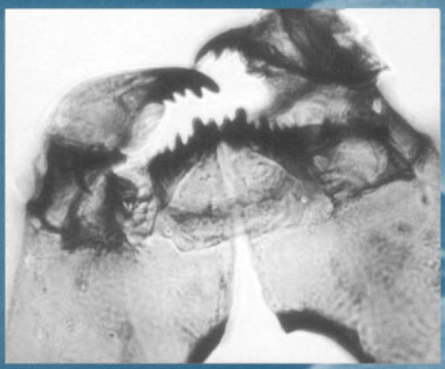
Tracking Environmental Change Using Lake Sediments

Volume 4

Zoological Indicators

Edited by
John P. Smol, H. John B. Birks
and William M. Last



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Tracking Environmental Change Using Lake Sediments.
Volume 4: Zoological Indicators

Developments in Paleoenvironmental Research

VOLUME 4

Tracking Environmental Change Using Lake Sediments Volume 4: Zoological Indicators

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DEDICATION

Dedicated to the memory of Dr. Thomas M. Frost.

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PREFACE

Paleolimnology is a rapidly developing science that is now being used to study a suite of environmental and ecological problems. This volume is the fourth handbook in the *Developments in Paleoenvironmental Research* book series. The first volume (Last & Smol, 2001a) examined the acquisition and archiving of sediment cores, chronological techniques, and large-scale basin analysis methods. Volume 2 (Last & Smol, 2001b) focused on physical and chemical methods. Volume 3 (Smol et al., 2001), along with this book, summarize the many biological methods and techniques that are available to study long-term environmental change using information preserved in sedimentary profiles. A subsequent volume (Birks et al., in preparation) will deal with statistical and data handling procedures. It is our intent that these books will provide sufficient detail and breadth to be useful handbooks for both seasoned practitioners as well as newcomers to the area of paleolimnology. These books will also hopefully be useful to non-paleolimnologists (e.g., limnologists, archeologists, palynologists, geographers, geologists, etc.) who continue to hear and read about paleolimnology, but have little chance to explore the vast and sometimes difficult to access journal-based reference material for this rapidly expanding field. Although the chapters in these volumes target mainly lacustrine settings, many of the techniques described can also be readily applied to fluvial, glacial, marine, estuarine, and peatland environments.

This current volume focuses on zoological indicators preserved in lake sediments, whilst Volume 3 focused on terrestrial, algal, and siliceous indicators. The taxonomic divisions between these two books, however, are not exact, as some zoological indicators are discussed in Volume 3 (e.g., protozoa, rotifers, sponges) because these groups are typically studied using techniques often associated with palynologists or diatomists. Hence, it was more practical to cover these topics there.

Many people have helped with the planning, development, and final production of this series. In addition to the hard work provided by the authors, this publication benefitted from the technical reviews furnished by our scientific colleagues, many of whom remain anonymous. Each chapter was typically examined by two external referees as well as the editors. In order to assure readability for the major target audience, we asked many of our graduate students to also examine selected chapters; their insight and questioning during the reviewing and editorial process are most gratefully acknowledged. The staff of the Environmental, Earth and Aquatic Sciences Division of Kluwer Academic Publishers are commended for their diligence in production of the final presentation. In particular, we would also like to thank Ad Plaizier, Anna Besse-Lototskaya (Publishing Editor, Aquatic Science Division), and Rene Mijs (former Publishing Editor, Biosciences Division) for their long-term support of this new series of monographs and their interest in paleoenvironmental research. John Glew (Queen's University, PEARL) designed our logo. Finally, we would like to thank our respective universities and colleagues for support and encouragement during this project.

THE EDITORS

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AIMS AND SCOPE OF *DEVELOPMENTS IN PALEOENVIRONMENTAL RESEARCH* SERIES

Paleoenvironmental research continues to enjoy tremendous interest and progress in the scientific community. The overall aims and scope of the *Developments in Paleoenvironmental Research* book series is to capture this excitement and document these developments. Volumes related to any aspect of paleoenvironmental research, encompassing any time period, are within the scope of the series. For example, relevant topics include studies focused on terrestrial, peatland, lacustrine, riverine, estuarine, and marine systems, ice cores, cave deposits, palynology, isotopes, geochemistry, sedimentology, paleontology, etc. Methodological and taxonomic volumes relevant to paleoenvironmental research are also encouraged. The series will include edited volumes on a particular subject, geographic region, or time period, conference and workshop proceedings, as well as monographs. Prospective authors and/or editors should consult the series editors for more details. The series editors also welcome any comments or suggestions for future volumes.

EDITORS AND BOARD OF ADVISORS OF *DEVELOPMENTS IN PALEOENVIRONMENTAL RESEARCH* BOOK SERIES

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Contents of Volume 1: ***Tracking Environmental Change Using Lake Sediments: Basin Analysis, Coring, and Chronological Techniques.***

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Applications of seismic sequence stratigraphy in lacustrine basins. *Christopher A. Scholz*

Ground penetrating radar applications in paleolimnology. *Brian J. Moorman*

Shoreline and basin configuration techniques in paleolimnology. *Dorothy Sack*

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Cladocera and other branchiopod crustaceans. *Atte Korhola & Milla Rautio*

Midges: Chironomidae and related Diptera. *Ian R. Walker*

Coleoptera and Trichoptera. *Scott A. Elias*

Oribatid mites. *Torstein Solhøy*

Bryozoan statoblasts. *Donna R. Francis*

Ostracoda. *Jonathan A. Holmes*

Freshwater molluscs. *Barry B. Miller & Michael J. S. Tevesz*

Fish. *W. P. Patterson & G. R. Smith*

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SAFETY CONSIDERATIONS AND CAUTION

Paleolimnology has grown into a vast scientific pursuit with many branches and subdivisions. It should not be surprising, therefore, that the tools used by paleolimnologists are equally diverse. Virtually every one of the techniques described in this book requires some familiarity with standard laboratory or field safety procedures. In some of the chapters, the authors have made specific reference to appropriate safety precautions; others have not. The responsibility for safe and careful application of these methods is yours. Never underestimate the personal risk factor when undertaking either field or laboratory investigations. Researchers are strongly advised to obtain all safety information available for the techniques they will be using and to explicitly follow appropriate safety procedures. This is particularly important when using strong acids, alkalies, or oxidizing reagents in the laboratory or many of the analytical and sample collection/preparation instruments described in this volume. Most manufacturers of laboratory equipment and chemical supply companies provide this safety information, and many Internet and other library resources contain additional safety protocols. Researchers are also advised to discuss their procedures with colleagues who are familiar with these approaches, and so obtain further advice on safety and other considerations.

The editors and publisher do not necessarily endorse or recommend any specific product, procedure, or commercial service that may be cited in this publication.

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1. ZOOLOGICAL INDICATORS IN LAKE SEDIMENTS: AN INTRODUCTION

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This volume is a continuation of the previous three books in this series (Last & Smol, 2001a,b; Smol et al., 2001), which collectively attempt to summarize the major approaches and techniques used by paleolimnologists to track long-term environmental change. Broadly defined, paleolimnology is the study of the physical, chemical, and biological information stored in lake deposits. In most cases, lake sediments are considered the primary archives,

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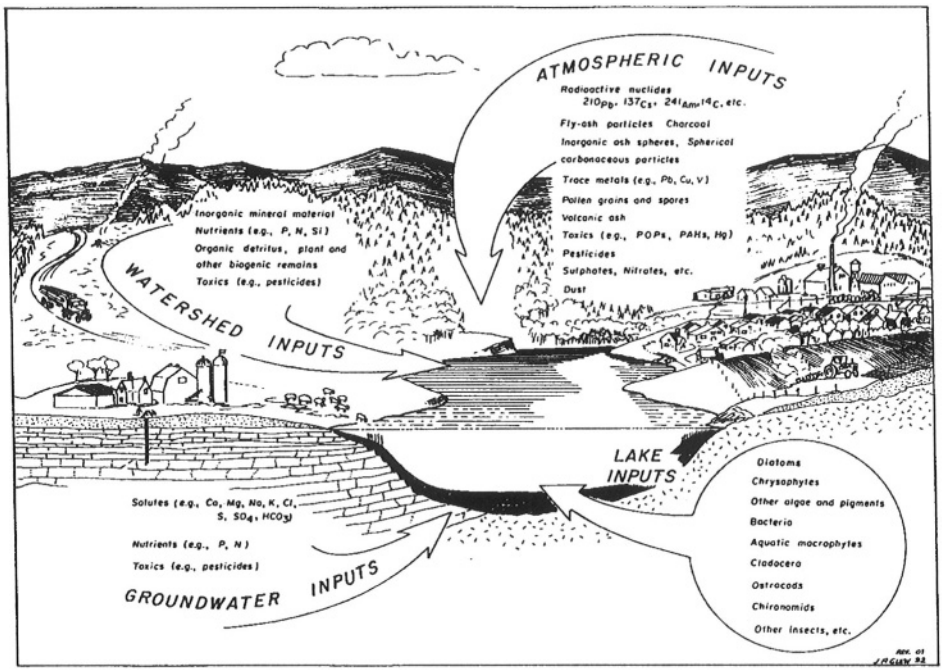

Figure 1. Schematic diagram showing the accumulation of allochthonous and autochthonous indicators used by paleolimnologists to track long-term environmental change (modified from Charles et al., 1994).

however other deposits (e.g., sediments from rivers, bogs, wetlands, marshes, estuaries, and so forth) also contain important proxy data of past environmental change, and many of the approaches discussed in this book can be equally applied to these environments. The amount of information stored in sediments is staggering, with both allochthonous and autochthonous sources of proxy data (Fig. 1), and so it soon became clear to the series editors that several books would be required to summarize some of the commonly used methods. These books build on the foundation set by previous compilations of paleoenvironmental techniques, such as Gray (1988), Warner (1990), and especially Berglund (1986). The latter has been the standard reference for about 15 years. Moreover, Frey's (1964) review remains a classic publication that contains a wealth of historical references on the use of invertebrate indicators in paleolimnology.

As we hope to capture in these current volumes, many new approaches and techniques are now available to paleolimnolgists. The first two books in this series deal with physical and chemical techniques. Volume 1 (Last & Smol, 2001a) includes chapters on field work, such as core collection and sectioning, basin analysis techniques, and dating sedimentary profiles. Volume 2 (Last & Smol, 2001b) summarizes the many chemical techniques that paleolimnologists use to describe and interpret sedimentary profiles.

Volumes 3 and 4 of this book series focus on the biological information we can glean from sediments, with some example applications. Volume 3 (Smol et al., 2001), which contains 15 chapters that deal primarily with terrestrial, algal, and siliceous indicators, is

closely related to the subject matter contained in this book. Smol et al. (2001) includes chapters on topics such as pollen, stomates, macrofossils, charcoal, fungi and non-pollen palynomorphs, as well as semi-terrestrial indicators, such as testate amoebae. This is followed by six chapters dealing with siliceous microfossils, such as diatoms, chrysophytes, ebrideans, phytoliths, sponges, and siliceous protozoan plates. Volume 3 concludes with two chapters that use chemical techniques to track biological populations (i.e., biogenic silica, fossil pigments), followed by a glossary and index.

This current volume completes the collation of methods and approaches that are concerned with primarily zoological indicators preserved in lake sediments. It should be noted, however, that some invertebrate groups are included in Volume 3. For example, some of the microfossils described in the non-pollen palynomorph chapter (van Geel, 2001) include invertebrates such as rotifers, and certainly the protozoa described by Beyens & Meisterfeld (2001) are zoological. These invertebrate indicators were included in Volume 3 because the methods used for these microfossils are similar to those used for pollen analysis. Similarly, siliceous protozoan plates (Douglas & Smol, 2001) and sponge spicules (Frost, 2001) are included in Volume 3, as the laboratory methods used for these siliceous microfossils are similar or identical to those used for diatom analyses (Battarbee et al., 2001)

Although paleolimnological applications are discussed throughout this book, only cursory comments are made on the statistical and quantitative approaches that have been developed to interpret the proxy information gleaned from sediments. A separate volume on statistical and data handling approaches is currently in preparation (Birks et al., in preparation).

As we noted in Volume 3, paleolimnology has progressed at a tremendous rate over the last few decades, with biological approaches often leading many new initiatives. These are exciting times for paleoenvironmental research. We hope these current volumes capture this progress, and will aid the next generation of paleolimnologists in their investigations.

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2. CLADOCERA AND OTHER BRANCHIOPOD CRUSTACEANS

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Keywords: Cladocera, evolution, habitat ecology, taxonomy, fossil remains, applications to paleoecology, training set, transfer functions

Introduction

Lake sediments contain a variety of organic and inorganic remains that may be used to track the history of a lake or its catchment. Shells, head-shields, post-abdomens and claws of Cladocera are among the most frequently found animal remains in sedimentary deposits. They have played an important role in providing information on various environmental events and disturbances affecting lake status, such as climatic changes, trophic oscillations, acidification, and water-level changes. Yet, one major problem has been to relate sediment core findings to animal ecology. As in the case of other organism groups, many contradictory records and opinions have been presented concerning their paleoecology and indicator value of cladocerans.

This chapter provides a brief overview of the use of Cladocera and other invertebrate groups of the crustacean class Branchiopoda in paleoecological research. We focus on Cladocera and only briefly discuss other branchiopod groups that may have value as paleo-indicators. We first discuss the biotic and abiotic factors responsible for the present-day production, distribution, and abundance of these animals, as such information is obviously critical for meaningful interpretations of paleoassemblages (Whiteside & Swindoll, 1988). The methods will not be discussed in full; instead, readers are referred to existing review articles, foremost of which are Frey (1979, 1986a) and Hann (1989), who also provide excellent summaries of other aspects related to cladoceran research.

Cladocera

Evolution, morphology, and reproduction

Living representatives of the crustacean class Branchiopoda fall into four orders: Cladocera (water fleas), Anostraca (fairy shrimps), Notostraca (tadpole shrimps), and Conchostraca

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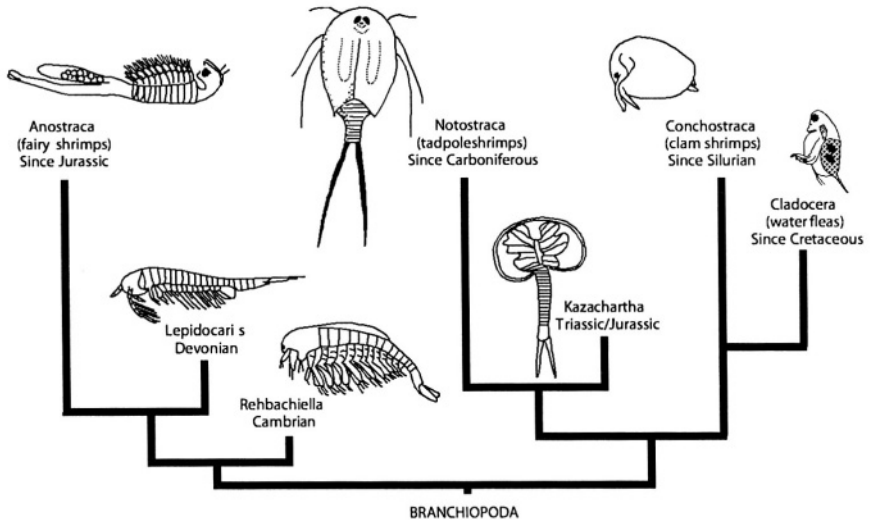


Figure 1. Phylogenetic differentiation of the four living orders of the Class Branchiopoda and some extinct branches. Modified from http://mailbox.univie.ac.at/Erich.Eder/UZK/index2.html.

(clam shrimps) (Fig. 1). The order Cladocera is an old group of microscopic branchiopod crustaceans (size generally smaller than 1 mm) known at least from the mid-Mesozoic era. These tiny crustaceans can inhabit almost any kind of freshwater habitat from large lakes to ponds, and even small ditches, puddles and water-filled tire ruts. Cladocerans have even been found in moss growing on trees in rain forests several meters above the ground (Green, 1997). The greatest abundance of species is usually found in the vegetation at margins of lakes and ponds. It is a major component of the micro-crustacean fauna in freshwater lakes and ponds playing multiple roles in aquatic ecosystem, such as by being an active grazer on algae, detritus and various heterotrophs (Edmondson, 1957; Nilssen, 1978), by regenerating nutrients back to primary producers and bacteria (Järvinen & Salonen, 1998), and by serving as food for fish and planktivorous organisms (Black, 1993; Tolonen, 1998; Dodson & Hanazato, 1995). Some are herbivores (plant eaters) while some are carnivores (animal eaters); some species like *Polyphemus pediculus* (Linnee, 1761) and *Cercopagis pengoi* (Ostroumov, 1891) are voracious predators preying upon small animals, mostly other water fleas.

Recent molecular evidence suggests that the Cladocera is a monophyletic group (Crease & Taylor, 1998; Hanner, 1997), in contrast to previous classification schemes, which divided the Cladocera into four orders (e.g., Dodson & Frey, 1991). The order Cladocera is now divided into four suborders (Anomopoda, Ctenopoda, Onychopoda and Haplopoda), 11 well-defined families (Daphniidae, Moinidae, Bosminidae, Macrothricidae, Chydoridae, Sididae, Holopedidae, Polyphemidae, Cercopagidae, Podonidae, and Leptodoridae) and about 80 genera, consisting of an estimated 400 or so species worldwide, roughly 100–150 for each continent (Rowe & Hebert, 1999). More than 90 cladoceran taxa are known to inhabit European inland waters alone. However, taxonomic revisions in all families are underway so that the numbers of genera and species are likely to increase.

The first modern Cladocera developed in the Jurassic period 150 million years ago from the ancestral crustaceans during the period of the supercontinent Pangea (Smirnov, 1971b). Although the evolutionary history of many ancestral branchiopods began from the sea, only a few cladoceran species are found in marine systems today. In general, the present-day ability of cladocerans to regulate osmotic pressure is poor (Frey, 1993). There are only few taxa (e.g., *Podon polyphemoides* (Leuckart, 1859), *Evadne nordmanni* (Lovon, 1836)) that can be considered strictly oceanic. However, several cladoceran taxa, such as *Bosmina longispina maritima* (P. E. Müller), prefer brackish-water environment (Viitasalo et al., 1995; Ojaveer & Lumberg, 1995), whereas some cladoceran forms are characteristic to inland saline lakes which commonly lack fish predators (Reynolds, 1979; Bos et al., 1996).

The split of Pangea into Laurasia and Gondwanaland defined the first geographical dispersal of the order. For example, most of the species in the subgenus *Ctenodaphnia* seem to be restricted to fish-free waters in the Gondwanaland (Sergeev & Williams, 1983). At present, species richness is highest in mid-northern latitudes and decreases towards the tropics and poles (Fernando, 1980; Kerfoot & Lynch, 1987; and references therein). Subtropical and tropical environments seem to lack certain taxa, such as *Holopedium, Polyphemus,* and *Leptodora* entirely (Fernando, 1980), whereas in Antarctica no limnetic cladocerans have been found despite extensive sampling (Heywood, 1983). There is also a general decline in the mean body size of cladocerans from temperate toward tropical and arctic regions (Gillooly & Dodson, 2000).

The geographical trend in cladoceran communities may be partly a function of geological history, including the presence or absence of pathways for dispersal such as river networks, lake-systems or dispersal barriers (Carter et al., 1980). On the geological time scale, the vast numbers of north temperate lakes are exceptional, releatively recent products of the Pleistocene glaciation. The isolated nature of these lake basins promotes speciation, yet their relatively short geological life spans favor life histories characterized by immigration and regional patterns. The rare and scattered lakes of the tropics are more typical of the long-term geographical norm. Freshwater aquatic ecosystems in the tropics are usually river-dominated systems, characterized by oxbow lakes and numerous temporary pools and other water bodies subject to wet-dry season fluctuations. Therefore, speciation or differentiation in the community structure of plankton in the tropics is not promoted by terrestrial isolation barriers as in more northerly regions (Kerfoot & Lynch, 1987).

On the other hand, the presence and absence of cladocerans in different regions of the world can be attributed to biotic factors, such as competition and predation (Brooks & Dodson, 1965; DuMont, 1994). Also latitudinal differences in primary production, nutrient regeneration, and oxygen avalibility may have contributed to the broad-scale patterns in cladoceran communities (Lewis, 1995). In general, the much larger range of environmental conditions in temperate lakes and the greater number of ecological niches in which species can live could have led to the greater number of species in temperate regions. Meanwhile, the recent study by Gillooly & Dodson (2000) strongly emphasizes the role of temperature in controlling the population dynamics of Cladocera in lakes across latitudes.

The distribution of Cladocera is controlled mainly by two factors: their capacity for dispersal and their tolerance to various environmental conditions. The first includes both the capacity of an organism to move or be easily transported. The second refers to an organism's ability to survive physical, chemical and biological pressures in their new

habitat. For example, organisms restricted to deep and/or cold hypolimnetic waters have a reduced capacity for dispersal (Carter et al., 1980). The ability of cladocerans to reproduce parthenogenetically and to produce transportable resting eggs (see below) makes dispersal easier for these organisms than for some other crustacean zooplankton, such as Copepoda (Carter et al., 1980). Despite a relatively good ability for dispersal, very few species of Cladocera, if any, are at present considered cosmopolitans with a worldwide distribution. Improved genetic techniques have recently been used to modify and change past taxonomic designations, with significant splitting of several established taxonomic units and the description of new ones. As a result, the distribution patterns of several species have changed (Scwenk et al., 1995; Ender et al., 1996).

The present-day Cladocera show some degree of structural variation, including cyclical morphological variability, although no major morphological changes have been detected during the last 11 000 years (Frey, 1962, 1976). Furthermore, the few published records from the last interglacial stage in Europe (Eemian: Frey, 1962) and North America (Sangamonian: Hann & Karrow, 1984, 1993) suggest no morphological changes in any cladoceran species between interglacial species and their modern counterparts.

Most of the cladoceran species can be described as follows: their appendages have a flattened leaf-like structure and the coxopodite bears a flattened epipodite or gill. In addition to their role in respiration, the appendages are used for filter feeding and frequently for locomotion as well. Most species have a short body and well-developed carapace, which completely covers the limbs so that there is no external evidence of segmentation. The only exceptions to this pattern are the Polyphemidae, Leptodoridae, Cercopagidae, and Podonidae. Individuals from these families have a reduced carapace that only covers the brood chamber. The head protrudes anteriorly and bears a pair of disproportionally large and powerful second antennae, which the animal uses to row itself upwards through the water in a series of jerks. The head also bears the first antennae (antennules) and a single compound eye and paired nauplius eye (Fig. 2).

Reproduction in the Cladocera is unusual. During most of the growing season, reproduction is via unfertilized female-bearing eggs, which develop directly in a dorsal brood chamber. As conditions deteriorate (e.g., overcrowding, limited food availability, temperature exceeds limits, oxygen depletion), males are produced parthenogenetically and diapausing eggs are predominantly generated sexually (gamogenesis). For example, the abundance of headshields of ephippial *Chydorus piger* Sars females in Holocene sediments of a lake in northern Finnish Lapland led Sarmaja-Korjonen (1999) to suggest that the species responded to the harsh conditions at the extreme limits of its northern distribution by gamogenetic reproduction. There are no naupliar stages. The offspring are born with a complete set of appendages and a well-developed shell. As a successful breeding may yield 5–10 juveniles that, in turn, can reproduce themselves after 1–2 weeks, cladoceran populations can increase at exponential rate (Amoros & Van Urk, 1989). Due to this highly effective mode of reproduction, faunal communities can respond rapidly to changes in the environment.

The diapausing eggs are enclosed within several protective membranes, including a modified part of the carapace, the entire structure consituting an ephippium. The transportation of the ephippia over vast distances via birds and insects enables cladocerans to colonize new water bodies very rapidly, such as recently isolated coastal lakes or cut-off river meanders (Frey, 1958; Korhola, 1990). Reproduction and colonization are further

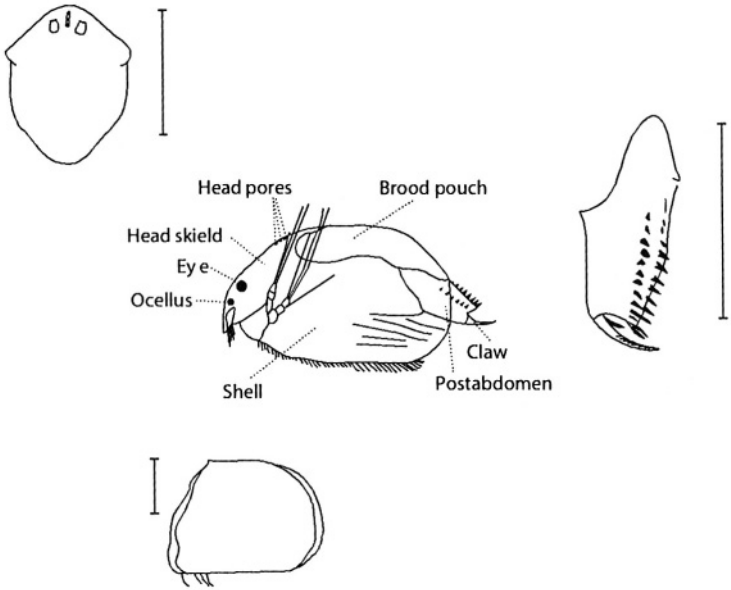


Figure 2. Living Cladocera and their most important body parts used in the identification of a fossil animal. A headshield, with details of the head pores, is shown in the upper left corner of the figure; a postabdomen with claw is shown in the right hand side of the figure; and a complete carapace is drawn in the lower part of the figure.

aided by the high resistance of the eggs against desiccation, extensive temperature changes, digestion, corrosion, or biodegradation (Amoros & Van Urk, 1989).

Preservation in the sediment

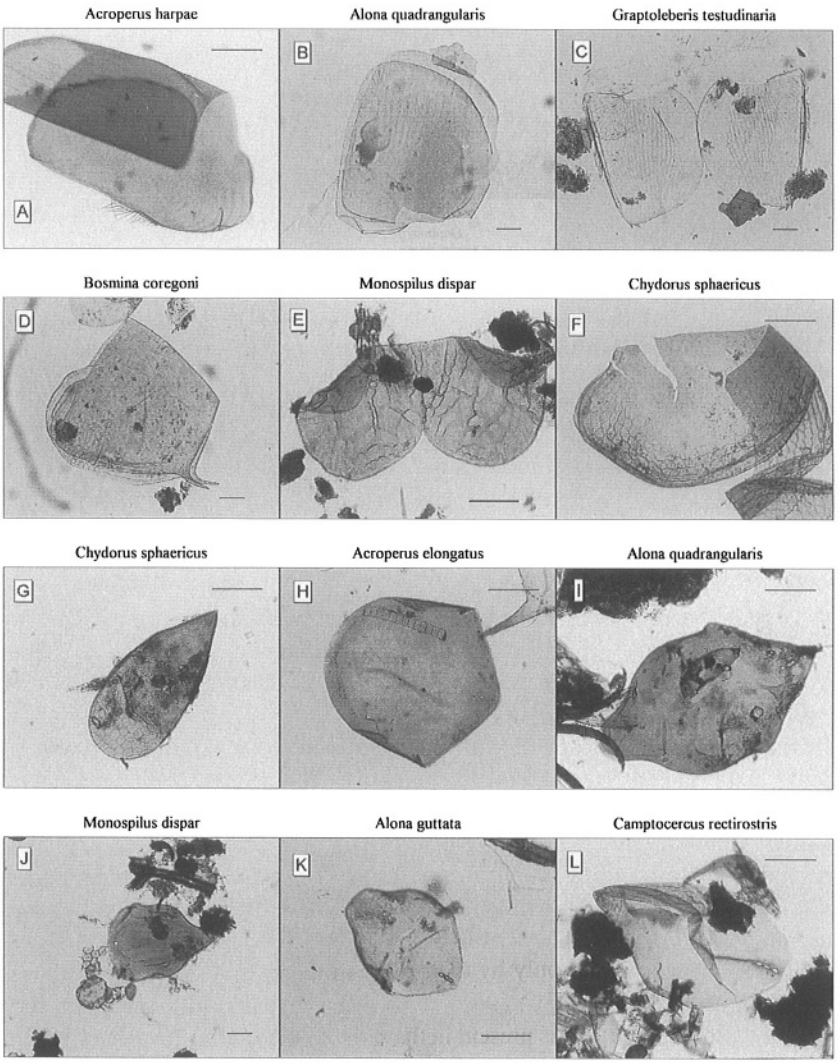
After death, several processes modify the remains of organisms to produce fossils. The most important factor affecting the preservation of species assemblages in deep-water sediments is the chemical composition of the different body parts, which determines how well the remains are preserved in sediments.

Zooplankton disarticulate at death (or after the process of molting) into a variety of exoskeleton parts, such as carapaces, post-abdomens, claws, mandibles, segments of antenna (only Copepoda) and head-shields (only Cladocera), which are identifiable to varying degrees (Figs. 2 and 3). The chitinous skeletal structures of Cladocera preserve better than soft-bodied Copepoda, resulting usually in a shift from Copepoda-dominating water column material to Cladocera-dominating sediment trap and fossil material—i.e. in the sediments copepods no longer are detectable (Rautio et al., 2000; Fig. 4).

Chitin is very inert chemically, yet all cladoceran chitin may not be equally resistant to biological degradation. Deevey (1964) studied in detail the differential preservation of Cladocera from the viewpoint of the constitution of the chitin. He found that certain crystalline structures in the chitin polymers are more hydrated and thus better preserved.

A major constraint for paleolimnological investigations is that only the Chydoridae (a taxon-rich group of benthic, mostly mud- or macrophyte-dwelling cladocerans) and

Bosminidae (a planktonic group) are well preserved in terms of all skeletal components (Hofmann, 1987; Hann, 1989). Remains of Chydoridae and Bosminidae usually preserve quantitatively, which means that the variation in absolute numbers and relative abundances among species as recovered from sediment samples can be translated, with some reservations, to the total production of the original living population. The remaining nine families are either selectively preserved, or do not leave any identifiable remains. For example, planktonic Daphniidae, a key component of aquatic ecosystem, are poorly preserved because their exoskeleton is too fragile to survive decomposition and attack by fungi; in deeper



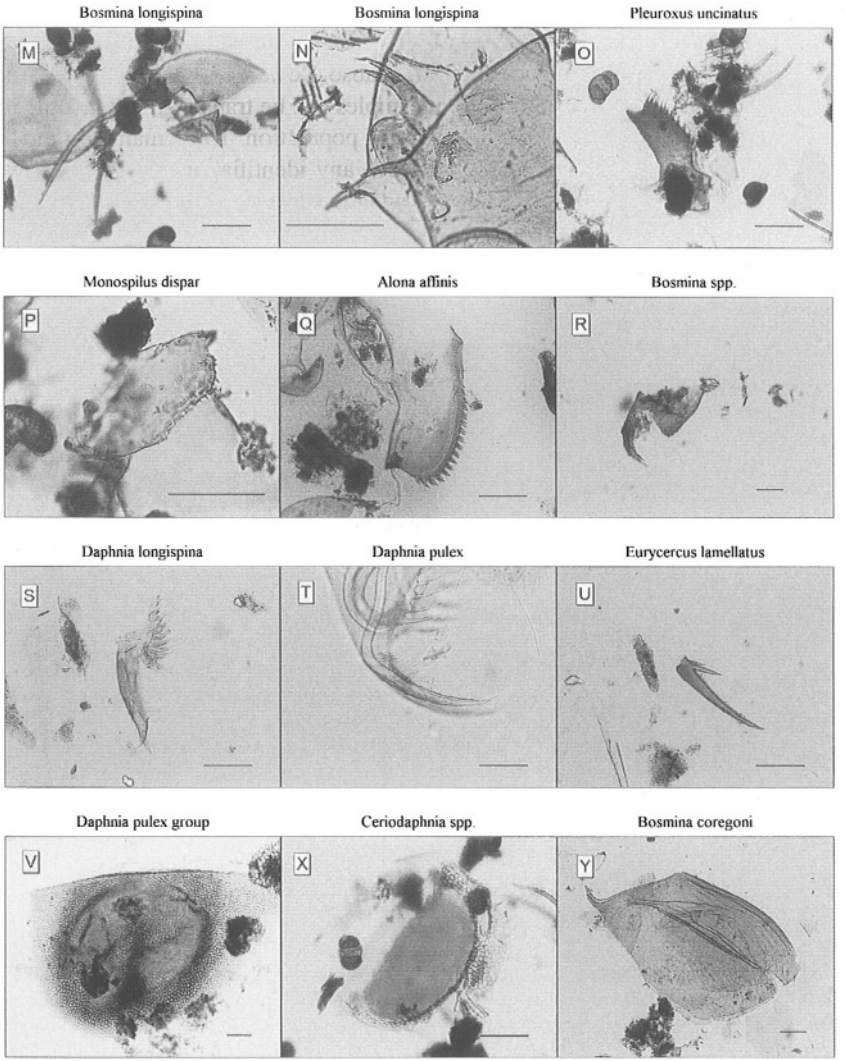


Figure 3. Selected fossil remains of Cladocera from Poland, Finland, UK, and California (U.S.A.). The photographs were taken by Gavin Simpson, Krystyna Szeroczyñska, David Porinchu, Kaarina Sarmaja-Korjonen, Mari Hakojärvi, MR and AK during the Cladocera workshop held in Helsinki in fall 2000. All scale bars represent 100 μm. A–F *carapaces*. G–M *head shields* with *head pores*. N–R *postabdomens*. S–U *claws* (T = modern specimen with Nematoda). V–Y *ephippia*.

sediments they are represented only by their post-abdominal claws (Fig. 3S), mandibles, and ephippia.

A large reservoir of ephippia is present in the sediments of lakes and estuaries, of which a proportion may remain viable for several years or even decades (Moghraby, 1977; Moritz, 1987; Marcus et al., 1994; Viitasalo & Katajisto, 1994). Periodic recruitment of hatchlings to the pelagic population may contribute significantly to changes in cladoceran population

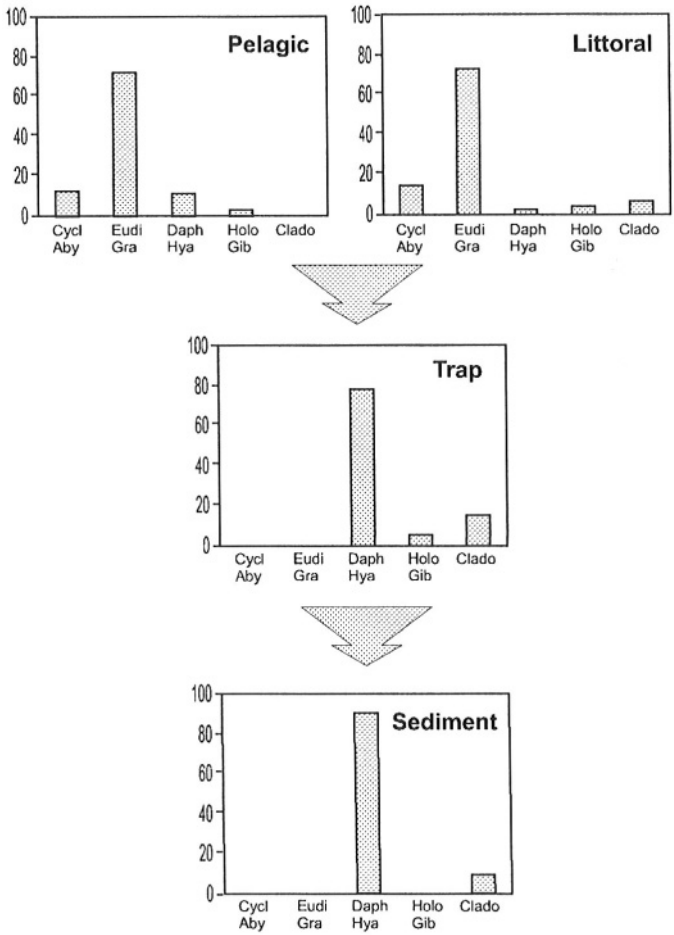


Figure 4. Distribution of zooplankton in the major habitats of the subarctic Lake Saanajärvi, Finnish Lapland, and the transportation and loss or gain of species between different steps of sedimentation. Cycl Aby = *Cyclops abyssorum*, Eudi Gra = *Eudiaptomus graciloides*, Daph Hya = *Daphnia hyalina*, Holo Gib = *Holopedium gibberum*, Clado = *Bosmina longispina, Chydorus sphaericus, Alonella nana, Alonella excisa, Alona quadrangularis, Alona affinis, Acroperus harpae, Acroperus elongatus and Eurycercus lamellatus*. Adapted from Rautio et al. (2000).

density, species composition, and clonal structure (Carvalho & Wolf, 1989). Whereas intact ephippia with resting eggs are characteristic to superficial sediments, empty ephippial cases are know to survive for thousands of years (Fig. 3V–Y).

Despite the selective preservation of Cladocera remains, Frey (1960), nevertheless, suggested that probably all Cladocera species leave some kind of remains in sediment—a concept that has, indeed, gained some support from a very detailed study by Cotten (1985). She was able to identify remains of 71 cladoceran taxa representing 9 families from the surface sediments of 46 lakes in eastern Finland—i.e., a far larger collection of remains than is usually recovered in the course of routine investigations.

The fossil record of zooplankton is, thus, quite variable between the different taxonomic groups, both in terms of the degree of taxonomic resolution that can be achieved and the faithfulness of the fossil record. Moreover, the distribution and abundance of cladoceran remains is affected by several *in situ* lake factors, including movement and mixing of sediments by burrowing organisms (bioturbation), lake morphology, water depth and associated water movements. Therefore, in lake studies of Cladocera microfossils, caution should be exercised when drawing conclusions based on the observation of single, small-volume samples. On the other hand, some taxonomic groups, such as the Chydoridae, are preserved so well that the sediment of the deepest basin can be considered a better collector of these animals than years of extensive water column sampling. Indeed, in many cases, hints of new species can been obtained from subfossil material (e.g., Sarmaja-Korjonen et al., 2000).

Habitat ecology and sensitivity to different environmental factors

Different species of Cladocera are not distributed randomly in various types of environments: some species have wide ecological tolerances and are able to colonize various types of aquatic environments, whereas other taxa are more restricted to particular conditions and narrower ecological niches (Flössner, 1964; Amoros, 1980). Although major environmental requirements for several species are roughly the same, single lake or pond communities usually contain only a limited number of species (Patalas, 1964; Löffler, 1969; Hebert & Hann, 1986; Rautio, 1998, 2001).

As Cladocera are only one component of a lake's ecosystem, their abundance and distribution is affected to some extent by other organisms. The important role of Cladocera in the overall functioning of an ecosystem makes them good indicators of changes in the food web and trophic cascades. As the success of many aquatic species is, on one hand, dependent on the phytoplankton as their food supply and, on the other hand, is controlled by predators, Cladocera rapidly responds to changes in trophic interactions.

Changes in phytoplankton species dominance may lead to resource competition among selectively feeding zooplankton favoring species with less-defined feeding patterns (Rothaupt, 1990). For example, during periods of filamentous cyanobacteria blooms, selective feeders such as *Bosmina* may become a dominant component of the cladoceran community, because they are able to avoid ingestion, whereas less-selective feeders, such as *Daphnia,* may suffer either from mechanical interference by filaments or toxins produced by algae (Kerfoot & Kirk, 1991; Henning et al., 1991). Because resource competition and interference are indirect mechanisms affecting populations (not directly acting between the species), there is no unifying way or concept to describe these relationships among herbivorous zooplankton. In contrast, predation is an interaction in which the mechanisms directly involve the biota in question. Therefore, it is conceivable that fish behavior, for example, directly influences pelagic predator-prey relationships (Brooks & Dodson, 1965; Zaret & Kerfoot, 1975; Zaret, 1980). Fish usually reduce the number of zooplankters as well as alter their size-regime; the greater the predation pressure by fish, the more biased is the size structure of zooplankton community. Fish usually select larger prey, whereas with invertebrate predation, small-sized individuals are effectively removed (Brooks & Dodson, 1965; Nilssen, 1978).

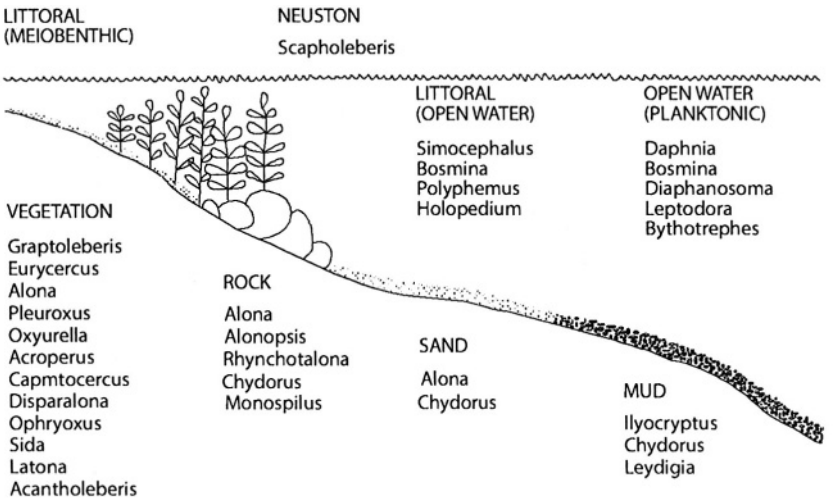


Figure 5. The major ecological niches of Cladocera and different microhabitats within the littoral-benthic habitat: vegetation, rock, sand, mud, and the neuston. Modified from Hann (1989), so that the examples of the species associated with the different sub-habitats have been re-considered and updated from Hofmann (1987), Whiteside & Swindoll (1988), Korhola (1990), and Nilssen & Sandøy (1990).

Cladocera are known to be highly responsive to the substrata they inhabit (Flössner, 1964; Hann, 1989). Within a lake, Cladocera 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 (Fig. 5). Species that have high site-specific requirements to different microhabitats are especially valuable indicators of different environmental conditions and changes therein. For instance, lake-level fluctuations may induce changes in suitable habitat composition for different species of Cladocera by changing the relative proportions of littoral-pelagic habitats, and further changes within the littoral zone (Mueller, 1964). Many studies have recognized the importance of lake depth in influencing the cladoceran distributions (e.g., Whiteside, 1970; Sarvala & Halsinaho, 1990; Korhola et al., 2000).

Many cladoceran species appear to be adapted to a wide range of (seasonal) temperature changes (Meijering, 1983), although their growth and reproduction is slower in cold water (Allan, 1976; Allan & Goulden, 1980; Goss & Bunting, 1983; Frey & Hann, 1985; Moore et al., 1996) and their optimum temperatures are usually at the higher side of the tolerance range. Temperature has also been shown to be critical to the body size of cladocerans (Gillooly & Dodson, 2000). In addition, several investigations have documented the general importance of temperature and other climate factors to zooplankton biomass (e.g., George & Harris, 1985) and diversity (e.g., Patalas, 1990; Stemberger et al., 1996).

DeCosta (1964) reports a clear distributional pattern among Cladocera over a latitudinal range of 17 °C, and Harmsworth (1968) classified the European cladoceran species as 'arctic', 'sub-arctic', 'north temperate', and 'south temperate' according to their latitudinal affinities. In a geographical survery of littoral Crustacea in Norway, Sandøy & Nilssen (1986) found many chydorid taxa to be related to altitude and geographic regions.

Rautio (1998, 2001) also noted that altitude, either directly (dispersal and colonization abilities) or indirectly (temperature, amount of vegetation), was the main factor controlling crustacean species compositions in small ponds in Finnish Lapland. However, there are probably no, or only a few, true cold stenothermal species among these animals, so these crustaceans may lack proper 'northern' representatives (Frey, 1988).

Most of the cladocerans prefer oligotrophic and dilute (low ionic strength) waters. Many studies document strong correlations between common chemical variables (e.g., specific ions, pH, alkalinity, conductivity) and cladoceran composition (reviewed by Brett, 1989; Marmorek & Korman, 1993). As a rule, a decrease in faunal diversity for rapidly changing values with all these parameters is expected (Synerholm, 1979; Fryer & Forshaw, 1979; Chengalath, 1982). For example, decreasing species diversity as a result of a pH decline has been reported both in North America (e.g., DeCosta, 1975; Yan & Strus, 1980) and in Europe (e.g., Fryer, 1980; Sandøy & Nilssen, 1986). The critical pH value, below which even tolerant taxa begin to decline, is said to be ≈5.0 (DeCosta & Janicki, 1978; Fryer, 1980). However, not all studies have confirmed these results (Uimonen-Simola & Tolonen, 1987). Caution should be exercised when interpreting the changes in cladoceran species diversity as these can be produced by multiple factors, including external perturbations such as climatic changes (see below) and natural catastrophes (Tsukada, 1967).

Whiteside (1970), in his pioneering study dealing with chydorid assemblages and water quality in 77 Danish lakes, found a negative relationship between most taxa and pH, alkalinity, and conductivity. He also noted trends of decreasing faunal diversity with increasing alkalinity, with most diverse assemblages occurring in clear-water lakes with low pH. However, a closer analysis revealed that the chydorid diversity was, in fact, significantly controlled by habitat availability (Whiteside, 1970). The more polluted lakes were characterized by fewer and a less diverse assemblage of rooted macrophytes, and thus did not contain littoral Cladocera that are strictly associated with vegetation (Whiteside & Harmsworth, 1967; Korhola, 1990). Whiteside & Swindoll (1988) have discussed the factors that may confound the relationships of cladoceran species to water chemistry.

Methodological aspects

Frey (1986a) and Hann (1989) offer excellent summaries of major steps involved in cladoceran slide preparation and examination, including some recommendations and discussion about the reliability and constraints of various methods. As no major re-considerations or innovations in the laboratory techniques have occurred since those publications, only a brief overview of the sampling strategies, slide preparation and identification of remains is given here.

Where to collect samples from?

There are two major habitats in lakes that are normally inhabited by Cladocera: the open-water planktonic and the littoral benthic habitat. The abundance and species composition of a cladoceran community not only varies between these two environments, but also within them. For example, littoral taxa are not distributed randomly over the benthic habitat, but

instead prefer particular substrates, such as rock, sand, mud and vegetation (Whiteside et al., 1978; Whiteside & Swindoll, 1988; Korhola, 1990).

In most cases, paleolimnological investigations of cladoceran assemblages are based on sediment profiles collected in the central (or deepest) part of a basin. This practice is based on the observation that the remains of chydorid cladoceran species from different microhabitats in the littoral zone are passively transported offshore (e.g., via currents generated by wind), and mixed with remains of limnetic taxa before they are incorporated into the sediments (Frey, 1988). Thus, sediment deposited in the central area of a lake is thought to represent a spatially and temporally integrated sample of the cladoceran communities that have lived in different habitats in the lake.

Frey (1960) tested the above assumption by analyzing an offshore sample for its cladoceran remains in five lakes in Wisconsin, U.S.A., intensively studied for their living crustacean populations for about 30 years (original monitoring work referenced in Frey, 1960). He found that all the species, except one, encountered by the traditional method of collecting intact animals were recovered from the sediment samples, in addition to which six extra species were recorded that had not been found during the intensive monitoring program. This led Frey (1960: 687) to state that "A list of species, at least chydorids, occurring in a given body of water can be obtained with least expenditure of time and greatest assurance of completeness from an examination of the sediments".

The subsequent studies by Mueller (1964), DeCosta (1968), Goulden (1969), Binford (1982), and Boucherle (1982) have demonstrated that all samples of surficial offshore sediments yield approximately the same relative proportion of Cladoceran remains, including littoral chydorids. These results suggest that the entire cladoceran fauna is sufficiently well represented in samples taken from surficial muds of the lake's pelagic region, regardless of the initial ecological niches of the individual taxa (Kerfoot, 1981). However, the integration of taxa from various habitats is not complete anywhere in a lake, which means that subfossil assemblages do not completely represent living communities. In fact, a recent study in the Belauer See, Germany, in which surface sediments were analyzed along a network of transects covering the entire lake bottom, revealed that the major sedimentation pattern of Cladocera was produced by direct *in situ* deposition of remains (Hofmann, 1998). Thus, in any sediment-based study on Cladocera, one must always remember that the assemblages we are dealing with are only secondarily composed assemblages. The consequences of this information to paleolimnological interpretations are further discussed in Hofmann (1987).

The conditions and processes that affect the distribution and deposition of remains should be taken into consideration when planning the sampling strategy. These include, *inter alia,* morphometric properties, mixing, sediment focusing, re-deposition, input of both organic and inorganic material from the catchment, bioturbation, and changes in lake level (see Dearing, 1986). In general, in large or shallow lakes, in bathymetrically complex basins, and in wind-stressed conditions, sediment distribution mapping by systematic coring or echosounding may be necessary for locating the major sedimentation areas. The optimal coring site and the quantity and type of samples to be taken will, however, be ultimately determined by the purpose of the study. For example, if one's intention is to examine general lake ontogeny or species successions, analysis of one central master core is probably the best choice. In contrast, several cores, which more adequately represent the entire sedimentation environment, are needed for a more detailed analysis of a particular event within a lake (Hann, 1989). As the consequences of many perturbations, such as water-level change, are

most pronounced in the littoral zone, inshore sediments should also be studied to achieve a proper understanding of environmental change. Until now, such multiple-core sampling across the whole basin has not been fully utilized.

How to prepare slides?

Cladocera remains are usually relatively abundant in lake sediments; typically there are several thousand fragments of Cladocera per cm^3 of fresh sediment. The volumes needed for identification and counting range from $1\,cm^3$ to more than $10\,cm^3$ depending on the sediment type; organic gyttja is typically rich in Cladocera, whereas mineral sediments are generally Cladocera-poor.

Different sediment types require somewhat different methods before Cladocera remains can be identified. Frey (1986a) summarizes, in detail, the various treatments needed. All methods include some chemical treatments, although this increases fragmentation and degradation of the remains and thus makes identification more difficult. Enumeration of remains from sediments with a high content of inorganic material is often difficult due to the inorganic matrix obscuring the remains. As outlined by Frey (1986a), hydrofluoric acid (HF, a procedure which has significant safety risks) may be used to help remove inorganic material, while hydrochloric acid may be used to remove carbonates. However, acid treatments can lead to the dissolution of remains (DeCosta, 1968; Hann, 1989). Unnecessarily harsh chemicals, such as strong acids or HF, should therefore be avoided. Due to risk of fragmenting, we also recommend not to centrifuge and not to use a magnetic bar in any step involved in the process. Heating should be at 70–80 °C and boiling should be avoided.

Quantifying the samples to a volume or weight basis may add an important dimension to the data. For example, quantitative data provide information on the degree of preservation of the remains, which may be very helpful when interpreting the results. Under favorable circumstances, quantification of the remains may also allow a direct estimate of past production of the organisms. However, Kerfoot (1974) discusses the difficulties in relating the accumulation rates of cladoceran remains to animal abundance. According to him, accumulation rates are only indirectly related to animal abundances, because of the problems of shedding of exuviae, differential transportation, and temperature-related turnover rates. Cladoceran growth takes place through the moulting of the shell or carapace, and the formation of a new larger carapace. Depending on the number of moultings during its lifespan, each individual generates a different number of exuviae, and hence skeletal fragments (Frey, 1986a).

We recommend the following gentle method for all sediments, including the mineral ones:

1. In a 250 ml beaker placed on a hotplate, mix a volumetric sample of sediment and 150ml of a 10% KOH solution. Heat to approximately 70–80°C for 30min (or 1 h in the case of highly organic-rich sediment) with constant gentle stirring. Mixing is recommended to be done manually by using a glass rod instead of a magnetic stirrer which may cause unnesessary fragmentation of remains.

2. Pour the KOH-sediment mixture onto a $50\,\mu m$ sieve and wash under running tap water until the rinsing water comes through clear. The fine material passing the screen

should be examined microscopically to check for the possible loss of fine exoskeletal fragments.

3. Transfer the residue retained on the screen into a 5–15 ml tube with a screw-cap, depending on the amount of remains in the sample, with a gentle jet of tab water. It requires some practice not to use too much water but still transfer all the reamins into the tube. Add 2–3 drops of safranin-glycerin solution to color the Cladocera remains in the sample. Several drops of formalin or alcohol can be added as a preservative. The volume of the sample at this point should be noted in order to quantify the counted sample later.

4. Quantitative slides are prepared by pipetting 200 μl of the well-stirred sample onto an object glass, which will be covered with a 24 x 50 mm cover slip and counted using magnifications 100–240×. Permanent slides can be made by using glycerin as a mounting medium and nail varnish as a cover slip seal.

5. Usually two slides are sufficient for identifying at least 200 remains, which is the minimum number recommended for counting. All Cladocera remains found (e.g., carapaces, headshields, ephippia, and postabdominal claws) should be tabulated separately, but only the most frequent body part for each taxon should be used for estimate of species abundance. If the two halves of the bilateral carapace have come apart, as is often the case with some of the larger species (e.g., *Eurycercus, Leydigia*), one half should be counted as half an individual. Badly fragmented remains should only be counted if they contain a clear diagnostic feature (Goulden, 1969). If total biomass production or annual fluxes to the sediment are to be determined, then processed samples must be counted entirely.

6. Calculate the counted portion of the sample to "remains per cm^3" by using the volumetric information of the sample prepared, diluted sample in the tube, and the proportion of the sample counted.

Identification of remains

The number of species that are preserved in sediments is rather small. However, not all taxa have yet been recognized. Also, there are very likely more physiological races and ecotypes within particular species than was originally thought (Frey, 1986b). Thus, our ecological interpretations of Cladocera are hampered by taxonomic uncertainty for several species.

Unfortunately, there is no single 'standard' identification manual available that could be used as a starting point for the identification of sub-fossil Cladocera. Instead, each analyst is required to collect such information from various literature sources, such as research reports, faunistic summaries, and illustrated keys. Frey (1986a) gives a comprehensive list of publications that are useful for identification of cladoceran remains. Perhaps the most practical and also widely used of these are Brooks (1957, 1959), Frey (1958, 1959, 1960, 1962, 1965, 1982), DeCosta (1964), Goulden (1964), Goulden & Frey (1963), Megard (1967), Scourfield & Harding (1966), and Smirnov (1971a, 1978). Other relevant literature sources for species identification, not mentioned in Frey (1986a), include Frey (1980, 1985),

Deevey (1964), Deevey & Deevey (1971), Flössner (1972), Flössner & Kraus (1977), Hofmann (1978, 1984), Chengalath & Hann (1981), Hann (1980, 1989), Pennak (1989), Lieder (1983a-c, 1986), Dodson & Frey (1991), Fryer (1993), and De Melo & Hebert (1994).

The many kinds of Cladocera fragments found in sediments cannot be confidently identified for all species, but due to the pioneering work by Frey (1958, 1959), identification of head shields and carapaces of Chydoridae has become relatively easy. The carapace (Fig. 3A–F) is almost always the most frequent chydorid skeletal fragment found, but examination of head shields (Fig. 3G–M) is recommended, because they often carry the best diagnostic features to differentiate species of some genera (LRC Core Facility Handbook, 1997). The identification of the chydorid head shield is done on the basis of the size, shape and ornamentation of the head shield, as well as the number, size and location of the head pores (Fig. 3G–M). These fragments can, in most cases, be identified to species. Yet, some difficulties do exist in the separation of certain chydorid remains, in particular those of small *Alona* species. Other problems concern the exact identification of species from the often fragmentary remains found in sediment.

The taxonomy of *Bosmina* has been problematic despite several attempts at clarification. Few other freshwater genera exhibit such a variety of phenotypes. The publications by Hofmann (1978, 1984), Nilssen & Larsson (1980), and Lieder (1983a–c, 1986) are particularly useful for *Bosmina* identification. Furthermore, Nilssen et al. (1980) describes seasonal morphological variability in *Bosmina.*

The cladoceran web site by Rowe & Hebert (1999) contain a useful and updated list of the *Daphnia* species known to occur in North America, with detailed descriptions and photos of each species. The taxonomy is largerly based on Colbourne et al. (1996).

The use of Cladocera in tracking environmental change

The study of Cladocera began in Denmark in the late 18^{th} century and then spread to other countries in northern Europe. The earliest occasional recordings of cladoceran remains in sediment material were already made in the late 19^{th} century. However, it was only until the work of Frey (1958, 1959), who brought these analysis into a more systematic level, that stimulated the use of Cladocera research in paleolimnology. Since then, cladocerans have been used for many paleoenvironmental applications.

The classical approach to relate fossil assemblages to environmental conditions involves the indicator-species approach. However, a common conclusion emerging from the numerous studies on cladoceran remains is that the ecological indicator value of individual cladoceran species is rather low. Instead of single species, interpretations should be based on the overall structure and composition of the assemblage. In order to interpret the remains of Cladocera in lake sediments in a meaningful way, it is essential to know the regional relationships of cladoceran assemblages to the environmental factors that are responsible for their distributions and abundance in the same or in comparable present-day systems.

The so-called calibration set (or training set) approach, in which modern taxon data are sampled from surface sediment samples of a large number of lakes distributed along an environmental gradient of interest (e.g., pH, temperature, nutrients), is one of the best and quickest means of gathering information about environmental variables regulating

the distributional patterns of cladoceran assemblages in present-day lake environments. With the collection of each surface sediment sample, detailed environmental information concerning the lake and its catchment is also gathered. Multivariate analysis techniques are then used to identify the environmental parameters most strongly correlated with the species distributions. Once the important variables influencing the taxon distributions are identified, quantitative predictive models or transfer functions can be developed using a variety of calibration approaches (for more details, see Charles & Smol, 1994; Birks, 1995, 1998).

Below, a few examples of the applications of cladoceran research are summarized. We give examples of more traditional studies where the emphasis is on qualitative descriptions, but also deal with more recent attempts towards quantification of key environmental parameters. Further examples of applications are provided by, for example, Frey (1979, 1986a), Hofmann (1987), Hann (1989), and Szeroczynska (1998).

Climatic change

A number of studies have used cladoceran records to infer past climates. These studies have usually demonstrated relative changes rather than providing quantitative estimates of climatic variables. The community response of Cladocera to changes in the physical environment is generally reflected by species diversity measurements (Hofmann, 1987). Several investigations (e.g., Goulden 1964; Hofmann, 1983, 1993; Flössner, 1990; Korhola & Tikkanen, 1991) have documented that species-poor cladoceran assemblages dominated in lakes in Europe during late-glacial times, whereas they were replaced by a more diverse fauna at the onset of the Holocene. The scanty chydorid fauna during late-glacial times consisted of cold-tolerant forms such as *Chydorus sphaericus, Acroperus harpae, Alona affinis, A. quadrangularis,* and *Alonella nana.* Such sub-arctic/arctic species composition (*sensu* Harmsworth, 1968) is thought to reflect cool climatic conditions, whereas climatic warming at the onset of the Holocene is indicated by an increase in species diversity due to the emergence of less cold-tolerant Cladocera taxa (Hofmann, 1987). However, Hann & Warner (1987) interpret the increase in species diversity from late glacial to post-glacial times as a response to limnological conditions (e.g., change in sediment characteristics, increase in rooted aquatics) rather than to climate.

In an attempt to separate local effects from regional influences upon lakes, Harmsworth (1968) analyzed cladocerans from a deep sediment core from a lake in the English Lake District and compared his results with a nearby lake, previously studied for subfossil cladocerans by Goulden (1964). The overall cladoceran stratigraphies in the two sites were remarkably similar in their percentage compositions, stratigraphic distributions and absolute numbers, suggesting that the records were of regional significance. Two processes that may have been responsible for these similar trends were increased productivity from late-glacial to post-glacial times, and 'morphometric eutrophication' (gradual filling-in). Both these processes are governed, to some extent, by climate.

Whiteside (1970) studied two Holocene sequences in Denmark for their fossil Cladocera and concluded that climate was the most important factor causing changes in species assemblages. However, only one of the study lakes was found to be particularly sensitive to climatic change, whereas in the other lake, the effect of climate was probably dampened

due to its chemical stability, as well as the large size and the specific morphological features of the lake. Thus, different lakes, even in the same geographic area, may respond differently to climatic forcing depending on their overall chemical and physical characteristics.

In a multi-proxy study of recent sediments of sub-arctic lake Saanajärvi, northwestern Finnish Lapland, a striking shift from the benthic to plankton-dominated cladoceran assemblage was observed starting at the turn of the 20^{th} century (Korhola et al., in press). This change was accompanied by species shifts in several other biological indicators such as in diatoms, chrysophytes, and plant pigments, suggesting a marked ecosystem response. The change paralleled the pronounced rise in mean annual temperature between the mid-19^{th} century and the 1930s reconstructed for the site using site-specific meteorological data, as well as long-term instrumental records from nearby climate stations. The first principal components analysis (PCA) axis of the planktonic Cladocera was found to be significantly correlated with the reconstructed mean annual temperature. Increased thermal stabilization due to rising epilimnetic temperatures was hypothesized to have been the most important causative factor for the observed biological change (Korhola et al., in press).

Lotter et al. (1997) made the first attempt to quantify the relationship between climate and cladoceran assemblages. They concluded that physical factors, including water depth, temperature and area of silicate bedrock, contributed markedly to the distributions of cladoceran taxa in 68 small alpine lakes along an altitudinal gradient from 300 to 2350 m in Switzerland. Quantitative inference models for mean summer air temperature were then developed for both planktonic and benthic life-forms of Cladocera, using weighted averaging partial least squares (WA-PLS) and linear-based partial least squares (PLS) regression (Lotter et al., 1997). After screening the data for outliers, the prediction accuracy of the temperature models in terms of root mean square error of prediction (RMSEP) was 1.6 °C for benthic Cladocera (WA-PLS) and 1.8 °C for planktonic Cladocera (PLS).

Similarly, distinct changes in the composition of surface-sediment cladoceran assemblages were found along an ecoclimatic sampling gradient comprising 53 subarctic lakes in northern Fennoscandia (Korhola, 1999). The multivariate approaches with variance partitioning procedures and associated Monte Carlo permutation tests demonstrated that the greatest proportion of faunal compositional variation was associated with changes in the physical environment, of which lake depth, substrate, and water temperature were among the most important contributors. Using total Cladocera, a one-component PLS model provided a jaccknifed RMSEP = 1.19 °C for water temperature. However, the data indicate a rather weak relationship ($r^2_{jack} = 0.30$) between the measured and PLS-inferred temperature, which is likely due to the short and uneven temperature gradient caused by the poor preservation of cladoceran remains in the coldest lakes in the data set. Thus, the Finnish Lapland cladoceran inference model for predicting lake-water temperatures should be considered, in many respects, tentative and should be improved in the future.

The Cladocera—temperature model developed by Lotter et al. (1997) has thus far been applied to late-glacial sequences of the classic Swiss study site, Gerzensee, with promising results (Lotter et al., 2000). Not only was the distinct cooling during the Younger Dryas recorded, but also many finer-scale climatic oscillations, such as the early Preboreal climatic cooling (Preboreal oscillation, PBO), can be identified on the basis of the cladoceran temperature reconstruction (Fig. 6). There is generally a good correspondence in Gerzensee between temperatures predicted using Cladocera and the reconstruction made by pollen, as well as the oxygen-isotope record. However, the cladoceran-inferred

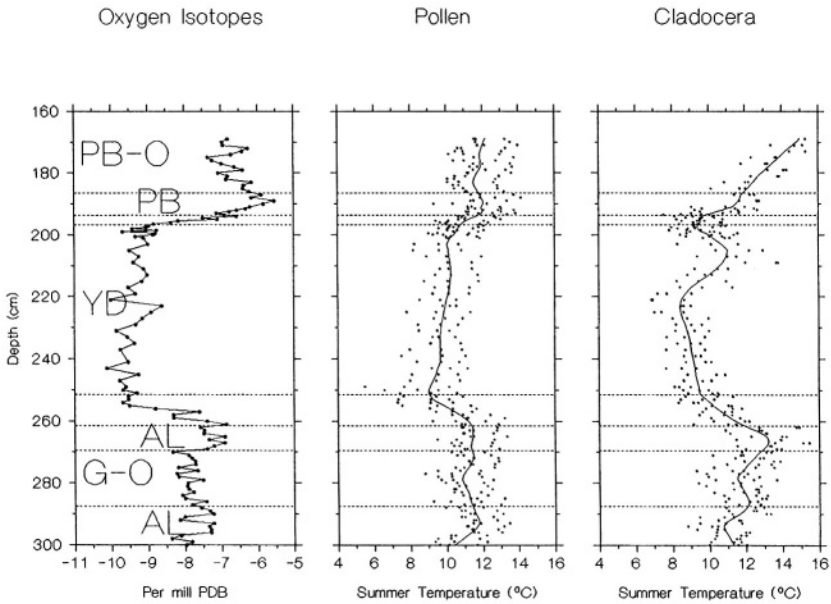


Figure 6. The chydorid-inferred summer-temperature for the late-glacial of Gerzensee plotted against the oxygen-isotope stratigraphy and the pollen-inferred summer temperatures. A combined reconstruction has been carried out both for pollen and Cladocera using PLS, WA, and WA-PLS models. The dots mark the sample-specific summer temperatures, whereas the solid lines represent LOWESS smoothed (tension = 0.1) summer temperature reconstructions. PB-O = Preboreal oscillation; YD = Younger Dryas cold phase; AL = Allerød; G-O = Gerzensee oscillation. Slightly modified from Lotter et al. (2000).

reconstruction suggests generally warmer summers than the pollen-based reconstruction, while there is no evidence for a cooling synchronous to the Preboreal oscillation in the oxygen-isotope record.

The Swiss Cladocera—temperature model has additionally been used to infer summer temperatures from the late-glacial cladoceran assemblages at Kråkenes lake, western Norway (Duigan & Birks, 2000). Although the general pattern of temperature changes was revealed, the cladoceran model again yielded systematically higher temperatures compared with the other proxies used. In this case, the difference was belived to be due to different ecological conditions in the Swiss training set lakes determined by high altitude and low latitude.

Lake level changes and lake terrestrialization

Cladocerans inhabit different habitats in lakes with their primary occurrence between limnetic and littoral zones, and among rock, sand, vegetation, and soft mud in the littoral zone. The bosminid and chydorid assemblages may thus yield information about factors that affect the relative importance of these habitats, such as lake morphometry (ratio between the open water area and the inshore area), occurrence and extent of rooted aquatics, and degree of terrestrialization (Amoros & van Urk, 1989).

Mueller (1964), on the basis of morphometric measurements in three lakes in Indiana, determined a planktonic/littoral (P/L) ratio to describe the volume of the planktonic zone relative to the littoral zone floor. He then investigated the horizontal distribution of cladoceran remains in surficial sediments along transects across the lakes, and found that the relative proportion of littoral to planktonic remains was subject to consistent changes with increasing depth and distance from the shore. Thus, the changing littoral-planktonic proportion of remains in sedimentary cores may be useful as an indicator of the areal changes between the shallow-water and open-water zones, and the relative dominance of littoral or planktonic production following periods of a lake's expansion or reduction. As littoral area increases relative to planktonic volume, there should be a corresponding increase in littoral Cladocera reflecting an increase in the type of habitat needed for a littoral fauna. Earlier, Brehm et al. (1948) used the relative abundance of chydorid and planktonic species to indicate periods of expansion and contraction of lake area.

Several attempts have since been made to use the ratio of planktonic to littoral cladocerans to indicate historical fluctuations in lake levels (Alhonen, 1970, 1972; Whiteside, 1970; Amoros & van Urk, 1989; Korhola, 1990, 1992; Hyvärinen & Alhonen, 1994; Szeroczynska, 1998; Sarmaja-Korjonen & Alhonen, 1999; Sarmaja-Korjonen & Hyvärinen, 1999). Mikulski (1978), for example, found the P/L ratio to reflect closely the lake-level changes inferred by other methods, while Bradbury & Whiteside (1980) demonstrated changes in the open-water area using both diatoms and Cladocera. Similarly, Hyvärinen & Alhonen (1994) studied two small closed-basin lakes in Finnish Lapland for both diatoms and Cladocera. Based on the low occurrence of planktonic cladocerans and diatoms between about 8000 and 4000 BP, the authors suggested that water levels were considerably lower then than today.

Meanwhile, many arguments have been put forward against the use of such a simple P/L ratio to reconstruct changes in bathymetric development and water depth (see Hofmann, 1998 and references therein). For example, rising nutrient levels and associated changes in lake trophy may favor the planktonic element relative to the littoral component without any change in water level (Crisman & Whitehead, 1978). Also, a shift in the plankton community from well preserved taxa (e.g., *Bosmina*) to weakly preserved taxa (e.g., *Daphnia*) may affect the relative proportion of planktonic *versus* littoral taxa in the subfossil record. Moreover, as the genus *Bosmina* is an important diet item both for fish and invertebrate predators, changes in food webs may also change the planktonic-littoral relationships (Nilssen, 1978). For example, in a small clear-water lake in southern Finland, the proportion of planktonic Cladocera increased from around 30% in the early 20th century to current values of ca. 70% as a result of increased acidification and associated declines in fish predation (Uimonen-Simola & Tolonen, 1987). Caution should therefore be exercised when interpreting the changes in P/L ratio solely in terms of water level fluctuations, as many additional abiotic and biotic factors can affect the ability of various littoral and planktonic forms to thrive (Whiteside & Swindoll, 1988; Hofmann, 1998).

In order to circumvent at least some of the above-stated problems, several sites in a region should preferably be studied for lake-level changes (Sarmaja-Korjonen & Hyvärinen, 1999). It is highly unlikely that consistent trends in the P/L ratio observed over wide areas could be explained, for example, by changes in predation or by habitat changes of a kind that were not specifically the consequences of external events, such as climatically induced fluctuations in water level (Korhola, 1992). In addition, interpretations should not be based

solely on the P/L ratio, but should include all the information available from an ecological analysis of the preserved assemblages.

Korhola (1990, 1992) tested how water-depth changes are reflected by the entire cladoceran fauna in sediment cores taken from former lakes which were filled in by sedimentation and transformed into mires at the beginning of the Subboreal chronozone. He classified the chydorid species into three habitat groups: 1) restricted to vegetation, 2) associated to vegetation, and 3) bottom dwellers. Stages in hydrosereal succession were reflected in the cladoceran record by the disappearance of benthic species (bottom dwellers) and a reciprocal increase of exclusively phytophile species. The P/L ratio closely followed the relation between open water and the macrophyte zone as a function of time.

Habitat preferences of Cladocera were also successfully used by Amoros & Urk (1989) and Jurasz & Amoros (1991) in their investigations of the history of overgrown meanders of the River Rhône in France. A reverse in the hydroseral succession caused by a progressive rise in the mean water level was inferred from the cladoceran remains (Jurasz & Amoros, 1991). Thus, important information about the physiographical development of a water body can be achieved by the analysis of subfossil Cladocera.

Korhola (1999) analyzed the relationship between surface-sediment cladoceran assemblages to lake depth in more detail in 53 small subarctic lakes in Finnish Lapland using multivariate statistical approaches. From the 28 physical and chemical variables measured, lake depth was identified as explaining the greatest proportion of variance in the cladoceran taxon data. A quantitative inference model was developed for lake depth using the entire cladoceran assemblage (Korhola et al., 2000). The prediction accuracy of the 2-component WA-PLS Cladocera—lake depth model was 1.56m as assessed by leave-one-out cross-validation (depth range in calibration lakes = 0.87–27.0 m).

The Finnish Cladocera—lake depth model (Korhola et al., 2000) has been tentatively applied to a small kettle-hole lake in northwestern Finnish Lapland to infer changes in Holocene water levels (Fig. 7). The site is located on a large aquifer of a fluvio-glacial esker reflecting regional water balance. The lake is presently 6.2 m deep, and contains 1.58 m of Holocene sediments. The quantitative inference model applied to the subfossil cladoceran assemblages suggests that the lake was ca. 8 m deep (6.2 m + 1.58 m = 7.8 m) in the early Holocene. Lake level then experienced a marked drop of 4–6 m in mid-Holocene times, with the lowest phase between 6000 and 4000 cal. yr. B.P. This was followed by a gradual increase in water depth during the latter half of the Holocene, suggesting increased climatic humidity in the area. The inferred value of 5.8 m for the uppermost sample corresponds well with the present measured depth (6 m) of the lake, giving some credence to the model. In general, the inferences are closely comparable with the humidity patterns previously suggested for Finnish Lapland by Hyvärinen & Alhonen (1994).

Bos et al. (1996, 1999) have also created a transfer function for predicting lake-level changes from cladoceran assemblages found in surface-sediments in lakes from the Interior Plateau of British Columbia, Canada. However, this transfer function has thus far not been used to reconstruct past lake-level changes in the region.

Lake trophy

Cladocerans are considered to be sensitive to changes in trophic status and are, therefore, used by many authors to study patterns of both natural and anthropogenically-caused lake

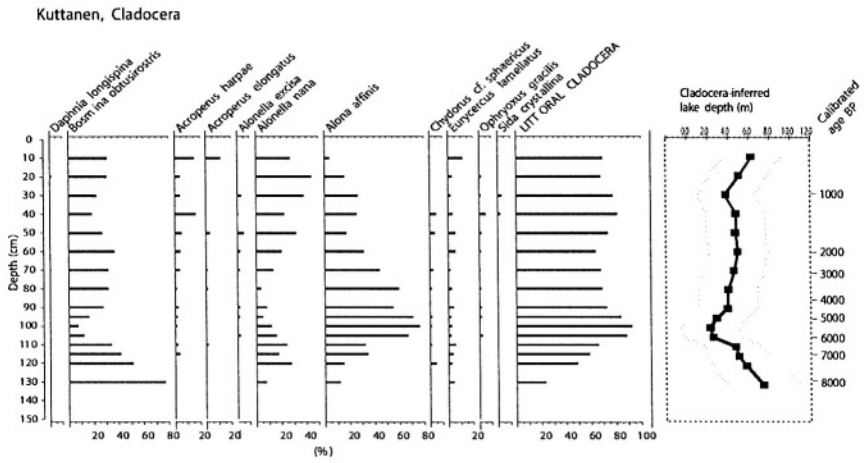


Figure 7. Cladocera relative frequency diagram of selected taxa and reconstructed Holocene lake level changes with sample-specific errors of the Lake Kuttanen in Finnish Lapland using the northern Fennoscandian cladoceran calibration data set of 53 lakes and a WA-PLS 2-component model (Korhola et al., 2000). The entire cladoceran fauna was used in the reconstruction. For the interpretation and accuracy of the results, see text. Reconstruction previously unpublished.

eutrophication (e.g., Whiteside, 1970; Alhonen, 1972, 1985; Birks et al., 1976; Boucherle & Züllig, 1983; Hofmann, 1986, 1996; Binford, 1986; Korhola 1990; Szeroczynska, 1991). However, Whiteside & Harmsworth (1967) demonstrated the negative relationship of chydorid species diversity to nutrient input, whereas Harmsworth & Whiteside (1968) presented evidence suggesting that the densities of cladoceran remains were not closely related to lake primary production.

According to Hofmann (1987), littoral cladocerans respond to eutrophication only if their inshore habitats are affected. In contrast, obvious and sometimes dramatic changes in bosminid species composition and abundance may be directly related to changes in trophic conditions. The widely-observed species replacement of *(Eu)bosmina longispina* by *Bosmina longimstris* is considered a classical example of eutrophication (Goulden, 1964; Deevey, 1969; Crisman & Whitehead, 1978; Hofmann, 1978). Using varved sediments of Lake St. Moritz, Switzerland, Boucherle & Züllig (1983) demonstrated that this species turnover may occur extremely rapidly, within a single year, as a response to eutrophication, in this case caused by increased tourism in the area. Similarly, Hann et al. (1994) used laminated sediments in Lake 227, Canada, to demonstrate a striking community response of Cladocera to experimental eutrophication. In some Polish waters, a rapid emergence of *B. longirostris* has been documented resulting from Mesolithic and Neolithic settlement (Szerozynska, 1991, 1998).

Hofmann (1977, 1978, 1983, 1987) has interpreted species replacements and morphological alternations within the subgenus *Eubosmina* (from *B. longispina* to *B. coregoni* f. *kessleri,* and finally to *B. coregoni* f. *coregoni)* as indicative of a progressive increase in trophic state from oligotropic, through mesotrophic, to more eutrophic systems in recent time. However, as pointed out by Nauwerck (1991), only in the case of *Bosmina longirostris* are such interpretations consistent with long-term monitoring data (Müller, 1985;

Nauwerck, 1988), whereas in *Eubosmina,* conclusions rely on indirect observations (e.g., Patalas & Patalas, 1966). An *a priori* interpretation of eutrophication should perhaps be avoided, as food supply and feeding patterns may also contribute to the composition of *Bosmina* populations (Müller, 1985). Nilssen (1978), for example, argued that succession of *Bosmina* might be more closely related to predatory interactions than to trophic state.

Lotter et al. (1998) found a statistically significant relationship between benthic cladoceran assemblages and epilimnetic total phosphorus (TP) concentrations in a set of small alpine lakes in Switzerland. While benthic Cladocera yielded a transfer function for total TP with a prediction accuracy, after cross-validation, of $0.28 \log \mu g\ TP\ l^{-1}$ (sreened data), only a very weak relationship was found between planktonic Cladocera and TP. The minor influence of TP on planktonic Cladocera was also noted by Jeppesen et al. (1996) in their study on planktivorous fish and trophic patterns in Danish lakes.

Brodersen et al. (1998) re-sampled 32 of the Whiteside's (1970) original 70 Danish lakes for water chemistry and surface-sediment cladocerans in an attempt to trace possible changes in the trophic state of the systems concerned during the 27-year time period between the two sampling endeavors. Using canonical correspondence analysis, they discovered a strong relationship between the species data and lake total phosphorus (TP) concentrations, which enabled them to establish a chydorid-based model to infer TP by weighted averaging, with a bootstrapped coefficient of determination of 0.79 and prediction error of $0.24\ \mu g \log TP\ l^{-1}$. Clear changes in TP concentration were observed in some of the study sites when the model was applied to the original data set lacking TP measurements.

Recently, Bos (2000) analysed sediment cores from two lakes from central British Columbia, Canada, that experienced known changes in trophic state and/or changes in fish populations, for cladoceran microfossils. Reconstructions of TP were made using weighted-averaging models based on a 50-lake calibration set that spanned oligotrophic through eutrophic lakes in the Prince George region. Contemporaneously, changes in the size of daphnid postabdominal claws were used to infer past changes in fish planktivory. Changes in the cladoceran assemblages and inferred TP levels were found consistent with the cultural eutrophication that is believed to have occurred. According to this study, the Cladocera promise to be a useful management tool, and may also be able to answer key ecological questions related to long-term changes in nutrients and fish within lakes.

Acidification

Several paleolimnological studies have found distinct changes in the composition of cladoceran assemblages in association with evidence of acidification (Fryer, 1980; Brakke, 1980; Brakke et al., 1984; Arzet et al., 1986; Krause-Dellin & Steinberg, 1986; Uimonen-Simola & Tolonen, 1987; Steinberg et al., 1988; Nilssen & Sandøy, 1990; Korhola, 1992; Paterson, 1994; Havas & Rosseland, 1995). Increasing acidity is usually shown as changes in community interactions, loss of acid-sensitive species, declines in species richness, and changes in total cladoceran biomass and abundance. Decreasing species diversity in recently acidified lakes has been reported in North America (e.g., DeCosta, 1975; Yan & Strus, 1980; Paterson, 1994) and Europe (e.g., Fryer, 1980; Brakke et al., 1984).

Krause-Dellin & Steinberg (1986) used cluster analysis to assign the chydorid species found in the surficial sediments of 23 lakes in the European Alps into five pH categories according to their abundances. Multiple linear regression was then used to establish a

regression equation ('index C') to explore the relationship of the established pH groups to mean water pH. When applied to three sediment cores with cladoceran counts, a good correspondence was found between the pH reconstructed from index C with methods using diatoms. However, Hofmann (1986), Flössner (1990) and Szeroczyncka (1998) have expressed some reservations concerning the method. According to Hofmann (1986), the model overestimates the significance of pH and underestimates the effect of various other environmental factors governing the species abundance and chydorid community structure. Moreover, many chydorid taxa seem to show a bimodal response to pH. For example, *Chydorus* cf. *sphaericus* is a taxon that often predominates in highly eutrophied lakes with summer pH even above 9 (Hofmann, 1986), yet it can equally well be found in numbers in acid lakes and bog waters with pH below 5 (Korhola, 1992). Despite these difficulties, cladocerans have potential in quantitative reconstruction of lakewater pH, as shown in the subsequent study by Huttunen et al. (1988) in Finnish lakes.

Paterson (1994) examined cladoceran remains in three Adirondack Park (New York) lakes, which, according to diatom evidence (Charles et al., 1990), had become strongly acidified in recent decades. In all of the study cores, the greatest changes in net accumulation rates, relative abundance of species, and species richness of Cladocera occurred in recently deposited sediments. The primary correspondence analysis (CA) ordination axes scores for each lake were found to be highly correlated with diatom-inferred pH. Reduced species richness was also seen in acidified Norwegian lakes studied by Nilssen & Sandøy (1990), with a disappearance of the acid-sensitive plankters such as *Daphnia longispina, Bythotrephes longimanus, Leptodora kindtii,* and *Bosmina longirostris,* whereas littoral taxa such as *Alona intermedia, Alona guttata, Alonella exigua,* and *Ophryoxus gracilis* were also extirpated. In contrast, although there were shifts in the relative abundances of cladoceran species, no declines in species number were found in six Finnish lakes which were strongly acidified during the past ≈30 years (Uimonen-Simola & Tolonen, 1987).

Natural acidification can also cause dramatic changes in cladoceran assemblages. Examination of subfossil diatoms suggest that Lake Pieni Majaslampi in southern Finland was subjected to extremely pronounced natural acidification during its early developmental phases, with pH falling rapidly within the first ≈2000 years of lake's post-glacial history to pH 5.0 (Korhola & Tikkanen, 1991). The rapid early Holocene acidification was shown in the cladoceran succession by the replacement of *Bosmina longimstris* by *Bosmina (Eubosmina) longispina* (Fig. 8), and an increased number of acid-tolerant chydorid species, such *as Alonella excisa* and *Alona nana.* According to Nilssen & Sandøy (1990), a particularly sensitive pH interval for many aquatic organisms, including Cladocera, is pH 5.5–5.2, and the diatom evidence suggests such a change in pH for Pieni Majaslampi for the time period in question.

At the present time, *Bosmina longispina* characterises most acidified lakes in northern Europe (Sandøy & Nilssen, 1986; Uimonen-Simola & Tolonen, 1987; Nilssen & Sandøy, 1990), whereas *B. longirostris* is often the sole dominant planktonic Cladocera in acidified lakes in North America (Charles et al., 1990; Paterson, 1994). Among the chydorid Cladocera, *Alonella excisa, Alona rustica,* and *Acantholeberis curvirostris* appear to be associated with acid environments (Krause-Dellin & Steinberg, 1986; Nilssen & Sandøy, 1990). For example, in a broad-scale geographical survey in Norway, *Alonella excisa* was found to occur in >90% of lakes with pH less than 5.0 (Sandøy & Nilssen, 1986). However, as it has been shown that several chydorid species do not have cosmopolitan distributions

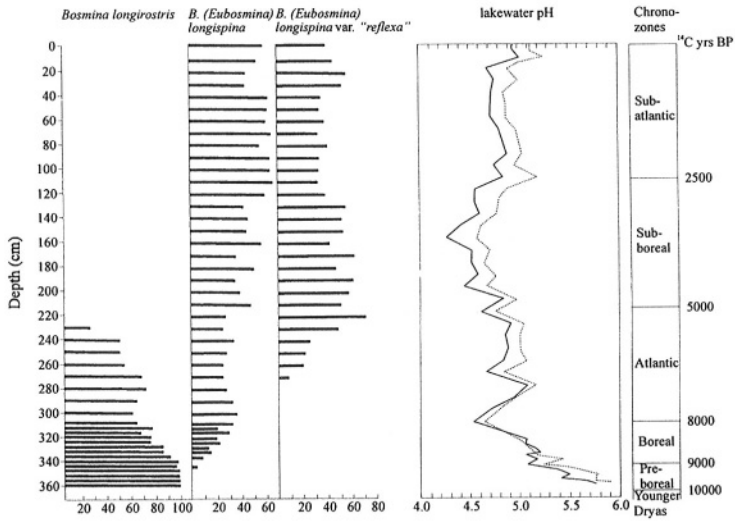


Figure 8. Holocene *Bosmina* succession at Pieni Majaslampi, southern Finland, plotted against diatom-inferred lakewater pH. pH reconstruction is based the Finnish HAPRO diatom calibration data-set (Huttunen & Turkia, 1990) comprising either all 89 lakes (broken line) and a subset of 63 lakes (solid line) with pH <6.8. The lake has experienced a pronounced natural acidification during its early development. Modified from Korhola & Tikkanen (1991).

(Frey, 1986b), any direct use of ecological information of species provided by papers on remote ecosystems should be avoided.

Although some cladoceran species, especially in the plankton, show a clear physiological relation to pH, species shifts and overall simplification of cladoceran assemblages in acid lakes are apparently not only due to pH. Quite often these changes are related to other factors such as predation, changes in aquatic vegetation, and high metal concentrations (Havens & DeCosta, 1987; Uimonen-Simola & Tolonen, 1987; Nilssen & Sandøy, 1990; Paterson, 1994). While the effects of metal contamination are generally difficult to identify, the patterns related to predation pressures are detectable in the sediments by recording the size of Cladocera(Hrbácek, 1969; Nilssen, 1978; Salo et al., 1989; Jeppesen et al., 1996). For example, Nilssen & Sandøy (1990) found small specimens of *Bosmina* to have comparably larger mucro length in acid fishless lakes in Norway, which was most obviously due to adaptation to increased invertebrate predation. Furthermore, laboratory studies have shown *Bosmina* to develop a larger mucro and rostrum in response to copepod predation (Kerfoot, 1977).

Future of cladoceran research

In the recent years, palaeoecology as a discipline has been changing from a predominantly desription-orientated subject to a more exact science with capabilities to provide quantitative data on environmental change (Birks, 1998). From this information, it is now possible to generate and test hypotheses, define natural variability, and evaluate models. The examples

given above concerning quantitative research using Cladocera demonstrate the enormous potential of using modern training data-sets along with rigorous statistical techniques in deriving more accurate information of past limnological and environmental changes. In addition to the parameters described above, attempts have also been made to reconstruct changes in water color using cladoceran fossils (Huttunen et al., 1998). Bos et al. (1996, 1999) have further developed transfer functions for salinity, conductivity, and lake levels on the basis of cladoceran assemblages found in surface-sediments in lakes from the Interior Plateau of British Columbia, Canada. However, these transfer functions have thus far not been used to interpret and reconstruct past environmental changes in this region.

Despite the major recent advancements in cladoceran research, there are still many gaps in our understanding of these organisms (Hann, 1989). In order to make more meaningful paleoenvironmental interpretations, more information is needed on the biogeography, taxonomy (even with the most common species), distribution and ecology of modern species. Although considerable research has been completed on cladocerans in some regions of the world, we do not yet know how many species occur in different parts of the world, and what are their ecological characteristics, feeding habits or behavior. Studies based on the transfer function approach are valuable, but other approaches are more appropriate to answer questions concerning biogeography and evolution.

The rapidly evolving techniques in genetics may provide a useful new tool in paleolimnology. Molecular ecology has, thus far, only rarely been used in paleo-research. Hairston et al. (1999) hatched ancient *Daphnia* eggs from Lake Constance, Germany, and were able to show rapid evolutionary responses to nutrient level changes in the species genetics. DNA can already be separated from unhatched eggs and new techniques are constantly under development to separate it from subfossil remains. Genetic markers may eventually provide tools to study not only speciation but also clonal variation within species. In addition to community analyses and changes in species abundances over time, individual species responses to shifts in the environment can also be recorded. Cladocera are especially useful test organisms for such molecular techniques because they reproduce parthenogenetically, and therefore there are clonal differences in tolerance to various environmental variables, such as temperature (Carvalho, 1987). If these clonal changes can be quantified, we will reach a new level in paleolimnology and will be able to provide better and more realiable information concerning historical events.

Finally, it should be noted that all the recent advances in palaeocological coring techniques, sampling protocols, taxonomic and analytical quality control, statistical data treatment, quantification, and interpretation of ecological information could be directly transferred to cladoceran palaeoecological work. Moreover, considerable attention is being now devoted to the possibility of rehabilitating aquatic systems to re-establish "natural ecological conditions" (as expressed, e.g., in the 'European Union Water Directive'). Analysis of subfossil Cladocera offers an opportunity to help assess what "natural conditions" were, to reconstruct the past biota of lakes, and to analyze biotic responses to recent anthropogenic pressures. Cladoceran analysis may therefore help answer some of the leading ecological questions of our time. This rich fossil fauna clearly deserves more attention.

Other crustacean branchiopods

The three other crustacean branchiopod groups can be considered 'living fossils' because their basic body characteristics have remained the same for millions of years. The most

complete fossil record belongs to the Notostraca, whose remains are found from a wide range of deposits, dating back from the Carboniferous to the Recent. However, their earliest known member is the fossil fairy shrimp *Rehbachiella kinnekullensis* found in Upper Cambrian sediments (Walossek, 1993). Recent changes in ecological conditions of natural habitats have often been fatal to these organisms. For example, Löffler (1993) reports that eight of the sixteen known Austrian large branchiopod species are extinct, primarily due to agricultural activities and artificial changes of hydrologic conditions.

Similar to Cladocera, the other branchiopod crustaceans have the following features: flat, biramous and setose trunk appendages, gringing mandibles associated with reduced first and second maxillae, last body segment with a pair of short to long cecopods, and legs modified for swimming and/or food gathering (Pennak, 1989; Kerfoot & Lynch, 1987). In comparison to Cladocera, the representatives of the other three orders are relatively large-bodied; body length ranges from millimeters to centimeters: Anostraca 7–100 mm, Notostraca 10–58 mm and Concostraca 2–16 mm (Kerfoot & Lynch, 1987).

Anostracans differ from the other large branchiopods in having stalked compound eyes and in not having any shield (carapace) covering the body. They are backstrokers, as their ventral side is oriented to the light. The limbs are continuously filtering food particles (microorganisms and organic matter) out of the water (Dexter, 1959). Notostracans possess a large, shield-like carapace, a fused pair of eyes on top of the carapace, and a segmented abdomen. They have 35 to 71 pairs of ventral appendages called phyllopods (phyllo = "leaf" and pod = "feet"), which beat in a wavelike motion from front to back and propelling the animal. Notostraca are omnivorous, and they dig around in the mud using the frontal part of their shield, searching not only for plankton but also for larger prey such as worms, chironomid larvae and even tadpoles (Thorp & Covich, 1991). Anostracans, often associated with notostracans, are also part of their prey.

Conchostracans have internal compound eyes and a large protective bivalve shield, which covers the entire body. Swimming in a staggering style, they use the second antennae in addition to their legs. Conchostraca filter food particles out of the water or stirred-up mud. The reproductive mode of clam shrimps can be obligately sexual, hermaphroditic or partenogenetic. Conchostracans develop very quickly (depending on temperature, adult individuals could be found within a few days after inundation) and are thus well adapted to the extreme conditions of astatic water bodies.

All three orders are widely distributed geographically. However, the large crustacean branciopods have a limited number of species, which are generally found in ephemeral aquatic habitats (e.g., vernal pools, road ditches, springs, temporary lakes), an environment with very few aquatic predators, especially fish (Kerfoot & Lynch, 1987; Thorp & Covich, 1991; King et al., 1996). These crustaceans are slow-moving and have no defenses against direct predation by fish. They are readily consumed if there is a temporary connection of their living environments to more permanent water bodies containing fish (Pennak, 1989).

Tadpole shrimps are characteristic of shallow, saline lakes and ponds of arid environments, whereas fairy shrimps and clam shrimps occupy temporal waterbodies of semiarid regions (Wetzel, 1983). Notostraca are essentially benthic, living near the bottom of water bodies, where they move with their ventral side down, whereas Anostraca and Conchostraca are common in the plankton. However, Conchostraca may spend much time on the ground of temporary puddles, sometimes almost entirely dug into the mud just like mussels. Occurrence and species compositions of the large branchiopods are partially dependent

on hydrology, temperature, and water chemistry (Hathaway & Simovich, 1996; King et al., 1996). They have been classified according to their temperature tolerance to cold-stenothermal species, thermopilic and eurythermal species (e.g., Flössner, 1972). However, the temperature classifications are mostly observational and have no experimental data, as of yet, to support these observations.

A key adaptation of these animals to a transient (e.g., alternately wet and dry) environment is the numerous degradation-resistant cysts (eggs) they produce. For example, a female tadpole shrimp may produce thousands of cysts during her life span. Adult females have an ovisac where the mature eggs are continuously moved to be supplied with oxygen. These cysts can also withstand high temperatures, drying out, and frost, while embedded in the top layers of the soil sediments, and can remain dormant and viable for months or even years while waiting for suitable environmental conditions to initiate their hatching. Another strategy for adapting to temporary and harsh environments is reaching sexual maturity rapidly (in as little as three weeks). Rapid sexual maturity allows these organisms to hatch, mature, and produce numerous cysts quickly, thereby effectively adapting to short-lived environments. This temporal isolation (separated by time) allows them to occupy a harsh environment to which few predator species have adapted.

In suitable conditions, the cysts (or eggs) of the large branchiopods are preserved in sediments and can be extracted as pan of routine cladoceran analysis. Although not yet fully utilized in the context of paleolimnological research, the remains of these crustaceans may have high indicator value, for example, in tracing past changes in fish populations in various types of aquatic environments. Their cysts may also provide information about rapid environmental changes in particular in extreme environments, such as arctic ponds and saline lakes of arid regions. The sensitivity of the large branchiopods to water temperature is also well established (Flössner, 1972). For instance, the hydrological and thermal differences of the Austrian Danube River flood plains were reflected by the large branchiopod fauna so that cold-stenothermal species were found along the Morava floodplain during spring inundations, whereas species preferring warm water were found along the Danube floodplain during high waters in summer (Eder et al., 1997).

Bos et al. (1999) recorded anostracan remains along with other branchiopods from surface-sediment samples of 33 closed-basin saline lakes from British Columbia, Canada. They found the planktonic anostracan species *Anemia franciscana* to be restricted to sites with highest salinity in the data set. Calibration models were developed to infer lake-water salinity, conductivity, and lake level from the species composition of anostracans and cladocerans.

Summary

The order Cladocera is an old group of microscopic branchiopod crustaceans known at least from the mid-Mesozoic era. They are among the best-represented groups of aquatic animals that leave remains in lake sedimentary deposits. Their high potential for paleoecological research is based on high ecological (microhabitat) diversity, easy dispersal between lakes, and short generation times. These factors enable them to closely track environmental change, without the timelags associated with some other paleoecological methods. However, the extraction of information from fossil assemblages is not easy, as because many biotic and abiotic factors are involved.

The examples reported demonstrate the value of Cladocera as indicators of a variety of environmental changes and disturbances affecting lake status, such as climatic changes, trophic oscillations, acidification, and water-level changes. In general, planktonic *Bosmina* and *Daphnia* species are sensitive to changes in lake trophic state, predation, lake transparency, and acidification status, whereas littoral chydorid assemblages are responsive to changes in substrate type and macrophytes within the littoral zone. During the past decade, the transfer-function approach has been successfully applied to a wide range of environmental problems using Cladocera. The preliminary results indicate that these crustaceans can be effectively used to provide reliable quantitative data on environmental changes once high-quality and extensive calibration data-sets are obtained. Taking into account the limitations of the analysis (e.g., differential preservation), it is possible to successfully use cladoceran remains for a wide spectrum of paleoenvironmental investigations.

The other groups of branchipod crustaceans (Anostraca, Notostraca and Conchostraca) have not been fully utilized in paleolimnological research, but they may have considerable potential in reconstructing, for example, former fish status and rapid changes in extreme environments. The Branchiopoda promise to be a useful tool in paleolimnological reconstruction.

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3. MIDGES: CHIRONOMIDAE AND RELATED DIPTERA

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Introduction

Among insects, the chitinous larval remains of the order Diptera (true flies) are most abundant in lake sediments, and thus have proven to be especially useful in palaeoenvironmental studies. Within this large and diverse group, however, remains of the Chironomidae (non-biting midges) greatly exceed the remains of all other Diptera in abundance. Only a few other families—the Chaoboridae (phantom midges), the Ceratopogonidae (biting midges or "no-see-ums"), and the Simuliidae (black flies)—are sufficiently common to be of much interest to palaeoecologists. Each of these families is principally aquatic in its larval form, although the Ceratopogonidae and Chironomidae comprise some terrestrial or semi-terrestrial species. Head capsules are the principal remains of the Chironomidae, Ceratopogonidae and Simuliidae that can be recovered from lake sediments (Fig. la, b, c, d, f). Identification of the Chaoboridae relies instead upon the larval mandibles (Fig. 1e).

Overview of life cycles and ecology

Chironomidae ("Non-biting midges")

Since chironomid remains (Fig. 1a, b) are far more abundant than those of any other insect in lake sediments, this chapter will focus especially on their attributes. The Chironomidae are holometabolous insects, developing from an egg, through a series of four larval instars, before pupation, and finally emergence as an adult insect.

For aquatic species, the eggs are deposited by adults on, or in, the water. The egg stage is usually brief, but may vary markedly in duration from one species to another. In lentic species the first instar larva is typically planktonic, and is sometimes referred to as the larvule. The larvule will eventually settle to the bottom, shed the thin, chitinous cuticle

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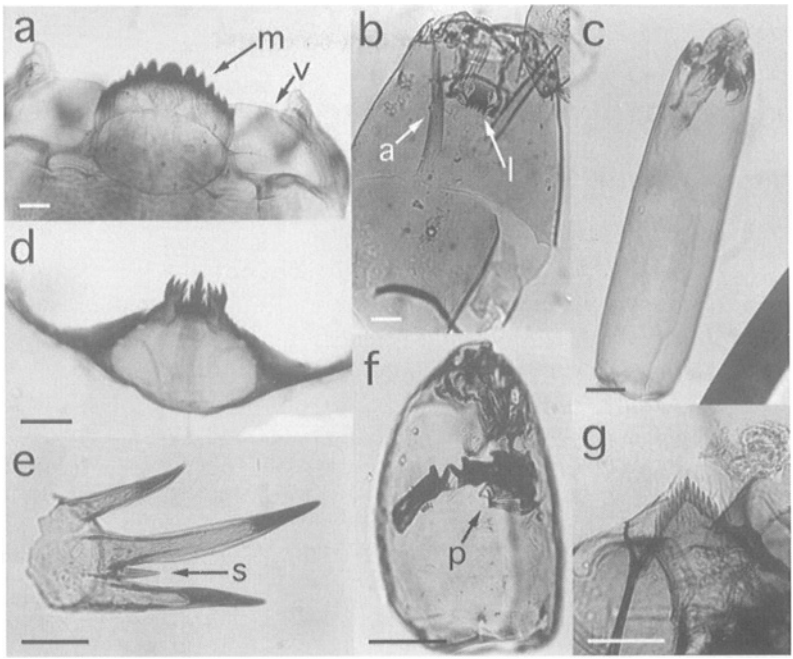

Figure 1. Representative remains of some common Diptera: a) mentum (m) and ventromental plates (v) of *Glyptotendipes* (Chironomidae), b) Pentaneurini head capsule (Chironomidae) with ligula (l) and retracted first antennal segments (a), c) *Bezzia* type head capsule (Ceratopogonidae), d) hypostoma of *Prosimulium* (Simuliidae), e) mandible of *Chaoborus flavicans* (Meigen) (Chaoboridae) (s = subordinate tooth), f) *Dasyhelea* type head capsule (Ceratopogonidae) with pharyngeal complex (p), g) head capsule of Culicidae, including toothed hypostomal plate. Horizontal bar in lower left corner of each photograph represents 0.05 mm.

which surrounds the thorax and abdomen, and progress to the next instar. A more or less strongly sclerotized head capsule is also shed with the cuticle (Walker, 1987).

Three subsequent episodes of growth and ecdysis (shedding of the head capsule and cuticle) define the remaining larval instars. The second, third and fourth instar larvae are mostly bottom-dwellers (benthic), although larvae of some species (e.g., *Sergentia coracina* (Zetterstedt)) are at least partially planktonic. The larvae vary tremendously in their feeding habits. Many are detritivores or filter-feeders, while others graze on algae and bacteria, or burrow into either wood or aquatic plants. Some, for example the Tanypodinae, are omnivorous, preying on other midge larvae or aquatic invertebrates, as well as eating other matter.

The littoral zone is home to most lentic Chironomidae, but some species occur in the profundal zone. A few bright-red, hemoglobin-containing species (e.g., *Chironomus plumosus* (Linnaeus) and *C. anthracinus* Zetterstedt) are able to tolerate prolonged periods of hypolimnetic anoxia. Many other chironomids inhabit streams, while some are typical of moist soils, peats, littoral marine environments, pitcher plant leaves, or even dung. Chironomids are known from every continent, being distributed from tropical rain forests to high arctic and alpine tundra. Only three species occur on the Antarctic mainland, although a few others are known from the Antarctic islands (Cranston, 1995).

In most Chironomidae, each larval instar is progressively longer in duration than the one preceding. During the fourth (pre-pupal) larval instar, the thoracic segments eventually become markedly enlarged, and with ecdysis, the insect is transformed to a pupa. The pupa is normally a short-lived stage in which the body form is reorganised from that of a larva, to an adult (imago). The pupa will migrate to the water surface, where the dorsal thoracic cuticle will split, allowing the adult to emerge. The adults of at least some species may feed on nectar, but the adults are typically short-lived. Their wings and small-size potentially allow the adults to disperse widely, colonising new habitats (Armitage et al., 1995).

The entire chironomid life-cycle varies greatly in duration. Most tropical species are probably multivoltine (completing several generations in one year), whereas most temperate taxa are univoltine or bivoltine. In the arctic, Butler (1982) noted two *Chironomus* species required seven years to complete one generation.

In sediments, the head capsules shed by third and fourth instar larvae during ecdysis, and the remains of individuals that died as larvae, are most abundant. Due to differential preservation, early instar remains are less abundant in sediments. Iovino (1975) demonstrated that the chitin in first and second instar head capsules is resorbed prior to ecdysis. Pupal thoracic horns and adult hypopygia have also been recovered from sediments (e.g., Hofmann, 1984; Bitušík & Kubovčík, 1999) but are much less common than head capsules in lake sediments.

A more complete synopsis of chironomid biology and ecology is provided by Armitage et al. (1995).

Related Diptera

Being closely related holometabolous aquatic insects, the Ceratopogonidae, Simuliidae, Chaoboridae, Culicidae and Thaumaleidae have life cycles that much resemble those of chironomids. All develop through the same sequence from egg to larva to pupa to adult. The Ceratopogonidae, Culicidae, Chaoboridae and Thaumaleidae always have four larval instars, but the number of larval instars varies from four to nine in the Simuliidae.

Ceratopogonidae ("Biting midges " or "No-see-ums")

In terms of ecology, the Ceratopogonidae (Fig. 1c, f) most resemble the Chironomidae. They are widely distributed among benthic standing water and semi-terrestrial habitats, but are much less common than chironomids. The biting habit of the adults, a feature which distinguishes them from Chironomidae, can be a severe annoyance, and serves as a vector for the spread of several viruses and parasites.

Simuliidae ("Blackflies" or "Buffalo gnats")

As larvae, the Simuliidae (Fig. 1d) are found exclusively in streams, where they cling to hard surfaces. Most species feed on fine organic matter suspended in the current. They typically secure themselves in the current by depositing a pad of silk threads on a rock or log, clinging to the silk by means of recurved hooks which surround the posterior proleg. Most species capture suspended food particles via labral fans which continually filter stream water as it passes near the mouth. Black fly larvae are often most abundant in plankton-rich waters immediately downstream of lakes, probably because suspended food is abundant, whereas

the concentrations of suspended mineral matter are low. The adult female flies commonly require a blood-meal for egg development, and their bites are a severe annoyance, especially in the boreal forest/taiga biome. They are sometimes vectors for diseases, such as "river blindness"; and massive outbreaks of some species have killed cattle (Giller & Malmqvist, 1998). They essentially have a world-wide distribution, but do not occur in Antarctica.

Culicidae ("Mosquitoes ")

Larval mosquitoes (Fig. 1g) are planktonic filter-feeders. Generally they are restricted to small, fishless lakes, ponds, puddles and other standing water habitats. Unlike most other Diptera discussed in this chapter, the larvae typically need access to atmospheric oxygen to breathe. Breathing is accomplished via a siphon situated near the dp of the abdomen. *Mansonia* larvae use the siphon to penetrate aquatic plants where oxygen in the aerenchyma (pith) is available, but most species breathe at the water surface.

Female adult mosquitoes typically require a bloodmeal. Their bites are a great annoyance, and are responsible for the transmission of several diseases, including malaria.

Chaoboridae ("Phantom midges ")

The larvae of *Chaoborus* (Fig. le) are unusual among aquatic insects, being essentially transparent, and in having a planktonic larval habit. Hydrostatic organs are used to regulate the buoyancy of the larvae, and thus their position in the water column. Prehensile antennae are used to sweep small planktonic prey from the water. Most species avoid visual predators (principally fish) via pronounced diel vertical migrations from the epilimnion into the hypolimnion or benthos. *Chaoborus americanus* (Johannsen) does not migrate, and is restricted to fishless lakes.

Unlike the other Diptera discussed here, mandibles are the principal remains of Chaoboridae preserved in sediments.

Methods

Sediment processing

The methods best used to isolate midge remains vary considerably depending on the nature of the sediments. For small, shallow forest-lakes, 1 cm^3 of sediment will usually yield 50 to 100 head capsules. In glacial lakes, and in late-glacial sediments, larger samples are frequently required. Although acetolysis is too corrosive for use in midge analyses, many of the digestion procedures parallel those used in pollen analysis; thus, readers may wish to consult pollen texts (e.g., Fægri et al., 1989) for additional details concerning these methods or possible alternative preparations (see also Bennett & Willis, volume 3).

Sample processing (Fig. 2) typically begins by deflocculating the sample in 5% KOH. The KOH solution may be gently heated to quickly deflocculate the sample. Barbara Lang (pers. comm.) has discovered that a brief sonic bath can be useful in breaking apart marl. Although freeze-dried sediments appear to be suitable for analysis, air dried material (e.g., a core that has dehydrated in storage) should be avoided. If only air-dried samples are available, the sediment should initially be put in hot water for 30 to 60 minutes, and deflocculated slowly (perhaps over several days) in a cold KOH solution.

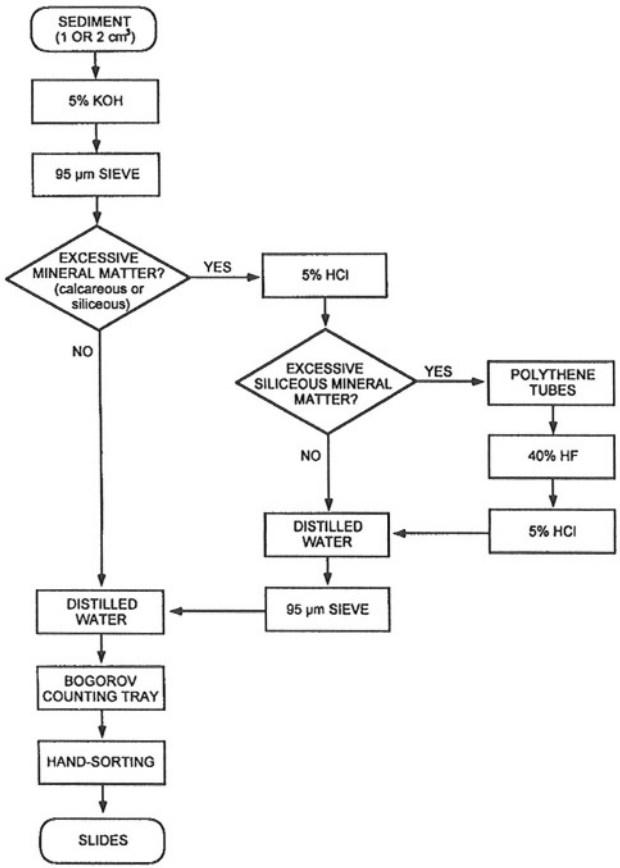

Figure 2. Flow diagram depicting the methods used to prepare sediments for analysis of fossil midges.

The deflocculated sample is then washed with distilled water on a 95 μm sieve to eliminate clay and other fine sediment components. At this stage, pebbles and other large debris may be hand-picked from the sieve, washed over the mesh, and then discarded. Although coarser meshes have sometimes been used, large numbers of midge remains will then be lost (Walker & Paterson, 1985). Many chironomid palaeoecologists use a pair of nested sieves (e.g., 95 and 150 μm) to collect remains during the final wash. They argue that it is quicker and easier to pick the remains as two size fractions.

If the sample contains carbonates, most may be eliminated in cold 5% HCl. The reaction should be allowed to proceed until the sediments no longer effervesce when fresh HCl is applied.

Sand and other coarse siliceous matter may be eliminated in cold, concentrated (approx. 50%) HF. In preparation for HF digestion, the sediment should be concentrated by centrifugation in polythene tubes; the HCl acid residues may then be decanted, and the HF applied. The sediment should be allowed to stand for about 24 hours and stirred occasionally to allow the HF digestion to proceed.

The HF processing step is rarely necessary, and should normally be omitted. The extreme dangers of HF burns and systemic poisoning, even on exposure to small drops (Burke et al., 1973; Shelley, 1995), dictate that HF always be handled cautiously, in a fumehood equipped with a HF resistant Lexan® sash. In case of spills, topical treatment of burns with calcium gluconate gel is the most effective first-aid treatment (Treviño et al., 1983; Bracken et al., 1985), to be immediately followed by the attention of a physician. The calcium gluconate paste may be prepared by mixing 2.5 g calcium gluconate USP into 100ml of either KY® jelly or another surgical water-soluble lubricant (Shelley, 1995). This paste should be prepared in advance, so that it will be immediately available to the technician.

Following digestion, the HF is diluted with distilled water, and the sediment is again concentrated by centrifugation. Once the HF has been decanted, the sediment should be washed in 5% HCl to eliminate silicofluoride crystals, before being thoroughly rinsed with distilled water on a 95 μm sieve. Ultimately, the residue retained on the sieve is washed with distilled water into a beaker or other suitable sample container. It is advisable to use warm water in this wash; if cold water is used the midge remains tend to become trapped on bubbles that form as dissolved gases are gradually released from the cold water. Use of distilled water is recommended for washing the remains, especially since tap water in hard water regions may cause crystals to form on the head capsules once they have air-dried, and because midges are occasionally found living in water distribution systems.

Ultimately the midge remains must be hand-picked from the sediment concentrate. This is most easily achieved by examining small aliquots of the aqueous concentrate in a Bogorov counting tray (Gannon, 1971) at 25 to 50 ×. To facilitate picking from the tray it is important to dilute the concentrate with distilled water and to smooth the meniscus with a pin or forceps along the length of the groove. Remains caught in the meniscus are most easily collected at 25 × magnification, whereas remains that have settled to the bottom of the groove should be sorted at 50 × magnification to ensure that the smallest, first and second instar, remains are not overlooked. Midge remains may be collected from the tray using fine forceps, a micro-pipette, or a platinum wire loop.

Although some analysts pick midge remains from ethanol, recent safety guidelines recommend that prolonged exposure to ethanol vapours should be avoided. Because there is ample opportunity for incidental sorting of head capsules by, for example, size while being picked, the process is a non-random procedure; consequently, once picking of a sample begins, the entire sample must be picked to avoid bias in the final result.

It is worth noting that all of the procedures used to concentrate the remains are likely to damage head capsules, or at least result in the loss of some of the mouthparts used in their identification; thus, whenever possible, the number of processing steps should be minimised. Ideally, the analyst should pick midge remains from raw, untreated sediment (e.g., Velle, 1998)—but, this will greatly increase the time required to pick remains from each sample. If head capsule concentrations are exceptionally low, then the paraffin or kerosene floatation methods used by beetle palaeoecologists may be useful (see Elias, this volume).

Apart from Walker & Paterson's (1985) assessment of KOH and sieve sizes, no experiments have been conducted to assess the impact of various processing techniques on head capsule recovery. This is an important area for future research.

Identification

Microscopy

In order to be identified, the midge remains must ultimately be transferred to microscope cover glasses, and mounted in an appropriate medium. The standard procedure in my laboratory is to transfer the remains direcdy from the Bogorov counting tray into a bead of distilled water, resting on a No. 1 thickness, 12 mm round cover glass. After the bead of water has air dried, a drop of Entellan® is used to secure the cover glass to a microscope slide.

Other procedures may be needed depending on the mounting medium selected for use. Canada Balsam and Euparal® have long been used as mounting media, and the slides have remained transparent; thus, these media may be preferred. The permanence of other mounting media is not so well known. When using Euparal®, the specimens should be dehydrated in successive baths of 80% ethanol, 100% ethanol, and Euparal essence before mounting.

In my laboratory, we mount up to fifty midge remains on a single cover glass, and do not concern ourselves with orienting individual head capsules. The head capsules are identified by repeatedly traversing the cover slip at about 100×, but with routine identification generally being accomplished at 400 × under bright-field illumination. For critical identification, it is sometimes necessary to examine mouthparts of individual remains in detail at 1000×. Phase contrast and differential interference contrast microscopy may provide better resolution. Scanning electron microscopy is rarely used in chironomid work.

To facilitate identification, many palaeoecologists prefer to mount fewer head capsules per cover slip (e.g., six), with the ventral side of the head capsule oriented such that it faces the analyst on the finished slide. The coverslip may also be pressed, if desired, to spread any mouthparts retained with the head capsule. While this orientation of the head capsules allows taxonomic precision to be maximised, much time is consumed in the process. Individual researchers need to consider the costs and benefits accompanying these alternatives, and which technique best suits their goals.

By failing to distinguish among larval instars, Carter (2001) believes that palaeoecologists are over-looking useful palaeoenvironmental information. Measurements of gular length are useful for distinguishing among instars, and are best determined on carefully oriented specimens.

Recently several researchers (Palmer, 1998; Heiri & Lotter, 2001; Quinlan & Smol, 2001) have independently addressed the question, "How many head capsules must be identified from a sample, to reliably infer past environmental conditions?". A consensus appears to be emerging that a minimum of 50, and preferably close to 100 individuals should be identified. This result will be model dependent. Because tolerance-downweighted and weighted averaging partial least squares models are more sensitive to the abundances of rare taxa, such models will likely require larger counts than simple weighted averaging models.

Taxonomic Literature

Chironomids: Identification of fossil Chironomidae is based principally on the mentum (= hypostoma), ventromental plates, and other structures, especially mouthparts, associated with the larval head capsule (for more detail, see Hofmann, 1971). Key taxonomic references for the Holarctic region (North America, northern Eurasia and northernmost Africa) include larval keys and diagnoses, provided by Oliver & Roussel (1983) and Wiederholm (1983).

Unfortunately, conventional taxonomic literature frequently relies on diverse body parts, many of which are rarely preserved with fossils. Recently, Schnell (1998) has provided some useful guidelines for chironomid identification as a part of the MOLAR project, and some specialised keys (e.g., Hofmann, 1971; Walker, 1988; Verschuren, 1997; Rieradevall & Brooks, 2001) have been developed for fossil work. The keys have limited geographic coverage; thus the Holarctic fauna is relatively well known, but identification of larvae from other zoogeographic regions relies on a widely scattered literature. Verschuren (1997) provides the taxonomic basis for future work in east Africa, but no comparable compilation is available for the Neotropical, Oriental, or Australian faunal regions.

Chaoborus: Several taxonomic references are useful in identifying larval and adult Chaoboridae (e.g., Sæther, 1970; Borkent, 1979), but are not well suited for use with fossil material. Fortunately, Uutala (1990) provides keys to distinguish among the mandibular remains of many of the common North American species, although some closely related species, such as *Chaoborus punctipennis* (Say) and *C. astictopus* Dyar & Shannon, are indistinguishable as subfossils. Differentiation to subgenus is generally possible on the basis of the size, shape and position of the subordinate tooth associated with each mandible. No keys have been specifically developed for Eurasian subfossils, but since the Chaoboridae are less diverse in the Palaearctic, and since Palaearctic taxa are closely related to Nearctic species (Borkent, 1981), Uutala's (1990) keys should be easily adapted for Palaearctic work. Species of *Chaoborus* are known from all continents, apart from Antarctica (Borkent, 1993). They are thus likely to be useful as palaeoindicators throughout the world.

Ceratopogonidae, Culicldae and Thaumaleidae: Useful keys to the larval Ceratopogonidae are not yet available. Two distinct ceratopogonid larval types are apparent however: 1) "*Bezzia* type", with very long, slender head capsules (Fig. 1c), and 2) "*Dasyhelea* type", with shorter, more broad head capsules (Fig. 1f). The presence of a unique pharyngeal complex in the head, consisting of the epipharynx, hypopharynx and pharyngeal sclerites, serves to distinguish ceratopogonid remains from the superficially similar head capsules of Chironomidae (Hribar & Mullen, 1991; Armitage et al., 1995).

Culicidae have rarely been reported as subfossils, and subfossil keys are not available. Verschuren et al. (1999), however, were able to describe their stratigraphy in an east African soda lake.

Walker & Heiri (unpublished) have recently discovered head capsules (Fig. 3) of seepage-flies (Thaumaleidae) in sediments of a Swiss Alpine lake. Their larvae occur only in madicolous habitats (seeps or thin films of water flowing over rocks and other substrates). Because thaumaleid larvae are poorly known (Sinclair, 1996), identification of the head capsules is likely difficult.

Simuliidae: Like the Chironomidae, black fly larvae are commonly differentiated on the basis of the teeth of the hypostoma. Currie & Walker (1992) have developed a key for subfossils of North American species groups. Because of the importance of the hypostoma to larval identifications, reference to conventional taxonomic literature (e.g., Currie, 1986) may be helpful in other regions. Rück et al. (1998) used black fly remains as an indicator of shifts between lacustrine and fluvial environmental conditions.

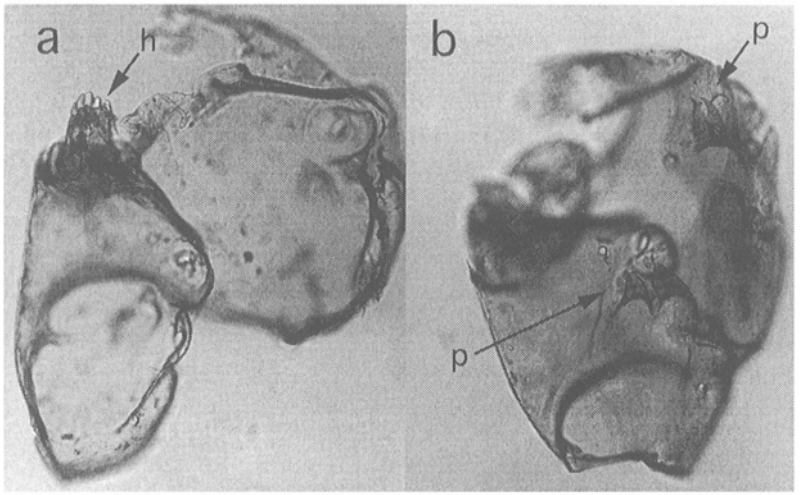

Figure 3. Remains of Thaumaleidae from Bachalpsee, Switzerland: a) head capsule with hypostomal teeth (h), b) view of protuberances (p) on dorsal surface of head capsule (note trilobed protuberance in upper right of photo). Horizontal bar in lower left corner of each photograph represents 0.05 mm.

General taxonomic considerations

With the growth of interest in midge palaeoecology, large palaeoecological working groups are developing with an interest in refining the art of subfossil identification, and a proposed standard taxonomic coding system has been developed (Schnell et al., 1999). Interest has especially concentrated on improved taxonomic resolution within such large and cumbersome taxa as the tribe Pentaneurini and subtribe Tanytarsina. With regard to making decisions on appropriate levels of identification, Brodersen (1998: 16) provides excellent advice:

> *"It is often found that the results of numerical analysis are very similar at different taxonomic resolution. This, however, does not have to be the rule. Decisions about identification levels should always depend on the purpose of the study, the level of sensitivity required, the type of analysis being used and the group of organisms of primary interest (Resh & McElravy, 1993). Provided that the primary (species-) identification is reliable and that well defined distributional/autecological differences between two phenotypic closely related taxa really exist, such taxonomic species aggregation will inevitably [cause] loss in analytical information. However, if the identification is doubtful and two aggregated taxa display the same distributional patterns along (trophic) gradients, any attempts to split the aggregation may instead introduce noise..."*

Conceptually we may therefore consider that an optimum exists with respect to taxonomic resolution (Fig. 4). It is clear that information will be lost if the level of identification is too coarse. Conversely, while increased taxonomic resolution seems desirable, there is some danger that misidentifications will increase rapidly as the required level of identification is increased, and thus, that little or no benefit will be realised (Fig. 4). This danger may be minimized by assigning all counts to a single analyst, and by maintaining a photographic reference collection of subfossil "type" specimens. However, projects are

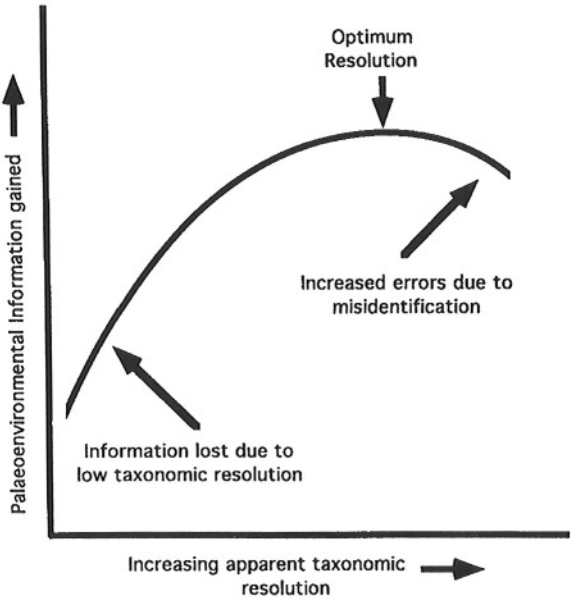

Figure 4. Conceptual model portraying optimum taxonomic resolution for palaeoecological reconstructions.

now being developed which involve a series of analysts, distributed among a multitude of laboratories, and residing in different countries. Despite frequent meetings to harmonise the taxonomic treatment among analysts, it is especially difficult to overcome the limitations imposed by geography. Ultimately, it may not benefit the project to push the required level of identification too far. Having a better understanding of the original classification, the primary analyst (the analyst who establishes a transfer function) will likely favour a higher taxonomic resolution than his colleagues (other analysts trying to apply the transfer function). It is important that all analysts in the group appreciate this problem.

Improved access to electronic communication and especially the world wide web (WWW) is proving very useful in maintaining taxonomic consistency within and among research groups. To illustrate this potential, Walker (1996–2000) developed a WWW site, "The WWW Field Guide to Subfossil Midges". The website includes recommendations for sample processing and identification, similar to those presented in this chapter. However, it also provides means for sharing instantaneously a photographic reference collection and identification keys with other researchers. Indeed it enables consultation with the reference collection, simultaneously by researchers from throughout the world. Currently the website has the disadvantage of impermanence (i.e., it is constantly changing), but this is also an advantage; as new subfossil types are discovered and keys are refined, they may be quickly incorporated into the website, whereas a conventional publication (on paper) is soon obsolete. The advantage becomes more apparent given the costs of producing and distributing paper, and the fact that revised editions of conventional publications are slow to appear. No costs are incurred in revising and distributing the electronic copy.

While interest in chironomid palaeoecology grows, and the ability to distinguish among taxa improves, there is a danger that analysts may develop a nomenclature that does not

clearly convey the taxonomic uncertainty that often accompanies subfossil identifications. Unless a species can be unambiguously assigned to a specific species, it should not be so designated. Use of an appropriate suffix (e.g., type or group), as is done in pollen analysis (e.g., Fægri et al., 1989; Bennett & Willis, volume 3), is adequate to convey this uncertainty to other researchers. For example, reference to "*Corynocera oliveri* type" clearly conveys that the specimen may be *Corynocera oliveri* Lindeberg, but could also belong to a similar looking species. Since other researchers are unfamiliar with the uncertainties inherent in the subfossil identifications, and may wish to reconstruct, for example, the past distributions of specific species through time, it is essential that analysts not mislead these researchers via over-confident nomenclature. It is sobering to recall that a very large proportion of midge species have never been described, especially in their larval form.

Indicator potential

Brief history of use and development of indicator potential

Midge remains were first used as palaeoenvironmental indicators by Gams (1927). Although their significance as hypolimnetic oxygen indicators and potentially as palaeoclimatic indicators (e.g., Andersen, 1938) had been demonstrated, they were not commonly used in palaeoecological studies until the 1980's, and especially the 1990's. The history of their early development as palaeoenvironmental indicators is well documented in reviews by Frey (1964, 1976, 1988), Stahl (1969), Hofmann (1971,1986,1988), Crisman (1978,1988), Brugam (1984), Walker (1987, 1993, 1995), and Sadler & Jones (1997). Their increased use in recent years can be traced to the development of increasingly large surface-sample data sets, documenting the distributions of midge taxa with respect to climate (e.g., Walker & Mathewes, 1989; Walker, 1991; Walker et al., 1991a, 1997; Lotter et al., 1997; Olander et al., 1997, 1999), salinity (Walker et al., 1995), lake productivity (Brodersen & Lindegaard, 1997, 1999a; Brodersen, 1998; Lotter et al., 1998), and hypolimnetic anoxia (Quinlan et al., 1998), and to the development of models for quantitatively inferring past environmental conditions from their remains. These developments have provided a more solid basis for interpreting fossil stratigraphies. However, perhaps more importantly, the quantitative inferences of, for example, climatic changes as °C and salinity changes in $g.L^{-1}$ are much more readily understood and appreciated by other palaeoclimatologists and palaeoecologists than the qualitative evidence provided by even the most dramatic changes in species abundance.

Today, midges are widely respected, especially as indicators of climatic change (e.g., Wilson et al., 1993; Levesque et al., 1993a, 1993b, 1994, 1997; Heinrichs et al., 1997; Walker et al., 1997; Lotter et al., 1999; Ammann et al., 2000; Brodersen & Anderson, 2000; Brooks & Birks, 2000a, 2000b, 2001). Upon reviewing various palaeolimnological methods, Battarbee (2000: 107) concluded that chironomid analysis is the "most promising biological method for reconstructing past temperature". They are being increasingly used as indicators of eutrophication (e.g., Douglas & Murray, 1987; Itkonen & Olander, 1997; Quinlan et al., 1998; Francis, 2001). In North America, the Chaoboridae are serving as valuable indicators of fish presence/absence, and thus, as means to document the impact of acidification on fish populations (Johnson et al., 1990; Uutala, 1990; Kingston et al., 1992; Uutala et al., 1994; Uutala & Smol, 1996).

Palaeotemperature

In the last decade, perhaps the most dramatic advances in midge palaeoecology have been in the area of palaeotemperature inference. Suites of surface samples collected across treeline in Canada (Walker & Mathewes, 1989; Walker, 1991; Walker et al., 1991a, 1997; Walker & MacDonald, 1995), Finland (Olander et al., 1999), Switzerland (Lotter et al., 1997) and Sweden (Larocque et al., 2001) have demonstrated consistent patterns in faunistic composition across gradients of both latitude and elevation. Among the Chironomidae, most members of the tribe Chironomini (subfamily Chironominae) are clearly warm-adapted, whereas the subfamilies Orthocladiinae and Diamesinae tend to dominate in arctic and alpine lakes. Similarly, the distributions of individual *Chaoborus* species suggest that *Chaoborus* species differ significantly with respect to cold tolerance (Lamontagne et al., 1994). *Chaoborus trivittatus* (Loew) seems to be most cold tolerant, with a distribution extending into the arctic and alpine, whereas members of the subgenus *Sayomyia* are distributed from temperate to tropical environs (Borkent, 1981; Lamontagne et al., 1994).

The patterns revealed by these surface-sample collections have greatly facilitated the qualitative interpretation of midge stratigraphies in climatic terms (e.g., Hofmann, 1993; Levesque et al., 1996; Brooks, 1996, 1997, 2000; Brooks et al., 1997a, 1997b; Sadler & Jones, 1997; Hirvenoja, 1998; Smith et al., 1998; Barber et al, 1999; Lowe et al, 1999; Mayle et al, 1999). However, by using the surface sample datasets as a template, a series of midge-temperature inference models has now been developed via weighted averaging, and weighted averaging partial least squares regression (Walker et al, 1991a, 1997; Lotter et al., 1997, 1999; Palmer, 1998; Olander et al., 1999; Brooks & Birks, 2000a; Larocque et al, 2001). While these models rely principally on the indicator potential of the Chironomidae, some of the models incorporate *Chaoborus* and Ceratopogonidae remains in the calculations.

Quantitative palaeotemperature reconstructions (e.g., Fig. 5) are obtained by applying these models to fossil stratigraphies, and these have provided dramatic evidence for late-glacial (Walker et al, 1991b; Wilson et al, 1993; Levesque et al, 1993a, 1993b, 1994, 1997; Cwynar & Levesque, 1995; Lotter et al., 1999; Brooks & Birks, 2000a) and Holocene (Palmer, 1998; Velle, 1998; Pellatt et al., 2000) climatic change. An assessment of these models conducted by Lotter et al. (1999) indicates that the midges are robust indicators of climatic change. Although many of the current models were developed to infer summer surface-water temperature, Livingstone et al. (1999) argue that future models should instead be developed to infer summer air temperature (e.g., Olander et al, 1999; Brooks & Birks, 2000a), a variable of more immediate interest to palaeoclimatologists. Reliable long-term air temperature data are generally much more readily available than water temperatures.

Water depth

Like temperature inferences, lake water-level fluctuations have been considered especially useful for understanding past climate dynamics (e.g., Mason et al, 1994). Thus, the possibility that past water levels might be reconstructed from midge records has been the focus of two recent studies (Hofmann, 1998; Korhola et al, 2000). Furthermore, surface sample surveys have consistently identified lake depth as one of the most important variables regulating midge distributions (e.g., Walker et al, 1991a; Walker & MacDonald, 1995).

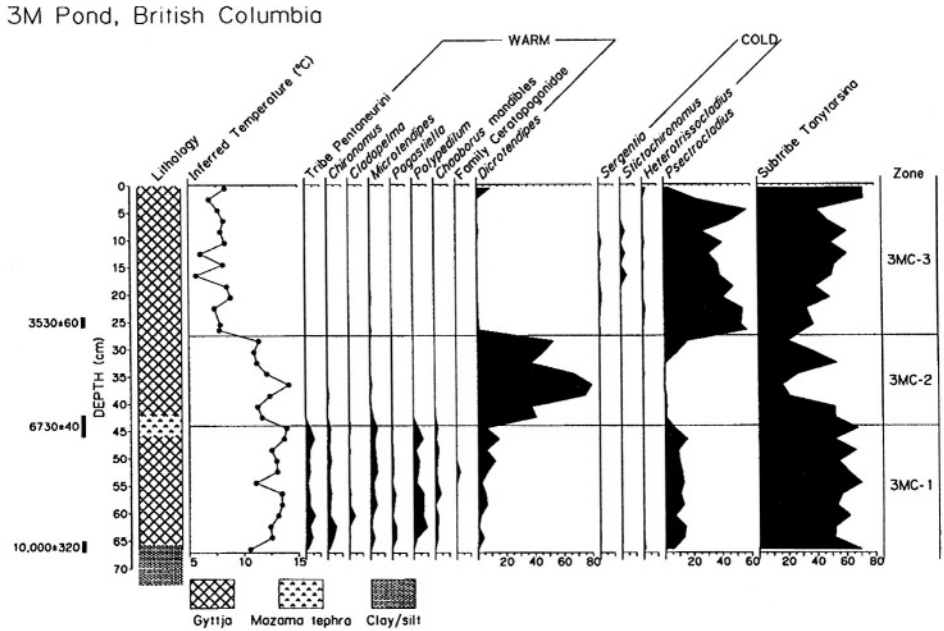

Figure 5. Holocene stratigraphy of 3M Pond, British Columbia, Canada, indicating radiocarbon dates, sediment lithology, midge-inferred temperature, and percent abundance of selected common midge taxa (Pellatt et al., 2000).

Based on the distributions of midges in Finnish lakes, Korhola et al. (2000) developed transfer functions for inferring lake depth from midge fossils. Nevertheless, Korhola et al. (2000) note that there are difficulties in separating the effects of lake depth and water temperature since these variables are negatively correlated in the training data set. Furthermore, the RMSEP of 0.49 obtained on $\ln(x + 1)$ transformed water depths indicates that the inferred water level changes would need to be large (e.g., a water depth increase of about 3 to 4×) to be significant statistically. Walker (unpublished) developed similar transfer functions based on midge distributions in eastern Canadian lakes, with similar results.

Since stream discharge from open basin lakes changes dramatically with water level (e.g., doubling or tripling with a water-level increase of less than 0.5m (Mason et al., 1994)) large water-level changes in open basins are unlikely, and midge-depth models are likely not sufficiently sensitive to provide useful proxy records. Closed basin lake levels are much more climatically sensitive, and in these instances midges may provide more useful inferences.

These conclusions are all based on surface samples collected from the point of maximum depth in lakes, and therefore may only apply to the validity of water-level records derived from cores taken in a similar position. As Hofmann (1998) indicates, cores of littoral or sublittoral sediments may provide more sensitive water-level records. Because lake levels (and salinity) may lag significantly behind climatic changes (Langbein, 1961; Mason et al., 1994), caution must be exercised in their interpretation.

Palaeosulinity

Palaeosalinity has attracted interest because it can be considered as a proxy for evaporation/precipitation balance (Walker et al., 1995; Heinrichs et al., 1997, 1999, 2001). Walker et al. (1995) developed a midge-salinity transfer function for closed basin lakes in western Canada. Application of the model to saline lake cores from south-central British Columbia, has provided complete postglacial salinity records for three lakes in the region (Heinrichs, 1995; Heinrichs et al., 1997, 1999, 2001). The salinity changes are probably largely attributable to climatic events, although the possible influence of volcanic tephra deposition and late-glacial meltwater discharge cannot be discounted.

Verschuren and co-workers have pioneered similar research in east Africa (Mees et al., 1991; Verschuren, 1994, 1997; Verschuren et al., 1999, 2000a, 2000b; De Deyne, 1999). Surface samples collected from diverse habitats have clearly demonstrated the importance of salinity, water depth and specific benthic habitats to the midge fauna of Lake Naivasha, Kenya (De Deyne, 1999). Furthermore, using a multiproxy approach, Verschuren et al. (2000a) were able to reconstruct the history of both salinity and water level for the Crescent Island Crater basin, and to relate the inferred climatic episodes to historical accounts of the political stability and economic prosperity of the region.

Palaeosalinity records from coastal lakes might also assist reconstructions of past sea-level change (e.g., Hofmann, 1987).

Productivity/hypolimnetic oxygen

The use of midges as indicators of lake trophic status, productivity and hypolimnetic oxygen can be traced to the early work of Thienemann (1921), and is therefore a well-established practice in palaeolimnological research. In the past decade, research has focused on developing mathematical models to quantify the relationships between midges and these variables. In North America, Quinlan et al. (1998) have developed a method for reconstructing hypolimnetic oxygen deficits from midge remains. In a series of recent studies, Quinlan and co-workers (Hall et al., 1999a, 1999b; Clerk et al., 2000; Little & Smol, 2000; Little et al., 2000; Quinlan & Smol, 2000) have used the midges to reconstruct the eutrophication histories of Canadian lakes. In Europe, Lotter et al. (1998) and Brooks et al. (2001) have developed models to infer total P, whereas Brodersen (1994) and Brodersen & Lindegaard (1997, 1999a) have developed means to reconstruct trophic changes, as chlorophyll *a*, in shallow Danish lakes.

Acidification

The acid rain controversy of the 1980's focused many palaeolimnologists' efforts on the task of reconstructing the impact of acidification on freshwater ecosystems. Midge records from Europe (e.g., Henrikson & Oscarson, 1985; Olander, 1992; Schnell & Raddum, 1993; Guilizzoni et al., 1996; Schnell & Willassen, 1996; Ilyashuk & Ilyashuk, 2001), Canada (Johnson & McNeil, 1988; Johnson et al., 1990) and the Adirondack Mountain region of New York state (Uutala, 1986) reveal the changes in midge communities that accompanied acidification.

In conjunction with this work, phantom midges (*Chaoborus* spp.) have proven especially useful as indicators of past fisheries in North America (Johnson et al., 1990; Uutala, 1990; Uutala et al., 1994; Uutala & Smol, 1996). *Chaoborus americanus* (Johannsen), a common and widely-distributed North American species, is easily preyed upon by fish, and thus occurs only in fishless lakes. Its recent appearance in lakes of the Adirondack (New York) and Sudbury (Ontario) regions provides a valuable indication of fish extirpation (Uutala, 1990; Uutala et al., 1994; Uutala & Smol, 1996). No comparable work has been conducted in Europe, where a closely related and ecologically similar species, *C. obscuripes* (van der Wulp), occurs (Borkent, 1981).

Other environmental assessments

Over and above their use in the previously mentioned studies, fossil midges are being widely used for environmental assessments. Klink (1989) and Mayer & Johnson (1994) have used midge remains to assess the extent of environmental degradation in highly polluted aquatic systems, whereas Miskimmin & Schindler (1994) used midge (especially *Chaoborus*) and micro-crustacean remains to examine the impacts of fishes and piscicides on lake community composition. In an innovative study, Eggermon (1999) compared surficial deltaic sediments derived from disturbed and pristine catchments in Lake Tanganyika to assess the impact of land disturbance and subsequent soil erosion on midge communities.

Future directions

The advances in midge palaeoecology over the last decade have been particularly striking. Midges are now widely used in Quaternary studies, including some archeological investigations (e.g., Dayton, 1986). Quantitative models have been developed allowing detailed inferences of temperature, salinity, hypolimnetic O_2 and total phosphorus. Although Walker (1995) lamented that midge palaeo-research was largely limited in distribution to North America and northern Europe, the rapid growth of midge palaeoecological research based in Africa (e.g., Verschuren, 1994, 1996, 1997; Verschurenetal., 1996, 1999, 2000a, 2000b; De Deyne, 1999; Eggermont, 1999), South America (Massaferro, 1994, 2000; Ariztegui et al., 1997; Massaferro & Corley, 1998), Australia (Schakau, 1993), New Zealand (Schakau, 1993), and the Mediterranean region (Guilizzoni et al., 1992; Massaferro et al., 1993; Lami et al., 1994; Massaferro, 1994) has been particularly exciting.

It is increasingly difficult to foresee where future developments are most likely. However, new research is sorely needed 1) to address the role of various taphonomic processes in shaping subfossil assemblages, 2) to investigate the impact of sample processing techniques on subfossil recovery and identifications, and 3) to quantitatively assess the impact of taxonomic resolution on palaeoenvironmental reconstructions. Given that midge palaeoecologists are now armed with a multitude of transfer functions as yet little used, it is certain that these models will be further refined, and widely exploited in the drive for increasing precision and accuracy in palaeo-reconstructions.

Brodersen & Lindegaard's (1999b) analysis of the past and present distribution of *Corynocera ambigua* (Zetterstedt) reveals that we still have much to learn with regard

to the environmental controls on midge distributions. Similar investigations of chironomid ecology and the physiological controls on species' distributions are needed to better understand the limits to Dipteran palaeoenvironmental reconstructions.

Chironomid palaeoecological studies are now highly refined in northern hemisphere research; thus major advances are perhaps more likely to occur in southern hemisphere and equatorial research where the ecology and systematics of midges is slowly becoming better understood, but the attention of a new generation of chironomid palaeoecologists is needed.

Summary

Although the remains of Chironomidae are most abundant in lake sediments, the remains of other aquatic Diptera, including Ceratopogonidae, Chaoboridae, Culicidae, Simuliidae and Thaumaleidae, are also preserved. Standard methods for sample preparation and subfossil identification are reviewed. Subfossil Dipteran remains have been especially useful as palaeotemperature indicators, but are also being used to provide proxy evidence of past changes in salinity, lake productivity, hypolimnetic anoxia, water depth, acidification and fisheries. Although prior work has been concentrated chiefly in Canada and northern Europe, growing interest in fossil Diptera has stimulated new research in African, South American, Australian and New Zealand ecosystems.

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4. COLEOPTERA AND TRICHOPTERA

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Introduction

Insects are one of the most important groups of animals preserved in the Quaternary fossil record. Over the past 50 years, the field of insect fossil research has developed into a fully-fledged discipline within Quaternary science, beginning with Coope's (1959) ground-breaking work in Britain. Insect remains from lake sediments, as well as from bogs, fluvial sediments, and other types of organic deposits, are now commonly used to reconstruct paleoenvironmental conditions, especially paleoclimates (Elias, 1994). The extraction of insect fossils from organic-rich sediments is relatively easy and inexpensive, although the identification of specimens may be considerably more arduous. This chapter discusses the extraction, identification, and paleoenvironmental interpretation of insect fossils found in Quaternary lake sediments.

Sampling of insect fossils

Insect exoskeletons, including adult Coleoptera (beetles) and larval Trichoptera (caddisflies), are found chiefly in anoxic sediments that contain abundant organic detritus. Other groups of insects commonly found in such sediments include ants (Order Hymenoptera, family Formicidae) and true bugs (order Heteroptera). Ants, in particular, can be used to reconstruct terrestrial paleoenvironments (see Francoeur & Elias, 1985; Mackay & Elias, 1992). This chapter focuses mainly on beetles and caddisfly larvae.

Insects decompose rapidly in well-oxidized sediments, leaving either thin, partially preserved sclerites or no trace. Water-lain sediments are generally the best source of insect fossils, because water acts to concentrate the insects. Lakes and ponds (including kettle-holes) serve as reservoirs that collect insects, and sediments that accumulate in these waters act rapidly to cover their remains, preventing oxidation. The best lake sediments for study are those that contain abundant organic detritus, comprising a mixture of plant macrofossils, insect exoskeletons, and other organic debris (Elias, 1994). Detritus-rich sediments usually

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accumulate in the littoral zone of a lake. Sediments particularly rich in organic detritus are found where a small stream enters a lake, because the flotsam carried by the stream tends to settle-out rapidly where the stream enters the standing water. Oxbow lakes, formed when a bend in a large stream becomes cut-off from the main channel, accumulate a sequence of organic sediments representing the transition from fluvial to lacustrine environments, often finishing with in-filling by mire vegetation.

For the purposes of fossil beetle analysis, the aim in sampling these sediments is to obtain at least one liter of organic detritus per sample. Depending on site characteristics, this may or may not be possible, and some kinds of deposits (e.g., organic-rich sediments from deltaic deposits where streams enter lakes) may yield large numbers of insect fossils even though the sample size is less than one liter. If only a small fraction of the sediment is composed of organic detritus, then very large volumes of sediment must be obtained. Generally, the quantity of sediment obtainable by piston coring of lacustrine sediments is insufficient to yield adequate amounts of detritus. While some success has been achieved by taking multiple, large diameter cores (for instance, from the Mount Ida Ridge pond site in Colorado, see Elias, 1985), this is not often practical, and may be hampered by difficulties in correlating the horizons between cores, unless numerous marker horizons are present (Hoganson & Ashworth, 1992). The best results are obtained by sampling exposures of sediments, either natural or man-made. Natural exposures include cutbanks of streams, and ocean and lake bluffs. Man-made exposures include gravel and clay pits, irrigation ditches, trenches, and building sites. In some circumstances, large quantities of sediment must be wet-screened to obtain the requisite liter of organic detritus. For instance, the author screened as much as one hundred kilograms of sediment per sample from thaw lake deposits exposed at a coastal bluff on Bristol Bay, Alaska, in order to obtain sufficient detritus for fossil insect study. In such cases, wet screening with a bucket sieve allows the rapid concentration of organic detritus out of silty sediments in the field. Generally speaking, it is preferable to sieve samples indoors, to avoid contamination from modern insects.

Organic-rich lake sediments are generally made up of detritus dispersed in sand, silt, and clay. For insect fossil analysis, the best results are obtained from organic detritus in silts. Silt readily disaggregates and separates from the organic fraction in water screening, and its limited compressibility ensures that insect fossils are preserved in their original shape (Coope, 1986).

Extraction of insect fossils from sediment

The sequence of steps in extraction and mounting of insect fossils is summarized in Figure 1. Fossil insect extraction is relatively safe, cheap and easy. No costly chemicals or equipment are required, and less time is needed than for the preparation of pollen or diatom samples. The only lengthy process that may be involved is the pre-treatment of samples to disaggregate the organic detritus from calcareous sediments and clays (see Fig. 1 for a summary of these methods). Such procedures may require hours, days, or weeks (Elias, 1994).

Once disaggregated organic detritus is obtained, the next step is to wet sieve the sample. This process removes fine particles, such as silt, that may fill the concavities of rounded insect sclerites, such as head capsules and the elytra of some weevils. If the silt is not removed, the affected sclerites may not rise to the top in the subsequent kerosene flotation procedure (see below). The standard sieve mesh size for this is 300 μm. Some fossil

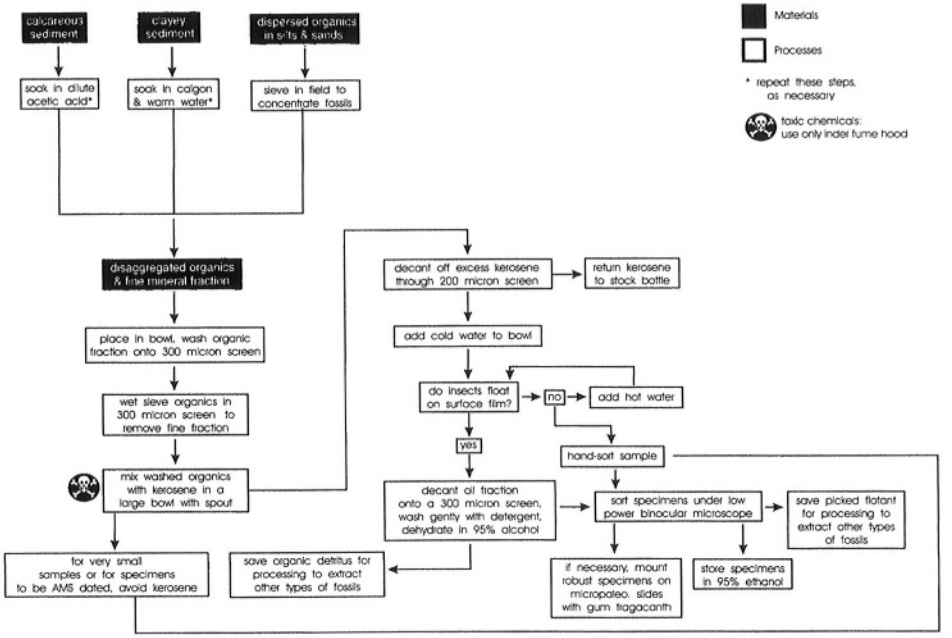

Figure 1. Summary diagram outlining the procedures for the extraction of insect fossil remains from various types of organic-rich sediments.

beetle workers prefer a slightly finer screen size (200–250 μm) (Coope, 1986), and the study of caddisfly larvae requires even finer sieves (Williams, 1988). If collaborations are to be made with researchers studying these animals, either duplicate samples are taken from the same horizon, or the $<300\ \mu$m fractions of samples are retained for study by other specialists.

The damp, screened detritus is placed in a large bowl with a spout, or a rectangular dishpan, and processed by kerosene flotation to isolate and concentrate insect fossils. This must be done in a room with good ventilation, or under a fume hood. Kerosene or other lightweight oil is gently worked into the sample by hand for several minutes. The oil adheres to the insect sclerites but not to the plant detritus. The excess kerosene is decanted from the bowl and filtered into the stock bottle through a fine screen (200–300 μm) over a funnel. Since oil and water do not readily mix, the kerosene comes away cleanly, and may be used repeatedly. Cold water is vigorously added to the oily detrit is in the bowl, with the aid of a hose. The temperature of the water is important because my temperature differential between the sample and the water will alter the flotation (i.e., warm layers rise above cold layers). In most cases, nearly all of the insect sclerites will rise to the top, and float at the oil-water interface. Within 15–60 minutes, most of the plant remains sink to the bottom of the bowl, allowing the concentrated insect remains at the top to be decanted onto a screen, then washed gently in liquid detergent and dehydrated in 95% ethanol before sorting.

Sometimes, for reasons not yet understood, the kerosene flotation fraction has a very low yield, even though the sample may be rich in insect fossils (Elias, 1994). This can only be ascertained by checking both the flotant and plant residue fractions. Not all insect parts

Figure 2. Insect fossil remains in petri dish of alcohol, ready to be sorted. Most of the specimens visible here are beetle remains. Photo by the author.

are equally buoyant, even when coated with oil (Morlan & Matthews, 1983). For instance, the head capsules of heavily sclerotized beetles are sometimes too dense to float in water.

Small samples (less than 500ml of detritus) should be sorted through completely under the microscope, rather than processed with kerosene. Also, samples that may need to be submitted for radiocarbon dating should not be exposed to kerosene. Kerosene flotation samples may be stored after washing. Samples washed in a fungicidal detergent may be stored in water for long periods without suffering fungal growth. This allows the sample to be picked in water, rather than alcohol. However, long-term storage of picked specimens should be in alcohol, since it retards fungal and bacterial attack. Specimen sorting is done under low power (10×) binocular microscope in either alcohol or water (Fig. 2). Only ethyl alcohol (ethanol) should be used for sorting and storing insects. Methanol releases toxic fumes, and isopropyl alcohol forms a cloudy solution when mixed with water. Some workers add a small amount of glycerine to vials of ethanol, to retard evaporation (Elias, 1994).

Robust, well-sclerotized insect remains, such as beetles, bugs, and ants, may be mounted with gum tragacanth (a water-soluble glue) onto micropaleontological slides with cover slip and aluminum holder. However, many specimens shrivel and break as the glue dries, so it is best to leave most specimens in alcohol. The micropaleontology slides have a rectangular cavity, 3 mm deep. The specimens are glued to the floor of this cavity.

Specimen identification

The identification of Quaternary insect fossils is a challenging task, made more difficult by a lack of suitable identification keys. Most dichotomous keys written for the identification of modern insects require entire specimens, or even a series of specimens of both sexes. Such fossil material is rarely available. Fortunately, there are some exceptions to this rule.

Some monographs on beetle families and genera include numerous illustrations, including useful photographs and line drawings, either of complete specimens or of prominent sclerites (head capsules, pronota, and elytra) that are also found in the fossil record. For instance, Lindroth (1961–1969, 1985, 1986) present good illustrations of the ground beetles (Carabidae) Canada, Alaska, and Fennoscandia, respectively. It is also possible to gain some familiarity with regional faunas by looking through monographs with abundant, accurate illustrations. Browsing through a series of good photographs or line drawings (for instance, those in White, 1983), may provide clues useful in specimen identification. An interactive CD-ROM program (Lawrence et al., 2000) has recently been developed to aid students and researchers in the identification of beetles at the family and subfamily level. This guide provides excellent illustrations of many exoskeletal features. Matching a fossil specimen and an illustration (either exact or nearly so) can be an important first step in its identification; this greatly reduces the amount of time involved in comparing fossil and modern specimens in a museum collection.

Most Quaternary insects are identified through direct comparison with modern, identified material. It is necessary to develop familiarity with the insect fauna that lives in a study region before attempting to identify insect fossils from that region. Moreover, the paleoecological reconstructions based on insect assemblages from a given study region must be based on a sound knowledge of the ecological requirements and interactions of the species found in the fossil assemblage. While some information may be gleaned from the literature, there is no substitute for prolonged study of modern material and hands-on experience, gained by years of observing, collecting, and identifying modern insects from a given region. This is a somewhat daunting task, as the beetle fauna of North America comprises more than 30,000 species in 98 families (White, 1983). The fauna of Eurasia is at least as large. Clearly, no single entomologist can be expected to retain a comprehensive knowledge of the beetle fauna of a whole continent. Therefore paleoentomologists often seek the assistance of specialists in various families. Most of these taxonomists work in national museums of natural history, such as the British Museum (London), the Smithsonian Institution (Washington, D. C.), and the Canadian National Collection of Insects (Ottawa). Other specialists are scattered in colleges and universities, in government agricultural and forestry offices, and elsewhere. Ultimately, however, it is the fossil worker's responsibility to verify any identifications made by taxonomic specialists. Fortunately, the fauna of any single region is much smaller than the fauna of a whole continent, especially if the study region is in the higher latitudes, where species diversity is greatly diminished.

The exoskeletons of beetles, caddisfly larvae, and some other insects and arachnids, exhibit a multitude of features useful in the separation of fossils to orders, families, genera and species. The general success rate for the identification of fossils beetles (based mainly on head capsules, thoraces, and elytra) to the species level is about 50% (Coope, 1986). That is, about half of the major sclerites in a given fossil assemblage will eventually be identified to species. This success rate varies from region to region. British workers have had far greater success with some samples. For instance, Coope & Angus (1975) identified nearly 90% of the species in the fossil beetle assemblages from Isleworth, England. Of course, many insect body parts, such as leg segments, antennal segments, and abdominal sclerites, can not even be identified to the family level.

Remarkably, lacustrine sediments generally yield more terrestrial than aquatic beetle specimens (Elias, 1994). This is probably due to a combination of factors, including greater

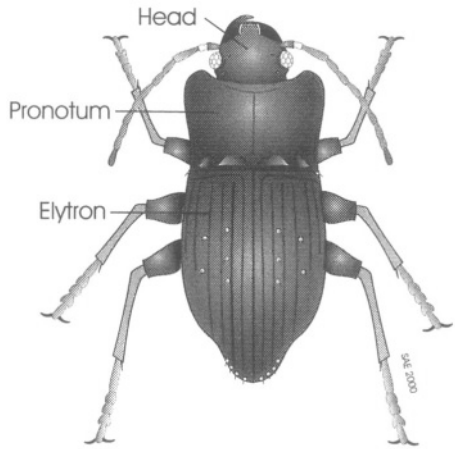

Figure 3. Generalized drawing of a ground beetle, showing parts of the exoskeleton commonly used for fossil identification.

species diversity in terrestrial habitats, and the concentration of wind-blown specimens in catchment basins (Elias, 1985). One reason beetles preserve so well in sediments is that many species' exoskeletons form a hard, armor-like case over their bodies. Therefore, the major sclerites are heavily sclerotized plates. The main exoskeletal parts that preserve in sediments are the head capsule, the pronotum (the dorsal thoracic shield), and the wing covers, or elytra (Fig. 3). Many of these plates are ornamented with a number of characters that are preserved for as long as the sclerites themselves are preserved. These characters include striations (either isolated or in rows), ridges (carinae), grooves, tubercles, punctures, setae (or points of attachment of setae, if these have broken-off), scales, and rows of teeth. Each of these features have character states that may exhibit a wide range of variation from one taxon to another. For instance, punctures range from deep to shallow and broad to narrow; they may contain a seta or not; they occur in dense patches, in rows, in small groups, or are widely dispersed; the shape of punctures varies from round to oblong to quadrate, and so on.

Microsculpture, some of which is visible only at high magnification (150–200×), is part of the exoskeleton of most insects. Microsculpture is very useful in identifying fossil beetles, because the microlines do not degrade or alter with time, and their pattern is remarkably constant within species. A few beetles are devoid of microsculpture, giving them a shiny appearance. Others have patches of microsculpture only at the margins of the pronotum and apex of elytra. Many species are completely covered with very dense patterns of reticulate lines, often in diagnostic shapes. These range from isodiametric meshes to longitudinally or transversely elongated meshes. In some species, the meshes are broken into transverse rows of very fine lines. These serve as diffraction gratings that cause iridescence. Other beetles have a very dull, mottled appearance because of dense, granular microsculpture and ornamentation.

Metallic coloration is fairly common in beetles, especially in the families Cicindelidae (tiger beetles), Carabidae (ground beetles), Scarabaeidae (dung beetles and chafers), Buprestidae (metallic wood-boring beetles), Meloidae (blister beetles), and Chrysomelidae

(leaf beetles). These colors result from light interference from thin films of the cuticle. Some metallic-colored fossil specimens become darkened through t me, but the metallic sheen reappears when the fossils are wetted.

In contrast to metallic coloration, pigment-based colors may or may not be preserved in insect fossils. Sclerites that were originally yellow, orange, and red tend to thin, become frail, and fade to pale yellow through time, whereas dark brow for black coloration due to tanning of chitin may persist (Coope, 1959). Hence, the black spots on a ladybird beetle (Coccinellidae) may preserve longer than the red or orange background which disappears, leaving only the spots. However, pigmented ornamentation such as spots, stripes and maculae persist well enough in most fossils to serve as identification aides. In fact, coloration patterns are sometimes diagnostic in identifying species of ground beetles, predaceous diving beetles (Dytiscidae), ladybird beetles (Coccinellidae), leaf beetles (Chrysomelidae), and other families.

The head capsules of many families of beetles contain useful features, including the shape, position, and size of eye sockets, the position and shape of mouthparts (many mandibles are found separately from head capsules, but their position and points of attachment on the head can be determined even when the mandibles are absent), the shape of the frontal region (between the eyes) and the shape of the clypeus (anterior to the frons). In weevils (Curculionidae), the front of the head is produced into a snout or proboscis. The elongated first segment of weevil antennae generally fit into grooves along the snout. The size and shape of the snout, and the shape and position of antennal grooves are important taxonomic features.

The dorsal prothoracic shield, or pronotum, is often useful in beetle identification. In some families, such as most ground beetles and predaceous diving beetles, the pronotum is often a broad, flat plate that is completely divided from the ventral part of the prothorax. Fossil pronota of these families are usually found detached from their associated thoracic sclerites. In other families, including weevils, it is more-or-less cylindrical and fixed to ventral sclerites, forming a dome-like covering around the thorax. The lateral margins of beetle pronota may be straight or sinuate. Some pronota are smooth and shiny, others are heavily sculptured and rugose, or covered with scales or setae. The overall size, shape, and texture of many pronota provide enough information to enable an identification to the family or genus level. Pronota of ground beetles often provide the best characters for species determinations; only the male genitalia are more diagnostic.

Elytra are the modified fore wings of beetles that are reinforced, protective covers for the hind wings and the abdomen. In fact, the name for the beetle order, Coleoptera, means "sheath winged". Elytra may be pliable and leathery or very hard and inflexible. Few leathery elytra are preserved as Quaternary fossils. As with pronota, beetle elytra range from relatively flat to very convex. Most beetle families have elytra that taper apically and cover the abdomen (or at least all but the last one or two segments). However, some have truncated elytra that leave several abdominal segments exposed. These families include Staphylinidae (rove beetles), some Silphidae (carrion beetles), and Histeridae (hister beetles). The usefulness of elytral characters for fossil identification varies greatly from group to group. Some elytra contain sufficient diagnostic characters to allow a species identification; others may not even be identifiable to the generic level. Inside the abdomen of male beetles is the aedeagus, or male genitalia. This is also partially sclerotized, and so preserves well in lake sediments.

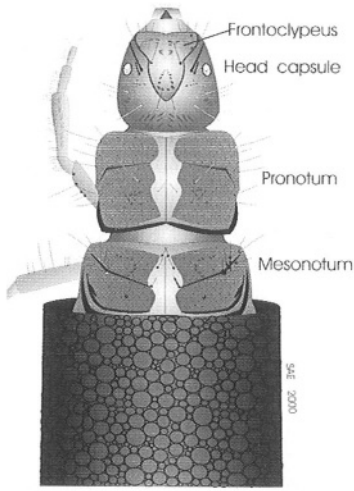

Figure 4. Generalized drawing of a caddisfly larva, showing parts of the exoskeleton commonly used for fossil identification.

Caddisfly (Trichoptera) larvae are aquatic, and sclerites from the head capsule and thorax of caddisfly larvae are abundant in some lacustrine sediments. The frons and clypeus of caddisflies are fused into a single sclerite, called the frontoclypeus (Fig. 4). Besides the overall shape of the frontoclypeus, it also contains a number of other diagnostic features, including the position of setigerous punctures along the margins, surface sculpturing, and the size, shape, and coloration of muscle scars that are revealed in transmitted light (Fig. 5). The pronotum and mesonotum are also useful for identification (Williams, 1988). The cases built by caddisfly larvae are occasionally found in ancient lake sediments (Elias, 1994). The size and shape of cases, as well as the materials used in their construction, are often diagnostic to the family or genus level. Good illustrations of modern North American caddisfly larvae are contained in Wiggins (1977). Though more rare, fossils of adult caddisflies have also been found,

Paleoenvironmental interpretation

There are several aspects of beetle taxonomy and ecology that are key to their interpretation in the fossil record. First is the enormous diversity of beetle species. More than one million species of beetles have been described (Crowson, 1981), with perhaps several million more awaiting description, mainly from tropical regions. Because they are so numerous, beetle species are also ecologically diverse. Nearly all conceivable freshwater and terrestrial habitats on this planet are occupied by beetles, from the hottest deserts to the high Arctic regions. Second is their taxonomic stability through much of the Quaternary and beyond. Studies of Late Tertiary and Early Pleistocene fossil assemblages (Böcher, 1989; Matthews, 1977) have demonstrated that most species have remained morphologically constant for at least one million years, and some species have remained constant for many millions

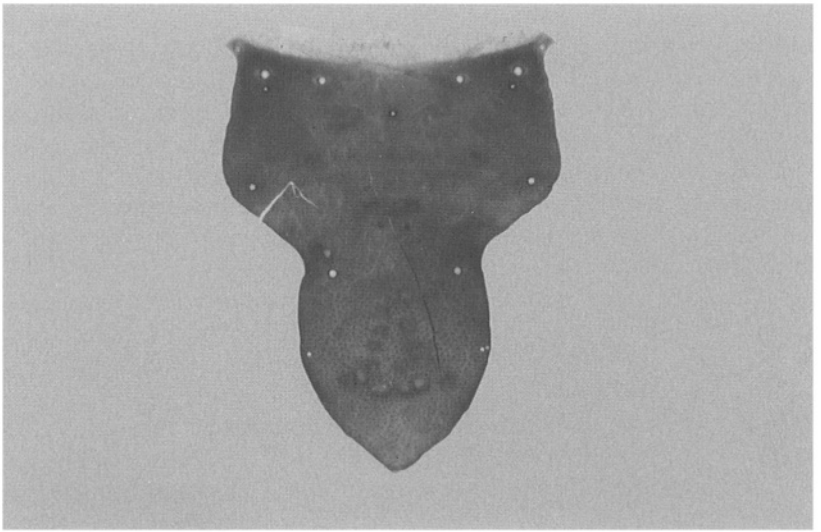

Figure 5. Frontoclypeus of a fossil caddisfly larva, showing muscle scars (dark patches) and points of attachment of setae (small white dots, mainly near the margins of the sclerite. Photo by the author.

of years. Third, beetles are highly mobile organisms, able to respond to environmental pressures by migrating to new regions in just a few years.

Given these three features, diversity, stability, and mobility, it is possible to use fossil beetle assemblages to make paleoenvironmental reconstructions that are remarkably detailed and precise. As mentioned above, the many diagnostic exoskeletal features of many beetles allows a large number of specimens to be identified to the species level. Armed with a lengthy species list from a fossil assemblage, the investigator need only collect modern ecological and distributional data from the literature and from museum specimens. These modern data may be applied directly to the fossil assemblage, because of species constancy through the Pleistocene.

Plant-feeding beetles are an important element in fossil reconstructions, because they provide information on past plant communities, including the composition of plant communities (both aquatic and terrestrial), and the health and age class structure of forests. According to Arnett (1973), the majority of phytophagous beetles feed on the leaves and flowers of plants (7950 North American species in 25 families), but a considerable number live under the bark of trees, or in rotting wood (4025 North American species in 24 families). Some phytophages feed on a wide variety of plants, but many are associated with a few or only one host plant species. The fossils of these beetles provide data on ancient plant communities, even when the plants' pollen signature is sparse or lacking (Elias, 1982). The best kinds of studies employ a multidisciplinary approach, in which paleobotanical and paleoentomological studies are done on duplicate sets of samples.

In general, predators and scavengers receive the most attention in paleoclimatic reconstructions, because they are not tied to specific types of vegetation. While some predators and scavengers are eurythermic (adapted to a broad range of thermal conditions), many are stenotherms which are adapted to only a narrow thermal environment. Stenotherms may rapidly colonize a region, as long as the climatic conditions are suitable. When climatic con-

ditions change, stenotherms depart with equal rapidity. Predators and scavengers are usually the only beetle species used in the Mutual Climatic Range (MCR) method of paleoclimatic reconstruction (Atkinson et al., 1986). Though the majority of species in most lacustrine fossil assemblages represent terrestrial habitats, predaceous diving beetles, whirligig beetles (Gyrinidae), water-scavenger beetles (Hydrophilidae) and a few other predaceous and scavenging families are also used in paleoclimatic reconstructions (Atkinson et al., 1986).

Tests of paleoclimatic reconstructions employing terrestrial or aquatic species show that both groups usually yield the same paleotemperature estimates. This result may seem surprising, given that water beetles live in a thermally-buffered environment. However, it appears that macroclimatic conditions dominate the thermal regime of lacustrine environments. However, caution must be used in paleotemperature reconstructions based on lacustrine faunas of at least some regions. A recent study of Swiss alpine lakes (Livingstone et al., 1999) has shown that summer surface water temperatures in that region are consistently 3–5 °C warmer than air temperatures, and that local topographic and limnological conditions exert considerable influence on surface water temperatures of alpine lakes. Another problematic case involves the study of faunas living in or near huge, proglacial lakes near the end of the last glaciation (Ashworth, 1977). In such faunal assemblages, the chilling effects of large volumes of glacial meltwater seem to have affected species composition rather strongly. Regional sites that were distant from such lakes had faunas that yielded paleotemperature estimates 3–5 °C warmer than those from sites near proglacial lakes (Elias et al., 1996). Thus it appears that proglacial lake sediments yield insect faunas that are unreliable for regional paleotemperature reconstructions. Although the cooling effects of the glacial meltwater depressed mean summer temperatures, they had no appreciable effects on mean winter temperatures, presumably because the water surfaces froze over in winter (Elias et al., 1986).

Caddisfly larvae provide valuable information on the waters they inhabit, as many species have narrow thermal tolerances, as well as being sensitive to the trophic status and pH of the water. Some species require specific substrates and build larval cases from particular substances (sand grains of a certain size, reeds, and even snail shells) (Wiggins, 1977). Quantitative paleotemperature reconstructions have also recently been made on the basis of caddisfly larval analyses. For instance, one recent study (Solem & Birks, 2000), documented a series of changes in thermal regime in a Norwegian lake from the late glacial interval to the early Holocene, including a 5–8 °C cooling during the Younger Dryas period.

Paleotemperature reconstructions

The principal method of paleotemperature estimation from fossil beetle assemblages is the MCR method (Atkinson et al., 1986). The basic principle of this method lies in establishing the climatic range, or "climate envelope" of beetle species found in fossil assemblages, then estimating past climatic conditions based on the overlap of the climate envelopes of these species. This method uses presence/absence of species rather than relative abundance, which may vary considerably, depending on depositional environments). The climate envelope represents the boundaries of a species' climatic tolerances for given parameters, such as mean temperature of the wannest (TMAX) and coldest (TMIN) months. A species need not occupy the whole of its potential range, nor do we need to have a complete picture of its geographic distribution. For an adequate climatic envelope

to be constructed, all that is needed is a determination of the climatic tolerances of a species, based on the climatic parameters within its known range. This is a great advantage over the previously used geographical overlap method (Atkinson et al., 1986). In order for the geographic overlap method to succeed, the species in a given fossil assemblage must have modern ranges that overlap. The climatic conditions in the overlapping region are used to estimate the conditions that supported the fossil assemblage. This method sometimes fails, because individual species have undergone independent distributional shifts during and after the Pleistocene, so that even if a fossil assemblage is composed of species all adapted to a certain style of climate, those species have since dispersed in various directions, and are not necessarily living together in any single region today. This is not to say that the species in question are climatically incompatible, just that their modern ranges may not overlap. For instance, cold adapted species that were part of Pleistocene lowland communities in Britain have gone their separate ways in the Holocene; some live in the alpine tundra zones of the Alps, Pyrenees and other high mountains; others are found today only in arctic tundra regions of Scandinavia and northern Russia (Coope, 1978).

Once the climatic envelope for each species is established, the climate indicated by the whole assemblage may be taken to lie within the area of overlap of the climatic ranges of all the species in the assemblage. Beetles are especially well-suited to this technique, because many species have clearly defined thermal tolerances. The climate envelopes are plotted on graphs whose axes are the mean temperature of the warmest month of the year (TMAX) and the temperature range between warmest and coldest months (TRANGE). The latter serves as an index of degree of seasonality. Principal components analysis of the mean monthly temperature from 495 meteorological stations in the Palearctic region shows that over 96% of the variance in temperature regime for the Palearctic is described by two groups of variables, which can be interpreted as TMAX and TRANGE (Atkinson et al., 1986). Predicted TMAX and TMIN values were found to differ in slight but systematic ways from observed values. Specifically, MCR estimates for colder sites were higher than expected and estimates for warm sites were cooler than expected. Linear regressions of predicted on observed values have yielded formulae that have been used to calibrate fossil assemblage reconstructions in Europe (Walkling & Coope, 1996), temperate and boreal regions of North America (Elias et al., 1996), and Alaska (Elias et al., 1999).

These regressions yield calibrated estimates that are reasonably precise. The r^2 value for the European regressions are 0.94, and the standard errors of the regressions were ±0.83 °C for TMAX and ±2.4 °C for TMIN (Atkinson et al., 1987). The r^2 value for the regressions of the North American data sets is likewise 0.94, and the standard errors of the regressions were ±0.8 °C for TMAX and ±2.4 °C for TMIN. The accuracy of mean July temperature reconstructions is therefore greater than the accuracy of mean January temperatures. This makes ecological sense because nearly all beetles are active during the summer, while most are inactive during mid-winter.

Summary

The remains of beetles and caddisfly larvae are often abundant and well-preserved in Quaternary lacustrine sediments. The degree to which these remains can be determined to the species level, combined with the ecological diversity of these groups, allows pa-

leoentomologists to develop detailed paleoenvironmental reconstructions. These reconstructions provide information on ancient substrates, water temperature, air temperature, and regional vegetation (both aquatic and terrestrial). Constancy of species through more than one million years allows us to use ecological and distributional data from modern specimens to interpret fossil assemblages. The strength of the paleoclimate 'signal' in the fossil insect record allows us to quantify paleotemperature estimates through the MCR method.

Some regional examples from Europe serve to illustrate the quality and kinds of paleoenvironmental reconstructions that have been drawn from fossil insect assemblages from lake sediments. Swiss lake sediments have produced valuable late glacial insect assemblages at a number of sites. At Lobsigensee on the Swiss Plateau (Elias & Wilkinson, 1983), fossil beetle and caddisfly larval assemblages change abruptly from an arctic and alpine fauna to a temperate, boreal fauna at about 13,000 yr BP. The shift from arctic and alpine to temperate insect assemblages coincides with pollen spectra including tree birch, willow and juniper in the Bølling pollen zone (Ammann et al., 1983). The earliest insect faunal assemblage from the Champreveyres site at the lake of Neuchâtel (Coope & Elias, 2000) has been dated at about 13,000 yr BP. This assemblage reflects temperate conditions, so the timing of the transition from last glacial climates predates this assemblage. The presence of thermophilous beetles in early late glacial assemblages suggests that the climate was warm enough to have sustained mixed deciduous forest by at least 12,500 yr BP, although regional forests of modern composition seem not to have been established until the Holocene, more than 2,000 years later.

In Sweden, Lemdahl (1988) documented late glacial climatic changes from insect fossil assemblages extracted from sediments at Lake Byson. These faunas show an initial late glacial amelioration slightly later than in Britain (ca. 12,600 yr BPvs. 13,000 yr BP), but of a similar intensity. In contrast, the Swedish vegetation shows a gradual change in the early late glacial, or Bølling pollen zone, Lemdahl (2000) also identified beetle and other insect fossils from Late glacial and early Holocene sediments from Kråkenes Lake in Norway. Compared with other late-glacial faunal assemblages from Scandinavia, the Kråkenes assemblages are rather poor in species. The water beetles found in the Allerød are characteristic of a poorly vegetated clear-water lake. The terrestrial fauna is indicative of dwarf-shrub and moss vegetation. The start of Younger Dryas cooling is marked by a sharp, rapid decline in the number of species; most of the Younger Dryas zone is almost devoid of beetle remains. The subsequent recovery in the numbers and diversity of both aquatic and terrestrial species at the Younger Dryas/Holocene transition is very rapid. After an initial pioneer stage, beetles associated with dwarf-shrub heath and willow scrub appeared, but no obligate tree or forest taxa were recorded. MCR temperature reconstructions suggest that the Allerød period was colder and more continental than present. The near absence of beetles in the Younger Dryas probably reflects very cold conditions. A rapid temperature rise at the start of the Holocene resulted in a warmer and more continental climate than present.

The mixture of terrestrial and aquatic insect taxa in studies such as these produce detailed paleoenvironmental information on terrestrial vegetation, soils, and climate, in addition to paleolimnological data. Probably the greatest weakness in paleoentomological research is simply that it has been underutilized in so many regions of the world. There is tremendous potential for future research in this field, as more students receive the necessary training in fossil insect identification and assemblage interpretation.

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5. ORIBATID MITES

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Introduction

Mites (Acari) are members of the Chelicerata, within the class Arthropoda. They are placed in the two orders Anactinotrichida (= Opilioacariformes + Parasitiformes of other authors), and Actinotrichida (= Acariformes) to which the suborder Oribatida belongs. The average free-living mite is barely perceptible to the sharpest eyes, as Walter & Proctor (1999) note in their inspiring book on mite ecology, evolution, and behaviour. There are three characteristic mite features shared with other chelicerates, which distinguish them from insects. The first is the occurrence of paired chelicerae and palpi in the oral region. The second is four pairs of legs in adults and the three nymphal instars (but three pairs in the larvae, a feature only shared with the subclass Ricinulei). The third characteristic feature is the division of the body into an anterior region, the prosoma, and a posterior region, the opisthosoma. In Acari the opisthosoma is modified in a very characteristic way: an anterior part bearing the chelicerae and palps forms a gnathosoma which articulates against the remaining part of the body called the idiosoma (see Alberti & Coons, 1999, for details). Systematics, biology, evolution, and the astonishing morphological and ecological variation among mites are well illustrated in the general books listed in Appendix 1.

The suborder Oribatida consists of about 11,000 described species which is roughly estimated to be between 10% and 30% of the true global diversity of this group (Walter & Proctor, 1999). Most new species are likely to be discovered in the tropics and little explored "hotspots", like the Himalayas.

Almost all the mite remains found in lake sediments belong to the Oribatida. The size of these mites usually varies between 0.13 and 1.00mm. They might therefore easily be overlooked in the sediments or lost during sieving and extraction procedures unless special precautions are taken to recover them.

Oribatid mites are known as fossils back to the Middle Devonian period (Norton et al., 1988, 1989) and Early Ordovician (Bernini et al., 2002), and an overview of pre-Pleistocene records is given by Labandeira et al. (1997). Their abundant occurrence in most bog sediments was first recorded by Nordenskiold (1901), but only in recent decades has

J. P. Smol, H. J. B. Birks & W. M. Last (eds.), 2001. *Tracking Environmental Change Using Lake Sediments. Volume 4: Zoological Indicators.* Kluwer Academic Publishers, Dordrecht, The Netherlands.

their potential as indicators of paleoclimate and paleoenvironments been fully recognised. This requires identification to species, and Knülle (1957), Haarløv (1967), Karppinen & Koponen (1973, 1974), Erickson (1988), Schelvis & van Geel (1989), Krivolutsky et al. (1990), Schelvis (1990, 1997), Drouk (1997), and Solhøy & Solhøy (2000) all rely on precise species determinations as far as possible. In many other recent studies, their full potential has not been utilised and they are listed only as Oribatei, oribatids, oribatid mites or Cryptostigmata (e.g., Bennike & Böcher, 1994; Garry et al., 1997).

Lake and bog sediments usually cover the time span since the last glaciation, but remains of oribatids can also be found, like beetle fragments (see Elias, this volume), in interglacial and pre-Quaternary sediments and in different types of buried soils (Elias, 1994).

This brief overview will mainly treat the techniques used to recover fossil oribatids from lake and bog sediments, how their presence and abundance can aid in the reconstruction of the local plant communities of the catchment area, and give hints about changes in climate and variation in water and soil conditions and lake level fluctuations. This account draws heavily from information in Knülle (1957), Erickson (1988), Schelvis (1990), Drouk (1997) and Solhøy & Solhøy (2000).

Brief history

Reports on subfossil mites date back to Nordenskiold (1901) who identified 24 oribatid taxa from bog sediments of a Finnish site. All except one specimen could be identified to the species level and their modern Latin names are given by Karppinen et al. (1979). Paul & Ruoff (1927, 1932) listed about 25 species from *Carex-Hypnum* bog sediments in Germany, determined by the eminent German acarologist Carl Willmann. Knülle (1957) discussed this species list and he was able to identify 21 of these species.

Several other works from this early period mentioned recovering a few oribatid mites, but almost no interpretations were made of these records (e.g., Stark, 1925; Steinecke, 1929; Hoogenraad, 1935). Most of these earlier works are listed and partly discussed in Knülle (1957) and Frey (1964). The work of Knülle (1957) treated subfossil oribatid mites from *Sphagnum* peat bogs in northwest Germany, from sand-buried peat of inland sand dunes, and brown moss peat and gyttja deposits of former eutrophic water bodies. Although no dating was done, by precise determination of most of the specimens and a knowledge of the present-day distribution and habitat selection of the species found, a rather good reconstruction of the paleoenvironment was possible.

Frey (1964), in his account of remains of animals in Quaternary lake and bog sediments, gave an overview of the main findings to that date. He remarked (p. 79): "As is readily apparent, most of these records of mites in freshwater sediments are very vague, and being incidental to other studies, they do not begin to represent the potential of the group. Here, certainly is a fertile field for further exploration and study. The surface has been scratched only enough to reveal the potential treasures beneath". How right he was.

More recent overviews dealing with subfossil oribatid mites were those of Karppinen et al. (1979) of northern Europe and Greenland, Golosova et al. (1985) of northern Siberia and Krivolutsky & Druk (1986), who provide a general overview, giving species lists and several illustrations.

Erickson (1988) gave a review of the type of information which could be extracted from oribatid remains in lake sediments, especially of their usefulness in reconstructing

lake level variations by the variation in the abundance of *Hydrozetes oryktosis* Woolley and *Limnozetes* cf. *rugosus* (Sellnick). He also classified the preservation state of the fossil mites into five categories from perfect to imperfect ones, which could aid in interpretation of data.

Krivolutsky et al. (1990) published a book in Russian on fossil oribatid mites. Although not easily accessible to those not mastering Russian, many of the taxa mentioned are illustrated by drawings or photos.

The most recent important works on oribatids from lake and bog sediments are those of Drouk (1997) and Solhøy & Solhøy (2000). Drouk (1997) gave a good overview of possibilities and problems in the reconstruction of Quaternary environments. Of special interest are the references and discussions of many Russian studies, but his table and figures are difficult to interpret. For the notation "acarological analysis" (analysis of oribatid mites in sediments), he refers to his doctoral thesis (Drouk, 1986) and the review by Krivolutsky & Druk (1986).

Solhøy & Solhøy (2000) studied the fossil oribatid remains from a "master" core from Kråkenes, western Norway as a part of a multidisciplinary study (Birks et al., 1996; see J. Paleolim. vol. 23, no 1, 2000, which is entirely devoted to the results from this project). The period covered by the oribatid analysis was from just after deglaciation to the early Holocene (12,300–9,200 ^{14}C yrs BP = 14,100–9,950 calibrated yrs BP). From the records of 38 identified species and the fluctuations in the abundance of adults through the core with 1 cm resolution, it was possible to indicate rather convincingly a succession pattern which showed variation in climate and resulting habitats around the lake (Fig. 1; see also Birks et al., 2000). The main strength of this study is the high resolution of the core, abundant radiocarbon dates, identification to species of all the adult oribatids present, documentation of the species' present-day distributions and habitat requirements, and support from the multidisciplinary approach.

Outline of methods

1. *Sample collection and storage*

For site selection and sampling, reference is made to H. H. Birks (volume 3). In future studies on mites from lake and bog sediments, they should be a component of multidisciplinary studies on the same cores (cf. Birks & Wright, 2000). Since oribatid mites are mainly associated with aquatic vegetation or washed or blown in from terrestrial vegetation and litter close to the lake, the methods used for macrofossils by H. H. Birks (volume 3) also apply to oribatids.

As for many other arthropod fossil taxa, it is important to have large diameter cores (currently in use ca. 10cm, e.g., Nesje, 1992) to obtain sufficient material for high resolution studies. Storing of the cores at 4°C may be sufficient, but if the cores are stored for several years they should be deep-frozen since the oribatid mite cuticle can be attacked by micro-organisms making identifications to species more difficult or impossible.

2. *Sample preparation from cores*

To get the highest precision in evaluating changes in oribatid composition through the cored sediment, 0.5 or 1.0 cm intervals of the core should be analysed. With a core diameter of

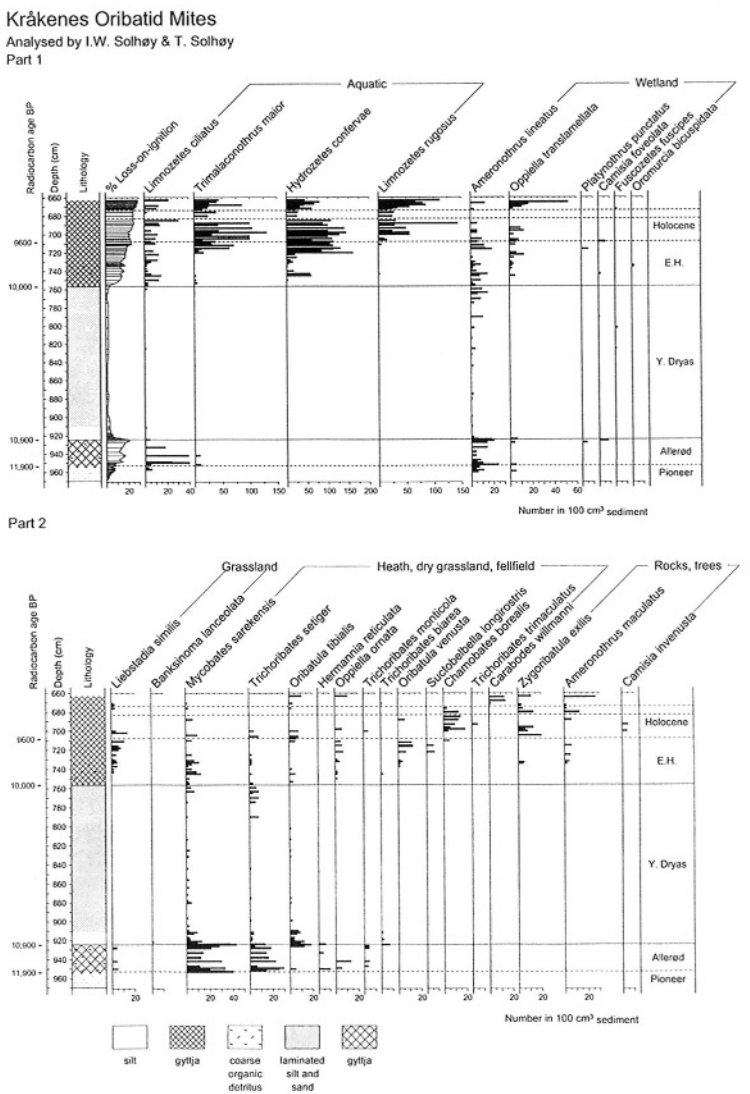

Figure 1. Stratigraphic profiles of oribatid species from Kråkenes Lake, Norway, shown as number of adult mites in 100 cc wet sediment. Note changing concentration scales. Only species that could be associated with known habitat preferences are shown. Part 1: Aquatic species and wetland dwellers. Part 2. Species living in mesic and dry to extremely dry habitats such as grassland, heath and lichens on rocks and trees. Pioneer = Pioneer period, Y. Dryas = Younger Dryas, E.H. = Earliest Holocene. The E.H./Holocene boundary is placed at the first record of *Betula* (tree) fruits, the other zone boundaries mark lithostratigraphical changes. The lithology is described by Birks & Wright (2000). Modified from Solhøy & Solhøy (2000); used with permission.

10–11 cm, this should equal 40 and 80 cm^3 respectively. In the Kråkenes lake sediments, we found 0–220 adult specimens per 100 cm^3 in the pioneer phase and Allerød period, 1–90 specimens in Younger Dryas, and 15–410 specimens in the early Holocene (Solhøy & Solhøy, 2000). In other types of sediment, the number may be inadequate and several parallel cores may be needed.

It is important that the sediments are completely disaggregated, since the mites are easily concealed in sediment clumps (Erickson, 1988; Drouk, 1997). This can be done in distilled water, 70% ethanol or in dilute sodium pyrophosphate ($Na_4P_2O_7 \cdot 10H_2O$), similar to plant macrofossils (H. H. Birks, volume 3). Erickson (1988 obtained very good results with ethanol using a test tube shaker, but care should be taken with a shaker since legs, setae and valves may easily be lost. Our lab prefers a gentle jet from a plastic syringe and additional mechanical disaggregation. Very humic sediments can be soaked in 10% NaOH and calcareous sediments treated with 10% HCl. The sediments can then be sorted directly. Caution must be used with all these chemical treatments.

Several workers prefer to sieve the sediment sample to get rid of the finest particle section. If that is done, it is of utmost importance to use the correct mesh size during sieving so the smaller specimens are not lost. A 125 μm sieve is recommended for plant macrofossils and will retain most of the oribatids. Mesh sizes of 80–100 μm sieve sizes should be used to collect the smallest species in the suctobelbid and oppioid genera, remains of the smallest immature stages, and identifiable parts of the bigger oribatids (e.g., notogaster, prodorsum).

Often a rather violent spray of tap water or alcohol is used to get the finest material through the sieve. But great care should be taken so there will be no damage to the remains, i.e. loss of legs where they are intact, loss of body setae, genital and anal valves, and breaking up of the body along the fissures. More effort and trials should be placed on sorting the sediments by placing them directly in 70% ethanol and then sorting small quantities at a time, well dispersed in a glass petri dish. Alternatively, they can be sorted and counted in a grooved perspex sorting tray (Bogorov sorter with a groove 5 mm deep and 5 mm wide) as used for chironomid head capsules (Brooks, 1997; Brooks & Birks, 2000; Walker, this volume).

3. Sample preparation from large sediment samples

If the sediments are not from cores, but from trenches, eroded banks, peat exposures or archaeological sites, it is often possible to obtain great quantities of material, either directly or by concentrating the organic fraction of sandy sediments (Elias, 1994, this volume). The insect and mite remains can be recovered by flotation techniques, either after field or laboratory washing through a 100 μm screen, or directly from the sediments. These techniques, using kerosene or in some cases calcium chloride solution or heptane, were first described by Coope (1968) and are thoroughly described by Elias (1994) for extracting insect remains. However, beetle workers often prefer to wash the remains through a 300 μm sieve, which is too coarse for oribatid remains. Kerosene is added and worked into the sediment, the excess decanted and cold distilled water is added. The arthropod fragments are found in the water/kerosene interface. The fragments must be washed with a detergent, rinsed in water, and dehydrated and sorted in alcohol (Morgan, 1988, and on the internet: Quaternary Entomology Laboratory, Univ. Waterloo,

URL: http://www.science.uwaterloo.ca/earth/qsi/qellab.html). Schelvis (1990, 1997, 1998) has used the technique (with reference to Kenward, 1974) to recover oribatids from archaeological samples and it has been widely used by Russian workers (Krivolutsky et al., 1990). It has also been used by Klinger et al. (1990) in Alaska, but they would have lost smaller oribatids using a 300 μm sieve prior to flotation. On the other hand, Niemi (1985) using a 125 μm sieve was able to recover a high number of small species, although from five 0.5 kg samples of soil she only recovered 343 individuals.

Drouk (1997), referring to Drouk (1986) and Krivolutsky et al. (1990), described a technique used by Russian workers applying 5–7 consecutive alternations of drying the sediment and flotation in distilled water. The dried mite remains will very often trap an internal air bubble when the material is flotated, and continue to float after most of the plant remains have sunk. The efficiency of this method is claimed to be more than 90% recovery (checked by hand picking). A drawback of this method, in my opinion, may be that the dry mites change form and structure and are therefore more difficult to determine, although they can be "softened" again in glycerol or lactic acid.

A heptane flotation method used successfully to recover microarthropods from grassland soils (Walter et al., 1987) seems also to be worth consideration, although to my knowledge it has never been used for fossil mites.

Coetzee (2002) used the flotation method described by Fain & Hart (1986) for house dust mites to recover mite fossils from sediments. The sediments were disaggregated in 80% ethanol and then a saturated NaCl-solution was added. The density difference caused the mites to float to the surface, but no efficiency estimates were given. This simple method should therefore be further tested for extraction efficiency with different types of sediments.

4. *Mite picking*

To remove the mite remains from the suspension, I strongly recommend the use of a set of 2–4 wide-bore glass Pasteur pipettes with different sized openings to accommodate the different sized oribatid remains. To get good control on the suction of the mites into the pipette, I have attached a capped length of a 20–30 mm long rubber tubing closed in the end by a rubber stopper. This allows for a more gentle transfer and selective picking of the mites out of the glass petri dish as compared to the use of a Pasteur pipette and bulb.

The mites can be transferred to small watch glasses for counting and preliminary separations into families, genera, artificial groups or even some easily recognisable species.

The magnification by the stereomicroscope for routine sorting is usually 12×, but it is often also necessary to scan the petri dish at 25× to be sure that most of the small species and immature forms have been detected. Often it is an advantage to alternate between the black and white backgrounds under the sorting dish, i.e. examining the same sample twice at the same magnification. For most samples, a white background will probably be the best option.

A sample of mite remains should be stored in 70% ethanol. Many workers prefer to add 5% glycerol to the alcohol to keep the mites more soft and to save the sample if the alcohol should evaporate. The sample is best stored in a small glass tube 6 × 34mm and sealed with a small cotton plug, allowing no air in the tube. The advantage of such a small tube is that all the mites inside the tube can easily be removed by turning the tube upside down

(the surface tension forces will keep the liquid in the tube) and emptied into a glass watch glass with alcohol by placing the mouth of the tube under the surface of the alcohol.

For storing purposes, the small tube is placed upside down in a bigger glass or plastic tube, also filled with alcohol and sealed off with a cotton plug, and also containing a label with all necessary information (Baker, 1999). Good-quality paper, which survives prolonged immersion in alcohol, is needed, and the information should be written with Indian ink or a soft (2B) lead pencil. The tubes are placed in an inverted position in airtight jars with enough alcohol to cover the tubes. Each jar should contain a label describing its content.

An alternative compact storing method of mite samples has been brought to my attention by Dr. Josef Stary, Inst. Soil Biology, Ceske Budejovice, Czech Republic, which utilises the small microwell plates with lids used for cell growth. Each sample is placed in glycerol in a well and the position of the individual sample is identified by a code attached to the lid. There is no evaporation of the glycerol, even after several years, and, because of the glycerol's great viscosity, these plates can also be sent by mail to other researchers.

5. *Identification*

The mites are identified at high magnification (100–l000×) with a good quality compound-light microscope, preferably with phase contrast and differential interference contrast. Prior to examination, the cuticle must be rendered transparent and in freshly collected individuals the internal tissue must be removed. The most effective clearing agent is concentrated lactic acid, but some workers prefer 60% lactic acid or lactophenol. I have always used concentrated lactic acid with excellent results for most individuals, but dilute lactic acid may be more appropriate with weakly sclerotized forms (Norton, 1990). The clearing process can be done at room temperature over several days to weeks in the same small vials where the samples have been stored by just adding some lactic acid and letting the alcohol evaporate, or by heating them to 60–70 °C on a hot plate as temporary mounts in lactic acid on a cavity slide.

Most, if not all, of the identification should be done in temporary mounts and the specimens returned to alcohol or glycerol, which will keep the specimens in far better condition than in permanent mounts. A major advantage of temporary mounts is that the specimens can be moved into different positions during examination, which is absolutely necessary for observing all the morphological structures relevant for identification.

Procedure: Use a cavity microscopic slide and place a drop or two of lactic acid into it. Half cover the cavity with a cover-slip and place specimens in the lactic acid using soft entomological forceps, a fine brush or a needle after the alcohol has been drained off. Several specimens can be placed simultaneously, but there should not be too great differences in size. The individuals are moved into the desired position and often fixed between the cover-slip and the cavity floor by fine threads of copper wire (cords of a telephone cable) attached to a pin. The specimen position can also be manipulated by moving the cover-slip. After examination, the specimens are transferred back to alcohol or glycerol. The procedure is also described by Grandjean (1949), Krantz (1978), Coineau (1984) and Travé et al. (1996).

Permanent mounts should only be used for building up a reference collection. For mites the most preferred mountants have been Berlese fluid or Hoyers medium; detailed

procedures and how to prepare these mountants (and others as well) are described by Krantz (1978), Brown (1997) and Baker (1999), and discussed by Upton (1993). The edge of the cover slip must be ringed to prevent drying and also to ensure that the mountants do not take up moisture from the air. For ringing the cover slip, use two or three layers of nail varnish, Glyceel™ or Glyptal™ insulating varnish (Baker, 1999).

Norton (pers. com.) suggested that the most useful permanent slides are those in which the mite is mounted in a small depression or "pit" made by a tungsten-carbide dental drill. Several different depths can be made to accommodate different sized mites. There are several advantages: the mite is not crushed, a normal amount of medium is used and the mite can be re-mounted in a different position. For reference or teaching slides, two mites of the same species and instar are mounted in the same pit, one in dorsal and one in ventral position. When the mite needs to be dissected before mounting to observe specific morphological details, Norton (pers. com.) advises to mount the separate small pieces under separate small cover slips, positioned around the central pit where the thick body parts are mounted.

When the mite remains are cleared in lactic acid and mounted temporarily or permanently, they are ready for identification.

A key to the world genera of oribatids is given by Balogh & Balogh (1992) and they also provide a line drawing of a representative species from nearly all genera. The key is rather complicated to use, but can probably be simplified by the aid of regional checklists (see Appendix 1) to eliminate many genera not present in the region under consideration. Most new genera (and species) published after that can be found in the annual publications of Bibliographia Oribatologia (see Appendix 1). Norton (1990) provides a concise and good family-level key for "beginners" to common adult oribatid mites from North America north of Mexico, which also may work well for northern Palearctic faunas. Balogh & Mahunka (1983) provided a useful book for species identification of "primitive" ("lower" or "macropyline") oribatids of the Palearctic region, but Norton (1984) discusses a large number of problems in using it, especially for those inexperienced in work with oribatids. Covering mid and northern Europe, Willmann (1931) combined with Sellnick (1960) is still useful for the experienced worker, although outdated in many ways. A useful book for the European and Siberian oribatid fauna is that of Gilyarov (1975), dealing with the species of the former USSR, unfortunately in Russian (but an English translation exists at the Agriculture and AgriFood Canada Library, Ottawa, Canada).

For the Iberian Peninsula, Pérez-Íñigo has published keys for the Oribatei, Poronota (1993) and Gymnonota I (1997). There is also circulating among oribatologists some unpublished identification lists of some geographic areas and efforts are made to get these published and to construct new ones.

However, for as reliable identifications as possible, it is necessary to consult papers dealing with revisions of specific taxa (e.g., Colloff, 1993), descriptions (e.g., Behan-Pelletier, 1997), redescriptions (e.g., Solhøy, 1997), monographs (e.g., Olszanowski, 1996) or overviews (e.g., Reeves & Behan-Pelletier, 1998) and other papers figuring species.

Care should be taken in checking the identity of a fossil species and it should preferably be checked against determined material and by a specialist. A major problem is that several described genera and species are badly in need of revision, and another problem is that subtropical and tropical areas are full of undescribed species. Even in well-studied geographical areas, several species have frequently been misinterpreted, misidentified and confused.

One solution for scientists wanting to work with fossil oribatid mites is to start with regional species lists and build up a reference archive of drawings and descriptions for as many species as possible and from various authors representing the same species. A reference collection is also indispensable, containing both fossil material and field collected specimens. Properly identified species can also be obtained by exchanges of material with specialists or museum collections, but identifications should still be treated with caution. For quick comparisons, a collection of field collected species as permanent slides is of great help. But it is also necessary to have a reference collection of species in alcohol or glycerol, since proper comparisons and species determinations require inspections of all sides and different angles and illuminations. This is very important when determining imperfectly preserved fossil oribatid remains (see Erickson, 1988, where he grades the quality of his fossils into five classes), or where the keys probably do not work, as Angus (1997) has vividly described for Pleistocene fossil beetles.

Indicator potential

Oribatid mites certainly have considerable potential in reconstructing local plant communities and other environmental variables at a site. In several areas, such as many parts of Europe, some in Japan and North America, most of the subfossil remains can be identified to the species level by an experienced oribatologist (but the numbers of these in most countries are few or nil!). This is the first prerequisite for a reliable reconstruction of the conditions that they experienced. But a good reconstruction is only possible if their present-day distributions and ecological optima and tolerances are documented from published reports and the analysis of modern training sets from a variety of habitats at many local sites. Even for comparatively well known areas, such as Scandinavia, Britain, The Netherlands, and Germany, several hundreds, maybe even a few thousands of samples are needed before more quantitative models can be developed as for some other arthropod taxa (e.g., Coleoptera, Chironomidae).

The species assemblages found in lake sediments will be a mixture of limnic, wetland and terrestrial species (Erickson, 1988; Solhøy & Solhøy, 2000). All or several of the species in the genera *Aquanothrus, Heterozetes, Hydrozetes, Limnozetes, Malaconothrus, Mucronothrus, Naiazetes, Platynothrus, Punctoribates Tegeocranellus, Trhypochthoniellus, Trimalaconothrus, Zetomimus,* and some other genera live on vegetation in the lake or at its margins. Their densities probably fluctuate due to variations in temperature, pH, and nutrition status, and the species assemblages may also change over time (Solhøy & Solhøy, 1997, 2000). Behan-Pelletier & Bissett (1994), in their account of Canadian peatland oribatids, noted that most of the *Limnozetes* species (Fig. 2) were present in acidic bogs and bog pools (pH 4.4–4.7) and absent from an eutrophic fen. They also noted that species richness varied among bogs, and preliminary data suggested highest species diversity in domed bogs and lowest in kettle bogs and fens (see also Behan-Pelletier, 1989). Markkula (1986a, b) thought that declines in densities of *Limnozetes* (*ciliatus* (as *sphagni*) and *rugosus*) were associated with declines in peat moisture, especially created by afforestation and associated drainage. In bogs composed of hummocks and hollows, she found a distinct terrestrial oribatid assemblage in the hummocks with *Limnozetes* absent, and more limnic species in the hollows. The same results, comparing hummocks and hollows, were found by Tarras-Wahlberg (1961) and Popp (1962).

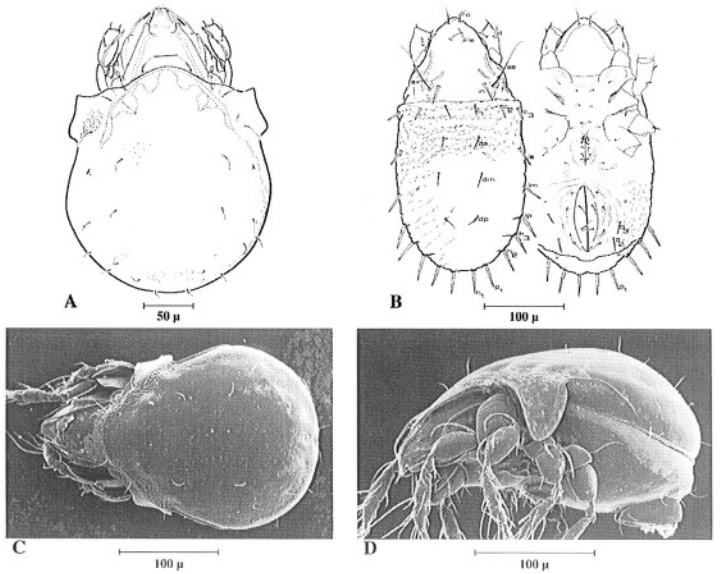

Figure 2. *Limnozetes onondaga* Behan-Pelletier from saturated *Sphagnum* at the edge of a non-acid "trout-pond", Cortland, New York State, U.S.A. A: Dorsal aspect of adult. B: Dorsal (left) and ventral aspect of tritonymph. C: SEM of dorsal aspect of adult D: SEM of lateral aspect of adult. *L. onondaga* is a parthenogenetic species as are all the known species of *Limnozetes*. From Behan-Pelletier (1989); used with permission.

The genus *Hydrozetes* (Figs. 3 & 4) occurs in most lakes, tarns, bog pools and even in very wet fens where they often are found in great densities. They may be more abundant in eutrophic than in oligotrophic water bodies (pers. obs.). About 20–30 species are described with a known distribution from the Arctic (Bennike, 2000) to the tropics (Fernández & Travé, 1984). Their remains are often abundantly preserved in lake sediments (Frey, 1964; Erickson, 1988; Solhøy & Solhøy, 2000), and hence have been reported from many paleoecological studies, although often only determined to the genus level. A reliable species determination is hampered by the confusion about the identity of the described species and the genus is in badly need of a revision. Fernández & Travé (1984) list the known species and supported synonyms together with excellent illustrations of a new species and subspecies. Grandjean (1948) provides outstanding figures of some European species (see Figs. 3 & 4), but note that his *H. incisus* n. sp. is *H. thienemanni* Strenzke. Fernández & Athias-Binche (1986) and Athias-Binche & Fernández (1986) analysed the population dynamics of *Hydrozetes lemnae* (Coggi) associated with the duckweed *Lemna gibba* L.

Species of *Hydrozetes, Limnozetes* and other aquatic taxa, will certainly have considerable potential for lake reconstructions provided that the taxonomic uncertainties are resolved and enough training sets of modern analogues are available. In Kråkenes Lake sediments, *Hydrozetes confervae* (Schrank) was the most abundant mite in the sediment from the earliest and early Holocene (Fig. 3A). The observed density fluctuations were hypothesised to reflect variations in the productivity of the lake (Solhøy & Solhøy, 2000).

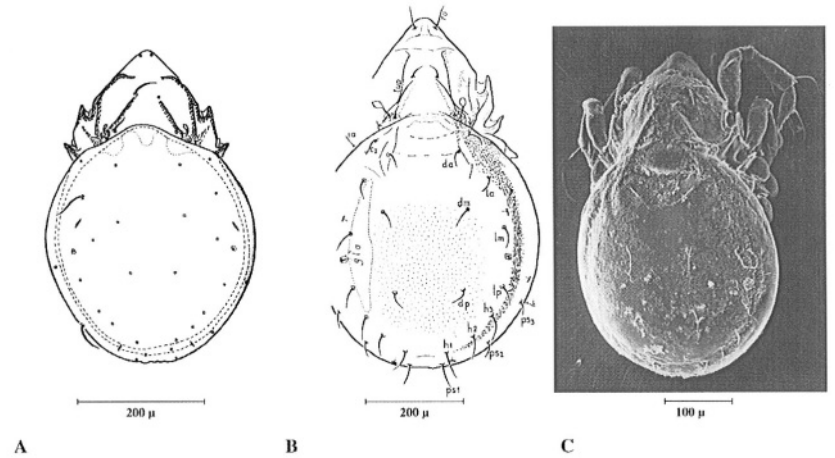

Figure 3. Adults of the genus *Hydrozetes*. A: Fossil specimen of *H. confervae* from the early Holocene, Kråkenes Lake, coastal western Norway. Age about 9,100 ^{14}C yrs. B: *H. thienemanni* S renzke from Seine-et-Oise, France. C: *H. lemnae* Coggi from an aquarium at the Zoological Institute, University c f Heidelberg. A: Drawing by Ingrid W. Solhøy in 1993. B: from Grandjean (1948); used with permission. C: Pho .o by Gerd Alberti.

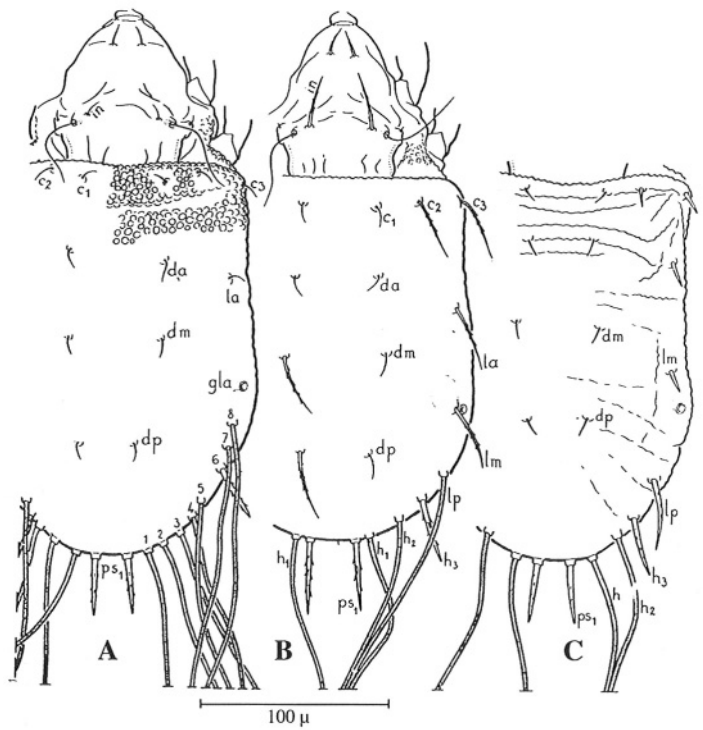

Figure 4. Tritonymph of *Hydrozetes parisiensis* (A), *H. lemnae* (B) and *H. thienemanni* (C). From Grandjean (1948); used with permission.

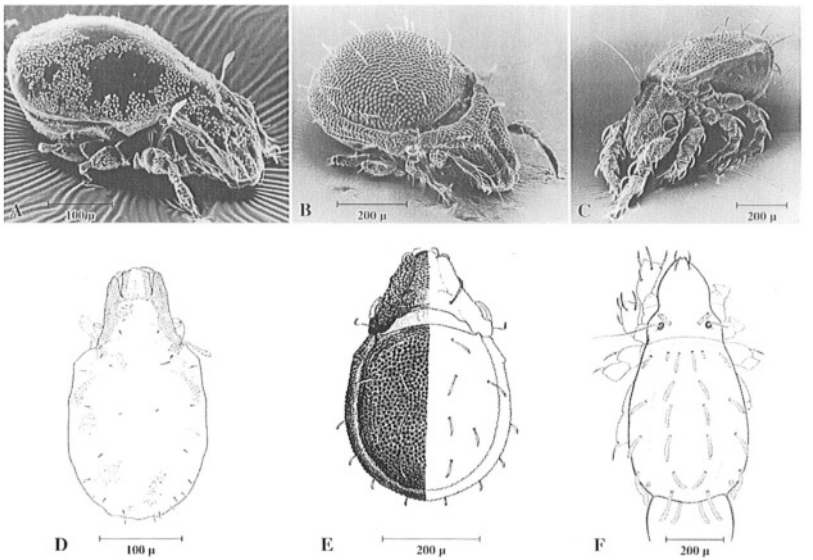

Figure 5. SEMs of three common terrestrial oribatid mites (A–C) and the same species illustrated as line drawings (D–F). A & D: *Tectocepheus velatus* (Michael). A widespread and ubiquitous species found on all continents except Antarctica. In Tibet up to 5,100 m a.s.l. B & E: *Carabodes forsslundi* Sellnick. May be a synonym of *C. ornatus* Storkan. A Palearctic species, in the Nordic countries mostly found in moss, litter and on trees in coniferous woodland and subalpine birch forest. C & F: *Nothrus silvestris* Nicolet. Has a Holarctic distribution, common in various types of woodland and in mesic to wet meadows. A–C: from Alberti & Coons (1999), D: from Nübel-Reidelbach (1994), E: from Sellnick & Forsslund (1953) and F: from Seniczak & Zelazna (1992); used with permission.

In the study by Erickson (1988) of Glovers Pond, USA, it was suggested that abundances were related to lake level variations, which influenced lake productivity.

The semi-aquatic species *Naiazetes reevesi* Behan Pelletier was at first only known as Quaternary fossils in Hiscock site, New York State from a fibrous, gravelley layer older than 8500 yrs (Jennings, 1993, Erickson pers. com. to Behan-Pelletier). It was found living in large numbers in a narrow zone of decaying sedges and grasses at the edge of a small pond (Behan-Pelletier, 1996) and could probably be a good indicator species of lake level fluctuations.

The contribution of terrestrial oribatids to lake sediments is varied, and in principle most of the species of the local environments of a lake can be flushed or blown into the lake (Fig. 5). Solhøy & Solhøy (2000) distinguished between species of the following broad habitat groups: wetland, grassland, heathland, rocks and trees, and, in addition, generalists with a wide occurrence and no specific habitat association recorded so far (Figs.1 & 6). A few species with unknown preference were also found. Several of the species in the habitat groups could further be associated with an alpine and/or arctic distribution pattern, thus allowing for more precise habitat reconstructions.

With more precise knowledge of the distribution and microhabitat selection of oribatid species, it should be possible in the future to refine and link the species assemblages to more precise vegetation communities and even plant taxa. For instance, *Ameronothrus maculatus* (Michael) is only abundant on certain species of lichens on rocks at lower

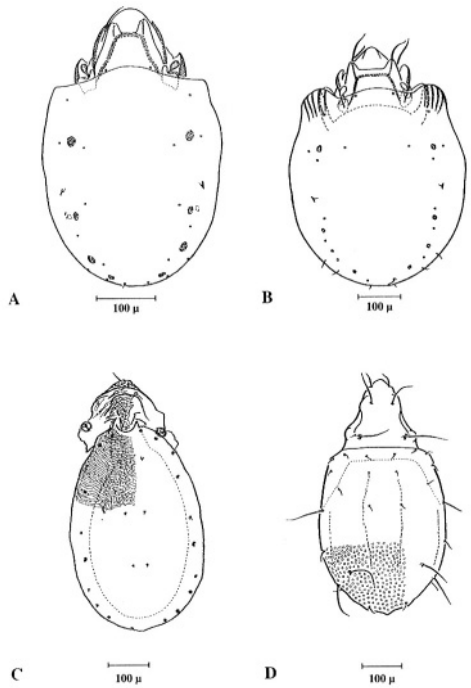

Figure 6. Four characteristic species from the fossil oribatid assemblage found in the sediments from Kråkenes Lake, coastal western Norway (See Solhøy & Solhøy, 2000 for details, where four other species are illustrated). A: *Trichoribates setiger* (Trägårdh). Specimen from Younger Dryas, ^{14}C age about 10,100 yrs. The present-day distribution in Fennoscandian mountains is above tree-line, often in alpine meadows. B: *Trichoribates monticola* (Trägårdh). Specimen from Allerød, ^{14}C age about 11,800 yr. At present a mountain species in Fennoscandia on exposed ridges and fellfields. C: *Amerronothrus maculatus* (Michael). Specimen from the early-Holocene, ^{14}C age about 9,100 yrs. Today's records from Norway are associated with rock lichens (e.g., *Xanthoria*) and occasionally tree lichens in lowland, mostly coastal areas. D: *Trimalaconothrus maior* (Berlese), synonym: *T. novus* (Sellnick). Specimen from the early-Holocene, ^{14}C age about 9,150 yrs. The Fennoscandian distribution today is in bogs, fens, pools and lake margin vegetation to about 1,300 m a.s.l. Drawings by Ingrid Wunderle Solhøy in 1993.

elevations (less than 500 m a.s.l.) in western Norway and *A. lapponicus* Dalenius in a few nitrophilous lichens in the low to middle alpine areas. *Mycobates sarekensis* (Trägårdh) is common on alpine lichen heath vegetation, while *Carabodes willmanni* Bernini occurs abundantly in similar lichen-rich dry heathlands at low altitude. Solhøy & Solhøy (2000) list several other habitat associations for the Kråkenes late glacial and early Holocene fossil assemblage.

In recent years, more information has been documented about arboreal oribatid mites and their possible association with tree species (i.e., Travé, 1963; Wunderle, 1992; Walter & Behan-Pelletier, 1993; Behan-Pelletier & Winchester, 1998; Winchester et al., 1999). Judging from these and other studies, oribatid mites could help reconstruct the arrival and possible succession of trees. Fossil arboreal oribatids could also contribute to recording

possible changes in tree-line positions during the Holocene. Both trees and shrubs have a rather species-rich oribatid fauna, and some may even be associated with only a single tree/shrub genus or even a single or a few species. For instance, *Dentizetes ledensis* Behan-Pelletier is so far known only from leaves of *Ledum groenlandicum* (Oeder) Hult (Behan-Pelletier, 2000). In tree ecosystems, oribatids are often associated with bark, epiphytic lichens and mosses (Wunderle, 1992; Winchester, 1997; Winchester et al., 1999) and may be specific to these microhabitats, or in leaf domatia as discussed by O'Dowd & Willson (1991) and Walter & O'Dowd (1995). Once the distribution and ecology of these mites are properly known, their fossils will contribute significantly to habitat reconstruction around a lake.

There are also several oribatid species associated with marine littoral and brackish water habitats (e.g., in the families Ameronothridae, Fortyuniidae, Hermanniidae, Oribatulidae, Scheloribatidae and Selenoribatidae). They can probably be used to reconstruct marine transgressions and, together with fresh and brackish water species, changes in salinity in lagoons, deltas, and lakes cut off from the sea. Oribatid species of the marine littoral also show a temperature-related geographic distribution, and usually occur in sufficiently high abundance and have a robust exoskeleton. These attributes may result in good preservation in some sediments of sheltered littoral habitats and aid in temperature reconstructions. The same probably applies to old inland salt lakes, but the oribatid fauna of these habitats is virtually unknown.

In the Baltic Sea, Bennike et al. (1998) recorded undetermined oribatids from submarine early-Holocene lake marl deposits containing macroscopic remains of wetland and terrestrial invertebrate and plant taxa. The uniform low number of species throughout the cores would probably not add much new information to the reconstructions made from the presence of other taxa, but points to potential applications of oribatids even in these types of sediments.

Oribatids are also found in interglacial sediments and Quaternary sediments of considerable age (Krivolutsky et al., 1980; Krivolutsky & Druk, 1986; Krivolutsky et al., 1990; Schelvis, 1992; Bennike & Böcher, 1994; Coetzee, 2002). Their preservation quality has been variable, but in some studies they have been shown to be well preserved, thus allowing for species determinations, especially by Russian workers (Krivolutsky et al., 1990). From a late-Tertiary beaver pond on Ellesmere Island, Canada, Behan-Pelletier & Ryabinin (1991) reported the oribatid mite *Proteremaeus macleani* Behan-Pelletier, which is not known presently from North America, but only in the Kolyma Highlands, Siberia. Coetzee (2002) found the three species *Discoppia cylindrica* Pérez-Íñigo, *Ramusella* sp. and *Protoribates capucinus* Berlese in a 125,000 yrs old sediment layer at Florisbad thermal spring, South Africa, representing the last interglacial (warm) period, and with *P. capucinus* not found in the area today, probably because of insufficient soil moisture. These paleoecological reconstructions have, however, been of limited precision, often due to insufficient material and lack of a multi-disciplinary approach.

In Dutch archaeological studies, Schelvis (1990) established ecological groups of oribatid mites based on an extensive sampling programme of recent faunas. Oribatids were used as indicators of heath, moorland, woodland, grassland and "solid" (i.e., moss and lichens on solid surface) habitats. These broad habitat groups were further subdivided into 1–4 subgroups based on variations in substrate moisture. His ecological grouping also used information from northern Germany based on Knülle's (1957) work on "isovalent groups",

which in turn was influenced by Strenzke's (1952) work on oribatid communities. This approach is certainly a valuable one, which deserves to be developed further.

Fossils of other mite groups, e.g. the Gamasina and Uropodina, have also proved to be valuable indicators in archaeological excavations, as several species are associated with human settlements and in particular with dung of domestic animals (Schelvis, 1990, 1997; URL: http://home.planet.nl/~scarab.schelvis/home.html).

Summary

Fossil oribatid mites in lake and bog sediments can greatly assist in paleoenvironmental reconstructions. However, they must be sufficiently abundant, be reliably determined to the species level, and enough high quality "training sets" or other information on factors governing extant distribution and community composition must be available. The dating of the sediments must also be adequate and the conclusions reached by studying mite assemblages should be supported by data from other groups of organisms, using multidisciplinary approaches.

Oribatid mites occur in marine and brackish water littoral sediments, saltmarshes, as part of lake ecosystems, in bogs and fens, in all types of soils, and in most saxicolous and arboreal habitats. With many species preserved in fossil sediments, their indicator potential can complement conclusions reached from other proxy indicators. One important strength is that they originate *in situ* or from the nearby surroundings of the study site.

Local mite communities are often reasonably rich in species and their fossil occurrence in lake sediments can give clues to the existence of local microhabitats (e.g., lichen communities) and climatic and edaphic conditions not readily revealed by other fossils. Contrary to many winged insects, the dispersal power of mites is lower, and problems associated with long-distance dispersal are therefore negligible.

Once more precise ecological data sets and long-term population ecology studies of extant aquatic taxa become available, past shifts in oribatid assemblages can hopefully be used to reconstruct environmental variables such as temperature, lake chemistry, ice cover, and lake-level fluctuations. More biogeographic data with respect to climatic and edaphic variables are also needed. Modelling can also be done with assemblages of terrestrial species, but it is important to realise that these fossil assemblages are less representative than aquatic assemblages. Many unknown factors contribute to the inwash of terrestrial species, and re-sedimentation can also be a potential problem for interpretation.

Some terrestrial and freshwater oribatids have a wide tolerance to environmental conditions, and are thus less reliable indicators. Nonetheless, many taxa are stenotopic, and therefore their paleoecological potential is considerable and as yet underutilized.

In the future, it may also be possible to develop models using, for example, the Mutual Climatic Range (MCR) method for temperature reconstructions (Elias, this volume) or other transfer functions (e.g., Birks et al., 2000), using oribatid mites.

Some possible directions for future developments in fossil oribatid studies of lake and bog sediments can, in my personal and pragmatic view, be summarised as follows:

1. Studies of mite remains should be incorporated into multidisciplinary studies, and the extracted specimens should be properly stored in museum collections, except those needed for reference collections.

2. Preserved mite material from many previous and ongoing paleoecological studies should be analysed or reanalysed in the light of present knowledge.

3. Methods for extracting mites from sediments should be further studied, compared, modified, and improved. Possible problems should be clearly identified.

4. Manuals for identifying fossil mite taxa should be developed. Much effort should be put into the development of interactive databases of species and genera illustrations, and these made available on the Internet.

5. More taxonomic revisions, species redescriptions and descriptions should be undertaken for many genera, especially in the aquatic or wetland oribatid genera of *Hydrozetes, Limnozetes, Malaconothrus, Nanhermannia* and *Trimalaconothrus.* But more genera can be added as needed.

6. "Training sets" of modern assemblages should be developed, further refining our knowledge of distribution patterns related to environmental factors.

7. Much more information on microhabitat distribution and plant-oribatid mite associations are needed.

8. The use of mites in archaeology should be continued and expanded along the lines developed by Schelvis (1990, 1997).

9. New researchers should be trained in the identification and interpretations of both fossil and extant mite assemblages.

With the present neglect and disappearance of acarology in many countries (Walter & Proctor, 1999), these goals will be hard to achieve in the near future. However, with the paleoecological potential of oribatid mites as described in this account, and documented by Solhøy & Solhøy (2000), and the importance of mites in general, convincingly described in the seminal book by Walter & Proctor (1999), this trend could be reversed.

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Appendix 1

Checklists and catalogues of oribatid faunas

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6. BRYOZOAN STATOBLASTS

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Introduction

The Bryozoa (Phylum Ectoprocta), also known as Polyzoa in some older literature, is a group of small, sessile, colonial, filter-feeding animals. The majority of the members are strictly marine, but there are at least 65 freshwater species worldwide (Wood & Wood, 2000). The phylum is divided into three classes: the Stenolaemata which are exclusively marine; the Gymnolaemata which are mostly marine but have a few freshwater members in the order Ctenostomata; and the Phylactolaemata which are exclusively freshwater. Only species in the Phylactolaemata produce encapsulated dormant structures called statoblasts, and thus this discussion will be confined mainly to this group.

Colonies consist of fused individuals or zooids and each zooid consists of two parts: the body wall or cystid, and the polypide which includes the internal organs (Figs. 1, 2). Colonies grow by budding, and individuality in these animals is blurred. Even the body cavities of the zooids are connected (Wood, 1989). The polypide has a ring or U-shaped double row of ciliated tentacles, called a lophophore (Fig. 1). The lophophore can be drawn into the body wall, or extended for feeding. The outermost layer of the cystid is secreted material and may be gelatinous or chitinous cuticle, and colony form varies from gelatinous masses to tubular, thread-like structures. The resemblance of some colonies to mosses led to the name Bryozoa, coined by Ehrenberg (Brusca & Brusca, 1990). Colony size can vary from a few millimeters to huge masses weighing several kilograms (Wood, 1989).

The freshwater bryozoans inhabit both still and flowing water and have a world-wide distribution, appearing on every continent except Antarctica (Wood, 1991). Bushnell (1973) gives the northernmost limit for distributions as 75 °N latitude in Novaya Zemlya and Spitzbergen, and the southern limit at 55 °S, Tierra del Fuego. The highest elevation with

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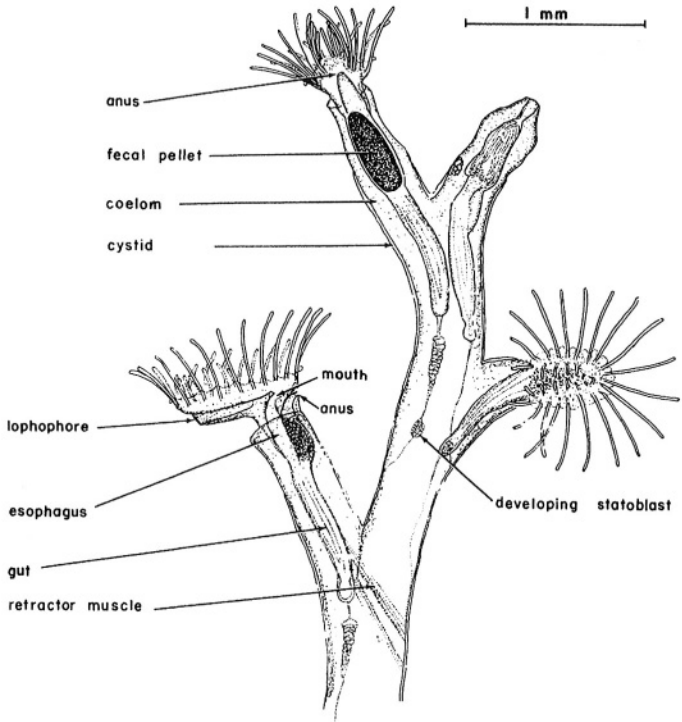

Figure 1. A generalized diagram of a plumatellid bryozoan showing the basic body plan. Modified from Wood (1989).

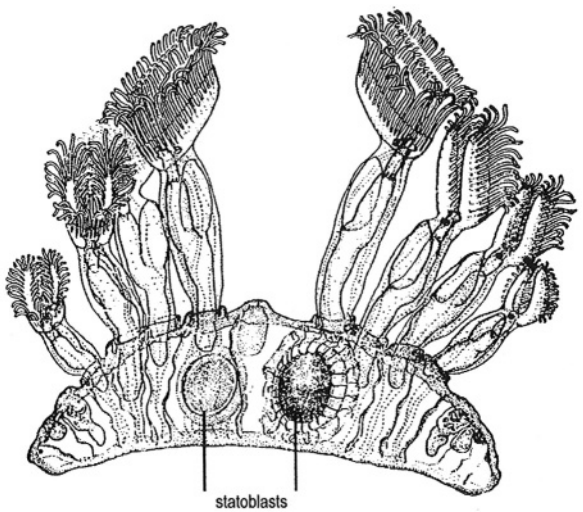

Figure 2. Cross section through a colony of *Cristatella mucedo*. Arrows point to developing (left) and mature (right) statoblasts. Modified from Hyman (1959).

recorded collections is at Lake Titicaca, 4151 m asl. In regions where no collection records exist, it is probably due to the fact that no investigators have attempted collections (Wood, 1991). But new localities and range extensions are continually being reported (Rao, 1973; Ricciardi & Lewis, 1991; Ricciardi & Wood, 1992; Smith, 1993; Wood & Okamura, 1999). Because of their small size, bryozoans are frequently overlooked in collections of freshwater invertebrates. They have a reputation for being difficult to collect and study, a reputation which some authors feel is unjustified (Wood, 1989). Despite the fact of their widespread distribution and common occurrence whenever collections are made, and that they can be dominant in terms of biomass in littoral communities (Raddum & Johnsen, 1983), the group is still not well known. More information is needed on taxonomy and systematics, physiology and ecology, and biogeography. Brown (1933) stated that the taxonomy as well as the ecology has been badly neglected in America. Many authors still lament our lack of knowledge of these animals (Wood, 1991; Ricciardi & Reiswig, 1994).

Although bryozoans are usually associated with shallow water habitats, they have also been collected from deep water. The greatest depth recorded (for *Fredericella sultana)* is 170m in Lake Lucerne, Switzerland (Zschokke, 1906; in Bushnell, 1973). Rawson (1953) reports collection of *F. sultana* at 33 m depth in Great Slave Lake, N.W.T., Canada. Macrophytes are frequently cited as a preferred substrate for bryozoan colonies (Pennak, 1989; Wood, 1991), but they also inhabit a variety of other substrate types, including submerged wood and trash, metal, bridge supports, etc. (Pennak, 1989; Wood, 1989), and even hard-packed mud and sand (Ricciardi & Reiswig, 1994). Shells of unionid clams, both living and dead, are also a frequently used substrate (Bushnell, 1966; Curry et al., 1981; Ricciardi & Reiswig, 1994). Prolific growth of a bryozoan on zebra mussels (*Dreissena polymorpha*) in a Lake Michigan harbor was shown to inhibit recruitment of the zebra mussel larvae (Lauer et al., 1999). Bryozoans are also known to foul water pipes and filters, clog wastewater treatment facilities, and attach to the undersides of boats (Dendy, 1963; Shrivastava & Rao, 1985; Pennak, 1989; Wood & Marsh, 1999). As well, bryozoan colonies also serve as habitat for a diverse epizooic community of protozoans and invertebrates (Bushnell & Rao, 1979; Kaminski, 1990; Ricciardi & Reiswig, 1994). Bryozoans can dominate periphyton or littoral communities (Raddum & Johnsen, 1983) and may contribute significantly to nutrient cycling in lakes (Sørensen et al., 1986; Kaminski, 1991). Several fish and invertebrate predators feed on both colonies and statoblasts (Dendy, 1963; Bushnell & Rao, 1979; Ricciardi & Reiswig, 1994).

Statoblasts

Phylactolaemate bryozoans produce encapsulated, asexual buds called statoblasts. Statoblasts consist of two chitinous valves with yolky material and regenerative cells enclosed within. These cells are capable of germinating and producing a new colony when conditions are favorable. The statoblasts function as reproductive, survival, and dispersal agents, and can survive freezing, desiccation, and other stresses (Brown, 1933; Bushnell, 1974; Bushnell & Rao, 1974). Statoblast valves are made of sclerotized chitin, and are well preserved when buried in lake sediments. These valves can be recovered from sediment samples along with other microfossil remains and provide information on past aquatic environments.

There are three basic types of statoblasts (Wood, 1991): 1) floatoblasts, which are buoyant and floating; 2) sessoblasts, which are sessile, and cemented to a substrate or to the colony itself; and 3) piptoblasts, which are neither buoyant nor attached, and only produced by *Fredericella* spp. Some bryozoans such as *Plumatella* are capable of producing both floatoblasts and sessoblasts. Statoblast morphology has proved to be distinctive among species and is an important tool in identifying living bryozoans (Wood, 1979; 1996). Statoblasts vary in size, shape, and surface decoration, and the presence or absence of hooks and spines (Figs. 3, 4). Each valve consists of an outer periblast and an inner capsule. The periblast has an outer ring called an annulus and a center region termed the fenestra. In floatoblasts, the annulus consists of gas-filled cells. The two valves of one statoblast are not equal but consist of dorsal and ventral valves (Fig. 3, 4); the dorsal valve of floatoblasts having a larger annulus, so that the statoblast floats dorsal side up (Bushnell & Rao, 1979). The periblast is usually more substantial than the capsule, and has features that are useful for identification (Wood, 1979), which has positive implications for their use in paleolimnological studies. Statoblasts range in size from 0.2 mm up to 1 mm in diameter in *Pectinatella* and *Cristatella* (Pennak, 1989). Although statoblasts probably have a high natural rate of mortality (Pennak, 1989), statoblast valves recovered from lake sediments could represent both ungerminated or germinated ones, as the valves fall away from the new colony as it grows, or after the colony degenerates (Rogick, 1941). Or the valves may have even have passed through the guts of various animals such as fish and ducks (Brown, 1933).

Methods

A measured volume of wet sediment sample is placed in a 100 ml beaker. The amount of sediment to be processed may depend on the concentration of statoblasts present in the samples. Concentrations can vary greatly. In Douglas Lake, Michigan sample volumes ranged from 1 to 5 cm^3 (Francis, 1997). One advantage of the method is that sorting of statoblasts can be done in conjunction with other microfossil analyses, such as chironomid analysis. The method presented here is a version of the chironomid method (Walker, this volume). Statoblasts are often recovered along with plant macrofossils as well (see Birks, this volume).

If carbonates are present in the sediments, the first step in processing is the addition of 10% HC1 to the sample. The sample can then be allowed to sit overnight, or until no more bubbles of CO_2 are being evolved. The HC1 is then removed from the sample by washing through a 100 μm Nitex nylon bolting cloth sieve with distilled water. A small sieve can easily be made by gluing a circle of Nitex cloth into a ring manufactured for home canning jars, using silicone sealer or aquarium sealant as the glue.

The residue remaining on the sieve is flushed back into the beaker, and about 50 ml of 5% KOH is added. The beaker is then heated gently on a hot plate (about 85 °C, do not boil) for 15 minutes. This deflocculation step removes much of the organic material in the sample. The sample is rinsed again thoroughly through the 100 μm sieve and returned to the beaker by flushing with distilled water. The sample is now ready for sorting. Gloves and goggles should be worn when handling the HC1 and KOH, and work should be performed in a fume hood.

Sorting can be done under a dissecting microscope at 50 x using a Bogorov sorting tray (Gannon, 1971). Aliquots of sample (which should now consist of the resistant residue in

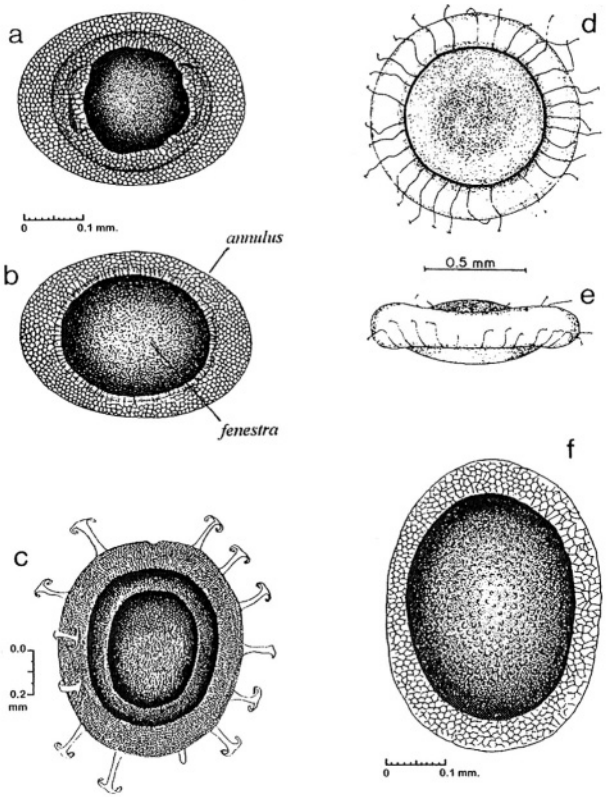

Figure 3. Examples of bryozoan statoblasts. a. Dorsal valve of *Plumatella repens* floatoblast. b. Ventral valve of *P. repens* floatoblast, with annulus and fenestra indicated. c. *Pectinatella magnifica* floatoblast. d. Dorsal valve of *Cristatella mucedo* floatoblast. e. side view of *C. mucedo* floatoblast. f. *Plumatella* sp. sessoblast. a, b, and f from Rogick (1940), c from Rogick & Brown (1942), d and e from Wood (1989).

aqueous solution) are transferred to the counting tray using a pipette. All of the sample is then examined, and statoblasts removed. This can be accomplished using fine forceps or a fine wire loop. The statoblasts should be transferred to small vials containing 70% ethanol if identification is to be carried out at a later time. All statoblasts must be removed from the entire volume of cleaned sample if the procedure is to be quantitative. A statoblast valve should be counted as one half of a statoblast.

Identification

Statoblasts are important in the identification of living specimens, and several authors give details of preparation, and keys to identification. Normal light microscopy is usually sufficient for identification (Wood, 1979), however, new studies on some *Plumatella* species show morphological differences that can only be detected by SEM (Wood, 200la). For

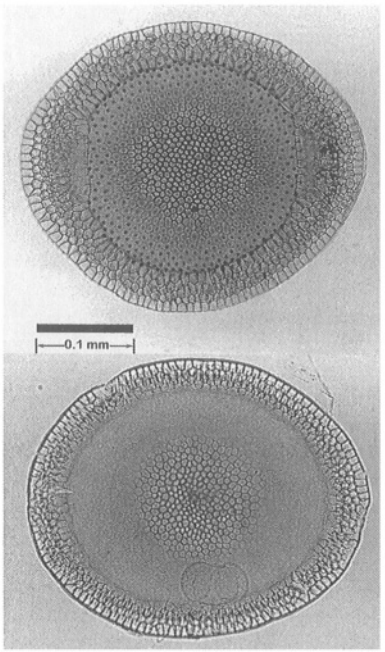

Figure 4. Fossil statoblasts of *Plumatella nitens* from Douglas Lake, Michigan sediments. Top: dorsal valve, bottom: ventral valve with a pollen grain underneath the lower edge. Photos by M. Edlund.

methods of preparing statoblasts for examination by SEM, readers are referred to Wood & Wood (2000). Statoblasts for light microscopy may be permanently mounted in media such as Canada Balsam, Euparal®, or synthetic media (after dehydration in alcohol), but Wood (1979) recommends water mounts as faster and easier, retaining photographs of the statoblasts as permanent records. In either case, further treatment of the statoblasts may be necessary, to break apart the components of each valve, the periblast and capsule. The statoblasts are treated again in hot KOH solution, and then transferred to water. Teasing with fine needles will separate the periblasts and capsules if necessary. Wood (1979) recommends 20% KOH heated in bowls of porcelain depression plates to near boiling, the statoblasts are placed in the hot KOH for 2 minutes, then transferred to cool distilled water. This step may not always be necessary with fossil material. Valves are sometimes encountered in which the capsule is already separated from the periblast. On the other hand, one also encounters intact statoblasts, with both valves still clinging together.

Keys to the living freshwater Bryozoa include many characters and descriptions of statoblasts, as well as colony morphology. Keys can be found in Pennak (1989), Wood (1989, 1991), and Mundy (1980). A separate key to statoblasts of freshwater bryozoans of eastern Canada is given in Ricciardi & Reiswig (1994). The monograph of Lacourt (1968) also includes a key to statoblasts but is difficult to use. Detailed descriptions of statoblast morphology of several genera are presented in Wood (1979). A new key which includes statoblast characters is presented by Wood (2001b) and has excellent illustrations.

Statoblast characters are also given in species descriptions such as those of Wood (1996), Smith & Wood (1995), and Wood & Okamura (1999).

Statoblasts in sedimentary records

A brief review of literature on Statoblasts recovered from sedimentary samples is presented. This is by no means an exhaustive list of all the literature. Only three genera of bryozoans have been recorded thus far in paleoecological studies: *Plumatella, Pectinatella,* and *Cristatella mucedo,* with *Pectinatella* being very rarely reported. Frey (1964) lists two reports of *Paludicella* Statoblasts in surficial sediments in Sweden (Munthe, 1895; Trybom, 1888), but *Paludicella* is in the class Gymnolaemata that do not produce Statoblasts, so these are probably misidentified specimens. Frey (1964) provides a good review of the literature on sedimentary Statoblasts published up to that point. Many of the references are pollen and macrofossil studies, and Statoblasts are only mentioned briefly, and not found in very great abundance (for example, Mitchell, 1940, 1941; Allison et al, 1952; Harmsworth, 1968; Warner et al., 1987). Crisman (1988) also gives a short review and indicates that Statoblasts are often mentioned in the palynological literature. The Statoblasts recovered are often of *Cristatella mucedo,* which are large and very distinctive (Fig. 3). *Cristatella mucedo* is also a circumpolar species of north temperate regions, where pollen analysis has classically been done. Pollen work usually involves examination of only a small amount of sediment material (see Bennett & Willis, volume 3), and so workers may have only encountered a few Statoblasts in any one sample. *Plumatella,* the other genus reported in palynological studies, is common and widely distributed and a prolific producer of Statoblasts, hence giving them a better chance to be found in sediments. *Fredericella* is another genus that is cosmopolitan and often abundant, but the Statoblasts have never been reported from sediment samples. This may be in part due to low Statoblast production, typically only 1 to 2 sessoblasts per zooid (no floatoblasts), whereas *Plumatella* can produce up to 27 Statoblasts per zooid (Bushnell, 1973).

First reports of fossil Statoblasts appeared in the 1890s (Frey, 1964), including that of Wesenberg-Lund (1896) who provided descriptions and illustrations of *Plumatella* and *Cristatella* Statoblasts from postglacial deposits. Although most fossil Statoblasts have been recovered from late Pleistocene and Holocene lake deposits, the oldest Statoblasts date from the Permian. Vinogradov (1996) reported Statoblasts of three genera (*Plumatella, Hyalinella,* and *Stephanella*) from Permian, Jurassic, Cretaceous, and Miocene deposits from Kazakhstan and Russia. Kuc (1973) recovered *Cristatella mucedo* Statoblasts from the Beaufort Formation on Banks Island, Canadian Arctic, which is dated late Tertiary/early Pleistocene.

Most fossil Statoblasts are found in organic gyttja deposits, but Bennike et al. (1998) have recorded *Cristatella* in marl sediments. Lavoie & Payette (1995) found *Cristatella* in peat deposits in Québec, and Kuc (1973) also recovered *Cristatella* from peat deposits in the Canadian Arctic. *Plumatella* is most often associated with gyttja deposits. Statoblasts have also been recovered from reservoirs in Spain (Prat & Daroca, 1983), extinct lakes (Frey, 1958; Mitchell, 1940), and lacustrine layers in marine cores from the Baltic Sea (Bennike et al., 1998).

The first stratigraphic profile of fossil Statoblasts and their use in interpreting environmental history was given by Deevey (1942) in a core from Linsley Pond, Connecticut. He

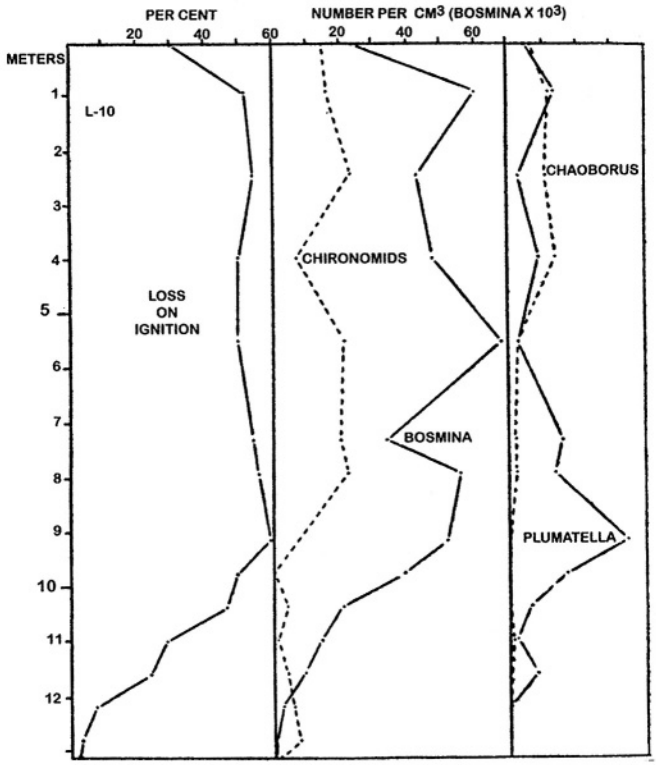

Figure 5. Core L-10 from Linsley Pond, Connecticut (Deevey, 1942). Microfossils are numbers per cm^3 of sediment.

was also the first to suggest that statoblasts could provide indirect evidence of macrophyte abundance. Deevey was interested in lake development, or the succession of lake types, and found that initially the profiles of percent organic matter and number of Bosmina were sigmoid curves, much like the sigmoid curves for the growth of organisms or populations. The maximum abundance of *Plumatella repens* statoblasts coincided with the maximum amount of organic matter in the core. Following that, there was a decline in statoblasts (Fig. 5). Deevey's interpretation was that the *Plumatella* decline reflected a decline in macrophytes (a common substrate for bryozoans), which in turn reflected shading by phytoplankton as productivity of the pond increased. Prior to this, high water transparency had permitted macrophytes to grow to greater depths, hence providing more substrate for bryozoans. In support of this idea, epiphytic diatoms also declined at the same time as did statoblasts.

Deevey also included the only report of fossil *Pectinatella magnifica* statoblasts, from the early spruce-fir period. Since this species favors warmer waters, he interpreted this to indicate the water was at a warmer temperature than was indicated by the terrestrial vegetation present at the time. This interpretation is not surprising in light of recent work

showing that lake surface water temperatures are about 3 to 5 °C higher than air temperatures (Livingstone et al., 1999).

The Linsley Pond history was later reinterpreted by Vallentyne & Swabey (1955). Because the zone of maximum statoblast abundance coincided with what appeared to be increased frequency of breakage of pollen grains, statoblasts, and *Bosmina* carapaces, they felt mis zone represented increased redeposition from the littoral region into the deep sediments, and not a time of high transparency and macrophyte growth. However, possible reasons for the high rate of redeposition during that time are lacking.

Frey (1958, 1962) recovered both *Plumatella* and *Cristatella* statoblasts in conjunction with fossil Cladocera studies. Frey (1958) interpreted *Plumatella* statoblasts in Alleröd age (warm interstadial period) sediments from a small extinct lake in Germany as indicating a favorable climate, particularly as they occurred with sponge spicules and high numbers of chironomids. In lacustrine deposits in Denmark of Eemian interglacial age, Frey (1962) found a peak in *Plumatella* statoblasts in the early part of the moist oceanic phase. He compared this with the maximum found by Deevey in Linsley Pond, and invoked a similar interpretation, that there was also a maximum of submersed aquatic plants at that time, associated with climate amelioration and increased productivity.

Stahl (1959) recovered fossil *Plumatella* statoblasts from a lake core in Indiana during a study of the development of dipteran fauna. Stahl noted a correlation between the numbers of statoblasts and the abundance of *Sergentia* (Chironomidae) head capsules. However, it can be seen from his profile that there is also a general correlation between statoblast numbers and the total number of chironomid head capsules recovered. Unfortunately, only seven core samples were examined for statoblasts, and Stahl refrained from making any interpretations of the findings. In Lago di Monterosi, Italy, Goulden (1970) counted *Plumatella* statoblasts along with many other types of animal fossil remains. The abundance of statoblasts was correlated with that of turbellarian cocoons, and the abundance of both may have been related to fluctuating water levels.

Profiles of *Plumatella* statoblasts in a core from Lake Nojiri in Japan are presented by Tsukada (1972). These bryozoans were abundant from 11,500 to 4,500 ^{14}C years BP, then declined and numbers remained low up to the present (Fig. 6). Tsukada felt that the lake became deeper at the time of the statoblast decline, resulting in less macrophyte coverage and hence a lower bryozoan population. This is corroborated by an increase in planktonic Cladocera such as *Bosmina longirostris* during the deeper water phase (4,500 to present). Another interesting aspect of this core are the two volcanic ash layers. Statoblast numbers declined dramatically at these points, which fits nicely with the evidence that bryozoans can not tolerate high turbidity and fine siltation (Cooper, 1988).

In a study of six Greenland lakes, Fredskild et al. (1975) found statoblasts of *Cristatella mucedo* during the late hypsithermal period, (3,600 to 2,600 ^{14}C years BP) in one of the lakes, Comarum Sø. They interpreted this time period as a climatic optimum, particularly since *Cristatella* is not known from Greenland today. Bennike & Böcher (1992) also found *Cristatella mucedo* statoblasts in Greenland, in a coastal cliff deposit which dates to a warm interval in late Oxygen Isotope Stage 5 (just before the last glacial advance). Seven statoblasts were isolated from a 10kg sample taken near Thule Air Base, on Western Greenland.

Plumatella repens has also been recovered in Greenland sediments. Björck et al. (1994) found these statoblasts at only one level in a core from Lake Boksehandsken, Jameson Land,

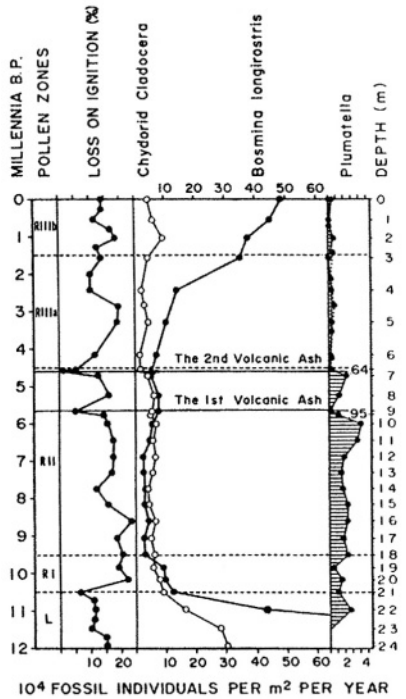

Figure 6. Accumulation rates of Cladocera and *Plumatella* remains in Lake Nojiri, Japan. Modified from Tsukada (1972).

of approximate age of 8000 years, and probably indicating higher summer temperatures than at present. Occurrence of *P. repens* statoblasts was much more frequent in two lakes in Disko, West Greenland (Bennike, 1995). The statoblasts are present from about 4000 ^{14}C years BP to sub-recent samples, but abundance fluctuates. No interpretations were offered. In a study of four other West Greenland lakes, Bennike (2000) found *P. repens* to be abundant in the two freshwater lakes cores, but virtually absent from the two lakes with high salinity.

In a study of three Minnesota lakes, Birks et al. (1976) counted statoblasts of both *Cristatella mucedo* and *Plumatella.* They were interested in documenting stratigraphic effects of cultural eutrophication during the last 100 years. Increases in statoblast abundance were correlated with increases in aquatic plant pollen and macrofossils. Greatest abundance of bryozoans occurred in Lake Sallie in the recent sediments, reflecting increasing productivity due to cultural eutrophication. However, it can not be determined whether bryozoans are responding to an increase of available substrate or increasing nutrients and food availability.

Lavoie & Payette (1995) used statoblasts of *Cristatella mucedo* as well as other plant and animal macrofossils to trace the development of a palsa peatland in northern Québec, Canada. Statoblasts were most abundant from 5850 to 4400 ^{14}C years BP, as were cladoceran ephippia, when the area was peatland with scattered ponds, and the site had open

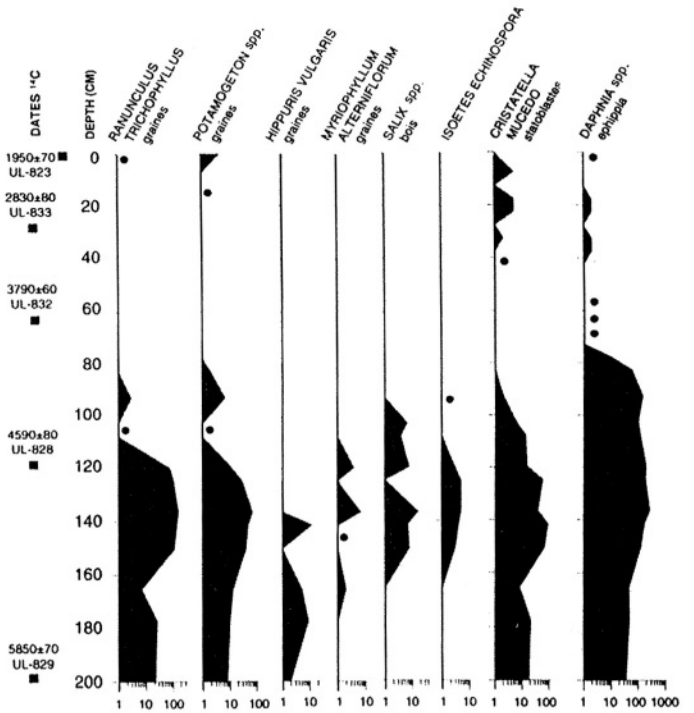

Figure 7. Selected profiles of plant and animal macrofossils, including *Cristatella mucedo*, from a study of peatland development in northern Québec. Modified from Lavoie & Payette (1995). Numbers are per 200 cm^3 of peat.

water (Fig. 7). During one period, dry conditions apparently prevailed, as statoblasts and ephippia disappeared, as well as macrofossils of aquatic plants. A raised palsa was formed at the site about 1950 ^{14}C years BP.

Probably the greatest numbers of statoblasts reported from sediments come from Douglas Lake in Michigan (Francis, 1997). The number of *Plumatella nitens* statoblasts per cm^3 ranged as high as 140 (Fig. 8). In two cores from this lake, statoblast abundance declines abruptly at a time corresponding to heavy logging in the watershed in 1880. The decline may have been due to heavy siltation associated with the logging operations, or a decline in macrophyte abundance. A concomitant decline in littoral chironomid head capsules suggests major disturbance in the littoral zone.

Only one attempt has been made to collect surface-spectrum data for bryozoans. Crisman et al. (1986) made a survey of surficial sediments from 30 shallow Florida lakes. In lakes with less than 50% of the bottom covered with macrophytes, they found a positive correlation between statoblast accumulation rate and macrophyte cover. In lakes in which macrophyte cover was greater than 50%, this relationship was reversed, suggesting that at high levels of macrophyte abundance, the lake would be dominated by epiphytic algae and phytoplankton used for food by bryozoans would be at low concentrations. Thus the bryozoans may be food limited in lakes with greater than 50% coverage of macrophytes. In lakes with less

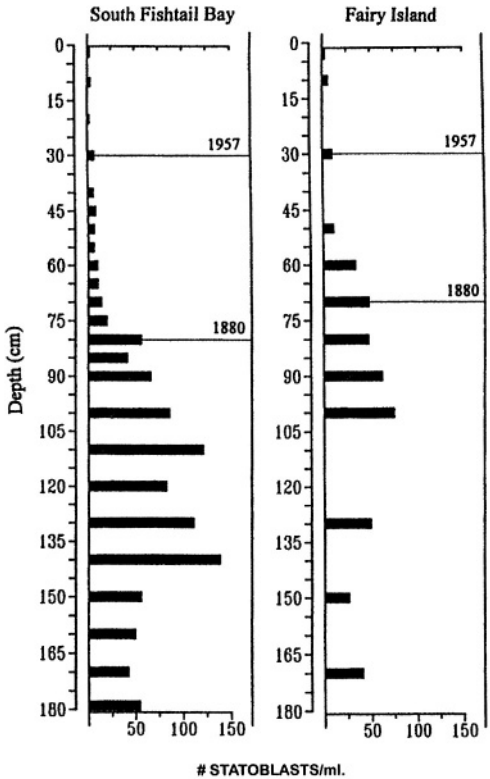

Figure 8. Statoblasts of *Plumatella nitens* in two cores from Douglas Lake, Michigan. Modified from Francis (1997).

than 50% coverage, statoblast abundance was positively correlated with trophic state. No species designations were given in this paper.

Indicator Potential

Fossil bryozoan statoblasts have thus far been used in interpretations of water-level fluctuations or the presence of open water and aquatic conditions, the extent of macrophyte or littoral zone development, disturbances in the littoral zone, lake trophic state, and temperature/climate. Although bryozoans can be found in a wide range of habitats and conditions, some specific things can be noted about several species, and current research indicates that more information is being accumulated. *Plumatella* constitutes the largest group of freshwater bryozoans, and they produce the most statoblasts, more than twice that of other genera (Bushnell, 1973), and which can be identified to species level. *P. casmiana* is associated with alkaline waters (Bushnell, 1968; Ricciardi & Reiswig, 1994). *P. emarginata* is more common in streams than other Plumatellidae (Bushnell, 1974; Karlson, 1991; Wood, 1991) and is also stenothermal, not tolerating very high or very low temperatures

(Bushnell, 1974). *P. fungosa* is usually collected from solid substrates such as rocks and bridge supports (Bushnell, 1974). *P. nitens* is believed to be restricted to northern North America (Wood, 1996). *Cristatella mucedo* is circumpolar, in colder north temperate areas (Bushnell, 1968). Statoblasts of this species have been recovered from many northern sites (Kuc, 1973; Matthews, 1974; Fredskild et al., 1975). *Pectinatella magnifica* is a warm water species, particularly abundant in the southern United States (Dendy, 1963; Everitt, 1975). *P. magnifica* is very intolerant of siltation/turbid waters (Cooper & Burns, 1984). *Pectinatella* and *Cristatella* are least adapted for turbulent water habitats because of their gelatinous colony structure (Bushnell, 1973).

Work on *Cristatella mucedo* by Toriumi (1943) suggested that some statoblast characteristics for this species may be temperature-dependent. Statoblasts collected during the colder months had smaller diameters and fewer spines than those collected during the summer. Unfortunately, no water temperature data were collected during the study. Shotton et al. (1965) hoped to use this information to infer climate change during the Hoxnian interglacial period (about 250,000 years BP) from *Cristatella mucedo* statoblasts recovered from lacustrine sediments in Nechells, England. However, they found no systematic trend in variation of either spine number or statoblast diameters that they could correlate with a climate change from late-glacial to temperate. Variation of statoblast characteristics in response to environmental conditions has received little attention since then, and is an area of research that would bear further exploration.

Although in general, all freshwater bryozoans have been found most often in clean or only mildly polluted habitats (Bushnell, 1974), some species can tolerate organic and other pollution. *Plumatella repens* has been reported from several habitats polluted with livestock wastes (Rogick & Brown, 1942; Dendy, 1963; Bushnell, 1974). *P. emarginata* also seems to tolerate some organic pollution (Bushnell, 1966). In studies of heavy metal toxicity, several authors have found bryozoans to be more sensitive than other invertebrates (Bushnell, 1974; Mundy, 1981; Pardue & Wood, 1980). Mundy (1981) found *Cristatella mucedo* to be particularly sensitive to low levels of copper. Bushnell (1974) also tested the sensitivity of *P. casmiana* to organic pesticides and found evidence of impaired feeding, reduced budding, abnormal behavior, and increased mortality. He also exposed *P. casmiana* Statoblasts to city sewage and found that many remained viable and produced normal colonies.

Sensitivity to siltation or high turbidity has been noted by Ellis (1965) for *Cristatella mucedo* in England. *Pectinatella magnifica* also seems to be intolerant of heavy silt (Cooper & Burris, 1984). Cooper (1988) tested the tolerance of *P. magnifica, Plumatella repens,* and a sponge to suspended sediments in laboratory experiments and found that although all three species were sensitive, *P. repens* showed the highest rates of mortality. Cooper felt that *P. repens* was more sensitive to sediment than to the pesticides and sewage as tested by Bushnell (1974).

Substrate availability is clearly a limiting factor for bryozoans (Wood, 1991). Because macrophytes are a frequently used substrate by many species, statoblast abundance in lake sediments is often used to infer the extent of macrophyte and littoral zone development in lakes, or water-level fluctuations. Studies of preference of freshwater bryozoans for specific species of plants as substrate have not been conclusive. Brown (1933) stated that *Plumatella* in Douglas Lake avoided *Chara* as a substrate, but other workers have found abundant colonies on *Chara* (Shrivastava & Rao, 1985). Bushnell (1966) did a detailed

survey of plant-bryozoan interactions and found little evidence for species specificity. The correlation of bryozoan abundance with macrophyte abundance needs more quantitative work, the only work in that area thus far having been done by Crisman et al. (1986).

Some limitations on the use of bryozoan statoblasts in paleolimnological interpretations include the fact that they are not always abundant in sediment samples, and large quantities of sample may have to be examined to obtain significant numbers. Greater limitations result from our lack of knowledge of the ecology of these invertebrates. More information is needed particularly on the relationship of bryozoan species to their macrophyte substrates, the relationship between population size and numbers of statoblasts produced, as well as the taphonomy of statoblasts and what factors control deposition of statoblasts. The buoyant floatoblasts could be flushed from lakes before they could be deposited. Free statoblast valves from germinated colonies (or from being broken apart) may have a greater probability of ending up in deep lake sediments were cores are usually taken. Most studies make the assumption that statoblast numbers deposited in sediments are a reflection of population size of bryozoans, and this assumption needs to be explored.

Conclusions and future directions

Frey (1964) believed that fossil statoblasts had great potential because they could be recognized to species level, and are abundant enough for quantitative studies, with the reservation that much more information was needed on factors controlling statoblast production and population size. The paleolimnological community seems finally to be moving toward realizing Frey's vision. Increasing interest in fossil statoblasts is shown by the number of papers published in recent years, including Crisman et al. (1986), van Geel, et al. (1989), Björck (1994), Bennike (1995), Francis (1997), Bennike et al. (1998), to name only a few.

The indicator potential of members of the family Plumatellidae has a great deal of promise for paleoecology. They are the largest group of freshwater bryozoans, prolific producers of statoblasts, and widely distributed throughout the world. The resistant statoblasts can be carried by wind, water, and other animals, making potential for dispersal and colonization of new habitats high. The many species can be identified based on statoblast morphology using simple light microscopy, and more work on statoblast morphology is continually being published. In addition, there is in general more interest in freshwater bryozoans, with an increasing amount of work being done on all aspects of their ecology including dispersal strategies (Karlson, 1992), relationships with other organisms (Joo et al., 1992), feeding and food preferences (Richelle et al., 1994), statoblasts survival (Smyth & Reynolds, 1995), reproduction (Uotila & Jokela, 1995), and genetics and population biology (Okamura, 1997; Hatton-Ellis et al., 1998). Taxonomy and species distributions are also receiving increased attention (Smith, 1992; Wood & Backus, 1992; Smith & Wood, 1995; Wood, 1996; Wood & Okamura, 1999).

In terms of paleolimnological research, bryozoan statoblasts have particular potential in multiproxy studies of environmental change. It is hoped that researchers will continue to produce stratigraphic profiles of statoblasts from different areas of the world. The more information that is gathered, the more we can learn about these animals as environmental indicators. Topics that clearly require more research include identification of fossil statoblasts to the species level, collection of surface-spectra data, and the taphonomy and deposition of statoblast valves. Crisman et al. (1986) also suggest that stratigraphic sequences could be

used to study long-term population dynamics of freshwater bryozoans, an intriguing idea that has not been acted upon.

Summary

Bryozoans are small, sessile, colonial, filter-feeding animals that live in shallow waters of lakes, streams, and other aquatic habitats. Freshwater bryozoans are distributed worldwide, and can be important components of littoral communities in terms of biomass, nutrient cycling, and community structure. Freshwater species produce statoblasts by asexual reproduction. Statoblasts consist of two chitinous valves enclosing germinal tissue that can grow into a new colony. The valves can be recovered from lake sediment samples and often identified to the species level. Methods for removal and study of statoblasts in sediment samples are reviewed. Statoblasts are often recovered in conjunction with other types of fossils, including pollen, plant macrofossils, and insects. A review of work on fossil statoblasts reveals increased interest in their use as indicators of climate, lake-level fluctuations, extent and development of littoral zones and macrophyte coverage, and pollution. Increasing interest in the ecology, population dynamics, and systematics of extant faunas bodes well for improvements in the use of bryozoan statoblasts as paleolimnological tools. There is a great need for research on both modern and fossil assemblages.

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7. OSTRACODA

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Introduction

Ostracods are small, bivalved aquatic crustaceans that secrete shells of low magnesian calcite. Adults are typically 0.5 to 3 mm long. Ostracods are common in all types of non-marine waters with neutral to alkaline pH. They are frequently abundant and well preserved in lake sediments. Ostracods may also occur in slightly acidic waters, but their shells are rarely preserved in the sedimentary record in such environments.

Ostracods are sensitive to a range of ecological factors including habitat type, nutrient status and the salinity, temperature and chemical composition of their host water. Furthermore, the trace element (especially Mg and Sr) content and stable isotope ($^{18}O/^{16}O$ and $^{13}C/^{12}C$) ratios of their shells reflect important limnological variables such as water temperature, water chemistry and productivity. More recent geochemical applications of ostracod shells include their use in $^{87}Sr/^{86}Sr$ analyses and radiometric dating, including radiocarbon and uranium series. Overall, ostracods have excellent potential in palaeolimnology.

Despite this potential, ostracods have received less attention from Quaternary palaeoecologists than many other microfossil groups. This has arisen partly because of a perception, probably unwarranted, that non-marine ostracods are difficult to identify to species level and that taxonomic confusion reigns within the group. Moreover, there is a lack of quantitative ecological information for many taxa and geographical regions and a dearth of modern ecological training sets. However, the use of ostracods in multi-proxy palaeolimnological investigations has grown markedly over the last decade or so as more information about the modern ecology is being amassed. Furthermore, increased use has been made of ostracod shells in geochemical studies. There have been several reviews of the group published during this time that are relevant to palaeoecologists, including De Deckker & Forester (1988), Carbonel et al. (1988), Holmes (1992), Löffler (1997) and Griffiths & Holmes (2000) on the general applications of non-marine ostracods: Holmes (1996b) specifically reviewed the geochemical applications of ostracods.

J. P. Smol, H. J. B. Birks & W. M. Last (eds.), 2001. *Tracking Environmental Change Using Lake Sediments. Volume 4: Zoological Indicators.* Kluwer Academic Publishers, Dordrecht, The Netherlands.

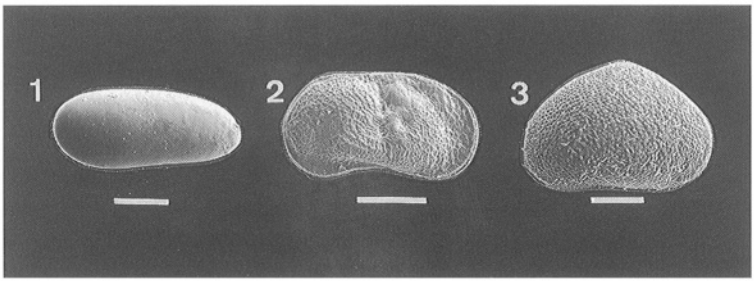

Figure 1. Scanning electron micrographs of a single representative of each of the non-marine ostracod superfamilies. Each picture shows an external lateral view of a valve. 1. Darwinuloidea. *Darwinula stevensoni* (Brady & Robertson, 1870). Female, right valve. Recent, Mooghaun Lough, Co. Clare, Ireland. 2. Cytheroidea. *Limnocythere inopinata* (Baird, 1843). Female, right valve. Recent, An Loch Mór, Co. Galway, Ireland. 3. Cypridoidea. *Sarscypridopsis aculeata* (Costa, 1847). Female, left valve. Recent, An Loch Mór, Co. Galway, Ireland. Scale bars = 200 μm.

The aim of this chapter is to provide a state-of-the-art overview of ostracods and their use in Quaternary palaeolimnology. It begins with an outline of ostracod structure and biology: a brief account of non-marine ostracod taxonomy is also provided. Next, the chapter considers the ecological factors controlling ostracod occurrence, with particular emphasis on those factors that can be quantified, and/or are of palaeoenvironmental significance. Techniques for the extraction, identification and study of ostracods are examined, including geochemical analysis. Finally, possible future developments are outlined.

Biology and taxonomy

Structure and morphology

An ostracod's body is completely enclosed within a calcareous carapace, which is composed of two shells, or valves (Fig. 1), which are hinged dorsally and partially enclose the limbs and body parts. Although it is the shells that are commonly preserved in sediments, much taxonomic work relies on examination of the body parts.

The outer surfaces of non-marine ostracod shells are often smooth, although some may be ornamented, like their marine counterparts. However, in contrast to marine taxa, the hinge of non-marine taxa is relatively simple, often consisting of a bar and groove. The adductor muscles effect the closure of the two valves. The point of attachment of the adductor muscles onto the shell may form prominent muscle scars on the internal surface of the shell (Fig. 2) and these scars may have taxonomic significance at higher levels. Kesling (1951) discusses the terminology of ostracod carapaces (Fig. 2) at length. Ostracod carapaces are formed by the calcification of the outer of two layers of epidermal tissue, which is termed the outer lamella; the inner lamella is only partially calcified. The carapace appears to be formed from ions taken from the host water at the time of calcification (Turpen & Angell, 1971).

The carapace surrounds a largely-unsegmented body, together with seven or eight pairs of appendages. The appendages are variously associated with movement, feeding and copulation: detailed functional and terminological descriptions are given in Athersuch et al. (1989) and Henderson (1990).

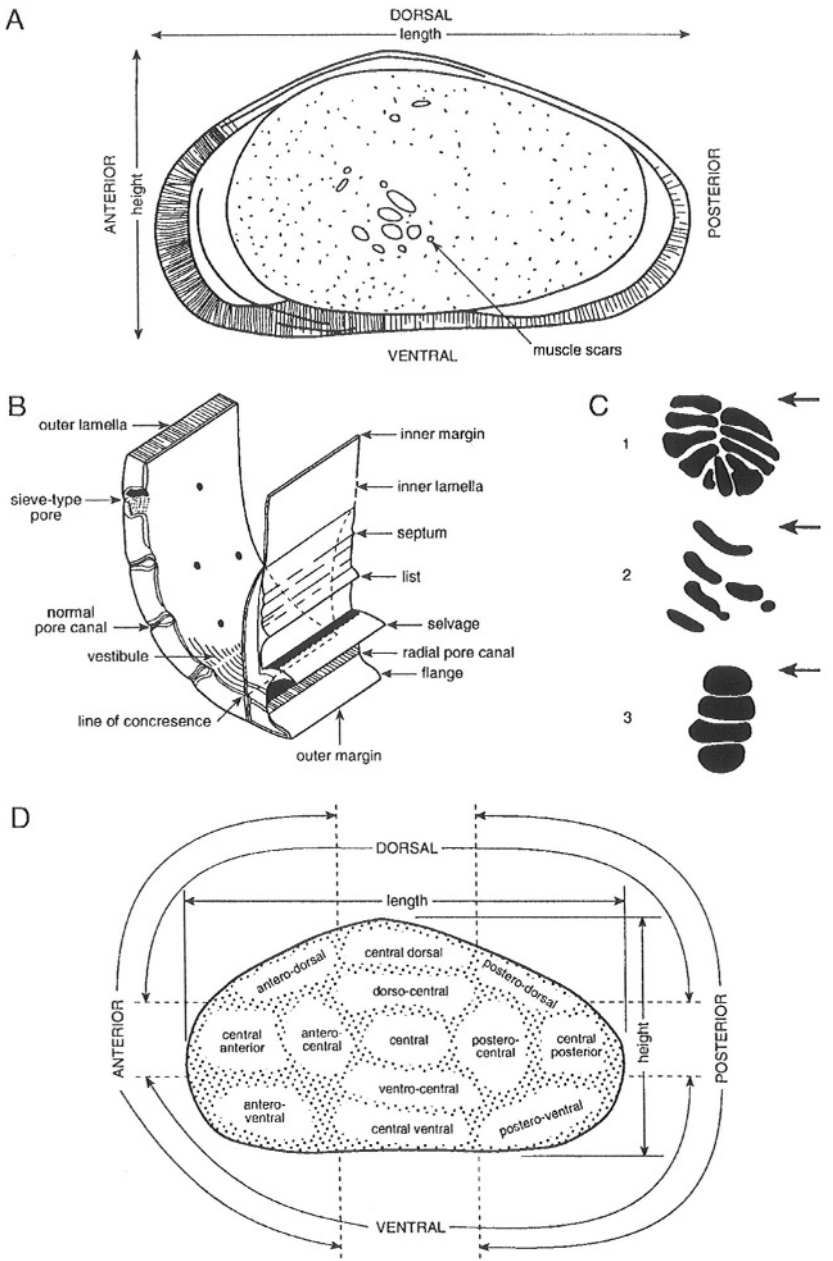

Figure 2. Structure of an ostracod carapace and associated terminology. A. Internal view of the right valve of *Eucypris heinrichi* Diebel & Pietrzeniuk, 1978 (redrawn from Diebel & Pietrzeniuk, 1978a). B. Section through an ostracod valve margin (redrawn from van Morkhoven,1962). C. Pattern of adductor muscle scars in the three superfamilies of non-marine Ostracoda: 1. Darwinuloidea; 2. Cypridoidea; 3. Cytheroidea. Arrows point to the posterior. (From Griffiths & Holmes, 2000). D. Ostracod shell terminology (adapted from van Morkhoven, 1962).

Reproduction, growth and life-cycles

Ostracods reproduce sexually or parthenogenetically: in the latter case, populations contain only females. Geographical parthenogenesis is known amongst some species (e.g., Home et al., 1998). For sexual populations the degree of sexual dimorphism varies. For some species male and female shells are readily distinguished whereas in others, those of the two sexes are all but identical. In some strongly dimorphic taxa, the male shells tend to be inflated posteriorally, in response to the need to accommodate the large genitalia. In others, the female may show posterior inflation of the shell to provide a brood space for the eggs and juvenile instars.

Ostracods lay eggs. Following hatching of the nauplius larva, the animal grows by moulting, generally eight times between the hatching of the egg and the adult. The adult stage is often designated 'A', with the first growth stage (instar) designated A-8, and then subsequent stages designated A-7, A-6 and so on, to the adult stage. In addition to a change in size (Fig. 3), growth involves an increase in the degree of calcification and complexity of the shell, together with modifications to the complement of appendages. Frequently, the shape of the shell becomes more adult-like with each moult, although in some cases, it is difficult to identify juveniles to species level with certainty based on the shells alone. An instar series for a species often resembles the adult female in terms of shape, although this is not always the case. The adult shell form is not attained until the final moult. In sexual populations, males are often not recognisable until the adult stage, although sexual dimorphism may become apparent in juvenile moult stages in some species.

The life span of an ostracod varies markedly between species, from as little as several weeks, to several years (Delorme, 1978). Moreover, the time taken to reach maturity is not constant, and is also dependent on environmental conditions. Most taxa show some degree of seasonality in their distribution. This is especially the case for ostracods adapted to desiccation, whose life-cycle is coupled to the seasonal drying of the waterbody.

Higher-level taxonomy

All non-marine ostracods belong to the order Podocopida. Within this order there are three superfamilies that occur in non-marine environments, namely the Darwinuloidea, the Cytheroidea and the Cypridoidea (Martens et al., 1998) in order of increasing number of genera (around 5, 20 and 100 respectively: Holmes & Home, 1999). Distinction between the three superfamiles is most clearly made on the basis of the adductor muscle scars. In the Darwinuloidea, they show a clear 'rosette' pattern; in the Cytheroidea they form a near-vertical row with four or five components; in the Cypridoidea, they are more clustered, but generally very different to those of the two other superfamilies (Fig. 2). A more detailed discussion of taxonomy is beyond the scope of this chapter, although techniques for identification are examined below.

Ecology

The factors that control the presence and abundance of a given species include habitat characteristics and the nature of the host water. The former category includes the

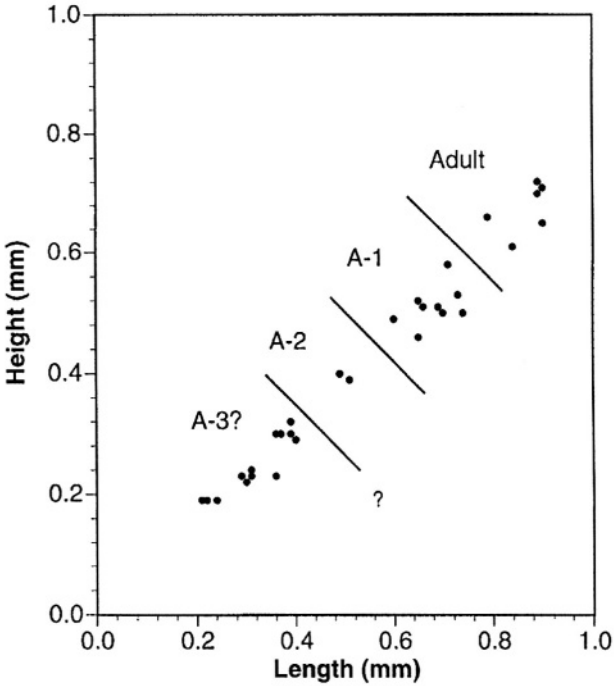

Figure 3. Size-dispersion diagram of valves of *Cypretta brevisaepta* from late Quaternary sediments in Jamaica (from J. A. Holmes, unpublished).

size, energy level and permanence of the waterbody together with the depth at the site, presence and types of aquatic plants, availability of food and predation. Water characteristics include temperature, pH, dissolved oxygen content, salinity and ionic composition. Palaeoecologically, the most important of these factors are hydrological habitat type, temperature, salinity and ionic composition; most attention will therefore be paid to these factors. Ostracod shells that are preserved in lake sediments may have calcified within the zone of groundwater discharge (e.g., springs and seeps): thus many species respond at least in pan to the physical and chemical characteristics of groundwater (Forester, 1991).

Hydrological habitat characteristics

It is possible to classify many non-marine ostracod species into habitat-preference groups. This may allow reconstruction of the general environment of deposition of a sedimentary sequence where the associated waterbody is either no longer present, or has undergone substantial change through time. For example, Absolon (1973) assigned many Central European species into spring-, stream-, pond-, lake-, groundwater- and temporary-water affinity groups.

Many ostracods are able to withstand desiccation. Juveniles of some species survive prolonged desiccation through torpidity (e.g., Horne, 1993). Moreover, many cypridoidean species produce desiccation-resistant eggs. The occurrence of such ostracods in the fossil record may point to past seasonal desiccation. Many ostracods crawl on, or burrow into, their substrate (e.g., members of the genera *Cytherissa, Limnocythere* and *Candona*) whereas others (e.g., *Cypridopsis*) are strong swimmers. However, even the swimming forms tend to stay within the shelter of aquatic macrophytes: there are no truly planktonic species.

Water depth also appears to be an important control, especially in large lakes. Mourguiart & Carbonel (1994) have noted the clear depth-zonation of species in the large lakes of the Bolivian Altiplano and used this relationship to reconstruct Quaternary water-depth and lake-level histories. It seems likely that such depth zonation is not a simple response to water depth, but is linked to the depth distribution of aquatic plants within the lake (e.g., Bridgwater, 1995; Holmes, 1997, 1998), which is, in turn, a response to light availability, together with inputs and outputs of surface water and groundwater.

Salinity

Ostracods appear to be sensitive to salinity, in terms of total dissolved ions, although there are many euryhaline taxa. In non-marine waters, salinity rise may be a response to evaporative concentration as a result of climatic drying (e.g., De Deckker & Forester, 1988; Holmes et al., 1997), marine intrusion in coastal lakes (e.g., Holmes et al., 1995) or human-induced pollution (e.g., Taylor & Howard, 1993). A number of authors have compiled salinity tolerance data for non-marine species (e.g., Keyser, 1977; De Deckker, 1981b, 1988; Carbonel et al., 1988; Neale, 1988) (Fig. 4). Salinity can affect both the species diversity and abundance of ostracods. There is often a rise in both diversity and abundance with salinity up to the calcite branchpoint (the point during evaporative evolution at which calcite precipitation takes place, but often taken to be the dividing line between fresh and saline waters). Beyond the branchpoint, diversity decreases but abundance further increases (De Deckker & Forester, 1988) (Fig. 5).

Solute Composition

The lack of a simple relationship between ostracod occurrence and salinity has led several workers to suggest that the ionic composition of the water may be a more important control than salinity *per se*, even though these two factors are frequently related. For example, Forester (1983) noted that certain saline-lake ostracods did not co-exist in nature despite having similar salinity tolerances. He showed that anion composition was an important control, and suggested that the occurrence of certain taxa could be depicted on anion ternary diagrams (Fig. 6). A means of depicting both the salinity tolerance and ionic preferences of ostracods species is to plot their occurrence as a function of salinity and the alkalinity/Ca ratio of the host water. As lake water evaporates, it follows one of several different pathways of solute evolution depending on its initial composition. Many species of ostracod appear to be especially sensitive to the alkalinity/Ca ratio (see, for example, Curry, 1999). Ionic preferences of ostracods have also been noted by Carbonel & Peypouquet (1983), Peypouquet et al. (1983), Carbonel et al. (1987), Smith (1993), and Taylor &

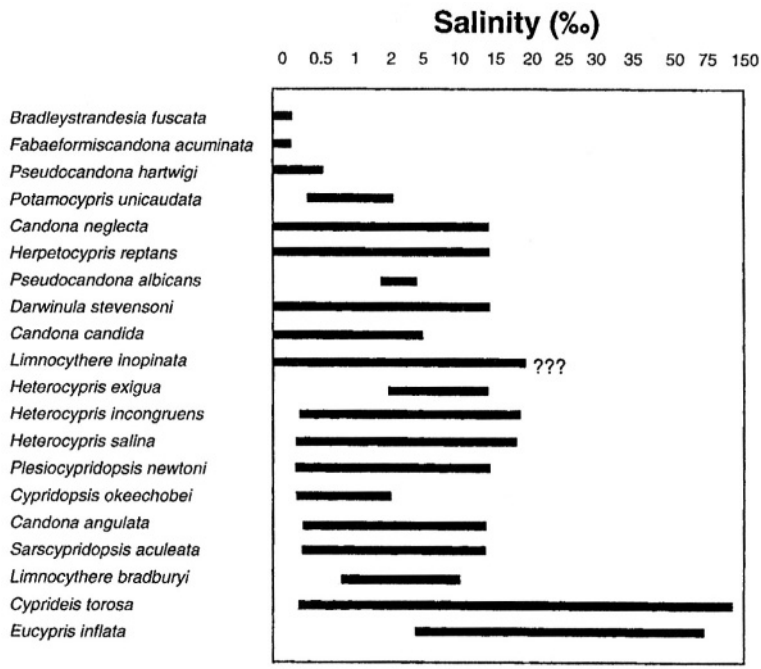

Figure 4. Salinity tolerances of selected non-marine ostracod species (from information in De Deckker, 1981a and Neale, 1988).

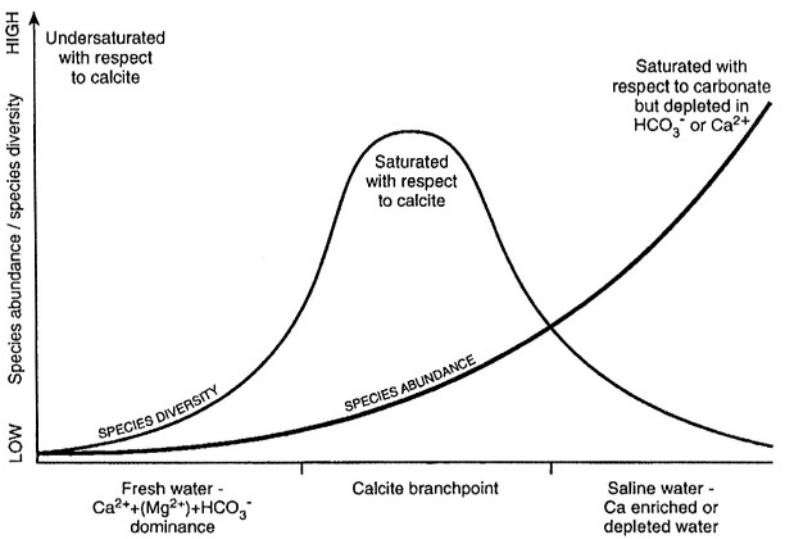

Figure 5. Relationship between ostracod species diversity and abundance, and salinity in non-marine waters. For further explanation, see text (after De Deckker & Forester, 1988).

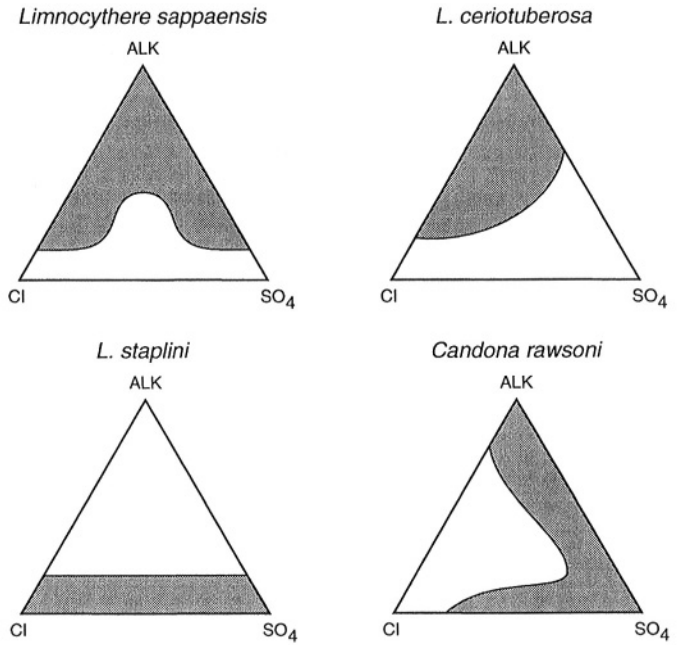

Figure 6. Schematic representation of the occurrence of four non-marine ostracod taxa in hydrochemical space shown by the shaded area on anion trilinear diagrams (from information in Forester, 1983, 1986).

Howard (1993). A knowledge of such preferences is important for the reconstruction of long-term solute histories of lakes (e.g., Smith et al., 1992).

Water temperature

Some ostracods species are limited latitudinally, suggesting that temperature is an important control on ostracod occurrence. Limited information is available on the temperature preferences of non-marine ostracods (e.g., Tab. I). Despite this lack of data, it is known that water temperature will influence the occurrence (e.g., Delorme & Zoltai, 1984), growth rate, size, and life span (e.g., Martens et al., 1985) of individual species. Although the range of temperatures that a species can tolerate may be high, most species have narrower optimum temperatures at which their productivity is at a maximum (e.g., Forester, 1987).

Ecological, palaeoecological and geochemical techniques

Sampling of ostracods from waters and lacustrine sediments

Modem environments: Living ostracods are often collected for taxonomic or ecological work, most usefully along with all associated environmental information. In general, the

Table I. Temperature ranges of selected non-marine ostracod species.

Species	Temp. (°C)	Locality	Notes	Source
Candona rawsoni	5.5 to 30.2	Canada	Bottom-water temperature	1
Candona renoensis	0.0 to 31.0	Canada	Bottom-water temperature	1
Cyclocypris ampla	3.0 to 29.5	Canada	Bottom-water temperature	1
Cytherissa lacustris	5.5 to 18.0	Canada	Bottom-water temperature	1
Ilyocypris gibba	14.0 to 29.5	Canada	Bottom-water temperature	1
Limnocythere staplini	8.0 to 32.0	Canada	Bottom-water temperature	1
Fabaeformiscandona caudata	3.4 to 27.0	Canada	Bottom water temperature	2
Candona subtriangulata	2.6 to 19.2	Canada	Bottom water temperature	2
Tonnacypris glacialis	−1.57 to 12.58	Europe	Summer air temperature range	3
	5.95		Summer mean air temperature	
	±3.18		Standard deviation	

1. Delorme, 1969; 2. Delorme, 1978; 3. Griffiths et al., 1998.

nektic and benthic forms must be sampled using different approaches. Deeper environments can be sampled using grab samplers, such as the Ekman, although these produce large quantities of substrate and users report difficulty with quantification (e.g., Smith, 1991). Coring devices that produce core-top samples generate smaller amounts of sediment, yet the samples are more readily quantified (e.g., Smith, 1991). Coring devices may also be used in shallower waters where grab samplers will fail to function. Some workers use zooplankton nets with mesh sizes of 250 μm to sample shallow waters, especially for those ostracods that show a preference for macrophytes rather than the substrate. However, quantification can be difficult.

Once collected, the sample is either preserved on site or cooled for subsequent picking or preservation in the laboratory. Some workers prefer to pick samples wet under low magnification (× 20–30) using a stereo-zoom microscope: this enables ostracods to be extracted alive. Others may pick a wet fixed sample (30% ethanol to kill the animals with valves open, which aids dissection, followed by 90% ethanol to limit subsequent deterioration). Yet others freeze dry the sediment and pick dry. In many cases, the sample is initially sieved to remove the fine and coarse fractions (see below under 'Fossil sequences'). In preserved samples, ostracods that are articulated and have limbs present and in good

condition are generally assumed to have been living at the time of collection. This is an important consideration, since most modern sampling of the benthos will include material that is essentially subfossil. Wet ostracods are generally stored in 90% ethanol in small vials: dried ostracods are stored in microfossil slides (e.g., Biotech, Reigate, UK). If dissection is required, the protocol of Athersuch et al. (1989) is recommended. Ostracod shells are best examined under a stereo–zoom binocular microscope. For general examination, incident light and a magnification of up to about ×50 is sufficient, although detailed examination requires higher magnification (up to ×100). Fines structures can be enhanced by staining (e.g., malachite green, food colourings) or immersion in water or glycerine.

The extent to which a single ostracod sample can be used in the interpretation of a fossil sequence is open to debate. Of much greater use is a time series of ostracod assemblages and associated environmental variables, such as water temperature and chemistry. However, such information is necessarily more time consuming to collect.

Sedimentary sequences: The extraction of ostracods from Quaternary sediments involves disaggregation of the sediment, size separation and picking. Most workers advocate picking from dry sediment. Disaggregation should involve the least aggressive treatment possible to avoid damage to the ostracod shells (e.g., Hodgkinson, 1991). Techniques that have been used include dispersal in water, followed by drying and rehydration (e.g., Robinson, 1980), freeze-thaw with saturated salt solution (e.g., Glauber salt, $Na_2SO_4.10H_2O$ or $NaHCO_3$) (e.g., Smith, 1991), freeze drying (e.g., Delorme, 1989), hydrogen peroxide treatment (e.g., De Deckker, 1982a,b) and Calgon (sodium hexametaphosphate) treatment (De Deckker, 1979b). Choice of technique will depend on the nature of the sediment. Drying and rehrydration is usually only effective in disaggregating sediments that are poorly consolidated. Freeze-thaw treatment is effective at disaggregating marls and other sediments that are not organic rich. Neither of these physical disaggregation techniques appears to cause significant damage to ostracod shells. Hydrogen peroxide (5–10% v/v) removes organic matter and helps to disaggregate marl, although in the presence of organic matter will dissolve carbonates. Calgon is effective at dispersing clays, although can cause etching of microfossils (e.g., Hodgkinson, 1991).

Following disaggregation, the sediment is generally wet sieved through both fine-mesh (maximum size limit between 63 and 250 μm) and coarse-mesh (>5 mm) sieves to leave the size fraction that contains most adult and later juvenile instars. Although earlier instars will usually be found in the fine fraction, these are often not identifiable to species level and are disregarded in many studies. Sieving is also used to separate the ostracod-bearing sediment into size fractions to aid picking. The choice and number of sieve sizes will depend on the aims of the study. Typical sieve sizes used include 500, 250, 180 and 125 μm. The sieved material is finally oven- or freeze-dried before ostracod extraction (Fig. 7). An oven temperature of 105°C is often used, although a lower temperature is warranted (e.g., <40°C) if the ostracods are to be used in amino-acid racemization studies (e.g., McCoy, 1988).

Debate surrounds the number of valves that should be picked in order to obtain a representative sample. Some authors (e.g., De Deckker, 1979b) have picked all ostracod material, although this is often precluded by very high shell concentrations. Subsampling may involve picking between 300 and 500 valves. If the dry weight of the sediment is recorded and the picked proportion of each sieve fraction is known, the concentration, both

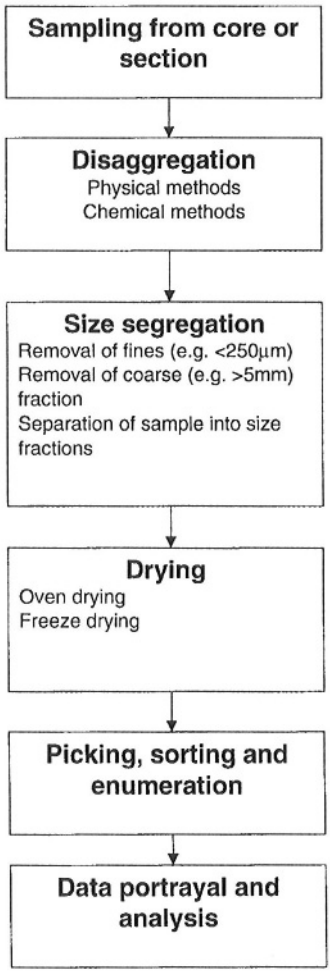

Figure 7. Flow diagram for treatment of sediment samples for ostracod extraction.

total and for each species, can be estimated: this is usually expressed as valves per gram of sediment (e.g., Holmes, 1998). Typically, the removal of the fine fraction by sieving means that the earlier moult stages are not recorded. Many workers justify their exclusion on the grounds that juveniles are difficult to identify to species level. Carapaces, where present, are always counted as two valves. Broken valves are generally excluded from counts, although a note of their approximate abundance is often made, since this may be of palaeoenvironmental significance. However, this practice should be used with care: some large taxa (e.g., *Cypris bispinosa* Lucas, 1849, and some members of the genus *Herpetocypris*) have fragile shells that are often poorly preserved in sediments.

Fossil ostracod data are plotted stratigraphically, often using software such as TILIA GRAPH (e.g., Grim, 1991). Species may be listed in taxonomic order, first appearance

order or grouped according to their environmental preferences, depending on the aims of the study. Both percentage and absolute abundance plots may be used: each has its relative merits (see, for example, Horne & Slipper, 1992; Paul, 1992). Sometimes, distinction is made between adults and juveniles of a species.

Identification of ostracods

The carapace features that are most useful for identification include size of the adult, gross and detailed shape, ornamentation and muscle-scar patterns. Many of these features, however, may show quite marked intra-specific variability.

There are a number of pitfalls in identification of which readers should be aware. Juveniles are especially difficult to identify to species level if adult representatives of the species are not present within the assemblage. This is a problem with the difficult genus *Candona sensu lato,* the juvenile specimens of which are commonly referred to '*Candona* spp. juveniles' in many studies (e.g., De Deckker, 1979b). Some ostracods may have markedly asymmetric valves, such that the left and right valve may appear to belong to different species if they are not articulated. The genus *Physocypria,* for example, includes species with marked valve asymmetry. In sexual populations, care should be taken not to refer adult males and females to different species. Ecophenotypic variation in size, shape and especially ornamentation may also cause problems. This is especially so in the genus *Ilyocypris*, where noded and un-noded specimens have been referred both to the same and to different species (e.g., Van Harten, 1979). Finally, there are a number of problematical taxa, the identification of which is difficult. One of the best examples is the genus *Candona s.l.* (see, e.g., Absolon, 1978), which has since been subdivided into several genera (e.g., Meisch, 2000).

There is no single volume that can be used to identify non-marine ostracods. Instead, the reader must consult mainly regional literature, which is of variable quality. For Europe, the work of Meisch (2000) is the standard reference, although this only covers western and central Europe. Other works include those of Sywula (1974) and Henderson (1990). Parts of Africa (notably east and southern Africa) are well served by the series of papers by Martens (1984, 1985, 1990a,b,c, 1992a,b, 1995), together with McKenzie (1977). In North America, readers are referred to the papers of Delorme (1970a-d, 1971a), together with earlier monographs by Hoff (1942) and Tressler (1966) whereas works on the Ostracoda of South America and the Caribbean islands are covered by the checklist of Martens & Behen (1994). Hartmann (1964), Victor & Fernando (1979, 1982) and Okubo (1990a,b) deal with the non-marine ostracods of Asia. Finally, the papers of Chapman (1963) and De Deckker (1977, 1979a, 1982a,b, 1983) deal with Australasia. This list, whilst not comprehensive, provides readers with an entry point into the literature. Many of the aforementioned works also provide some ecological information.

Palaeoecology

A considerable amount of palaeoenvironmental information can be obtained without identifying a taxon. The overall age structure of a population (i.e., the relative abundance of adults and the different instars of a species) can indicate the presence of transport. If the adults and

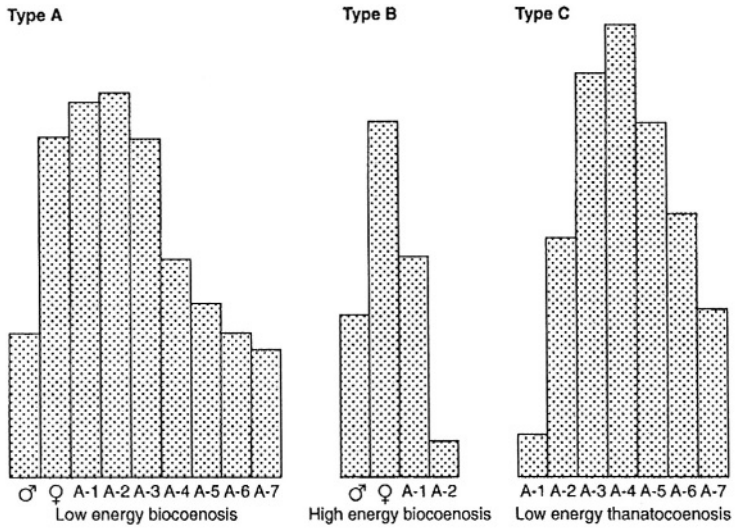

Figure 8. Some examples of ostracod population age structure histograms and their environmental association (redrawn from Whatley, 1988). Type A represents an assemblage that has been subject to negligible transport. Type B represents transport by under high-energy conditions, in which early moult stages are removed, leaving only the adults and later moult-stage juveniles. Type C represents the 'end product' of low-energy transport of earlier moult-stage juveniles from the original death assemblage.

all juvenile instars (allowing for the smallest size fraction examined) are present within an assemblage, it is unlikely that significant *post mortem* transport has taken place (Whatley, 1988). However, the absence of either adults, or earlier instars from an assemblage suggests that there has been some degree of transport (Fig. 8).

Valves to carapace ratios of adult specimens also reflect transport. *Post mortem* disarticulation of adult ostracods will tend to occur in higher-energy environments. In low-energy conditions and with rapid burial (i.e., high rates of sedimentation), valves will tend to remain articulated. The presence of a large number of juvenile carapaces suggests juvenile mortality (since moulting leads to disarticulation), which may arise from the rapid onset of an unfavourable environment. Finally, dissolution, mechanical breakage and the presence of overgrowths on shells indicate reworking and diagenesis, although breakage of valves can occur during coring and sample preparation.

Notwithstanding the above, most palaeoecological work relies on the identification and enumeration of individual taxa. Ostracod workers have tended not to use sophisticated statistical techniques to analyse palaeoecological data; certainly not as routinely as for other fossil groups. Examples of the use of cluster analysis (e.g., Holmes et al., 1998), various ordination techniques (e.g., Griffiths et al., 1996; Mezquita et al., 1999) and transfer functions (e.g., Mourguiart et al., 1992) to analyse and manipulate modern and fossil data can be found in the literature. However, most work involves environmental reconstruction based on the known ecological preferences of each species. In many cases, this reconstruction is qualitative. However, some workers have used quantitative approaches based on modern analogue or autecological methods (e.g., Smith et al., 1992).

Table II. Selected examples of ecophenotypic variations in the carapaces of non-marine Ostracoda and their environmental significance.

Species	Characteristic	Environmental significance	Reference
Cyprideis torosa	Noding	Salinity	Kilenyi, 1972
	Sieve-pore shape	Salinity	Rosenfeld & Vesper, 1977
Cytherissa lacustris	Noding, reticulation	Nutrients, carbonate saturation	Carbonel et al., 1990
Heterocypris symmetricus	Elongation	Salinity	McKenzie, 1971
Limnocythere africana	Reticulation	Mg/Ca ratio of water, ionic composition and concentration	Carbonel et al., 1988
Mytilocypris henricae	Elongation	Salinity	Martens et al., 1985

Considerable interest has also surrounded the palaeoecological significance of ecophenotypic variations in carapace morphology. Characteristics such as noding and strength of reticulation have all been used to deduce palaeoenvironmental conditions (Tab. II), although many of these characteristics lack firm experimental evidence to link them to environment, and so should be used with care in palaeoenvironmental reconstruction.

Palaeoecological work has involved reconstruction of a number of limnological variables. Detailed examination of each of these is beyond the scope of this chapter; readers are directed to the following references for further information. However, the main variables that have been reconstructed in past studies are outlined below, together with some of the more important findings.

Salinity and solute composition: Ostracods have been used as palaeosalinity indicators in two main contexts: first, in basins that are more-or-less hydrologically closed in subhumid to semi-arid regions, where salinity variations relate primarily to changes in effective precipitation; second, in coastal lakes, where salinity changes are a result of variations in marine intrusion.

The existence of an extensive dataset of modem ostracod occurrence and hydrochemical data for North America (e.g., Forester, 1983, 1986; Delorme, 1989; Smith, 1993) has allowed quantitative reconstructions of salinity and solute composition to be made for a number of North American late Pleistocene and Holocene lacustrine sequences (e.g., Smith, 1991; Smith et al., 1992; Curry, 1997) using modern analog and autecological techniques (e.g., Smith et al., 1992) (Fig. 9). Such techniques have been less commonly applied outside North America, owing to the lack of comparable training sets. However, ostracods have been used as palaeo-water chemistry indicators in Southern Europe (e.g., Anadón et al., 1986), Africa (e.g., Cohen et al., 1983; Holmes et al., 1998), Australia (e.g., De Deckker 1982a,b) and China (e.g., Sun et al., 1995).

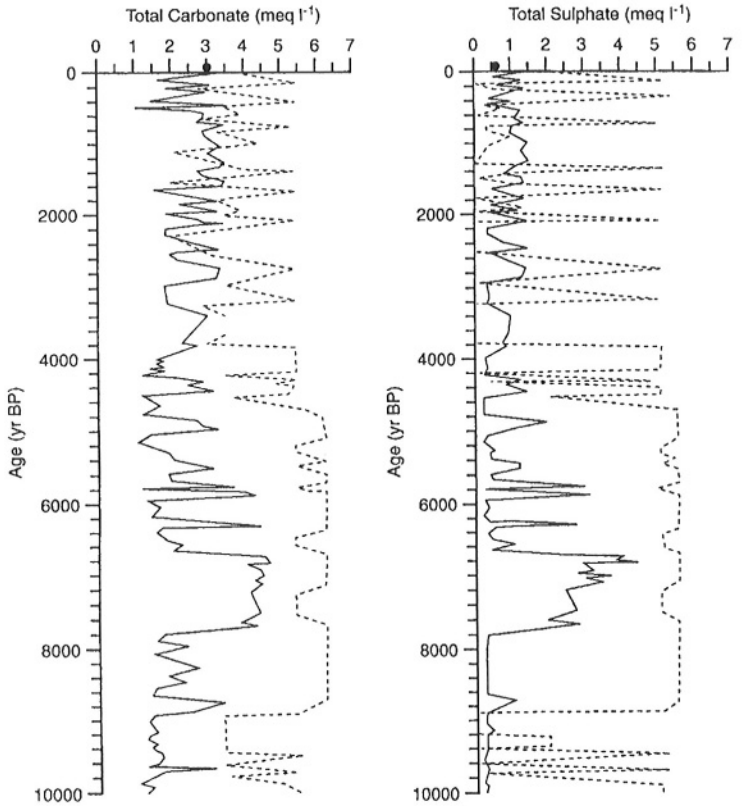

Figure 9. Reconstructed sulphate and carbonate for Elk Lake, Minnesota, based on ostracod assemblages. In each graph, the solid line indicates the mean value reconstructed using an autecological method (e.g. Delorme, 1989) and the dashed line is the best estimate from the modern analogue technique. Present-day values for the lake are shown by a black dot (redrawn from Smith et al., 1992).

Ostracod faunas from marine waters tend to be distinct from those of most non-marine waters, since marine waters have a differing ionic composition, which is dominated by Na and Cl, and a low alkalinity/Ca ratio (Forester & Brouwers, 1985). Ostracods can thus be sensitive indicators of marine intrusion into non-marine coastal lakes and wetlands: they have been used to reconstruct salinity changes in such environments in a number of studies (e.g., Alcala-Herrera et al., 1994; Gunter & Hunt, 1977; Holmes, 1996a).

Palaeotemperature: Despite the fact that ostracods have critical water temperature requirements for survival, hatching of eggs and completion of life cycle, few studies have used them in quantitative palaeotemperature reconstruction. An exception is the work of Forester et al. (1987), in which the mean annual temperature of Elk Lake, Minnesota (USA) was reconstructed using modern ostracod training sets and the modem analog technique. The temperature sensitivity of some species is reflected in differences between

palaeogeographical and modern distributions (e.g., Griffiths et al., 1998). Other studies that have used ostracods as indicators of past temperature include Delorme (1969, 1971b), Delorme et al. (1977), Delorme & Zoltai (1984), Forester & Smith (1994).

Lake-level variation: The best example of lake-level reconstruction comes from the work of Mourguiart and colleagues (Mourguiart et al., 1992; Mourguiart & Carbonel, 1994; Wirrman & Mourguiart, 1995). They have used the depth distribution of ostracods in lakes on the Bolivian Altiplano to develop ostracod-water depth transfer functions. These functions, in turn, have been used to reconstruct the lake level history of Lake Titicaca. Holmes (1998) recognised that deep-water and shallow-water phases of Wallywash Great Pond, a small Jamaican karstic lake, were dominated by the ostracods *Cypretta brevisaepta* Furtos, 1936 and *Candonopsis,* respectively. This relationship was used to identify qualitatively successive deep and shallow periods of the lake (Fig. 10), which are in good agreement with evidence from inorganic geochemistry and facies variations (Holmes, 1998). Finally, Bridgwater (1995) used ostracod assemblages to identify deep and shallow phases of Lake Pátzcuaro in Central Mexico.

Hydrological Habitat: many studies have used the general ecological preferences of ostracods to determine such variables as general environmental setting, palaeohydrological habitat type, the energy level of the water and water permanence, generally in a qualitative way. Examples include De Deckker, (1979b), Robinson (1980), Preece et al. (1986) and Bridgland et al. (1999).

Geochemistry

The geochemical analysis of lacustrine carbonates has the potential to reveal information about variables such as past water temperature, salinity and the lake's carbon cycle. The use of ostracod shells as a source of carbonate for geochemical analysis dates back to the mid-1970s for stable isotopes (Fritz et al., 1975) and the early 1980s for trace elements (Chivas et al., 1983), even though earlier work had hinted at their geochemical potential (e.g., Kesling, 1951). Under certain circumstances, there are distinct advantages to using ostracod shell carbonate over 'bulk' carbonate in geochemical studies. First, by using ostracod shells, one can be certain of the mineral phase being analysed. Second, the use of ostracods avoids inclusion of any detrital carbonate. Third, because an ostracod shell is secreted over a very short time, its composition is a temporally-specific reflection of water conditions. Therefore, if information about the seasonal cycle of growth is known for the species in question, very close constraints can be placed on the timing of carbonate formation. Fourth, if information about the depth preferences is known for the species in question, very close constraints can be placed on the location of carbonate formation. However, it is important to remember that ostracods are organisms whose shell formation is under biochemical control. They may thus be geochemically distinct from inorganic authigenic calcite (e.g., Ito, volume 2).

Oxygen and carbon isotopes: The $^{18}O/^{16}O$ ratio of ostracod carbonate is a function of the water temperature and the $^{18}O/^{16}O$ ratio of the water at the time of shell formation, together with any vital effects. The $^{18}O/^{16}O$ ratio of lake water is a function of a number of factors, including the average ratio of precipitation over the drainage basin, basin hydrology

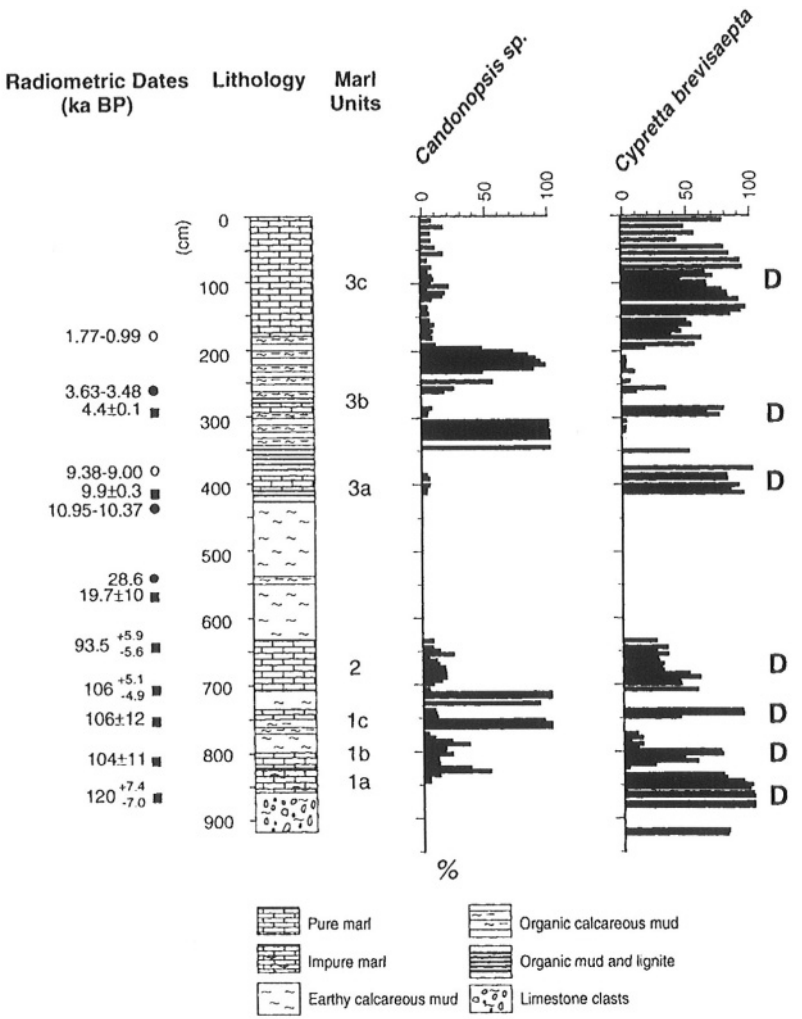

Figure 10. Variations in the relative abundance of the ostracods *Candonposis* sp. and *Cypretta brevisaepta* in late Quaternary sediments from Wallywash Great Pond, Jamaica. Deep-water phases (D), represented by the numbered marl units, are associated with a large proportion of *C. brevisaepta* whereas the intervening shallow-water phases have greater abundance of *Candonopsis* sp. (adapted from Holmes, 1998).

and the evaporative evolution and residence time of the lake (Kelts & Talbot, 1990). The relative importance of each of these factors will vary from basin to basin. In hydrologically-closed basins in sub-humid to semi-arid regions, for example, the ratio of evaporation to precipitation is likely to be the primary control (e.g., Holmes et al., 1997) whereas for deep lakes with an isothermal hypolimnion, the air-temperature-controlled $^{18}O/^{16}O$ ratio of precipitation is the main factor (e.g., von Grafenstein et al., 1996). It is now well established

Table III. Vital offsets for $\delta^{18}O$ in selected non-marine ostracod species (from von Grafenstein et al., 1999).

	Vital offset ($\delta^{18}O$‰) compared to equilibrium calcite
Candoninae	$+2.2 \pm 0.15$
Darwinula stevensoni	$+0.73 \pm 0.23$
Cytherissa lacustris	$+1.2 \pm 0.23$
Limnocythere inopinata	$+0.78 \pm 0.20$

that ostracods do not form their shell in oxygen-isotope equilbrium with their host water. Vital offsets from equilibrium are positive compared to precipitation of calcite in isotopic equilibrium with the host water (Tab. III), for reasons that are poorly understood (von Grafenstein et al., 1999).

Carbon isotope fractionation is little affected by temperature: the $^{13}C/^{12}C$ ratio of ostracod carbonate reflects the $^{13}C/^{12}C$ ratio of the dissolved inorganic carbon (DIC) from which the shell is formed. The isotopic composition of the DIC is a function of the degree of CO_2 exchange with the atmosphere, uptake rate of CO_2 and other inorganic carbon species for aquatic photosynthesis, rates of decay of organic matter within the lake, microbial processes and dissolution of carbonates within the catchment (Kelts & Talbot, 1990). Lake water chemistry will also influence the isotopic composition of the DIC. As with oxygen isotopes, the relative importance of the different factors will vary between lakes. For further information on isotopic systematics of lacustrine carbonates, see Ito (volume 2).

Trace-element chemistry: It is generally assumed that trace elements that are co-precipitated with the ostracod shell carbonate have been derived from the host water and are therefore indicative of concentrations within the water (e.g., Turpen & Angell, 1971).

Previous work has focussed on Sr and Mg determinations, often of single shells, with results presented as molar ratios (see Holmes, 1996b, for a review). The relationship between trace elements in ostracod carbonates and waters is often described using a partition coefficient (K_D value):

$$K_D[M]_{(T)} = \frac{(M/Ca)_{ostracod\ shell}}{(M/Ca)_{host\ water}}, \quad (1)$$

(where M is the element concerned and T is the temperature of the water at the time of shell formation; M/Ca are molar ratios) (Chivas et al., 1986) (Tab. IV).

For Sr, the Sr/Ca ratio in ostracod shells is positively correlated with the Sr/Ca of the water at the time of shell formation, although Sr is strongly discriminated against during shell formation, so that K_D values are much lower than unity (Chivas et al., 1986). For Mg, the Mg/Ca ratio of an ostracod shell is positively correlated with the Mg/Ca ratio of the water and with water temperature. As for Sr, $K_D[Mg]$ values are less than unity. $K_D[M]$ values are genus specific (e.g., Chivas et al., 1986) and are not applicable to juvenile specimens (Chivas et al., 1983) or under all water chemistry conditions (e.g., Xia et al., 1997; Wansard et al., 1998; De Deckker, et al., 1999). Further complications may occur as a result of the anion dependence of the free-metal concentrations of the cations

Table IV. Selected K_D values for the uptake of Sr and Mg into ostracod calcite.

Genus/Species	K_D [Sr]	K_D [Mg]	Reference
Australocypris & *Mytilocypris*	0.208±0.061 F, n=89		Chivas et al., 1986
Candona rawsoni	0.406 L	0.0024 L (25° C)	Engstrom & Nelson, 1991
Cypretta	0.306±0.0.069 F, n=31	0.0142±0.0088 F, n=31 (29.8–32.5° C)	Holmes et al., 1995
Cyprideis	0.474±0.061 F, n=37 0.475±0.057 L, n=32	0.0046±0.0007 L, n=15 (25° C)	Chivas et al., 1986
Darwinula stevensoni	0.175±0.006 F, n=6	0.0101±0.0003 F, n=6 (22 °C)	Palacios-Fest, unpublished data (in Palacios-Fest et al., 1994)
Limnocythere	0.350±0.058 L, n=16		Chivas et al., 1986
Herpetocypris brevicaudata	0.195±0.013 L, n = 14 (adults) 0.198±0.009 L, n = 7 (juv.)	0.0171±0.0018 L, n = 16 (adults) (12.4–23.3 °C) 0.0208±.0008 L, n = 8 (juv.) (12.4–23.3 °C)	Wansard & Roca, 1997

L = laboratory culture, F = field collection, juv. = juveniles.

(Engstrom & Nelson, 1991). Only the free metal ion co-precipitates with calcite, yet the total concentration is generally determined in water chemistry assessments. Some prior knowledge of the modern water chemistry of the lake in question, together with the trace-element systematics of the species, is therefore vital for the successful palaeolimnological application of M/Ca ratios in ostracod shells.

In some lakes, where Ca behaves conservatively with respect to salinity change, Sr/Ca_{water} and Mg/Ca_{water} may covary with salinity; thus the Sr and Mg content of ostracod shells when coupled may be regarded as an indicator of water salinity and temperature. However, these relationships are by no means universal for all lakes (e.g., De Deckker et al., 1999) and must be established from modern limnological investigations.

Despite the complications, the trace-element content of ostracods from lacustrine sequences has been used successfully in a number of settings to reconstruct palaeosalinity in subhumid to semi-arid regions (e.g., Chivas et al., 1985; Holmes et al., 1997; Yu & Ito, 1999) and marginal-marine environments (e.g., Holmes, 1996a; Holmes et al., 1995) and to reconstruct past water temperatures (e.g., Wansard, 1996). Some studies have used coupled trace element and isotope determinations on the same ostracod shells (e.g., Chivas et al., 1993). Moreover, there have been additional geochemical studies using ostracod shells, for example in radiocarbon dating (e.g., O'Hara et al., 1993), uranium-series dating (Bischoff

et al., 1998), amino acid racemization studies (e.g., McCoy, 1988) and strontium isotope analysis (e.g., McCullough et al., 1989).

Future Directions

Over the past decade, ostracods have moved from relative obscurity to prominence in palaeolimnology. Over the next few years, developments in the following areas will ensure that their influence continues to grow:

1. Further developments in taxonomy, especially of problematical groups;
2. Further understandings of modern ecology of species, including the developments of more abundant and better quality training sets;
3. More information about the life-history of individual species;
4. Further understandings of isotope and trace-element systematics of individual species;
5. Additional investigations into the use of other isotopes (e.g., $^{87}Sr/^{86}Sr$) and trace metals (e.g., Fe, Mn).

These developments could be achieved through modern collection and monitoring of ostracods and there environments, taxonomic studies and *in vitro* cultures.

Summary

Ostracods are small bivalved crustaceans that are common in non-marine waters. They secrete shells of low-Mg calcite, which are often well preserved in Quaternary sediments. Ostracods are sensitive to a range of ecological factors, of which habitat type and the chemical composition are potentially most valuable for palaeoenvironmental work. Furthermore, ostracod shells provide a source of carbonate for geochemical analysis, including trace elements and stable isotopes. Despite past under-representation of ostracods in palaeolimnology, recent advances in the understanding of their biology, taxonomy, ecology and shell chemistry have led to them becoming used almost routinely in environmental reconstruction alongside other indicators. This chapter reviews the palaeolimnological significance of ostracods by providing an outline of their biology, taxonomy and ecology, together with an account of the main palaeoenvironmental techniques and their application.

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8. FRESHWATER MOLLUSCS

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Introduction

Fossil freshwater molluscs shells are among the most commonly encountered macroscopic animal remains recovered from Quaternary lacustrine sediments. They are particularly abundant in calcareous sediments which reflect deposition in non-acidic waters. The North American freshwater molluscan fauna includes at least 227 species of "freshwater mussels" (Unionacea) (Fig. 1), 33 native species of "fingernail clams" (Pisidiidae) (Fig. 2) and about 500 species of gastropods (Fig. 3) (Burch, 1975a,b; 1989).

Nonmarine molluscs have been reported from a broad range of sedimentary deposits, which include wind-blown silt deposits (Miller et al., 1994a); cave, sinkhole and fracture/fissure sediment accumulations (Parmalee & Oesch, 1972; Miller et al., 1994b); alluvial, floodplain (Miller & Kay, 1981; Keen, 1990; Preece, 1999), and back-water channel deposits (Miller, 1983); lagoonal (Miller & Thompson, 1990; Karrow et al., 1995), littoral (Magny et al., 1995) and deepwater lacustrine sediments (Colman et al., 1990); and fen peat (Miller & Thompson, 1987). Some species, such as the bivalve *Pisidium conventus,* are widely distributed (e.g., Holarctic distribution), while others, such as *Pisidium ultramontainum,* are relatively restricted geographically (e.g., known only from localities in southwestern Oregon and northern California) (Burch, 1975a).

Studies of Quaternary nonmarine molluscs have resulted in significant contributions. They have been used to reconstruct former stream confluences (Taylor, 1965; Miller, 1976), provide a basis for biostratigraphic zonation of sedimentary sequences (Miller et al., 1979; 1985; Miller & Kott, 1989; Keen, 1990) and reconstruct local habitat and climatic conditions

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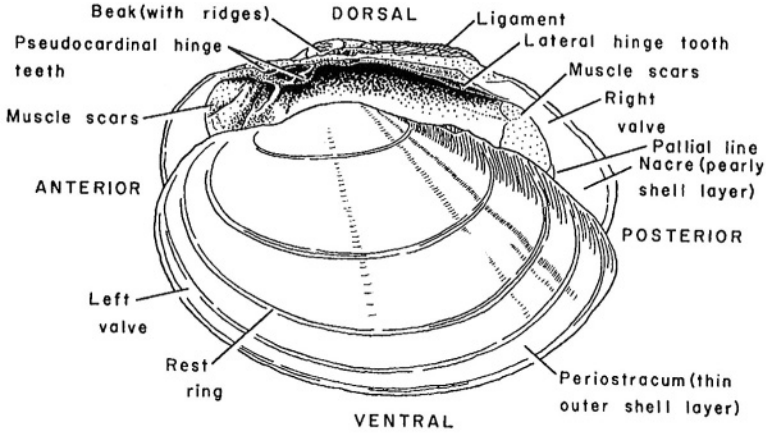

Figure 1. Shell characteristics of unionacean bivalves (from Cvancara, 1983).

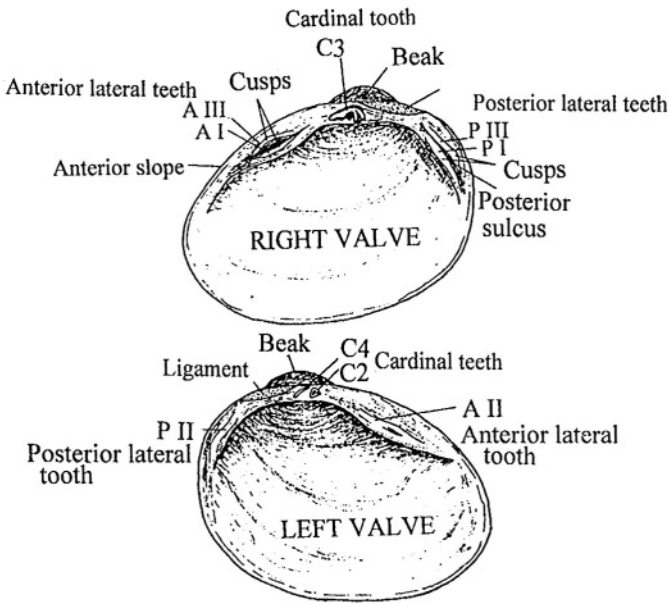

Figure 2. Shell characteristics of pisidiid bivalves (from Mackie et al., 1980).

(Sparks, 1961; Taylor, 1960; 1965; Ložek, 1986; Rousseau et al, 1990; Keen, 1990). In recent years, analysis of stable isotope ratios from molluscan shell aragonite has provided detailed information on productivity, water sources and temperatures of the environments in which the molluscs lived (Colman et al., 1990; Tevesz et al., 1996; 1997; Miller et al., 1998; Bonadonna et al., 1999; Leng et al., 1999). Amino-acid studies of shell protein

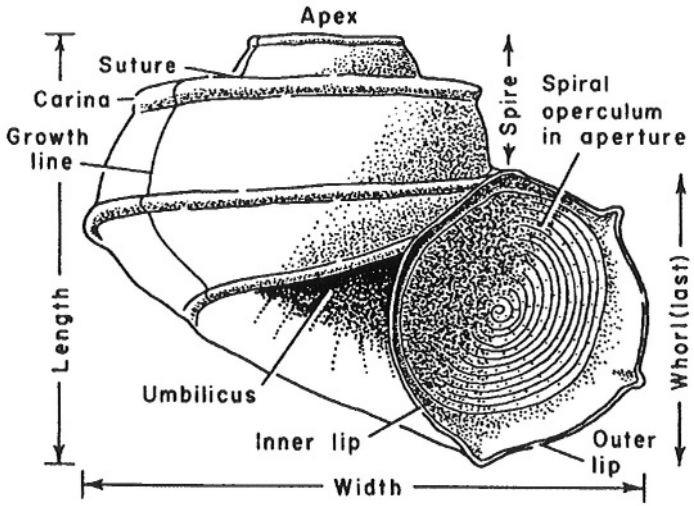

Figure 3. Shell characteristics of freshwater gastropods (from Cvancara, 1983).

have provided information about the relative ages of fossil assemblages and a method for estimating post depositional effective temperature histories of fossil sites (Clark et al., 1989; Miller et al., 1993; Miller et al., 1994b).

The quality of shell preservation varies greatly. Individuals from some sites may retain the external organic layer (periostracum) and original shell color patterns (Miller & Bajc, 1989). Although good preservation is generally the rule in Holocene lacustrine sediments, there are deposits, usually enriched with plant material, in which the shells have been etched and pitted to the point of almost complete destruction (Miller & Thompson, 1987).

Prior to the 1950's, the study of Quaternary nonmarine molluscs was commonly descriptive and resulted in the production of a faunal list for a site. Information on mollusc abundance and stratigraphic occurrence at a site was usually not provided (Baker, 1920; Ložek, 1986). During the second half of the 20th century, analysis of nonmarine molluscs entered a new phase in which quantification of the data was emphasized. La Rocque (1952, 1960) and several of his students (e.g., Reynolds, 1959; Zimmerman, 1960) were among the first in North America to collect sequential samples, count the molluscan content of each sample, and plot these data as line graphs similar to pollen diagrams. Workers in Europe applied similar methods to the study of nonmarine Quaternary molluscan sequences (Sparks, 1961; Ložek, 1964; Sparks & West, 1959, 1970; Piechocki, 1977; Digerfeldt et al., 1997; Böttger et al., 1998; Preece & Bridgland, 1999). Other workers have attempted to reconstruct precipitation and temperature changes in Quaternary sequences by applying transfer function analysis to molluscan assemblages from loess (Rousseau, 1991).

The sections that follow focus on analytical techniques that are primarily applied to the study of North American Quaternary freshwater molluscan sequences from lacustrine

deposits. This chapter draws freely from review articles by Miller & Bajc (1989) and Miller (1990).

Field methods

Fortuitous exposures of Holocene lake deposits may occur naturally as a consequence of wave action along the shore of a lake (Gutschick & Gonsiewski, 1976) or by the erosive action of a stream incised into lacustrine sediments (Miller et al., 1985). Many Holocene sites have become available for study through the serendipitous location of human excavation activities (Coope et al., 1997) or as a result of archeological excavations (Bridgland et al., 1999). Fossil molluscs in these exposures are often bleached white and may stand out in sharp contrast against the color of the enclosing sediments. All but the smallest shells (<2 mm) can usually be seen with the naked eye.

Sequential bulk samples are usually collected at 5 to 10cm intervals. The sampling interval and the size of the samples should be commensurate with the following: the thickness of the units being studied, the abundance of the molluscs, and the objectives of the study. Some workers contend that a 1–2 kg sample should usually be adequate for molluscan analysis and that if molluscs were scarce in this size sample, the site would probably be unsuitable for analysis (Sparks, 1964). In contrast, La Rocque (1966) and his students collected samples of about $4500\,cm^3$ in 5 cm increments. Ložek (1986) suggests that in calcareous sediments where molluscs are usually abundant, samples between 1000 and $2000\,cm^3$ should be adequate; but where molluscs are less abundant, a sample of 5000 to $10{,}000\,cm^3$ may be necessary.

If large quantities of sediment must be processed and a nearby source of water is available, shells could be extracted from the matrix by using a screen washing technique similar to the one described in Hibbard (1949). The 1 mm-mesh screen washer permits most of the sediments to pass through, while retaining a volumetrically much reduced residue of fossils and sediment that may be taken back to the laboratory.

Although serendipitous access to Holocene deposits is welcome, there still is a need for collecting methods in which the investigator decides the best location to sample for a specific research project. There are a number of coring devices that have been developed to sample in different types of unconsolidated soft sediment that are well suited for sampling small organisms such as diatoms, cladocera and ostracods, etc. (Aaby & Digerfeldt, 1986). However, because the size of individual shells of freshwater molluscs may range from a few mm to near 200 mm in length, a wide diameter coring device is preferred. A vibracorer, which can provide sediment cores encased in a 7.6cm diameter, thin walled aluminum pipe, is often used to recover molluscs from soft, unconsolidated sediments. (Miller & Thompson, 1987,1990; Miller & Mullet, 1990; Smith, 1992; Miller et al., 1998). The use of a 7.6 cm diameter pipe during vibracoring greatly increases the probability of recovering relatively complete large mollusc specimens and usually provides sufficient shell materials in a 5 cm interval for quantitative analysis of the core.

Most lacustrine molluscs tend to live in relatively shallow water. Studies involving large, deep lakes, as well as smaller lakes with steeply slopping margins, should include some cores from near shore. Although near shore cores are more likely to include erosional hiatuses during low water events, they will increase the probability of recovering an adequate sampling of the molluscs.

Laboratory methods

Extraction

Extraction of molluscs from the enclosing sediment usually starts by drying the sample to remove most of the interstitial water. The sample is then immersed in a container of cold water. After several hours of soaking, the sediment will usually disaggregate, and mollusc shells, ostracodes (see Holmes, this volume), insects (see Elias, this volume), seeds, and plant fragments (see Birks, volume 3) may float to the surface where they may be decanted into a sieve. The fossils remaining in the water-sediment slurry are then poured through a stacked series of sieves (2.0 mm to .071 mm mesh diameter). Washing under a gentle spray of tap water flushes the fine silt and clay through the sieves and breaks down small clods of sediment that do not completely disaggregate during soaking.

If this simple procedure does not succeed in freeing the shell, the material may have to be redried, soaked in a solution of sodium hexametaphosphate, sodium carbonate, and bicarbonate of soda at room temperature, with occasional stirring until the sediments disaggregate. This process can be accelerated by boiling or placing the sample in an ultrasonic cleaner. This residue of shell, organic matter and the coarse-grain fraction from the sediment retained in the sieves are then dried, labelled and stored in vials.

Identification and counting

The molluscs from these washed residues are dried and then identified to species under a low-power (10×–40×) binocular microscope. In general, the preserved shell characteristics of most Holocene freshwater molluscs appear to have undergone little evolutionary change during this interval, thus making it possible to assign most fossil shells from this interval to living species. A basic principle in the interpretation of fossil shells assumes that shells referred to living species interacted with the environment in a manner similar to their living counterparts. There are a number of publications available for identification of living freshwater molluscs that can also be used to identify fossil Holocene molluscs (e.g., Ložek, 1964; Graham, 1988; Adam, 1960; Germain, 1930-1; Clarke, 1973, 1981; Burch, 1975a,b, 1989; Mackie et al., 1980; Jokinen, 1983, 1992). Ideally, the reference books should be used in conjunction with comparative materials from museum collections. Ultimately, the identifications should be confirmed by a specialist.

The identified materials are then counted. Some workers try to identify shell fragments and include them in the species counts (Ložek, 1986). Although shell fragments of some gastropods can confidently be assigned to species, it is certainly not true for many species. Therefore, if changes in species abundance counts are used to interpret habitat changes, it is probably best to exclude these fragments from the totals to avoid prejudicing the counts in favour of those species that can be so identified. These laboratory methods are summarized in Figure 4.

Data interpretation

Several different approaches have been used to extract information from sampled molluscs on the paleoecology of a fossil site. One commonly used method groups the fossil species

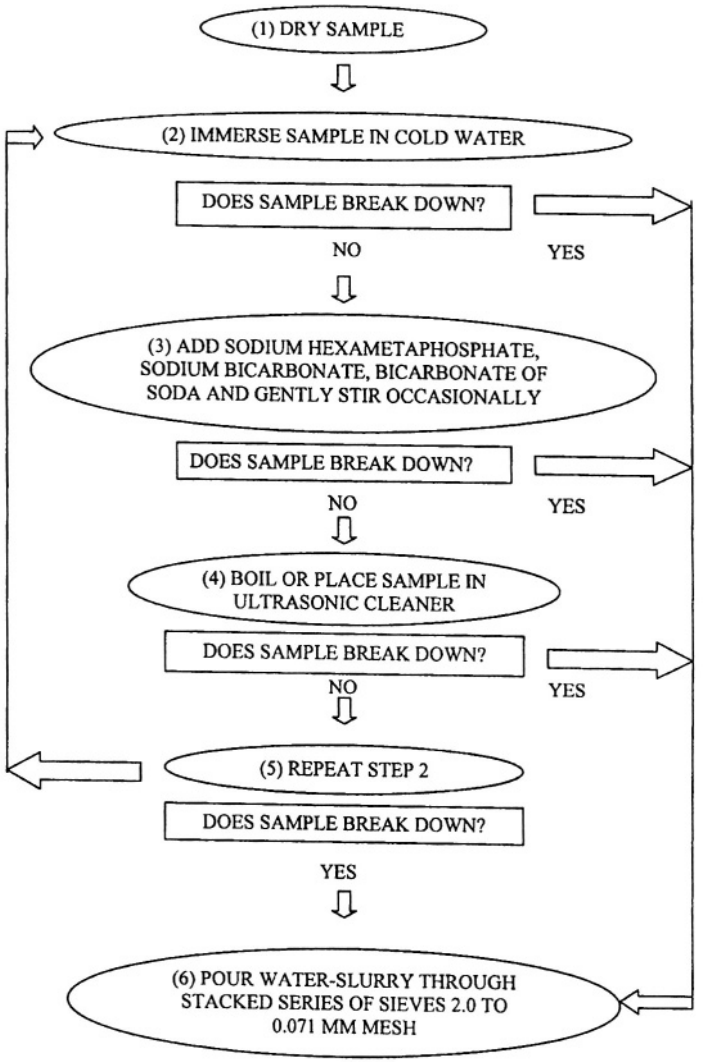

Figure 4. Flow chart showing sample preparation steps.

from each horizon into ecologic assemblages based on the habitat preferences of their living relatives. Although it is true that most species may be found in a range of habitats, many of them seem to occur more frequently or are more abundant in only a few (e.g., Ložek, 1964; Harman & Berg, 1971; Clarke, 1973, 1979a,b; Cvancara, 1983; Jokinen, 1983, 1992; Pip, 1986; Mouthon, 1999). Clarke (1979a,b) has suggested that several species of gastropods and of pisidiid bivalves appear to be guides to trophic lake levels (Tab. I). The list of indicator species, however, should be considered provisional because the trophic level of the lakes

Table I. Lake trophic level indicator gastropod species (modified from Clarke, 1979a).

OLIGOTROPHIC	
Lymnaea atkaensis	
MESOTROPHIC	
Cincinnatia cincinnatiensis	*Physa gyrina latchfieldi*
Helisoma corpulentum vermilionensis	*Somatogyrus subglobosus*
EUTROPHIC	
Viviparous georgianus	*Campeloma decisum*
Physa hordacea	*Promenetus exacuous*
Menetus cooperi	*Planorbula armigera*
Armiger crista	*Physa nuttalli*
Cipangopaludina cninaensis	*Ferrissia fragilis*
Physa concolor	*Fossarria truncatula*
Laevapex fuscus	*Helisoma corpulentum whitevesi*
Helisoma trivolvis binneyi	*Amnicola limosa*
Amnicola walkeri	*Radix auricularia*
Radix peregra	*Fossaria feruginia*
Marstonia decepta	*Lyogyrus ranum*
Acella haldemani	
VERNAL	
Stagnicola caperata	*Gyraulus circumstriatus*

was assessed solely on qualitative observations. A second method arranges the fossils into groups on the basis of the modern geographic distribution of their living counterparts. If the fossil materials include extant species that are no longer living near the collection site, the fossil assemblage can be compared to the closest area with a similar assemblage of living molluscs. Lastly, the fossil assemblages might contain species that may be indicative of specific environmental condition.

The habitat association method starts with species identifications of the fossils. The fossil molluscs are then counted and sorted into ecologic groupings that reflect the species associations of their extant analogs (Tab. II). Individual species abundance counts for each major habitat grouping may be represented in a table that at least presents the two major habitat groupings: terrestrial and aquatic. The percentage and absolute abundance of individuals within each grouping may be then plotted as a series of stacked bars or histograms against the stratigraphic position of the sample. Data presented in this manner will graphically illustrate habitat variations through time (see examples in Ložek, 1964, 1965; Sparks & West, 1970; Piechoki, 1977; Miller & Thompson, 1987,1990).

Regional differences in faunas might require additional subdivisions within these major habitats to accommodate the molluscs at a given site. In central Europe, for example, Ložek (1964, 1986) was able to assign all of the Quaternary aquatic mollusc species to just one aquatic habitat grouping. Nine of the 10 habitat groupings he had created were based on

Table II. Habitat and faunal list for core 11, Cowles Bog (modified from Miller & Thompson, 1987).

Habitat Group 1. Terrestrial species of wooded, damp lowlands; close to water; moist areas available throughout the year beneath twigs, bark, logs.

Carychium exiguum
Hawaiia miniscula
Discus cronkhitei
Gastrcopta contracta
Strobilops labyrinthica
Vertigo morsei
Deroceras laeve
Gastrocopta tappaniana
Nesovitrea electrina
Euconulus fulvus
Stenotrema leai
Vertigo milium

Habitat Group 2. Bodies of water with areas of submerged vegetation; subject to significant seasonal drying.

Bakerilymnaea dalli
Fossaria obrussa
Gyraulus circumstriatus

Habitat Group 3. Eutrophic, perennial water bodies; no significant seasonal drying; with dense stands of submerged aquatic vegetation.

Gyraulus parvus
Promenetus exacuous
Stagnicola elodes
Gyraulus deflectus
Planorbula armigera
Armiger crista
Amnicola walkeri
Acella haldemani
Lymnaea stagnalis
Ferrissia parallela

Habitat Group 4. Perennial, mesotrophic to eutrophic water bodies, containing submerged aquatic vegetation.

Amnicola limosa
Planorbella campanulatum
Goniobasis livescens
Helisoma anceps
Marstonia decepta
Valvata tricarinata

terrestrial mollusc associations. In contrast, workers in Great Britain found it useful to use four groupings just for the aquatic molluscs (Sparks, 1961; Sparks & West, 1970). Ložek (1986) suggested that the differences between the central European and British aquatic habitat classifications are probably due to the nature of the deposits being studied. The central European materials were mostly from loess deposits that were dominated by terrestrial species, whereas the British studies dealt mostly with freshwater and wetland deposits that contained mostly aquatic species.

A variety of methods have been utilized to extract paleoclimate information from nonmarine molluscs. Some workers (e.g., Sparks, 1961; Harris & Pip, 1973; Hibbard & Taylor, 1960; Miller & Kay, 1981; Keen, 1990; Ložek, 1964) divide the molluscs on the basis of their modern distribution patterns into what are considered climatically significant groupings. In the continental interior of North America, Taylor (1960) recognized 5 broadly defined distribution patterns. Taylor suggests that the southern distributional limits of the northern group in the interior plains appear to be controlled by high summer temperatures, because some members of this group can and do extend further south at higher elevations

in the Appalachian and Rocky Mountains. The northern limits of the southern group is probably constrained by some combination of the length and severity of the winter. Several species in this group range further north along the Atlantic coastal plain where the ocean exercises a moderating effect on the climate (Taylor, 1960). Members of the eastern species group range varying distances onto the Great Plains. West of the Mississippi River, there is a general decrease in eastern species diversity from east to west that appears to correspond to the precipitation gradient, which also decreases from east to west. The distribution of this group appears to be controlled primarily by available moisture and frequency of drought. Taylor recognized two additional distributional groupings of molluscs, one consisting of species that occur over most of North America and a small group of species for which distribution data were inadequate. Miller (1975) and Miller & Kay (1981) have lumped these last two groupings into a general group that includes species which are either extinct, have inadequate range data, or are so widely distributed that they are not useful for making climatic interpretations.

Although these groupings are somewhat subjective because some species are not assignable to any one group (e.g., the gastropod *Succinea ovalis* could with equal justification be considered a member of either the northern or the eastern group), the distributional patterns are real and on a regional scale are apparently controlled by climate.

Fossil species diversity and abundance within the northern, southern and eastern groups are compared to the geographic groupings of the extant molluscan fauna at or near the fossil site (Miller, 1975; Miller & Kay, 1981). Changes in abundance of species within these groupings are usually interpreted as responses to climate change. If, for example, there is a great increase in northern group taxa in the fossil assemblage relative to what is now living in the area, the fossils could be interpreted as having lived at a time when the local climate included cooler summer temperature. Ideally, the molluscs from several dated sites in an area should be studied to identify local environmental microclimatic effects that might otherwise prejudice the climate interpretation.

For example, *Promenetus exacuous,* a common aquatic gastropod in many Illinoian faunas from the southwest Kansas area, is still living in the area, but is restricted to one cold water artesian-fed pond. The nearest living *P. exacuous* occurrences to the pond are several hundred kilometers to the west, in the Rocky Mountains, and to the north, in northern Nebraska (Taylor, 1960). This disjunct occurrence appears to be related to the cool, artesian water that supports the pond fauna. The presence of *P. exacuous* at a number of different localities in southwest Kansas during the Illinoian might not be due to the existence of similar cool water seeps in the area during the Pleistocene. Rather its presence in these deposits more likely indicates cooler summers. Constraints on the inferred summer temperatures can be made by comparing the temperatures along the southern limits of the northern group species that are absent from the modern fauna of the fossil site.

An application of this method is illustrated by Miller (1975), who compares seven Late Wisconsinan molluscan faunas from southwestern Kansas-northwest Oklahoma with the modern extant molluscs of this area. In other studies, an area of sympatry for the majority of the extant faunal elements is established, and the climate of the overlap area is considered to be an approximation of climatic conditions locally at the time the fossil assemblage lived (Taylor, 1960, 1965; Miller, 1966).

Some species may develop shell modifications in response to stressed habitat conditions. For example, in some species of *Ferrissia* that have been subjected to desiccation, the shell

may develop a septum that partially closes the aperture (Basch, 1963; Richardot, 1978). Fossil septate forms of *Ferrissia* are known from some deposits, where their presence is considered *prima facie* evidence for the former presence of temporary water habitats at or near the fossil site (Miller & Kay, 1981). In general, environmental analysis based on this type of inference from the molluscs is usually compatible with interpretations derived from independent study of other elements of the biota (e.g., Hibbard & Taylor, 1960; Coope et al., 1997; Bridgland et al., 1999; Gao et al., 2000) and suggests that these approaches are capable of producing reasonable reconstructions.

Geochemical approaches

Trace chemistry

The calcium carbonate shells of molluscs usually contain trace amounts of exotic elements and ions. These may be incorporated into the crystal lattice, absorbed onto the shell surface or into the organic matrix, or occur as separate mineral phases within the shell. Analysis of these substances by a variety of techniques, including atomic absorption spectrophotometry, neutron activation analysis, inductively coupled plasma analysis, and mass spectrometry have allowed workers to use marine mollusc shells to distinguish between marine and freshwater environments, and, in some cases, attempt to determine paleotemperature and paleosalinity (Dodd & Stanton, 1990).

Research on the trace and minor element chemistry of freshwater mollusc shells is more limited and has mainly been used to infer anthropogenic environmental loading by comparing recently collected specimens with historic samples. Mollusc soft tissues are used for this purpose as well. The trace chemistry of freshwater molluscs is used to monitor environmental pollution because the presence of some contaminants in the shell and soft tissues has been correlated with the presence of contaminants in the environments were the molluscs were living (Forester, 1980; Imlay, 1982; Tevesz et al., 1989). Nevertheless, the factors controlling the trace chemistry of freshwater molluscs in relation to environmental chemistry are incompletely understood. Dermott & Lum (1986), for instance, found that trace metal levels in *Elliptio complanata* (freshwater mussel) shells may not be directly related to environmental levels because uptake of the elements/ions by the mussels is affected by factors such as availability during growth periods and physiology. Thus additional work is needed in order to refine the usefulness of using the trace chemistry of freshwater molluscs shells to make accurate inferences about the water chemistry history of lakes.

Stable carbon and oxygen isotope ratios

The $^{18}O/^{16}O$ ratios of skeletal carbonate precipitated in oxygen isotopic equilibrium with ambient water may provide useful estimates of water temperature and salinity. Because the theory behind the use of these ratios is reliably explainable and because physiological effects are often minor, $^{18}O/^{16}O$ ratios are widely used in paleoenvironmental and paleoclimatic reconstruction. Interpretation of $^{13}C/^{12}C$ ratios is more difficult because of microenvironmental and physiological effects on the carbon isotope composition of shells (Dodd & Stanton, 1990; Barrera & Tevesz, 1990). In all, $^{18}O/^{16}O$ ratios and $^{13}C/^{12}C$ ratios of marine

and freshwater mollusc shells, as well as the biomineralized tissues of other taxa, have been used to determine paleotemperatures, climatic trends, the amplitude of seasonal changes, and long term trends in the isotope composition of ocean and lake waters; to distinguish marine from non-marine environments and determine paleosalinity; to measure rates of shell growth, estimate season of death, water depth, primary productivity, and polar ice volume (Barrera & Tevesz, 1990).

Oxygen isotope ratios of carbonate are usually expressed as δ values or per mil (parts per thousand) differences from a standard. For example, $\delta^{18}O$ is defined as:

$$\delta^{18}O(‰) = \frac{\left(^{18}O/^{16}O\right)_{sample} - \left(^{18}O/^{16}O\right)_{standard}}{\left(^{18}O/^{16}O\right)_{standard}} \times 1000. \quad (1)$$

An equation similar to (1) defines $\delta^{13}C$. Carbon and oxygen isotope values from biogenic carbonate are usually reported relative to the PDB or related standards (Dodd & Stanton, 1990).

Paleoenvironmental usefulness of mollusc carbonate

Epstein et al. (1951, 1953) compared the oxygen isotope values of seawater and shell carbonate from molluscs collected from areas with recorded seasonal temperatures. Epstein & Lowenstam (1953) and Lowenstam (1961) found that bivalves, gastropods, and brachiopods precipitate their shells in isotopic equilibrium with ambient water. Nevertheless, they further noted the taxa which they analyzed did not record the full range environmental temperatures. [The notion of "equilibrium precipitation" means that the shells are being deposited in isotopic equilibrium with ambient water, and therefore record environmental conditions at the time of shell deposition, instead of merely reflecting the physiological processes of the organism—a condition referred to as "vital effects". Vital effects could potentially obscure the environmental signal recorded by the organism in its shell.] Many additional studies have confirmed the fact that isotope studies of mollusc shells provide reliable historical records of temperature, salinity, and seasonality (Mook & Vogel, 1968; Killingley & Berger, 1979; Wefer and Killingley, 1980; Jones, 1981; Jones et al., 1983; Krantz et al., 1984; Barrera & Tevesz, 1990; Barrera et al., 1990, 1994; Leng et al., 1999).

Isotopic records from freshwater mollusc shell carbonate

Isotope analyses of freshwater mollusc shells include those by Keith et al. (1964), Fritz & Poplawski (1974), Abell (1982, 1985), Godwin (1985), Cerling et al. (1988), Dettman & Lohmann (1993), Fastovsky et al. (1993), Dettman (1994), Tevesz et al. (1996), Böttger et al. (1998), Bonadonna et al. (1999), and Leng et al. (1999). Fritz & Poplawski (1974), for example, investigated the relation of the stable isotope composition of freshwater mollusc shells to environmental variables and were able to confirm the usefulness of the shells of several species for paleoenvironmental and paleoclimatological work. Dettman & Lohmann (1993) and Dettman (1994) analyzed shell aragonite samples and ambient water temperature and $\delta^{18}O$ water values for several unionid bivalve species and concluded that their shells were deposited in oxygen isotopic equilibrium with ambient water. Although

Fastovsky et al. (1993) suggested that unionid *Elliptio complanata* exhibited disequilibrium precipitation, subsequent studies of the shells the fingernail clam *Sphaerium striatinum* and the unionid *Pyganodon grandis* (Tevesz et al., 1996) support the ideas of Dettman (1994) that freshwater bivalves precipitate their shells in oxygen isotopic equilibrium with ambient water. In all, most studies confirm the usefulness of stable isotope ratios of freshwater mollusc shells as reliable sources of paleoenvironmental and paleoclimatic data.

Interpretation of oxygen isotope ratios

The $\delta^{18}O$ values from biogenic carbonate precipitated in marine environments have been used to provide paleotemperatures and estimates of global ice volume (Savin et al., 1975). In freshwater environments, $\delta^{18}O$ values are less useful for determining paleotemperatures because factors such as water mass source, isotopic composition of meteoric water, and evaporation often have a greater influence on the oxygen isotope ratio of the precipitated carbonate than does temperature (Stuiver, 1968, 1970; Fritz & Poplawski, 1974; Cerling et al., 1988; Kelts & Talbot, 1990; Schwalb et al., 1995). Nevertheless, changes in oxygen isotope values from shells can provide an indication of temperature change by indicating the effect of temperature on evaporation. Relatively high $\delta^{18}O$ values, for instance, may be interpreted as indicating high evaporation/precipitation ratios, which are considered to reflect relatively warm, dry conditions, while relatively low values could indicate cooler and more moist times (Stuiver, 1968, 1970).

Downcore variation in the oxygen isotope ratios of mollusc shells from lakes have been used to define important aspects of the paleoenvironmental and paleoclimatic history of lakes. For example, in the case of the Laurentian Great Lakes of North America, these include a history of lake level changes, the identification of times when glacial melt-waters were important constituents of lake waters, and indications of warming and cooling climate trends (Colman et al., 1990; 1994a,b; Lewis & Anderson, 1992; Forester et al., 1994; Rea et al., 1994a,b; Tevesz et al., 1998). In addition, detailed sampling of individual shells may provide a record of not only relative temperature but also the relative intensity of seasonal changes in weather patterns (Dettman, 1994).

Stable carbon isotope record

The stable carbon isotope composition of calcium carbonate precipitated in fresh waters is a function of the isotopic composition of the dissolved inorganic carbon (DIC). Schelske & Hodell (1988), for instance, reported that the $\delta^{13}C$ of calcite precipitated during the summer in Lake Ontario reflects the isotope composition of carbon dissolved in lake water at the time of summer stratification. Delta ^{13}C data from marine and lacustrine environments have been used as proxies of photosynthesis, respiration, and decay. For example, during photosynthesis ^{12}C is preferentially fixed by phytoplankton, which results in the production of ^{13}C-poor organic matter and a diminution of ^{12}C in the dissolved carbon reservoir in the water mass. Shell carbonate precipitated from these waters will therefore have relatively high $\delta^{13}C$ values. In contrast, ^{12}C-enriched CO_2 is released into the water during respiration and decay, and shells precipitated under these conditions will have relatively depleted $\delta^{13}C$ values. Stable carbon isotope data have also been used to monitor the exchange of CO_2

between water and the atmosphere, where they have been proven useful as indicators of paleoproductivity and have also provided signatures for tracing water masses (Stuiver, 1968, 1970; Fritz & Poplawski, 1974; Cerling et al., 1988; Kelts & Talbot, 1990; Schwalb et al., 1995; Tevesz et al., 1997).

In addition to the isotopic composition of DIC, physiological factors likely also affect the stable carbon isotope composition of mollusc shells. For instance, Tanaka et al. (1986) found that mollusc shells contain a high percentage of metabolic carbon. In addition, Dettman (1994) did not find a straightforward relationship between freshwater bivalve shell $\delta^{13}C$ and water DIC $\delta^{13}C$. Instead, measured shell values were more negative than predicted values. Because these offsets were consistent within species, trends in intra-species values are still useful for inferring environmental changes.

Summary

Freshwater mollusc shells are among the best and most extensively preserved fossils in lacustrine sediments. These molluscs are useful because they occur in a broad range of paleoenvironments. As a result, they have been used to reconstruct former stream confluences, provide a basis for biostratigraphic zonation of sedimentary sequences in lake basins, and reconstruct habitat and climatic conditions. Because many Quaternary and particularly Holocene species found in lacustrine sediments are extant, knowledge of the taxonomy, ecology, distribution, and biogeochemistry of living representatives has considerable value for reconstructing ancient environments and climates.

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9. FISH

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Introduction

Freshwater fish remains are abundant in some water-laid sediments in every time period since the Ordovician. Fish fossils and associated data are useful to estimate conditions in paleoenvironments because living fish respond directly to chemical and physical parameters as well as geological processes (Schaffer, 1972; Behrensmeyer & Kidwell, 1985; Wilson, 1988a, 1988b; Weigelt, 1989; Martin, 1999). Known habitat restrictions of fish and other organisms yield environmental evidence in the fossil record. This evidence is seen first as presence or absence of indicator organisms, but also as in the form of clues about the death and transport of the organisms (taphonomy). Taphonomic information comprises observations not only from transport and decay of carcasses, but also from coprolites that indicate food habits and microorganisms (Bradley, 1946), evidence caused by feeding processes (Gregory et al., 1974; ate & Evans, 1994; Wilson, 1987), and biogeochemistry of clasts and concretions (Martill, 1988; 1991). These lines of evidence are subject to evaluation by standard experimental, sedimentary, and geochemical methods (Tan & Hudson, 1974).

Many fish live in and are often restricted to habitats that are distinctive depositional environments, as observed by fishermen everywhere. As fossils, species and higher taxonomic groups may provide ecological and environmental evidence about ancient bodies of water (Grande, 1980). Inference from the presence or absence of species or other taxonimic groups is less direct than taphonomic evidence, because environmental interpretation requires the assumption that the fossil organisms had habitat requirements analogous to those of their recent counterparts (Elder & Smith, 1984, Elder & Smith, 1988; Wilson, 1988b). The contribution of fish paleoecological analogy to paleolimnology is limited to

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situations in which members of evolved groups of fishes share constrained relationships to such things as current or wave energy, gradient, elevation, temperature, oxygen, salinity, alkalinity, and other chemical conditions in lakes and streams. The basic premise is that ecological and evolutionary responses of fishes—their adaptive shapes, physiology, and especially restriction to aspects of water chemistry, energy, and temperature—are products of long-term interactions between geological processes and natural selection, paralleling the well-known responses of micro-organisms like foraminifera or plants like redwoods to their environments (e.g., Wolfe, 1971). When environments are too ancient to permit evolutionary/ecological analogies based on the relatedness of groups of organisms (Trewin, 1986), or generalities based on observable features such as body shape, evidence is limited to sedimentology, taphonomy, and geochemistry.

Fractionation of isotopes in geochemical systems is proving to be a powerful toolkit for reconstructing temperature, seasonality, salinity, and pathways of incorporation of inorganic and organic carbon sources in foodwebs (e.g., Swart et al., 1993; Patterson et al., 1993; Drummond et al., 1993). Isotope geochemistry of fish otoliths and bones promises to become a new field in itself, but the classical tools—stratigraphy, taphonomy, and taxon adaptations—still provide basic information not available by other means. Herein we present the types of information that may be derived through the analysis of fish remains recovered from sediment in eight categories.

Establishing the stratigraphic framework

Reconstructing the timing of sedimentary events is fundamental to understanding paleoenvironments (Wilson & Barton, 1996; Smith et al., in press). Evolutionary and ecological processes are often helpful. Fishes and mollusks, for example (Taylor & Smith, 1981), evolve through time slowly and species are restricted to limited times and sedimentary basins. Their evolved responses are recognizable in the fossil record over tens of thousands to millions of years.

Short-term ecological responses, such as rapid growth rates or polymorphic tooth forms, may be observed on a geologically instantaneous time scale. Evolved changes enable stratigraphic diagnosis of sedimentary units whose boundaries may be indistinct because lacustrine depositional units are often formed by reworking earlier formations. Fishes and other fossils provide an index of time to which the physical and chemical changes can be linked (Wilson, 1977, 1996; Grande, 1980; Bell et al., 1989; Smith 1987). These may be calibrated through their known time range in nearby sequences. The evidence thus obtained assists interpretation of the time scale of observed ecological succession as well as the geographic extent of aquatic systems.

Fish are often integral, interacting parts of depositional systems. When lakes are oxygenated to the bottom, benthic inhabitants disturb the bottom while feeding or hiding from predators. Benthic feeders stir up sediments while locating and consuming benthic crustaceans, mollusks, and fishes. Bioturbated sediments may show evidence of fish burrows, nests, concavities, and traces that differ according to the species and sizes of the fishes in the fauna and indicate limnological conditions required for these behaviors and these taxa (Johnson et al., 1984). Observations from submersibles in Lake Superior showed that benthic sculpins disturb soft sediments to a depth of 3-4 centimeters when hiding, or 7-10 cm when nesting (Smith, unpublished data). Predatory freshwater cods create meter-scale

trenches as traps for prey fishes. These allow reconstruction of history from upper sediment layers when bottom conditions permit employment of a sediment camera from a submersible or ROV (Boyer et al., 1989, 1990). Such evidence from behavioral ecology has the potential to constrain estimates of depth, temperature, and oxygen concentration. Interpretation of these traces in the ancient sedimentological record requires outcrop exposures that can be brushed out or recorded by acetate peels. Because the scale of sedimentological features ranges from tens of centimeters to meters, the evidence would not be recognizable in cores. The identity of the organisms causing the trace fossils requires associated presence of identifiable bony remains.

Geomorphology and paleohydrology

Knowing when and where lakes overflowed, drained, and had connections to neighboring lakes (paleohydrology) is important to paleolimnology because it permits reconstruction of the limits and sources of ancient lakes. Aquatic organisms such as fishes, mollusks, and crayfish may be faithful indicators of past aquatic connections, for example, because their presence in sediments of now-separate basins indicates continuous habitat in ancient times, as noted by early naturalists (Cope, 1883; Jordan, 1905). Fish, mollusk, and crayfish species are restricted to water habitat, therefore comparison of species distribution patterns in ancient sediments and recent basins can indicate stream captures, separation of watersheds by tectonic and volcanic barriers, connections among lakes (Hubbs & Miller, 1946), and former lake outlets (Wheeler & Cook, 1954). Occasionally, fish-derived evidence for past drainage connections is reinterpreted as transfer of aquatic organisms on birds' feet (Brown & Rosen, 1995; Spencer & Patchett, 1997). However, ecological tests of alternative hypotheses (Taylor, 1960, 1985; Smith et al., 1982) in western North America always support interpretations based on population ecology, rather than interpretations that rely on dubious rare occurrences, especially where integrated faunas are involved (Taylor, 1985), or where geomorphic data corroborate the biogeographic hypotheses (Smith et al., in press). Chance transport of fish eggs on birds' feet or adult fish in water spouts might be invoked to explain isolated occurrences that are inexplicably "out of place," but whole, ecologically congruent faunas require biogeographic connections through ecological and geochemically compatible habitats. Analysis of communities is important, because different species have non-congruent adaptations for dispersal.

Geochemical investigations add strength to hypotheses regarding fish migrations (Kennedy et al., 2000; Joukhadar et al., in press). Analysis of trace elements, calcium and strontium ratios, and stable isotopes in accretionary skeletal structures, can indicate whether paleoenvironments had connections to the sea (Koch et al., 1992; Shuck et al., in prep.) by documenting marine isotopic composition in migrants that have fed and grown in the sea (Patterson, 1999; Ivany et al., 2000). Bones and otoliths in particular offer the most promising chemical record of paleoenvironmental information that may be recovered from fish.

Otoliths

Otoliths are accretionary aragonite structures precipitated within the ears of most teleost fish making them readily analyzed structures, when available. Otoliths are common teleost

fossils that are found in a wide variety of sedimentary environments as old as the Devonian period (e.g., Nolf, 1995). Well-preserved aragonitic otoliths can be recovered from sedimentary rock dating back at least to the Jurassic (Patterson, 1999), unconsolidated sediment (e.g., Smith & Patterson, 1994), and archaeological deposits known as middens (e.g., Patterson, 1998; Wurster & Patterson, 2001). Otoliths are most commonly recovered by sieving unconsolidated or loosely consolidated sediment. Similarly, otoliths can be recovered from clay and shale that has been broken up by sonication and then sieved. Nolf (1995) provides an excellent summary on the secular distribution of fossil otoliths and their use as taxonomic paleoenvironmental indicators.

Taxonomic identification to the species level is relatively straightforward because otoliths are morphologically distinct (e.g., Nolf, 1995). Modern fish are often restricted to characteristic environmental conditions and life histories, so that related fossil assemblages can be used to reconstruct paleoenvironmental conditions (including bathymetry, ecology, and climate). Otoliths can often be found throughout sequences of rock and sediment, where they offer the potential of providing long-term secular environmental trends, but they are perhaps most valuable as snapshots of paleo-limnology and paleo-weather as revealed by microchemistry.

Thin sections of otoliths reveal annual (and sometimes daily) accretionary growth rings that represent different life stages that may be microsampled for isotopic analysis. Microsampling isolates time-specific aragonite from these growth rings that record temperature and other life history information as changing $\delta^{18}O_{(CaCO_3)}$ and $\delta^{13}C_{(CaCO_3)}$ values (Patterson et al., 1993; Smith & Patterson, 1994; Patterson, 1998; Wurster & Patterson, 2001). Fish that occupy a single environment throughout life will record seasonal conditions for that environment (e.g., seasonal temperature variation in shallow water). Migratory fish will record environmental conditions along the migratory route (e.g., freshwater to marine, or shallow to deep-water transitions). Transitions to marine water and/or cold water will each result in an ontogenetic (life history) increase in isotope values (Patterson, 1999,2000; Patterson et al., 2000; Ivany et al., 2000). The laminar bone of fish vertebrae and scales is accretionary, displaying clearly visible annual growth rings. However, isotope analysis of apatite requires time-consuming wet chemistry and offline extraction techniques to quantitatively separate oxygen from the phosphate radical for isotope analysis (O'Neil et al., 1994). Other bones may be resorbed and re-grown during the life of the animal, erasing previously stored isotope information. Otherwise, temperature and $\delta^{18}O_{(H_2O)}$ values are stored as $\delta^{18}O_{(PO_4)}$ values in a manner similar to that of carbonate ($\delta^{18}O_{(CaCO_3)}$). For example, deepwater sculpin (*Myoxocephalus thompsoni*) live at approximately 4°C throughout their adult life, thus precipitating bone apatite and otolith carbonate as $\delta^{18}O_{(PO_4)}$ and $\delta^{18}O_{(CaCO_3)}$ values, respectively. Because the temperature of the water is 4°C and the isotope value of the bone and carbonate can be determined, the $\delta^{18}O_{(H_2O)}$ value can be calculated using empirical temperature fractionation relationships (e.g., Patterson et al., 1993; Smith & Patterson, 1994).

Evaporation/precipitation

$\delta^{18}O$ values of lake-water can serve as an important indicator of precipitation, evaporation, recharge and residence time. Determination of $\delta^{18}O$ values of paleo-water is generally difficult because fractionation relationships require data for both temperature and water

$\delta^{18}O$ values (Fricke & Rogers, 1997). $\delta^{18}O_{(H_2O)}$ values of paleo-lakes can be calculated if the thermal life history of a fish can be constrained. For example, stenothermic species (such as the deepwater sculpin) are restricted to a narrow range of temperatures by the thermal activity range of their enzymes. If this preferred temperature is quantified, $\delta^{18}O$ values of fossil carbonate (fish otoliths) or phosphate (fish bone) can be used to quantify $\delta^{18}O_{(H_2O)}$ values. Fossil fish and modern relatives that belong to the same taxonomic group often have similar thermal tolerances.

Deep, temperate, dimictic lakes that contain deepwater fish are easier to analyze because carbonate from otoliths or bones of benthic fishes in such lakes with a hypolimnion at 4°C enable solving the equation with oxygen isotope values from tissues grown at 4°C. For example, $\delta^{18}O_{(PO_4)}$ and $\delta^{18}O_{(PO_4-CO_3)}$ values of fossil deepwater sculpin, *Myoxocephalus idahoensis,* permit calculation of paleo-water $\delta^{18}O_{(H_2O)}$ values in Pliocene Lake Idaho (Idaho, USA), because *Myoxocephalus* is restricted to hypolimnic 4°C water (Smith & Patterson, 1994). $\delta^{18}O_{(H_2O)}$ values of seasonally cool lakes can also be determined using eurythermic fishes with a characteristic minimum growth temperature by assuming that the highest $\delta^{18}O_{(CaCO_3)}$ value each season equates with the minimum growth temperature (Patterson et al., 1993; Patterson, 1998; Wurster & Patterson, 2001). Because temperature (minimum growth temperature in this instance) and $\delta^{18}O_{(CaCO_3)}$ value are known, $\delta^{18}O_{(H_2O)}$ values can be calculated.

Seasonal variability from micromilled otoliths

The accretionary nature of otoliths coupled with recent advances in micromilling technology (Patterson et al., 1993; Wurster et al., 1999) enable extraction of high-resolution aliquots of aragonite that represent a time averaging of a few weeks to as little as several hours. These samples provide a proxy for details of paleoclimate (Smith & Patterson, 1994; Patterson, 1998; Wurster & Patterson, 2001) and life history (Joukhadar et al., in press; Patterson et al., 2000) at a resolution that was previously unobtainable. Micromilled otoliths yield $\delta^{18}O$ and $\delta^{13}C$ values that reflect temperature and metabolism for restricted times and habitats.

A polished otolith thin section attached to a stage beneath a fixed micro-milling head, is viewed on a large-screen monitor through a color digital camera (Fig. 1). Growth bands (analogous to tree rings) generally resulting from variable accretion rates in biogenic carbonates are digitized in real-time as a series of three-dimensional coordinates (Fig. 2a). Intermediate coordinates are interpolated using a cubic spline fit through the digital points (Fig. 2b). Intermediate sampling paths, which mimic less visible daily growth banding, are in turn calculated between digitized curves. Sampling path arrays guide three high precision actuators, which position the sample stage relative to the fixed micro-milling head. A fourth actuator provides vertical control of the digital color camera (compensating for vertical movement of the z-axis stage actuator) keeping the specimen image focused.

The micromill uses a diamond dental drill bit to mill discrete carbonate sample aliquots from the otolith. Since the dental drill bit is significantly larger than the requisite width of the sample path, removal of discrete samples requires that the sample paths (for example $15\,\mu m$) are milled perpendicular to growth axes using the edge of the drill (Fig. 2c). The width of the carbonate milled depends on the total number of intermediate paths calculated. The volume of sampled carbonate depends on the length, width, and depth of the sample

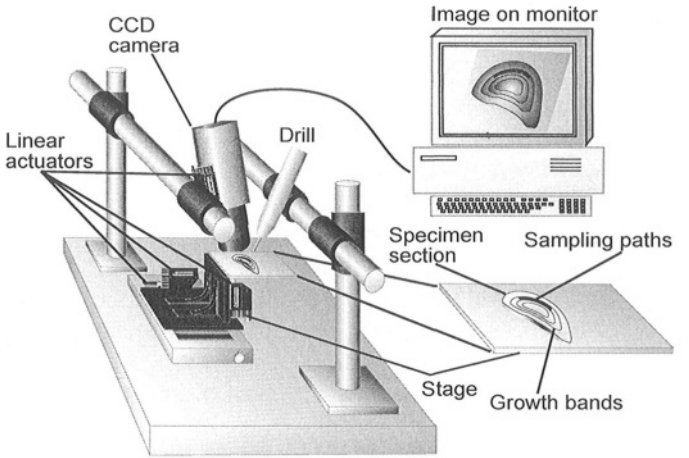

Figure 1. Schematic of micromilling apparatus. Specimen is attached underneath a fixed dental drill and viewed on large screen monitor via color digital camera. Computer-control drives motion controller via IEEE-488 interface, and permits stage manipulation in three directions via three micropositioning actuators (after Wurster et al., 1999).

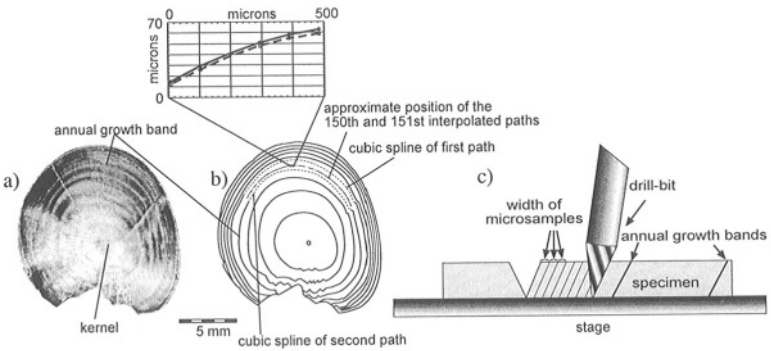

Figure 2. Illustration showing how carbonate is extracted from sample paths narrower than dental drill width. Note how first sample is coarsely drilled without extracting high-resolution time-specific carbonate. High-resolution samples are later extracted by milling carbonate from specimen using dental drill bit. Note micron-scale widths of subsequent sample paths (after Wurster et al., 1999).

path, and mass is calculated from the volume using the density of the sampled mineral. Current mass spectrometer technology using automated carbonate preparation systems for analysis usually requires $\sim 20\ \mu g$ of carbonate. Although the length function is determined by the morphology of the specimen, manipulation of both depth and width functions is possible. The depth function is selected by increasing or decreasing the drill depth (z-axis). The width function is determined by the number of intermediate paths between any two digitized paths (the greater the number of intermediate sampling paths, the higher the resolution and the lower the sample size and mass). Carbonate samples are manually collected with a small scalpel while viewing the specimen on the large screen monitor. Each sample is stored in a stainless steel vessel, which is placed in numbered brass convoys prior to analysis.

Stable isotope values of lacustrine fish

As with $\delta^{18}O_{(PO_4)}$ values, application of $\delta^{18}O_{(CaCO_3)}$ values to paleotemperature requires that the $\delta^{18}O_{(H_2O)}$ value be determined. There are currently two methods for determining the $\delta^{18}O_{(H_2O)}$ value of ancient freshwater using mineral elements of fishes; micromilling of otoliths with specific thermal growth requirements (Patterson et al., 1993), paired-species analysis (Smith & Patterson, 1994), or a combination of the two techniques. Paired-species analysis uses a cold-water obligate benthic fish such as a deep-water sculpin (restricted to 4°C) to obtain $\delta^{18}O_{(H_2O)}$ values. Once paleo-water $\delta^{18}O_{(H_2O)}$ values are constrained, warm water stenothermic and eurythermic species can be analyzed by micromilling to interpret seasonal variation in surface-water temperatures that are directly related to atmospheric conditions (Patterson et al., 1993; Patterson, 1998). If the eurythermic species has a minimum thermal tolerance for growth, the highest isotope value each year will represent carbonate precipitated the minimum growth temperature (Patterson et al., 1993; Smith & Patterson, 1994; Patterson 1998). For shallow-water species these water temperatures correspond to mean weekly atmospheric temperature (Patterson et al., 1993; Wurster & Patterson, 2001). Thus, shallow-water fish can provide a detailed record of atmospheric temperature for the past. The resolution obtainable from these structures is easily suitable for reconstructing paleoclimate in great detail. The recent advances are sufficient to generate records that essentially represent paleo-weather data.

Stable isotope evidence from river-dwelling fish

Fish remains recovered from rivers provide additional hydrological and climatological information while presenting a different challenge because $\delta^{18}O_{(H_2O)}$ values may vary to a greater degree than lakes on an intra- and inter-annual basis. The seasonal maximum $\delta^{18}O_{(CaCO_3)}$ value used to calculate $\delta^{18}O_{(H_2O)}$ may change each year, reflecting different sources and amounts of seasonal precipitation. For example, otoliths of freshwater drum (*Aplodinotus grunniens*) were micromilled and analyzed to determine $\delta^{18}O_{(H_2O)}$ values and summer maximum temperatures of the Holston River in Tennessee for the last 5,500 years (Wurster & Patterson, 2001). Significantly, it appears that this technique has the sensitivity to discern individual storm events if sufficient precipitation enters the watershed (Fig. 3). During the late Hypsithermal, summer temperatures were generally higher than in the modern and tropical storms have been proposed by models to be more frequent (Emanuel, 1987; Gutowski et al., 1994). In Figure 3, the late season apparent rise in temperature during year 4 is interpreted to represent tropical storm moisture that is known to have significantly lower $\delta^{18}O_{(H_2O)}$ values due to the high degree of distillation (e.g., Lawrence & Gedzelman, 1996). By examining otoliths through a sequence of sediment or rock, secular variation in temperature and $\delta^{18}O_{(H_2O)}$ values can be derived (Patterson, 1998; Wurster & Patterson, 2001). Figure 4 presents temperature and $\delta^{18}O_{(H_2O)}$ values for the South Fork of the Holston River in Tennessee, derived from a series of otoliths recovered from the Eastman rockshelter archaeological site at Eastman TN. Otoliths range in age from 5,500 to 300 years old. Oxygen isotope analysis should now permit tests of climatic hypotheses based on taxon habitat as the basis for inference (e.g., Smith, 1963; Shoshani & Smith, 1996), which are ambiguous because of the conflation of amount of water and temperature effects (Cross, 1970).

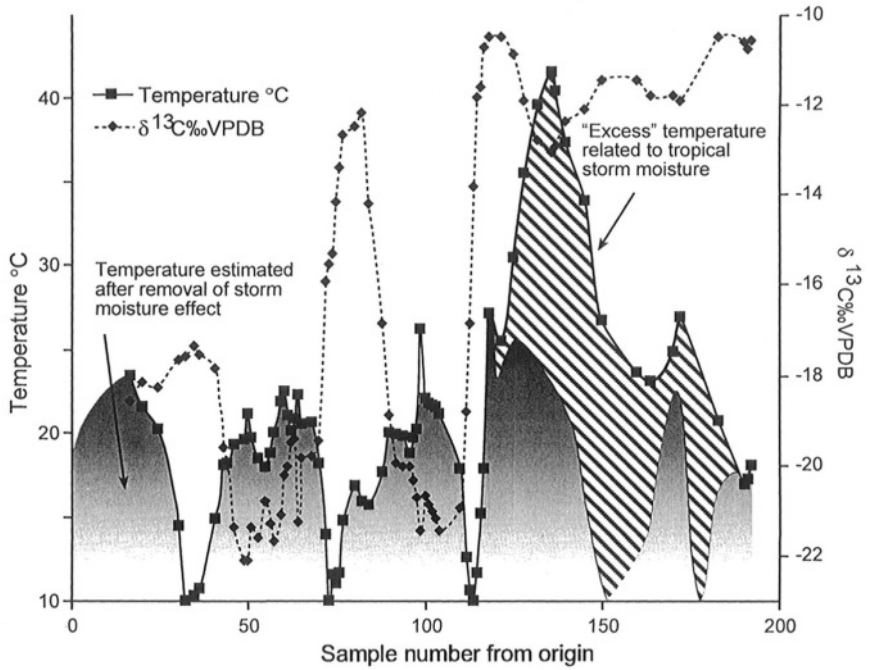

Figure 3. $\delta^{13}C_{(CaCO_3)}$ values and temperatures (calculated from $\delta^{18}O_{(CaCO_3)}$ values) from a 2,900-year-old Freshwater Drum otolith recovered from the Eastman Rockshelter archaeological site in Tennessee, USA. Samples represent a three-day resolution in temperature and metabolism. $\delta^{18}O_{(CaCO_3)}$ values have been converted to temperatures assuming that the highest $\delta^{18}O$ value each year represents carbonate precipitated at 10 °C. The apparent peak temperatures in year 4 are well above the thermal tolerance for this species. These values are interpreted to represent incursion of highly distilled tropical moisture during at least one storm event. $\delta^{13}C$ values which are predominately a function of metabolic rate do not indicate excessively high temperatures, thus we invoke a large decrease in $\delta D_{(H_2O)}$ value at the end of the summer (data from Wurster & Patterson, 2001).

Lake depth, salinity, oxygenation, temperature

Coldwater fish such as trout and whitefish are indicators of cool waters and possibly cold paleoclimate (Rogers et al., 1985, 1992; Firby et al., 1997). Ambiguity arises because coldwater fish are also indicators of water depth. Other indicators of depth-sediment texture, lack of scavenger action and other indicators of anoxia, and sedimentary context are sometimes difficult to interpret. Behavior of decaying carcasses may provide depth estimates when low temperatures, salinity, and (or) pressures constrain bacterial action (Allison et al., 1991). Fossil evidence of the nature of carcass decay and disturbance by scavengers is therefore an important link in connecting paleolimnological evidence to paleoclimate analysis.

Fish evidence for depth and sedimentation rates in the lake deposits of the Miocene Clarkia Formation, in the St. Maries River basin, Idaho, suggested conclusions different from those provided by plant fossils (Elder & Smith, 1985, 1988). Freshwater conditions were indicated by the fact that two of the taxa present are restricted to fresh water and warm climate was indicated by the restriction of one of the fish families present to warm

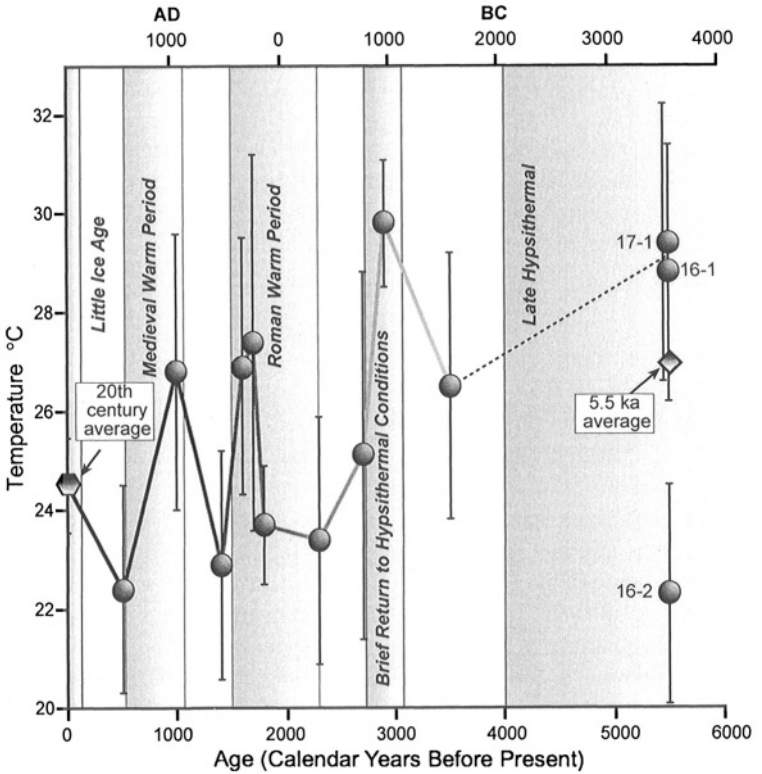

Figure 4. Estimated maximum summer temperature and average $\delta^{18}O_{(H_2O)}$ values from 5.5 ka to 0.3-1.0 ka derived from intra-otolith $\delta^{18}O_{(CaCO_3)}$ values of 14 sagittae recovered from the Eastman. Bars represent variation in estimated temperature using calculated $\delta^{18}O_{(H_2O)}$ +1‰ and are not representative of error. Twentieth-century average maximum temperature is plotted for comparison. Modern $\delta^{18}O_{(H_2O)}$ value (collected 3/24/99, at the approximate seasonal start of fish growth) is included for comparison (data from Wurster & Patterson, 2001).

waters. The evidence of minimal but observable scavenger action (by crayfish or snails) on decaying fish established occasional oxygenation to the lake bottom, despite the warm water habitat. Constraints on the depth of the lake were quantified by experimental work that established the relationship between pressure and temperature in the flotation of dead fish by bacterial decay gases. At temperatures above 16 °C, pressure equivalent to 10m of water are required to keep bubbles of decay gases from accumulating and floating positively buoyant fish carcasses (Elder & Smith, 1985). Thus, application of fossil observations and laboratory experiments provides evidence for depth and temperature.

Mass mortality layers are assemblages of fossil organisms that died in a catastrophic event, as indicated by their concentration in a single stratum. The cause of death is usually anoxia or an increased concentration of CO_2 or decay gases released by turnover, or sudden temperature change. Combinations of ecological, taphonomic, and taxonomic interpretation are usually required. There is a limited signal indicating cause of death in the posture and decay pattern of the dead fish. Anoxia causes distended gill chambers and

concave-up distortion of the vertebral column. Scavenger disturbance indicates presence of oxygen; absence of scavengers indicates anoxia. Death assemblages also provide detailed information about limnological conditions of life and population dynamics (Wilson, 1980, 1988a, 1988b; Bell et al., 1989).

Exceptionally rich faunas may also contribute to chemical information. The diverse fish, mollusk, and ostracod faunas of the Pliocene Glenns Ferry Formation, Idaho, are represented by massive amounts of calcite, aragonite, and apatite, consistent with the presence of alkaline, but not saline, nutrient-rich conditions, confirmed by abundant biogenic oolite (Swirydczuk et al., 1979, 1980).

Rates of lacustrine sedimentation

Sedimentation rates are important to paleolimnological interpretation, but are sometimes controversial. Tree leaf chemistry and distinct sediment laminae (Smiley & Rember, 1985) in the Miocene Clarkia Formation, St Mary's drainage, Idaho, suggested rapid sedimentation in a small lake. Many species of tree leaves recovered from the formation are fresh in appearance (leaves and fish retain some original pigment and organic chemistry for a few moments after being exhumed; i.e., until oxidized), suggesting that burial was nearly instantaneous, in a storm event. However, fish taphonomy contradicts this conclusion (Elder & Smith, 1985). Long periods of slow decay in cold water, with minimal sedimentation and minimal scavenger action, are indicated by the presence of small fans or splays of scores of minute (1 mm) fin-ray bones, dispersed evenly across the bottom up to 4 cm away from the fins of the fishes by gentle currents after extensive decay. Slow decay and exposure to slow, unidirectional currents for several months are indicated by the graded dispersion of the fine bones (lepidotrichs). Laminar sediment couplets (presumably annual, on the basis of the above observations) are about 1 mm thick, further suggesting slow, gradual, sedimentation rates (Smith & Elder, 1985). Some sedimentary layers are penetrated by the decaying bodies of the fishes.

Lake vs. stream habitats

High vs. low energy environments are not always easily diagnosed because constraints on sediment sources do not permit the full range of clasts and sediment textures (Pickard & High, 1985). Lacustrine and low energy fluvial habitats may have identical sediment particle sizes. The first step in analysis is to determine the energy level in the local paleoenvironments; the lateral and vertical relations of these will point to lacustrine vs fluvial settings. Fish can help support inferences made on the basis of sediment textures. Lacustrine and low-energy habitats in general are indicated by fossils belonging to groups that live primarily in lakes (the method of taxonomic analogy) and also by presence of fish with a ratio of body depth to length exceeding 0.3, such as bluegill sunfish or other deep-bodied fish (the method of ecomorphology). Certain taxonomic groups are restricted to lowland lakes in modern settings, for example, catfish, sunfish, bass, perch, drum, or pikes that normally live in eastern North American lakes lower than 1200m above sea level. It is probable that co-occurrence of fossil relatives of these groups indicates similar restriction (Lundberg & Smith, 1978; Smith et al., 2000), but this general method of inference, alone,

is weak because it ignores the possibility of change in physiology or behavior of the indicator organisms (Binford et al., 1985). Inferences about habitats are now testable by isotopic analysis and by the ecomorphological approach. The analysis of body shapes that function in restricted ecological settings (ecomorphology) has potential for providing tests of hypothesized low-energy waters. Just as large, smooth-margined leaves indicate moist tropical climates (Wolf, 1971), absence of deep-bodied fish from a community indicates high-energy environments. Deep-bodied sunfish, cichlids, pupfish, suckers, minnows, and characins, for example, inhabit low-elevation, low-energy environments (Perrine, 2000).

Elevation

The identification of relative elevation above sea level in the sedimentological record is problematical. It is especially difficult to determine whether a lake existed on a high plateau or a lowland, because the modern elevation of the sediments is not good evidence for the original elevation of the body of water. River sediments are easier if the broad lateral context of the basin is well known, but may be ambiguous. The problem may be approached as an issue of energy in the depositional system, similar to the analysis of above, because of the correlation between elevation, gradient, and current velocity. Fish may contribute to the solution to this problem because only slender fishes such as sculpins, darters, and trouts inhabit high-gradient streams. Deep-bodied fishes such as sunfish, bass, carp-suckers, buffalofish, carp, or cichlids inhabit low-gradient streams (with a mix of slender-bodied fishes). The occurrence of any of the deep-bodied fish in a fossil fauna indicates low gradients and elevations lower than 1200 m (Perrine & Smith, in prep.). A survey of modern fish habitats in the United States, Mexico, South America, and Madagascar indicates that deep-bodied, spiny-rayed fish such as sunfish and cichlids (Perciformes) are not naturally found above 1200m in elevation (Perrine & Smith, in prep.). Hydrodynamic pressures on deep-bodied fish apparently eliminate them from swift currents. Therefore access to high elevation lakes as well as high elevation fluvial environments is eliminated.

Exceptional cases of lakes and low-gradient rivers in basins perched at high elevations are possible, but these are especially short-lived in geological time, so time and high-gradient barriers in rivers interact to keep deep-bodied fishes from these environments. Such settings are usually inaccessible because they are separated from lowlands by downstream barriers of high gradient. Known cases of low gradients at high elevations, in low latitudes, such as the Peruvian and Bolivian Andes and Mexican Plateau, are not inhabited by deep-bodied, spiny-rayed fish.

Summary

Taphonomic and taxonomic data from fishes are used to identify physical, chemical, and ecological conditions in ancient environments.

1) Temperatures of ancient environments are estimated by oxygen isotopic ratios in aragonitic otoliths or apatite of bone, as well as by presence or absence of fish that belong to known warm-water or cold-water groups.

2) Analysis of the conditions of death, scavenger disturbance, and carcass decay may enable identification of cold, stratified lakes and estimation of oxygen, water chemistry,

and sedimentation patterns.
3) Climatic seasonality can be analyzed as temperatures recovered by isotopic analysis of aragonite or apatite growth rings representing different seasons. The growth bands in these accretionary structures are micromilled from growth rings and analyzed in a mass spectrometer.
4) Salinity is indicated by presence or absence of fish with narrow salinity tolerance (stenohaline) in contrast with fish that are broadly tolerant of salinity (euryhaline fish).
5) Migrations are determined by microsampling different years of life, as represented in oxygen isotopes in otoliths or bone, and recovering evidence of travel to distinctive chemical environments.
6) Current energy and elevation may be indicated by fish body-shapes and taxon-diagnostic adaptations. Deep-bodied fishes are restricted to waters with low current or wave energy.
7) Hydrographic connections, lake spillovers, and stream captures are indicated by biogeographic patterns of species distributions. Fish in adjacent but separate hydrographic basins indicate former continuous fish habitat between the basins.

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Glossary, Acronyms and Abbreviations

^{210}Pb dating: Method of absolute age determination based on the decay of radioactive lead-210, which is formed in the atmosphere. It rapidly attaches itself to aerosol particles, and settles to the Earth's surface. Lead-210 activity in lake sediments provides an indication of their age for the last ~ 150 years.

Acari: See mites.

acarology: The study of mites and ticks.

accretionary structure: A structure that has grown by addition of layers to the outside.

acetolysis: Sample preparation technique used to destroy excess organic matter in sediments via a hot 9:1 solution of acetic anhydride and concentrated sulphuric acid. Commonly used in preparation of sediments for pollen analysis.

Actinotrichida: One of the two major taxonomic divisions of the Acari, characterised among other things by the occurrence of normal body and leg setae containing "actinochitin", which alters the wave direction of polarised light.

adductor muscles: In Ostracoda, the muscles that effect valve closure. They are attached to the inner valve surface more-or-less centrally. Also refers to muscles with a similar function in bivalve molluscs and brachiopods.

aedeagus: Male reproductive organ of insects.

aerenchyma: Plant tissue consisting of large dead air-filled cells with thin walls. Forms the pith commonly found in stems or culms of emergent aquatic macrophytes. Provides pathway from atmosphere to roots for oxygen needed in root respiration.

Allerød: Warm interstadial period that occurred at the close of the Weichselian (or latest) Glacial Stage in Europe, approximately 11,800 to 11,000 ^{14}C years before present (about 12,700 - 13,900 calibrated yr B.P.).

allochthonous: From elsewhere, as opposed to autochthonous (produced *in situ*). Used, for example, for organic matter that may be imported from elsewhere, or for organisms.

amino acid: Organic molecules found in proteins.

Anactinotrichida: One of the two major taxonomic divisions of the Acari in which the body and leg setae do not contain "actinochitin", cf. Actinotrichida.

annulus: Outer ring of a bryozoan statoblast valve consisting of large, sclerotized chambers usually containing a gas for buoyancy. Term is used in the description of other organisms, such as chrysophyte cysts.

antenna: One of a pair of mobile appendages on the heads of insects, crustaceans, etc., that are often whiplike and respond to touch and taste, but may be specialized for swimming or attachment.

antennae: Plural of antenna.

antennal grooves: Grooves along the head capsule of weevils (snout beetles) that hold the antennae in place.

apatite: A mineral group including calcium phosphate of bone and certain shells.

aragonite: A carbonate mineral found in mollusc shells and other invertebrates that is an orthorhombic form of $CaCO_3$, trimorphous with calcite.

arboreal: Living above the ground in trees and bushes.

articulated: In Ostracoda, an articulated specimen is one in which the valves are attached at the hinge. The valves are articulated in the living animal but become disarticulated after moulting and, sometimes, following the death of the animal. Term also used for other organisms.

autecology: The ecology of an individual species.

autochthonous: From within, as opposed to allochthonous, which is material from elsewhere. Used, for example, to describe material, such as aquatic invertebrates, which are produced within a lake basin.

benthic organism: An organism that lives on the bottom of a lake or stream.

benthic: Relating to the lake or ocean floor; the deepest part of the lake.

benthos: Collectively, all organisms living on or in the bottom of a lake, stream or other body of water.

Berlese: Antonio Berlese, famous Italian acarologist, the author of numerous mite species, inventor of the Berlese funnel for extracting arthropods from soil and litter, and the Berlese fluid as a mounting medium.

biocoenosis: The living assemblage of organisms.

biogenic origin: Of biological origin.

bioturbated sediment: Sediment that has been modified by action of an organism, often bearing information about living conditions of that organism. May be a problem in some systems if the sedimentary profile is mixed.

biramous: Structure of crustacean appendages which are divided into two parts.

bivoltine: Producing two generations per year.

Bryozoa: Small, sessile, colonial, filter-feeding animals. Phylum Ectoprocta; also known in older literature as Polyzoa.

Bogorov counting tray: A plankton counting tray developed by Bogorov. With the aid of a dissecting microscope, zooplankton are counted in a sinuous groove cut into a transparent perspex plate. In paleolimnology, also used for sorting insect remains from sediment samples.

bucket sieve: A large metal bucket with the bottom removed and a sieve screen inserted near the bottom.

budding: Form of asexual reproduction in which a new individual grows from the body of the parent individual. Bryozoan colonies grow by budding.

CA: Correspondence analysis.

caddisflies: Insects in the order Trichoptera; the larvae are aquatic, the adults fly mainly near water.

calcareous: Refers to the presence of $CaCO_3$.

calcite: A carbonate mineral composed of calcium carbonate; $CaCO_3$.

calcite branchpoint: During progressive evaporative evolution of a waterbody, the point at which the water becomes saturated with respect to calcite, at which time there is a tendency for precipitation of the mineral calcite to occur.

calibration set: A present-day reference data-set ("training set") for modeling purposes. Typically includes the analysis of indicators preserved in the surface sediments (e.g., top 1 cm of a set of reference lakes). See training set.

Canada balsam: Type of mounting medium for making permanent microscope slides, made from balsam (*Abies balsamea*) resin.

canonical correspondence analysis (CCA): A constrained ordination technique based on correspondence analysis, but where the ordination axes are constrained to be linear combinations of the supplied environmental (predictor) variables.

carapace: The thick, hard, chitinous shield that covers part of the body of crustaceans (e.g., Cladocera). In Ostracoda, the carapace is generally calcified and consists of two valves, the left valve and the right valve, which are joined along a dorsal hinge.

carina: An elevated ridge or keel.

CCA: Canonical correspondence analysis.

ceratopogonid: Biting midge or "no-see-um". Minute biting flies belonging to the family Ceratopogonidae.

chelicerae: First pair of appendages of an arachnid that have been modified for food collecting, most often in the forms of fangs with one fixed and one movable digit. Males of many predatory mites in the suborder Gamasida also use the chelicerae for sperm transfer.

Chelicerata: Arthropods where the body consists of a cephalothorax or prosoma and an abdomen or opisthosoma. The first of the feeding appendages is the chelicerae that gives the group its name, and they have no antennae.

chitin: Long-chain, nitrogen-containing polysaccharide compound found in the exoskeletons of arthropods, cell walls of fungi, and bryozoan statoblasts, etc. Resistant to deterioration when buried in lake sediments.

chydorid: Chydoridae; family in the suborder Cladocera.

cichlid: A member of the family Cichlidae—common freshwater fish of the southern hemisphere, characterized by spiny median fins and deep body shapes, at least in low gradient waters at low elevations.

circumpolar: Distributed around the north or south polar regions.

clade: A natural group of species that includes all of the descendants of a common ancestor and is diagnosed by shared, advanced features. Membership in a clade implies some shared predictive qualities.

Clarkia: A Miocene lacustrine fossil locality in the St. Marys Basin, Idaho, noted for its preservation of leaves containing DNA and original pigments.

clasts: Sedimentary particles, originating as detrital rock fragments as well as shells, bones, and other biological hard parts.

climate envelope: The set of climatic conditions found within the geographic range of a species.

clypeus: The part of the head of an insect, anterior to the frons, to which a upper lip (labrum) is attached.

concretions: A nodular sedimentary rock made of matrix precipitated from solution, with a mineral or biogenic nucleus.

coprolite: A fossil feces, often containing information about the digestive tract and the food habits of the organism that made it.

correlation coefficient (r): A statistical index which reflects the strength of the relationship between two variables.

correspondence analysis (CA): An ordination method that simultaneously ordinates samples and variables (species), and maximizes the correlation between sample and variable scores. It is widely used in ecology because it assumes a unimodal response of species variables to underlying gradients.

cosmopolitan: Widely distributed.

coxopodite: The primary basal segment of an appendage, representing the primitive limb basis.

Crustacea: A phylum or subphylum of Arthropoda. Most crustaceans are aquatic.

cyclical morphological variability: Morphological changes in the shape of the organism that are induced mainly by predation, making the handling of the prey more difficult to the predator; typical in, for example, cladocerans.

cyst: A thick-walled, protective membrane enclosing a cell, larva, or organism.

cystid: The body wall of a zooid (individual) in a colony of Bryozoa (Ectoprocta).

deep-bodied fish: A fish shaped like a sunfish, with the body depth equal to 0.3 to 0.5 of the body length. Interpreted as indicative of aquatic habitats with low current or wave energy.

deflocculate: To break up loose aggregates of sediments, usually by physical and chemical means.

detrital carbonate: The carbonate component of sediment derived from erosion of pre-existing carbonate rock or sediment. In lake sediments, detrital carbonate is generally derived from the weathering and inwash from carbonate rocks within the lake's catchment.

detritivores: Organisms that feed on decaying organic matter (i.e., organic detritus), such as the finely-disseminated organics in lake sediments.

diapausing egg: An egg that is under suspended development and growth accompanied by decreased metabolism. It is often correlated with seasonal changes.

DIC: Dissolved inorganic carbon.

dichotomous key: A key to the identification of a taxonomic group, in which the key characters are split into couplets.

diffraction gratings: Microscopic lines, impressed on the surface of, for example, an insect exoskeleton, that refract light.

dimictic lake: A lake that experiences two periods of mixing per year, caused by temperature fluctuations that bring the upper and lower waters to the same temperature and density.

disarticulate: To separate or cause to separate at the joints.

disarticulated: In Ostracoda, a disarticulated specimen is one in which the two valves of the carapace are separated. Disarticulation occurs during moulting and often following death of the animal.

dissolved inorganic carbon (DIC): Inorganic carbon dissolved in lake water, consisting primarily of free CO_2, bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}) in varying proportions. The relative proportions of the different inorganic carbon species are strongly pH-dependent.

domatia: Tufts of hair, often in small pits, on the underside of a leaf and inhabited by mites and other minute arthropods. First described by the Swede Axel Lundström more than a century ago as acarodomatia (i.e., mite houses). May have a positive function in harbouring predatory and fungivorous mites as a plant defence.

dorsal hinge: In Ostracoda, the line of attachment of the left and right valves. In most lacustrine species, the hinge is relatively simple. The word hinge is also used to refer to an analogous line of attachment for the shells of bivalve molluscs.

dorsal prothoracic shield: The first dorsal sclerite on the thorax of a beetle, expanded to cover the rest of the thorax, also called the pronotum.

ecdysis: Periodic shedding (moulting) of the exoskeleton to allow for further growth in insects, Crustacea, and other arthropods.

echo-sounding: A navigation and position-finding device that determines depth by measuring the time taken for a pulse of high-frequency sound to reach the sea/lake bed or a submerged object and for the echo to return.

ecoclimatic: A combination of climatic and ecological factors.

ecomorphological methods: The use of functional constraints in structural shapes of organisms to infer environmental characteristics such as temperature or current energy, in contrast to the method of taxonomic analogy.

ecophenotypic: A variation in an organism that is the direct result of interaction with the environment, for example robustness caused by exercise.

ecotype: A group of organisms within a species that is adapted to different environmental conditions and therefore differ from one another in structure and physiology.

Ectoprocta: See Bryozoa.

Eemian: The most recent interglacial stage; named from marine deposits along a small stream in the eastern Netherlands.

Eemian Interglacial Stage: Interglacial period preceding the last major ice advance (Weichselian glacial stage) in Europe during the late-Pleistocene. The warm Eemain stage is correlated with the Ipswichian Interglacial of Britain, the Riss-Würm Interglacial of the Alpine region of Europe, and the Sangamon Interglacial of North America.

effective precipitation: The balance of precipitation to evaporation and evapotranspiration.

elytron: The anterior leathery or chitinous wings of beetles, which cover the hind wings and often the abdomen.

entomology: The study of insects.

epidermis: The outer layer of cells of an organism.

epilimnion: Warm water region near the surface of thermally-stratified lakes.

epipharynx: In insects, a lobe or plate borne on the palate. In Chironomidae, more specifically, the ventral surface of the labrum ("upper lip").

epipodote: An exite of the coxopodite; often a gill-bearing organ.

epizooic: Referring to animals living on other animals or using other animals as a substrate for attachment.

Euparal®: Trade name for mounting medium used for making permanent microscope slides.

euryhaline: A species, capable of tolerating a wide salinity range.

eurythermic: An organism tolerant of a broad range of temperatures (in contrast to stenothermic).

eutrophic: Of lakes and similar habitats rich in organic and mineral nutrients and supporting an abundant plant and algal life, which, in the process of decaying, may deplete the oxygen supply for benthic animal life.

evaporative evolution: The chemical evolution of a water as a result of progressive evaporation. With significant evaporation, a saline brine may form, the chemical composition of which is in part dependent on the chemistry of the dilute input water and the degree of evaporation.

exoskeleton: The protective or supporting structure (external skeleton) covering the outside of the body of many animals, such as the thick cuticle of arthropods.

extant species: A species that is not extinct; currently living.

fenestra: Central region of a bryozoan statoblast valve.

filamentous cyanobacteria: Long slender chains of cells into which a group of bacteria containing a blue photosynthetic pigment and formerly regarded as algae (blue-green algae).

filter-feeders: Organisms which feed by filtering other organisms or food particles from water.

fin-ray bones: Formally "lepidotrichs"; the small (ca. 1 mm) bony platelets that make up the fin rays of fishes. After death, decay, and fossilization, these can be interpreted as indicators of current strength and direction on ancient lake bottoms.

floatoblast: Type of bryozoan statoblast having a buoyant ring of cells, released as free-floating disseminules, effectively dispersing the species to new localities.

flotant: The portion of material in the flotation procedure that floats to the top of the liquid.

flotsam: Floating debris.

fractionation (of isotopes): Separation of one isotope from another of the same element, usually a result of different bond strengths.

frons: The frontal sclerite of the head capsule of insects, posterior to the clypeus.

frontoclypeus: On the head capsules of caddisfly larvae, the fused frons and clypeus sclerites.

fungicidal detergent: A detergent that contains fungus-killing ingredients.

gamogenesis: Another name for sexual reproduction.

gastropod: A member of the Class Gastropoda (Mollusca).

gnathosoma: A secondary body region peculiar to the mites and mainly formed from parts of the palpal and cheliceral segments.

Gondwanaland (Gondwana): One of the two ancient supercontinents produced by the first split of the even larger supercontinent Pangaea about 200 million years ago, comprising chiefly what are now Africa, South America, Australia, Antarctica, and the Indian subcontinent.

growth rings: Layers of a mineral, such as aragonite, in an accretionary structure, such as a clam shell or fish otolith.

gum tragacanth: A water-soluble glue, made from a gum obtained from various Asian or East European leguminous plants (especially *Astragalus gummifer*).

gyttja: Type of lacustrine sediment with high organic content. Coprogenous sediment containing the remains of all particulate organic matter, inorganic precipitations, and minerogenic matter. The word is of Scandinavian origin.

head capsule: Resistant chitinous exoskeleton (sclerites) that encloses the head of some insects (e.g., larval midges and black flies).

head-shield: The protective outer covering of the head in Cladocera.

hermaphroditic: An individual that has both male and female reproductive organs.

heterotrophs: Organisms that use complex organic compounds to manufacture their own organic constituents. Compared to autotrophic organisms, such as plants.

Holarctic: The Nearctic region (North America) and the Palaearctic region (Eurasia north of the Himalayas, the northern part of the Arabian Peninsula, and Africa north of the Tropic of Cancer).

holometabolous: Insects with complete metamorphosis (i.e., life cycle includes a pupal stage).

Hoxnian interglacial stage: Period thought to be between the third and fourth major Pleistocene glaciations in Britain. It is correlated with the Holstein Interglacial Stage in Europe, the Mindel-Riss Interglacial in alpine Europe, and the Yarmouth Interglacial in mainland North America.

Hoyers medium: A modification of the Berlese fluid and the most widely mountant used for many invertebrates when making permanent slides. Consists of a mixture of glycerol (20 ml), chloral hydrate (200 g), crystalline gum arabic/acacia (30 g) and distilled water (50ml). The solid material is dissolved and the fluid filtered.

hydroseral succession: The succession from aquatic environment to terrestrial habitat (i.e., from open water to mire); filling-in.

hydrostatic organs: In phantom midges, gas-filled structures which regulate the buoyancy of the larva, and thus its position in the water column.

hypolimnic waters: Those colder strata of a lake below the thermocline, which is the zone of rapid temperature change.

hypolimnion: Cold water region at the bottom of thermally-stratified lakes.

hypopharynx: In insects, a mouthpart located in a median ventral position, just anterior to the labium.

Hypsithermal: Interval in the Holocene with mean temperatures higher than the present ones. It includes the Boreal, Atlantic, and Subboreal climatic intervals, roughly from 10,500 BP to 2,500 calibrated years BP. It varies in its age in different pans of the world.

idiosoma: The region of a mite body that does not belong to the gnathosoma.

Illinoian: The name used in most of North America for the penultimate glacial stage.

imago: Adult stage of insect life cycle.

***in vitro* culture:** A culture of organisms undertaken in the laboratory to allow the opportunity for close control on environmental conditions or detailed observation of the organisms, or both.

inference model: Prediction or calibration model; transfer function.

inner lamella: In Ostracoda, the inner covering of the body parts: it is composed mainly of chitin.

instar: In the life cycle of arthropods, the interval between two moults (shedding of the exoskeleton).

integrated fauna: An assemblage of animals that lives together and is characterized by a particular history.

interglacial stage: Between glacial stages.

ionic strength: The measure of ionic concentration in water.

iridescence: A lustrous rainbow-like play of color caused by differential refraction of light waves that tends to change as the angle of view changes.

isotopic fractionation: The enrichment or depletion of different isotopes of an element during natural processes. Isotopic fractionation is most important in the lighter elements: in environmental systems, these include hydrogen, carbon, and oxygen. Fractionation arises because certain chemical and physical properties of molecules depend on the relative atomic mass of the constituent atoms. Natural processes in which fractionation occurs include evaporation of water, chemical precipitation of minerals such as calcite, and photosynthesis.

isovalent group: Term proposed by the German acarologist Willi Knülle in 1957 for a group of oribatid species in which the local distribution is determined by some environmental factor(s) (e.g., soil moisture, not restricted to a special vegetation type). The group of species is defined by their frequency and abundance.

Jurassic: The second period of the Mesozoic era, between the Triassic and Cretaceous periods, lasting for 45 million years during which dinosaurs and ammonites flourished.

kettlehole: A typically steep-sided basin, commonly with little surface drainage, in glacial drift deposits (especially outwash), formed by the melting of a large, detached block of stagnant ice.

labium: The "lower lip" or posterior-most mouthpart in insects.

labral fans: In larval blackflies, fans of setae (hairs) attached to the labrum ("upper lip"), and used for filtering minute organisms and other food particles from the water.

laminar bone: Bone that grows in layers. These are often useful as growth layers that may be sampled for isotopes or trace elements to reconstruct history.

larvule: First instar larva of a non-biting midge (Family Chironomidae).

leave-one-out cross-validation: Computer-intensive resampling technique that is used in model validation to provide more realistic estimates of model parameters.

lentic: Pertaining to standing water (e.g., lakes, ponds, puddles).

limnetic taxa: Species inhabiting the open water of lakes down to the depth of light penetration.

littoral communities: Groups of plants and animals living in the shallow waters at the edges of lakes and ponds.

littoral zone: The zone in a lake or pond extending from the shore through to the depth at which plants are rooted. Typically, the shallow, near-shore regions of a water body.

lophophore: Feeding organ possessed by bryozoans, with ciliated tentacles, for capturing suspended food particles from the surrounding water and directing them to the mouth.

macrofossil: Fossil that is visible to the naked eye.

macula: A colored mark, larger than a spot.

madicolous: Pertaining to seeps and thin films of flowing water.

magnesian calcite: Calcite in which Mg replaces some of the Ca atoms in the crystal lattice. Two types are recognised: low-Mg calcite (<4 mole % Mg in calcite) and high-Mg calcite (>4 mole % Mg in calcite).

malachite green: A stain that is commonly used to highlight, amongst other things, structures in carbonate microfossils.

mandible: Either of a pair of mouthparts in arthropods that are usually used for biting and crushing food. The lower jaws of an insect.

marl: Type of lake sediment with a high concentration of carbonates.

maxilla: Any member of one or two pairs of mouthparts in arthropods used as accessory jaws.

MCR: Mutual climatic range method.

mesonotum: The middle of three sclerites on the dorsal surface of an insect.

mesotrophic: Aquatic ecosystems with intermediate amounts of nutrients and plant and algal life.

microhabitat: The smallest part of the environment that supports a distinct flora and fauna.

microlines: Microscopic lines impressed on the surface of, for example, insect exoskeletons.

micromilling technology: Methods for grinding small quantities of calcium carbonate from growth rings of of accretionary structures such as otoliths, usually controlled by a computer.

microsculpture: In entomology, microscopic sculpture, including striations, punctures, and meshes, on the surface of sclerites.

mites: The subclass Acari; but often the expression mites and ticks is used in English. Includes arachnids within the size of 0.09 mm (some gall mites) to 30 mm (some ticks). Separated from all other arachnids except spiders by inconspicuous or absent somatic segmentation. Distinguished from spiders by the absence of a pedicel, a structure in spiders that connects the abdomen with the rest of the body.

molluscs: A member of the Phylum Mollusca (also spelled mollusks).

molting: To shed (e.g., a cuticle). Also spelled moulting.

monophyletic: Relating to a single ancestral group of organism.

morphometric eutrophication: Filling-in of a waterbody due to eutrophication and associated macrophyte expansion.

moult stage: One of several growth stages of an ostracod between moulting. There are commonly nine moult stages up to the adult stage in Ostracoda.

multivoltine: Producing several generations per year.

mutual climatic range (MCR) method: A method of paleoclimatic reconstruction in which the climate envelopes of the species in a fossil assemblage are overlapped to determine their intersection, or mutual climatic range of the assemblage.

nektic: Actively swimming organisms (i.e., the nekton) inhabiting open water, which are able to swim independently of water currents.

Neotropical: South American faunal region, extending north to the Tropic of Cancer.

nitrophilous: Preferring habitats rich in nitrogen, often supplied by animal droppings.

noding: In Ostracoda, the presence of intermediate-sized protuberances on the shell.

notogaster: A shield covering the dorsal, lateral and posterior body region in oribatid mites (i.e., the part of the body behind the second pair of legs). Often with ornamentation important for species determination.

obligate benthic fish: Fish that are negatively buoyant and unable to swim off the bottom for more than a few seconds. In temperate lakes, these are therefore restricted to cold waters and therefore useful in paleolimnology.

obligately sexual: Able to reproduce only sexually.

oligotrophic: Aquatic ecosystems poor in nutrients and plant and algal life, and rich in oxygen.

omnivorous: Eating food of both animal and vegetable origin, or any type of food indiscriminately.

ontogenetic: The stages of growth in an organism.

ontogeny: The entire sequence of events involved in the development of an individual organism. Also used to describe the development of ecosystems.

ooids: Small calcium carbonate nodules, chemically or biogenically precipitated.

opisthosoma: The more posterior part of the two body regions in arachnids (cf. prosoma).

osmotic pressure: The pressure necessary to prevent osmosis into a given solution when the solution is separated from the pure solvent by a semipermeable membrane.

Ostracoda: A microscopic (generally 0.5 -1 mm long, although there are exceptions) class of aquatic Crustacea, generally having a calcified, bivalved carapace enclosing a body that is generally unsegmented.

otolith: An ovate, accretionary calcium carbonate concretion from any one of six ear chambers of a fish; useful to paleolimnologists because its daily and annual growth rings carry abundant information about the food, temperature, and water experienced by the fish.

outer lamella: In Ostracoda, the thick, calcified, outer layer that is enclosed in layers of chitin, which protects the body and appendages.

ovisac: A capsule or sac in which egg cells are produced.

oxbow lake: A U-shaped bend that becomes cut off from the main channel of a river to form a typically small curved lake lying on the flood plain of a river and constituting the remnant of a former river meander.

Oxygen Isotope Stage 5: One of a number of climatic stages identified by stable oxygen isotope studies of marine sediments. Stage 5 (130,000 to 74,000 years BP) includes the last interglacial (5e, about 12,000 to 13,000 years BP).

Palaearctic: Region comprising Eurasia north of the Himalayas, the northern part of the Arabian Peninsula, and Africa north of the Tropic of Cancer.

palpi: Second pair of appendages in a mite and all other arachnids situated near the mouth. Can often be modified with a special function (e.g., sensory, anchoring in some parasitic mites, raptorial and/or prey manipulation in some predatory mites).

palsa: Low mound (1-6 m in height) consisting of a cap of peat overlying a dome of frozen mineral strata, found in northern lowlands in the discontinuous permafrost zone.

Pangea: The ancient supercontinent, comprising all the present continents joined together, which began to break up about 200 million years ago.

parthenogenesis: A type of reproduction, occurring in, for example, cladocerans, in which the unfertilized ovum develops directly into a new individual. A means of reproduction whereby offspring are formed from eggs that are unfertilised. Parthenogenetic populations lack males.

partition coefficient: A coefficient that describes the partitioning of trace elements from water into a mineral such as calcite. For carbonates, a partition coefficient for a trace metal is given by the atomic ratio of the trace metal to calcium in the mineral divided by the ratio in the water from which the mineral precipitated.

PCA: Principal components analysis.

pelagic: Open-water area of the lake or sea.

periblast: Outer portion of a bryozoan statoblast valve, having species-specific morphology and ornamentation.

periostracum: Thin proteinous external layer covering most mollusc shells.

pharyngeal complex: In Ceratopogonidae, a unique complex in the head, consisting of the epipharynx, hypopharynx and pharyngeal sclerites.

pharyngeal sclerites: Hardened plates associated with the pharyngeal (throat) region.

phenotype: The physical constitution of an organism as determined by the interaction of its genetic constitution and the environment.

phyllopods: Group of Crustacea that possess paired ventral appendages called phyllopods (from Greek: phyllo = "leaf" and pod = "feet"), which beat in a wavelike motion from front to back and act as propulsion.

phytophagous: Plant-feeding.

phytophilous: Animal that thrives on plants; associated with aquatic plants.

pigmented ornamentation: Surface sculpturing on an organism that contains color patterns due to pigments.

piptoblast: Type of bryozoan statoblast that is neither buoyant nor attached, and only produced by members of the genus *Fredericella.*

pisidiid: A bivalve member of the mollusc Family Pisidiidae.

planktivorous: Animal that eats plankton.

P/L ratio: See planktonic/littoral ratio.

planktonic/littoral (P/L) ratio: The ratio of open-water organisms to near-shore thriving, shallow-water taxa.

polypide: The retractable portion of a zooid (individual) in a colony of Bryozoa (Ectoprocta) which contains the internal organs.

post-abdomen: The posterior part of the body behind the thorax.

Preboreal climatic cooling: Rapid climatic oscillation phase at the early part of the Preboreal in the early Holocene that had a duration of between ~ 150 and 260 years.

Preboreal oscillation: See above.

pre-pupal: Pertaining to the time or events prior to the pupal stage in insect life cycles.

principal components analysis (PCA): A numerical technique for the analysis of a multidimensional data set based on the identification of orthogonal linear combinations of variables that are selected to capture as much of the total variance in the data as possible.

proboscis: In beetles, the protuberance, or snout, on the head of weevils (Curculionidae) or allied families, bearing the mouth parts and antennae.

prodorsum: The dorsal and lateral cuticle of the anterior region in oribatid mites called proterosoma, which are all structures anterior of an easily seen furrow called the sejugal furrow.

profundal: Pertaining to deep-water bottom habitats in lakes (i.e., at depths where respiration exceeds photosynthesis).

proleg: In larval insects, a short unsegmented appendage on the ventral surface of the thorax or abdomen. Distally, often equipped with a series of minute hooks. Usually paired and used for locomotion.

pronotum: The first dorsal sclerite on the thorax of a beetle, expanded to cover the rest of the thorax, also called the dorsal prothoracic shield.

prosoma: The anterior one of the two body regions of an arachnid. In oribatid mites, the border between them is usually ill defined.

pupation: Development of the pupa from a larval insect.

r: Correlation coefficient.

r^2 value: The square of the correlation coefficient, a measure of dependence between two variables. It gives the proportion of the variation in one variable that is accounted for by the other. Also known as the coefficient of determination.

residence time: For a lake, the amount of a substance (e.g., water, solutes) in the lake divided by the flux of the substance into or out of the lake.

reticulation: Surface ornamentation consisting of a net-like patterning.

Ricinulei: Also Ricinuleida by some authors. A tropical arachnid order of 5 -10 mm long, slow-moving and predatory soil animals with about 50 species found in Africa and America.

RMSEP: Root mean squared error of prediction.

root mean squared error of prediction: Standard error of the differences between the observed and inferred values of an environmental variable in an inference model. Commonly calculated for training sets as an assessment of predictive power. It should be based on leave-one-out cross-validation to avoid bias and over-optimistic estimates.

safranin-glyserin solution: A solution for sample coloring and preservation.

Sangamon: Stratigraphic name referring to the last interglacial stage in North America. The term is a name for a paleosoil widespread in the central United States. Correlated to the Eemian in Europe.

saxicolous: Inhabiting or growing among rocks (e.g., saxicolous lichens, mosses and mites).

sclerite: In entomology, a chitinous plate, especially the rigid portions of the exoskeleton bounded by sutures of softer cuticle.

sclerotized: Hardened by scleroprotein, waxes, calcium or other substances apart from chitin.

sculpin: A member of the fish family Cottidae, usually benthic and usually found in cold, northern waters.

SEM: Scanning electron microscopy.

semi-terrestrial habitats: Peats, seeps, waterlogged soils.

septate forms: A term used to describe some ancylid gastropods with an apertural septum.

septum: A partition that partially closes the aperture of some ancylid gastropods.

sessoblast: Type of bryozoan statoblast that is cemented to the surface on which the colony grows, ensuring a suitable substrate for the next generation.

seta: A hair-like appendage developed as an extension of the epidermal layer. In normal form, a slender rigid or bristly sense organ of body and legs, which has a mechanoreceptive function. Can also occur in modified forms with other sense functions.

setae: Plural of seta.

setigerous puncture: A puncture on the surface of insect exoskeleton, containing a seta.

sexual dimorphism: Marked differences in form between males and females of a species.

sieve pore: In Ostracoda, a pore that intersects the valve surface approximately at right angles and which is partially closed off by a sieve-like structure.

slender fishes: Fishes with a torpedo-like body shape adapted to rapid swimming or strong currents, characterized by a body depth less than 30% of the body length, for example a trout.

speciation: The evolutionary development of a biological species, as by geographical isolation of a group of individuals from the main stock.

spiny-rayed fish: Members of the vast group of perch and bass-like fish, with spines in the median fins. The body is often deep relative to its length (sunfish shaped) and the fish is more adapted to maneuvering than to speed. In the fossil record, these indicate habitats with low current or wave energy.

statoblasts: Encapsulated buds produced asexually by freshwater Bryozoa (Ectoprocta), consisting of two chitinous valves enclosing yolk and germinal tissue. Statoblasts are an important means of reproduction, dispersal, and survival of unfavorable conditions.

stenothermic: An organism that is restricted to a narrow range of temperatures (in contrast to eurythermic).

striations: Fine, impressed lines on the surface of the exoskeleton or other structure.

subfossil: A specimen that is found under fossil conditions (e.g., sediments), but is relatively young on the geological time scale (i.e., post-Pleistocene). Usually belongs to an extant taxon.

substratum: The nonliving material on which an animal or plant grows or lives.

taphonomy: The study of all of the geological, chemical, and biological processes that changed a fossil from the time of death of the organism until it becomes a fossil. The conditions of death and decay, as revealed by the form of fossils, may provide information on, for example, oxygen, stratification, depth, and temperature of ancient lakes.

taxonomic analogy: The method of inferring ancient environmental conditions from the presence of groups of organisms whose modern representatives are restricted to certain habitats. The method assumes some predictive generality across all members of a group (see clade), ancient and modern.

taxonomy: The naming and classification of organisms.

tephra: Volcanic ash; fine-grained sediment consisting of glass shards ejected during a volcanic eruption.

ternary diagram: A means of displaying water chemistry data on triangular axes. Separate diagrams are used for the major cations (Ca + Mg and Na + K) and anions (HCO_3 and CO_3, Cl and SO_4). In each case, the proportions of the ions, in equivalents, are plotted.

terrestrialization: Filling in of water body due to sedimentation, see hydroseral succession.

thanatacoenosis: A fossil assemblage that does not represent an assemblage of living organisms, the components of which have been brought together after death: in an aquatic system, this is often by current action.

thaw lake: A lake that forms when a land surface collapses due to thawing of ice-rich permafrost. The thawing develops where water ponds on the surface.

thoracic sclerites: Sclerites of the thorax.

thoracic segments: In insects, the three body segments behind the head. The segments which bear the legs and wings of adult insects.

TMAX: The mean temperature of the warmest month of the year. This abbreviation is used in the mutual climate range method.

TMIN: The mean temperature of the coldest month of the year. This abbreviation is used in the mutual climate range method.

topical treatment: Treatment applied to a surface of the body.

trace element: A minor, non-rock-forming element that may be useful in reconstructing the history of a rock or sediment or organism. The term also refers to elements present in very low concentration in a water or mineral.

training set: A set of species collected from modern sites along with relevant environmental data, often related to one another using a series of quantitative transfer functions. Training sets form the basis for quantitative paleoecological reconstruction when used in conjunction with fossil or subfossil assemblages. Used to generate transfer functions or inference models. See calibration set.

TRANGE: The difference between TMAX and TMIN values, used as an index of climatic continentality (i.e., the greater the TRANGE, the greater the difference between summer and winter temperatures). This abbreviation is used in the mutual climate range method.

transfer function: A mathematical function that describes the relationship between biological species and environmental variables that allows the past values of an environmental variable (e.g., pH, temperature) to be inferred from the composition of a fossil assemblage.

tritonymph: The last of the three nymphal instars (stages, stases by some authors) in an oribatid mite and most other mites. The other nymphal stages are proto- and deuteronymph. In many oribatids, the nymphs are very unlike the adults and the moult from tritonymph can be viewed as a metamorphosis, as in many insects. The nymphs can, in general, be distinguished from adults by a weaker sclerotisation (i.e., a softer cuticula). Separation of nymphal stages is by the number of genital papillae (i.e., one pair in the protonymph, two pairs in the deuteronymph and three pairs in the tritonymph and the adult). These papillae, located beneath the genital valves, are easily seen in specimens cleared in lactic acid.

tubercles: In entomology, a small, round protrusion on the surface of the exoskeleton.

univoltine: Having one generation per year.

valve: In Ostracoda, one of two halves of the carapace, which are hinged dorsally in living specimens and in articulated fossil or subfossil material. Also refers to one of the two halves of the shell of bivalve molluscs and the frustule of diatoms.

ventral sclerites: Sclerites on the ventral portion (underside) of the exoskeleton.

ventral: Relating to the front part of the body; towards the belly.

vibracorer. A device used to collect subsurface samples that usually consists of a length of aluminum irrigation pipe attached to a vibrating head that vibrates the pipe into the soft sediment.

vital effects: For biogenic carbonates, the deviation from the isotopic composition of material that has been precipitated in isotopic equilibrium, as predicted thermodynamically. Such vital effects may arise from the incorporation of metabolic CO_2 into the biogenic carbonate and commonly affect their oxygen ($^{18}O/^{16}O$) and carbon ($^{13}C/^{12}C$) isotope ratios. Whereas oxygen isotope vital effects for many biogenic carbonates are negative (i.e., the carbonates are depleted in the heavier isotope), in ostracod carbonate they are positive. The reason for this is poorly understood.

vital offsets: See vital effects.

WA: Weighted averaging.

WA-PLS: Weighted averaging partial least squares.

weighted averaging (WA): In environmental reconstruction, a numerical technique to derive transfer functions by estimating species optima from a calibration training set (WA regression), and then using these optima to estimate the past value of an environmental variable from a fossil assemblage (WA calibration). The species optima and tolerances are estimated from the weighted averages and weighted standard deviations, respectively. Used in developing organism-environment transfer functions.

weighted averaging partial least squares (WA-PLS) An extension of two-way weighted averaging and calibration where two or more components, that utilize the residual structure in the modern biological data, are used to improve the predictive power of the transfer function.

Younger Dryas: A cold reversal in the late-glacial warming trend during the glacial/Holocene transition. It occurred between ca. 12,700 and 11,500 calibrated yrBP(ca. 11,000-10,000 ^{14}C yr BP). The climatic changes occurred rapidly in decades or less. They are registered most strongly around the North Atlantic region, in ice cores and in the biological and sedimentary records in marine and terrestrial sediments. The term "Younger Dryas" is now more precisely defined as Greenland Stadial 1 (GS-1) in the GRIP ice core. Named after the plant *Dryas octopetala,* which has now an arctic-alpine distribution.

zooid: One of the physically connected, morphological units comprising a colony of Bryozoa (Ectoprocta). Each zooid consists of the polypide and adjacent body wall or cystid.

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