

The use and application of freshwater midges (Chironomidae: Insecta: Diptera) in geographical research

David F. Porinchu^{a,*} and Glen M. MacDonald^{b,c}

^aDepartment of Geography, California State University, Long Beach, Long Beach CA 90840–1101, USA

^bDepartment of Geography, University of California, Los Angeles, Los Angeles CA 90095-1524, USA

^cDepartment of Organismic Biology, Ecology and Evolution, University of California, Los Angeles, Los Angeles CA 90095-1524, USA

Abstract: The potential of applying the analysis of freshwater midges (Chironomidae) for current questions in geographical research is examined. Chironomids are cosmopolitan in distribution and frequently the most abundant insects found in freshwater ecosystems. The capacity of the family to tolerate large gradients of pH, salinity, depth, oxygen concentration, temperature and productivity enables members of the Chironomidae to occupy virtually every available niche present in freshwater environments.

In addition to wide distribution and abundance, Chironomidae are well suited for paleolimnological studies because the larvae possess chitinous head capsules which are well-preserved in lake sediment and relatively easily recovered and identified. As a result, chironomids are increasingly being used to track a number of natural and anthropogenically induced limnological changes resulting from atmospheric contamination, eutrophication and increased lake water salinity. Other areas in which subfossil chironomid analysis has provided valuable insight include climate change, phylogenetics and biogeography and aquatic ecosystem dynamics and development.

Details describing the biology and ecology of the Chironomidae that are directly relevant to their use in paleoenvironmental and biogeographical studies are presented. The methodology describing the recovery and identification of subfossil chironomid remains is reviewed. A generalized overview of the statistical methods that are commonly employed in relating the modern distribution of chironomids to specific aspects of the environment, i.e., the calibration dataset approach, is briefly discussed. Case studies that highlight the various uses and applications of chironomid analysis in areas of paleoenvironmental and biogeographical research relevant to geographers are described. Lastly, the current status of chironomid research in academic geography is discussed and suggestions of potential future research directions are made.

Key words: aquatic ecosystems, biogeography, biomonitoring, chironomids, climate change, environmental change, paleoclimatology, paleolimnology

*Author for correspondence. E-mail: porinchu@geog.ucla.edu

I Introduction

The chironomid family (Insecta: Diptera: Chironomidae), commonly referred to as non-biting midges to distinguish them from the biting midges (Insecta: Diptera: Ceratopogonidae), are frequently the most abundant insect found in freshwater ecosystems (Cranston, 1995). The biotopes occupied by chironomids are extremely varied because of the ability of individual chironomid species to tolerate large gradients of pH, salinity, depth, oxygen concentration, temperature and productivity (Armitage, 1995). Their broad species-specific tolerances to large environmental gradients enable chironomids to be the most widely dispersed, free-living, holometabolous insects in the world (Armitage *et al.*, 1995). Midges are an extremely important component of the aquatic ecosystem; they are a valuable source of food for freshwater fish, insectivorous birds and other aquatic organisms, they play an important role in the cycling of nutrients through the aquatic ecosystem and they serve as a critical nexus between primary producers and secondary consumers.

Chironomids have long been used by limnologists and aquatic ecologists as biotic indicators to classify lakes in terms of trophic status and hypolimnetic oxygen concentration. Biogeographers have studied the geographic distribution of the Chironomidae to reconstruct the biogeographical histories of continents (Brundin, 1966; Cranston and Oliver, 1987; Ashe *et al.*, 1987). Chironomids are now increasingly being used by paleolimnologists to reconstruct past lake conditions and to assess the impact of environmental change and pollution on the structure and function of aquatic communities. Although many techniques are available to reconstruct past environmental conditions, the last two decades have seen a remarkable increase in the use of paleolimnology to address fundamental questions, including: the impact that anthropogenic disturbance has had on aquatic ecosystems; the inherent variability present in the aquatic environment; and the response of aquatic communities to past periods of environmental change. While many biological proxies are used in paleolimnological analyses, widespread use of chironomid analysis is relatively recent and, as a result, the utility of subfossil chironomid analysis is not well known within the geographical community. Areas in which subfossil chironomid analysis has provided valuable insight include climate change, water quality studies and aquatic ecosystem dynamics. These are all areas that biophysical geographers have long been interested in and should continue to play a role in further developing.

There are five key reasons why chironomids are increasingly being used in paleolimnological studies: (1) they are sensitive to key environmental variables such as temperature and dissolved oxygen, i.e., they are stenotopic; (2) they have relatively short life cycles; (3) the adults are mobile, (4) the larvae possess chitinous head capsules that are well-preserved and identifiable in lake sediment and; (5) they are abundant, enabling high-resolution studies and the statistical treatment of results. The mobility of the adults in conjunction with their short life cycles enable chironomids to respond rapidly to environmental change, likely resulting in distributions that are near equilibrium with their surrounding environment (Walker and MacDonald, 1995; Porinchu and Cwynar, 2002). Several papers reviewing the use of chironomids in paleoecology and environmental change research have been published (Frey, 1964; Stahl, 1969; Hofmann, 1971a; Hoffman, 1986, 1988; Walker, 1987, 1995, 2001); however none of the previous review papers place the use of subfossil chironomid analysis explicitly in

the context of geographical research or have been addressed to those working in geography. The primary focus of this paper is to provide an overview of the methodology associated with subfossil chironomid analysis and to present examples of their use and application in geographical research. We will first present the details of chironomid biology and ecology that are relevant for biophysical geographers interested in using subfossil chironomids to reconstruct past environmental and aquatic ecosystem conditions. We will also touch on the classic use of modern chironomid collections for phylogenetic research by biogeographers. We are hoping that this paper will serve to introduce geographers to the exciting avenues of research that are currently being pursued in subfossil chironomid research.

II Biology and ecology

1 Classification and systematics

The Chironomidae consists of ten subfamilies worldwide (Malloch, 1917; Edwards, 1929; see Oliver and Roussel, 1983, for a more up-to-date description of chironomid systematics). Of the ten subfamilies, three have extremely limited geographical ranges and/or size; the *Chilenomyiinae* is limited to a single species, *Chilenomyia paradoxa*, that has only been found in southern Chile (Brundin, 1983a), the *Aphroteniinae* is a pauperite subfamily consisting of four genera and is limited to the southern hemisphere (Brundin, 1983b), and the *Buchonomyiinae* consist of a single genus *Buchonomyia* with three species that have only been found in the western Palaearctic, Iran, Burma and Costa Rica (Walker, 1987). The *Telmatogetoninae* have a global distribution but are predominately associated with marine intertidal environments. Two of the subfamilies, *Podominae* and *Diamesinae*, are predominantly associated with lotic environments (running waters). The *Prodiamesinae* incorporates three anomalous genera that were previously classified as belonging either to the *Orthocladiinae* or to the *Diamesinae* (Sæther, 1976). The three remaining subfamilies, the *Tanypodinae*, the *Orthocladiinae* and the *Chironominae*, are the subfamilies that are most commonly encountered in freshwater ecosystems.

There was a great deal of confusion in early chironomid systematics and the reader is referred to Oliver and Roussel (1983) and Ashe (1983) for reviews detailing the nature and causes of this confusion. The early 1980s saw the publication of a volume detailing the systematic position of the Holarctic larval Chironomidae (Wiederholm, 1983), as well as a volume that catalogued the world's chironomid genera (Ashe, 1983). These two publications have helped, in large part, to standardize the naming conventions associated with the Chironomidae.

2 Geographic range and species richness

Geographically, the Chironomidae are probably the most widely ranging family of aquatic invertebrates, with their geographical distribution exceeded only by collembolans and mites (Armitage *et al.*, 1995). Chironomids are found from the Tropics to the Arctic and Antarctic regions. In terms of freshwater aquatic insects the Chironomidae contain the largest number of aquatic species. Estimates of the global species richness

of the Chironomidae range from 8000 to 20 000 species (Coffman, 1995). Midges comprise approximately 25% of the freshwater macroinvertebrate group (Cure, 1985). In Europe, where the fauna has been widely studied, approximately 1400 species have been described (Fittkau and Reiss, 1978).

3 Life cycle

Chironomids are holometabolous insects, i.e., they experience complete metamorphosis. They progress through four life-history stages (egg, larvae, pupae, adult), with the majority of their life cycle spent in the larval stage. For the vast majority of Chironomidae the immature stages are aquatic, however, the immatures of a few species are found in semi-terrestrial and terrestrial environments.

The typical chironomid life cycle begins with the depositing of an egg mass imbedded within a gelatinous matrix on the water surface (Figure 1). This egg mass generally becomes attached to firmer substrates present at or near the water surface, e.g., macrophytes, leaf litter or shoreline. The rate of egg development is primarily dependent upon temperature, with competition (intra- and interspecific), pH,

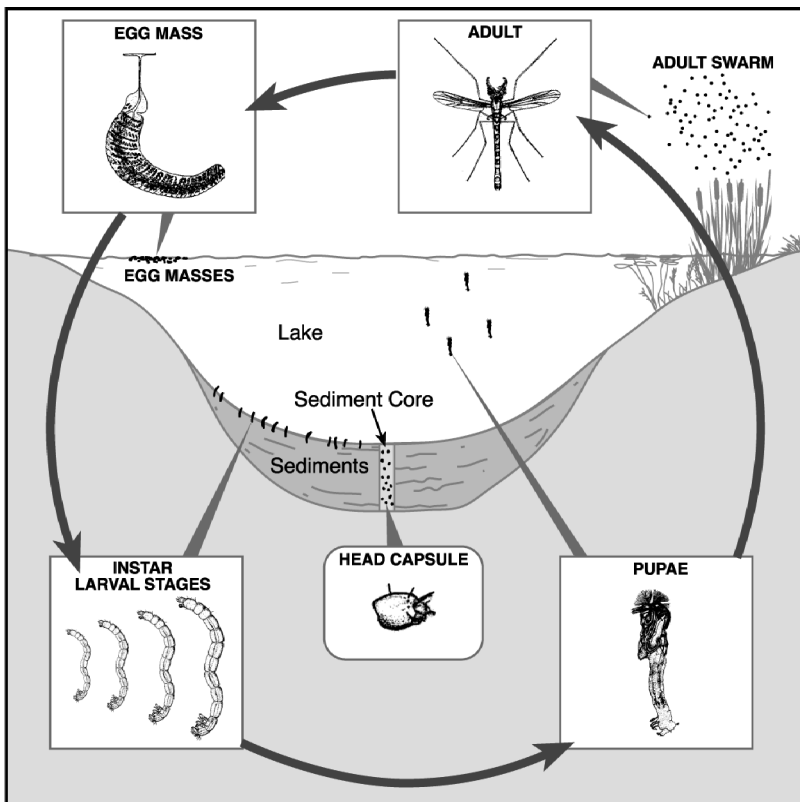


Figure 1 Typical life cycle of aquatic Chironomidae. Not to scale
Source: modified from Brodersen and Anderson (2000).

photoperiod, salinity and oxygen concentration also playing important roles (Pinder, 1995). It takes from a few days to a month for the eggs to hatch and the first of four larval instars to emerge (Figure 1). The larvae undergo ecdysis (periodic shedding of the exoskeleton) three times resulting in the 2nd to 4th larval instars, respectively, with the majority of the larval period spent in the 4th larval instar stage. The larvae, which appear maggot-like in form, become progressively larger as they proceed through the instar stages with 4th instar-larvae ranging from 1 to 20 mm in length. The pupal phase is relatively short-lived. It is during the pupal phase that the larvae metamorphose into the adult form, with the pupae rising to the water surface, shedding its exuviae and the adult emerges. Adult chironomids appear quite similar in appearance to mosquitoes, however, they lack scales on their wings and do not have a lengthy proboscis. Adult males form aerial swarms into which females enter, pair-off and mate (Figure 1). In temperate regions, generally, a life cycle can be completed in one year, whereas in high latitude regions it may take up to several years (Tokeshi, 1986). It has been demonstrated that some of the more common chironomid taxa found in cold, arctic waters take between two and three years to complete one generation (Oliver, 1971; Welch, 1976; Lindegaard and Jónasson, 1979).

4 Habitat

Most paleoenvironmental research on chironomids relies on subfossil chironomid remains (head capsules) recovered from lakes (Figure 1). Lentic environments can be split into three broad zones: profundal, littoral and sublittoral. The profundal is the zone of the lake in which there is insufficient light to support photosynthesis and, as a result, it generally consists of fine sediment and is free of vegetation (Wetzel, 2001). The littoral zone consists of the shallow near-shore and shore area of a lake and is characterized by coarser sediment and rooted aquatic macrophytes. The sublittoral is the transition zone found between the littoral and profundal zones. The differential effects of abiotic factors, such as wind, light, substrate, oxygen concentration and temperature, on the littoral and profundal zones results in the development of the characteristic chironomid communities typifying each zone. Other factors that are important in affecting the distribution of chironomids within the aquatic environment include the quantity and quality of food, intra- and interspecific competition and species-specific physiological adaptations.

A number of studies have identified substrate as an important determinant of chironomid community composition and species distribution (McGarrigle, 1980; Pinder, 1980; Winnell and White, 1985). Chironomid species tend to be associated with particular substrates during their larval stage. Some of the substrates that are utilized include; hard rock such as boulders, coarse gravel, pebbles and stones, soft sediment (sand and silt), submerged wood and macrophytes. Vegetation increases the amount of potentially available habitat and most studies indicate the existence of a positive relationship between the presence of macrophytes and chironomid taxon abundance and diversity (Driver, 1977; Moore, 1980; Verschuren *et al.*, 2000b). Members of both the Orthocladinae and the Chironominae mine in plant tissue (Van der Velde and Hiddink, 1987) and submerged wood (Cranston and Oliver, 1988).

The soft sediment that typifies the profundal of many lakes generally consists of fine

sediment (sand and silt), particulate organic matter and inorganic precipitations. The presence of particulate organic matter can lead to the development of reducing oxygen conditions in the water column a few millimetres above the mud–water interface, limiting the amount of oxygen available for aerobic respiration. Many chironomid taxa construct and live in cases or tubes consisting of mud, silt and/or sand, which extend above this zone of low oxygen concentration and enable them to obtain sufficient amounts of oxygen (Konstantinov, 1971). Some members of the Chironominae, such as *Chironomus* and *Sergentia*, possess haemoglobin and can tolerate the low oxygen conditions often associated with highly eutrophic lakes.

III Morphology

As with other nematoceros Diptera, chironomid larvae are characterized by a well-developed, exposed, nonretractile head capsule and a narrow, segmented body (Cranston, 1995). Typically, the chitinized head capsule of chironomid larvae is the only feature of the larvae that is resistant to decomposition. In general, there are two features present on Orthocladiinae and Chironominae subfossil head capsules that enable generic identification, the ventromental plate and the mentum (Figure 2). The nomenclature for these features follows Wiederholm (1983). The mentum is a toothed, double-walled plate, with the size, shape, number and orientation of the teeth serving as a diagnostic. The ventromental plates are lateral or posterolateral extensions of the mentum and vary from being very poorly expressed in the Orthocladiinae to very well-developed in most Chironominae. Mandibles are another feature that are sometimes found associated with subfossil head capsules. The number and orientation of the mandibular teeth can serve as a valuable diagnostic and can help improve the taxonomic precision of the identifications of Orthocladiinae and Chironominae. In most cases the characteristics of the mentum and the ventromental plates can be used to identify subfossil Orthocladiinae and Chironominae remains to the generic level. However, in certain cases, specific determinations may be possible, e.g., *Zalutschia zalutschicola*.

The two features generally used for identification of Tanypodinae specimens are the number of teeth present on the ligula and the size and shape of the antennae. The ligula is a medially located, toothed plate that forms part of the feeding apparatus in the Tanypodinae. Until recently taxonomic determinations of subfossil Tanypodinae remains have been limited, for the most part, to the sub-Tribe level owing to the limited number of diagnostic features that are preserved on subfossil Tanypodinae head capsules. However, the recent publication of an identification guide to subfossil Tanypodinae based on cephalic setation will enable generic identification of all Holarctic Tanypodinae (Rieradevall and Brooks, 2001).

IV Preservation and deposition of head capsules

One of the assumptions implicit in the paleolimnological approach is that the biological remains preserved in lake sediment are related to the former community from which they are derived. However, it is important to recognize that the chironomid

assemblages preserved in profundal sediment cores are the end result of a number of processes operating within the lake basin (and sometimes outside the basin; Frey, 1988). One of the areas in chironomid ecology and paleoecology that has yet to be adequately addressed is the extent to which the thanothocene (death assemblage) is representative of the extant community. In order to address this question a greater understanding of

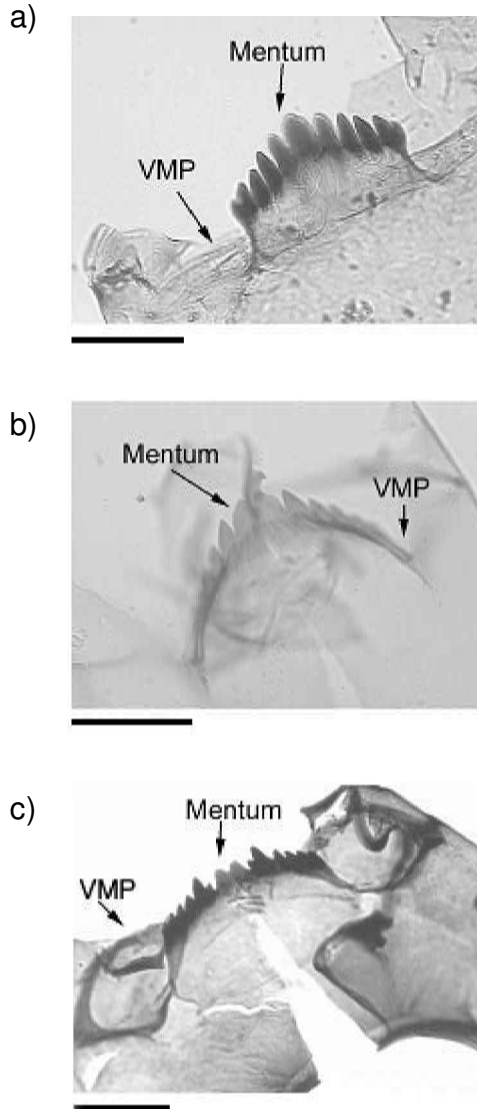


Figure 2 Photomicrographs of subfossil chironomid remains recovered from the Sierra Nevada, USA. VMP, vetromental plate. (a) *Tanytarsina* (Chironominae: Tanytarsini), (b) *Psectrocladius* (Orthocladiinae), (c) *Microtendipes* (Chironominae: Chironomini). Photographs are light micrographs taken on a Nikon transmission light microscope at 20 ×. Scale bar = 100µm

the processes of preservation and deposition of chironomid remains and the degree to which head capsules persist over time is required.

As described previously, the larval stage of the chironomid passes through four larval instars and typically only the remains of the 3rd and 4th instar tend to be well preserved in lake sediment. Iovino (1975) demonstrated, using the chitin-iodine test, that head capsules of the 3rd and 4th instars of *Chironomus attenuatus* contained a greater concentration of chitin than the early instars and, as a result, were likely more resistant to decomposition. This may explain, in part, why early instars are poorly represented in lake sediments. If the head capsules of certain chironomid species or the head capsules from different larval instar stages are subject to differential dissolution, decomposition and/or fragmentation, they will be under-represented in lake sediment. For example, some authors have suggested that the remains of the Tanypodinae tend to be under-represented because of fragmentation (Walker *et al.*, 1984). Also in question is whether the persistence of head capsules is dependent on the source of the head capsules; are head capsules that are produced by ecdysis (periodic shedding of the exoskeleton) more resistant to dissolution than head capsules that result from the 'premature' death of the larvae (Walker, 1987). The role of voltinism (number of generation produced per year) must also be accounted for; bi-voltine and multivoltine species will produce a greater number of head capsules given the same relative abundance. Yet, given these limitations, the few studies that have explicitly addressed the question of the representativeness of the 'death assemblage' have provided evidence that there is good agreement between the biocenose (extant faunal assemblage) and the thanothocene (Iovino, 1975; Walker *et al.*, 1984).

Very little work has been done to assess how well chironomid assemblages recovered from a single profundal core reflect the whole lake community. As Hofmann (1986) points out, it is important to keep in mind that the site of sedimentation of chironomid remains is not necessarily the habitat of the living organism. A number of authors have cautioned that the transport of littoral taxa offshore is heavily dependent on site-specific conditions and that deep-water cores may not adequately represent the faunal heterogeneity present in a given lake (Frey, 1988; Hofmann, 1998). Iovino (1975) determined that in an Indiana lake, chironomid head capsules are found at their highest concentrations where they lived; however, he also determined that deep-water cores from a shallow Florida lake were well mixed, with littoral taxa well represented in the deep-water sediment cores. A number of other studies have also demonstrated that offshore movement and the incorporation of the head capsules of littoral taxa in deep-water sediment occurs (Wiederholm, 1979; Brodin, 1982). Schmah (1993) analysed surface sediment along transects from heterogeneous environments in Bodensee-Untersee to determine whether the subfossil chironomid remains preserved in deep water cores can accurately capture the diversity of the entire, extant chironomid community. Based on her results, Schmah concluded 'profundal sediments in particular represent an integration of chironomids from the entire lake' (Schmah, 1993: 107).

As many chironomid species are tube-building, burrowing organisms found in oxygenated and typically bioturbated environments, it is logical to assume that some vertical mixing of head capsules occurs in lake sediments. Little is known to what degree this occurs and it is likely to differ for different types of lakes and sediments. Given that chironomid burrows may extend a few centimeters into the sediment (Ford, 1962), it would not be unexpected to find vertical mixing of subfossil head capsules of

a similar magnitude occurring. However, as some authors point out, it may be possible to overcome some of the inherent difficulties associated with studying extant aquatic invertebrate communities by relying on the assumption that subfossil assemblages preserved in lake sediment have been somewhat integrated over space and time (Anderson and Battarbee, 1994; Brodersen and Lindegaard, 1997; Verschuren *et al.*, 2000b).

V Methodology

1 Chironomids and the paleolimnological approach

Implicit in any paleolimnological reconstruction of past environments using biotic proxy indicators are the following assumptions: (1) strong relationships exist between the biota and the environmental variable of interest; (2) the proxy leaves identifiable remains in lake sediment; and (3) the lake sediment can be dated by using radiometric techniques (Smol *et al.*, 1995). Quantitative paleolimnological reconstructions involve two steps; (1) establishment of a modern calibration dataset; and (2) applying a transfer function to infer environmental or aquatic ecosystem conditions from subfossil assemblages.

The first step requires the development of a surface sediment calibration set or training set (Moser *et al.*, 1996). The most recently deposited sediment within a lake (the uppermost 0.5–1.0 cm) is referred to as surface sediment and it represents the sediment that has accumulated in the lake basin over the last few years (generally <10 years) (Holmes *et al.*, 1989). A large suite of lakes, usually greater than 50, are sampled for their surface sediment, with the geographic extent of the area sampled dependent upon the environmental variables of interest and the specific region in which the sampling is being carried out (Moser *et al.*, 1996). One of the most important aspects of the sampling design involves ensuring that the gradient of interest is maximized and that the lakes in the calibration set are evenly distributed along this gradient. Sampling a suite of lakes across an ecotonal boundary can provide a sharp gradient in climate and vegetation and may reduce the spatial extent required to capture a large range of variation in the environmental variable of interest (Walker and MacDonald, 1995; Porinchu and Cwynar, 2000).

During surface sediment collection, measurements of physical and limnological variables are made and water samples for water chemistry analyses are collected (Smol *et al.*, 1995; Moser *et al.*, 1996). Variables measured in the field include surface lake water temperature, lake depth, pH, Secchi depth, conductivity and salinity. Water samples collected in the field are later analysed for trace metal concentration, dissolved organic carbon, chlorophyll *a* and nutrients. Other variables that are often also used to characterize the training-set lakes include catchment size, composition of surrounding vegetation, pedology, geology and local and regional climate data (Moser *et al.*, 1996).

Multivariate statistical techniques, including ordination, are used to identify which of the measured environmental variables have a statistically significant relationship to the distribution of the organism in question (Birks, 1995, 1998; Jongman *et al.*, 1995). Detrended correspondence analysis (DCA) of the biological data is used to identify the

length of the environmental gradients sampled. The length of the faunal composition gradients in the calibration dataset identifies whether linear methods, such as redundancy analysis (RDA), or unimodal methods such as canonical correspondence analysis (CCA), are appropriate for constrained ordination (ter Braak and Prentice, 1988; ter Braak and Verdonschot, 1995; Pienitz *et al.*, 1995). The relationship between a specific environmental variable and species distribution is quantified in the form of a transfer function (mathematical formula that express the values of an environmental variable as a function of faunal composition data). A statistical technique commonly used for the development of transfer functions is weighted-average regression and calibration (Hall and Smol, 1992; Pienitz *et al.*, 1995, 2000; Reavie *et al.*, 1995; Moser *et al.*, 1996). The robustness of the transfer functions can be evaluated through the use error estimation techniques, e.g., crossvalidation, jackknifing and/or bootstrapping (Birks *et al.*, 1990; Birks, 1998). The transfer function(s) can then be applied to down-core biological assemblages to reconstruct past environmental conditions.

2 Sample recovery and processing

There are many methods of recovering surface sediment and late Quaternary sediment from the lakes that are typically sampled in subfossil chironomid research. The primary goal of all sediment sampling techniques is to recover a lacustrine sediment profile as complete and undisturbed as possible. Some of the more commonly used surface samplers include; Hongve (Hongve, 1972), HON-Kajak (Renberg, 1991), Glew (Glew, 1991), Nesje (Nesje, 1992) and modified KB corer (Glew, 1989). For even finer temporal resolution, frozen corers (Renberg, 1981) have also been employed. An excellent review of gravity-based lake sediment coring and sediment extrusion methods is presented by Glew *et al.* (2001). The two types of corers commonly used to recover late Quaternary lake sediment are chamber samplers or piston samplers, i.e., Russian sampler (Jowsey, 1966) and modified Livingstone piston sampler (Wright, 1991). For further detail on late Quaternary lake sediment sampling a review by Aaby and Digerfeldt (1986) is recommended.

The volume of sediment required to recover a sufficient number of subfossil head capsules (50–100) varies from lake to lake (see Walker, 1987, for examples); it has been our experience that 1–2 ml of sediment is sufficient. However, this may not always be the case, especially with inorganic lateglacial sediment and also with very flocculent surface sediment (Porinchu *et al.*, 2002). We have sampled lateglacial sediment from the Sierra Nevada, CA, USA, with head capsule concentrations as low as five head capsules per millilitre and as high as 1300 head capsules per millilitre. One of the highest concentrations of reported midge remains in lake sediment comes from Eight Lake, Alaska, where Livingstone *et al.* (1958) recorded up to 8000 head capsules per millilitre. The high variability in head capsule concentrations emphasizes the importance of taking multiple sediment cores at each lake to ensure that a sufficient amount of sediment is available for analysis

The methodology associated with processing and identifying chironomid remains in lacustrine sediment generally follows a standard procedure (Warwick, 1980; Walker and Paterson, 1985; Hofmann, 1986; Walker, 1987, 2001). Although the approaches in individual laboratories vary slightly, the overall principal remains the same – careful

separation of the subfossil chironomid head capsules from the sediment matrix using mild chemical treatment and sieving.

The first step in processing involves disaggregating the sediment sample chemically with a 5–10% KOH solution at 30°C for 30 minutes. The warm KOH serves to break up colloidal matter without damaging the midge remains. In some cases harsher chemical treatments are required if excess calcareous (cold 10% HCL – addition of fresh HCL should continue until no further reaction is observed) or siliceous material (cold 49% HF – sample should be allowed to stand in HF for 24 hours, with occasional, careful stirring) are present. However, it is important to note that the morphological features preserved on the head capsule that are used for identification can easily be damaged by these harsher treatments (particularly HF) and these harsh chemical treatments should be used only when absolutely necessary. A method that has been used to isolate head capsules from marl sediment with minimal damage and good success involves the use of a sonic bath (Barbara Lang, personal communication, 2000). Once the sediment sample has been chemically treated it is passed through a sieve in order to remove finer sediment such as clay and fine organic matter. A number of different approaches have been taken with regards to sieving: Hofmann (1986) suggests splitting the sediment sample into two fractions (>200 μm and 100–200 μm) in order to improve the ease of sorting, whereas others have suggested using sieves of various sizes to prevent the loss of the smallest head capsules (Walker and Paterson, 1985). However, as the 4th instar head capsules are rarely less than 120 μm in size, a sieve with a 95 μm mesh should retain subfossil head capsule remains while eliminating much of the finer material.

The material that is retained by the mesh should be well rinsed and backwashed into a beaker with distilled water. Generally, the sample is sorted immediately following sieving to prevent the development of fungal hyphae which obstructs sorting. However, if the sample is not sorted immediately it can be refrigerated for a short period of time (few days) or preserved with 80% ethanol for longer periods. Sorting of samples should take place in a counting chamber, e.g., petrie dish, watch glass, Stender dish or a Bogorov plankton counting tray (Warwick, 1980; Walker, 1987). The chironomid remains are distinguished, sorted and hand-picked from the sediment concentrate using a stereo dissection microscope at magnifications of between 25 and 50 \times . Once the head capsules are located they are transferred to a glass coverslip using fine forceps, micropipette or platinum wire loop.

There are a number of methods and media used for the permanent mounting of midge remains (Warwick, 1980; Wiederholm, 1983; Walker and Paterson, 1985; Hofmann, 1988), however we will limit our description to what we find to be the most straightforward and least time-consuming. When the chironomid remains are transferred from the sorting chamber to a glass coverslip they should be arranged dorsal side up in a drop of distilled water. Each cover slip can hold approximately 50–75 head capsules without being overcrowded. However, when working in a new geographic area or with novel chironomid fauna, it is recommended that mounts of individual specimens should be created in order to develop an accessible reference collection. Once the drop of water has evaporated the coverslip is mounted: Permount[®] (not available in the USA) and Entellan[®] are mounting media that are commonly used to create permanent slides. Other mounting media such as Canada Balsam and Euparal[®] have also been used to mount slides with good success. The permanently

mounted larval specimens are generally identified and enumerated at 400× using a transmitted light microscope with phase contrast or interference optics.

3 Identification of subfossil remains and count sums

The majority of the identification keys that exist for chironomid larvae deal with identifying living individuals and rely on diagnostic features that are rarely preserved with subfossil specimens (for example, see Epler, 1995, 2001). However, there are a few sources that enable the identification of subfossil larval chironomid taxa. The primary source are the illustrations present in Wiederholm's (1983) diagnoses and key to the chironomid larvae of the Holarctic region. Other valuable sources for identification of northern high latitude and northern temperate subfossil chironomid larvae include Oliver and Roussel (1983), Sæther (1976) and Walker (1988). Country-specific keys exist for the UK (Cranston, 1982) and the Netherlands (Moller-Pillot, 1984a,b). For the identification of rheophilic larval midge taxa, which may be encountered in lacustrine sediment, Simpson and Bode (1980) provide excellent photos and diagnoses. The vast majority of taxonomic literature available to paleolimnologists studying subfossil chironomid remains is limited to the temperate, sub-arctic and arctic portions of the northern hemisphere, with other regions covered by keys that are limited in their geographic scope. No comparable compilation of the taxonomy of subfossil remains from the southern hemisphere (Neotropics, Orient or Australia) is available (Walker, 2001). However, recent work by Verschuren (1997) and Eggermont and Verschuren (2003a, 2003b) has expanded knowledge of the taxonomy of subfossil chironomids in equatorial east Africa and Cranston (2000) has made available an on-line key to the Chironomidae of Australia.

The taxonomic resolution of the identifications of subfossil chironomid remains has been increasing over the last decade. Suggestions of the appropriate taxonomic resolution to use in studies that are interested in identifying community-level changes have been presented by a number of authors (King and Richardson, 2002). It has been suggested that increasing taxonomic resolution will improve the predictive ability of inference models by providing further useful ecological data that we are currently unable to take advantage of (Brooks and Birks, 2001). However, as Brodersen (1998) points out, one must weigh the loss of potentially valuable ecological data through the use of coarse taxonomic grouping, i.e., aggregating taxa, against the extraneous noise that can be introduced by splitting taxa when the identification is not certain.

The development of extensive regional paleolimnological training sets and the inclusion of subfossil chironomid analysis in these studies has led to the need to 'harmonize' taxonomy, i.e., to ensure that the same names are used for the same chironomid taxa. This is an area in subfossil chironomid analysis that is of serious concern and will require greater attention as time progresses. The most recent and complete attempt to 'harmonize' regional taxonomy developed within the MOLAR project. A project manual, entitled *Guidelines for the identification for chironomid larvae in the MOLAR project* provides recommendations for the most appropriate literature to use when identifying chironomid remains (Schnell, 1998). In order to facilitate the comparison of a number of different chironomid calibration datasets that have been developed in Europe in association with the MOLAR and CHILL projects, a follow-up

publication describes a standardized coding system for chironomids (Schnell *et al.*, 1999). Along with these publications, several taxonomy workshops have been held over the last few years to help chironomid researchers working on European datasets to improve and standardize identifications of subfossil chironomid remains. As of yet, no formal workshops have been held to help North American chironomid workers harmonize subfossil chironomid taxonomy. However, Walker (2000) has developed an on-line key, based predominately on chironomid taxa from Canadian temperate and sub-arctic lakes that will hopefully facilitate harmonization of naming conventions amongst North American researchers.

According to Quinlan and Smol (2001) 40–50 chironomid head capsules per sample are sufficient to develop quantitative inference models to reconstruct past environments. They also demonstrate that taxa deletion criteria, such as only including taxa that are present in two or more lakes with a relative abundance of 2%, greatly improved the statistical performance and predictive ability of their chironomid-based inference model. Another recent study addressed what effect low count sums had on quantitative reconstructions based on down-core assemblages (Heiri and Lotter, 2001). Using an existing dataset, the authors demonstrated that the variability of chironomid-inferred temperatures increased with decreasing count sums and that counts based on less than 50 head capsules suffered from a disproportionately large decrease in the stability of the inferred temperatures. While the authors suggest that enumerating 45–50 head capsules per sample is sufficient for applying their temperature inference model, they caution that the optimum number of head capsules to be enumerated in a given sample is heavily dependent on the properties of the inference model used and the diversity of taxa present in the sample. Another important point is that some inference models, such as those based on weighted-averaging partial least squares (WA-PLS) or models using tolerance down-weighting, are more sensitive to the presence of rare taxa and therefore larger count sums should be used in conjunction with these models (Walker, 2001).

VI Applications

1 Lake classification

The Chironomidae tend to dominate the profundal of deep, stratified lakes and are responsive to changes in hypolimnetic oxygen concentrations. As a result, they have been used extensively to classify lakes. The earliest chironomid-based lake classification system, relying primarily on the composition of the profundal community, was developed in the early twentieth century (Thienemann, 1918, 1921). Thienemann's (1921) typology was later modified by others, who suggested that factors such as lake-water temperature, trophic status and food quality and quantity were important determinants of chironomid community composition (Brundin, 1949, 1958; Sæther, 1979; Wiederholm, 1980). Brundin (1949, 1958) extended Thienemann's (1921) classification scheme by identifying five broad profundal chironomid associations. This benthic lake typology consisted of (1) ultra-oligotrophic *Heterotrissocladius subpilosus* lakes, (2) oligotrophic *Tanytarsus lugens* lakes, (3) mesotrophic *Stictochironomus rosenschöldi* – *Sergentia coracina* lakes, (4) eutrophic *Chironomus anthracinus* and *C. plumosus* lakes, and (5) dystrophic *C. tenuistylus* lakes (Table 1). Sæther (1975, 1979) further expanded Brundin's

Table 1 Lake classification scheme based on profundal chironomid fauna

Lake type	North America	Europe	Trophic status
I	<i>Heterotrissociadius oliveri</i> Sæther	<i>Heterotrissociadius oliveri</i> Brundin	Ultraoligotrophic
II	<i>Tanytarsus</i> sp. with <i>Monodiamesa tuberculata</i> Sæther and <i>Heterotrissociadius changi</i> Sæther	<i>Tanytarsus lugens</i> Kieffer with <i>Heterotrissociadius grimshawi</i> (Edwards) and <i>Heterotrissociadius scutellatus</i> (Goetghebuer)	Oligotrophic
II/III	<i>Chironomus atritibia</i> Malloch and <i>Sergentia coracina</i>	<i>Stictochironomus rosenschoeldi</i> (Zetterstedt) and <i>Sergentia coracina</i> (Zetterstedt)	Mesotrophic
IIIa b	<i>Chironomus decorus</i> Johannsen <i>Chironomus plumosus</i>	<i>Chironomus anthracinus</i> (Zetterstedt) <i>Chironomus plumosus</i> (Brundin) L.	Moderately eutrophic Strongly eutrophic
IV	<i>Chironomus</i> sp. with <i>Zalutschia zalutschicola</i>	<i>Chironomus tenuistylus</i> with <i>Zalutschia zalutschicola</i>	Dystrophic

Source: from Brundin, 1958; Sæther, 1975; Wiederholm, 1984; Lindegaard, 1995.

categories by identifying 15 characteristic profundal chironomid communities, correlated with measures of trophic status (concentrations of total phosphorous/mean lake depth or total chlorophyll *a*/mean lake depth), and extended the original European-based typology to North America (Table 1). The original typology and the later refinements relied almost exclusively on the composition of the profundal chironomid community, littoral chironomid taxa were not considered. As a result, these classification schemes are only appropriate for deep, stratified lakes (Hofmann, 1986).

It is important to note that generalizations based on changes in chironomid faunal composition do not take into account the site-specific conditions that may have had a significant influence on community composition (Brinkhurst, 1974). According to Warwick (1975) the distribution of chironomids in oligotrophic and mesotrophic lakes is a function of food availability not the annual minimum hypolimnetic oxygen concentration. Walker (1987) has questioned the interpretation of a number of studies that used changes in the temporal distribution of chironomid taxa to trace natural ontogenetic processes. Brinkhurst (1974), who provides an excellent review of the development of lake typology and classification systems, states that the 'establishment of discrete groups of lakes has always proved difficult' and goes further to cite E. Naumann (as translated by W. Kretschmar in Brinkhurst (1974: 8) who states

lake type is an abstract conception, representing a somewhat ideal classification of lakes with similar metabolic processes or biological production. (Brinkhurst, 1974: 8)

It is important to keep these points in mind when using the remains of subfossil chironomids preserved in lake sediment to either classify lakes or trace 'natural' ontogenetic processes.

2 Climate change

a Temperature reconstructions: There are a number of reasons that chironomids are sensitive to lake water and/or ambient air temperature. Studies have documented that the rate of egg and larval development are influenced by water temperature (Pradhan, 1945; Konstantinov, 1958; Oliver, 1971; MacKey, 1977; Anderson and Cummins, 1979). Water temperature can impact larval growth rates directly, by affecting bioenergetic relationships via altered larval feeding, assimilation and respiration rates, and indirectly, by affecting the quantity and quality of the food available (Tokeshi, 1995). Several studies have documented a high positive correlation between larval growth rates and water temperature (MacKey, 1979; Johannsson, 1980). It has also been demonstrated that atypically high water temperatures can result in reduced larval growth (Konstantinov, 1958). Water temperature has also been implicated in postponing both the pupation and emergence of adults across a broad range of aquatic insects (Danks and Oliver, 1972; Sweeney and Vannote, 1981). The timing of eclosion (emergence from pupal case) of most chironomids that have been studied tends to be synchronized by photoperiod, but also, at least in part, by water temperature (Kureck, 1979; Titmus, 1979; Butler, 1980). As Brodersen and Lindegaard (2000) demonstrate, most of the Chironomidae that they studied in a shallow Danish lake required water temperatures of 18°C to initiate emergence. Temperature-dependent emergence is critical for taxa that are multivoltine; if sufficiently high temperatures are not reached early in the season a

second emergence may not occur, which may affect the relative abundance of these taxa in the sediment. Chironomids are also indirectly affected by water and air temperature. With increasing temperature (water and/or air) there are changes in trophic relationships. Typically, an increase in water temperature results in an increase in lake productivity, which in turn affects food availability (quantity and quality) (Cummins and Klug, 1979). Increased lake productivity can also lead to a decrease in hypolimnetic oxygen concentrations. The interaction of these factors will affect the species composition of the chironomid community within a given lake.

Subfossil chironomid remains have long been used as a qualitative source of information to describe past climate conditions. Lateglacial sediments from both the littoral and profundal zone of northern European lakes contain cold stenothermic taxa such as *Heterotrissocladius subpilosus*, *H. grimshawi*, *Sergentia coracina* and *Tanytarsus lugens* (Brundin, 1949). Increased water temperatures associated with post-glacial climatic amelioration appear to have restricted these taxa to the profundal of stratified lakes and eliminated them completely from unstratified lakes (Hofmann, 1983). Higher water temperatures enabled the colonization of the littoral zone by diverse, warm-adapted chironomid assemblages (Frey, 1988).

In recent years there has been an explosion in the number of training sets that have been used to develop transfer functions relating the modern distribution of chironomids to surface and/or air temperature. These transfer functions allow quantitative reconstructions of past temperatures. There has been some geographical discrimination evident in the location of these training sets; the majority are located in the temperate and sub-arctic regions of the northern hemisphere. The first study that quantified the relationship between chironomids and summer surface water temperature in the form of a transfer function was based on lakes in eastern Canada (Walker *et al.*, 1991a) (Figure 3(a), 3(b) and 3(c)). A number of studies were undertaken following the publication of Walker's original training set and now chironomid-based inference models for air and/or water temperature exist for the Swiss Alps (Lotter *et al.*, 1997), Northern Finland (Olander *et al.*, 1999), Western Norway (Brooks and Birks, 2000a), Norway and Svalbard (Brooks and Birks, 2001), Northern Sweden (Larocque *et al.*, 2001) eastern Canada (Walker *et al.*, 1997; Lotter *et al.*, 1999) and the Sierra Nevada, CA, USA (Porinchu *et al.*, 2002) (Table 2).

A number of papers using chironomids to reconstruct summer surface water temperature variability in eastern Canada during the lateglacial period were published in the early to mid-1990s (Walker *et al.*, 1991b; Wilson *et al.*, 1993; Levesque *et al.*, 1993, 1994, 1997; Cwynar and Levesque, 1995). Work by Levesque and colleagues identified the presence of a previously unrecognized centennial-scale climate oscillation that occurred just prior to the Younger Dryas (Figure 4(a) and 4(b)). The Killarney Oscillation (KO), as they termed it, was characterized by a 2–3°C depression in surface lake water temperatures and was correlative with the Gerzensee Oscillation (Levesque *et al.*, 1993). Further work by Levesque identified the existence of strong southeast to northwest thermal gradients in this region during the lateglacial period; ~4.6°C/100 km (pre-KO, pre-YD, and post-YD) and ~16.0°C/100 km (mid-KO) (Figure 4(a) and 4(b)). Levesque *et al.* (1997) suggest that the existence of these large temperature gradients was partly a result of the proximity of their study sites to the southern margin of the Laurentide ice sheet.

Recent work in western Europe using lateglacial and Holocene chironomid

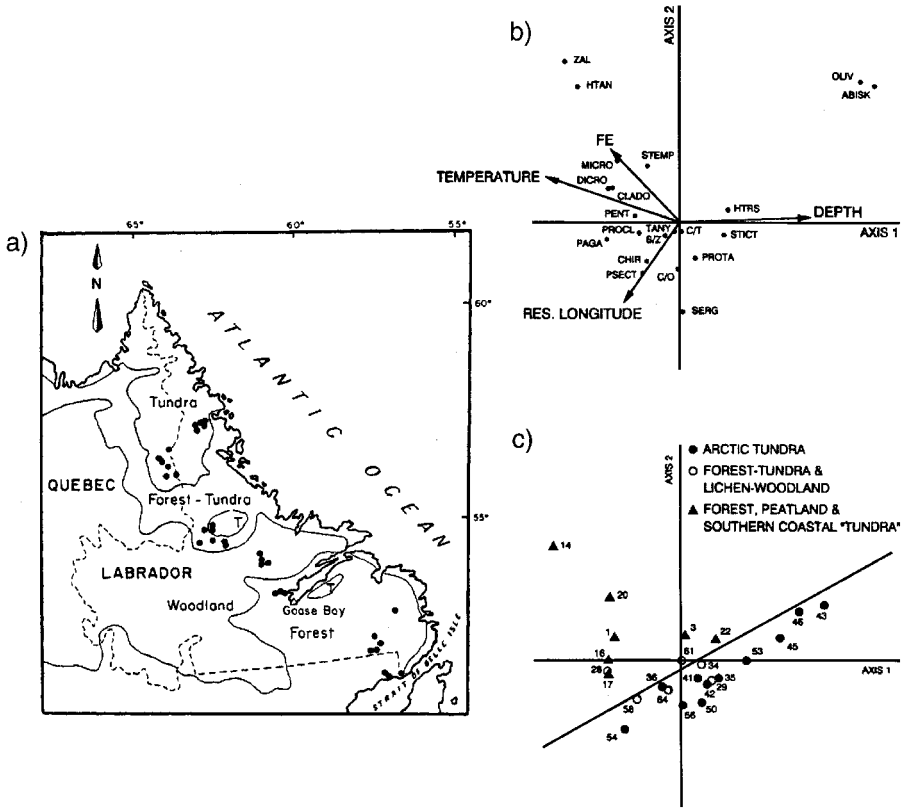


Figure 3 (a) Location of study sites incorporated in Walker *et al.* (1991a), (b) species–environment and (c) site–environment bi-plots, illustrating the relationship between study sites, species composition and environmental variables. Ordination diagrams and analyses based on canonical correspondence analysis (CCA), incorporating 21 chironomid taxa in 24 lakes. Surface water temperature gradient spanned by dataset was 10.40°C. Notice that CCA axis 1, which captures 22% of the variance in the distribution of chironomids, is strongly correlated to surface water temperature (correlation coefficient –0.79)
 Source: modified after Walker *et al.* (1991a).

assemblages to reconstruct paleotemperature regimes has further refined our understanding of the magnitude and timing of temperature change in this region (Brooks, 1997; Brooks and Birks, 2000a,b, 2001; Rosén *et al.*, 2001). Brooks and Birks (2001) have recently published quantitative air and water temperature inference models based on a calibration dataset incorporating 111 lakes from Svalbard to southern Norway. They have applied the air temperature model to the chironomid assemblages in a sedimentary sequence recovered from Whitrig Bog, Scotland, to develop a high-resolution temperature reconstruction spanning the Holocene and lateglacial period (Brooks and Birks, 2000b, 2001). Immediately following deglaciation, air temperatures

Table 2 Comparison of the existing chironomid-based inference models for surface lake-water temperature and mean July air temperature

Study	Study area	No. of lakes	No. of taxa	Model	r^2_{jack}	RMSEP (°C)	Range of gradient (°C)	RMSEP as % of gradient	Max bias (°C)
<i>Water temperature</i>									
Walker <i>et al.</i> (1997)	Eastern Canada	39	34	WA-PLS (2 component)	0.88	2.26	21	10.76	2.40
Olander <i>et al.</i> (1999)	Northern Finland	53	38	MAT (6 matches)	0.43	1.48	9.3	15.91	1.90
Brooks and Birks (2000a)	Western Norway	44	81	WA-PLS (1 component)	0.30	2.22	12.4	17.90	5.29
Brooks and Birks (2001)	Svalbard – Norway	111	119	WA-PLS (3 component)	0.86	2.13	22.7	9.83	2.84
Porinchu <i>et al.</i> (2002)	Sierra Nevada, USA	44	44	WA (classical)	0.73	1.2	8.5	14.1	0.90
<i>Air temperature</i>									
Lotter <i>et al.</i> (1997) ^a	Swiss Alps	50	58	WA-PLS (2 component)	0.849	1.370	6.4	21.4	1.668
Lotter <i>et al.</i> (1999)	Swiss Alps	51	40	WA-PLS (2 component)	0.844	1.470	13.4	11.0	2.743
Lotter <i>et al.</i> (1999)	Eastern Canada	39	51	WA-PLS (2 component)	0.852	1.544	14.0	11.0	1.704
Lotter <i>et al.</i> (1999)	S. Alps & E. Canada	90	57	WA-PLS (2 component)	0.813	1.741	16.0	10.9	3.753
Olander <i>et al.</i> (1999)	Northern Finland	53	38	WA-PLS (2 component)	0.497	0.866	6.4	13.5	2.925
Brooks and Birks (2000a)	Western Norway	44	81	WA-PLS (1 component)	0.69	1.13	8.3	13.6	2.65
Brooks and Birks (2001)	Svalbard – Norway	109	119	WA-PLS (3 component)	0.94	0.90	12.1	7.4	3.09
Larocque <i>et al.</i> (2001)	Northern Sweden	100	48	WA-PLS (2 component)	0.649	1.13	7.4	15.7	2.101

Notes: The number of lakes and the number of taxa included in each study, the jack-knifed values of the coefficient of determination (r^2_{jack}) and the root mean square error of prediction (RMSEP) from each study, as well as the range of summer surface water temperature and air temperature encompassed by the studies (range of gradient), the RMSEP expressed as a percentage of the gradient length and the maximum bias (maximum bias) of each of the models are indicated. The type of model used in each study is also indicated: WA-PLS (weighted averaging partial least-squares), MAT (modern analogue technique), WA (weighted averaging).

^aVariable reconstructed in Lotter *et al.* (1997) is mean summer air temperature.

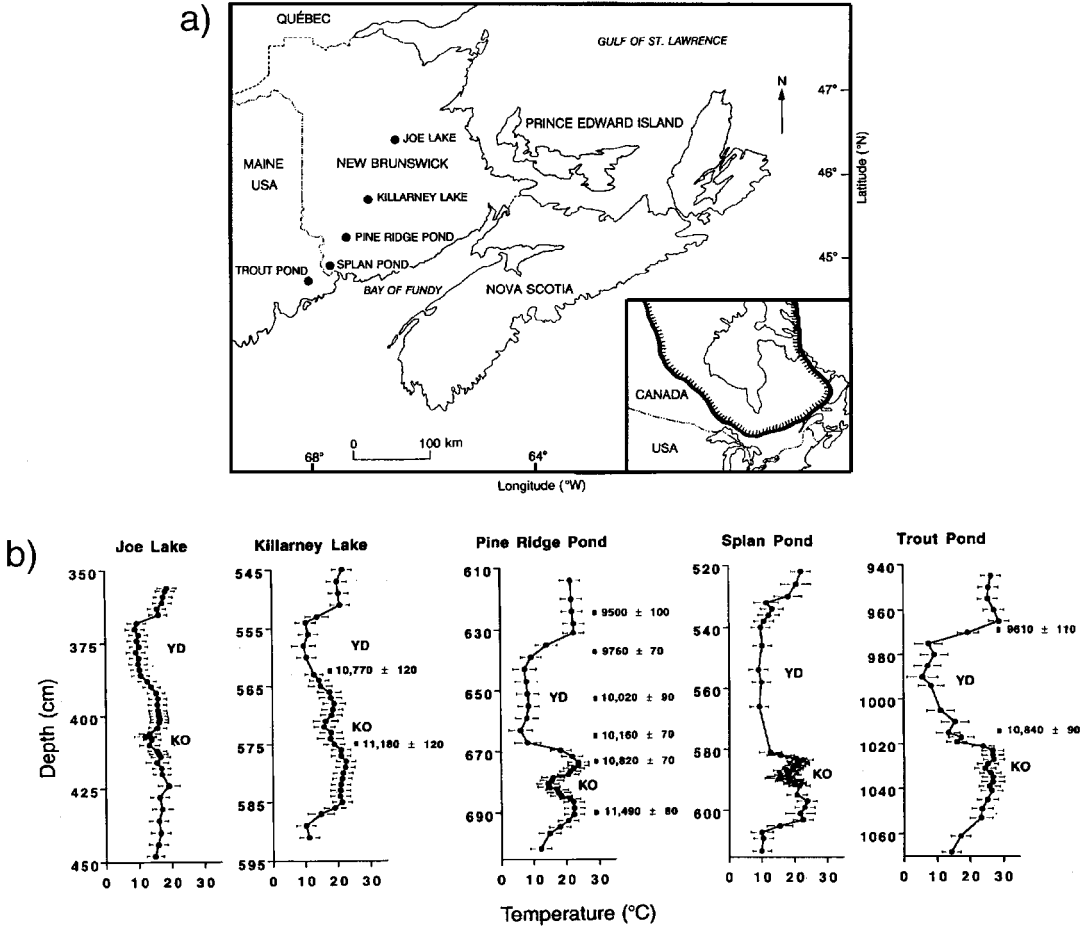


Figure 4 (a) Location of study sites discussed in Levesque *et al.* (1997), (b) chironomid-based temperature reconstructions illustrating the effects of the Killarney Oscillation and the Younger Dryas on surface water temperature at each of the study sites. Reconstructed summer surface water temperature and sample specific error estimates are indicated

Source: modified after Levesque *et al.* (1997).

were approximately 6°C, however warming was rapid and temperatures soon rose to approximately 10.5–12°C (Figure 5). Post-glacial warming was interrupted by four dramatic cold oscillations of varying lengths when temperatures plunged between 2 and 5°C. Although poor chronological control on the core prevents a direct comparison with cold events known from other sites in the circum-North Atlantic region, the authors suggest that the events evident at Whitrig Bog may be correlative with the Aegelsee Oscillation, the Gerzensee Oscillation and the Younger Dryas. To date only two quantitative chironomid-based reconstructions of lateglacial and/or Holocene temperature has been made outside the circum-North Atlantic region or central Europe (Palmer *et al.*, 2002; Porinchu *et al.*, 2003).

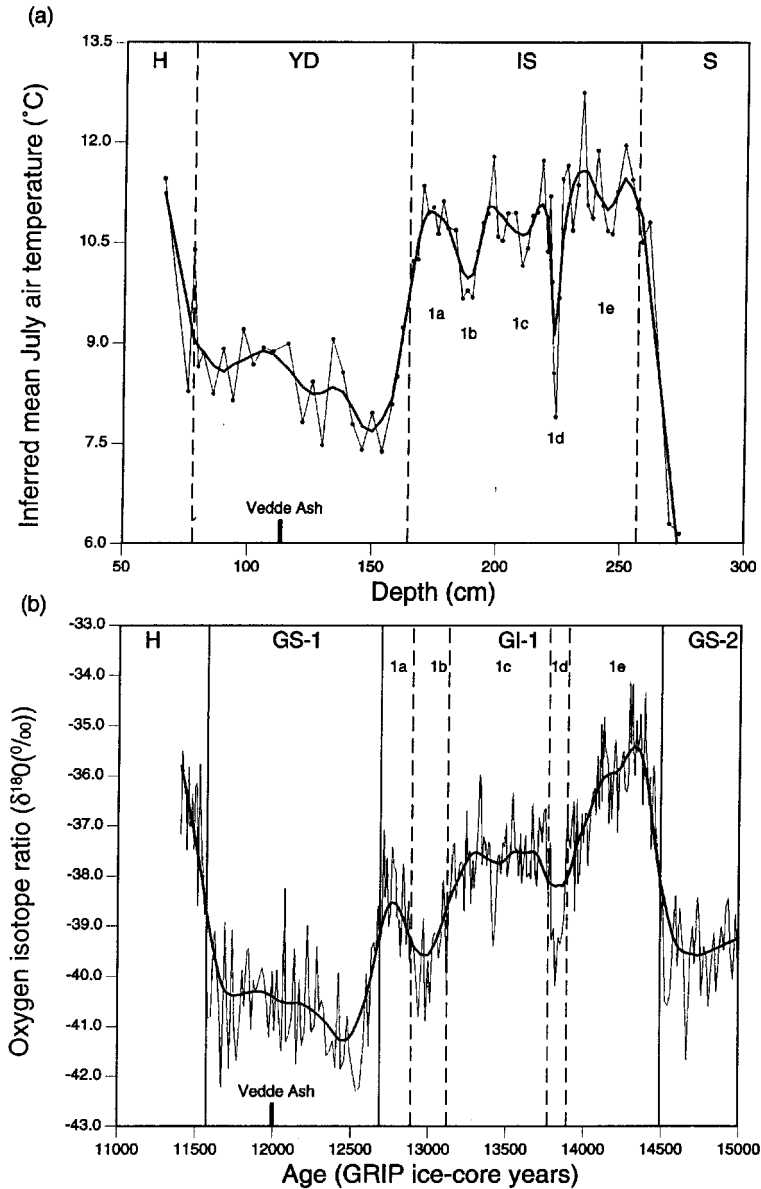


Figure 5 (a) Chironomid-based reconstruction of mean July air temperature at Whitrig Bog, Scotland, compared with (b) the GRIP oxygen isotope record. The presence of the Vedde Ash is indicated in both plots. A tentative correlation between the GRIP isotope stratigraphy and the chironomid-based temperature reconstruction for Whitrig Bog are illustrated. See Brooks and Birks (2000b) for details regarding the development of the GRIP timescale chronology. Both curves have had a LOWESS smoother applied (span = 0.20; $\lambda = 2$)
Source: modified after Brooks and Birks (2001).

The other biological proxy that is often used to reconstruct lake water or ambient air temperature in paleolimnological studies are diatoms (Pienitz *et al.*, 1995; Lotter *et al.*, 1997). However, in all multiproxy paleolimnological studies that have incorporated diatoms and chironomids, chironomid-based inference models for lake water and/or air temperature outperform the diatom-based inference models. We suggest that the reason for this relates to the strong and direct influence that lake water chemistry, specifically nutrient availability and pH, has on the composition of the diatom flora. While temperature does indirectly affect diatoms by influencing lake productivity, in all calibration datasets it appears that diatoms are primarily responding to some aspect of changing lake water chemistry or habitat availability. As Battarbee (2000) has pointed out there still exists some doubt about whether diatom-based inference models for temperature can be used as an independent proxy to reconstruct past temperature regimes, especially for the lateglacial period. For these reasons, it appears that subfossil chironomid analysis provide one of the best paleolimnological methods available for reconstructing past temperature regimes.

b Hydrology: Changes in effective moisture and its resultant effect on lake levels and lake water residence times can greatly affect the faunal composition of the chironomid community present within a given lake. Changes in lake level can change the proportion and volume of the littoral and profundal zones, alter sediment distribution and deposition, reduce or eliminate the proportion of macrophytes present and affect the ionic composition, salinity, temperature and/or oxygen concentration of the system (Battarbee, 2000). The strong impact of lake depth on chironomid community composition has long been known (Thienemann, 1922; Brundin, 1949, 1958; Sæther, 1975). Taxa such as *Sergentia coracina*, *Tanytarsus lugens*, *Heterotrissocladius subpilosus* and *H. grimshawi* have been identified as common constituents of deep lakes, while taxa such as *Dicrotendipes*, *Microtendipes* and *Polypedilum* are associated with shallow water environments (Brundin, 1958; Sæther, 1975; Walker and Mathewes, 1989; Walker and MacDonald, 1995).

A number of studies, using the training-set approach, have indicated that depth has a statistically significant relationship to chironomid faunal composition (Walker *et al.*, 1991a; Quinlan *et al.*, 1998; Olander *et al.*, 1999; Larocque *et al.*, 2001; Porinchu *et al.*, 2002). However, as of yet only one inference model for reconstructing lake depth has been developed using chironomids (Korhola *et al.*, 2000). A two-component PLS model based on a 53 lake calibration dataset from northern Fennoscandia has an $r^2_{\text{jack}} = 0.70$, jack-knifed root mean square error of prediction (RMSEP) = 0.49 m (ln units) and a maximum bias of 0.39 m (ln units). This transfer function has yet to be applied to the subfossil chironomid assemblages preserved in lakes in this region to infer past changes in lake hydrology.

Some authors caution that faunal assemblages preserved in deep-water cores may often be insensitive to changes in lake level (Frey, 1988; Hofmann, 1998), while others suggest that reconstructing variables, such as depth, that are intrinsically related to lake morphometry may result in estimates of past hydrologic conditions that are bathymetrically nonsensical (Birks, 1998). It has also been noted that the depth distribution of certain taxa, including those that are both eurybathic and cold stenothermic, may naturally change during the normal course of lake development (Hofmann, 1988). For example Hofmann (1971b) has demonstrated, based on the analysis of sediment cores

from varying depths, that *Micropsectra coracina* migrated downward from the littoral zone into the profundal zone during the early post-glacial period. The change in the depth distribution of this typically profundal taxon during the immediate post-glacial period indicates the inherent difficulty in decoupling the relationship between water temperature and lake depth.

c Salinity: There are a number of physiological adaptations that freshwater aquatic organisms, including chironomids, have developed that enable them to tolerate moderate salinities, e.g., osmotic regulation. Most chironomids are limited to freshwater environments, however a limited number of taxa are associated with saline environments. Although a number of studies have described the distribution of midge flies in relation to salinity, Walker *et al.* (1995) point out that one of the principal difficulties that still remains in using midges as a proxy for paleosalinity lies in our insufficient knowledge of faunal-specific responses to salinity.

Until recently the use of subfossil chironomid remains as quantitative indicators of past changes in salinity has been limited. Paterson and Walker (1974) studied changes in the distribution of midge fauna in a saline Australian lake and identified notable variations in the abundance of *Chironomus duplex*, *Procladius paludicola* and *Tanytarsus barbatarsis*. They attributed these fluctuations to changes in the ionic composition of the lake resulting from variations in the lake's long-term evaporation:precipitation balance. A study of the benthic communities present in the shallow saline lakes of western Victoria, Australia indicated that taxa such as *Procladius* and *Chironomus duplex* typified low salinity lakes (1–13 g l⁻¹) and that *Tanytarsus barbatarsis* dominated higher salinity lakes (13–200 g l⁻¹) (Timms, 1983). The use of chironomids in reconstructing past changes in salinity has also been carried out in east Africa with good success (Verschuren, 1994; Verschuren *et al.*, 2000a,b).

Recent studies, the majority of which have been carried out in western Canada, have increased our understanding of the relationships that exist between chironomid taxa and salinity by providing new ecological data relating the contemporaneous distribution of chironomid fauna to variations in the ionic composition of regional lakes (Walker *et al.*, 1995). Heinrichs and his colleagues developed a two-component PLS inference model based on a 87-lake dataset that had an $r^2_{\text{jack}} = 0.76$, jack-knifed RMSEP = 0.44 g l⁻¹ and a maximum bias of 0.60 g l⁻¹ (Heinrichs *et al.*, 2001). This transfer function, which is based in part on an earlier calibration set developed by Walker *et al.* (1995), has been used to reconstruct Holocene salinity fluctuations in sub-saline and saline lakes located in the central interior of British Columbia (Heinrichs *et al.*, 1999, 2001).

The results from Kipoola Lake, currently a saline lake (9 g l⁻¹), indicate that the salinity during the immediate post-glacial period was much lower than at present, with the chironomid-inferred salinity less than 0.03 g l⁻¹ (Heinrichs *et al.*, 1999) (Figure 6). The chironomid community during this period was dominated by freshwater chironomid taxa, such as *Sergentia* and *Heterotrissocladius*. The chironomid-inferred salinities ranged between 1.0 and 3.5 g l⁻¹ for most of the remainder of the Holocene. Of particular interest in this record is the dramatic increase in the chironomid-inferred salinity that occurred immediately following the deposition of the Mount Mazama ash at 6730 ± 40 yr BP. The salinity of Kipoola lake waters rose approximately 450%, from 1.6 to 7.3 g l⁻¹, before decreasing to pre-Mount Mazama levels.

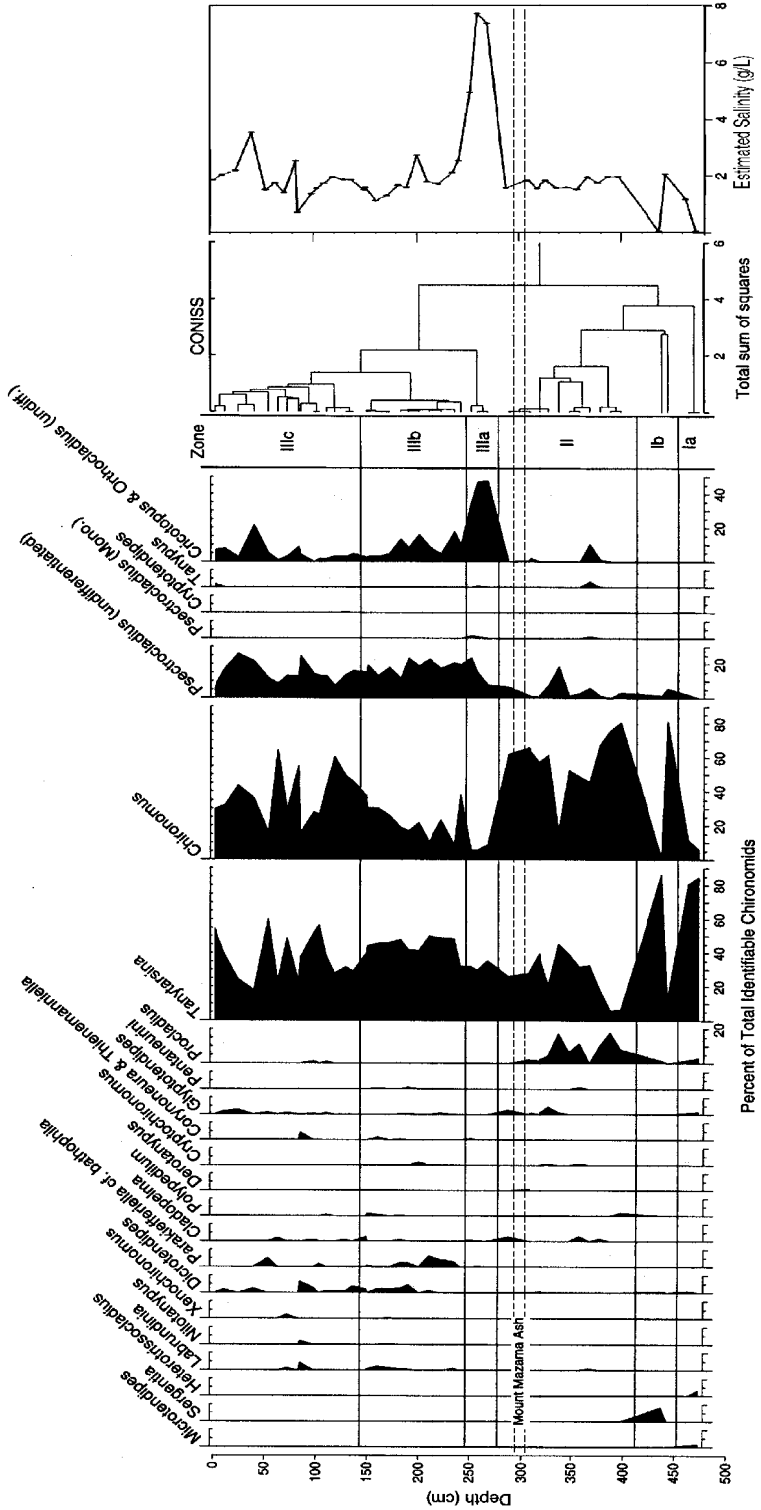


Figure 6 Chironomid percentage diagram from Kipoola Lake, British Columbia, Canada. Chironomids arranged in order of their salinity optima from left to right, with the exception of *Nilotanyppus*, *Psectrocladius* (subgenus *Psectrocladius*) and *Xenochironomus* for which no optima are available
 Source: modified after Heimrichs *et al.* (1999).

3 Treeline studies

The effect of climate on aquatic ecosystems and on the distribution of lentic organisms is especially pronounced at ecotonal boundaries such as treeline (MacDonald *et al.*, 1993). Latitudinal treeline and alpine timberline represent gradients in abiotic factors such as temperature and precipitation, and biotic factors such as vegetation cover and structure, ecosystem productivity and nutrient cycling and availability. Reconstructing past changes in latitudinal treeline and alpine timberline has long been of interest to paleoecologists and paleoclimatologists.

Recent work has illustrated that significant changes in chironomid assemblages occur across latitudinal treeline in north-central Canada (Walker and MacDonald, 1995), eastern Canada (Walker *et al.*, 1991a), Fennoscandia (Olander *et al.*, 1999; Larocque *et al.*, 2001) and northeastern Siberia (Porinchi and Cwynar, 2000) and across altitudinal timberline in the Canadian Cordillera (Walker and Mathewes, 1989), the Swiss Alps (Lotter *et al.*, 1997) and in California's Sierra Nevada (Porinchi *et al.*, 2002). Porinchi and Cwynar (2000) argue that the position of circumpolar treeline, which is approximated by the position of the mean July 10°C to 12.5°C isotherm (MacDonald, 2002), indirectly affects chironomid fauna by differentiating the taxa found in cold tundra lakes (<10°C) from the warmer, forested lakes (>10°C) found south of treeline. It is clear from these studies that treeline serves as an important biogeographical and ecological boundary with regards to the distribution of chironomids.

Porinchi and Cwynar (2000) characterized the chironomid communities present in a suite of lakes spanning treeline in northeast Siberia and quantified the relationship of the faunal assemblages to their contemporaneous environment (Figure 7(a) and 7(b)). Ordination analyses of the species abundance data indicated that the chironomids were responding to a climate–vegetation gradient, with treeline serving to demarcate chironomid taxa associated with tundra lakes from those associated with lakes in forested catchments. Taxa such as *Paracladius*, *Stictochironomus*, *Abiskomyia* and *Parakiefferiella* cf. *nigra* are found more commonly in oligotrophic, tundra lakes, while taxa such as *Microtendipes*, *Glyptotendipes*, *Psectrocladius* and *Zalutschia zalutschicola* are restricted to the more productive, forest lakes. Knowledge of the modern distribution of chironomids in the region was used to interpret the late Quaternary chironomid assemblages recovered from a small tundra lake and to develop qualitative reconstruction of past climate and treeline position for this region (Porinchi and Cwynar, 2002). Relating the chironomid-inferred evidence for lateglacial and Holocene climate change to the pollen and stomate evidence analysed from the same core provided some interesting insights (Figure 7(a) and 7(c)). The pollen evidence (Pisaric *et al.*, 2001) indicates the presence of a strong Younger Dryas signal and the chironomid assemblages present during this period suggested that climatic deterioration had occurred between 10 000 and 11 000¹⁴C yr BP (Porinchi and Cwynar, 2002). The results of the subfossil chironomid analysis were valuable because they provided investigators with an independent means of assessing the timing and rate of past climate change in this region.

4 Geomorphology: fluvial applications

The importance of substrate on chironomid distribution and community composition

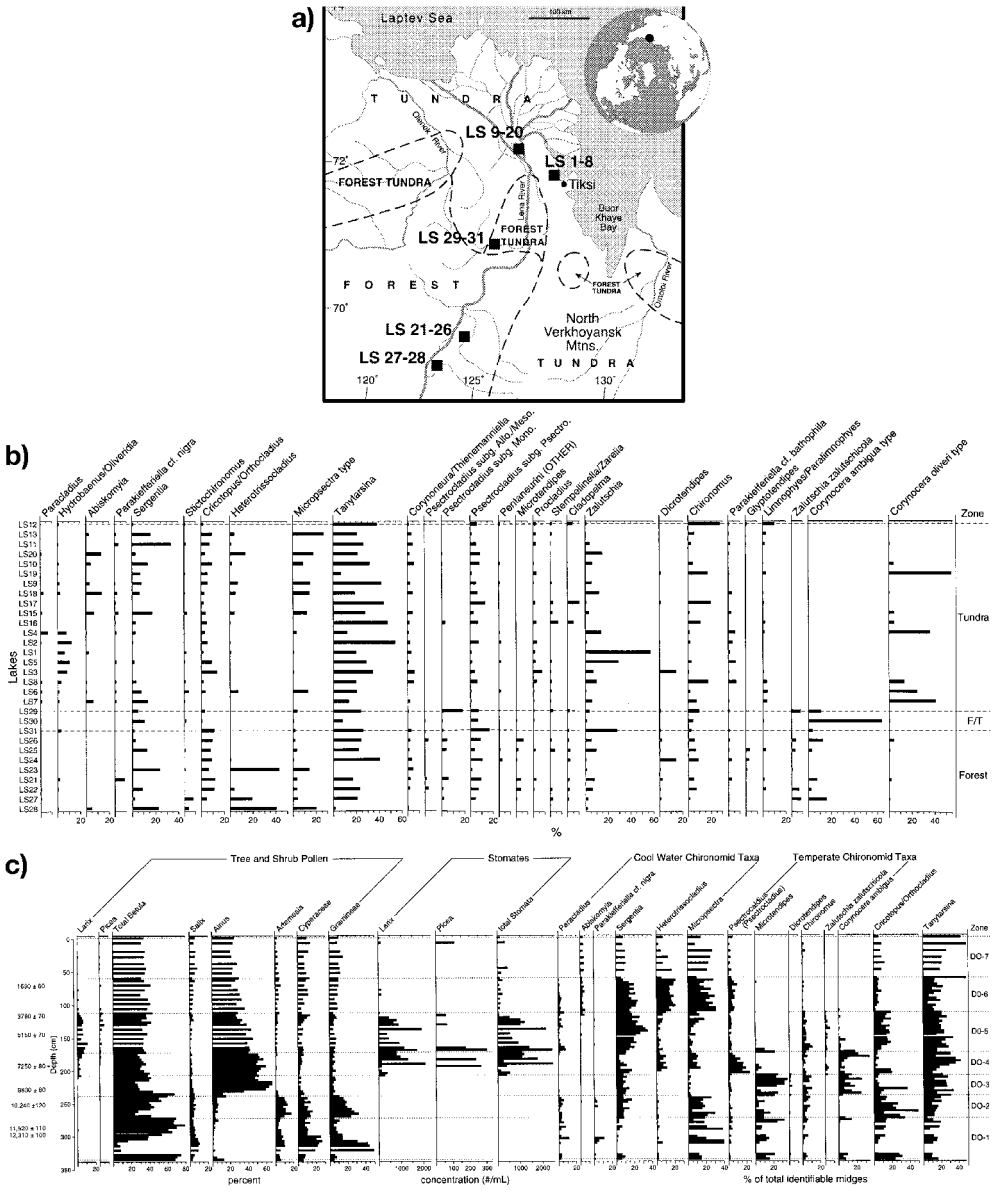


Figure 7 (a) Map depicting the location of the lakes incorporated in the surface sample training set for the Lena River region and the location of LS9 (Dolgoye Ozero). (b) Chironomid percentage diagram illustrating the modern distribution of chironomids from a transect of lakes crossing circum-polar treeline in the Lena River region, Russia. (c) Composite diagram from Dolgoye Ozero incorporating the major pollen, stomate and chironomid taxa. Zonation of the diagram based on CONISS analysis of chironomid percentage data
Source: modified after Porinču and Cwynar (2000, 2002); Pisarić *et al.* (2001).

has been well demonstrated (Lindegaard-Petersen, 1971; Pinder, 1980; Minshall, 1984). The preference of certain chironomid taxa for particular substratum is also well known (McLachlan, 1969; Cantrell and McLachlan, 1977; Oliver and Roussel, 1983). However, to date, only two studies have interpreted and addressed the paleoecological significance of finding larval remains of rheophilic chironomid taxa within lacustrine sediment. These two studies have illustrated the value of using chironomid remains to reconstruct landscape development.

Klink (1989) studied floodplain deposits located in abandoned river channels of the Lower Rhine River in the Netherlands. This work was undertaken, in part, to determine what steps were required to mitigate the effects of river engineering on the macro-invertebrate stream communities by identifying the pre-disturbance composition of these communities (Amoros and Van Urk, 1989). A layer of coarse sand, found at the base of sediment cores recovered from abandoned river channels, was assumed to represent the bed of the former active river channel. The silt lying immediately above this sand layer was sampled for insect remains, including Chironomidae. Using available historical sources, Klink was able to identify the timing of river abandonment and thereby determine the nature of the chironomid communities that typified the Lower Rhine River prior to the channel being abandoned.

A study conducted by Rück *et al.* (1998) reconstructed the influence of changing fluvial input on a lacustrine system using both sediment characteristics and faunal insect assemblages (Figure 8). A 14.53-m core was recovered from Tugulnuit Lake in the southern interior of British Columbia, Canada. The authors found that prior to approximately 4000 yr BP the chironomid community within the lake was dominated by taxa generally associated with standing waters or the slower reaches of flowing waters. Such taxa included *Chironomus*, *Cricotopus/Orthocladius* and *Tanytarsina*. Other taxa present, but at relatively low levels, included *Dicrotendipes* and *Pseudochironomus*, both of which are generally associated with lentic environments. After approximately 4000 yr BP, the lentic taxa decreased in relative abundance and taxa commonly associated with lotic or running waters, such as *Brillia/Euryhapsis*, *Eukiefferiella/Toetenia*, *Rheocricotopus*, *Doithrix/Pseudorthocladius* and *Corynoneura/Thienemanniella* increased in abundance. The remains of taxa that are associated with mineral substrates (*Paralauterborniella*) and sandy substratum (*Robackia*) were also found. Associated with the increase in lotic chironomid taxa were the appearance of Simuliidae (black fly) larvae and an increase in the sand component of the sediment. Simuliids are, for the most part, restricted to running waters (Currie and Walker, 1992). The increase in rheophilic chironomid taxa and sand, along with the appearance of Simuliidae remains, suggests that stream or river incursion into Tugulnuit Lake must have occurred during this period. At approximately 3700 yr BP the chironomid community returned to its pre-4000 yr BP composition with taxa typifying lentic waters increasing in abundance, lotic taxa decreasing in abundance and Simuliids extirpated. The authors suggest that a change in the Okanagan River's course or a large flooding event may have been responsible for the changes evidenced by the subfossil chironomid remains and sediment lithology.

It is clear from the studies described above that valuable information detailing geomorphological processes and landscape evolution can be derived by careful and detailed study of lacustrine sediment properties and the larval chironomid remains contained within. However, this incipient field will require much further work before results will be able to be interpreted with consistency.

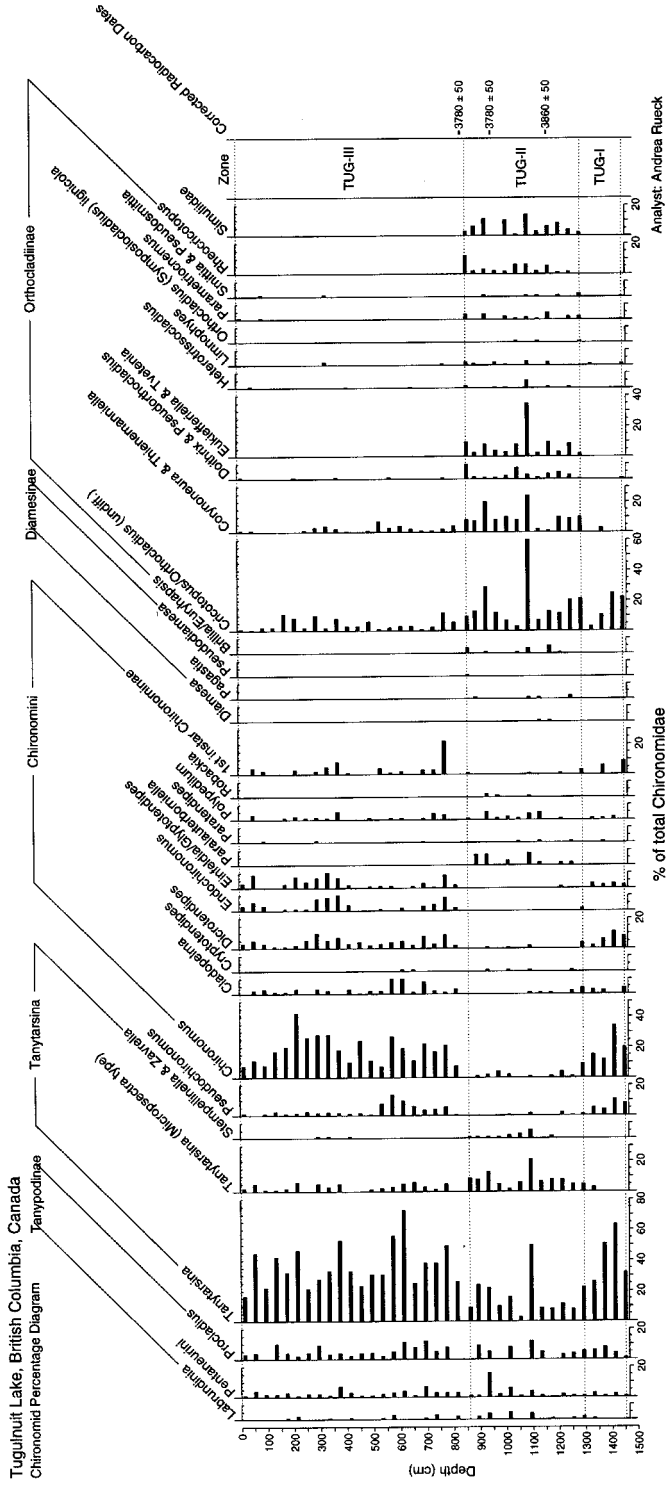


Figure 8 Selected chironomid taxa from Tuguluit Lake, British Columbia, Canada. Zones based on stratigraphically constrained cluster analysis as implemented by CONISS.
 Source: modified after Rück *et al.* (1998).

5 Biomonitoring

The use of freshwater organisms for biomonitoring of streams and lakes began in the early twentieth century, however the last few decades have seen a great deal of progress and an expansion of their use (Rosenberg, 1993; Rosenberg and Resh, 1993). Any attempt to manage, remediate or restore aquatic ecosystems to their 'natural' or pre-cultural disturbance conditions will require baseline data on the biological, physical and chemical characteristics of the lake. Recent studies have used subfossil chironomid analysis to assess whether eutrophication, acidification and fish stocking have impacted lake ecosystems.

a Eutrophication: Eutrophication, which has long been identified as a serious pollution problem (Carson, 1962; Likens, 1972), may result from increased nutrient availability, decreased residence time of lake water or changes in intra-lake biotic interactions and/or lake morphometry (Whiteside, 1983). However, increased inorganic nutrient supply is the causal agent most often cited as responsible for the increased productivity that many lakes experienced during the mid- to late- twentieth century (Wetzel, 2001). Increased input of inorganic nutrients, such as phosphorous and nitrogen, tends to increase the productivity of primary producers which, in turn, alters the physical and chemical properties of lakes. These changes are reflected in the species composition of the flora and fauna within the lake and the geochemical properties of the lake sediment (Whiteside, 1983).

One of the most important physical changes that occurs during extreme eutrophication is a steep decline in dissolved oxygen. Some researchers have related the community composition of profundal chironomid assemblages to hypolimnetic oxygen concentration (Thienemann, 1920; Brundin, 1949, 1956). However, other researchers have suggested that such changes in chironomid community composition may more strongly represent changes in nutrient availability (Sæther, 1979; Wiederholm, 1980). In either case, an argument can be made for the use of chironomids in the biomonitoring of eutrophication.

There are a number of physiological and behavioural characteristics that enable certain chironomid larvae to tolerate the low oxygen levels that commonly exist at the mud-water interface in eutrophic and hyper-eutrophic lakes. Many chironomid larvae possess invertebrate haemoglobin, which has a high affinity for oxygen, enabling respiration in situations of extremely low ambient oxygen (Cranston, 1988). Many chironomid taxa also inhabit tubes that span the mud-water interface within which they undulate their bodies to facilitate water movement and oxygen uptake (Heinis *et al.*, 1994; Lindegaard, 1995). Also, some Orthoclaadiinae taxa are small and mobile, enabling them to migrate to areas with suitable oxygen concentrations and food availability (Wiederholm, 1984).

Many researchers have used the remains of subfossil chironomids as indicators of the trophic status of lakes and to assess the nature of lake ontogeny in relation to its nutrient history (Deevey, 1942; Hofmann, 1978; Warwick, 1980; Wiederholm, 1980; Walker *et al.*, 1993; Lang and Lods-Crozet, 1997; Little and Smol, 2000, 2001; Quinlan and Smol, 2001). Typically, with increasing eutrophication the benthic chironomid community follows a successional pattern from a *T. lugens*-dominated community to a community dominated by *Chironomus* spp. (Wiederholm, 1979; Warwick, 1980), and

with the development of anoxic conditions associated with further eutrophication, the remaining chironomid taxa may be replaced by an oligochaete-dominated community (Johnson *et al.*, 1993). There have been a number of quantitative inference models developed for estimating lake trophic status based on subfossil chironomid analysis; these models reconstruct trophic status either directly by reconstructing total phosphorous concentration (Lotter *et al.*, 1998; Brooks *et al.*, 2001) or indirectly by reconstructing anoxic factor (Quinlan *et al.*, 1998), chlorophyll *a* concentration (Broderson and Lindegaard, 1999), volume-weighted hypolimnetic oxygen concentration (Quinlan and Smol, 2001) and hypolimnetic oxygen concentration (Zoe Ruiz, personal communication, 2001).

Work by Clerk and colleagues on a sediment core recovered from the west basin of Peninsula Lake, a large (853 ha), deep ($Z_{\max} = 34$ m), oligotrophic ([TP] = $8.0 \mu\text{m l}^{-1}$) lake in central Ontario, Canada, has provided interesting insights into changes in hypolimnetic anoxia and nutrient levels resulting from recent (<300 years) anthropogenically induced disturbance (Clerk *et al.*, 2000; Quinlan and Smol, 2001). Using a multiproxy approach (historical data, pollen, diatoms and chironomids) changes in epilimnetic water quality and average volume weighted hypolimnetic oxygen concentration (avg[VWHO]) were quantified using transfer functions developed by Hall and Smol (1996) and Quinlan and Smol (2001). The chironomid analyses indicated that pre-disturbance (prior to 1870) assemblages consisted primarily of taxa associated with well-oxygenated conditions such as *Heterotrissocladius*, *Protanypus*, *Micropsectra* type and *Parakiefferiella* cf. *nigra* (Figure 9). Following ca. 1870, when a grist-mill was established and an increase in land-clearance, road construction and lakeshore development occurred, a pronounced change in the chironomid assemblages was evidenced. An increase in the relative abundance of taxa such as *Chironomus*, *Procladius*, *Polypedilum* and *Tanytarsus* s. lat. occurred. These taxa are associated with eutrophic lakes that are generally characterized by lower available hypolimnetic oxygen levels. As disturbance pressures decreased in the mid-1960s an increase in taxa such as *Parakiefferiella* cf. *nigra*, *Heterotrissocladius* and *Sergentia* occurred, suggesting the beginning of a return to higher hypolimnetic oxygen concentrations.

A chironomid-based avg[Volume Weighted Hypolimnetic Oxygen] inference model developed by Quinlan and Smol (2001) was applied to the Peninsula Lake chironomid stratigraphy to quantitatively reconstruct changes in down-core avg[VWHO] values (Figure 9). Prior to European settlement chironomid-inferred concentrations of VWHO were between 8 and 10 mg l^{-1} , however these values decreased fairly rapidly following European settlement and reached 5 mg l^{-1} by the early to mid-twentieth century. The chironomid inferred avg[VWHO] suggest that there has been some improvement in water quality during the later part of the twentieth century with avg[VWHO] rising to approximately 8 mg l^{-1} . The changes in subfossil chironomid assemblages and the chironomid-inferred avg[VWHO] reconstruction correspond well with the fossil diatom changes, diatom-based inferences of TP and geochemical data (Quinlan and Smol, 2001).

b Acidification: Limnological studies have played a large role in documenting the effects that acid rain has had on aquatic ecosystem structure and function in large parts of eastern North America and Europe during the late nineteenth and twentieth centuries. Particularly affected were areas with granite bedrock and poorly buffered

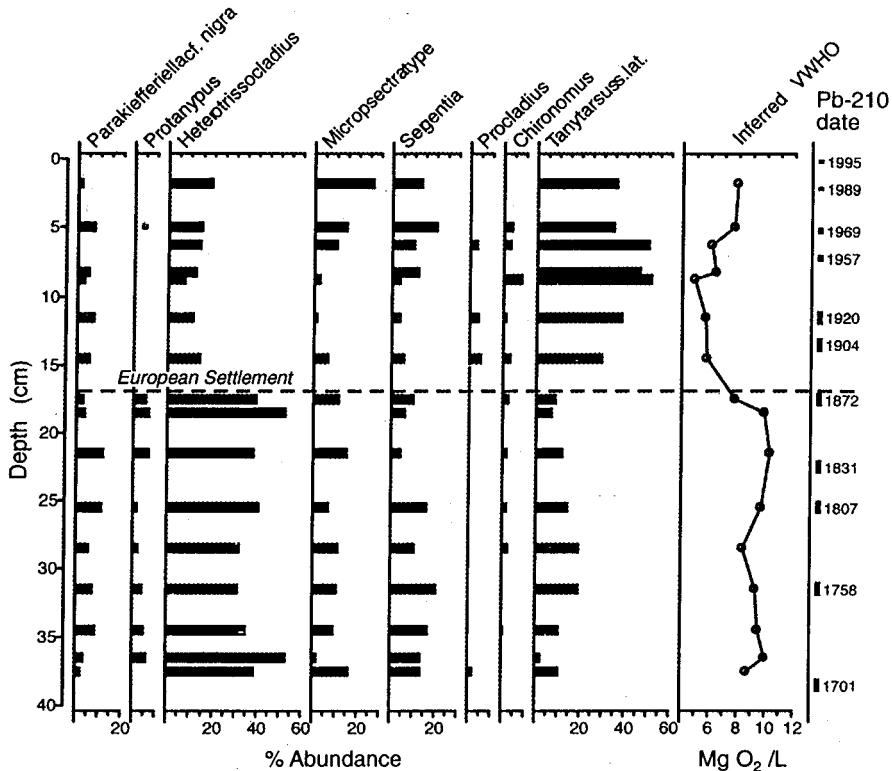


Figure 9 Stratigraphy of subfossil chironomid remains recovered from the west basin of Peninsula Lake. Percent abundance of chironomid taxa expressed as a percentage of total identifiable Chironomidae. Chironomid taxa are arranged from left to right in order of descending [avgVWHO] optima. Chronologic control is provided by Pb-210; the basal Pb-210 dates are italicized to reflect that they are based on extrapolation. The dotted line marks the onset of European settlement

Source: the chironomid stratigraphy is modified from Clerk *et al.* (2000) and chironomid-based inferences of [avgVWHO] are modified after Quinlan and Smol (2001).

soils, as exist in Scandinavia, southeastern Canada and northeastern USA (Wiederholm, 1984). These studies were able to document with exacting detail the effects that lowered pH had on the structure and function aquatic ecosystems.

Chironomus species have been associated with highly acidic lakes (Wiederholm and Eriksson, 1977; Raddum and Sæther, 1981). *Chironomus riparius* has been found in ponds located near Smoking Hills, NWT, Canada, with pH of 2.8 (Havas and Hutchinson, 1982), *Chironomus plumosus* has been found in acidic strip mine lakes with pH as low as 2.3 (Harp and Campbell, 1967), and Yamamoto (1986) documents the presence of *C. acerbiphilus* Tokunaga in a volcanic lake in Japan with pH of 1.4. The larvae of *C. riparius* found in the Smoking Hills ponds have significantly higher concentration of

haemoglobin than individuals found in circum-neutral waters. It has been suggested the higher levels of haemoglobin may increase the buffering capacity of the haemolymph allowing *C. riparius* to tolerate highly acidic waters (Jernelöv *et al.*, 1981).

A number of studies have used subfossil chironomid remains to identify the development and effects of anthropogenic acidification (Henrikson and Oscarson, 1985; Johnson and McNeil, 1988; Brodin, 1990). The faunal composition of contemporaneous chironomid communities has also been used to describe and classify lakes in terms of pH (Wiederholm and Eriksson, 1977; Walker *et al.*, 1985; Buskens, 1987; Johnson *et al.*, 1990; Halvorsen *et al.*, 2001). In general these studies document similar patterns occurring with acidification. Species diversity initially decreases, with the chironomid community increasingly dominated by a few acidiphilous taxa such as *Chironomus* spp. These taxa are initially present at high levels, but with continued acidification, abundances of even these acidiphilous taxa are dramatically reduced (Lindegaard, 1995). Similar patterns have been documented as occurring in streams (Simpson, 1983; Orendt, 1999).

A major research project entitled PIRLA (Paleoecological Investigation of Recent Lake Acidification) was undertaken in the mid-1980s to document the effects of acid rain on lakes in the Adirondack region of New York, USA. Changes in faunal composition of the chironomid community and *Chaoborus* spp. (phantom midges) in these lakes helped to identify the occurrence of rapid acidification in recent decades (Uutala, 1986; Charles *et al.*, 1987). A detailed study of sediment cores recovered from Big Moose Lake, New York, USA provided strong evidence of post-1950 increases in lake water acidity. The study was multiproxy in nature, incorporating sediment geochemistry, water chemistry analyses and a number of biological proxies, including diatoms, chrysophytes and chironomids. The chironomid analysis identified that a recent decrease in *Micropsectra*, *Zavrelia* grp. and Tanytarsini was statistically significant as was the recent increase in *Zalutschia* nr. *briani* (Figure 10). The authors point out that reductions in Tanytarsini taxa had been observed in acidified lakes in Scandinavia and that the recent increase in *Z. nr. briani* and the decrease in *Micropsectra* at Big Moose Lake had been observed in other acidic Adirondack lakes. An increase in the relative abundance of *Psectrocladius* (*P.*) was also observed at Big Moose Lake corresponding to similar trends observed in clear water acidic lakes in Scandinavia (Henrikson *et al.*, 1982). The authors suggest that the changes in the chironomid fauna of Big Moose Lake that occurred post-1950 are indicative of increased acidification.

c Fish introduction: In most freshwater ecosystems chironomid larvae are situated between the autotrophs (phytoplankton and benthic algae) and larger heterotrophs, such as fish, in terms of system energetics. As a result, chironomids play an integral role in maintaining the trophic structure of aquatic communities. The Chironomidae possess high amounts of protein, are easily digested and are known to act as growth promoters in fish diets (Armitage, 1995). These factors, together with the high relative abundance of chironomids in lentic waters, result in chironomids being an important dietary component of freshwater fish and other aquatic fauna (MacKey, 1979). The effect of fish predation on living chironomid larvae has been addressed in great detail (see table 17.2 in Armitage *et al.*, 1995). In general, larger, mobile larvae such as *Procladius* and *Thienemanniella* experience a more intense rate of predation than tube-dwelling taxa

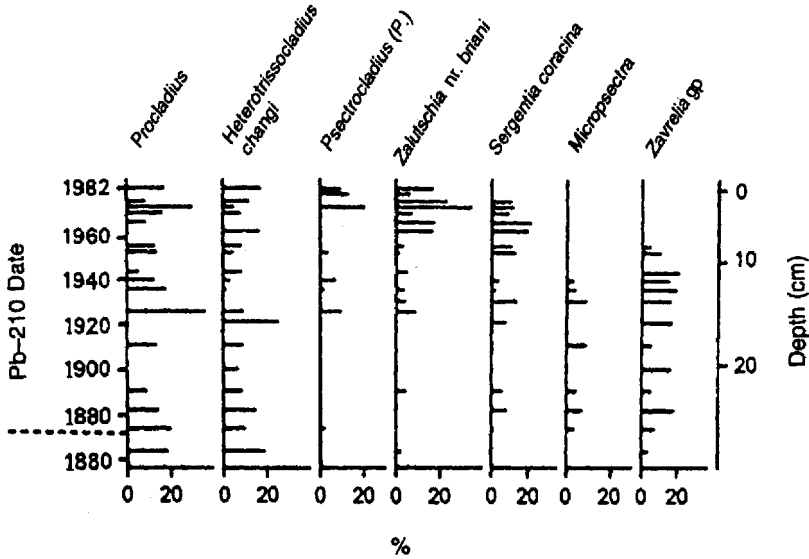


Figure 10 Chironomid percentage diagram incorporating important chironomid taxa from Big Moose Lake, New York, USA (core 5) illustrating the effects of recent acidification on the chironomid community. Relative abundance is expressed as percent of total head capsule count
 Source: modified after Charles *et al.* (1987).

(Armitage, 1995). Another group of chironomids that experience selective predation are the brightly coloured larvae belonging to the genus *Chironomus* (also known as bloodworms). The importance of the Chironomidae in fish diets suggests that fish introduction in aquatic systems should have a dramatic effect on chironomid community composition. However, as of yet, there has been little work carried out using subfossil chironomid remains to identify the timing of fish introduction into aquatic systems and to assess the impact of fish introduction on the composition of the chironomid community. This could be a fruitful area of future research.

6 Phylogenetic biogeography and cladistics

Historical biogeographers, particularly those interested in the application of cladistic approaches for reconstructing phylogenetics and geographical histories, have considered the ideas and work of Brundin (1965, 1967, 1972, 1988) to be of seminal importance. Although based on collections of living species rather than subfossil remains, this application of chironomid analysis deserves mention here because of its importance to geographic research. Brundin analysed and compared the chironomid fauna of the southern continents and New Zealand to produce cladograms testing the Gondwanaland concept, and inferred relative timing of the break up of the Southern continent.

Brundin points out in his publications that chironomids are ideal for analysis by phylogenetic biogeographers for several key reasons, including large modern diversity, rich

degree of morphological attributes and variation between different taxa, wide geographic distribution, and the relatively great age of the group.

The large number of species and wide range of morphological attributes and variations provides phylogeneticists with much data to compare extant species living in the same area or different areas. On the basis of morphological similarities and differences between species and higher taxa, phylogeneticists reconstruct the evolutionary histories of species and the geologic-geographic histories of the regions in which they occur.

The widespread distribution of living chironomid taxa, in terms of both geographic regions and freshwater aquatic habitats means that phylogeneticists can collect living specimens from almost any region of the Earth, ranging from the tropics to the Arctic and Antarctic. Thus, they can be used on a global scale to reconstruct geographic changes associated with plate tectonics.

The Chironomidae are an old group that have likely been present since at least the late Jurassic over 140 million years ago (Brundin, 1988). Fossils related to the modern subfamily Podonominae have been found in 130 million-year-old amber from Lebanon. Morphological analysis of this fossil chironomid, *Libanoclites neocomicus*, shows it is likely related to the extant northern hemisphere genera *Boreochlus* and *Paraboreochlus* and the southern hemisphere genus *Archaeochlus* (Brundin, 1988). The relatively great age of the Chironomidae means that the extant species can trace their lineages and history back through key plate tectonic events. The age of the Lebanese chironomid fossil and its relationship to both northern and southern hemisphere taxa show that chironomids evolved early enough to have been present prior to major plate tectonic events such as the break up of Laurasia and much of the fragmentation of Gondwanaland.

In a classic study of chironomid phylogenetics and continental history, Brundin collected specimens from South America, Africa, Australia, Tasmania, New Caledonia and New Zealand (Brundin, 1970, 1988). He concentrated on analysis of the morphological similarities and differences found in three subfamilies, the Podonominae, Aphroteniinae and the Diamesinae. These three subfamilies are largely found in cold stream habitats and are in large part restricted to the southern hemisphere, south of the tropics (the Diamesinae are not restricted to the southern hemisphere). Brundin found that the chironomid species from Australia and Tasmania were most closely related to those from South America, and then with New Zealand. The similarity with chironomid taxa from Africa was much less. Brundin concluded that this was consistent with plate tectonic theory which suggested that South America and Australia remained joined via Antarctica relatively late – until perhaps the Late Cretaceous to Eocene (65–50 million years ago) – while being well separated from Africa much earlier (Brundin, 1970, 1988). The connection between South America, Australia and Tasmania is now recognized as an important biogeographic track by traditional phylogeographers and panbiogeographers.

VII Status in geography

A perusal of the 'List of chironomid workers' found on Walker's chironomid homepage (<http://www.ouc.bc.ca/fwsc/iwalker/intpanis/>, last accessed 19 May 2003) indicates

that only six of the 500+ chironomid researchers listed are associated with geography departments. The vast majority of chironomid researchers are affiliated with ecology, zoology or limnology departments. However, the interest in using changes in the spatial and temporal distribution of chironomids to describe past and present environmental conditions in aquatic ecosystems is explicitly geographical in nature. Of the six chironomid researchers associated with geography departments five are interested in some aspect of paleoecology, paleoclimatology and/or paleolimnology. Paleoecology and paleoclimatology tend to be fairly well represented in geography departments; however paleolimnology (the above researchers notwithstanding) has tended to remain outside the purview of geography. As a result, the use of subfossil chironomid analysis as a proxy of historical and pre-historical environmental change is still not well developed in geography departments, especially in North America. While biogeographers are active in landscape-scale studies, these studies have traditionally focused on terrestrial systems. However, the aquatic system is an integral component of the landscape, and even more importantly, aquatic ecosystems act as information traps or archives collecting and preserving valuable information within their sediment. If the physical, chemical and biological signals that are present in this sediment can accurately be interpreted it will further increase our understanding of local landscape processes and regional environmental change. As geographers it behoves us to recognize the potential that exists with subfossil chironomid analysis and ensure that we contribute to its further development.

VIII Future research opportunities and challenges

As might be expected with a developing methodology there are a number of future opportunities and challenges facing geographers and others working with chironomid analysis. These opportunities and challenges exist in the realms of methodological refinement, improved development of empirical-based relations between chironomids and environment and application of chironomid analysis to substantive questions in paleoenvironmental reconstruction.

In terms of methodologies, the physical separation of chironomid subfossil from their surrounding sediment matrix remains a cumbersome and time-consuming manual process. It is possible that this could be made easier through physical or chemical manipulation of the sediment. It is likely that research will continue in this area. Similarly, our understanding of the bias that might exist if only part of the total head capsule concentration of a sediment sample is removed using current handpicking methods remains uncertain. This means that if some samples in a sequence have extremely high concentrations of capsules the entire concentration (which can range over 1000) is customarily picked and identified. Despite some work on this, a statistically based understanding of the biases in current head capsule separation and counting procedures remains weak. Although some research suggests that a total of 50 head capsules should provide a reasonable sample number, statistical work using modern plant and animal communities or fossil pollen counts has shown that acceptable identification totals depend upon the species richness and evenness of the sample. Finally, improved reference collections will lead to the identification of new morphological features that will provide for greater taxonomic resolution of subfossil

chironomid remains. It is hoped that harmonization of systematics and taxonomies will progress at a fast pace and facilitate the development of international and intercontinental comparisons of subfossil chironomid assemblages. The large increase in the number of regional calibration datasets that have been developed over the last decade has led to the need to harmonize the taxonomic naming conventions used in subfossil chironomid analysis. As many of the training sets have been developed in Europe there has been greater progress amongst European researchers than North Americans to standardize identifications of subfossil chironomid remains. As training sets are developed in new geographical regions, both the Web and in-person workshops should be used to encourage harmonization of subfossil taxonomy and naming conventions in these regions.

The development of training sets to empirically link chironomid taxa and assemblages to important environmental variables remains a clear opportunity. A number of studies using the training-set approach in northern temperate, sub-arctic and arctic lakes have determined that summer surface water temperature, ambient summer air temperature, lake depth, substrate, salinity and hypolimnetic oxygen concentration are important determinants of chironomid community composition. However, similar studies have not been carried out elsewhere, with large portions of South America, Central America, Australasia and Africa open to research. In addition, differences in accepted systematics and taxonomy has made the amalgamation of training sets from different regions difficult. The development of a hemisphere-wide training set for the boreal latitudes is a potential near-term opportunity.

Increasing taxonomic precision is being aided by studies relating the presence of contemporaneous larvae and pupae to the subfossil remains preserved in recently deposited lake sediment. The increase in taxonomic resolution should further improve our understanding of the ecological requirements of taxa, resulting in more accurate estimates of taxa optima and tolerances to specific environmental variables. However, readers are cautioned to weigh the potential benefits of more precise estimates of taxa tolerances and optima owing to improvements in subfossil chironomid taxonomy against potential increases in 'noise' resulting from imprecise or inconsistent taxonomy. As Brodersen (1998) rightly points out, the appropriate level of taxonomic resolution required in any study should be a function of the research questions being addressed by the study.

It is likely that given their breadth of technical facility, statistical ability and interest in methodology and spatial problems, geographers can and will play a significant role in methodological refinements, development of new training sets and application of chironomid-based inference models. However, it will also be important for geographers to develop the necessary taxonomic skills to identify subfossil midge remains and the ecological knowledge required to interpret chironomid stratigraphies. Of course, the developments of improved methodologies and empirical training sets are of little value in and of themselves. It is the application of chironomid analysis to a suite of environmental questions that offers the most exciting opportunities. Some of the most salient of these are outlined below.

In an age where the possibility of significant global warming in the near future has taken on a central role in scientific and public debate it is clear that research on past magnitudes and forms of climatic variation will remain a topic of much research by biophysical geographers. The ability of chironomid analysis to provide records of quan-

titative changes in water temperature, air temperature and salinity that have relatively high precision and fine temporal and spatial resolution is bringing the technique to the forefront of Holocene palaeoclimatology. There are worldwide needs and opportunities in furnishing such records of past climatic variations using chironomids. If we understand the past magnitude of natural climatic variations we can put postulated future changes into a proper context. In addition, we can use paleoclimatic records derived from chironomid analysis to examine how the climate system operates under altered conditions or the dynamics of its response to internal and external perturbations. Chironomid-based quantitative reconstructions of past climate conditions can also help to further improve the parameterization of the general circulation models (GCMs) that are currently being used to hindcast past climate events and simulate the effects of future climate change. These applications of chironomid analysis are really just beginning to take off and offer much opportunity for geographers.

The geomorphological applications of chironomid analysis are also just beginning to be tapped. Analysis of variations between lentic and lotic taxa in lake cores can provide evidence of past variations in fluvial inputs into lake systems. There is much in the way of opportunity for geomorphologists in the analysis of lotic chironomid assemblages from fluvial sediments in order to reconstruct past depositional environments and develop facies models. It is also possible that analysis of chironomids from estuarine and other near-shore aquatic environments may be useful in reconstructing estuary and beach formation, sea-level fluctuations, or reconstructing past disturbances such as hurricanes.

Another area that presents research opportunities to researchers is biomonitoring and restoration ecology. Any attempt to manage, remediate or restore aquatic ecosystems to their 'natural' or pre-cultural disturbance conditions will require baseline data on the biological, physical and chemical characteristics of the lake. This will entail using both historical records and neolimnological records to infer the nature of the pre-disturbance system in terms of its faunal composition, structure and function. Further study refining our knowledge of the species-specific response of midge larvae to various anthropogenic disturbances, e.g., logging, eutrophication, acidification, pollution, etc., is required in order to accurately interpret the conditions of the aquatic environment in which the larval chironomid remains were deposited.

Given the many opportunities and challenges outlined above, coupled with the technical accessibility of the chironomid methodology to biophysical geographers, it is likely that geographers will become increasingly interested in chironomid analysis and contribute to the development and application of the technique in a major way.

Acknowledgements

We thank H.J.B. Birks, R. Quinlan, M. Pisaric and M. Heinrichs for providing previously published data and/or images for inclusion in this paper, Larry Talbot for providing access to imaging equipment and Chase Langford (Department of Geography, UCLA) for producing some of the figures. We would also like to thank S.J. Brooks for providing valuable and constructive criticism of an earlier draft of this paper. Support for this paper was provided in part by NSF Regional Sciences grants to G.M.M. (BCS-9905350 and BCS-0135748) and an NSF Doctoral Dissertation Improvement Grant to G.M.M.

and D.F.P. (BCS-0101268) and a University of California, Dissertation Year Fellowship to D.F.P.

References

- Aaby, B.** and **Digerfeldt, G.** 1986: Sampling techniques for lakes and bogs. In Berglund, B.E., editor, *Handbook of Holocene paleoecology and paleohydrology* Chichester: John Wiley & Sons, 181–92.
- Amoros, C.** and **Van Urk, G.** 1989: Paleocological analyses of large rivers: some principles and methods. In Petts, G.E., Möller, H. and Roux, A.L., editors, *Historical change of large alluvial rivers: western Europe*. New York: John Wiley & Sons, 143–65.
- Anderson, N.H.** and **Cummins, K.W.** 1979: Influences of diet on the life histories of aquatic insects. *Journal of the Fisheries Board of Canada* 36, 335–42.
- Anderson, N.J.** and **Battarbee, R.W.** 1994: Aquatic community persistence and variability: a paleolimnological perspective. In Giller, P.S., Hildrew, A.G. and Raffelli, D., editors, *Aquatic ecology: scale, pattern and process*. Oxford: Blackwell Scientific, 233–59.
- Armitage, P.D.** 1995: The behaviour and ecology of adults. In Armitage, P.D., Cranston, P.S. and Pinder, L.C., editors, *The Chironomidae: the biology and ecology of nonbiting midges*. London: Chapman and Hall, 194–224.
- Armitage, P.D., Cranston, P.S.** and **Pinder, L.C.**, editors 1995: *The Chironomidae: the biology and ecology of nonbiting midges*. London: Chapman and Hall.
- Ashe, P.** 1983: A catalogue of chironomid genera and subgenera of the world including synonyms (Diptera: Chironomidae). *Entomologica Scandinavica Supplement* 17, 1–68.
- Ashe, P., Murray, D.A.** and **Reiss, F.** 1987: The zoogeographical distribution of Chironomidae. *Annales de Limnologie* 23, 27–60.
- Battarbee, R.W.** 2000: Paleolimnological approaches to climate change, with special regard to the biological record. *Quaternary Science Reviews* 19, 107–24.
- Birks, H.J.B.** 1995: Quantitative paleoenvironmental reconstructions. In Maddy, D. and Brew, J.S., editors, *Statistical modelling of Quaternary science data. Technical guide 5*. Cambridge: Quaternary Research Association, 161–254.
- 1998: Numerical tools in quantitative paleolimnology – progress, potentialities, and problems. *Journal Paleolimnology* 20, 307–22.
- Birks, H.J.B., Line J.M., Juggins, S., Stevenson, A.C.** and **ter Braak, C.J.F.** 1990: Diatoms and pH reconstruction. *Philosophical Transactions of the Royal Society of London (Series B)* 327, 263–78.
- Brinkhurst, R.O.** 1974: *The benthos of lakes*. London: Macmillan Press.
- Brodersen, K.P.** 1998: Macroinvertebrate communities in Danish lakes: classification and trophic reconstruction. Ph.D. Thesis, University of Copenhagen, Copenhagen, Denmark.
- Brodersen, K.P.** and **Anderson, N.J.** 2000: Subfossil insect remains (Chironomidae) and lake-water temperature inference in the Sisimiut-Kangerlussuaq region, southern Western Greenland. *Geology of Greenland Survey Bulletin* 186, 78–82.
- Brodersen, K.P.** and **Lindegaard, C.** 1997: Significance of subfossil chironomid remains in classification of shallow lakes. *Hydrobiologia* 342/343, 125–32.
- 1999: Classification, assessment and trophic reconstruction of Danish lakes using chironomids. *Freshwater Biology* 42, 143–57.
- 2000: The influence of temperature on emergence periods of Chironomidae (Diptera) from a shallow Danish lake, In Hoffrichter, O., editor, *Late 20th century research on Chironomidae: an anthology from the 13th international symposium on Chironomidae*. Aachen: Shaker Verlag, 313–24.
- Brodin, Y.-W.** 1982: Paleocological studies of recent development of the Lake Väckjösjön. IV. Interpretation of the eutrophication process through the analysis of subfossil chironomids. *Archiv für Hydrobiologie* 93, 313–26.
- 1990: Midge fauna development in acidified lakes in northern Europe. *Philosophical Transactions of the Royal Society London (Series B)* 327, 295–98.
- Brooks, S.J.** 1997: The response of Chironomidae (Insecta: Diptera) assemblages to Late-glacial climatic change in Kråkenes Lake, western Norway. *Quaternary Proceedings* 5, 49–58.
- Brooks, S.J.** and **Birks, H.J.B.** 2000a: Chironomid-inferred lateglacial and early-Holocene mean July air temperatures for Kråkenes lake, western Norway. *Journal of Paleolimnology* 23, 77–89.

- 2000b: Chironomid-inferred lateglacial air temperatures at Whitrig Bog, south east Scotland. *Journal of Quaternary Science* 15, 759–64.
- 2001: Chironomid-inferred air temperatures from Lateglacial and Holocene sites in north-west Europe: progress and problems. *Quaternary Science Reviews* 20, 1723–41.
- Brooks, S.J., Bennion, H. and Birks, H.J.B.** 2001: Tracing lake trophic history with a chironomid-total phosphorous inference model. *Freshwater Biology* 46, 513–33.
- Brundin, L.** 1949: Chironomiden and andere Bodentiere der südschwedischen Urgebirgsseen. *Report of the Institute of Freshwater Research, Drottningholm* 30, 1–914.
- 1956: Die bodenfaunistischen Seetypen und ihre Anwendbarkeit auf die Südhalbkugel. Zugleich eine Theorie der produktionsbiologischen Bedeutung der glazialen Erosion. *Report of the Institute of Freshwater Research, Drottningholm* 37, 186–235.
- 1958: The bottom faunistic lake type system and its application to the southern hemisphere. Moreover a theory of glacial erosion as a factor of productivity in lakes and oceans. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 13, 288–97.
- 1965: On the real nature of transantarctic relationships. *Evolution* 19, 496–505.
- 1966: Transantarctic relationships and their significance, as evidenced by chironomid midges. With a monograph of the sub-families Podonominae and Aphroteniinae and the astral Heptagytiae. *Kungliga Svenska Vetenskapsakademiens Handlingar* 11, 1–472.
- 1967: Insects and the problem of austral disjunctive distribution. *Annual Review of Entomology* 12, 149–68.
- 1970: Antarctic land faunas and their history. In Holdgate, M.W., editor, *Antarctic ecology*. London: Academic Press, 41–53.
- 1972: Phylogenetics and biogeography. *Systematic Zoology*, 21, 69–79.
- 1983a: *Chilenomyia paradoxa* gen. n. and *Chilenomyiinae*, a new subfamily amongst the Chironomidae. *Entomologica Scandinavica* 14, 33–45.
- 1983b: Two new aphrotenian larval types from Chile and Queensland, including *Anaphrotenia lacustris* n. gen., n. sp. (Diptera: Chironomidae). *Entomologica Scandinavica* 14, 415–33.
- 1988: Phylogenetic biogeography. In Myers, A. A. and Gillers, P. S., editors, *Analytic biogeography: an integrated approach to the study of animal and plant distributions*. London: Chapman and Hall, 343–69.
- Buskens, R.F.M.** 1987: The chironomid assemblages in shallow lentic waters differing in acidity, buffering capacity and trophic level in the Netherlands. *Entomologica Scandinavica Supplement* 29, 217–24.
- Butler, M.G.** 1980: Emergence phenologies of some arctic Alaskan Chironomidae, In Murray, D.A., editor, *Chironomidae. Ecology, systematics, cytology and physiology*. New York: Pergamon Press, 307–14.
- Cantrell, M.A. and McLachlan, A.J.** 1977: Competition and chironomid distribution patterns in a newly flooded lake. *Oikos* 29, 429–33.
- Carson, R.** 1962: *Silent spring*. Boston: Houghton Mifflin, 368 pp.
- Charles, D.F., Whitehead, D.R., Engstrom, D.R., Fry, B.D., Hites, R.A., Norton, S.A., Owen, J.S., Roll, L.A., Schindler, S.C., Smol, J.P., Uutala, A.J., White, J.R. and Wise, R.J.** 1987: Paleolimnological evidence for recent acidification of Big Moose Lake, Adirondack Mountains, N.Y. (USA). *Biogeochemistry* 3, 267–96.
- Clerk, S., Hall, R. I., Quinlan, R. and Smol, J.P.** 2000: Quantitative inferences of past hypolimnetic anoxia and nutrient levels from a Canadian Precambrian Shield lake. *Journal of Paleolimnology* 23, 319–36.
- Coffman, W.P.** 1995: Conclusions. In Armitage, P.D., Cranston, P.S. and Pinder, L.C., editors, *The Chironomidae: the biology and ecology of nonbiting midges*. London: Chapman and Hall, 436–46.
- Cranston, P.S.** 1982: A key to the larvae of the British Orthocladiinae (Chironomidae). *Scientific Publications of the Freshwater Biological Association* 45, 1–152.
- 1988: Allergens on nonbiting midges (Diptera: Chironomidae): a systematic survey of chironomid haemoglobins. *Medical and Veterinary Entomology* 2, 117–27.
- 1995: Systematics. In Armitage, P.D., Cranston, P.S. and Pinder, L.C., editors, *The Chironomidae: the biology and ecology of nonbiting midges*. London: Chapman and Hall, 31–52.
- 2000: The electronic guide to the Chironomidae of Australia. <http://entomology.ucdavis.edu/chiropage/index.html> (last accessed 5 October 2002).
- Cranston, P.S. and Oliver, D.R.** 1987: Problems in Holarctic chironomid biogeography. *Entomologica Scandinavica Supplement* 29, 51–56.

- 1988: Aquatic xylophagous Orthoclaadiinae – systematics and ecology (Diptera: Chironomidae). *Spixiana Supplement* 14, 143–54.
- Cummins, K.W. and Klug, M.J.** 1979: Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 10, 147–72.
- Cure, V.** 1985: Chironomidae (Diptera – Nematocera) aus Rumänien unter besonderer Berücksichtigung jener aus dem hydrographischen Einzugsgebiet der Donau. *Archiv Hydrobiologie Supplement* 68, 163–217.
- Currie, D.C. and Walker, I.R.** 1992: Recognition and paleohydrologic significance of fossil black fly larvae, with a key to the Nearctic genera (Diptera: Simuliidae). *Journal of Paleolimnology* 7, 37–54.
- Cwynar, L.C. and Levesque, A.J.** 1995: Chironomid evidence for lateglacial climatic reversals in Maine. *Quaternary Research* 43, 405–13.
- Danks, H.V. and Oliver, D.R.** 1972: Seasonal emergence of some high arctic Chironomidae (Diptera). *Canadian Entomologist* 104, 661–86.
- Deevey, E.S. Jr** 1942: Studies on Connecticut lake sediments III. The biostratonomy of Linsley Pond. *American Journal of Science* 240, 233–64.
- Driver, E.A.** 1977: Chironomid communities in small prairie ponds: characteristics and controls. *Freshwater Biology* 7, 121–33.
- Edwards, F.W.** 1929: British nonbiting midges (Diptera: Chironomidae). *Transaction of the Entomological Society of London* 77, 279–439.
- Eggermont, H. and Verschuren, D.** 2003a: Subfossil chironomidae from Lake Tanganyika, East Africa. 1. Tanytopodinae and Othoclaadiinae. *Journal of Paleolimnology* 29, 31–48.
- Eggermont, H. and Verschuren, D.** 2003b: Subfossil Chironomidae from Lake Tanganyika, East Africa. 2. Chironominae (Chironomini and Tanytarsine). *Journal of Paleolimnology* 29, 423–57.
- Epler, J.H.** 1995: *Identification manual for the larval Chironomidae (Diptera) of Florida*. Revised edition. Tallahassee FL: Florida Department of Environmental Protection, 317 pp.
- 2001: Identification manual for the larval Chironomidae (Diptera) of North and South Carolina. *A guide to the taxonomy of the midges of the southeastern United States, including Florida*. Special Publication SJ2001-SP13. Raleigh NC: North Carolina Department of Environment and Natural Resources, 526 pp.
- Fittkau, E.J. and Reiss, F.** 1978: Chironomidae. In Illies, J., editor, *Limnofauna Europaea*. Stuttgart: Gustav Fischer Verlag, 404–44.
- Ford, J.B.** 1962: The vertical distribution of larval Chironomidae (Dipt.) in the mud of a stream. *Hydrobiologia* 19, 262–72.
- Frey, D.G.** 1964: Remains of animals in Quaternary lake and bog sediments and their interpretation. *Ergebnisse der Limnologie* 2, 1–114.
- 1988: Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology. *Journal of Paleolimnology* 1, 179–91.
- Glew, J.** 1989: A new trigger mechanism for sediment samplers. *Journal of Paleolimnology* 2, 241–43.
- 1991: Miniature gravity corer for recovering short sediment cores. *Journal of Paleolimnology* 5, 285–87.
- Glew, J.R., Smol, J.P. and Last, W.M.** 2001: Sediment core collection and extrusion. In Last, W.M. and Smol, J.P., editors, *Tracking environmental change using lake sediments. Volume 1: basin analysis, coring, and chronological techniques*. Dordrecht: Kluwer Academic Publishers, 73–105.
- Hall, R.I. and Smol, J.P.** 1992: A weighted-averaging regression and calibration model for inferring total phosphorus concentration from diatoms in British Columbia (Canada) lakes. *Freshwater Biology* 27, 417–34.
- 1996: Paleolimnological assessment of long-term water-quality changes in south-central Ontario lakes affected by cottage development and acidification. *Canadian Journal of Fisheries and Aquatic Sciences* 53, 1–17.
- Halvorsen, G.A., Heneberry, J.H. and Snucins, E.** 2001: Sublittoral chironomids as indicators of acidity (Diptera: Chironomidae). *Water, Air and Soil Pollution* 130, 1385–90.
- Harp, G.L. and Campbell, R.S.** 1967: The distribution of *Tendipes plumosus* (Linné) in mineral acid water. *Limnology and Oceanography* 12, 260–63.
- Havas, M. and Hutchinson, T.C.** 1982: Aquatic invertebrates from the Smoking Hills, N.W.T., Canada. *Canadian Journal of Zoology* 61, 241–49.
- Heinis, F., Sweerts, J.-P. and Loopik, E.** 1994: Micro-environment of chironomid larvae in the littoral and profundal zones of Lake Maarsseveen I, the Netherlands. *Archiv Hydrobiologie* 130, 53–167.
- Heinrichs, M.L., Walker, I.R., Mathewes, R.W. and Hebda, R.J.** 1999: Holocene chironomid-

- inferred salinity and palovegetation reconstruction from Kilpoola Lake, British Columbia. *Géographie Physique et Quaternaire* 53, 211–21.
- Heinrichs, M.L., Walker, I.R. and Mathewes, R.W.** 2001: Chironomid-based paleosalinity records in southern British Columbia, Canada: a comparison of transfer functions. *Journal of Paleolimnology* 26, 147–59.
- Heiri, O. and Lotter, A.F.** 2001: Effect of low count sums on quantitative environmental reconstructions: an example using subfossil chironomids. *Journal of Paleolimnology* 26, 343–50.
- Henrikson, L. and Oscarson, H.G.** 1985: History of the acidified Lake Gårdsjön: The development of chironomids. *Ecological Bulletin* 37, 58–63.
- Henrikson, L., Olofsson, J.B. and Oscarson, H.G.** 1982: The impact of acidification on Chironomidae (Diptera) as indicated by subfossil stratification. *Hydrobiologia* 86, 223–29.
- Hofmann, W.** 1971a: Zur Taxonomie und Palökologie subfossiler Chironomiden (Dipt.) in Seesedimenten. *Ergebnisse der Limnologie* 6, 1–50.
- 1971b: Die postglaziale Entwicklung der Chironomiden und Chaoborus Fauna (Dipt.) des Schöhsees. *Archiv für Hydrobiologie Supplement* 40, 1–74. (English translation – Fisheries Research Board of Canada, Translation Series No. 2177).
- 1978: Analysis of animal microfossils from the Großer Segeberger See (F.R.G.). *Archiv für Hydrobiologie* 82, 316–46.
- 1983: Stratigraphy of Cladocera and Chironomidae in a core from a shallow North German lake. *Hydrobiologia* 103, 235–39.
- 1986: Chironomid analysis. In Berglund, B.E., editor, *Handbook of Holocene paleoecology and paleohydrology* Chichester: John Wiley & Sons, 715–23.
- 1988: The significance of chironomid analysis (Insecta: Diptera) for paleolimnological research. *Palaeogeography, Palaeoclimatology, Palaeoecology* 62, 501–509.
- 1998: Cladocerans and chironomids as indicators of lake level changes in north temperate lakes. *Journal of Paleolimnology* 19, 55–62.
- Holmes, R.W., Whiting, M.C. and Stoddard, J.L.** 1989: Changes in diatom-inferred pH and acid neutralizing capacity in a dilute, high elevation, Sierra Nevada lake since A.D. 1825. *Freshwater Biology* 21, 295–310.
- Hongve, D.** 1972: En bunnhenter som er lett a lage. *Fauna* 25, 281–83.
- Iovino, A.J.** 1975: Extant chironomid larval populations and the representativeness and nature of their remains in lake sediments. Ph.D. dissertation, Indiana University, Indiana, USA.
- Jernelöv, A., Nagell, B. and Svenson, A.** 1981: Adaptation to an acid environment in *Chironomus riparius* (Diptera: Chironomidae) from Smoking Hills, NWT, Canada. *Holarctic Ecology* 4, 116–19.
- Johannsson, O.E.** 1980: Energy dynamics of the eutrophic chironomid *Chironomus plumosus* f. *semireductus* from the Bay of Quinte, Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 1254–65.
- Johnson, J.H. and McNeil, O.C.** 1988: Fossil midge associations in relation to trophic and acidic state of the Turkey Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 45 (Supplement 1), 136–44.
- Johnson, M.G., Kelso, J.R.M., McNeil, O.C. and Morton, W.B.** 1990: Fossil midge associations and the historical status of fish in acidified lakes. *Journal of Paleolimnology* 3, 113–27.
- Johnson, R.K., Wiederholm, T. and Rosenberg, D.M.** 1993: Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates. In Rosenberg, D.M. and Resh, V.H., editors, *Freshwater biomonitoring and benthic macroinvertebrates*. New York: Chapman and Hall, 40–158.
- Jongman, R.H.G., ter Braak, C.J.F. and Van Tongeren, O.F.R.**, editors, 1995: *Data analysis in community and landscape ecology*. Cambridge: Cambridge University Press.
- Jowsey, P.C.** 1966. An improved peat sampler. *New Phytologist* 65, 245–48.
- King, R.S. and Richardson, C.J.** 2002: Evaluating subsampling approaches and macroinvertebrate taxonomic resolution for wetland assessment. *Journal of the North American Benthological Society* 21, 150–71.
- Klink, A.** 1989: The Lower Rhine: paleoecological analysis. In Petts, G.E., Möller, H. and Roux, A.L., editors, *Historical change of large alluvial rivers: western Europe*. New York: John Wiley & Sons, 183–201.
- Konstantinov, A.S.** 1958: Influence of temperature on the rate of development and growth of chironomids. *Doklady Akademii Nauk SSR (Soviet Socialist Republic)* 120, 1362–65.
- 1971: Ecological factors affecting respiration in chironomid larvae. *Limnologica (Berlin)* 8, 127–34.
- Korhola, A., Olander, H. and Blom, T.** 2000: Cladoceran and chironomid assemblages as

- qualitative indicators of water depth in subarctic Fennoscandian lakes. *Journal of Paleolimnology* 24, 43–54.
- Kureck, A.** 1979: Two circadian eclosion times in *Chironomus thummi*; (Diptera), alternately selected with different temperatures. *Oecologia (Berlin)* 40, 311–23.
- Lang, C. and Lods-Crozet, B.** 1997: Oligochaetes versus chironomids as indicators of trophic state in two Swiss lakes recovering from eutrophication. *Archive Hydrobiologie* 139, 187–95.
- Larocque, I., Hall, R.I. and Grahn, E.** 2001: Chironomids as indicators of climate change: a 100-lake training set from a subarctic region of northern Sweden (Lapland). *Journal of Paleolimnology* 26, 307–22.
- Levesque, A.J., Mayle F.E., Walker, I.R. and Cwynar, L.C.** 1993: A previously unrecognized lateglacial cold event in eastern North America. *Nature* 361, 623–26.
- Levesque, A.J., Cwynar, L.C. and Walker, I.R.** 1994: A multiproxy investigation of lateglacial climate and vegetation change at Pine Ridge Pond, southwest New Brunswick, Canada. *Quaternary Research* 42, 316–27.
- 1997: Exceptionally steep north–south gradients in lake temperatures during the last deglaciation. *Nature* 385, 423–26.
- Likens, G.E.** 1972: Eutrophication and aquatic ecosystems. In Likens, G.E., editor, *Nutrients and eutrophication: the limiting-nutrient controversy*. Lawrence KS: American Society of Limnology and Oceanography, 3–13.
- Lindegaard, C.** 1995: Classification of waterbodies and pollution. In Armitage, P.D., Cranston, P.S. and Pinder, L.C., editors, *The Chironomidae: the biology and ecology of nonbiting midges*. London: Chapman and Hall, 385–404.
- Lindegaard, C. and Jónasson, P.M.** 1979: Abundance, population dynamics and high production on zoobenthos in Lake Myvatn, Iceland. *Oikos* 32, 202–207.
- Lindegaard-Petersen, C.** 1971: An ecological investigation of the Chironomidae (Diptera) from a Danish lowland stream (Linding Å). *Archiv für Hydrologie Supplement* 81, 563–87.
- Little, J.L. and Smol, J.P.** 2000: Changes in fossil midge (Chironomidae) assemblages in responses to cultural activities in a shallow, polymictic lake. *Journal of Paleolimnology* 23, 207–12.
- Little, J.L. and Smol, J.P.** 2001: A chironomid-based model for inferring late-summer hypolimnetic oxygen in southeastern Ontario lakes. *Journal of Paleolimnology* 26, 259–70.
- Livingstone, D.A., Bryan, K. Jr and Leahy, R.G.** 1958: Effects of an arctic environment on the origin and development of freshwater lakes. *Limnology and Oceanography* 3, 192–214.
- Lotter, A.F., Birks, H.J.B., Hofmann, W. and Marchetto, A.** 1997: Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *Journal Paleolimnology* 18, 395–420.
- 1998: Modern diatom, Cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. *Journal of Paleolimnology* 19, 443–63.
- Lotter, A.F., Walker, I.R., Brooks, S.J. and Hofmann, W.** 1999: An intercontinental comparison of chironomid paleotemperature inference models: Europe vs. North America. *Quaternary Science Reviews* 18, 717–35.
- MacDonald, G.M.** 2002: The Boreal forest. In Orme, A., editor, *Physical geography of North America*. Oxford: Oxford University Press, 270–90.
- MacDonald, G.M., Edwards, T.W.D., Moser, K.A., Pienitz, R. and Smol, J.P.** 1993: Rapid response of treeline vegetation and lakes to past climate warming. *Nature* 361, 243–46.
- MacKey, A.P.** 1977: Growth and development of larval Chironomidae. *Oikos* 28, 270–75.
- 1979: Trophic dependencies of some larval Chironomidae (Diptera) and fish species in the River Thames. *Hydrobiologia* 62, 241–47.
- Malloch, J.R.** 1917: A preliminary classification of Diptera, exclusive of Pupipara, based upon larval and pupal characters, with keys to the imagines in certain families. *Bulletin of the Illinois State Laboratory of Natural History* 12, 161–409.
- McGarrigle, M.L.** 1980: The distribution of chironomid communities and controlling sediment parameters in L. Derravaragh, Ireland. In Murray, D.A., editor, *Chironomidae: ecology, systematics, cytology and physiology*. Oxford: Pergamon Press, 275–82.
- McLachlan, A.J.** 1969: Substrate preferences and invasion behaviour exhibited by larvae of *Nilodorum brevivucca* Freeman (Chironomidae) under experimental conditions. *Hydrobiologia* 119, 129–38.
- Minshall, G.W.** 1984: Aquatic insect–substratum relationships. In Resh, V.H. and Rosenberg, D.M., editors, *The ecology of aquatic insects*. New

- York: Praeger Publishers, 358–400.
- Moller Pillot, H.K.M.** 1984a: De larven der Nederlandse Chironomidae (Diptera) (Tanypodinae, Chironomini). *Nederlandse Faunistische Mededelingen* 1A, 1–227.
- 1984b: De larven der Nederlandse Chironomidae (Diptera) (Orthoclaadiinae). *Nederlandse Faunistische Mededelingen* 1B, 1–227.
- Moore, J.W.** 1980: Factors influencing the composition, structure and density of a population of benthic invertebrates. *Archiv für Hydrobiologie* 88, 202–18.
- Moser, K.A., MacDonald, G.M. and Smol, J.P.** 1996: Applications of freshwater diatoms to geographical research. *Progress in Physical Geography* 20, 21–52.
- Nesje, A.** 1992: A piston corer for lacustrine and marine sediments. *Arctic and Alpine Research* 24, 257–59.
- Olander, H., Birks, H.J.B., Korhola, A. and Blom, T.** 1999: An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia. *The Holocene* 9, 279–94.
- Oliver, D.R.** 1971: Life history of the Chironomidae. *Annual Review of Entomology* 16, 211–30.
- Oliver, D.R. and Roussel, M.E.** 1983: The insects and arachnids of Canada, Part II: The genera of larval midges of Canada-Diptera: Chironomidae. *Agriculture Canada Publication* 1746, 1–263.
- Orendt, C.** 1999: Chironomids as bioindicators in acidified streams: a contribution to the acidity tolerance of chironomid species with a classification in sensitivity classes. *International Revue Hydrobiologie* 84, 439–49.
- Palmer, S., Walker, I.R., Heinrichs, M., Mebda, R. and Scudder, G.** 2002: Postglacial midge community change and Holocene palaeotemperature reconstruction near treeline, southern British Columbia (Canada). *Journal of Paleolimnology* 28, 469–90.
- Paterson, C.G. and Walker, K.F.** 1974: Seasonal dynamics and productivity of *Tanytarsus barbitalis* Freeman (Diptera: Chironomidae) in the benthos of a shallow, saline lake. *Australian Journal of Marine and Freshwater Research* 25, 151–65.
- Pienitz, R., Smol, J.P. and Birks, H.J.B.** 1995: Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories of Canada. *Journal of Paleolimnology* 13, 21–49.
- Pienitz, R., Smol, J.P., Last, W.M., Leavitt, P.R. and Cumming, B.F.** 2000: Multi-proxy Holocene palaeoclimatic record from a saline lake in the Canadian Subarctic. *The Holocene* 10, 673–86.
- Pinder, L.C.V.** 1980: Spatial distribution of Chironomidae in an English chalk stream, In Murray, D. A., editor, *Chironomidae: ecology, systematics, cytology and physiology*. Oxford: Pergamon Press, 153–61.
- 1995: Biology of the eggs and first-instar larvae. In Armitage, P.D., Cranston, P.S. and Pinder, L.C., editors, *The Chironomidae: the biology and ecology of nonbiting midges*. London: Chapman and Hall, 87–106.
- Pisaric, M.F.J., MacDonald, G.M., Velichko, A.A. and Cwynar, L.C.** 2001: The lateglacial and post-glacial vegetation history of the north-western limits of Beringia, from pollen, stomates and tree stump evidence. *Quaternary Science Reviews* 20, 235–45.
- Porinchu, D.F. and Cwynar, L.C.** 2000: The distribution of freshwater Chironomidae (Insecta: Diptera) across treeline near the lower Lena River, northeast Siberia. *Arctic, Antarctic and Alpine Research* 32, 429–37.
- 2002: Late-Quaternary history of midge communities and climate from a tundra site near the lower Lena River, Northeast Siberia. *Journal of Paleolimnology* 27, 59–69.
- Porinchu, D.F., MacDonald, G.M., Bloom, A.M. and Moser, K.A.** 2002: The modern distribution of chironomid sub-fossils (Insecta: Diptera) in the Sierra Nevada, California: potential for paleoclimatic reconstructions. *Journal of Paleolimnology*, 28 355–75.
- Porinchu, D.F., MacDonald, G.M., Bloom, A.M. and Moser, K.A.** 2003: Late Pleistocene and early Holocene climate and limnological changes in the Sierra Nevada, California, USA, inferred from midges (Insecta: Diptera: Chironomidae). *Paleogeography, Paleoclimatology, Paleoecology*, 3166, 1–20.
- Pradhan, S.** 1945: Insect population studies: II. Rate of insect development under variable temperature in the field. *Proceedings of the National Institute of Sciences of India* 11, 74–80.
- Quinlan, R. and Smol, J.P.** 2001: Setting minimum head capsule abundance and taxa criteria in chironomid-based inference models. *Journal of Paleolimnology* 26, 327–42.
- Quinlan, R., Smol, J.P. and Hall, R.I.** 1998: Quantitative inferences of past hypolimnetic anoxia in south-central Ontario lakes using fossil midges (Diptera: Chironomidae). *Canadian Journal of Fisheries and Aquatic Science* 55, 587–96.

- Raddum, G.G. and Sæther, O.A.** 1981: Chironomid communities in Norwegian lakes with different degrees of acidification. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 21, 399–405.
- Reavie, E.D., Hall R.I and Smol, J.P.** 1995: An expanded weighted-averaging model for inferring past total phosphorus concentrations from diatom assemblages in eutrophic British Columbia (Canada) lakes. *Journal of Paleolimnology* 14, 49–67.
- Renberg, I.** 1981: Improved methods for sampling, photographing and varve-counting of varved lake sediments. *Boreas* 10, 255–58.
- 1991: The HON-Kajak sediment corer. *Journal of Paleolimnology* 6, 167–70.
- Rieradevall, M. and Brooks, S.J.** 2001: An identification guide to subfossil Tanypodinae larvae (Insecta: Diptera: Chironomidae) based on cephalic setation. *Journal of Paleolimnology* 25, 81–99.
- Rosén, P., Segerstrom, U., Eriksson, L., Renberg, I. and Birks, H.J.B.** 2001: Holocene climatic change reconstructed from diatoms, chironomids, pollen and near-infrared spectroscopy at an alpine lake (Sjuodjläure) in northern Sweden. *The Holocene* 11, 551–562.
- Rosenberg, D.M.** 1993: Freshwater biomonitoring and Chironomidae. *Netherlands Journal of Aquatic Ecology* 26, 101–22.
- Rosenberg, D.M. and Resh, V.H.,** editors, 1993: *Freshwater biomonitoring and benthic macroinvertebrates*. New York: Chapman and Hall.
- Rück, A., Walker, I.R. and Hebda, R.** 1998: A paleolimnological study of Tugulnuit Lake, British Columbia, Canada, with special emphasis on river influence as recorded by chironomids in the lake's sediment. *Journal of Paleolimnology* 19, 63–75.
- Sæther, O.A.** 1975: Nearctic chironomids as indicators of lake typology. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 19, 3127–33.
- 1976: Revision of *Hydrobaenus*, *Trissocladius*, *Zalutschia*, *Paratrissocladius*, and some related genera (Diptera: Chironomidae). *Bulletin of the Fisheries Research Board of Canada* 195, 1–287.
- 1979: Chironomid communities as water quality indicators. *Holarctic Ecology* 2, 65–74.
- Schmäh, A.** 1993: Variation among fossil chironomid assemblages in surficial sediments of Bodensee-Untersee (SW-Germany): implications for paleolimnological interpretation. *Journal of Paleolimnology* 9, 99–108.
- Schnell, O.A.** 1998: *Guidelines for the identification of chironomid larvae in the MOLAR project*. Norwegian Institute for Freshwater Research (NIVA) Report SNO 3710-97, Project Manual Annex A. Bergen, Norway: Department of Zoology, University of Bergen, Norway.
- Schnell, O.A., Rierdaevall, M., Granados, I. and Hanssen, O.** 1999: *A chironomid taxa coding system for use in ecological and palaeoecological databases*. Norwegian Institute for Freshwater Research (NIVA) Report Number 3710-97, Project Manual Annex B. Bergen, Norway: Department of Zoology, University of Bergen, Norway.
- Simpson, K.W.** 1983: Communities of Chironomidae (Diptera) from an acid-stressed headwater stream in the Adirondack Mountains, New York. *Memoirs of the American Entomological Society* 34, 315–27.
- Simpson, K.W. and Bode, R.W.** 1980: Common larvae of Chironomidae (Diptera) from New York State streams and rivers with particular reference to the fauna of artificial substrates. *Bulletin of the New York State Museum* 439, 1–105.
- Smol, J.P., Cumming, B.F. Douglas, M.S.V. and Pienitz, R.** 1995: Inferring past climatic changes in Canada using paleolimnological techniques. *Geoscience Canada* 21, 113–18.
- Stahl, J.B.** 1969: The uses of chironomids and other midges in interpreting lake histories. *Mitteilugen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 17, 111–25.
- Sweeney, B.W. and Vannote, R.L.** 1981: *Ephemerella* mayflies of White Clay Creek: Bioenergetic and ecological relationships among six co-existing species. *Ecology* 62, 1353–69.
- ter Braak, C.J.F. and Prentice, I.C.** 1988: A theory of gradient analysis. *Advances in Ecological Research* 18, 271–317.
- ter Braak, C.J.F., and Verdonschot, P.F.M.** 1995: Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57, 255–89.
- Thienemann, A.** 1918: Untersuchungen über die Beziehungen zwischen dem Sauerstoffgehalt des Wassers und der Zusammensetzung der fauna in Nord deutschen Seen. *Archiv für Hydrobiologie* 8, 316–46.
- 1920: Untersuchungen über die Beziehungen zwischen dem Sauerstoffgehalt des Wassers und der Zusammensetzung der Fauna in nord-deutschen Seen. *Archiv für Hydrobiologie* 12, 1–65.

- 1921: Seetypen. *Die Naturwissenschaften* 18, 643–46.
- 1922: Die beiden *Chironomus*-arten der Tiefenfauna der norddeutschen Seen. Ein hydrobiologisches Problem. *Archiv für Hydrobiologie* 13, 609–46.
- Timms, B.V.** 1983: A study of benthic communities in some shallow saline lakes of western Victoria, Australia. *Hydrobiologia* 105, 165–77.
- Titmus, G.** 1979: The emergence of midges (Diptera: Chironomidae) from a wet gravel-pit. *Freshwater Biology* 9, 165–79.
- Tokeshi, M.** 1986: Population dynamics, life histories and species richness in an epiphytic chironomid community. *Freshwater Biology* 16, 431–42.
- 1995: Production ecology. In Armitage, P. D., Cranston, P.S. and Pinder, L.C., editors, *The Chironomidae: the biology and ecology of non-biting midges*. London: Chapman and Hall, 269–92.
- Uutala, A.J.** 1986: Paleolimnological assessment of the effects of lake acidification on Chironomidae (Diptera) assemblages in the Adirondack Region of New York. Ph.D. Thesis, State University of New York College of Environmental Science and Forestry, Syracuse N.Y.
- Van Der Velde, G. and Hiddink, R.** 1987: Chironomidae mining in *Nuphar lutea* (L.) Sm. (Nymphaeaceae). *Entomologica Scandinavica Supplement* 29, 255–64.
- Verschuren, D.** 1994: Sensitivity of tropical-African aquatic invertebrates to short-term trends in lake level and salinity: a paleolimnological test at Lake Oloidien, Kenya. *Journal of Paleolimnology* 10, 253–63.
- 1997: Taxonomy and ecology of subfossil Chironomidae (Insecta, Diptera) from Rift Valley lakes in central Kenya. *Archive Hydrobiologie Supplement* 107, 467–512.
- Verschuren, D., Laird, K.R. and Cumming, B.F.** 2000a: Rainfall and drought in equatorial east Africa during the past 1,100 years. *Nature* 403, 410–14.
- Verschuren, D., Tibby, J., Sabbe, K. and Roberts, N.** 2000b: Effects of depth, salinity and substrate on the invertebrate community of a fluctuating tropical lake. *Ecology* 81, 164–82.
- Walker, I.R.** 1987: Chironomidae (Diptera) in paleoecology. *Quaternary Science Reviews* 6, 29–40.
- 1988: Late-Quaternary paleoecology of Chironomidae (Diptera: Insecta) from lake sediments in British Columbia. Ph.D. Dissertation, Simon Fraser University, Burnaby, Canada.
- 1995: Chironomids as indicators of past environmental change. In Armitage, P.D., Cranston, P.S. and Pinder, L.C., editors, *The Chironomidae: the biology and ecology of non-biting midges*. London: Chapman and Hall, 405–22.
- 2000: The WWW field guide to subfossil midges. <http://www.ouc.bc.ca/eesc/iwalker/wwwguide/> (last accessed 15 December 2002).
- 2001: Midges: Chironomidae and related Diptera. In Smol, J.P., Birks, H.J.B. and Last, W.M., editors, *Tracking environmental change using lake sediments. Volume 4: zoological indicators*. Dordrecht: Kluwer Academic Publishers, 43–66.
- Walker, I.R. and MacDonald, G.M.** 1995: Distributions of Chironomidae (Insecta: Diptera) and other freshwater midges with respect to treeline, Northwest Territories, Canada. *Arctic and Alpine Research* 27, 258–63.
- Walker, I.R. and Mathewes, R.W.** 1989: Chironomidae (Diptera) remains in surficial lake sediments from the Canadian Cordillera: analysis of the fauna across an altitudinal gradient. *Journal of Paleolimnology* 2, 61–80.
- Walker, I.R. and Paterson, C.G.** 1985: Efficient separation of subfossil Chironomidae from lake sediments. *Hydrobiologia* 122, 189–92.
- Walker, I.R., Fernando, C.H. and Paterson, C.G.** 1984: The chironomid fauna of four shallow humic lakes and their representation by subfossil assemblages in the surficial sediments. *Hydrobiologia* 112, 61–7.
- 1985: Associations of Chironomidae (Diptera) of shallow, acid, humic lakes and bog pools in Atlantic Canada, and a comparison with an earlier paleoecological investigation. *Hydrobiologia* 120, 11–22.
- Walker, I.R., Smol, J.P., Engstrom, D.R. and Birks, H.J.B.** 1991a: An assessment of Chironomidae as quantitative indicators of past climate change. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 975–87.
- Walker, I.R., Mott, R.J. and Smol, J.P.** 1991b: Allerød-Younger Dryas lake temperatures from midge fossils in Atlantic Canada. *Science* 253, 1010–12.
- Walker, I.R., Reavie, E.D., Palmer, S. and Nordin, R.N.** 1993: A paleoenvironmental assessment of human impact on Wood Lake, Okanagan Valley, British Columbia, Canada. *Quaternary International* 20, 51–70.
- Walker, I.R., Wilson, S.E. and Smol, J.P.** 1995: Chironomidae (Diptera): quantitative paleo-

- salinity indicators for lakes of western Canada. *Journal of Paleolimnology* 52, 950–60.
- Walker, I.R., Levesque, A.F., Cwynar, L.C. and Lotter, A.F.** 1997: An expanded surface-water paleotemperature inference model for use with fossil midges in eastern Canada. *Journal of Paleolimnology* 18, 165–78.
- Warwick, W.F.** 1975: The impact of man on the Bay of Quinte, Lake Ontario, as shown by the fossil chironomid succession (Chironomidae, Diptera). *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 19, 3134–41.
- 1980: Paleolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. *Canadian Bulletin of Fisheries and Aquatic Sciences* 206, 1–117.
- Welch, H.E.** 1976: Ecology of Chironomidae (Diptera) in a polar lake. *Journal of the Fisheries Research Board of Canada* 33, 227–47.
- Wetzel, R.G.** 2001: *Limnology: lake and river ecosystems*. San Diego CA: Academic Press, 1006 pp.
- Whiteside, M.C.** 1983: The mythical concept of eutrophication. *Hydrobiologia* 103, 107–11.
- Wiederholm, T.** 1979: Chironomid remains in recent sediments of Lake Washington. *Northwest Science* 53, 251–56.
- 1980: Use of benthos in lake monitoring. *Journal of the Water Pollution Control Federation* 52, 537–47.
- editor 1983: Chironomidae of the Holarctic region. Keys and diagnoses. Part I – Larvae. *Entomologica Scandinavica Supplement* 19, 457 pp.
- 1984: Responses of aquatic insects to environmental pollution. In Resh, V.H. and Rosenberg, D.M., editors, *The ecology of aquatic insects*. New York: Praeger Publishers, 508–57.
- Wiederholm, T. and Eriksson, L.** 1977: Benthos of an acid lake. *Oikos* 29, 261–67.
- Wilson, S.E., Walker, I.R., Mott, R.J. and Smol, J.P.** 1993: Climatic and limnological changes associated with the Younger Dryas in Atlantic Canada. *Climate Dynamics* 8, 177–87.
- Winnell, M.H. and White, D.S.** 1985: Trophic status of southeastern Lake Michigan based on the Chironomidae (Diptera). *Journal of Great Lakes Research* 11, 40–48.
- Wright, H.E.** 1991: Coring tips. *Journal of Paleolimnology* 6, 37–50.
- Yamamoto, M.** 1986: Study of Japanese *Chironomus* inhabiting high acidic water (Diptera: Chironomidae) I. *Kontyû, Tokyo* 54, 324–32.

