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Résumé de l'article

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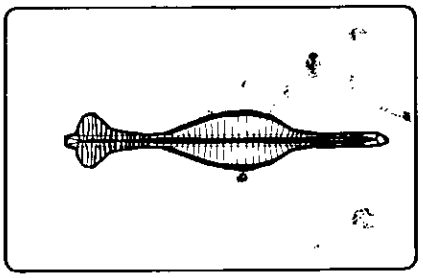

Methods in Quaternary Ecology #1. Freshwater Algae

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Summary
Morphological and biogeochemical remains of past algal populations can be recovered from most sedimentary deposits. The majority of these fossils are diatom valves, but many algal groups are preserved in some form. All algal taxa have specific ecological requirements, and therefore their stratigraphic distributions in sedimentary profiles can be used to infer past environmental conditions. This paper briefly reviews some of the ways that freshwater algal assemblages have been used in paleoecological studies, with an emphasis on North American research.

Introduction
The word "algae" has no real taxonomic meaning, except to circumscribe a diverse grouping of plants that share only a few characteristics. A simple, technical definition is that algae are non-vascular plants that contain chlorophyll *a* as their primary photosynthetic pigment and have simple reproductive structures (Trainor, 1978). Even these criteria are not met by all organisms generally considered to be algae (*e.g.*, some dinoflagellates are not photosynthetic). Nonetheless, the above is a useful working definition for a group of organisms whose classification includes upwards of 15 divisions (phyla) containing over 20,000 species.

One of the first tasks in any algal study is to outline the classification system one will be following — there are several (Round, 1973). Table 1 lists the class system I will be using. The Rhodophyceae (red algae) and Phaeophyceae (brown algae) are almost exclusively marine and are not considered here.

Historical Development
The study of algae, namely algology or phycology, was underway, at least in a minor way, since the time of Theophrastus (*ca.* 300 B.C.) — considered by many to be the father of botany. He divided the plant kingdom into three groups: trees, shrubs, and herbs. The latter category included the algae known at that time. Studies of microscopic forms, which incidentally include almost all of the freshwater taxa, only began after van Leeuwenhoek introduced the seventeenth-century scientific community to the microscope, and undoubtedly some of his "animalcules" were actually algae (Whitford, 1968).

Algae have a long fossil record, dating back to the first life forms of the Precambrian. Morphological fossils, which phycologists would immediately recognize as algae, were amongst the first living organisms, with blue-green algal forms recovered from two billion year old stromatolites (Schopf, 1975). Other sedimentary deposits, spanning many geologic time periods, also contain diverse algal assemblages (Round, 1981). Despite this rich record, my review is restricted to the discussion of algae from Quaternary freshwater deposits.

The fact that siliceous algae, such as diatoms, were well preserved in sediments was observed by the early phycologists. For example, Christian G. Ehrenberg (1854) made extensive use of diatomaceous deposits in his pioneering work with diatom systematics in Europe and Asia. Ehrenberg was also the first to write on North American diatoms, although he never visited this continent.

Patrick's (1984) history of diatom research in the United States is germane to this review, as little work was being done in Canada prior to the 1960s. The earliest account that I am aware of is the nineteenth-century study by Hinde (1877) on the Scarborough interglacial beds, where he noted three fossil diatom taxa, followed by Dawson's (1893) report of diatoms from what he believed were interglacial deposits near Rolling River, Manitoba. A few species lists of fossils identified from diatomaceous deposits in southern Canada also were compiled (Boyer, 1926).

Interestingly, a re-examination of the same interglacial beds where Hinde had noted diatoms and *Chara* almost a century earlier rekindled interest in the use of diatoms as paleoecological markers in Canada. Terasmae's (1960) palynological study of the Don Formation included a brief discussion of 20 diatom taxa. Later, Duthie and Mannada Rani (1967) re-investigated the site, and recorded over 200 diatom species; they concluded that the beds represented a freshwater river estuary.

Lasalle (1966) listed the diatoms he recorded in his primarily palynological studies in the St. Lawrence lowlands, and showed how fossil pollen and diatoms could be used together to reconstruct the paleoenvironments of the Champlain Sea. Shortly thereafter, Stockner (1971) assessed the applicability of diatoms as indicators of water quality, and Sreenivasa and Duthie (1973) published the postglacial diatom history of Sunfish Lake (Ontario). A large number of Canadian studies were soon to follow.

Morphological and Biogeochemical Fossils
The main requirement for any freshwater fossil is that it be insoluble in water, and that it be relatively resistant to bacterial decay and chemical solution. Despite these stringent pre-conditions, a lake's sediment contains a surprisingly large suite of indicators, with virtually every algal group represented (Table 1). I distinguish two main categories of algal fossils: morphological fossils, which maintain some morphological integrity in sedimentary deposits, and biogeochemical fossils, which are preserved in sedimentary profiles by chemical markers.

Morphological fossils are those that can be studied visually, although high resolution microscopy is usually required. These include the "hard parts" of an alga's structure, many of which are taxonomically diagnostic.

Table 1 **The dominant freshwater algal classes (Lee, 1980) and their morphological fossils. These algal groups are also represented by fossil pigments.**

CLASS	COMMON NAME	MORPHOLOGICAL FOSSIL
Cyanophyceae	blue-green algae or blue-green bacteria	vegetative and reproductive cells
Chlorophyceae	green algae	vegetative and reproductive cells
Euglenophyceae	euglenoids	vegetative and reproductive cells
Charophyceae	charophytes, stone worts, brittle worts	vegetative and reproductive cells
Dinophyceae	dinoflagellates	vegetative and reproductive cells
Cryptophyceae	cryptophytes	none known
Bacillariophyceae	diatoms	valves/frustules
Chrysophyceae	chrysophytes	statospores, mallomonadacean scales and bristles/spines

By far, the most widely studied are the siliceous valves of diatoms (Figures 1-3). Diatoms represent one of the most widely distributed and ecologically diverse group of algae, whose systematics is based on the size, shape, and sculpturing of their cell walls or frustules (one frustule is composed of two interlocking halves or valves). Because of their siliceous nature, diatom valves are usually well preserved in sedimentary deposits, where they can reach concentrations on the order of 10^9 per cm^3. Barber and Haworth (1981) provide a useful summary of the terminology used in diatom taxonomy, and Battarbee (1986) reviews the methodology and applicability of diatoms to paleoecological studies.

Chrysophycean algae similarly are represented in the fossil record by siliceous remains. All chrysophytes produce siliceous resting cysts known as statospores (Figures 4 and 5), the morphologies of which are often species-specific, and, like diatom valves, appear to have all the necessary characteristics to be useful paleoindicators. However, in contrast to diatom valves, the taxonomy of the cysts remains poorly documented, and in fact only about 5% of cyst morphotypes have been linked to known chrysophyte taxa. Several artificial classification systems have been proposed (*e.g.*, Nygaard, 1956) and used (*e.g.*, Carney and Sandgren, 1983), although rarely can paleolimnologists identify many fossil cyst morphs. These taxonomic shortcomings are being addressed by the International Statospore Working Group (ISWG), which has proposed a series of guidelines for describing statospores, even if their taxonomic identities are unknown (Cronberg and Sandgren, 1986).

Several common chrysophyte genera (such as those in the family Mallomonadaceae) are further characterized by an external armour of overlapping siliceous scales (Figure 6) and bristles or spines. Unlike the statospores, these species-specific scales have been studied extensively with the electron microscope, and presently the entire systematics of the Mallomonadaceae is based on the shape and sculpturing of the scales (Asmund and Kristiansen, 1986). Chrysophyte scales are usually well preserved in lake sediments, where they can be identified and enumerated alongside diatoms using the same preparations (Munch, 1980; Smol, 1980). Cronberg (1986a, b) and Smol (1987a) have reviewed the methodology and applicability of chrysophyte cysts and scales to paleolimnological analyses.

Most other algal groups also preserve morphological remains (Figure 7), although research on these has lagged behind the siliceous fossils. For example, vegetative remains of green algae, such as intact desmids or entire colonies of *Pediastrum*, are not uncommon in pollen preparations (Cronberg, 1986a; Frederick, 1981). Similarly, the resting stages and vegetative remains of other Chlorophyceae (Van Geel *et al.*, 1981; Livingstone, 1984), blue-green algae (*ibid.*), dinoflagellates (Norris and McAndrews, 1970), and charophytes (Burne *et al.*, 1980) are occasionally reported, although these indicators still represent a largely unstudied and probably underutilized paleoecological tool.

Past algal populations also can be inferred from biogeochemical fossils, most notably photosynthetic pigments and their derivatives (Brown, 1969). Chlorophylls have been useful in this regard, but carotenoids (*i.e.*, carotenes and their oxidized derivatives the xanthophylls) are more taxonomically specific, and can be used to trace the wax and wane of algal and photosynthetic bacterial groups. Fossil pigments are especially important in the reconstruction of populations that do not usually form morphological fossils. For example, cryptophytes can be traced by their specific carotenoid alloxanthin, blue-green algal populations by myxoxanthophyll, and so forth. Certain pigments are restricted to even lower taxonomic categories, such as oscillaxanthin (Brown and Colman, 1963), which is only found in some *Oscillatoria* and *Spirulina* species.

From a historical perspective, it is interesting to note that the pioneering Canadian research with pigments (Vallentyne, 1955, 1956; Brown, 1962) pre-dated much of the early work done on morphological fossils.

Field and Laboratory Techniques

Most sedimentary deposits contain at least some algal fossils. Field collection techniques are identical to those used for other paleoecological work. In general, sediment cores from lakes or bogs are retrieved using either gravity or piston corers (techniques reviewed by Aaby and Digerfeldt, 1986). The sediment is then extruded and sectioned at defined intervals. In some circumstances, fine resolution sampling is required (*e.g.*, the algae in a single varve). The sediment is then either impregnated with a resin and thin sectioned (Tippett, 1964), or a thin rind of sediment is adhered to a length of transparent tape from a longitudinal section of a frozen core (Simola, 1977). For certain specialized investigations, such as the study of sections (Terasmae, 1960), a systematic sequence of samples can be collected using a trowel or spatula.

Preparation procedures depend on the type of paleoindicators to be studied. Siliceous microfossils must first be separated from the sediment matrix by treatment with strong oxidizing acids, which digest any associated organic matter, followed by several rinses in distilled water (Battarbee, 1986). The resulting concentrate is then mounted on glass slides in a medium of high refractive index, such as Hyrax or Naphrax. Analyses can be prepared quantitatively by using evaporation trays (Battarbee, 1973) or by introducing a known quantity of exotic markers to the sediment, such as glass microspheres (Battarbee and Kneen, 1982). For non-siliceous microfossils, most procedures are similar to palynological preparations (Cronberg, 1986a; van Geel, 1986).

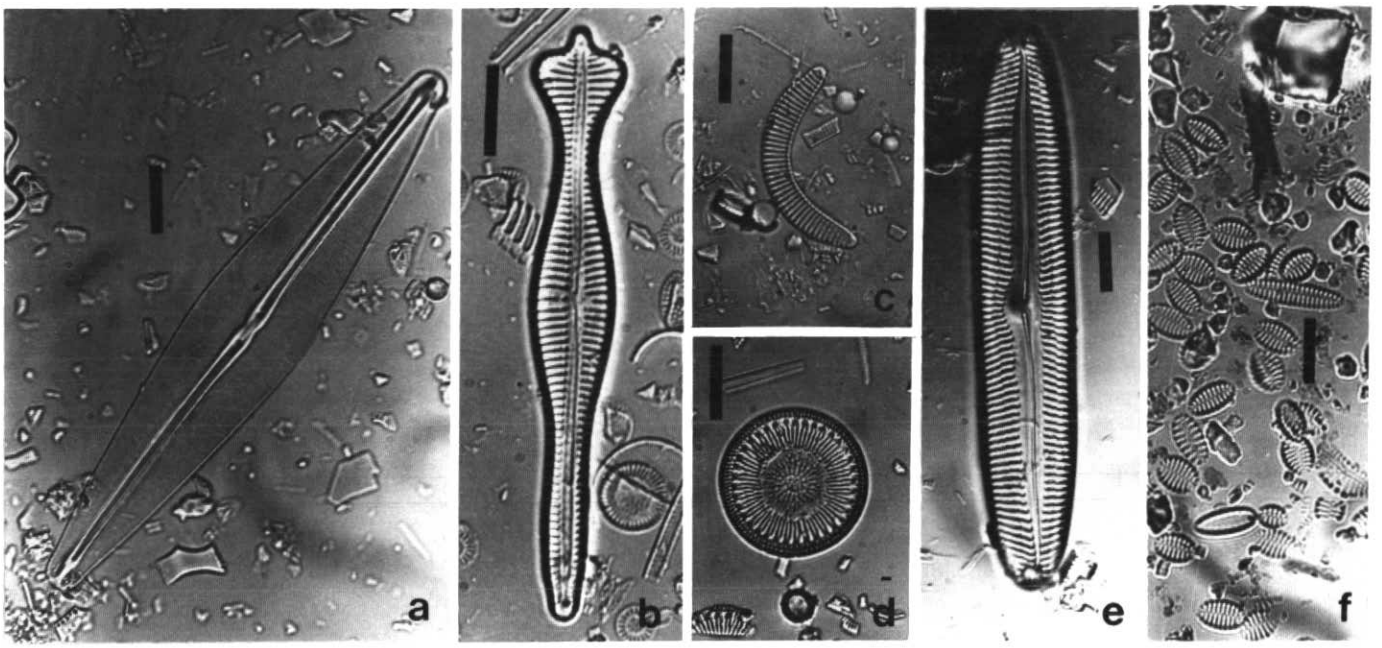
Morphological remains are usually identified and enumerated using high resolution optics (Figures 1, 4 and 7), although certain groups may require some scanning (Figures 3 and 5) or transmission (Figure 6) electron microscopy to confirm taxonomic identifications. Although the morphological taxonomy of most algal groups is based on systems that originated in the early nineteenth century, the single most important quality assurance/quality control problem in morphology-based paleoecology is consistent systematics.

Procedures for extracting fossil pigments and their derivatives are less standardized and more rigorous, and the validity of certain techniques continues to be an area of considerable debate. Isomers and the various pigment degradation products must all be considered (Brown, 1969). In general, analyses include the use of solvents, such as acetone and alcohol, to extract the pigments from the sediments. The extract is then separated into its various pigment components using chromatographic techniques. Spectrophotometry is often used to aid in identifying the pigments and their derivatives. In contrast to morphological microfossils, more stringent laboratory procedures (*e.g.*, working under dim lights, storage of sediments under a nitrogen atmosphera, *etc.*) are required to minimize degradative processes and to avoid the introduction of artifacts.

Applications

Many algal taxa have specific ecological requirements; therefore at least some information on past ecological conditions can be gleaned from a careful analysis of the algal assemblage the environment once supported.

Because of the large number of environmental factors that can potentially affect the size and composition of an algal community, the autecologies of many taxa are still poorly documented — but this shortcoming is being pursued aggressively and continued progress should be expected (Davis and Smol, 1986). An especially popular and successful approach has been the use of "calibration sets", *viz.* the study of algal microfossils in the recent sediments (*e.g.*, top cm, usually representing the last few years of sediment accumulation) in well studied lakes, and the correlation of these assemblages with modern environmental conditions. A variety of statistical techniques can then be applied to the data set, and transfer functions relating algal composition to environmental variables (such as pH; see papers in Smol *et al.*, 1986) can be constructed. Other measures of community structure, such as species diversity, have been used, but these approaches should be used with caution (Smol, 1981).



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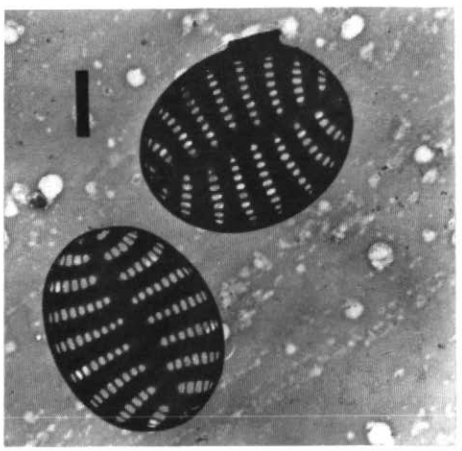

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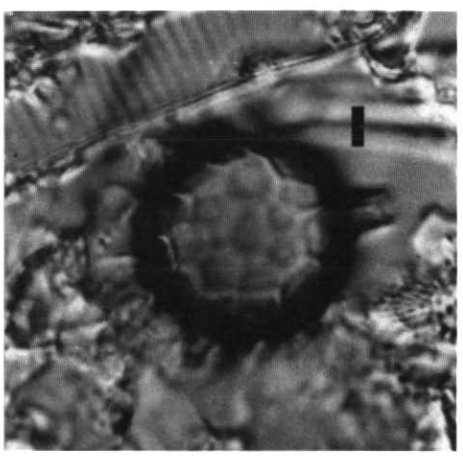

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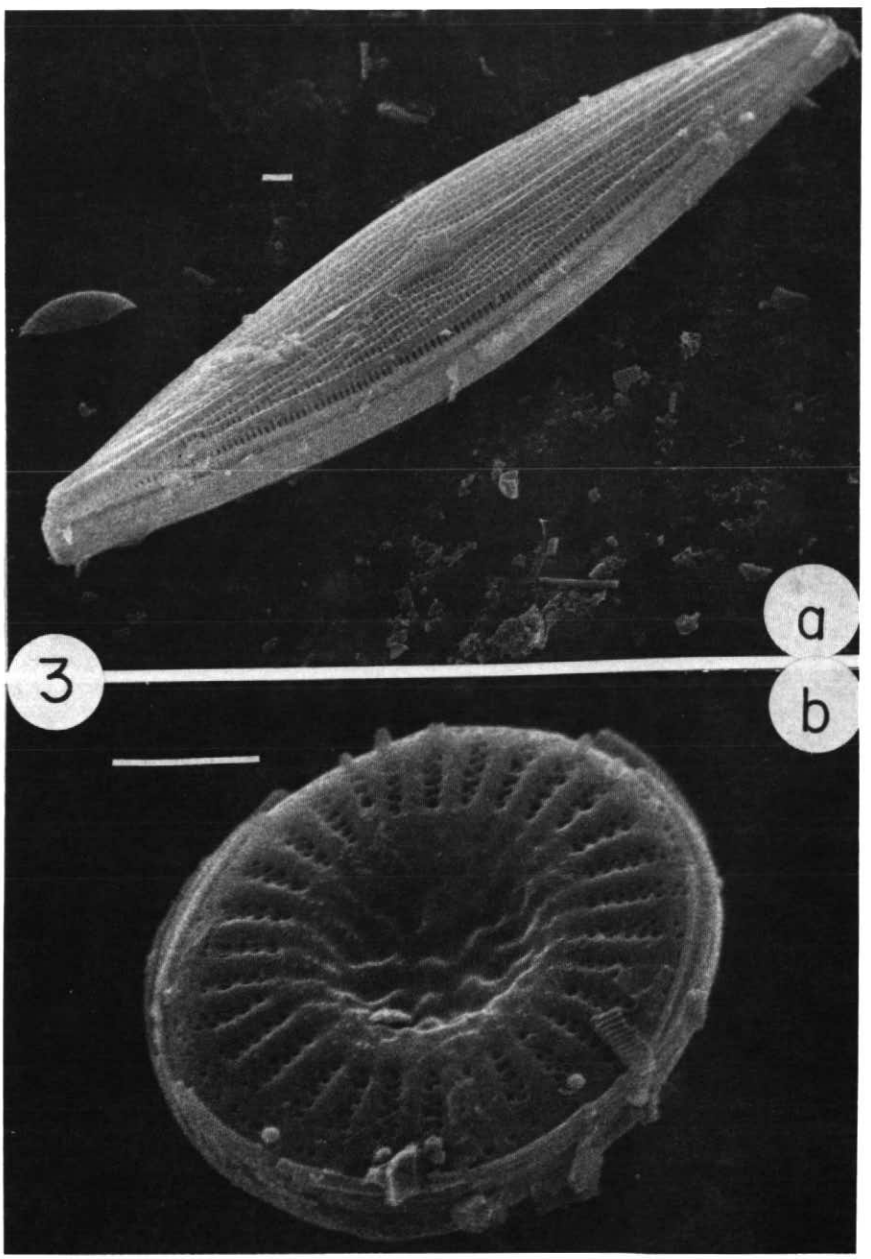

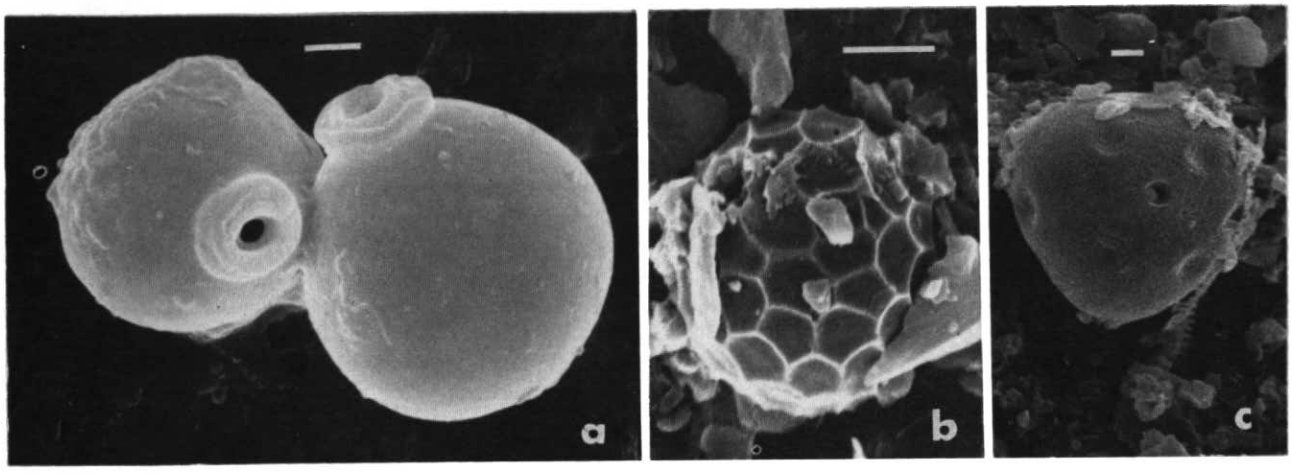

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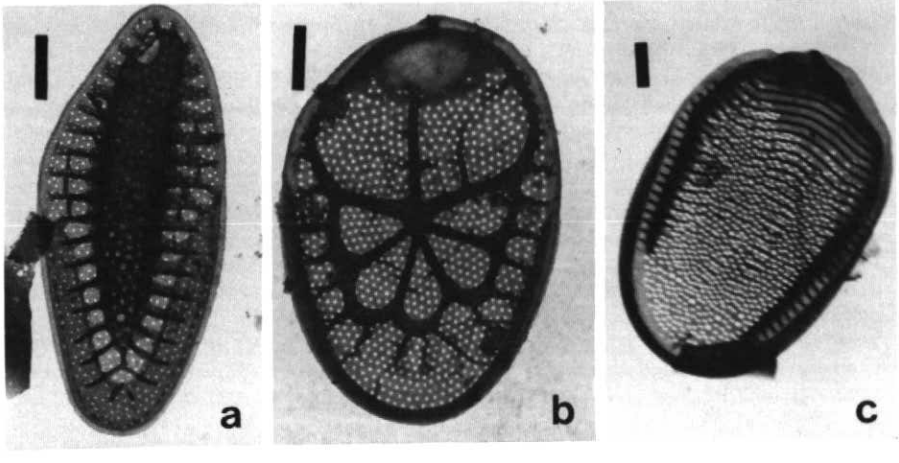

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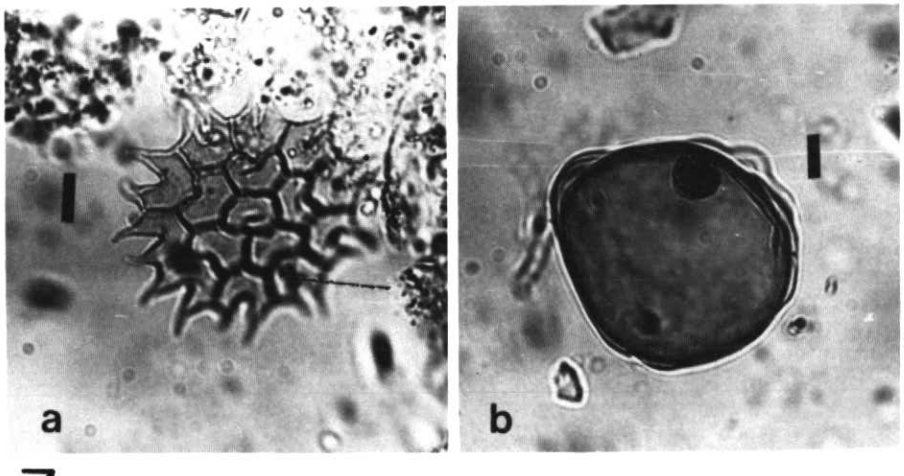

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Figure 1 *Light micrographs of fossil diatom valves. Scale bar = 10 μm.*
(a) Frustulia rhomboides *(Ehr.) DeT. — a common benthic diatom from shallow, acidic waters.*
(b) Gomphonema acuminatum *Ehr. — found in circumneutral, shallow waters.*
(c) Semiorbis hemicyclus *(Ehr.) Patr. — a shallow water, acidobiontic diatom.*
(d) Cyclotella comta *(Ehr.) Kütz. — a common planktonic diatom in non-acidic waters.*
(e) Pinnularia viridis *(Nitz.) Ehr. — a benthic diatom found in circumneutral waters.*
(f) *Small* Fragilaria *species from the sediments of a small lake from Northern Greenland. These diatoms are commonly found in the early post-glacial sediments of temperate lakes.*

Figure 2 *Transmission electron micrograph of some of the small* Fragilaria *diatoms shown in Figure 1 (f). The detail of the valve striation pattern can be seen. Scale bar = 2 μm.*

Figure 3 *Scanning electron micrographs of fossil diatom valves. Scale bar = 2 μm.* **(a)** Anomoeoneis serians *(Bréb.* ex *Kütz.) Cl. — a shallow water diatom from acidic waters.* **(b)** Cyclotella stelligera *Cl.* et *Grun. — a common planktonic diatom in many Canadian waters.*

Figure 4 *Light micrograph of a fossil chrysophycean statospore. Scale bar = 2 μm.*

Figure 5 **(a-c)** *Scanning electron microgrphs of chrysophycean statospores. Scale bar = 2 μm.*

Figure 6 *Transmission electron micrographs of chrysophycean scales. Scale bar = 0.5 μm.*
(a) Synura petersenii *Korsh. — a widespread species common in many water bodies.*
(b) Mallomonas hindonii *Nicholls — a chrysophyte characteristic of very acidic waters.*
(c) Mallomonas transsylvanica *Peterfi* et *Momeu — a relatively rare chrysophyte in most North American waters.*

Figure 7 *Light micrographs of non-siliceous algal microfossils. Scale bar = 20 μm.*
(a) Pediastrum *colony — these planktonic algae have been used to infer past changes in a lake's eutrophication.*
(b) *dinoflagellate cyst.*

Below, I briefly discuss some of the ways that algal assemblages have been used to infer past environmental conditions. Most of the examples deal with diatoms, but other algal groups are discussed where data are available.

Habitat. The life forms of most algae, and especially diatoms, are sufficiently well known that taxa can be categorized as having optimal growth either in the open water (phytoplankton) or attached in the littoral zone (periphyton). Often, the latter can be characterized further by the type of associated substrate, namely attached to plants (epiphytic), rocks (epilithic), sand grains (epipsammic), or mud (epipelic). Certain taxa are also characteristic of flowing waters (rheophilic; Patrick and Reimer, 1966), snow and ice (cryophilic; Lichti-Federovich, 1980), tree bark (corticolous; Cox and Hightower, 1972), and subaerial and aerial habitats, such as sandstone cliffs (Camburn, 1982) or even the hanging gardens at national monuments (Johansen *et al.*, 1983)! The paleoecologist can use the known life strategies of algae to reconstruct the relative size and composition of these different communities (*e.g.*, shallow water *versus* deep water forms), from which other environmental information can be deduced (*e.g.*, water level fluctuations).

Ritchie and Koivo (1975) related habitat preferences of diatoms to water level changes in the Lake Agassiz basin throughout postglacial time. They interpreted the abundance of planktonic diatoms in the early sediments as representing deposits of a large glacial lake. These communities were replaced by benthic floras as the lake gradually receded to the shallow pond, still present today. Björck and Keister (1983) also included diatom analyses to aid their interpretations of the Emerson Phase of Lake Agassiz. Manny *et al.* (1978) recorded fluctuations in the relative frequencies of planktonic and littoral taxa in a diatom stratigraphy from Wintergreen Lake (Michigan). They postulated that water levels have fluctuated in the past, which altered the size of the lake's littoral zone.

Osborne and Moss (1977) and Moss (1978) noted changes in the stratigraphic distribution of epiphytic diatoms in some Norfolk (UK) ponds. They believed that the decline in epiphytes indicated the elimination of macrophytes by the striking increase in planktonic forms and the resulting reduction in light transparency following eutrophication. Meanwhile, Jones *et al.* (1978) and Smol and Dickman (1981) attributed the decline in shallow water taxa to increased turbidity in their study lakes' littoral zones following road construction; the latter example was from a twentieth-century highway built in Algonquin Park (Ontario), the former was from a Welsh road built by the Romans in A.D. 74!

Hickman and Klarer (1981) recorded a decline in planktonic diatoms and a compensatory increase in epipelic forms about 6,600 years ago in Lake Isle (Alberta). This coincided with deposition of Mt. Mazama ash on the lake.

Florin and Wright (1969) identified a diatom assemblage characteristic of terrestrial habitats, along with wood debris and fungal spores, in the basal sediments of Kirchner Marsh (Minnesota). These data were interpreted as evidence for the persistence of stagnant glacial ice. The earliest sediments probably reflect the floor of a forest that once grew on the stranded ice block. Subsequently, the ice melted and a kettle lake formed, and planktonic diatoms began to dominate the assemblage. Haworth (1976) also found terrestrial diatoms in the late-glacial sediments of two Scottish lakes. She postulated that these diatoms were indicative of solifluction processes in the drainage basin.

Temperature. Algae are generally considered to be relatively poor indicators of climate, although temperature optima for some taxa have been suggested. Diatoms have been included in many studies to reinforce paleoclimate interpretations, especially in African lakes (*e.g.*, Richardson and Richardson, 1972; Stoffers and Hecky, 1978; Stager, 1984). Preliminary research on light and nutrient resource partitioning amongst African diatoms, and the relationships these variables have with climate, also provides interesting paleoecological possibilities (Kilham *et al.*, 1986).

In certain environments, the defined habitat requirements of algal taxa may be used to infer changes in past climate. Smol (1983, 1987b) suggested that in polar regions, such as the high arctic, algal microfossils may provide proxy data for paleoclimates because temperature changes are intimately related to the extent of snow and ice cover on high latitude lakes. Therefore, temperature determines the area of a lake that can be colonized by photosynthetic organisms. During cold summers, a portion of the lake's pelagic region may remain permanently covered by a raft of snow and ice, and therefore only shallow water, littoral species will thrive. As temperatures ameliorate, a larger portion of the lake is made available for algal growth, and progressively deeper water floras develop.

Similar reasoning might explain the abundance of shallow water diatoms in the late-glacial and early postglacial sediments of most lakes (*e.g.*, Sreenivasa and Duthie, 1973; Smol and Boucherle, 1985). Planktonic communities may have been late in developing because the cold temperatures characteristic of the late-glacial truncated the growing season in the pelagic region. Only later, as temperatures ameliorated and lake ice was less extensive, were deeper water algae more competitive.

Seasonality. Seasonal changes in algal populations have been the subject of intense study since the time of the first limnologists. Knowledge of the marked seasonality of certain algal groups has been exploited by paleoecologists to demonstrate that laminations in some lake sediments are annual deposits. For example, Tippett (1964), in a classic paper on varves in Ontario lakes, used the known seasonal distributions of diatoms and chrysophytes as evidence for the annual nature of the laminations. Other studies that examined algal fossils in varves, and related them to seasonal events, include Simola (1977), Battarbee (1981), and Peglar *et al.* (1984).

Conductivity/salinity. Water salinity is one of the most important factors influencing the distribution of algae. Much of the available data are for diatom species. Most diatoms can be characterized ecologically according to their salinity tolerances (*i.e.*, halobian spectrum; defined by Kolbe (1927), and subsequently modifed by Hustedt (1957)). Recent work on calibration sets indicates that diatoms may be characterized further by even more specific salinity variables, such as assemblages common to sodium carbonate—bicarbonate, sodium chloride, or calcium magnesium carbonate—bicarbonate waters (Gasse, 1986). The biostratigraphy of other algal remains, such as charophyte oospores (Burne *et al.*, 1980; Chivas *et al.*, 1986), also may be important paleosalinity indicators, and certainly warrant further work.

Alhonen (1971) used the known salinity tolerances for diatoms in Finnish sediment cores to document the stages in the development of the Baltic Sea. Similarly, Kjemperud (1981) traced the post-glacial isolation from the sea of eight Norwegian basins by recording the shift from marine, to brackish, and finally to freshwater diatoms in his sediment cores. Coincident with the shift to a freshwater flora, he also noted the presence of green algae, such as *Pediastrum* and *Botryococcus* colonies — further evidence that the water salinity had declined markedly.

Osborne and Moss (1977) and Buzer (1981) interpreted the presence of brackish and marine diatoms in their lacustrine sediments as evidence for marine transgressions. In the latter study, changes in dinoflagellate cysts were noted. Tuchman *et al.* (1984) recorded salinification in a Michigan lake based on a diatom profile, but this was due to seepage from a salt storage facility adjacent to the lake.

Paleosalinity interpretations may also be used to infer past climates and water levels, as these variables are closely related, especially in closed basins. For example, Bradbury (1971) delineated 15 diatom zones in a 46 m core from Lake Texcoco (Mexico). He suggested that past changes in water level resulted in drastic salinity changes, which were reflected by the diatom assemblages. These data indicated that Lake Texcoco had fluctuated from such extremes as a deep, freshwater lake with low salinity, to a shallow, brackish marsh. Stoermer *et al.* (1971) believed that lake level fluctuations were related to salinity changes during the ontogeny of Devil's Lake's in North Dakota.

Nutrients/eutrophication. Many algal taxa are relatively stenotypic with respect to their trophic requirements. Although a large number of nutrients may potentially limit algal

growth, the vast majority of temperate lakes are phosphorus limited. Not surprising, most paleoecological studies dealing with eutrophication have centered on phosphorus dynamics.

A lake may be enriched with nutrients from a variety of sources, ranging from the steady, albeit usually slow release of nutrients from the terrestrial system (natural eutrophication), to the greatly accelerated nutrient input resulting from human activities (cultural eutrophication). The latter includes direct sources, such as sewage input, as well as more diffuse sources, such as agricultural runoff.

Virtually every type of eutrophication process has been studied in the paleoecological record. Diatoms are the most widely used indicators; however, in contrast to most of the previous examples, other algal markers have been used. This is at least partially because other groups, such as blue-green or green algae, are usually more competitive in eutrophic waters. Most of the work on the blue-green algae is via pigments (Engstrom *et al.*, 1985), whilst the green algae are usually studied by their morphological fossils (Cronberg, 1986a). Chrysophycean scales (Munch, 1980; Smol, 1980) and statospores (Carney and Sandgren, 1983; Smol, 1985; Rybak, 1986) are also sensitive indicators.

Past trophic changes, unrelated to human activity, usually involve the use of cores spanning a lake's entire postglacial sedimentary history. Attempts at estimating paleoproductivity was a driving force for much of the early paleolimnological work (Wetzel, 1970; Adams and Duthie, 1976). Often, the apparent trophic shifts are related to a complex of interdependent factors. For example, in Little Round Lake (Ontario) diatom and chrysophycean microfossils (Smol and Boucherle, 1985) and fossil pigments (Brown *et al.*, 1977; Daley *et al.*, 1977) showed that the lake's trophic status changed over the past 11,000 years. These changes were attributed to cold temperatures during the lake's early history, watershed processes regulating erosion and nutrient release, and fluctuations in the lake's meromictic stability. One marked eutrophication event, which occurred around 4,800 years ago, was attributed to the effects of the decimation of hemlock trees in the lake's catchment (Boucherle *et al.*, 1986); a major change in forest composition that was most likely caused by a pathogen (Davis, 1981). The algal species shifts recorded at the "hemlock decline" were similar to those noted in Little Round Lake's recent sediments, with the latter coinciding with the arrival of European settlers and land-clearance in the late-1800s (Smol *et al.*, 1983).

Stockner (1978) reviewed most of the early Canadian work on eutrophication. Space limitations preclude a comprehensive update of the large number of studies that have focussed on cultural eutrophication, except to note that the limnological repercussions of activities such as road construction (Smol and Dickman, 1981), agriculture (Bradbury, 1975; Brugam, 1981), and sewage inputs (Stockner and Benson, 1971) have all been considered. Multidisciplinary approaches are the most instructive (Engstrom *et al.*, 1985).

Of particular interest to many North Americans is the quality of the water in the Great Lakes. Such large and deep bodies of water may provide special challenges to paleoecologists, but environmental reconstructions are still possible. Changes in diatom, chrysophyte, and green algal populations have all been used to document recent eutrophication changes (*e.g.*, Duthie and Sreenivasa, 1971; Frederick, 1981; Harris and Vollenweider, 1982; Stoermer *et al.*, 1985). An offshoot of these studies has been the quantification of biogenic silica in sedimentary profiles as an estimate of past diatom and chrysophyte populations (Schelske *et al.*, 1983, 1986). Such techniques have been applied to smaller lake basins (Newberry and Schelske, 1986).

In North America, cultural eutrophication is usually restricted to about the last 150 years; in Europe, cultural disturbances may date back thousands of years. For example, Cronberg (1982, 1986) recorded stratigraphic changes in green and blue-green algal microfossils from Lake Vaxjösjön (Sweden). Originally, the lake was oligotrophic, but it increased in primary production around A.D. 600 as a result of human activity in its drainage. Other investigators have traced the limnological impact of slash and burn agriculture and peatland drainage (Simola, 1983), hemp soaking (Battarbee *et al.*, 1980), fertilization by sea birds (Moss, 1978, 1979), and the effects of forest fires (Bradbury, 1986).

Table 2 The pH classification system for diatoms, as set up by Hustedt, (1937-39)

alkalibiontic	occurring at pH values above 7.0
alkaliphilous	occurring at pH values about 7, with widest distribution >7
indifferent	occurring equally on both sides of pH = 7
acidophilous	occurring at pH values about 7, with widest distribution >7
acidobiontic	occurring at pH values under 7, with optimum distribution at pH = 5.5 and under

pH/acidification. In recent years, paleolimnological studies on lake acidification have earned much credibility for paleoecological research in general. Presently, a large number of lakes in North America and northern Europe are acidic and devoid of higher life forms, such as fish. Acidic precipitation, related to cultural activities such as the smelting of ores or the burning of coal, has been suspected of acidifying these lakes. Without historical water chemistry data, causative factors are difficult to identify. Because a large number of diatoms and mallomonadacean chrysophytes are characteristic of restricted pH regimes, their stratigraphic distribution in affected lake sediments can be used to trace the timing, rates, and patterns of lake acidification. Much progress has been made in demonstrating the predictive information contained in fossil assemblages (Battarbee, 1984; Charles and Norton, 1986; papers in Smol *et al.*, 1986). In many ways, acidification studies provide a stellar example of the practical application of paleoecological techniques to environmental problems.

Hustedt (1937-1939) was the first to clearly recognize the pH specificity of diatom taxa. He identified diatoms from over 650 samples from Java, Bali, and Sumatra, concluding that the water's hydrogen ion concentration (pH) had the greatest influence on the composition of assemblages. The five categories he delineated in his pH classification system continue to be used commonly today (Table 2).

Nygaard (1956) expanded Hustedt's system by attempting to quantify past changes in lakewater pH. Nygaard proposed a series of indices that related the relative abundances of taxa in the various Hustedt categories to lakewater pH. The next major step towards quantification was by Meriläinen (1967), who used linear regression analysis to establish quantitative relationships between logarithms of Nygaard's indices and measured pH values. In recent years, many statistical techniques have been applied to diatom calibration sets (*e.g.*, Charles, 1985; Anderson *et al.*, 1986; Huttunen and Meriläinen, 1986; Taylor, 1986), and the predictive tools available to paleoecologists continue to be refined and improved (Davis and Smol, 1986). Most of the literature again relates to diatoms (Battarbee, 1984), although chrysophyte scales increasingly are being used to enhance and supplement interpretations (Smol *et al.*, 1984; Smol, 1986; Steinberg and Hartmann, 1986; Hartmann and Steinberg, 1986).

Paleolimnological studies have now been completed or are in progress for numerous affected regions, and recent declines in lakewater pH have been inferred for many sites using diatoms and chrysophytes (Charles and Norton, 1986). Inferred pH changes in the recent sediments of the affected lakes are far greater than those recorded throughout the Holocene. For example, in Upper Wallface Pond (New York) the diatom inferred pH declined from above 7

to about 5 from *circa* 12,000 to 8,000 years ago. The diatom inferred pH then remained relatively stable throughout the Holocene (Whitehead *et al.*, 1986) until the recent acidification stage, which was of a larger magnitude than recorded previously (Charles *et al.*, 1986). Similar trends were inferred using chrysophyte scales (Christie and Smol, 1986). Such studies have identified naturally acidic sites (*e.g.*, Ford, 1984, 1986).

Battarbee *et al.* (1985) used paleolimnological techniques to assess competing hypotheses for the onset of lake acidification in British lakes. Acid precipitation, heathland regeneration, afforestation, and natural acidification were all considered. The acid precipitation hypothesis was substantiated.

Although most pH reconstructions are concerned with the effects of acid deposition, a number of other types of studies have been completed. For example, Fritz and Carlson (1982) and Brugam and Lusk (1986) traced the recovery of acid strip-mine lakes in the midwestern states following the cessation of acid mine inputs; McKee *et al.* (1987) studied the effects of uranium mining and milling on Quirke Lake (Ontario); and Renberg (1986) showed that the present acid (pH = 3) state of Lake Blamissusjön (Sweden) was related to the oxidation of sulphides from nearby marine sediments, which were exposed as a result of isostatic uplift a few hundred years ago.

As with other aspects of paleophycological work, continued refinements of pH calibrations add additional autecological data for indicators. For example, Davis *et al.* (1985) showed that diatom assemblages may be quantified with respect to the water's total organic carbon (TOC), which can be used as an estimate of lakewater colour. With acidification, precipitation of coloured organic compounds with acid-mobilized metals often occurs, thus explaining the clarity of most acidified lakes. Metal concentrations, whose solubilities often are enhanced by acidic waters, have been implicated as factors responsible for the composition of diatom and chrysophyte assemblages (Charles, 1986; Dixit, 1986; Gibson *et al.*, 1987); however, work on calibration sets that can quantify these relationships are still in progress.

Conclusions

Paleophycological work has greatly increased our understanding of past aquatic environments. I have only gleaned a few studies from a myriad of publications dealing with sedimentary deposits. In addition, fossil algae have been used to reconstruct events that are totally unrelated to stratigraphic sequences. For example, archaeologists can trace the origins of pottery by the diatoms present in the potter's clay (Jansma, 1984), or forensic scientists used diatoms isolated from human tissues to determine if drowning was the cause of death of eight Greenlanders, who died in the fifteenth century (Foged, 1982). The applications are almost endless.

There are, of course, problems. The autecologies of many algal taxa are still poorly known, and this seriously hampers many investigations. Continued work with calibration sets, and the application of new and more powerful statistical approaches, will improve environmental reconstructions and predictive capabilities. This cannot be accomplished without continued improvements in taxonomic precision — often the biggest source of error in paleoecological studies. Other problems, such as poor preservation of key indicators (Round, 1964), bioturbation of the sedimentary sequence (Davis, 1974), or spatial variability in microfossil distribution (Dixit and Evans, 1986), can seriously limit interpretations. These problems, however, are not unique to paleophycological work.

Clearly, the best approach is a multi-disciplinary one that uses the widest variety of indicators possible; therefore any redundancies in the data set will provide internal checks on interpretations, and a more holistic trajectory of the lake's ontogeny can be inferred. In North America, this was demonstrated decisively by the PIRLA (Paleoecological Investigation of Recent Lake Acidification) project, where a variety of botanical, zoological, chemical, and physical paleolimnological techniques, coupled with state-of-the-art multivariate statistical treatments, were applied to stratigraphic studies of lakes in acid sensitive areas (Charles and Whitehead, 1986). The results exemplify the power of integrated approaches (Charles *et al.*, 1986, 1987).

During the last decade, there has been a tremendous surge of interest in paleolimnology, with fossil algal work often taking a leading role. The transition from purely descriptive studies, to attempts at using "indicator species", to the calculation of indices, to the development of transfer functions using sophisticated statistical and computer techniques has occurred over a relatively short time. Similarly, with advances in the technological tools available to paleoecologists, such as electron microscopy or high pressure liquid chromatography (HPLC), the suite of potential indicators will continue to grow. As the number of qualified researchers increases, progress will accelerate at an even faster pace. As a result, we can expect to have a clearer understanding of ecological and environmental processes — both modern and in the distant past.

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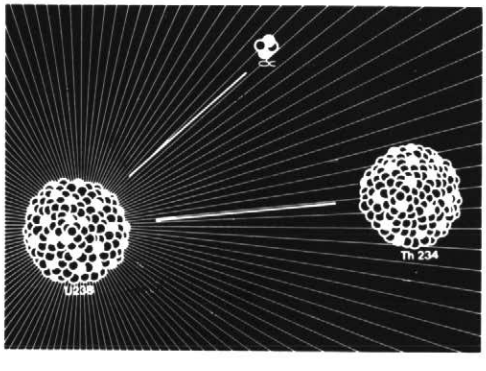

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