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Methods in Quaternary Ecology #6. Cladocera

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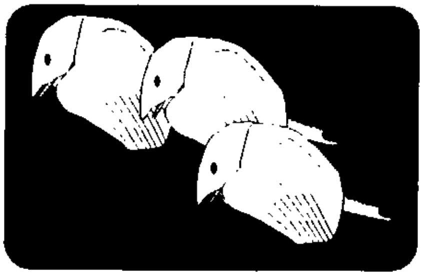
Article abstract

Cladocera are among the best represented groups of aquatic invertebrates that leave fossils in lake sediments. The skeletal fragments of Cladocera are abundant, can beidentified to species in most cases, and represent taxa from a variety of ecologicalniches in a lake. Unlike more conventional paleoecological indicators such as pollen orbeetles, Cladocera are not useful directly inpaleoclimatic reconstructions. Instead,Cladocera microfossii assemblages am uesiused to reconstruct past lacustrine environments, to investigate the effects of human disturbance (eutrophication, acidification, contaminants), and to assess long-term population and community changes. Improved understanding of the ecological tolerancesof living Cladocera, increased comparisons with analogue communities, and application of multivariate analytical methods will expand our interpretive capabilities for both modern and fossil assemblages. Once we understand how and why cladoceran communities responded to environment alevents in the past, we may be better able to predict the direction and magnitude of future change.



Methods in Quaternary Ecology #6. Cladocera

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Summary

Cladocera are among the best represented groups of aquatic invertebrates that leave fossils in lake sediments. The skeletal fragments of Cladocera are abundant, can be identified to species in most cases, and represent taxa from a variety of ecological niches in a lake. Unlike more conventional paleoecological indicators such as pollen or beetles, Cladocera are not useful directly in paleoclimatic reconstructions. Instead, Cladocera microfossil assemblages are best used to reconstruct past lacustrine environments, to investigate the effects of human disturbance (eutrophication, acidification, contaminants), and to assess long-term population and community changes. Improved understanding of the ecological tolerances of living Cladocera, increased comparisons with analogue communities, and application of multivariate analytical methods will expand our interpretive capabilities for both modern and fossil assemblages. Once we understand how and why cladoceran communities responded to environmental events in the past, we may be better able to predict the direction and magnitude of future change.

Introduction

The Cladocera, commonly known as water fleas, are a major component of the microcrustacean fauna in freshwater lakes and ponds. They occur in both the offshore (pelagic) regions, where the families Daphniidae and Bosminidae predominate, as well as in the shallow littoral zone where the diverse members of the family Chydoridae are most abundant. Among the chydorids, some species are found among submersed vegetation, whereas others more commonly live on sand, mud, or rocky substrata. In contrast to lakes, the microfauna of bogs are primarily macrothricids.

Cladocerans must moult their exoskeletons periodically in order to permit growth in size. This process occurs several times during the lifetime of each individual. The exoskeletons are chitin, a remarkable chemically inert material which preserves details of shell sculpturing, setae (or their attachment sites), as well as other features critical to species identification. Most fragments can be identified to species or at least can be assigned to a species group. These exoskeletons accumulate and become incorporated in the sediments. All exoskeletons (except the very earliest ones) produced by an individual appear to have an equal chance of being preserved.

Cladoceran exoskeletons are not preserved intact, but instead disarticulate into their component parts: head-shield, carapace, postabdomen, claws, antennules, mandibles, ephippia (Figure 1, 2). The majority of skeletal remains consist of members of the cladoceran families Bosminidae and Chydoridae. Other planktonic Cladocera are poorly preserved and are encountered rarely as fossils in the sediments except as post-abdominal claws, ephippia, and mandibles. However, in an extremely detailed study of Cladocera remains in surficial sediments of several Finnish lakes, Cotten (1985) identified a greatly expanded repertoire of fragments from other families.

This paper demonstrates the utility of Cladocera microfossil remains in the context of Canadian or North American research progress. Specifically, the intent is (a) to review briefly the historical development of the field in North America, (b) to describe the nature and occurrence of microfossils in lakes, and the methods of preparation and identification of remains, (c) to suggest how cladoceran fossils can provide a basis for inferring or reconstructing paleolimnological or paleoecological events, for expanding our biogeographical database, and for theoretical studies in community structure, development, and ecology, and lastly, (d) to provide suggestions for additional work in the area of cladoceran microfossil research to extend their usefulness in Quaternary paleoecology.

Historical Development

Examination of Quaternary fossil Cladocera began in the late 19th century in Europe, but not until the 1900s in North America. The majority of early literature records (see Frey, 1964) simply report the occurrence of a few Cladocera taxa with no attempt to reconstruct the entire cladoceran community or interpret the data in an ecological context. Deevey (1942) carried out the first quantitative study of animal microfossils in North America. The abundantly represented *Bosmina* exoskeletons proved useful in analyzing the developmental history of Linsley Pond (Deevey, 1942; Vallentyne and Swabey, 1955) and Rogers Lake (Deevey, 1964, 1969). These studies stimulated a number of fundamental investigations of accumulation of remains and sedimentation rate, and internal transport of fossils within a basin (Livingstone, 1957; Livingstone *et al.*, 1958).

A major break-through in cladoceran microfossil studies came with Frey's (1959) study of the headpores on the headshields of the chydorid Cladocera; the well-preserved headshields could now be identified to species. Goulden and Frey (1963) demonstrated that the 2 subgenera of the Bosminidae could be distinguished on the basis of the location of the headpores on the headshields. As the chydorid and bosminid remains are typically the most abundant in the sediments, this new diagnostic tool greatly improved the resolution of microfossil studies. Since those landmark studies, cladoceran microfossil evidence has been used to examine past ecological development of lakes in many parts of the world: temperate zone (Goulden, 1964; Megard, 1964; Harmsworth, 1968; DeCosta, 1968; Hofmann, 1978, 1986), tropical regions (Goulden, 1966a,b; Megard, 1967), and the Arctic (Bradbury and Whiteside, 1980).

One of the first systematic studies of fossil Cladocera in Canada was by Sreenivasa (1973). More recent investigations include: Warner *et al.* (1984), Hann and Karrow (1984), Smol and Boucherle (1985), Boucherle *et al.* (1986), and Hann and Warner (1987).

Field Sampling

The abundance and species composition of the cladoceran community vary greatly both seasonally and in different habitats within a lake. Fortunately, the remains of species from different microhabitats in the littoral zone, occurring in all seasons, appear to be integrated (to varying degrees) with remains of planktonic taxa in the deep-water sedimentary record (Frey, 1960; Mueller, 1964; Boucherle, 1982) as a consequence of redeposition of littoral remains offshore. Thus, the entire chydorid fauna of the lake will be represented in the sediments, and percentage species composition of the community can be determined by analyzing the microfossils in a sediment core (Goulden, 1969a).

The extent of integration of littoral and pelagic remains is a function of distance from shore and water depth (Mueller, 1964; Boucherle, 1982). Microfossil remains of littoral species are well represented in the littoral sediments, constituting a rapidly declining proportion of total cladoceran fossils with increasing distance from shore. In contrast, remains of planktonic species are rare in shallow-water sediments, and increase in abundance offshore. In some lakes, they appear to form a "concentration zone" at the top of the hypolimnion (Mueller, 1964), perhaps a function of lake morphometry. Nevertheless, this distributional feature must be taken into consideration in lakes where water levels have fluctuated, and where the concentration zone may periodically be represented in the core. Although the concentration of remains in the surficial sediment does vary across a lake basin, the percentage species composition of cladoceran remains is close to uniform in the deep-water sediments (Boucherle, 1982).

The design of strategies for sampling (both spatial and stratigraphic) must consider the mechanisms that affect sediment (and microfossil) redistribution as governed by basin morphometry. These include: changes in lake level, thermal stratification, sediment focusing, bioturbation, diagenesis, and resuspension (Hakanson, 1977; Davis *et al.*, 1984; Hilton, 1985; Dearing, 1986). In most instances, these difficulties have been ignored, and one central reference core (assumed to represent the integrated sedimentary record of the lake) has been obtained from the deepest part of a lake. This approach may be adequate in broad-scale regional comparisons of lakes. However, where the goal of the research is a more detailed understanding of the events within the catchment and waterbody, transects of cores or even a stratified or systematic design of core samples will be required to represent adequately the depositional environments. Methods for examining multiple-core correlation within time-stratigraphic units are available (Birks, 1986; Dearing, 1986), but have not been applied to cladoceran microfossil studies.

Coring of sediments, especially annually laminated sediments requires care to retrieve the stratigraphic sequences intact and with minimal distortion. Various types of freeze-corers have been designed for recent sediments (Huttunen and Meriläinen, 1978; Wright, 1980; Renberg, 1981). Gravity or piston corers are used to obtain longer sediment cores in lakes (Aaby and Digerfeldt, 1986).

Laboratory Techniques and Identification

Concentrations of cladoceran microfossils in lake sediment may vary from less than 100 to several hundred thousand per cm^3. To estimate the number of exuviae per cm^3 of fresh sediment for each species present at each level, different amounts of sediment must be processed according to the microfossil densities. The volumes assessed by preliminary determinations may range from as little as 1 cm^3 in gyttja to 10-20 cm^3 per stratigraphic level in mineral sediments.

Unnecessarily harsh chemical treatment is to be avoided as it may increase fragmentation or degradation of remains and make identification difficult. Frey (1986b) has summarized various treatments needed for different types of sediments. The main steps include: gentle heating and stirring of the

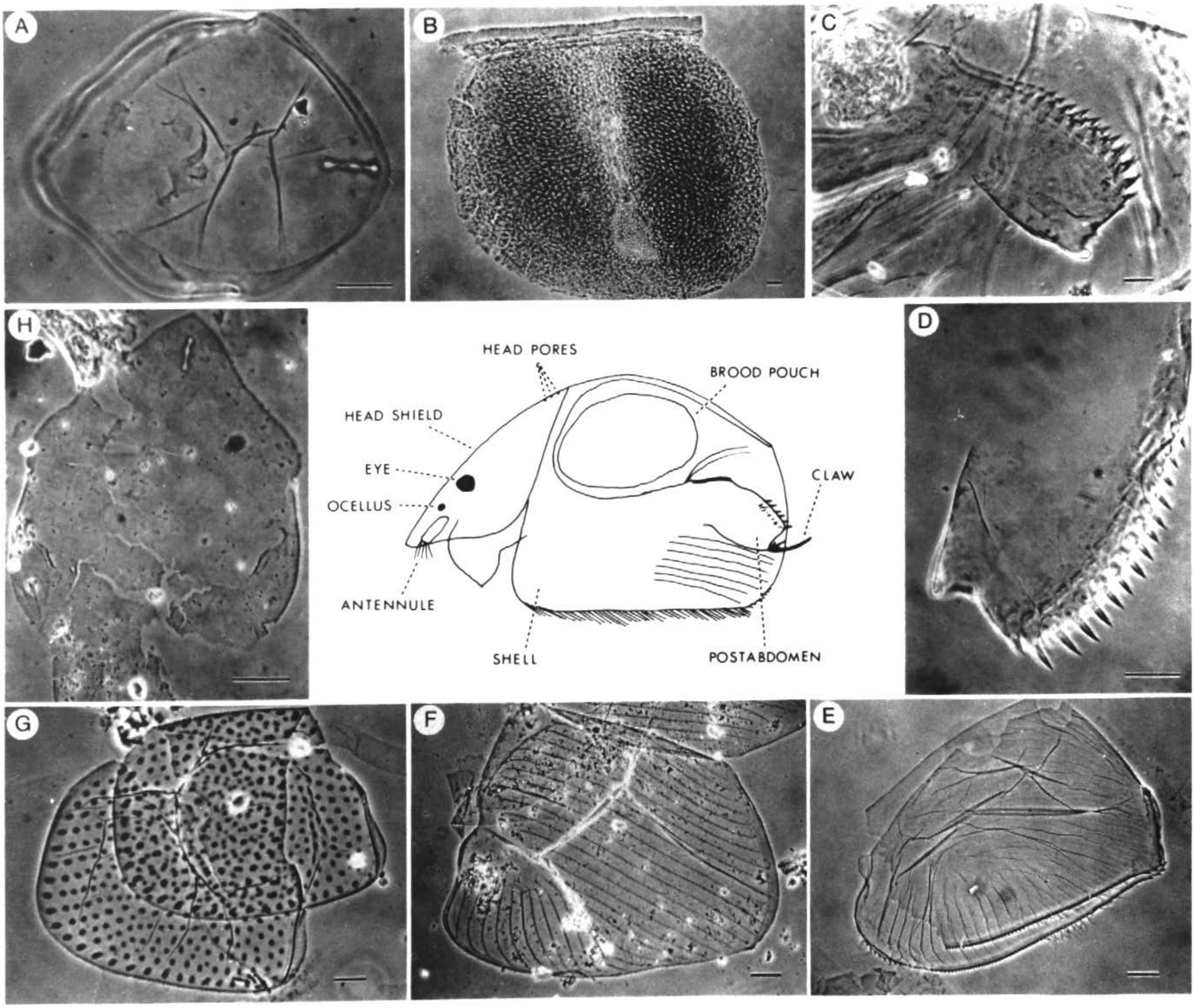

Figure 1 *Selected fossil remains of Cladocera from the Don and Scarborough Formations at Toronto, Ontario. All scale bars represent* 50 μm. *See Hann and Karrow (1984) for details.* **(a)** Alona circumfimbriata, *headshield;* **(b)** Daphnia *sp., ephippium;* **(c)** Alona quadrangularis, *postabdomen;* **(d)** Alona quadrangularis, *postabdomen;* **(e)** Pleuroxus denticulatus, *carapace;* **(f)** Acroperus *cf.* harpae, *carapace;* **(g)** Alona rustica, *carapace;* **(h)** Alona quadrangularis, *headshield.*

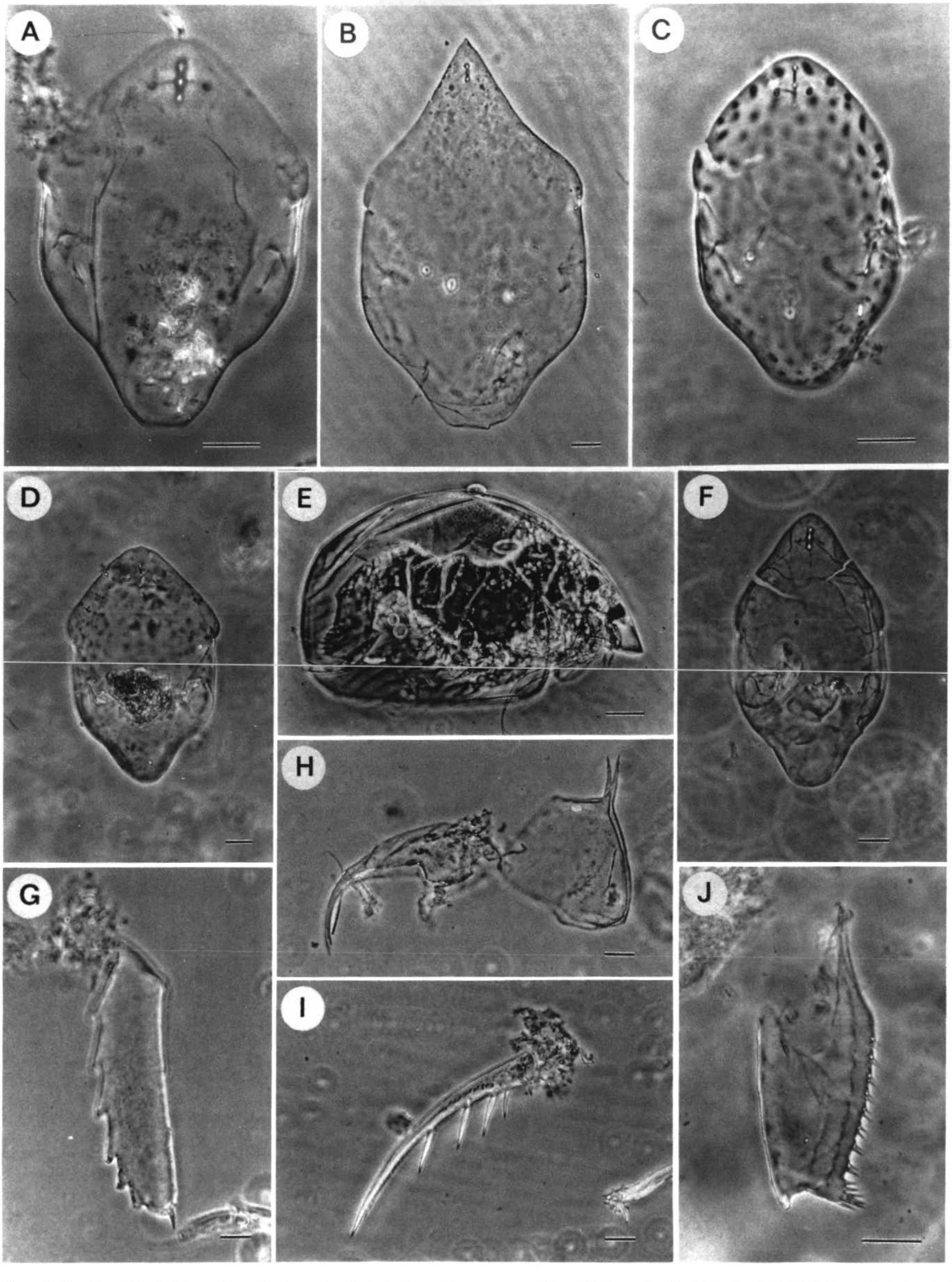

Figure 2 *Fossil remains of Cladocera from Manitouwadge, Ontario. All scale bars represent* 50 μm. **(a)** Alona cirumfimbriata, *headshield;* **(b)** Alona affinis, *headshield;* **(c)** Alona rustica, *headshield;* **(d)** Alona costata, *headshield;* **(e)** *Alona lapdicola, whole animal;* **(f)** Alona quadrangularis, *headshield,* **(g)** Sida crystallina, *antennal segment;* **(h)** Bosmina longirostris, *headshield and carapace;* **(i)** Sida crystallina, *postabdominal claw;* **(b)** Pleuroxus denticulatus, *postabdomen.*

sediment in 10% KOH, followed by careful sieving through a 37 μm mesh sieve to retain the smallest exoskeletal pieces. The residue retained on the screen is transferred to a vial and topped up to a known volume, with a few drops of formalin or alcohol added as a preservative.

To prepare quantitative slides, volumetric aliquots of the residue (typically 0.05 mL) are transferred to microscope slides using a precision pipette, with glycerin jelly as the mounting medium, lightly stained with lignin pink.

Identification of cladoceran microfossils is greatly assisted by a reference collection of slides of whole animals and moulted exoskeletons from the region under study. Literature sources useful for identification of North American material include Brooks (1959) and Pennak (1978). It is essential to supplement these sources with original literature descriptions of the many taxa not included therein or inadequately illustrated (Hann, 1981, 1982; Hann and Chengalath, 1981; Chengalath and Hann, 1981a,b; Frey, 1980, 1987). In addition, it has been clearly demonstrated that several chydorid species do not have cosmopolitan distributions, as previously assumed, and this pattern of more restricted distributions of species is undoubtedly prevalent (Frey, 1980; Michael and Frey, 1983, 1984). Hence, accurate identifications of taxa may often require use of primary species descriptions, and verification by taxonomic experts, familiar with the local fauna.

Numbers of each exoskeletal fragment (headshield, carapace, postabdomen, claw) are tabulated for each species. Of the several methods available for assessing population size for each taxon (see Frey, 1986b), a common choice is to use the largest category count as the estimate of species abundance at each level for each species. These numbers can be presented as (1) percentage that each species constitutes of the total at each level, (2) concentration (numbers per gram of dry sediment) or (3) accumulation rate (remains per $\text{cm}^3 \times$ sedimentation rate (cm/yr)).

The most common graphical representation of data is a relative frequency diagram for the most abundant taxa (Figure 3), and a plot of percentage littoral *versus* pelagic taxa throughout the stratigraphic record. Species diversity, typically estimated by the Shannon-Wiener diversity index, and equitability (Lloyd and Ghelardi, 1964) are also calculated for each level. If adequate dating of the sediment sequence is available, presentation of abundance diagrams constructed using all three computation methods listed above provides the most comprehensive basis for analysis. Each method has advantages and disadvantages in interpretation of the lacustrine sedimentary record (Brugam and Speziale, 1983; Binford, 1986). Renewed attention must be focussed on critical examination of statistical and analytical methods applied to fossil Cladocera communities (see Whiteside and Swindoll, 1988).

Uses and Applications in Paleoecology

A wide range of problems can be addressed using cladoceran microfossil assemblages: (a) paleolimnological and paleoecological reconstructions, (b) comparative regional limnology, (c) theoretical community ecology, and (d) biogeography (Frey, 1986a).

Cladoceran microfossil evidence provides a primary tool for the reconstruction of past lacustrine environments, from interglacial periods (Frey, 1962; Hann and Karrow, 1984) through to historical time (Kerfoot, 1974; Birks *et al.*, 1976; Brugam, 1978). In the only two studies of cladoceran microfossils in interglacial sediments, the Eemian in Europe (Frey, 1962) and the Sangamonian in North America (Hann and Karrow, 1984), no morphological change in any cladoceran species was detected between interglacial representatives and modern counterparts. Similarly, there was stability in species composition of the assemblage and the relative abundance of taxa was comparable to that in modern communities. Given this evidence of morphological and ecological uniformity in the

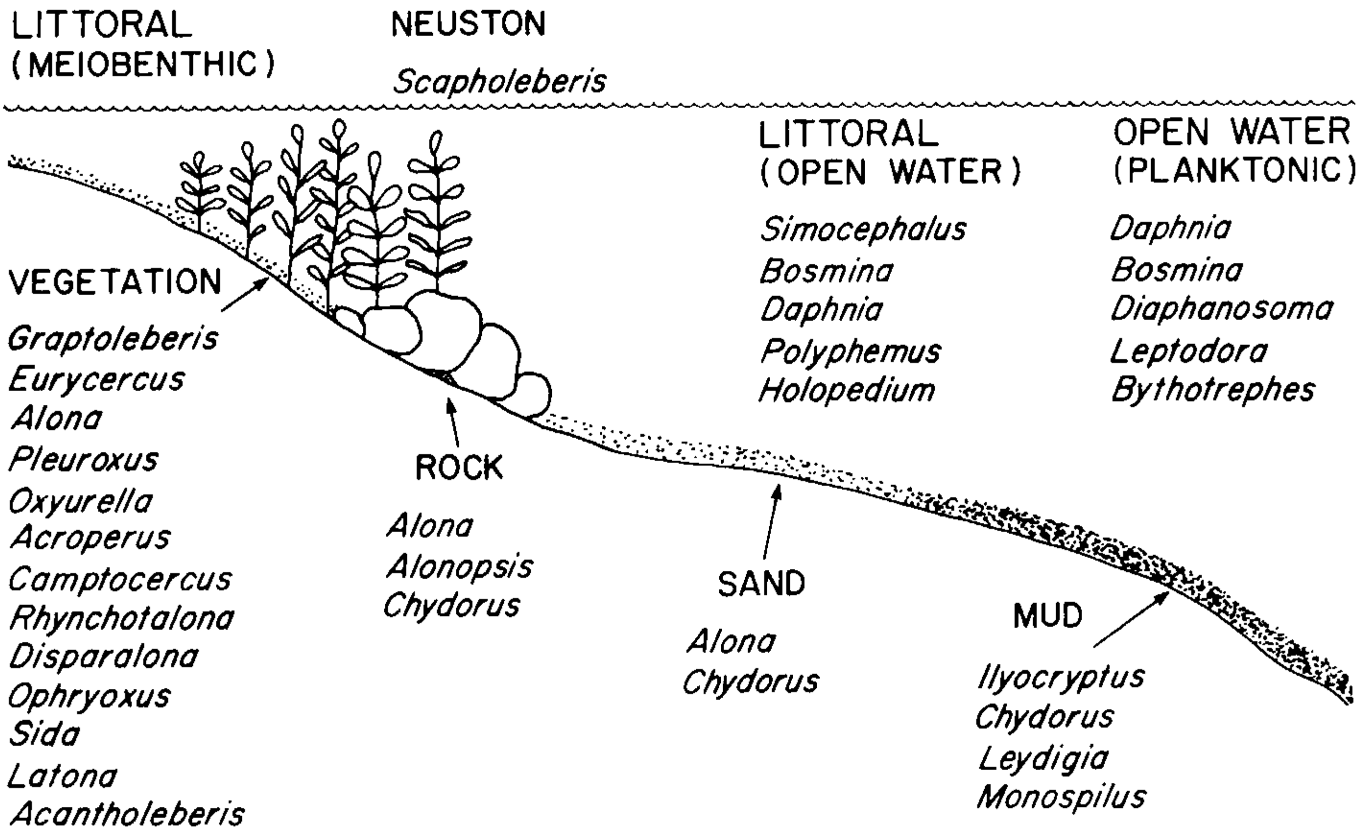

Figure 3 *Ecological niches occupied by Cladocera include: the pelagic zone with planktonic genera, the shallow water littoral zone with planktonic genera, and the littoral zone with meiobenthic genera segregated into several subhabits: vegetation, rock, sand, mud, and the neuston.*

cladoceran community, at least since the last interglaciation, modern ecological data can be validly used for paleoecological reconstructions within this time period.

Cladocerans inhabit diverse habitats, ranging from the littoral to the limnetic zone, and among vegetation, on rocks, sand, and other substrata in the littoral zone (Figure 4). By distinguishing the remains of littoral taxa from those that inhabited the limnetic zone of a lake, a planktonic/littoral (P:L) ratio can be determined. This reflects, in part, the relative volumes of the lake that have contributed remains to the sediments, and can be used to assess fluctuations in lake levels (Mueller, 1964; Alhonen, 1970) and, perhaps of greater significance, changes in littoral area providing habitat suitable for development of the littoral fauna. Chydorid Cladocera can be subdivided into vegetation- and substrate-dwelling groups (Quade, 1969; Whiteside, 1974; Whiteside *et al.*, 1978). The majority of chydorid species which have been carefully investigated are quite habitat-specific; for example, *Alona borealis* is typically found only in littoral habitats with sandy substrate, with little vegetation, and in nutrient-poor waters (Chengalath and Hann, 1981a). Therefore, the composition of the cladoceran assemblage recovered from the sediments can reveal a great deal about the lacustrine environment that existed in the past.

Do cladoceran microfossil assemblages reflect regional conditions in the watershed or local limnological conditions? Unlike the pollen record in lakes which is usually an amalgam from sources within the local catchment as well as from long distances, the Cladocera assemblage represents the product of the immediate aquatic environment, which greatly buffers the direct impact of climatic change. If cores can be obtained from a number of lakes in a region, it may be possible to separate the regional influences from the strictly local ones. Goulden (1964) and Harmsworth (1968) studied two small lakes in the English Lake District and found similar patterns of cladoceran relative abundance and distribution in time, suggesting parallel developmental histories. However, planktonic Cladocera predominated at EsthwaiteWater, while littoral forms were dominant at Blelham Tarn, probably a consequence of differing lake size and littoral zone area (Harmsworth, 1968). The overall similarity of the littoral chydorid community argues for regionally similar limnological parameters and composition of the macrophyte community, governed in turn by regional climatic impact on the watershed.

The abrupt decline in hemlock in eastern North America 4800 years ago (Webb, 1982; Allison *et al.*, 1986) provides another example of a broad scale environmental factor impinging upon the biota of lakes. Boucherle *et al.* (1986) studied the effects of the loss of hemlock from the watersheds of three lakes in southern Ontario. Although each lake experienced a change in trophic status, the response of the cladoceran community was unique in each lake, the differences probably related to lake size and the ratio of littoral to pelagic zone volume.

Thus, for two very different regional environmental factors, climate and hemlock decline, the evidence suggests that a hierarchical approach to interpreting the influence of environmental factors, as recommended by Hann and Warner (1987) and Warner and Hann (1987), will provide the most parsimonious result. This involves taking into consideration regional, local, and microhabitat characteristics, in turn, as contributing to the overall variation in community structure and composition.

Inference of paleotemperatures from cladoceran assemblages has drawn on studies relating present latitudinal distributions of Cladocera with climatic regimes (DeCosta, 1964; Harmsworth, 1968), classifying species as arctic, north or south temperate, or eurytopic. However, because of taxonomic difficulties (*e.g.*, north-south sibling species), geographic affinities are subject to considerable misrepresentation and must be approached with caution. Many of the more

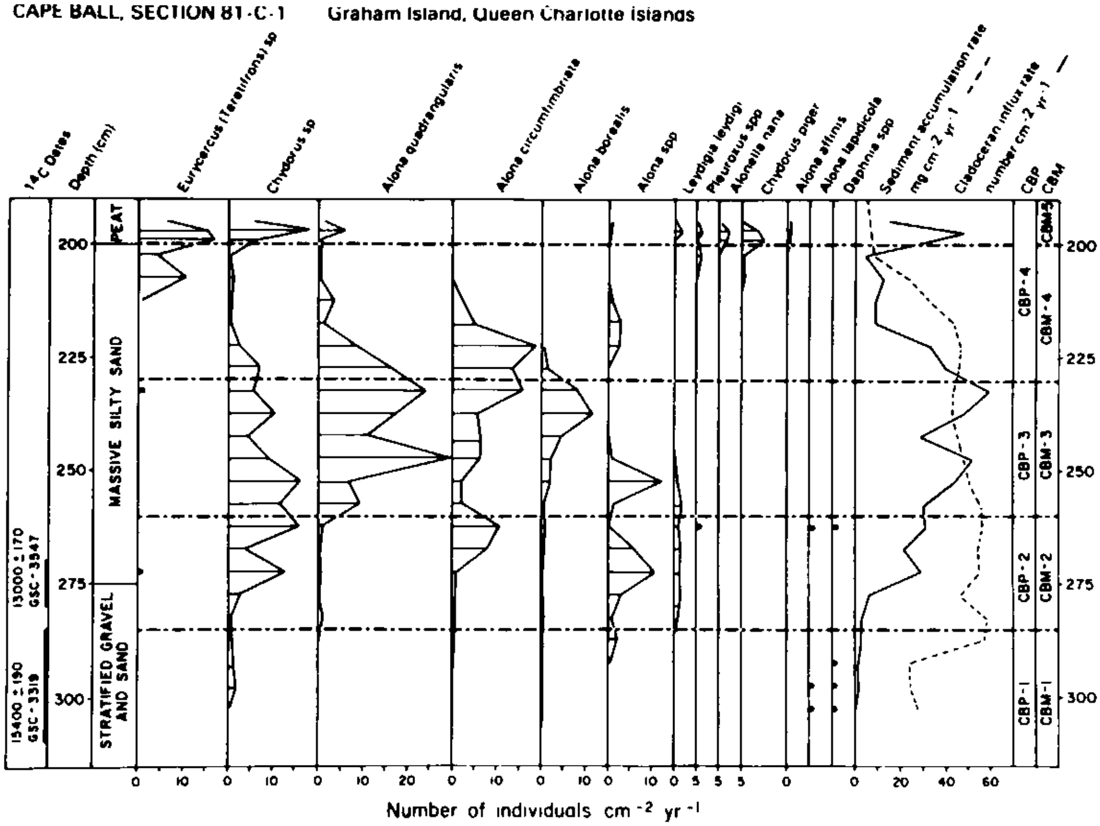

Figure 4 *Representative microfossil Cladocera diagram illustrating species accumulation rates, bulk sediment accumulation rates, and local pollen and macrofossil zones provided for comparison. Only those taxa comprising at least 5% of the total cladoceran number in one or more levels are included in the diagram. (After Hann and Warner, 1987).*

common taxa, as currently defined, have broad distributions and, thus, are not useful in climatic interpretations.

Species diversity as well as species composition change during development of a community through the sedimentary sequence. To interpret these patterns, comparison with modern analogue communities is a useful approach. As Whiteside (1970) pioneered application of the technique to chydorid assemblages, his study will be described in some detail. Whiteside (1970) examined assemblages of chydorid remains from surficial mud samples derived from 77 Danish lakes for which extensive limnological data were available. The lakes could be classified subjectively into 3 types (clear-water lakes, pond and bog lakes, and culturally disturbed clear water lakes), the groupings subsequently validated using multiple discriminant analysis of the limnological parameters. Analysis of correlations between individual chydorid species abundances in the surficial assemblages and limnological parameters revealed strong negative correlations between many species and alkalinity, pH, conductivity, and transparency.

More useful than relationships for individual species are those characterizing species assemblages. Multiple discriminant analysis (MDA) of average relative abundances (percentages) of microfossil chydorid species in each lake type provided a measure of the importance of species in defining a lake type by species. Generally, there was a good relationship between species groups and lake types, lending support to the hypothesis that chydorid assemblages can be used to reconstruct limnological conditions in paleoecological studies.

Whiteside (1970) next tested his modern analogue data from surficial chydorid assemblages against assemblages from cores of two Danish lakes, and attempted to infer past lake conditions. In one instance, Esrom Sø, use of the modern analogue communities as delimited by MDA was useful because the major factors affecting relative abundances in the past had been included in the original construction of the analogues. In Grane Langsø, in contrast, the analysis was less successful because the impact of climate during the developmental history of the lake was considerable, a factor which had not been incorporated into the initial survey data as the lakes were all within close geographic proximity. Hence, "the more accurate an investigator pinpoints the important factors (abiotic and biotic) affecting the distribution and abundance of organisms (and uses these factors to generate the discriminant function), the more accurate will be the description of that organism's niche" (Whiteside, 1970, p. 114), and consequently, the stronger the basis for interpretation of paleoassemblages (Whiteside and Swindoll, 1988).

Synerholm (1979) analyzed microfossil chydorid assemblages from surficial sediments in 32 lakes in Minnesota and North Dakota, on a transect from acidic, low conductivity waters in coniferous forest to circum-neutral pH waters in deciduous forest to alkaline waters with high dissolved ion concentration on the prairies. Each lake type had some characteristic chydorid species, although several species were generalists, occurring in all lake types. The strong negative correlation between chydorid species diversity and specific conductance found in this study supports the relationship detected by Whiteside (1970) between chydorid abundance and diversity and oligotrophic-type lakes of low productivity. Similarly, Whiteside and Harmsworth (1967) found a positive relationship between diversity and water transparency in 20 lakes in Denmark and in 14 lakes in northern Indiana, and an inverse relationship between species diversity and primary productivity.

Crisman (1980) examined subtropical chydorid assemblages in 52 lakes in Florida. The lakes were separated into three groups on the basis of four limnological parameters (phosphorus, conductivity, alkalinity, and Secchi disk transparency). Microfossil chydorid assemblages extracted from surficial sediment samples from the lakes were expressed as percentage representation by each species in each lake. Principal components analysis (R-mode) was used to examine the associations among individual chydorid species, and to define the limnological parameters controlling the groupings. The chydorid fauna was separated into soft-water and hard-water assemblages. Although both Synerholm (1979) and Crisman (1980) established the correlations between chydorid species and limnological parameters, neither attempted to use their analogues to interpret and reconstruct past lake development or examine chydorid community changes in their region.

Changes in species diversity have often been attributed to change in trophic status of the waterbody. Increased productivity of algae is typically associated with reduced transparency and decreased diversity of chydorid Cladocera. Other explanations must be considered, however, as emphasized by Whiteside (1983). For instance, increased overall productivity of the lake may be largely attributable to higher littoral zone productivity, primarily macrophytes. Thus, the available habitat for chydorids should increase, as would species diversity. In those few studies where remains of both cladocerans and aquatic macrophytes have been analyzed (Warner *et al.*, 1984; Hann and Warner, 1987), correlations of species diversity and overall concentration (remains/cm^3) or accumulation rates for the two groups lend support to this hypothesis.

The interaction of climate, morphoedaphic factors, and lake ontogeny with cladoceran community composition is complex. Only through incorporation of a variety of complementary indicator groups into the matrix, along with the Cladocera microfossils, can we hope to tease apart major controlling factors from significant interactions.

The species replacement of *Bosmina longispina* by *B. longirostris* is frequently considered indicative of eutrophication of the lake (Crisman and Whitehead, 1978; Hofmann, 1978). However, a change in dominant predators, for example, from planktivorous fish to invertebrate predators, could lead to the same replacement of a large bosminid by a smaller one. Kerfoot (1974, 1981) has demonstrated that a shift in major predators concurrent with nutrient enrichment could explain the changes in *Bosmina* morphology during the post-glacial history of Frains Lake, Michigan. The planktonic Cladocera community in Lake Harriet, Minnesota also responded primarily to change in predators rather than to trophic change (Brugam and Speziale, 1983). Changes in size structure and cladoceran community composition in Peter-Paul Lake, Michigan have been attributed to different predation intensity in two halves of the lake subject to contrasting experimental manipulation (Kitchell and Kitchell, 1980). Nilssen (1978) has summarized the major influence of vertebrate and invertebrate predators on the zooplankton community as recorded in the microfossil remains.

The impact of human disturbance can also be read in the recent microfossil record. The acidification history of lakes has been studied using short cores from lakes in sensitive areas and examining the response of the cladoceran assemblages (Paterson, 1985). The modern analogue approach was employed to examine the relationship between pH and subfossil chydorid assemblages in surficial sediment samples from 37 lakes and a core from each of 3 lakes in Maine (Brakke *et al.*, 1984). A positive relationship was observed between species richness, diversity, and pH. Using a cluster analysis technique, lakes with low pH tended to cluster together on the basis of their cladoceran community, as did high- and low-altitude lakes. In the cores, chydorid assemblages were analyzed and separation of clusters suggested levels at which pH change was likely to have occurred.

Cotten (1985) examined surficial sediment samples for cladoceran remains from 46 Finnish lakes and recovered 71 taxa belonging to 9 families. The relationship between lake parameters and cladoceran assemblages, assessed using a multivariate ordination technique, detrended correspondence analysis, revealed 5 lake types with distinctive cladoceran communities. Nutrient conditions, pH, and transparency were the chief lake discriminators. Transfer functions were developed to permit reconstruction of past lake conditions based on cladoceran remains recovered from lake sediments.

The chydorid Cladocera have been described as a taxocene, displaying taxonomic and ecological homogeneity (Deevey, 1969). Theoretical community ecology has gained from several pioneering studies of temporal variation in community structure of the chydorid fossil taxocene. Goulden (1966a,b, 1969a,b,c) defined three phases of development of the community: initially, diversity increases as species immigrate into a new habitat, then species numbers stabilize and equitability, or evenness, increases. Finally, species number, or richness, may increase slightly as additional rare species colonize the habitat. At this point in development, the chydorid community appears to fit the Type I or broken-stick model of MacArthur (1957), or any one of several other related distributions (Binford *et al.*, 1983). A taxocene will approach this condition gradually, as demonstrated for a variety of organisms (Tsukada, 1967; Goulden, 1969a; Deevey, 1969) in lakes around the world. Perturbations in species diversity or equitability may signal climatic change (Goulden, 1966a), catastrophic natural disturbances such as nearby volcanic eruptions (Tsukada, 1967), fire (Baas and Boucherle, 1984), eutrophication (Bradbury and Megard, 1972; Boucherle and Zullig, 1983; Brugam and Speziale, 1983; Hofmann, 1986), agriculture (Goulden, 1966b), or other human disturbances. As a consequence of disturbance, one species tends to become super-abundant and the others rare. When the disturbance ceases, the community readjusts and, depending upon the severity of the perturbation, may or may not return to the initial structure of the community. Examination of the effects of stress on the cladoceran community and subsequent recovery, as preserved and integrated in the sediments, may provide an excellent environmental monitoring tool that is only beginning to be refined.

Cladoceran remains have been used less extensively than plants or beetles to address biogeographic problems. In part, this stems from the long-held presumption of cosmopolitan distributions of most Cladocera. As the endemism of each continental faunule is recognized and documented, the utility of the Cladocera in testing vicariance theory or in examining colonization history is greatly enhanced.

Investigation of colonization patterns and timing of species invasions, governed by glacial advances and retreats, might be accomplished using cladoceran remains as suggested by Frey (1986a). In a study of cladoceran remains from a site on the Queen Charlotte Islands, British Columbia (Hann and Warner, 1987), a relatively high proportion of remains were recovered which represented unknown species, especially in the oldest sediments. Attempts are on-going to determine whether these unknown taxa were colonists from a refugium in Alaska or from the southern coastal regions, both areas for which the modern Cladocera are poorly studied.

Remains in the sediments may be used to define past ranges of well-delimited species. In particular, the presumed southward migration of northern taxa into southern United States at the time of the last glaciations may be detectable, or conversely, the northward expansion of ranges of southern taxa (Frey, 1986a). However, the occurrence of north-south sibling species pairs in several chydorid species (Hann, 1982; Shan and Frey, 1983), whose remains cannot be differentiated, complicates this historical sedimentary approach to colonization history.

In any paleoecological reconstruction, one must deal with differential preservation and distortions that may bias the interpretation. Deevey (1964) examined the fossilization process for selected zooplankton, finding that *Bosmina* exuviae fossilize well, in contrast to those of copepods which decompose rapidly.

Typically, the *Bosmina* headshield: carapace ratio is roughly equal to one, but can become distorted in zones of secondary deposition where breakage generally increases (Vallentyne and Swabey, 1955). No studies have systematically examined headshield:carapace ratios in chydorid remains, ephippia:parthenogenetic carapace ratios, nor other instances of marked distortion in representation of exoskeletal components. However, Deevey (1955) reported changes in frequency of ephippia of the overwhelmingly dominant *Pleuroxus hastirostris* in Pyramid Valley, New Zealand, perhaps in response to environmental stress. Goulden (1966a) concluded that changing ratios of carapaces of parthenogenetic females: ephippial females (of all Cladocera considered together) reflected response to fluctuations in water level.

Evidence has accrued suggesting that exuviae from early instars of bosminids and chydorids do not fossilize as well as those from later instars (Kerfoot, 1974; Culver *et al.*, 1981; Frey and Hann, 1985). Methods which take into account this selective preservation of exuviae are being developed (Hann, unpublished) prior to an attempt to estimate biomass of various components of the taxocene. Then it may be possible to evaluate past productivity of cladoceran species, and to correlate productivity of different trophic levels, as first suggested by Frey (1960).

Changes in species richness, diversity and the planktonic/littoral ratio in the sedimentary record are frequently used to assist paleoenvironmental reconstructions. In sediment stratigraphies where rates of sedimentation are relatively constant, diversity measures are representative of community structure. However, in recent sediment sequences particularly, patterns in diversity indices can be severely distorted by variable sedimentation rates (Smol, 1981). Although parallel responses in lakes to climate and regional geology can be useful in deriving empirical relationships (Duarte *et al.*, 1986), differences among lake histories can be indicative of unique events in a watershed or in the lake itself, *e.g.*, meromixis. As meromictic lakes often have annually laminated sediments, they are especially useful in paleoecological studies (Culver *et al.*, 1981; Smol and Boucherle, 1985).

Though Cladocera are useful in approaching a diversity of major problems in Quaternary ecology, nevertheless, there are several limitations that require refinement in their application to Quaternary problems: (1) There is a serious lack of ecological data for modern species, particularly relating to tolerances to physical, chemical and biotic parameters. Until such information becomes available, our ability to extrapolate from modern conditions of existence of a species into past analogous occurrence of the species is severely limited. (2) There do not appear to be well-defined "indicator" species in the Cladocera, although this may change as we recognize more and more species with clearly defined ranges, a radical reversal of the previously popular idea of globally distributed species (Frey, 1982, 1986a). Discrepancies in the literature regarding tolerance to various environmental factors for a given species may be coincidentally resolved. (3) Too little is known about distribution of cladoceran species generally, so that if a species occurs in small numbers in the fossil record, we cannot determine whether it is a rare species that is nonetheless well-established in the region, or if it is a broadly distributed common species that is infrequent at this locality because it is at the edge of its range. Therefore, ranges need to be defined in terms of relative abundance as well as occurrence (presence/absence).

Future Directions

To more fully realize the potential of Cladocera microfossil communities in Quaternary paleoecology, new approaches until now applied primarily to pollen analysis (Prentice, 1986) are necessary, particularly in the area of data analysis and interpretation. Whiteside's (1970) use of multiple discriminant analysis proved useful in defining axes upon which predetermined types of lakes could be differentiated. Chydorid assemblages could then be segregated into parallel groups. Cluster analysis, in attempting to define the groups themselves, has been used to distinguish pH-defined clusters of chydorid assemblages (Brakke *et al.*, 1984; Cotten, 1985; Paterson, 1985). Boucherle (1982) used a stratigraphically constrained clustering algorithm to delimit cladoceran zones, akin to the standard pollen zonation. This method provides an objective, quantitative approach to assessing change in the microfossil assemblage and merits further attention.

The use of modern analogue communities for comparison with microfossil assemblages must be expanded to encompass a broader range of habitat types. For a given region, if a catalogue of analogue communities are described from surficial sediment samples, then transfer functions developed using multiple discriminant analysis or detrended correspondence analysis (Gauch, 1982), can be used on down-core microfossil assemblages to make inferences regarding past environmental conditions (Cotten, 1985).

The absence of clear-cut indicator species of Cladocera has focussed attention on evaluating changes in the entire community. However, individual taxa of Cladocera may prove to be useful as pollution indicators. Deformities have been documented in a variety of chydorid species; in fact, some species have been described based on single deformed specimens. Morphological deformities in chironomids have been shown to have great potential as a screening technique for detection and assessment of contaminants in aquatic ecosystems (Warwick, 1985). The chydorids, too, may act as sophisticated environmental sensors, perhaps complementary to the chironomids, as the sediment-associated chydorids could be affected predominantly by sediment-bound contaminants, in contrast to species associated with the macrophytes or entirely free-swimming that would be influenced more strongly by contaminants in the water column. If particular contaminants could be shown to cause specific types of deformities or species-specific responses, the historical incidence of environmental contamination could be traced using the chydorid microfossil record.

Finally, preliminary attempts to examine the population structure and survivorship of certain species of Cladocera using microfossils have been successful (Frey and Hann, 1985). Detailed studies of such death assemblages using a matrix approach (Green, 1979) may permit estimation of life history parameters in populations over long periods of time.

Ultimately, the potential of cladoceran microfossils lies in providing a long-term record of response to environmental conditions, both stable and changing. The qualitative and quantitative responses to disturbance, whether physical or biotic, can be assessed and predictive models developed and tested. Understanding the processes that operated in the past will be the key to predicting the impact of present-day forces impinging on cladoceran populations in aquatic ecosystems. The clearest comprehension of the processes will come through a synthetic approach, integrating data derived from a wide variety of plant and animal fossil remains, and necessitating a co-ordinated multi-disciplinary approach.

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MINERALIZATION AND SHEAR ZONES

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