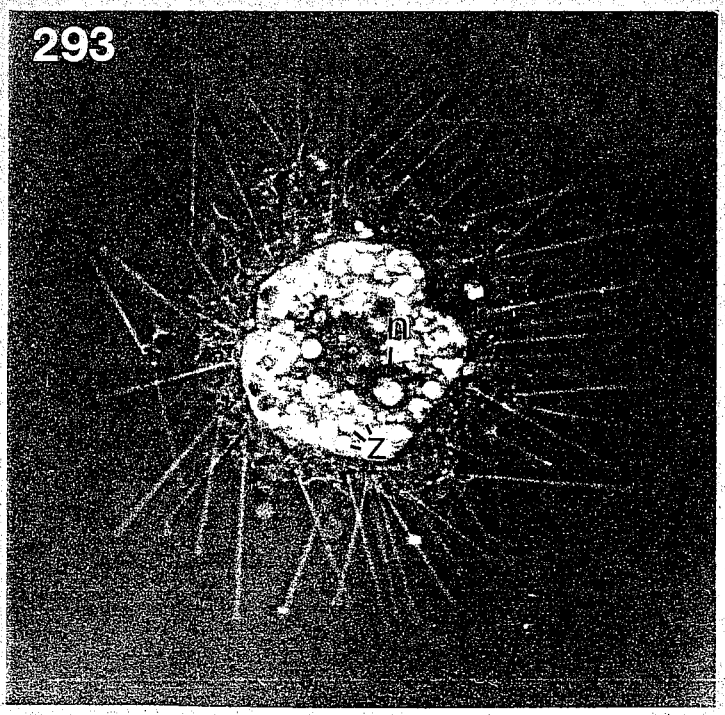

293
n
z


294
S3
S1
S2

The most noteworthy and characteristic feature of this species is its elaborate covering of scales. These occur in large numbers on a single cell (e.g. Fig. 290) and three types can be distinguished at high magnification (Fig. 294). Long, tubular scales resembling straight trumpets extend furthest from the cell, with their flared ends facing outwards. The more dense scale layer close to the cell includes flat oval scales and smaller scales which appear circular in end view but in side view can be seen to be funnel-shaped. Penard (1904) gave a careful description of these scale types which is remarkably accurate (compare Fig. 294 with his illustration: Penard, loc. cit., p. 194).

Further details of scale morphology are revealed by SEM and TEM examination of dried whole cells and detached scales. A single cell is illustrated as it appears in the LM and by the two EM techniques (Figs 295-6, 298); while TEM is appropriate for maximum resolution, the surface details visible with SEM are also of interest. In Fig. 296 (and detail, Fig. 297) the trumpet-shaped scales are seen to have open ends and to project from between the scales of the dense layer which covers the cell more completely. The external surface of this dense layer is made up from the open ends of the funnel-shaped scales, which are thus oriented with their closed tips towards the cell membrane as are the trumpet-shaped scales. Few oval scales are visible at the surface of the scale case; from other micrographs (e.g. Fig. 290 and Fig. 307, below) it seems likely that they are concentrated towards the inside of the scale case.

At higher magnifications the superior resolution of the TEM allows the sub-structure of the scale types to be seen (Fig. 299). An isolated scale of each type is also shown separately (Figs 300 - 302). The trumpet-shaped scales are homogeneous in appearance while scales of the other two types are constructed of material arranged in a meshwork pattern and surrounded by a tubular rim. A detail of the meshwork material is shown in Fig. 303; the component struts are ca. 40 nm wide. The closed ends of both the funnel-shaped and the trumpet-shaped scales are formed into

FIGS 295 - 304 *Raphidocystis tubifera*, II. LM, SEM and TEM examination of dried material.

Figs 295 - 298 Views of a single cell resting on copper grid.

Fig. 295: appearance of whole cell in LM, x 400 (anoptral contrast); arrows indicate limits of area visible in Fig. 297, below.

Fig. 296: appearance of the same cell in SEM, x 750; arrows as in previous Figure.

Fig. 297: SEM detail of cell surface, x 3,000; note distribution and appearance of scales (types s_1 and s_2).

Fig. 298: appearance of cell viewed with TEM, x 1,000; arrows as in Fig. 295.

Fig. 299: TEM detail of surface of cell, x 5,500, showing sub-structure of scales.

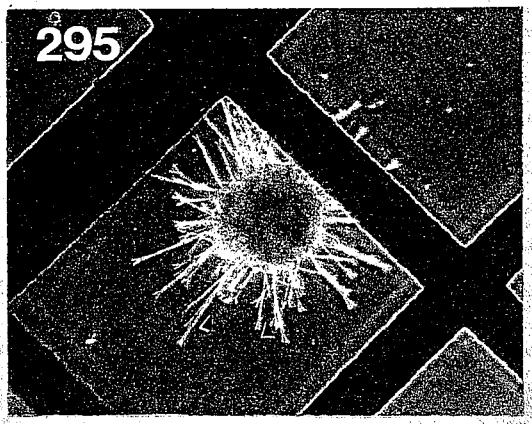
Fig. 300: TEM views of isolated trumpet-shaped scales (type s_1), x 3,000; a single bell-shaped scale also visible.

Fig. 301: TEM view of a detached bell-shaped scale (type s_2), x 7,000.

Fig. 302: TEM view of an isolated oval scale (type s_3), x 12,000.

Fig. 303: TEM detail of central portion of oval scale, x 35,000, showing structure of component material.

Fig. 304: TEM detail of flared ends of trumpet-shaped scales, x 9,000, showing fine serrations at tips.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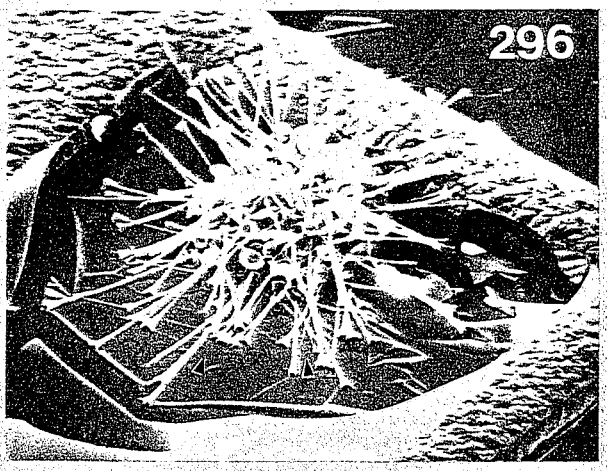
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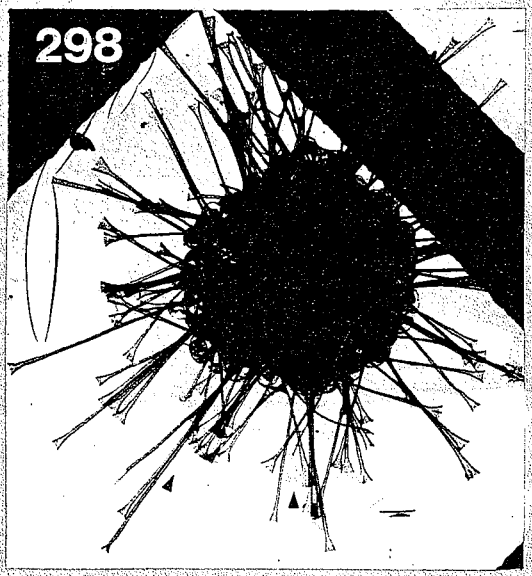
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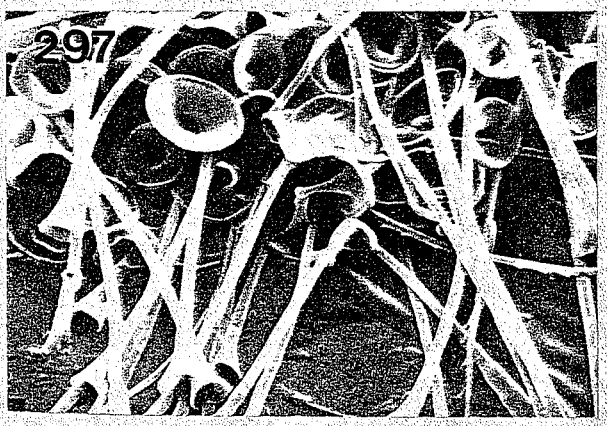
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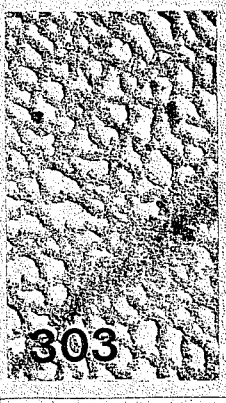
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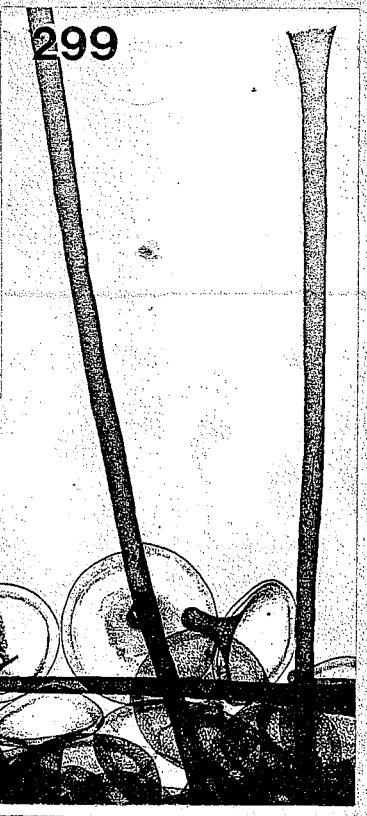
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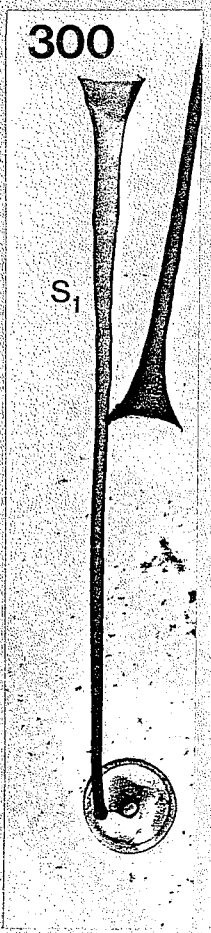
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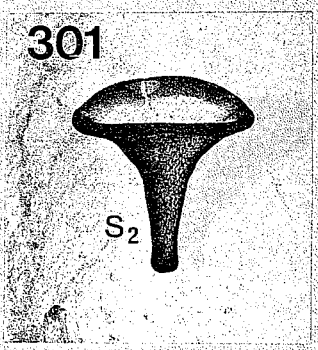
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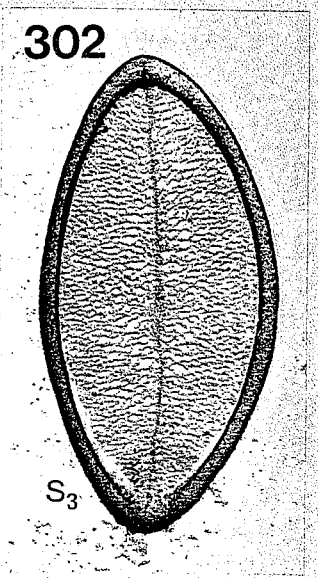
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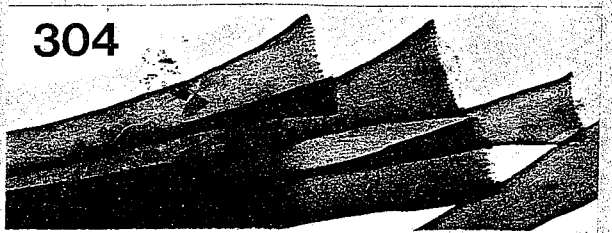

304

a globular tip; the open ends of the latter scales are finely serrated (Fig. 304). A narrow mid-rib is present on the oval scales (Fig. 302). It is the prominent rim of the two smaller scale types which allows them to be seen in the light microscope (cf. Fig. 294).

Preliminary tests (A. Rees, unpublished) indicate that the scales are insoluble in strong acids (HCl, H_2SO_4), consistent with the view of other authors (e.g. Penard, 1904; Grassé, 1953) that scales in the family Acanthocystidae (which includes Raphidocystis) are composed of silica.

Attempts to embed and section R. tubifera in mixed collections were unsuccessful owing to the infrequent occurrence of this organism in the plankton and its low numbers on each occasion. On its most recent appearance during the study period (October 1977) an effort was made to embed single cells, carrying them through the fixation and dehydration stages using micropipettes and embedding in a drop of resin on a glass cover-slip. Ca. 25 cells were treated in this manner but in most cases the cell was lost before the embedding was completed. One cell was successfully sectioned and some results are illustrated in Figs 305 - 310; although the fixation of the cytoplasm is unsatisfactory, certain details of interest may be seen.

In these sections the most prominent features within the cell are the presence of apparently mature scales within cytoplasmic vesicles (Fig. 305) and axopodia beneath the plasmalemma (Fig. 306). Several oval scales within vesicles were found; presuming this to be the mode of formation of the other scale types also, it is somewhat surprising that similar scales are not visible within the cytoplasm in light micrographs (e.g. Fig. 290): vesicles containing the trumpet-shaped scales should be the most clearly visible if present at the time of examination. Profiles of numerous retracted axopodia lie immediately beneath the cell membrane (Fig. 306), confirming the heliozoan nature of this organism; details of their microstructure have not been preserved (cf. Bardele, 1977).

Fig. 307 shows a section of the scale case taken some distance above the cell surface, which has possibly shrunk away from the scales in this preparation. The outer part

FIGS 305 - 310 *Raphidocystis tubifera*, III. TEM of sectioned material.

Fig. 305: part of sectioned cell, x 12,500, showing a few external scales (s) and an internal scale within scale vesicle (sv).

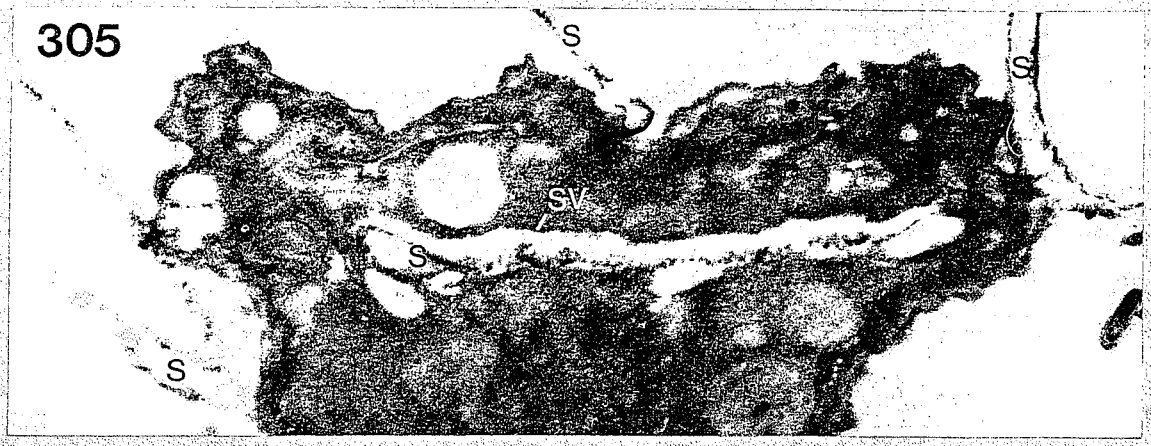
Fig. 306: peripheral region of cell, x 25,000, showing axopodia (ax) in T.S. beneath plasmalemma (pm).

Fig. 307: glancing section of scale case, x 6,000; note distribution of oval scales (arrows) and trumpet-shaped scales (arrowheads).

Fig. 308: detail of scales in section, x 8,000, showing the structure of each scale type (s_1, s_2, s_3).

Fig. 309: median longitudinal section of bell-shaped scale (type s_2), x 8,000.

Fig. 310: glancing longitudinal section of bell-shaped scale, x 8,000.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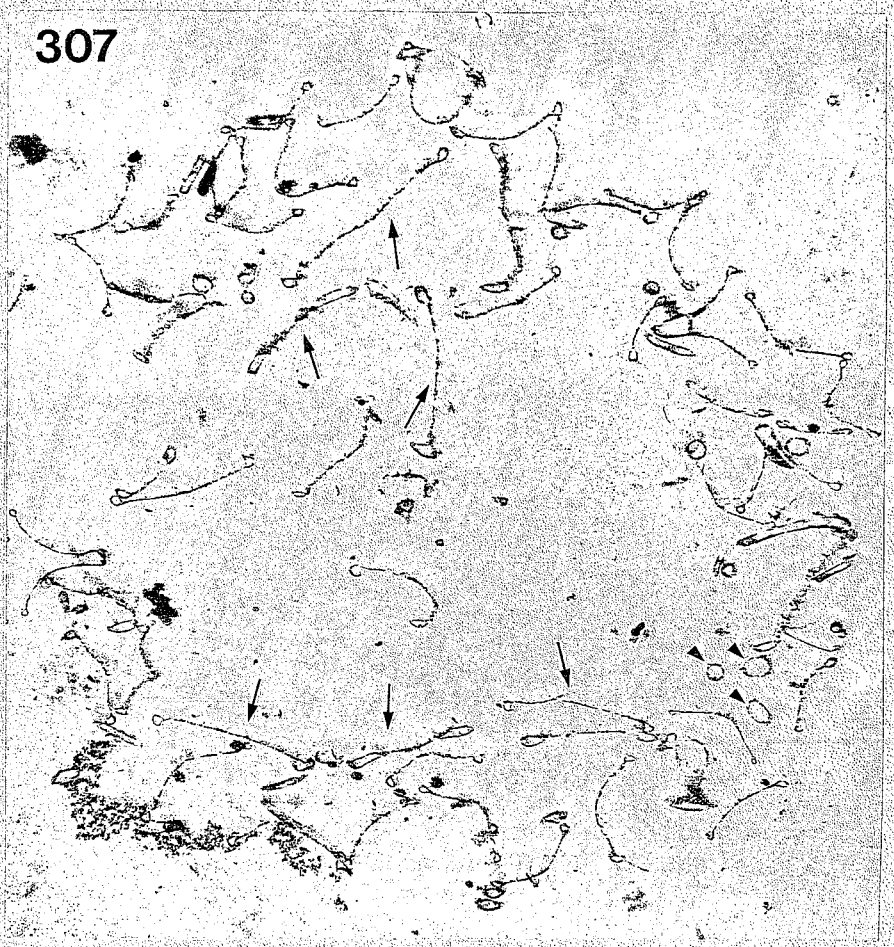
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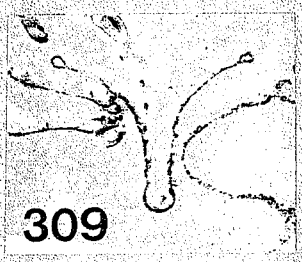
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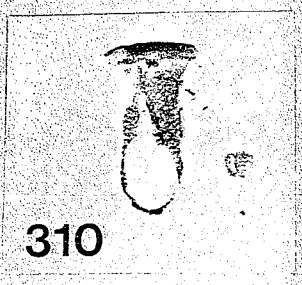
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of the scale case consists principally of the funnel-shaped scales, beneath which lie the flat profiles of the oval scales although the orientation of the latter is somewhat irregular. The trumpet-shaped scales appear to be concentrated in small groups at intervals among the other scales.

More details of the scale structure can be seen at higher magnification (Fig. 308). The trumpet-shaped scales are clearly hollow and are wider than the hollow rims of the other scales, even close to the cell surface where they are narrowest (see Fig. 300). The oval scales are distinctive when sectioned along their long axis but in other planes of section are of similar size and construction to the funnel-shaped scales, which may present profiles of various shapes depending on the part of the scale sectioned. The tubular rims of both these scale types appear to be formed in a similar manner, viz. from a rolled-up margin which retains a slight asymmetry. Median and glancing longitudinal sections of funnel-shaped scales are shown in Figs 309 and 310 and may be compared with the appearance of the whole scale in Fig. 301. Together these three micrographs illustrate the three-dimensional form of this scale type.

The investigations on R. tubifera described above illustrate the surface morphology of the species at a new level and will allow its features to be compared more accurately with those of other species when these become known. The formation of silicified scales in cytoplasmic vesicles contrasts with the origin of chitinous needles in a specialised organelle near the cell surface which is the only comparable process currently described in another heliozoan (Bardele, 1975). However, further investigations on well-fixed material are required before the details of the scale-forming process in R. tubifera are properly known. Many other species in the family Acanthocystidae produce silicified scales, usually of distinctive types (see Rainer, 1968) and complex mechanisms must control the form of the scales in each species.

GENERAL DISCUSSION

In the individual Discussions so far presented, the data from each Section have been examined within their immediate context and the most significant conclusions emphasised. The aim of this General Discussion is to consider in more detail specific points arising from the data, to attempt to relate various results which have previously been discussed in isolation and to review the main conclusions of the whole investigation. From the results obtained it is also possible to re-assess the validity of the approaches adopted for each part of the study and to suggest ways in which these might be modified or extended for future work.

Section 1 provides background information for the algal studies and evidence of the type of habitat for phytoplankton which Sawley Dene offers. Certain factors appear to be critical in determining this habitat type and the two of key importance may be identified as the chemical nature of the water and the basic hydrology of the lake basin. The lake has been shown to support "eutrophic" algal communities and these are found either in artificially enriched ion-poor waters or in naturally ion-rich alkaline lakes such as Sawley Dene. The water chemistry in turn reflects the nature of the superficial deposits over the catchment area whose distribution may be correlated with glacial events in the region (pp.14,15). Hydrological characteristics of the drainage basin result in a long retention time comparable with that of very much larger lakes (see p. 20); it is likely that an increased throughput of water would modify the "lake" nature of the plankton and possibly result in smaller algal crops and a more rapid, less predictable succession of communities (Dickman, 1969). The long retention time of Sawley Dene derives from the restricted catchment area which may again be related to the former glacial activity which resulted in the formation of the valley in which Sawley Dene now lies (p. 14).

Other factors will have some influence upon the character of the algal populations; worthy of note are the general shallowness of most of the lake area and the absence of

significant macrophyte cover. The shallow water column allows species normally characteristic of the epilimnion of a stratified lake (e.g. the blue-green algae) to coexist with some of the "bottom element" of such lakes (e.g. the Trachelomonas spp.) while partially excluding other species, e.g. Ceratium, for which stratification may bring a competitive advantage in other lakes. The shallow nature of the habitat brings an increased susceptibility to ice cover in winter which may adversely affect some algae but it would also result in less possibility of light-limitation at other times and may favour development of algal populations in early spring and during ice-free periods in winter. The absence of macrophyte cover removes a possible source of competition with algae for the available nutrients and allows free circulation of the water which thus provides a generally homogeneous habitat.

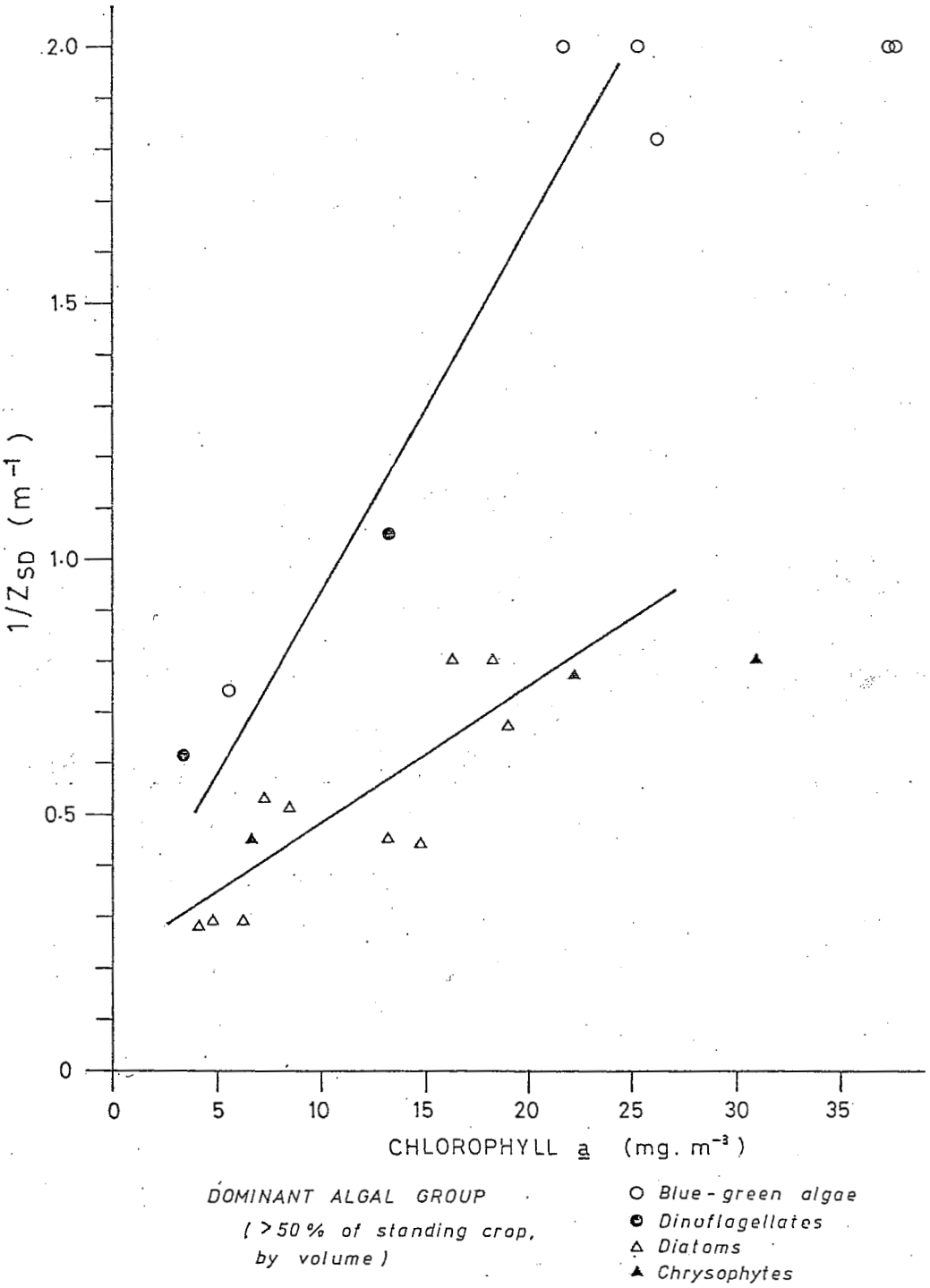
The temperature and dissolved oxygen data presented in Section 2 are of interest in that they indicate that Sawley Dene remains effectively unstratified over most of the summer period. The occurrence of algae typical of the nutrient-depleted epilimnion of a stratified lake in late summer must therefore depend on an alternative cause of nutrient-depletion; H.A. Cmiech (pers. comm.) found NO_3-N levels at or below 0.1 ppm over summer 1977 (wks 26b - 41b), together with undetectable levels of PO_4-P, and these low values may be explained as the result of uptake by algae coupled with virtual cessation of inflow during the summer months (see p. 18). Replenishment of nutrients in autumn is the result not of mixing within the water column (as in a stratified lake) but of resumption of significant runoff from the drainage area and inflow to the lake. This interpretation is consistent with the fact that the major diatom development does not take place until spring in Sawley Dene, whereas in larger lakes an important autumn peak may also be found (Round, 1971; Fogg, 1975) which utilises nutrients present over the summer period but previously unavailable to algae in the epilimnion.

The general similarity of the pattern of biomass peaks as expressed by chlorophyll a analyses, Secchi disc readings and calculations of total standing crop has already been noted (pp. 29, 57). However, it is clear that differences

in cell volume, chlorophyll content per cell and light-scattering power within and between algal species will preclude exact correspondence of the curves in each case and the extent of such divergence can be assessed in a preliminary way from the data available. Fig. 311 shows the relationship between chlorophyll a concentrations and turbidity values ($1/Z_{SD}$) on occasions when a specific dominant group could be recognised and it is apparent that the points are too scattered to be represented by a single function. Within the limitations of the data it appears that at least two separate relationships are involved, the blue-green algae requiring a different line to the diatoms; isolated points for dinoflagellates and chrysophytes suggest that these are closest to the blue-green and the diatom patterns, respectively. The discrimination between separate trends for different algal groups is important as this suggests one reason why previous authors (e.g. Carlson, 1977; Jones & Bachmann, 1978) have found only an approximate fit in generalised regressions involving Secchi disc data. Both the lines drawn on Fig. 311 intersect the Y-axis at a similar point ($1/Z_{SD}$ = 0.2 m^{-1}, i.e. Z_{SD} = 5 m); this corresponds to the theoretical maximum limit of visibility in the Sawley Dene water column, although it is worth noting that for at least one short period (wks 18c - 20c) this value was approached and may have been found to be exceeded had sufficient depth of water been available for the determination (see p. 29).

Plots similar to Fig. 311 but involving calculated standing crops (see p. 56) are of the same general form but fail to show such a clear distinction between these algal groups and show more scatter among outlying points. It is suspected that a combination of factors is responsible, partly the limited accuracy (on a linear scale) of the algal counts and the successive approximations in estimating the volumes of individuals, and partly genuine variability in the chlorophyll content of cells through the season. An impression of the latter variation may be gained from Table 10 where a considerable range of values is apparent within each group; the variation between mean values reflects either genuine differences or, more likely, counting inaccuracies or the presence of systematic errors

Fig. 311. Relationship between Z_{SD} and extracted chlorophyll on different dates.



in the volume determinations. Nevertheless, the mean values for the first three groups (blue-green algae, dinoflagellates and diatoms) are in good agreement with the approximate ratio of 4 µg chlorophyll *a* to 1 mm^3 algae suggested by Lund (in Ridley, 1970).

Only the more important algae are represented in the Sawley Dene species list (Table 4) and this reflects the emphasis of much of the present work on the occurrence of algal populations sufficiently dense to provide material for electron microscopy. Additional investigation would undoubtedly allow this species list to be enlarged (cf. the 73 species reported by Reynolds, 1973b, from Crose Mere and the 91 species identified by Moss & Karim, 1969, in Abbot's Pond) and investigation of other habitats (e.g. the lake margins, the surface of the sediments and possibly the upper basin) would add further records. Despite these limitations many of the species reported in Table 4 are not found in the only available survey of Yorkshire freshwater algae (West & West, 1901) and it appears that, in general, eutrophic sites such as those in the Sawley area were not investigated by these early workers and their colleagues. Sawley Dene itself could not have appeared in this work in any case since its date of (re-) construction post-dates that of West & West's "Alga-flora of Yorkshire" (see p. 13). The inclusion of light micrographs of the principal species (Figs 14 - 58) will allow the present determinations to be verified or amended if necessary by other workers in the future as well as illustrating the form of individuals in the Sawley Dene populations which may be of some interest for the more variable species. It is, of course, routine for EM-based identifications to be accompanied by the appropriate micrographs for verification (Section 4).

In the course of many ecological studies a considerable amount of time is spent counting individual algae under the inverted microscope. For some applications this effort is justified; in the present context, accurate counts enable population maxima to be measured and compared with results from elsewhere (Section 3) and from successive years in Sawley Dene (for blue-green algae see H.A. Cmiech, thesis in preparation) and they also allow the phytoplankton

Table 10. Ratios of chlorophyll a ($mg. m^{-3}$) to calculated algal volume ($\mu m^3 \times 10^6 ml^{-1}$) in tube samples on different dates, = μg chl. a per mm^3 algae.

Dominant algal group	Number of determinations	Mean value ($\mu g. mm^{-3}$)	Range	S.D.
Blue-green algae	14	3.2	0.9 - 6.4	1.60
Dinoflagellates	2	3.5	2.3 - 4.6	1.63
Diatoms	14	5.1	2.5 - 8.1	2.02
Chrysophytes	3	17.3	8.2 - 33	13.7

Table 11. Comparison of numbers of scale-bearing Chrysophyceae found in the present study with those found by Takahashi (1959 - 1978) in Japan.

Genus	Number of taxa from Sawley region	Number of taxa reported by Takahashi (1978)	Taxa common to both studies
Mallomonas	21	26	11
Mallomonopsis	3	6	2
Synura	4	11	4
Chrysosphaerella	1	2	1
Spiniferomonas	4	7	3
Paraphysomonas	4	5	3
total	38	56	24

standing crop to be analysed in some detail (Fig. 100). For many purposes, however, it appears that semi-quantitative determinations as described on p. 25 are adequate for representation of the phytoplankton periodicity (e.g. Fig. 59 and Appendix II) and the data given in Figs 65 - 99 show a generally good correlation between these and the algal counts. Partial exceptions occur only when some algae (Volvox, Ceratium and Microcystis) show a marked tendency to accumulate in the water column outside the collection range of the plankton net; for species which present problems for strict quantitative enumeration, e.g. owing to low concentrations as individuals ml^{-1} but high biomass (Gloeotrichia) or to non-random distribution in the counting chamber (Aphanizomenon), semi-quantitative estimation may even be preferable to inverted microscope counts.

The statistical procedures used in Section 2 produce a more complex summary of the data, incorporating as much semi-quantitative data on species periodicity as is available, which at the same time displays rates and directions of community change in a direct form. For this statistical method the simplicity of the semi-quantitative data is actually preferable to the algal counts, for which complex transformations would be necessary if they were to be used as the input data. A similar conclusion was reached by Ibanez (1974: cited in Legendre & Legendre, 1978) who suggests that a three-state scale (absent/rare, present, abundant) is as useful as more complex data for principal components analysis of marine zooplankton.

The major limitation of the present ordination is not the quantitative precision of the abundance values but the number of samples available for inclusion; even daily records could be incorporated which might then allow the small-scale changes implied by the present plots to be adequately represented. A limitation of a different kind is inherent in the two-dimensional graph which allows only two independent axes of variation to be considered; if thought desirable, a third axis could be calculated and compared with each of the other axes in turn on a separate plot, or a "three-dimensional" effect could be introduced similar to that used, for example, in chemistry to represent

the spatial structure of complex molecules. Certain authors (e.g. Anderson, 1971) have objected to the use of reference set methods such as the Bray & Curtis technique used here on theoretical mathematical grounds; however, as discussed earlier (p. 27), more sophisticated procedures such as principal components analysis (PCA) will tend to produce similar organisations of the data. Indeed, a reference set method is preferable if data from different sites or from separate years at the same site are to be compared, since a procedure such as PCA seeks to find new axes for every data set with the result that direct comparisons between the results of separate analyses are not possible.

Most of the discussion on the seasonal and geographical distribution of the principal phytoplankton organisms has been presented already (Section 3), excepting the blue-green algae whose periodicity is to be treated in a separate study by H.A. Cmiech. The most regular and prominent algae of Sawley Dene are Asterionella in winter/spring and Anabaena solitaria in late summer and in one sense these species may be said to characterise the lake. Asterionella is the most common spring diatom in many eutrophic lakes but Anabaena solitaria is comparatively rarely recorded, even as a subsidiary component of the plankton, suggesting that Sawley Dene as an "Anabaena solitaria lake" possesses some particularly individual characteristic. The nature of this is, however, obscure; the nearby, and generally comparable, Eavestone Lake (see Table 6) supported luxuriant growths of Aphanizomenon flos-aquae and Gloeotrichia echinulata when visited in July 1978 at a time when Sawley Dene was dominated by Anabaena solitaria. One possible indication of the environmental requirements of Anabaena solitaria is suggested by the fact that this alga was apparently favoured by the hot dry summer of 1976 in Sawley Dene and has occasionally appeared during similar periods in certain of the Shropshire Meres (Reynolds, 1973b, 1978 and pers. comm.); it is possible that the shallow nature and tendency towards summer stagnation in Sawley Dene regularly provide conditions of nutrient stress similar to those experienced at some other sites only in unusually hot or dry years.

The scale-bearing Chrysophyceae and the other organisms

surveyed in Section 4 were collected with minimal sampling through the study area, only some 20% of the Sawley collections being prepared as whole mounts for TEM examination (Appendix I) and one or two collections taken from each of the other sites in the area (Table 6). Some rarer organisms may have been missed through examination of only small portions of the net samples, while isolated scales and very small cells may not have been retained by the net during the original sampling. Nevertheless, the quantity of algal material provided by these collections is considerable and the chief limitations are the thoroughness with which any one sample can be studied together with difficulties of species identification from the frequently scattered and sometimes non-existent reports in the literature.

Repeated examination of portions of the same sample often reveals traces of additional species to those first noted and, to some extent, the microflora listed from a single site depends on the amount of study devoted to each collection in addition to the obvious effect of sampling frequency where such short-lived species may be concerned. It is therefore certain that the numbers of species quoted in Fig. 218 from various sites would be considerably extended with further study. Even so, it is interesting to compare the numbers found here with those found during the most comprehensive survey anywhere in the world to date, the 20 years' work of Takahashi (1959 to present, summarised in Takahashi, 1978) who has examined some 96 water-bodies in Japan (see Table 11). It is apparent that the present study has provided evidence of a significant number of species considering the limited samples taken within a restricted geographical area and, of these, over 60% have also been found by Takahashi (loc. cit.); this suggests that there are few effective barriers to dispersal of many species, even for those which may at present be known only from these two studies (e.g. several Spiniferomonas spp.). The distinction of taxa "new for Britain" is of little ecological significance since so few British waters have been studied in this respect; however, it does appear that certain species, e.g. Mallomonas hamata, are rare throughout the world and their occurrence is of particular interest.

The non-chrysophycean organisms treated in Section 4 present the greatest difficulties for ecological interpretation since so few of them have been reported by other workers. Belcher & Swale (1975, 1976, 1978) are among the few phycologists who have studied colourless scaled organisms; micrographs by other authors probably exist (e.g. Manton, unpubl. and Thomsen, unpubl., both cited in Gaarder et al., 1976) but remain unpublished either because of the absence of names for the organisms or because some of them may not be strictly "algae".

The affinities of some of the unidentified scales may become clearer if whole cells are found, particularly if these can be sectioned (e.g. Swale & Belcher, 1974 on Gyromitus and the present observations on Raphidocystis). At present, scales of a range of forms are known in the algal classes Chrysophyceae, Prymnesiophyceae, Prasinophyceae and some Chlorophyceae (see Leedale, in press) and have also recently been demonstrated in some Dinophyceae (Pennick & Clarke, 1977) and Bacillariophyceae (Crawford, 1974). Among the Protozoa, scales occur in several groups, notably in the Heliozoa (see p. 78) and in certain testate amoebae, e.g. Euglypha (Hedley & Ogden, 1973) and Cochliopodium (Bark, 1973). There are also problematical genera such as Gyromitus (Swale & Belcher, 1974) and Luffisphaera (Belcher & Swale, 1975), the systematic position of which is unknown.

Section 5 presents ultrastructural observations on the four species selected for detailed study but preliminary observations were also made on a number of other species before selection could be made. In general, sections of species not selected were either of little ultrastructural interest or were not of sufficiently high quality (e.g. because of problems of fixation or sectioning) to warrant continuation in the limited time available for the study of any one species. Nevertheless, other embedded material remains available for study at a later date although after this investigation it might be more valuable to develop similar studies at a new site.

The study of Paraphysomonas (p. 89) benefited from improvements in fixation and embedding techniques which have taken place subsequent to the study of Manton &

Leedale (1961) and these enabled new ultrastructural detail to be seen, particularly in respect of the preservation of membrane details and the sub-structure of flagella. The sections of ingested objects are also of interest since these shed some light on the feeding behaviour of the species in the wild in a way which might not necessarily be seen in culture. Scale-formation in Paraphysomonas and in Synura (p. 97) appears to follow a similar path although chloroplast ER, which is associated with the scale vesicles in Synura, is absent from the (colourless) Paraphysomonas cell and no specialised origin is apparent for the associated ER vesicles in this and other Paraphysomonas species (Lee, 1978; Hibberd, 1979). Wujek & Kristiansen (1978) suggest that the separate scale-containing vesicles are also derived from chloroplast ER in Mallomonas caudata but this interpretation is not unequivocally supported by their micrographs; the true origin of these vesicles remains obscure. The extent of direct ER or chloroplast ER activity in "moulding" the underside of the scale vesicle is also unresolved, since separate "tubular elements" are suggested to be associated with the rolling-up process involved in bristle formation in Mallomonas caudata (Wujek & Kristiansen, loc. cit.) and many features such as the ornamentation on the upper part of a Synura scale apparently form without close ER proximity (cf. Fig. 254 and Schnepf & Deichgraber, 1969).

Fixation of Peridinium from the wild resulted in good cell preservation and Berdach (pers. comm.) has suggested that freshly collected material may be more"robust" than cultured material and less susceptible to displacement or loss of flagella. The present study includes the first serial sections of an in situ transverse flagellum (see Rees & Leedale, in press); new details seen include the two types of flagellar hairs and the arrays of vesicles within the flagellar sheath. Within the Dinophyceae, flagellar hairs are more varied than in many other algal groups; Leadbeater & Dodge (1967b), Leadbeater (1971) and Dodge & Crawford (1971) report 10 nm diameter hairs, while Clarke & Pennick (1972) and Lee (1977) describe dinoflagellate flagella which bear scales in addition to hairs of various types. The combination of 5 nm and 20 nm diameter hairs does not

appear to have been reported previously in dinoflagellates but hairs of these dimensions occur in other algal groups (Sleigh, 1973). There is no evidence from the present sections that the 20 nm hairs of P. cinctum are tubular, as are mastigonemes in the Chrysophyceae (see Fig. 230 and Bouck, 1972).

In the living flagellum the flagellar strand remains relatively still while the axoneme undergoes regular contractions (see p. 101). The flagellum appears to be anchored to the cell at each end (Leadbeater & Dodge, 1967b) and Taylor (1975) postulated that additional anchoring threads might occur between the lower edge of the flagellum and the cingulum at intervals along its length. This suggestion has not been borne out by sections (e.g. Figs 268/269) and it is more likely that tensile forces within the strand are sufficient to support the flagellum in space within the cingulum. However, such a rigid strand would significantly inhibit the capacity of the axoneme to beat freely unless some decoupling system between the axoneme and strand were present; the arrays of vesicles discovered within the flagellar sheath could clearly fulfil such a role.

The propulsive model discussed by Leblond & Taylor (1976) is inadequate in the case of a helical axoneme as described here, where thrust may be generated over the whole of the axoneme path rather than at the upper edge of the flagellum only. Leblond & Taylor's model is based on S E M observations of axonemes with "hemi-helical" configurations but in view of the verification of a helical axoneme in P. cinctum it seems appropriate to question the validity of the S E M observations of these and some other authors, since it is possible that a helical axoneme may collapse so as to resemble a hemi-helix in dried preparations. Leblond & Taylor (loc. cit.: Fig. 6) illustrate an in situ flagellum of Thecadinium inclinatum which they describe as showing a "distorted wave form" but which conceivably possesses a helical axoneme. Herman & Sweeney (1977) describe the transverse flagellum of Gymnodinium splendens as hemi-helical but in one micrograph (their Fig. 3) a coiled structure is visible which might also be a flagellum with a helical axoneme. It is thus desirable that serial sectioning should be applied to transverse flagella of more

species of dinoflagellates in order to ascertain the true type or types of flagellar organisation in this group of organisms.

The detailed description of the surface morphology of Raphidocystis provides the second such study of a heliozoan, the first being that of Pinaciophora fluviatilis by Gaarder et al. (1976: as "Potamodiscus"), although these authors did not appreciate the heliozoan nature of the organism (see Belcher & Swale, 1978). Recognition of isolated scales as heliozoan in origin sheds light on the possible identity of other unidentified scales in the plankton (Section 4) although the structure of certain of these scales may also be reminiscent of those of the Chrysophyceae (e.g. Unknown species B, p. 81) and, indeed, the funnel-shaped scales of Raphidocystis tubifera have some similarity with the scales of the chrysophyte Paraphysomonas cylicophora (Leadbeater, 1972). A remote phylogenetic connection between these two groups of organisms has been suggested on other evidence by Davidson (1974), possibly through the Pedinellaceae which are currently considered to have a rather isolated position within the Chrysophyceae (see Hibberd, 1976). Further ultrastructural studies on scale-bearing Heliozoa might be expected to shed more light on the process of scale-formation and discover whether parallels exist between this and comparable processes in the Chrysophyceae.

The main results of this investigation have been described in earlier Sections and will be reiterated in the Summary (p. 121). To conclude the present Discussion it is perhaps appropriate to note the main areas within which the present work has shown that progress can be made. Firstly, the population data from Sawley Dene emphasise the uniqueness of every site and, to a lesser extent, of separate years at a single site and they lead to consideration of the factors which might exert the most significant influence on the character of the phytoplankton populations. Secondly, regular monitoring of a water body even with such straightforward field equipment as a plankton net and a Secchi disc can provide an acceptable summary of the phytoplankton periodicity and indicate the timing of development of population maxima for species which may be of particular

interest. Thirdly, investigation of plankton collections as whole mounts in the EM reveals a range of scale-bearing chrysophytes and other organisms which could not be detected by other means and which may be of fundamental ecological or taxonomic interest. Finally, routine EM sectioning and examination of wild material in mixed collections can display previously little-known ultrastructural features of cells which may in themselves be worthy of further study.

SUMMARY

Sawley Dene is a small (10 ha) lake in North Yorkshire, constructed ca. 80 years ago on the site of an old monastic fishpond. It lies in a channel associated with former glacial drainage but now by-passed by the principal rivers in the area; thus the lake is without an extensive catchment area and, despite its general shallowness (mean depth 2.2 m, max. depth 4.6 m), its theoretical retention time is long (ca. 6.5 months). The calcareous glacial drift in the drainage area results in the lake being alkaline (pH 7.6 - 8.2) although the underlying bedrock is Millstone Grit. The lake catchment contains pasture and mainly coniferous woodland together with a single human dwelling. The lake surface is relatively sheltered and there is no extensive macrophyte development.

Temperature profiles suggest that the main part of the water body is well mixed and that horizontal variations are unlikely to be significant. Small temperature gradients were detected following rapid surface heating or cooling during parts of summer 1976 but persistent stratification did not occur. Dissolved oxygen levels rarely fell to less than 20% saturation except at the mud-water interface at the bottom of the water column.

Algal biomass is highest in spring (March/April) and in late summer (August/September), the late summer peak being the most intense. The spring peak is due almost entirely to development of the diatom *Asterionella formosa* which can reach 1200 colonies ml^{-1} (spring 1977), yielding 15 - 20 mg m^{-3} chlorophyll *a* and associated with a decrease in Secchi disc visibility from at least 4.5 m (in periods of very low biomass) to ca. 1.25 m. The late summer peak is due largely to blue-green algae, of which *Anabaena solitaria* is the regular dominant (2,800 filaments ml^{-1} in summer 1976) although other blue-green algae (*Anabaena* spp., *Aphanizomenon flos-aquae*, *Gloeotrichia echinulata*, *Oscillatoria agardhii*) may also be prominent at times during the summer. Peak summer levels of chlorophyll *a* were 30 - 40 mg m^{-3} in 1976; Secchi disc visibility was typically 0.4 - 0.5 m each summer.

The annual succession typically comprises diatoms in winter and spring, chrysophytes and/or green algae in late spring - early summer, blue-green algae with some dinoflagellates in late summer and then an autumn period of low biomass before the development of diatoms in winter once more. Variation in the species composition and in the timing of each phase results in a distinctive pattern for each year which can be analysed statistically and represented in a graphical form. By this means patterns from different years can be compared and the main areas of divergence indicated; the path of the "community trace" through the year may also be examined in detail, exposing small-scale cyclic patterns superimposed on the annual trends which may reflect the influence of short-lived environmental fluctuations.

The species of algae recorded are typical of a eutrophic lake, comprising many species normally found in the epilimnia of larger, stratifying lakes during summer, together with a few species more characteristic of hypolimnia. Diatoms are relatively rare in summer, in contrast to the pattern in some other shallow lakes; dinoflagellates (e.g. Ceratium) are generally scarce although some development occurred during summer 1976; cryptomonads are less prominent than in many eutrophic lakes elsewhere. Sawley Dene appears to be somewhat distinctive in supporting large populations of Anabaena solitaria each summer, other species of blue-green algae being more frequent in lakes elsewhere.

Similar trends in patterns of algal biomass are shown whether these are represented by total calculated cell volume, extracted chlorophyll a, or by turbidity of the water (i.e. reciprocal of Secchi disc transparency readings); however, the degree of correspondence between the various measures of biomass varies according to the type of alga dominant: for example, blue-green algae appear to produce a greater turbidity per unit biomass (as cell volume or chlorophyll a) than do diatoms. More data would be necessary before accurate estimates of these relationships could be produced.

All the collections from Sawley Dene were examined in the light microscope and a number of them were also

prepared as whole mounts for EM examination, to identify small scale-bearing species. 17 species of scale-bearing chrysophycean flagellates were identified in the Sawley Dene samples, including species of Mallomonas, Mallomonopsis, Synura, Spiniferomonas and Paraphysomonas; scales of 13 non-chrysophycean organisms were also found, including species of Acanthocystis and Raphidocystis of the Heliozoa, a species of the colourless flagellate genus Gyromitus and a number of unknown organisms. A small number of samples were also taken from 6 other lakes and pools in the Sawley area for comparative purposes and these provided further morphological and ecological data for some of the Sawley species and yielded 21 more species of Chrysophyceae and 5 more non-chrysophycean species. Details of all the scale-bearing organisms found are given in a taxonomic treatment and certain new taxa are recognised, viz. Mallomonas pumilio var. "perforata", Mallomonas "clavoides", Mallomonopsis "minuta", Spiniferomonas bourrellii var. "simplex" and Paraphysomonas foraminifera var. "trifida". In addition, the new name Mallomonopsis calceolus is used for Mallomonas calceolus. Formal descriptions of the new taxa will be given elsewhere but provisional diagnoses are presented in an Appendix.

Most of the Chrysophyceae in Sawley Dene are widely distributed elsewhere; the rarer species tend to be restricted to acidic habitats and are thus absent from Sawley Dene. There are few studies of single sites elsewhere for comparison but it appears from the present investigation that water-bodies of the size of Sawley Dene have a relatively impoverished chrysophycean flora compared with smaller pools of similar alkaline status. Few conclusions can be drawn regarding the distribution of the non-chrysophycean species detected with the EM because of nomenclatural problems and the virtual absence of records from elsewhere.

Ultrastructural studies were carried out on freshly collected Sawley Dene plankton samples and sectioned material of four species was studied in detail. The colourless chrysophycean flagellate Paraphysomonas vestita was collected in January 1977, the pigmented chrysophyte Synura petersenii in February 1978 (the cells sectioned

originating from a separate pool ca. 2 km from Sawley Dene), the dinoflagellate Peridinium cinctum in June 1977 and the heliozoan Raphidocystis tubifera on a number of occasions between July 1976 and October 1977.

Sections of Paraphysomonas were compared with those from an early EM study of the same species (Manton & Leedale, 1961) and various new details were exposed. In the process of scale formation and release, the involvement of ER vesicles adjacent to the scale-forming vesicles was noted. Food vacuoles were found to contain ingested Paraphysomonas scales in addition to remains of recognisable extraneous organisms. Other features of interest include the occurrence of mastigonemes in intracellular vesicles, the form of the contractile vacuole and the fine structure of the flagellar transition region, all of which display typically chrysophycean features and so support the classification of this colourless species in the Chrysophyceae.

Colony structure in Synura is displayed in a series of sections approaching the centre of the colony. The posterior end of each cell is drawn out into a cytoplasmic "tail" which is still covered with scales almost to its tip. At the centre of the colony the cell membranes are without scales and those from ca. 16 cells interdigitate without fusing and without any apparent adhesive substance. Scales are formed in cytoplasmic vesicles which lie external to the chloroplast and are associated with a layer of chloroplast ER, parellelling the situation in Paraphysomonas except that in the latter species chloroplasts are absent and scale vesicles are associated with free ER in the cytoplasm. Schnepf & Deichgraber (1969) illustrated early stages of scale vesicle development in S. petersenii showing the chloroplast ER to act as a "template" for the lower surfaces of the scale outline; later stages in the present micrographs indicate that the chloroplast ER retracts from inside the scale leaving a cytoplasm-filled outline, the cytoplasm itself being withdrawn through gaps in the scale outline as mineralisation proceeds. A more complete scheme for scale production may thus be envisaged culminating in extrusion of the completed scale through the plasmalemma.

A cell of Peridinium was flattened to display its

thecal complement in the light microscope, allowing the species to be determined as P. cinctum. Sections of cells displayed the organisation of the cell components and included details of the cingulum with its complex transverse flagellum in situ; the latter organelle has a structure unique to the dinoflagellates and its precise form has been the subject of some speculation in previous accounts. Recovery of serial sections in tangential and radial planes allowed a three-dimensional model to be made which demonstrates the form of the flagellum and the spatial relationship of its component parts; these comprise a helically coiled axoneme lying external to a straight accessory strand, a single membrane surrounding the whole structure and groups of vesicles in the amorphous matrix between the axoneme and strand. It is suggested that the vesicles help to decouple the axoneme from the more rigid strand and enable the latter to generate thrust more effectively. The flagellum itself appears to maintain its position within the cingulum by internal forces without being tethered to the cingulum wall along its length as has been proposed by some other authors.

The surface scales of Raphidocystis and possible related species were encountered in whole mounts of mixed wild material and the three scale types of R. tubifera were studied in detail, not only as isolated scales but also attached to the cell surface in living and fixed material. Correlated light microscope, SEM and TEM examination of the same specimens reveals complementary details of scale morphology and arrangement; other details of scale fine structure are shown in sectioned material. R. tubifera has scales which are oval, bell-shaped and trumpet-shaped; they were originally described with the light microscope by Penard (1904) but have not previously been examined by modern methods. The scales appear to be formed in cytoplasmic vesicles but details of the process have not been elucidated.

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APPENDIX I. Dates of sampling visits to Sawley Dene.

1976	MARCH	wk	11a	11.3.76
	APRIL		14a	1.4.76
			18a	30.4.76
	MAY		21a	18.5.76
			22a	26.5.76
	JUNE		23a	3.6.76
			24a	10.6.76
			25a	17.6.76
			26a	25.6.76
	JULY		28a	8.7.76
			29a	13.7.76
			30a	20.7.76 *
			31a	28.7.76
	AUGUST		32a	4.8.76 ::
			33a	12.8.76
			34a	18.8.76
			35a	23.8.76
	SEPTEMBER		36a	1.9.76
			37a	9.9.76
			38a	16.9.76
			39a	21.9.76
			40a	29.9.76 ::
	OCTOBER		41a	6.10.76
			43a	18.10.76
			44a	28.10.76
	NOVEMBER		45a	4.11.76 ::
			46a	11.11.76
			47a	16.11.76
			48a	25.11.76
	DECEMBER		50a	7.12.76
			52a	20.12.76 ::
1977	JANUARY		2b	11.1.77
			4b	27.1.77 ::
	FEBRUARY		7b	16.2.77 ::
	MARCH		9b	4.3.77
			10b	11.3.77 ::
			12b	25.3.77
	APRIL		15b	15.4.77 ::
			17b	28.4.77
	MAY		19b	11.5.77 ::
			20b	17.5.77
			21b	25.5.77
			22b	31.5.77
	JUNE		24b	13.6.77
			25b	20.6.77
			26b	28.6.77

* lake sampled after 1200 h

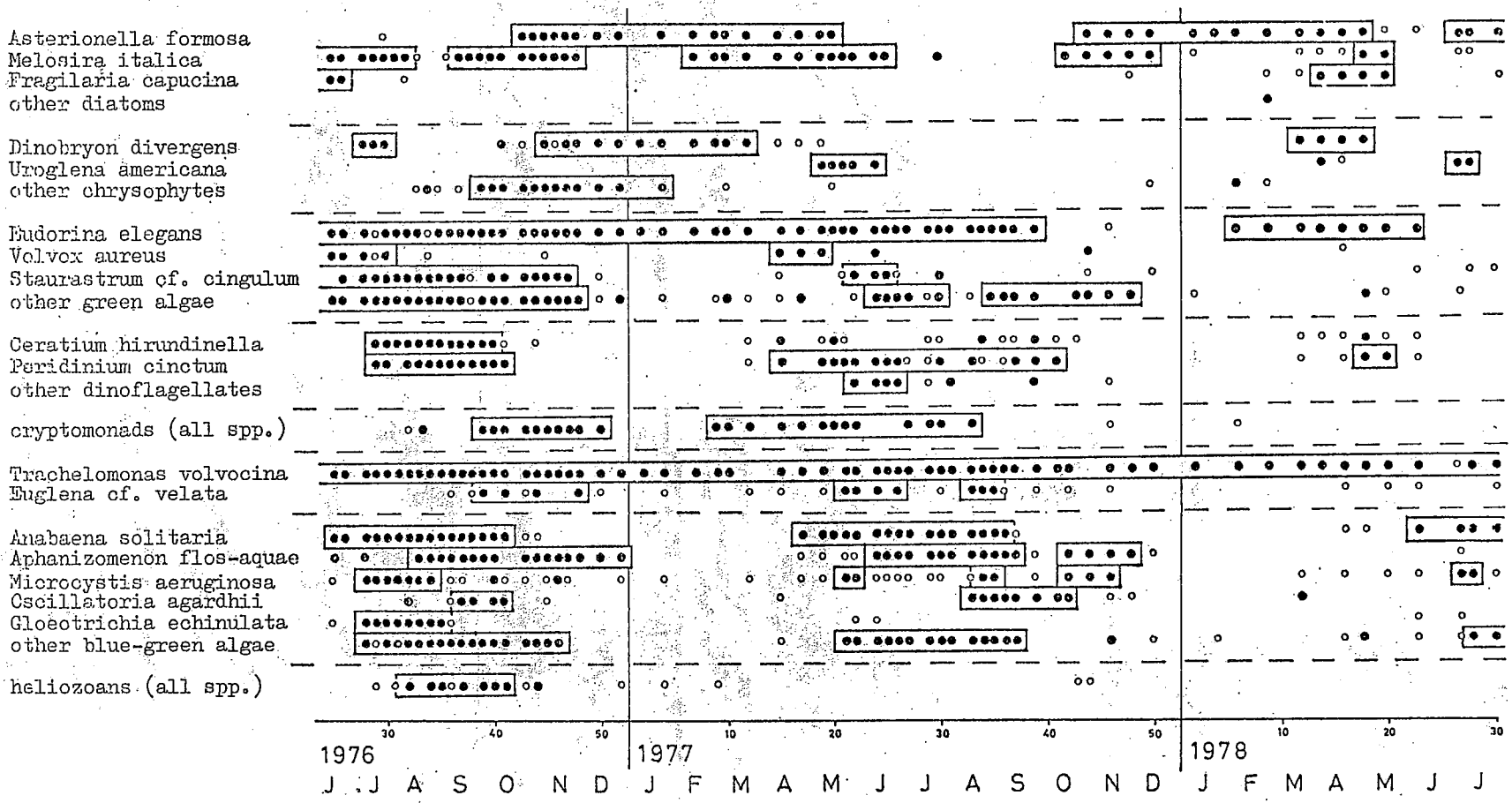
:: sample studied as whole mount in TEM

APPENDIX I, continued.

	JULY	27b	7.7.77	
		29b	17.7.77	
		30b	24.7.77	
	AUGUST	31b	4.8.77	
		33b	16.8.77	
		34b	24.8.77	*
		35b	31.8.77	*
	SEPTEMBER	36b	7.9.77	*
		37b	15.9.77	
		39b	30.9.77	
	OCTOBER	41b	10.10.77	
		42b	20.10.77	
	NOVEMBER	44b	3.11.77	
		46b	17.11.77	
		48b	28.11.77	*
	DECEMBER	50b	14.12.77	
1978	JANUARY	2c	12.1.78	::
		4c	24.1.78	::
	FEBRUARY	6c	6.2.78	::
		9c	28.2.78	::
	MARCH	12c	22.3.78	* ::
	APRIL	14c	5.4.78	::
		16c	20.4.78	::
	MAY	18c	4.5.78	
		20c	17.5.78	
	JUNE	23c	5.6.78	
	JULY	27c	3.7.78	
		28c	13.7.78	
		30c	24.7.78	

APPENDIX II. Summary of phytoplankton periodicity in Sawley Dene, based on net-tow records.

● = "sparse" → "dominant"
○ = "trace"



APPENDIX III. Statistical procedure used for non-parametric ordination, adapted from Bray & Curtis (1957).

(i) Initial organisation of data

This ordination is based on data for 18 species which exceed "trace" amounts over significant parts of the study period and for which full records exist. Each week's sample is treated individually and the abundance of each species tabulated for it, based on a 0 - 5 scale of abundance (see p. 25) to produce a table as follows:

samples	1 Asterionella	2 Melosira	3 Fragilaria	4 Dinobryon	5 Mallomonas acaroides	6 Uroglena	7 Eudorina	8 Volvox	9 Ceratium	10 Peridinium	11 Trachelomonas	12 Anabaena solitaria	13 Anabaena spiroides	14 Anabaena flos-aquae	15 Oscillatoria	16 Microcystis	17 Aphanizomenon	18 Gloeotrichia
25a	0	1	4	0	0	0	3	3	0	0	2	1	1	0.5	0	0.5	1	0.5
28a	0	4	0	3	0	0	3	2	0	0	1	4	0.5	0.5	0	1	1	1
29a	0	1	0	4	0	0	0.5	0.5	1	1	3	4	1	1	0	2	0	2
↓	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
27c	3	0.5	0	0	0	1	0	0	0	0	0.5	4	0.5	0.5	0	0.5	0.5	0
28c	2	0.5	0	0	0	3	0	0	0	0	1	3	0	0	0	1	0	0
30c	1	0	0.5	0	0	0	0	0	0	0	2	4	0	0	0	0.5	0	0

species

(63 samples in all)

(ii) Calculation of similarity between samples

$$\text{Coefficient of similarity, } C = \frac{2\,P_{mn}}{P_m + P_n} \qquad \text{(see p. 27)}$$

A specimen calculation comparing wk 25a (sample "m") with wk 28a (sample "n") is shown below:

species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
wk 25a	0	1*	4	0*	0	0	3*	3	0	0	2	1*	1	0.5*	0	0.5*	1*	0.5*
wk 28a	0	4	0*	3	0	0	3	2*	0	0	1*	4	0.5*	0.5	0	1	1	1

In this instance, $P_m = 17.5$, $P_n = 21$ and P_{mn} (the sum of the lesser values, indicated by *) = 11.

$$\therefore C = \frac{2 \times 11}{17.5 + 21} = 0.57$$

C = 0 would indicate total dissimilarity (i.e. no species in common between two samples); C = 1.0 would indicate that the samples are identical. In practice, C never reaches 1.0 due to the nature of sampling; the highest value found in the investigation, C_{max}, is used to indicate that samples are effectively identical: see (v), below.

(iii) Construction of matrix of C-values

Each sample can be compared with every other sample and a matrix of C-values produced, as in the example below. In practice, only those parts of the matrix where C-values are particularly high or low are of immediate interest, thus some parts of the matrix need not be filled in and some of the 1,953 comparisons for a 63 x 63 matrix are avoided. The example shows a partial matrix from the six samples given in (i), above.

Matrix of C-values

25a									
28a	0.57								
29a	0.39	0.62							
↓	..	..	..						
	..	..	..	..					
	..	..	..	..	..				
27c	0.28	0.44	0.41	..	..	..			
28c	0.16	0.35	0.35	..	..	..	0.70		
30c	0.31	0.38	0.45	..	..	..	0.63	0.50	
	25a	28a	29a	→			27c	28c	30c

(iv) Selection of reference sets - axis 1

Two samples are selected which are highly dissimilar and which also have many low C-values when compared with other samples. In the example above, such a pair would be 25a and 28c; in the complete data set, samples 9b and 35b were selected. These samples become the "reference sets" for axis 1. A table of C-values between every sample and the two reference sets is then drawn up; taking sample 30a as an example:

sample	C-value / 9b	C-value / 35b
...	..	..
...	..	..
30a	0.30	0.40
...	..	..
...	..	..

(v) Calculation of "floristic distance", D

The ordination is constructed using a measure of "distance" between samples rather than similarity; e.g. on a scale 0 - 100, D = 0 would indicate maximum similarity ($C = C_{max}$) and D = 100 would correspond to C = 0. Therefore:

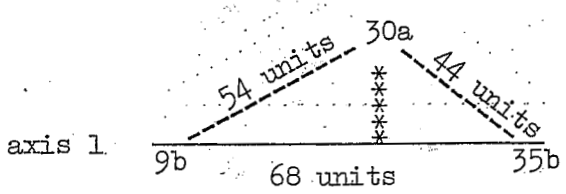
$$D = 100\ (C_{max} - C)$$

In the present instance, C_{max} = 0.84 and so, taking the example of sample 30a:

D (30a/9b) = 54 units; D (30a/35b) = 44 units

(vi) Calculation of sample coordinate on axis 1

Samples 9b and 35b are assigned extreme positions on axis 1 according to their floristic distance: for these two samples, C = 0.16 and thus D = 68 units. 9b is given the coordinate 0 and 35b the coordinate 68. Each sample is now placed so that its position on axis 1 reflects its comparative floristic distance from both sample 9b and sample 35b; thus, taking the example 30a as above:



The coordinate of sample 30a may be determined either by construction or by calculation as 37.5 units along axis 1. A similar procedure is carried out until axis 1 coordinates have been obtained for all the samples.

(vii) Selection of reference sets and calculation of coordinates for axis 2

A significant proportion of the variation within the data may not be represented on one axis alone, i.e. certain samples may occupy similar positions on axis 1 while retaining a high dissimilarity, shown by a low C-value. The matrix of C-values is examined for the most extreme example of such a tendency and two new reference sets selected to serve as extreme samples for axis 2. In the present data set, samples 28c and 43a fulfil these criteria, located at similar positions on axis 1 (coordinates 33.0 and 33.5 units, respectively) but showing high dissimilarity (C = 0.29, D = 55 units). Calculations are then carried out for each sample as in (iv) and (v), above, using the new reference sets, thus:

sample	C-value / 28c	C-value / 43a	D / 28c	D / 43a
...	..	..	..	..
...	..	..	..	..
30a	0.41	0.39	43	45
...	..	..	..	..
...	..	..	..	..

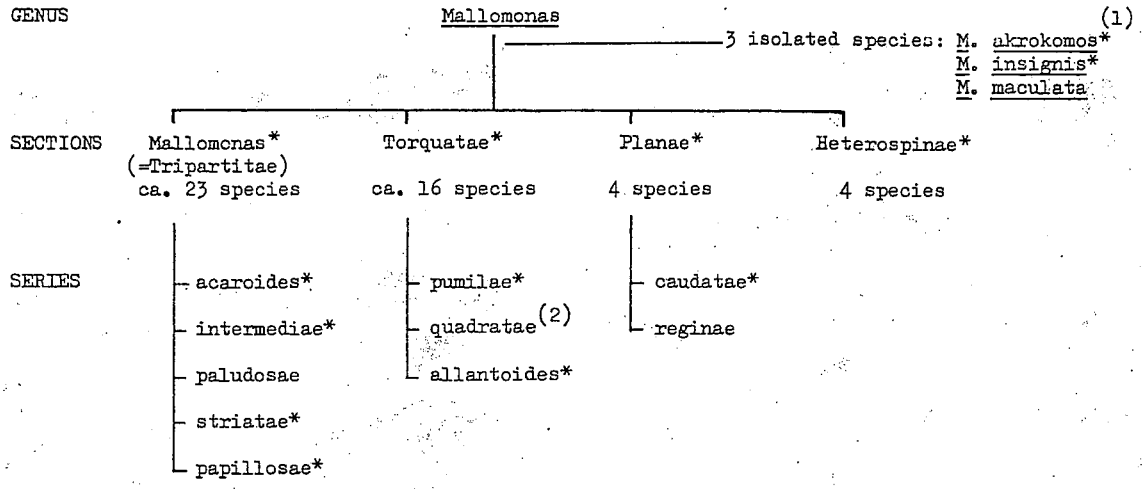
Using a similar procedure to that shown in (vi), above, sample 30a may be assigned a coordinate of 27 units on axis 2.

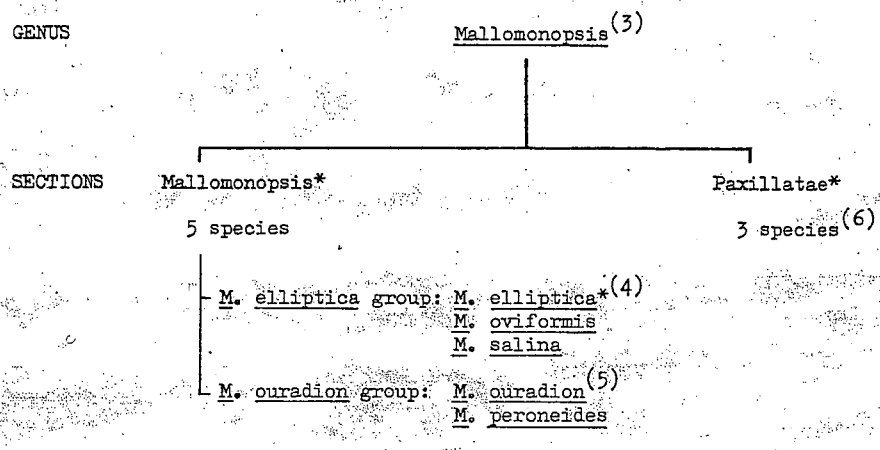
(viii) Location of sample on ordination plot

Sample 30a is positioned according to its coordinates (37.5, 27) on axes 1 and 2 and all other samples are positioned according to their own coordinates. Since the distances between samples are relative rather than absolute, there is no necessity to calibrate the axes in the resulting ordination, although the direction in which each axis proceeds should be shown. The same axes may be used for any subsequent ordination if the plots are required to be directly comparable; however, this may result in compression of information if the data sets are too different.

APPENDIX IV. Outline of subdivisions of the genera Mallomonas and Mallomonopsis, as adopted in the present treatment. For fuller information, see Peterfi & Momeu (1976) and Takahashi (1978).

Section 4 (pp. 58 - 87) includes representatives of those taxonomic groups marked * .





Notes (1) These three species have little in common with each other or with members of the currently recognised series

(2) This series is accepted by Peterfi & Momeu (1976) but not by some other authors, e.g. Takahashi (1978)

(3) Mallomonopsis is reduced to a subgenus of Mallomonas in the treatment of Peterfi & Momeu (1976)

(4) These species are distinguished as in Kristiansen (1975b)

(5) M. ouradion and M. peroneides are probably sufficiently distinct from the M. elliptica group to be placed in a separate Series

(6) This group contains M. paxillata, M. calceolus (transferred from Mallomonas) and the new species M. "minuta"

APPENDIX V. Provisional diagnoses for new taxa of scale-bearing Chrysophyceae (family Synuraceae).

Mallomonas pumilio Harris et Bradley, J. Roy. Microscop. Soc. 76, 1957, p. 45, var. "perforata" var. nov.

Cell oval to elongated, 8 - 10 µm x 3 - 5 µm, with single emergent flagellum. About 5 curved bristles, each ca. 5 µm long, borne singly on collar scales at cell anterior; minute spikes present on a few posterior scales. Collar scales asymmetric, 2.2 - 2.5 µm x 1.5 µm, with a small dome and a single prominent rib just inside the convex margin. Body scales diamond-shaped, ca. 2.0 x 1.5 µm, with single rib around posterior and part of anterior margin but with no dome. Some body scales at posterior end reduced in size.

Ornamentation on main part of scales resembles that displayed by M. pumilio sens. strict.: small ribs form a hexagonal pattern enclosing "rosettes" of pores in groups of 4-5. Var. "perforata" is distinguished by the posession of two additional rows of pores on anterior parts of all scale margins.

Type material from Brim Bray Pond, near Eavestone, North Yorkshire (N.G.R. SE 217687), collected February 1978. Type micrograph: Fig. 128.

Mallomonas "clavoides" sp. nov.

Cell elongated, 9 - 11 µm x 3 - 5 µm , with single emergent flagellum. 4 - 5 curved bristles, each ca. 5 µm long, borne singly on collar scales at cell anterior; minute spikes present on a few posterior scales. Collar scales asymmetric, ca. 3.5 x 2.5 µm; body scales diamond-shaped, ca. 2.5 x 1.8 µm, larger and less numerous on the cell than in the previous taxon. Scales heavily thickened around posterior margins with a peripheral rib and small comb-like extensions to the scale edge. Main part of scales bearing irregularly reticulate pattern of thickened ribs, with ca. 3 weakly defined pores in the spaces between. Scales resemble those of Mallomonas clavus Bradley, J. Gen. Microbiol. 37, 1964, p. 326, except that ribs are somewhat more thickened; cell differs from that of M. clavus in bearing minute posterior spikes instead of long spines.

Type material from Brim Bray Pond (details as for previous taxon). Type micrograph: Fig. 130.

Mallomonopsis calceolus (Bradley) comb. nov.
Basionym: Mallomonas calceolus Bradley, J. Gen. Microbiol. 37, 1964, p. 322.

Diagnosis as in Bradley, 1964, except that cells are now known to have two emergent flagella (see Belcher, 1969).

Mallomonopsis "minuta" sp. nov.

Cell round, ca. 5 μm diameter, details of flagella not known. Scales of one type, diamond-shaped but rounded at the posterior end, 1.6 - 1.8 μm x 1 μm, each with a V-rib but without a dome. Anterior portion of scale bearing a hexagonal array of papillae; posterior portion smooth except for U-shaped marking between V-rib and edge of scale. Each scale bearing a single curved bristle 2.0 - 2.5 μm long, flattened at base, with a pointed tip and a single sub-apical tooth.

Type material from Brim Bray Pond (details as for previous taxa). Type micrograph: Fig. 159.

Spiniferomonas bourrellii Takahashi, Bot. Mag., Tokyo 86, 1973, p. 76, var. "simplex" var. nov.

Cell round, ca. 7 μm diameter, with heterokont flagella and bearing oval plate scales and several long spines. Plate scales 1.2 - 1.8 μm x 2.2 - 2.5 μm, distinguished from those of S. bourrellii sens. strict. by the absence of a central lacuna and the presence of a short transverse strut as the only ornamentation.

Type material from Sawley Dene, Sawley, North Yorkshire (N.G.R. SE 263667), collected January 1978. Type micrograph: Fig. 176.

Paraphysomonas foraminifera Lucas, J. Mar. Biol. Ass. U.K. 47, 1967, p. 330, var. "trifida" var. nov.

Characteristics of whole cell unknown. Scales with round oval base-plate, 2.2 - 3.2 μm x 1.5 - 2.5 μm, of meshwork structure comprising concentric rings of pores outlined by delicate struts. Most scales also bearing a stout, tapering spine, 3 - 5 μm long, branching into three curving portions where it meets the base-plate. Var. "trifida" is distinguished from P. foraminifera sens. strict. by its three-branched spine bases and the more dissected nature of the scale base-plate.

Type material from Sawley Dene (details as for previous taxon). Type micrograph: Fig. 186.

ADDENDA

Since the completion of earlier parts of this thesis, certain additional information of relevance has become available to me.

Kristiansen (1979) gives details of 14 species of scale-bearing Chrysophyceae identified by EM from pools and lakes in North Wales, among which Mallomonas acaroides, M. tonsurata, M. hamata, Mallomonopsis (Mallomonas) calceolus, Paraphysomonas vestita, Synura petersenii, S. echinulata, S. sphagnicola and Spiniferomonas trioralis are in common with those found in the present study (Section 4, p. 60 et seq.). Mallomonas hamata, a very rare species, has also been recorded from Denmark a second time (Nygaard, 1975): cf. p. 69.

Thomsen (1978) illustrates scales of eight previously unknown types which he names as new species of the heliozoan genus Pinaciophora. Among these are scales identical to those of "Unknown species C" from Sawley Dene (see p. 81 and Figs 209 - 210) which are named Pinaciophora monopora Thomsen; these scales were found by Ø. Moestrup in a sample from Lake Esrom, Denmark.

Light-microscope observations on phagotrophy in Paraphysomonas vestita have been given by Richter (1975); his Figs 5 and 6 show ingested objects within vesicles which may exceed the normal cell diameter in width (cf. p. 91 and Figs 219, 220, etc.).

Bardele (1977) shows a transverse section of a cell of Acanthocystis which includes profiles of scales within cytoplasmic vesicles (cf. p. 107, Fig. 305); although the cytoplasmic preservation is good there is still no indication of how such vesicles arise (see remarks on p. 119).

Additional References

KRISTIANSEN, J. (1979). Observations on some Chrysophyceae from North Wales. Br. Phycol. J. 14: 231-241.

NYGAARD, G. (1975). New or interesting plankton algae with a contribution on their ecology. Biol. Skr. Dan. Vid. Selsk. 21: 1-107.

RICHTER, W. (1975). Der farblose flagellat Paraphysomonas vestita. Mikrokosmos 64: 266-273.

THOMSEN, H.A. (1978). On the identity between the Heliozoan Pinaciophora fluviatilis and Potamodiscus kalbei; with the description of eight new Pinaciophora species. Protistologica 14: 359-373.

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THE DINOFLAGELLATE TRANSVERSE FLAGELLUM: THREE-DIMENSIONAL RECONSTRUCTIONS FROM SERIAL SECTIONS[1]

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ABSTRACT

Serial sections through in situ transverse flagella of the dinoflagellate Peridinium cinctum *f.* irregulatum *(Lindem.) Lefèvre are presented. Three-dimensional reconstructions based upon tangential and radial series show a helically coiled axoneme lying external to and distinct from an accessory strand. Hitherto undescribed vesicles within the expanded flagellar sheath are suggested to provide a decoupling effect between axoneme and strand. The flagellar axis bears two types of hair but anchoring threads between cingulum and flagellum have not been found. Functional and taxonomic implications of these observations are briefly discussed.*

Key index words: axoneme; dinoflagellate; flagellum, Peridinium; *flagellum, model;* Peridinium; *sheath, flagellar; transverse flagellum, dinoflagellate*

Dinoflagellates are an ancient and phyletically isolated group of algae with several unique features of cell organization. In the order Peridiniales (Class Dinophyceae), a distinctive transverse flagellum encircles the cell within a surface groove, or cingulum. Early observations on its form and manner of beating were made by Kofoid and Swezy (6); more recent investigations have beem summarized by Leadbeater and Dodge (9) and Berdach (1). The flagellar sheath is expanded to encompass a looped or coiled axoneme and an accessory rod, the "striated strand" (7), but the precise relationship between the two has not been unequivocally resolved. Examination of dried whole flagella by transmission electron microscopy (TEM) suggested a helical axoneme coiled around the striated strand (8,9), whereas scanning electron microscopy (SEM) suggested hemihelical (4,10,16) or helical (1) configurations of the axoneme distinct from but parallel to the strand. Micrographs of individual sections of the flagellum in situ have been published without providing conclusive information on flagellar form (9,15).

Serial sections through a dinoflagellate transverse flagellum are presented here for the first time, together with three-dimensional reconstructions which allow all features of the flagellar axis to be viewed in their correct spatial relationships.

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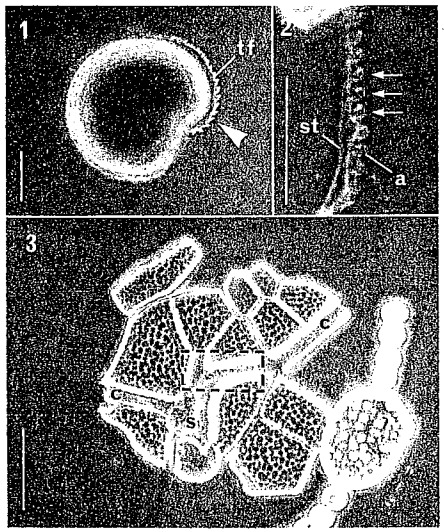
MATERIALS AND METHODS

Peridinium cinctum (O.F.M.) Ehrenb. occurred in net-plankton hauls taken from the surface waters of Sawley Dene, a small lake in Yorkshire, England (National Grid ref. SE 263667), during June 1977. Light microscopy was carried out on living and iodine-fixed cells using a Reichert Zetopan microscope. Spreads of thecal plates allowed the organism to be identified from Schiller (13) as *P. cinctum* f. *irregulatum* (Lindem.) Lefèvre. Samples for electron microscopy were fixed at 4 C for 2 h in 2% OsO_4 mixed 1:1 with 5% glutaraldehyde immediately prior to addition to the



NOTE: Abbreviations used in figures: *a* = axoneme; *c* = cingulum; *cw* = cingulum wall; *fm* = flagellar membrane; *fs* = flagellar sheath; *h* = hairs; *s* = sulcus; *st* = strand; *tf* = transverse flagellum; *tp* = thecal plate; *v* = vesicles.

FIGS. 1–3. Light micrographs of iodine-fixed *Peridinium cinctum*, Anoptral contrast. Scale = 20 μm. FIG. 1. Apical view of cell (ventral surface to right) showing transverse flagellum partly displaced from cingulum: arrow indicates location of the tangential series of sections. FIG. 2. Detached flagellum showing axoneme and flagellar strand: arrows indicate direction of approach for sectioning. FIG. 3. Flattened thecal plates showing ventral surface with sulcus and parts of cingulum: dotted rectangle indicates area in FIGS. 4–9. (Filament at right is bluegreen alga *Anabaena solitaria.*)

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MORPHOLOGY OF THE SCALES OF THE FRESHWATER HELIOZOAN *RAPHIDOCYSTIS TUBIFERA* (HELIOZOA, CENTROHELIDIA) AND ORGANISATION OF THE INTACT SCALE LAYER

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SUMMARY

Three types of isolated scales detected in freshwater plankton samples from Yorkshire, England, and British Columbia, Canada, are shown to belong to the heliozoan *Raphidocystis tubifera* Penard. New structural details of scales and whole cells have been revealed by scanning and transmission electron microscopy and these add to the original description based upon light microscopy. Previous records of this species are noted and its ecological and geographical ranges are briefly discussed.

RÉSUMÉ

Les auteurs démontrent que trois espèces d'écailles isolées, découvertes dans des échantillons de planctons d'eau douce provenant du Yorkshire, G.B., et de la Colombie britannique, au Canada, appartiennent à l'héliozoaire *Raphidocystis tubifera* Penard. Ils révèlent de nouveaux détails structuraux d'écailles et de cellules entières au moyen de la microscopie électronique, lesquels complètent la description originale de l'espèce basée sur la microscopie optique. Ils notent les signalisations préalables de l'espèce et discutent brièvement sa répartition écologique et géographique.

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PERIODICITY OF PHYTOPLANKTON OVER TWO SEASONS IN A SHALLOW EUTROPHIC LAKE

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