

Late Glacial and Holocene chironomid assemblages in 'Lac Long Inférieur' (southern France, 2090 m): palaeoenvironmental and palaeoclimatic implications

Emmanuel Gandouin, Evelyne Franquet

▶ **To cite this version:**

Emmanuel Gandouin, Evelyne Franquet. Late Glacial and Holocene chironomid assemblages in 'Lac Long Inférieur' (southern France, 2090 m): palaeoenvironmental and palaeoclimatic implications. Journal of Paleolimnology, 2002, 28 (3), pp.317-328. 10.1023/A:1021690122999 . hal-02959216

HAL Id: hal-02959216
https://amu.hal.science/hal-02959216

Submitted on 6 Oct 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Late Glacial and Holocene chironomid assemblages in 'Lac Long Inférieur' (southern France, 2090 m): palaeoenvironmental and palaeoclimatic implications

Emmanuel Gandouin and Evelyne Franquet*
*Laboratoire d'Ecologie des Eaux Continentales Méditerranéennes, Institut Méditerranéen d'Ecologie et de Paléoécologie, CNRS (UMR 6116), case 31, Faculté des Sciences de Saint Jérôme, F-13397 Marseille cedex 20, France; *Author for correspondence (e-mail: evelyne.franquet@univ.u-3mrs.fr)*

Received 10 March 2001; revised 7 August 2001; accepted in revised form 9 February 2002

Key words: Alpine lakes, Aquatic ecosystem reconstruction, Chironomids, France, Gyttja, Palaeolimnology, Trophic status

Abstract

Changes in lake water temperature and trophic states were inferred using chironomid fossil assemblages from 'Lac Long Inférieur' (Southern Alps, France). In the Late Glacial, a colder period, possibly analogous to the Younger Dryas, is characterised by a peak in *Micropsectra*, a cold stenothermic taxon. The increase in temperatures during the Late Glacial interstadial is indicated by a decrease in the percentages of cold stenothermic taxa (*Tanytarsus lugens*/*Corynocera oliveri* grp.) and by an increase in taxa linked to the development of vegetation in the littoral zone. The beginning of the Holocene is marked by the presence of taxa adapted to warmer and more eutrophic waters. During the Holocene, the progressive warming of the climate and increase in lake trophic status were indicated by the increase of eutrophic and warmer water indicators. An increase in tributary inflow into 'Lac Long Inférieur' was also inferred by the increase in rheophilous taxa, reflecting increased snowmelt. During the Subatlantic, the composition of the chironomid spectra suggests a re-cooling of the climate and/or a decrease in lake trophic status.

Introduction

The chironomid family is noted for its taxonomic richness, with nearly 10,000 species distributed globally (Cranston 1995), representing more than 20% of all freshwater insects in rivers and lakes. They colonise all terrestrial environments, from large lakes to the smallest ponds, and often dominate the benthos. As a result of their short generation times and the dispersal capacity of the winged adults, the Chironomidae appear to respond rapidly to environmental changes. For these reasons, they are used for lake typology, in particular for assessing lake trophic status and water quality (Saether 1980; Lindegaard 1995). Chironomidae fossils are increasingly used in palaeolimnology and palaeoclimatology. Recent knowledge of chironomid ecology, together with the development of transfer functions, has allowed for the reconstruction of palaeotemperatures (Walker et al. 1991a, 1997; Lotter et al. 1997; Olander et al. 1997; Brooks and Birks 2000). palaeosalinity (Walker et al. 1995), and oxygen and trophic levels (Lotter et al. 1998; Clerk et al. 2000; Francis 2001). To date, however, no palaeoecological studies based on the Chironomidae have been carried out in France.

Previous European studies in the alpine region have been on sites located at some distance from the 'Vallée des Merveilles', in Switzerland or in Italy (Lotter et al. 1997, 1998, 1999; Brooks 2000), or have concentrated principally on recent periods (Guilizzoni et al. 1996). Pollen analyses have shown that this part of the Alps is influenced by the Mediterranean climate (Beaulieu et al. 1984, 1994; Nakagawa 1998). The existing Nordic chironomid data do not appear to be

applicable to this area of the Alps: these new results will therefore be useful for potential future climate reconstructions.

This study is part of a multidisciplinary palaeoecological programme (palaeoentomology, palynology and dendroecology), designed to complete the reconstruction of the palaeoenvironment of the 'Vallée des Merveilles' and help understand long-term climatic processes in the French Southern Alps. This work was started by Beaulieu (1974, 1976, 1977). Regional events have been recently described using pollen and coleopteran analyses (Juhasz, unpublished; Ponel et al. (2001a, 2001b)). Our goal is to use chironomid analysis to provide information on local climatic and trophic signals from the Late Glacial to the Late Holocene.

Study area

The 'Lac Long Inférieur' (2090 m a.s.l.; 44° 03′47′′N; 7° 27′31′′E) is located in the southern French Alps, in the 'Vallée des Merveilles', near the Italian border (Figure 1a). The current Merveilles landscape is dominated by rocky outcrops, where schists and metamorphic sandstones have been scraped and polished by glacial action.

The vegetation of the 'Lac Long Inférieur' region belongs to the subalpine stage, more precisely to the mesophilous sub-series of *Pinus cembra* Linné and *Larix decidua* Miller series. At higher altitude (up to 2100 m a.s.l.), the alpine vegetation consists of grassland with *Festuca scabriculmis* (Hackel) K. Richter, *Potentilla valderia* Linné and *Festuca halleri* C. L. Allioni; screes are covered by *Thlaspi rotundifolium* ssp. *corymbosum* (Gaudin) Gremli. Locally, depressions with snow patches are occupied by dwarf willows and grass vegetation with *Alopecurus gerardi* D. Villars (Barbero et al. 1973).

The 'Vallée des Merveilles' is internationally known for its prehistoric paintings and evidence of early human colonisation (Lumley 1995). The valley is located at the junction of several large valleys (Vallée de la Miniera, Vallée de Valmasque, etc.). This crossroad position facilitated population movements between the different civilisations established in the peripheral plains. The 'Lac Long Inférieur' lies in an important watershed, which has been used for grazing

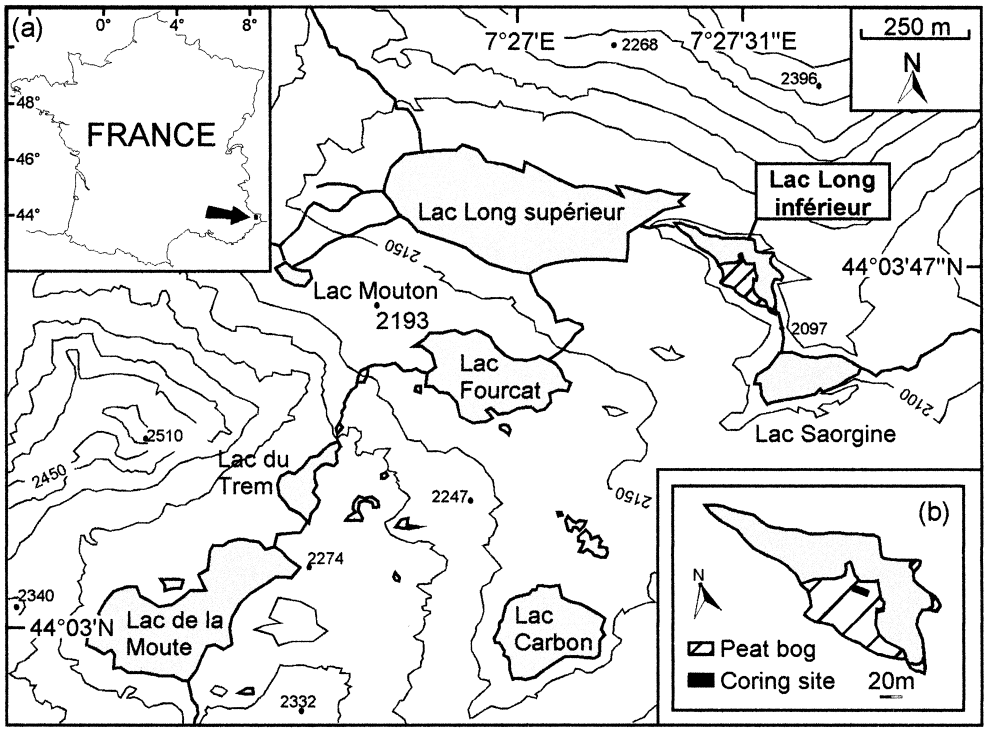


Figure 1. (a) Location of the site in France and general location of 'Lac Long Inférieur' (44° 03′47′′N, 7° 27′31′′E, Alpes-Maritimes, France). (b) Lake basin and coring site.

since the Neolithic. The Merveilles region is believed to be considered sacred by former populations (Romain 1995).

The lake basin is in siliceous bedrock and lies in a depression created by the Würmian glaciers. It is located downstream from the 'Lac Long Supérieur' and upstream from the 'lac Saorgine'. The basin is approximately 3 ha in area, and has a maximum water depth of 2 m. It is now nearly fully silted up and has been partly replaced by a Cyperaceae peat bog on its southwestern edge (Figure 1b). The presence of numerous fossil trunks buried in the peat bog suggests that the woodland was more developed in the past. At present, only rare isolated trees (*Larix decidua*) are found in the area around 'Lac Long Inférieur'. At lower altitudes (down to 1800 m a.s.l.), *Larix* woodland can be found. Pines are also present (e.g., *Pinus mugo* Turra, *P. uncinata* Miller ex. Mirbel, as well as *P. sylvestris* Linné) and are frequently associated with *Corylus* Linné.

Recent climatic data, from 1983 to 1998, are given in (Table 1) for two sites near the 'Vallée des Merveilles', 'Saint-Martin de Vésubie' (1550 m a.s.l.; 44° 04′N; 7° 15′E) and 'TENDE-Casterino' (1550 m a.s.l.; 44° 05′N; 7° 35′E). The climate is characterised by important annual precipitations (from 1100–1200 mm), July air temperature from 20–26 °C and January/February air temperatures from −0.6 to −6.8 °C. Using relationships between temperature and elevation (0.5 °C/100 m), it is possible to extrapolate that, at 2090 m, the 'Lac Long Inférieur' could be covered by ice from November to March.

Methods

Fieldwork

Sampling was carried out in October 1997 in a peat bog in the flattest area of the depression (Figure 1b). A Russian corer with a core diameter of 7 cm was used. The sequence consisted of five 1 m cores. The upper 10 cm of each core were discarded due to disturbance caused by the corer, and sediment is therefore missing between each of the successive sections.

Chronology

AMS radiocarbon dating of bulk sediment samples was used to determine the ages of the sediment at 7 points (137–139, 288–292, 326–330, 355–360, 481–483, 487–489, 509–513 cm). The calibrated age ranges are based on the INTCAL98 calibration, using the intercept method (Stuiver et al. 1998).

Chironomid subfossils

Samples of 5 cm^3 of sediment were taken every 10 cm (50 levels). The chironomid head capsules were isolated following the methods of Hofmann (1986). The sediment samples were deflocculated in a boiling solution of 10% KOH for 10 min. The solution was then sieved through a 100 μm mesh, and the residue was back-washed into a beaker using 90% alcohol, in which it was then stored.

Head capsules were mounted, ventral side up, onto glass slides using resin, and identified under a stereomicroscope at a magnification of 40× and 60×. Identifications were based on descriptions by Chernovskii (1949), Bryce (1960), Hofmann (1971), Bryce and Hobart (1972), Ferrarese and Rossaro (1981), Cranston (1982), Rossaro (1982), Wiederholm (1983), Schmid (1993).

Whole head capsules and fragments containing more than half of the mentum were counted as one head capsule. Fragments that were exactly half of a

Table 1. Climatic data for 'Saint-Martin de Vésubie' (1550 m a.s.l.; 44 ° 04′N; 7° 15′E) and 'TENDE-Casterino' (1550 m a.s.l.; 44° 05′N; 7° 35′E), from 1983–1998

	Saint-Martin de Vésubie (1550 m) from 1983–1998		TENDE-Casterino (1550 m) from 1983–1998	
Pr_{min} (mm)	48.2	February	56.9	February
Pr_{max} (mm)	136.3/122.8	October/April	147.6/154.1	October/April
Pr_{Annual} (mm)	1102.0	–	1243.0	–
T_{max} (°C)	25.9	July	20.1	July
T_{min} (°C)	−0.7	January	−6.8	February

Data were provided by 'Météo-France' (French weather office). Pr_{min}, minimal precipitation; Pr_{max}, maximal precipitation; Pr_{Annual}, annual precipitation; T_{max}, maximal temperature; T_{min}, minimal temperature. All values are means calculated from 1983–1998.

head capsule were counted as one half, and fragments that consisted of less than half of the mentum were excluded.

In general, a minimum of about 100 head capsules was counted for each sample. As Heiri and Lotter (2001), Quinlan and Smol (2001) have recently shown, counts of 50 head capsules should provided realistic estimates of environmental conditions.

The majority of the identifications were made to the genus level, and in rare cases to the species level. It was occasionally necessary to regroup the taxa into larger taxonomic categories, where morphological characteristics were too close to permit precise identifications (e.g., *Tanytarsus lugens*/*Corynocera oliveri*, *Eukiefferiella*/*Tvetenia*, *Cricotopus*/*Orthocladius*/*Paratrichocladius*, *Corynoneura*/*Thienemanniella* and *Parametriocnemus*/*Paraphaenocladius*). When the head capsules were damaged, the individuals were classified at the family, sub-family or tribe level, followed by the term 'indeterminate' (for example, Tanytarsini indeterminate).

Data analysis

The software GpalWin (Goeury 1997) was used to store the data and to produce the diagram of the subfossil chironomid communities. A cluster analysis of the coordinates obtained from a correspondence analysis (Benzecri 1973), using the Euclidean distance and the Wards criteria (Lebart et al. 1997), was performed to highlight the major changes in the chironomid assemblages. This method seems to be very near from the constrained single link method (Birks and Gordon 1985). Taxa that accounted for less than 2% of the chironomid sum at all levels were excluded from the analysis. Multivariate analyses were carried out using ADE-4 (Thioulouse et al. 1997). The richness is the number of taxa. Taxonomic diversity of the fossil assemblages was calculated using the Shannon index (H′) and the equilibrium of the community by the equitability (E) calculation (Frontier and Pichod-Viale 1998). Where $E = H'/H$; $H' = -\Sigma_i\, p_i \,\mathrm{Log}_2\, p_i$ (where p_i is the frequency of i^{th} species in the sample) and where $H = \mathrm{Log}_2\, S$ (where S is the taxonomic richness).

Results

Stratigraphy and chronology

The base of the core (555–469 cm) was composed of clayey gyttja. From 469–60 cm, the sediment consisted of a relatively uniform dark-brown gyttja. The upper part of the sequence is composed of a light beige gyttja. The top 25 cm of the core consisted of peat and has not been analysed, due to bioturbation. Results of the radiocarbon dates (AMS dating) obtained on the sediments are given in Table 2.

Chironomids

From 50 levels, 38 taxa have been identified. Selected taxa have been divided into three ecological categories: 'cold-water taxa' and 'warm-water taxa' and other indifferent (Walker and Mathewes 1987; Walker et al. 1991b; Brooks et al. 1997; Smith et al. 1998; Olander et al. 1999; Larocque et al. 2001). The chironomid diagram (Figure 2) has been divided into three major zones and seven sub-zones, each identified by cluster analysis. The number of zones and sub-zones was determined by the hierarchy level chosen in the cluster analysis.

Zone A (555–480 cm*)*
Taxonomic richness and equitability (Figure 3) in-

Table 2. AMS ^{14}C dates for sediments from the 'Lac Long Inférieur'

Depth (cm) Lab. no.	δ^{13}C	^{14}C age BP	Cal. age BP	
			1 σ (68%)	2 σ (95%)
137–139 AA 36512	−25.4	5678 ± 50	6497–6406	6622–6313
288–292 AA 36513	−24.6	8087 ± 58	9061–9000	9249–8781
326–330 AA 36514	−25.0	8692 ± 53	9711–9552	9891–9540
355–360 AA 36515	−24.6	8801 ± 54	10108–9701	10151–9585
481–483 AA 36516	−22.4	*10892 ± 80*	13003–12682	13145–12645
487–489 AA 36517	−21.3	*11263 ± 82*	13396–13142	13771–13007
509–513 AA 36518	−20.3	*11720 ± 79*	13840–13493	15129–13440

The calibrated age ranges are based on the INTCAL98 calibration using the intercept method (Stuiver et al. 1998). All measurements were done on bulk sediment. The dates in italics are considered too old.

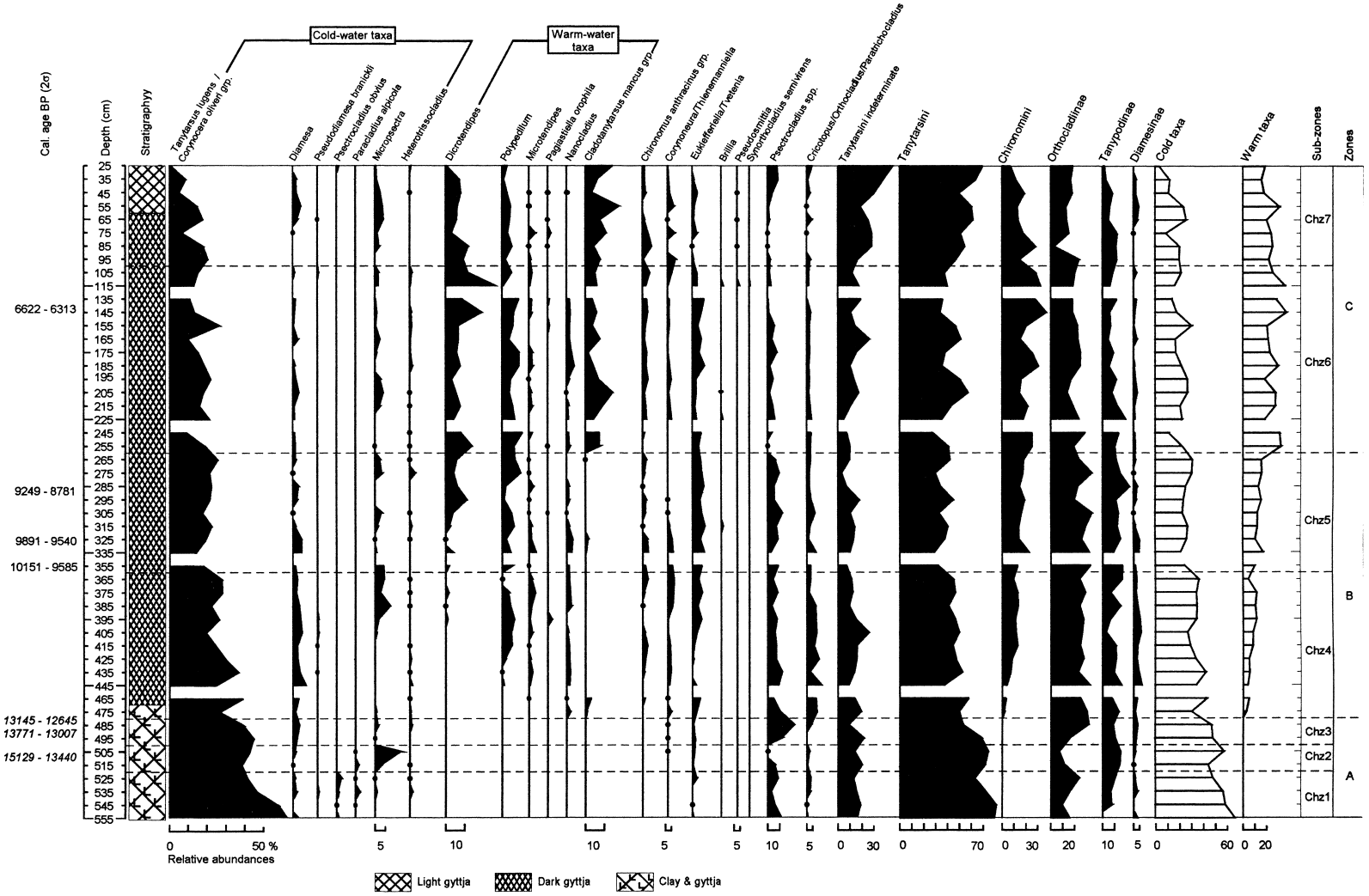


Figure 2. Chironomid percentages from 'Lac Long Inférieur' showing relative abundances (%) of chironomid taxa relative to depth (cm). The dots indicate occurrences of < 1%. Calibrated age B.P. (2σ) and core stratigraphy are shown on the left, whereas on the right, the different zones and sub-zones described in the text are shown.

crease through zone A. This zone is characterised by the absence of taxa adapted to warm water and by the unique occurrence in this zone of the cold stenothermic taxa *Paracladius alpicola* Zetterstedt (1–3%) and *Psectrocladius obvius* Walker (1–3%). This zone is divided into three sub-zones (ChZ-1, ChZ-2, ChZ-3).

Sub-zone ChZ-1 (555–520 cm) shows a regular decrease of the *Tanytarsus lugens* Kieffer/*Corynocera oliveri* group Kieffer (60–38%), together with a peak of Orthocladiinae (20%) at 525 cm.

Sub-zone ChZ-2 (520–500 cm) is marked by a peak of *Micropsectra* Kieffer (13%), higher values of the *Tanytarsus lugens*/*Corynocera oliveri* group (38–43%), and by low percentages of Orthocladiinae (< 10%). This drop is partly caused by a reduction in the number of *Psectrocladius* Kieffer spp., which reach a minimum value (< 1%).

Sub-zone ChZ-3 (500–480 cm) shows a slow decline of the *Tanytarsus lugens*/*Corynocera oliveri* group (45–40%) and an increase of *Psectrocladius* spp. (12–23%). The rheophilous taxa (*Diamesa* Meigen, *Eukiefferiella* Thienemann/*Tvetenia* Kieffer, *Corynoneura* Winnertz/*Thiennemaniella* Kieffer) are present at slightly higher percentages.

Zone B (480–260 cm*)*

Zone B is characterised by increased taxonomic richness and equitability, and there is a notable presence of taxa adapted to warm-waters. Taxa representative of flowing waters, such as *Corynoneura*/*Thienemanniella*, *Eukiefferiella*/*Tvetenia* and *Diamesa*, are also present in higher abundances. The zone is divided into two sub-zones (ChZ-4 and ChZ-5).

In sub-zone ChZ-4 (480–360 cm), taxonomic richness and equitability values continue to increase. The fourth sub-zone is marked by the presence of the Chironomini (*Chironomus anthracinus* grp. Zetterstedt, *Microtendipes* Kieffer, *Polypedilum* Kieffer and *Dicrotendipes* Kieffer), the tribe which groups taxa that are predominantly adapted to warm and temperate waters. *Nanocladius* Kieffer is also present. The *Tanytarsus lugens*/*Corynocera oliveri* group continues to dominate, at a lower abundance than zone A, and appears to decrease through the sub-zone. The *Cricotopus* van der Wulp/*Orthocladius* van der Wulp/*Paratrichocladius* Santos-Abreu group reaches a greater abundance during most of this sub-zone than elsewhere in the entire profile (average 8%). The rheophilous taxa, such as *Diamesa* (4–5%) and *Eukiefferiella*/*Tvetenia* (4–5%), are present at low but significant abundances.

In sub-zone ChZ-5 (360–260 cm), taxonomic richness and equitability both reach maximum values. This sub-zone is characterised by the start of a con-

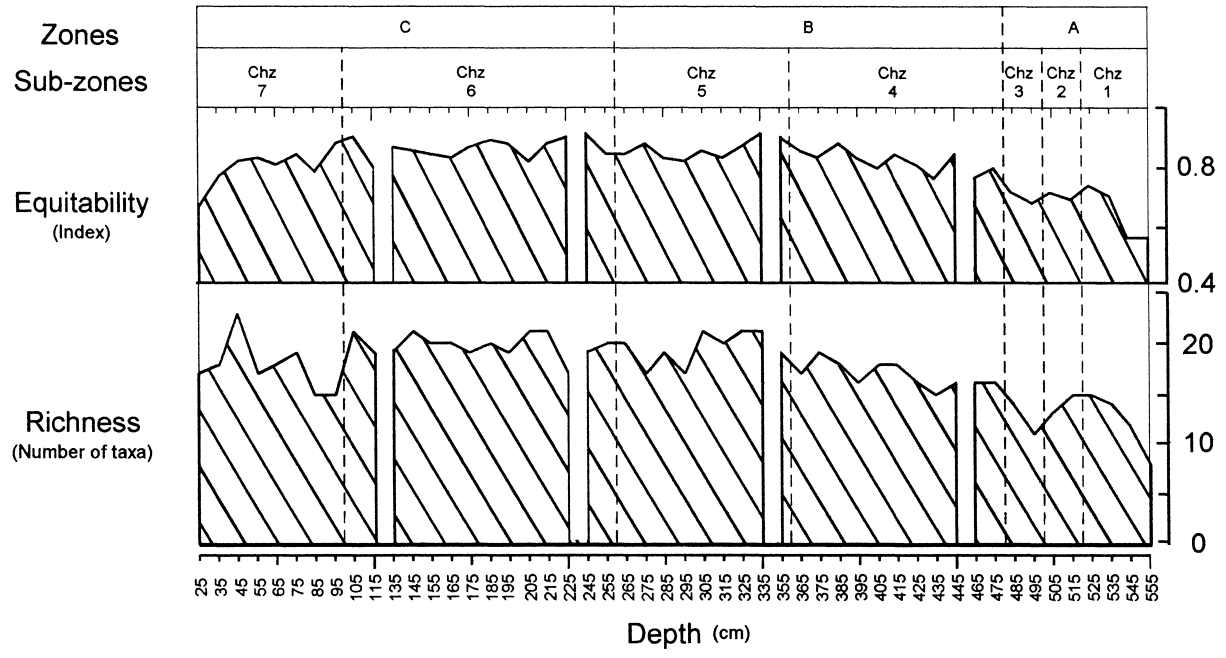


Figure 3. Changes in richness (number of taxa) and equitability (index), relative to depth (cm).

tinuous increase in *Dicrotendipes* and *Polypedilum* (11%). *Eukiefferiella*/*Tvetenia* (11%), also reaches maximum abundances within this sub-zone.

Zone C (260–25 cm*)*

Zone C is characterised, as was zone B, by the presence of taxa adapted to warm and flowing waters, such as *Corynoneura*/*Thienemanniella*, *Eukiefferiella*/*Tvetenia* and *Diamesa*. However, this zone differs from zone B by the continuous presence of the *Cladotanytarsus mancus* Walker group. Zone C has been divided into two sub-zones (ChZ-6 and ChZ-7).

Sub-zone ChZ-6 (260–90 cm) is marked by the start of a continuous increase in *Cladotanytarsus mancus* grp. Within this sub-zone, the cold stenothermic taxa fall to lower levels than those of the taxa adapted to warm-waters, which, with the exception of *Microtendipes* and *Pagastiella orophila* Edwards, remain continuously present. This sub-zone is notable for the dominance of *Dicrotendipes*, which reaches a maximum (27%) at a depth of 115 cm, then declines (27–10%). At this depth, taxa such as *Brillia* Kieffer, *Pseudosmittia* Goetghebuer and *Synorthocladius semivirens* Kieffer make a distinct appearance.

Sub-zone ChZ-7 (90–25 cm) is marked by a drop in the values of the *Tanytarsus lugens*/*Corynocera oliveri* group, with a corresponding increase in the Tanytarsini indeterminate group, which are present at relatively stable values throughout the rest of the sequence. The decrease of *Dicrotendipes*, which began at the end of the sixth sub-zone, continues in the seventh sub-zone (13–1%). The Chironomini group undergoes a general decline across this sub-zone. In the upper part of the sub-zone, equitability values drop noticeably (0.8–0.65), *Psectrocladius* spp. increase, and *Paratanytarsus* Thienemann & Bause and *Psectrocladius obvius* reappear.

Discussion

In zone A, the dominance of cold indicators such as *Tanytarsus lugens*/*Corynocera oliveri* grp. (Lotter et al. 1997; Brooks and Birks 2000), the exclusive presence of the genus *Paracladius* Hirvenoja, noted as a 'strongly cold-stenothermous taxon' by Walker et al. (1997), Pellatt et al. (1998), and the absence of most warm indicators suggest a cold environment, close to late glacial conditions. Brundin (1956) considered the *Tanytarsus lugens* group as oligotrophic taxa, offering further evidence that the waters were cold and oligotrophic at this time. This zone corresponds to sediments with low organic content, such as clay gyttja substrate. Levels of mineral elements in the sediments are closely related to variations in productivity and surface run-off from the watershed. The quantity of run-off is partially dependent on the vegetation cover, which in turn is partially dependent on climatic variables (Levesque et al. 1993). During the Late Glacial, therefore, the lacustrine environment had low levels of production, and was probably located in an open landscape, where erosional effects increased the minerogenic content of the sediment (Merilaïnen et al. 2000). This hypothesis is supported by the pollen reconstruction carried out by Beaulieu (1977), Ponel et al. (2001b), where high percentages of non-arboreal pollen were found during the Late Glacial, notably *Artemisia* and *Poaceae* (Figure 4).

The increase in taxonomic richness and equitability indicate that the lacustrine environment matured and increased in complexity throughout the Late Glacial. Ecological changes can be noted during this period. Zone A presents a similar trend in sub-zones ChZ-1 and ChZ-3, with a progressive increase in the temperature of the surface waters shown by decreases in the percentage of the cold stenothermic *Tanytarsus lugens*/*Corynocera oliveri* grp. (Lotter et al. 1997; Brooks and Birks 2000). In these sub-zones, the Orthocladiinae were probably able to expand with the development of an aquatic flora in the littoral zone (Pinder 1995), but there is no palaeobotanical evidence for this. In addition, the absence of the Chironomini in these two sub-zones suggests that this warming was limited, and water remained oligotrophic.

In the second sub-zone (ChZ-2), the peak of *Microspectra*, combined with an increase in the percentages of the *Tanytarsus lugens*/*Corynocera oliveri* group, appears to show a slight reversal in the progressive trends in temperature and trophic status. *Micropsectra* is currently dominant in Swiss lakes at an altitude greater than 2000 m (Lotter et al. 1997), or in Norwegian lakes where the average air temperature in July is close to or less than 8 °C (Brooks and Birks 2000). This second phase, therefore, appears to represent a period when the lake waters underwent a cooling, possibly the equivalent of the Younger Dryas. Whilst the evidence is too weak to attribute this sub-zone with confidence, this is in good agreement with a maximum of *Artemisia* and a minimum of *Pinus* in the pollen reconstructions (Ponel et al. 2001b), at a depth of 509–513 cm.

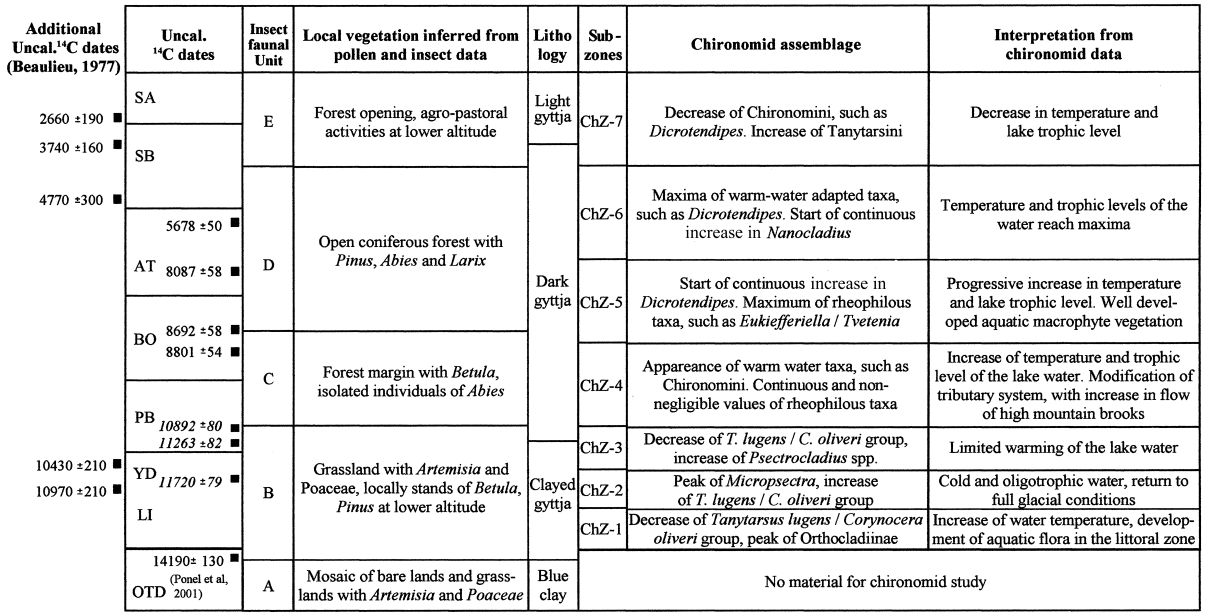


Figure 4. Correlation of lithology, pollen, insect records (Ponel et al. 2001b) and chironomid data. OTD – Oldest Dryas; YD-LI – Younger Dryas-Late Glacial Interstadial; PB – Preboreal; BO – Boreal; AT – Atlantique; SB – Subboreal; SA – Subatlantique. The chronostratigraphy is based on palynological work carried out by Beaulieu (1977) in Southern Alps. The dates in italics are considered too old.

The transition from the Late Glacial to the Holocene is marked by an important change in the composition of the chironomid assemblages. The amelioration of climate during this period resulted in the presence of taxa adapted to warm-waters and by the disappearance of certain cold stenothermic taxa, such as *Paracladius alpicola* and *Psectrocladius obvius*. The beginning of the Holocene was assigned to the same depth by the chironomid data as by the beetle data (Ponel et al. 2001b) (480 cm) (Figure 4). In addition, the transition from the Late Glacial to the Holocene is marked by an important change in the nature of the sediments, from clay gyttja to dark gyttja. The increased organic nature of the sediments is most likely the result of a lacustrine environment and a watershed supporting higher productivity during the Holocene, as well as a decrease in the erosion of the shore and the catchment area (Merilaïnen et al. 2000). Pollen data indicate that tree line was situated close to 'Lac Long Inférieur' at the beginning of the Holocene, during the Preboreal and the Boreal (Beaulieu 1977; Ponel et al. 2001b).

The dates obtained at 513–509, 489–487 and 483–481 cm differ markedly with the generally agreed ages for the regional chronostratigraphy, and are, in general, approximately 800–1000 years too old. The problem of dating has been discussed by Ponel et al. (2001b). The peak of *Micropsectra* at 505 cm, together with the appearance of taxa adapted to warm-waters between 485 and 475 cm (start of the fourth sub-zone), provide strong arguments to doubt the radiocarbon dates. We therefore propose that the Younger Dryas and the start of the Holocene are located respectively at these depths.

During the major part of the Holocene (ChZ-4, ChZ-5 and ChZ-6) water temperature and trophic status show a gradual increase. They both reach their maximum values in the sixth sub-zone, together with maximum values of thermophilous taxa such as *Dicrotendipes*, *Polypedilum* and *Microtendipes* (Hofmann 1983, 1984; Walker et al. 1991a). There is also a continuous presence of the thermophilous taxon, *Cladotanytarsus mancus* group (Serra-Tosio and Laville 1991; Brooks et al. 1997), currently found at mid-altitude in France. During this period, the increase in the number of ecological niches resulting from increased spatial heterogeneity benefit predator taxa. These include *Nanocladius*, which includes some species that are often found in the littoral zone of lakes (Hofmann 1971), and they profit from a better availability of food sources and of warming water. This results in an increase in the values of equitability and taxonomic richness. During the three sub-zones (ChZ-4 to ChZ-6), the chironomid assem-

blages appear to follow the natural evolution of the lake as it fills up.

The Holocene appears to be distinguished from the Late Glacial by a well-developed aquatic vegetation. This is highlighted by the high percentages of taxa frequently associated with aquatic plants, algae and the submerged parts of macrophytes, such as the *Cricotopus/Orthocladius/Paratrichocladius* group (Wiederholm 1983) or associated with vegetated ponds, e.g. the genus *Dicrotendipes* (Hofmann 1984; Brooks et al. 1997). These results are in good agreement with those of Beaulieu (1977) who found high percentages of monolete filicales, often associated with aquatic plants, and the sporadic presence of *Typha* Linné during the Preboreal and Boreal period.

During the Holocene, the presence of a typically rheophilous chironomid assemblage (with the groups *Eukiefferiella/Tvetenia*, *Corynoneura/Thienemanniella* and the genus *Diamesa*) probably represents a modification of the tributary system (Saether 1968; Rück et al. 1998), with inflows from high mountain brooks. The variations in tributaries inflows and hydrological conditions of 'Lac Long Inférieur' were also detected by Coleoptera and Trichoptera assemblages (Ponel et al. 2001b). Warming of the climate, with a longer and more marked spring season, would result in increased and more regular melting of snow at higher altitude, forming tributary streams in the watershed of the lake. These rheophilous species may have been resident in the lake, near the inflows of the tributary streams. Alternatively, the bodies of the rheophilous species may have been transported into the lake by tributary waters. In the fifth sub-zone (ChZ-5), the maximum in the rheophilous *Eukiefferella/Tvetenia* indicates progressive Holocene climate warming and an increase in the length of the warm season. However, it is highly probable that, in addition to the snowmelt from the glaciers, the increase in precipitation (shown by the regional extension of *Abies*, characteristic of the end of the Boreal and the start of the Atlantic period (Beaulieu 1977; Ponel et al. 2001b) increased the flow in the tributaries.

At 115 cm, the presence of rheophilous and xylophagous taxa, such as *Brillia* and *Synorthocladius semivirens* (Rossaro 1982; Wiederholm 1983; Walker and Mathewes 1989), suggest zones of accumulated vegetation debris in parts of the lake. This detritus, in particularly wood debris, were probably deposited in the lake by the tributaries. This indicates the possible existence of trees in the proximity of 'Lac Long Inférieur'. The development and survival of such a population during the sixth sub-zone would have been a result of favourable climatic conditions. Beaulieu (1977) and more recent studies (Ponel et al. 2001a, 2001b) have indicated a coniferous forest close to the 'Lac Long Inférieur'. The vegetation debris, which accumulated in the lake, may have raised the trophic levels of the water, which would explain the presence of the Chironomini, particularly *Dicrotendipes*. The decrease in percentages of *Dicrotendipes* at the end of the sixth sub-zone (ChZ-6) may indicate a decline in the trophic level of the lake, possibly from a decrease in the deposition of organic vegetal material in the lake. This would have been caused by either (1) a drop in the volume of water flowing through the tributaries, as the stocks of snow at high altitude disappeared during the climatic warming of the Atlantic; and/or (2) a decrease in the forest cover brought about by forestry and pastoral practices. This decrease in forest cover would have increased erosion, which is in agreement with the less organic sediment, indicated by a lighter colour above 61 cm. The Subboreal/Subatlantic limit, dated to approximately 2700 BP (Reille 1990; Magny 1995), is probably situated around this depth (61 cm). The reduction of the timberline at the end of the Subboreal and during the Subatlantic, caused by human pressure, was distinctly shown by Coleoptera analysis (Ponel et al. 2001a, 2001b), with the decrease of conifer-dependent insects.

It is equally probable that the similarity between the fossil assemblages of the seventh sub-zone and the Late Glacial, with dominance of Tanytarsini, decrease in warm-water taxa such as Chironomini and reappearance of *Psectrocladius obvius*, suggests a re-cooling of the lake waters. The low presence of the *Tantytarsus lugens/Corynocera oliveri* group, in apparent contradiction to a hypothesis of cooling, are probably an artefact, resulting from the poor preservation of the head capsules observed under stereomicroscope in the upper part of the profile (all species together). This bad preservation is possibly due to taphonomic problems. The low presence of this group could be equally result from shallow lake levels.

A comparison with other palaeoecological studies based on fossil chironomid larvae in other regions highlights the under-representation of the genus *Heterotrissocladius* Spärck in our sediments. This appears surprising, as this genus is currently frequently found in Canadian and Swiss alpine lakes at altitudes above 2000 m (Walker 1990; Lotter et al.

1997). Numerous palaeoecological studies have used *Heterotrissocladius* as an indicator of the Late Glacial in lacustrine sediments, where percentage peaks of *Heterotrissocladius* reveal particularly cold phases (Walker 1987, 1990; Walker and Mathewes 1987; Walker et al. 1991a, 1991b; Levesque et al. 1993; Smith et al. 1998). Walker and Mathewes (1987) confirm that the genus *Heterotrissocladius* is not found in warm climates. However, numerous other factors influence the distribution of Chironomidae species, for example the nature of the sediments (silica, limestone, etc.) (Lotter et al. 1997), salinity (Walker et al. 1995; Lotter et al. 1998) and/or acidity (Guilizzoni et al. 1996; Schnell and Willassen 1996). The low representation of *Heterotrissocladius* in the sediments of 'Lac Long Inférieur' is probably due to the influence of the Mediterranean climate in the southern part of the Alps. This potential influence of the Mediterranean climate and the siliceous nature of the substrate prevent the use of transfer functions developed for Nordic sites at 'Lac Long Inférieur'. It will therefore be necessary to develop a new transfer function, which will take into account the particularities of this region. Further research in this area appears necessary to obtain a better understanding of changes in climate at different temporal and spatial scales.

Livingstone and Lotter (1998), Livingstone et al. (1999) have shown that there are several factors that need to be taken into account before any climatic reconstruction is based on inference models. It is important to choose a site where local factors play a minor role. In the case of 'Lac Long Inférieur', the progressive in-filling of the lake probably had an important effect on water temperature, particularly in the more recent part of the sequence. As the lake became shallower, the amount of water to be heated would be reduced, favouring the establishment of warm-water taxa. The natural filling of the lake may therefore affect climatic interpretations based on sub-fossil assemblages of Chironomidae. This bias would result in an over-estimation of temperatures obtained from a transfer function. Equally, changes in the chironomid assemblages caused by a natural increase in the level of eutrophication of the lake waters could affect climatic interpretations.

Conclusions

The palaeoecological study of the fossil assemblages of Chironomidae, taken from the sediments of 'Lac Long Inférieur', has been shown to be an efficient tool for interpreting changes in water trophic levels and the major climate changes in a high mountain region of the southern Alps, during the Late Glacial and Holocene.

During the initial stages of development, the dominance of cold and oligotrophic indicators and the absence of most warm water indicators suggest a cold environment during the Late Glacial. During this period, in sub-zone ChZ-2, the chironomid assemblages are in good agreement with the pollen data, and may highlight a return to colder conditions, with a notable peak in *Micropsectra*.

During a second period (zones B and C), the progressive Holocene warming climate and increase in lake trophic status were indicated by the presence of more eutrophic and warm water indicators, such as the assemblage of Chironomini in the fourth and fifth sub-zone, and the Chironomini and *Cladotanytarsus mancus* group assemblage in the sixth sub-zone. During the Holocene, an increase in the inflow of tributaries into 'Lac Long Inférieur' was suggested by increases in rheophilous chironomid taxa, probably driven by increased snowmelt. In the seventh sub-zone, the chironomid data suggest a re-cooling of the climate and/or a decrease in lake trophic status.

Neither the chironomid data nor the previously published Coleoptera data detect any marked changes assorted with anthropogenic deforestation for pastoral purposes. The low level of anthropogenic impact on chironomid assemblages could offer a certain advantage for climatic reconstructions, notably temperature, in this Alpine region.

Acknowledgements

The study represents part of the palaeoecological program: 'Paléoenvironnement et Hominidés' (PeH), supported by the CNRS (the French Scientific Research National Center). The 'Parc National du Mercantour' provided logistic support and the necessary authorizations for the coring operations. The A.M.S. dating was carried out by T. Jull at the Laboratory of Physics and Atmospheric Sciences, at the University of Arizona. Recent climatic data were provided by 'Metéo-France' (the French weather office). We wish to thank Dr. Stephen J. Brooks, Mr. Oliver Heiri and all the members of the Chironomid workshop, which took place in Berne in March 2000, for valuable discussions on taxonomic problems. We would also like to thank Dr. Jacques Louis de Beaulieu, Dr.

Philippe Ponel, Dr. Valerie Andrieu-Ponel, Dr. Thierry Keller and Miss Imola Juhasz for fieldwork and comments. We are grateful to Dr. Isabelle Larocque, Dr. John P. Smol and an anonymous referee for corrections and valuable comments on this paper. Finally, we are grateful to Mr. Simon Brewer and Dr. Franck Torre who helped us to translate this paper.

References

Barbero M., Bono P.G., Ozenda P. and Mondino G.P. 1973. Carte écologique des Alpes au 1/100,000. Nice-Menton (R21) et Viève-Cuneo (R 20). Documents de cartographie écologique 12: 49–76.

Beaulieu J.L. 1974. Analyse pollinique des sédements holocènes du lac Long Inférieur (Alpes Maritimes). Rev. biol. écologie méditerranéenne 1: 97–104.

Beaulieu J.L. 1976. Contribution àl'histoire holocène de la végétation dans les Alpes méridionales françaises. Atti del Convegno intern. Sulla communité alpina nell'antichita Ce. SDIR: 195–202.

Beaulieu J.L. 1977. Contribution pollenanalytique à l'histoire tardiglaciaire et holocène de la végétation des Alpes méridionales françaises, Ph.D., Université Aix-Marseille III, Marseille, France 358 pp.

Beaulieu J.L., Clerc J. and Reille M. 1984. Late Weichselian fluctuations in the French Alps and Massif Central from pollen analyses. In: Mörner N.-A. and Karlén W. (eds), Climatic Changes on a Yearly to Millennial Basis. D. Reidel Publishing Company, pp. 75–90.

Beaulieu J.L., Richard H., Ruffaldi P. and Clerc J. 1994. History of vegetation, climate and human action in the French Alps and the Jura over the last 15,000 years. Dissertationes Botanicae 234: 253–275.

Benzecri J.P. 1973. L'analyse des données: II l'analyse des correspondances. Bordas, Paris, France, 620 pp.

Birks H.J.B. and Gordon A.D. 1985. Numerical Methods in Quaternary Pollen Analysis. Academic Press, London, UK, 317 pp.

Brooks S.J. 2000. Late-glacial fossil midge stratigraphies (Insecta: Diptera: Chironomidae) from the Swiss Alps. Palaeogeogr. Palaeoclim. Palaeoecol. 159: 261–279.

Brooks S.J. and Birks H.J.B. 2000. Chironomid-inferred late-glacial and early-Holocene mean July air temperatures for Kråkenes Lake, Western Norway. J. Paleolim. 23: 77–89.

Brooks S.J., Lowe J.J. and Mayle F.E. 1997. The late Devensian late Glacial palaeoenvironmental record from Whitrig Bog, SE Scotland. 2. Chironomidae (Insecta: Diptera). Boreas 26: 297–308.

Brundin L. 1956. Die bodenfaunistischen Seentypen und ihre Anwendbarkeit auf die Sühalbkugel. Zugleich eine Theorie der produktionsbiologischen Bedeutung der glazialen Erosion. Rep. Inst. Freshwater. Res. 37: 186–235.

Bryce D. 1960. Studies of the larvae of the British *Chironomidae* (Diptera), with keys to the *Chironominae* and the *Tanypodinae*. Trans. Soc. Brit. Ent. 14: 19–62.

Bryce D. and Hobart A. 1972. The biology and identification of the larvae of the Chironomidae (Diptera). Entomol. Gaz. 23: 175–217.

Chernovskii A.A. 1949. Identification of Larvae of the Midge Family Tendipedidae. The Zoological Institute of the Academy of Sciences USSR, Moscow, Russia, 280 pp.

Clerk S., Hall R., Quinlan R. and Smol J.P. 2000. Quantitative inferences of past hypolimnetic anoxia and nutrient levels from a Canadian Precambrian Shield lake. J. Paleolim. 23: 319–336.

Cranston P.S. 1982. A Key to the Larvae of the British Orthocladiinae (*Chironomidae*). Scientific Publication of the Freshwater Biological Association, London, United Kingdom, 62 pp.

Cranston P.S. 1995. Introduction. In: Armitage P.D., Cranston P.S. and Pinder L.C.V. (eds), The Chironomidae. Biology and Ecology of Non-Biting Midges. Chapman & Hall, London, UK, pp. 1–7.

Ferrarese U. and Rossaro B. 1981. Chironomidi, 1 (Diptera, Chironomidae: Generalità, Diamesinae, Prodiamesinae. Consiglio nazionale dell ricerche, Verona, Italy, 97 pp.

Francis D.R. 2001. A record of hypolimnetic oxygen conditions in a temperate multi-depression lake from chemical evidence and chironomid remains. J. Paleolim. 25: 351–365.

Frontier S. and Pichod-Viale D. 1998. Ecosystèmes, Structure Fonctionnement Evolution. Dunod, Paris, France, 447 pp.

Goeury C. 1997. Gestion, traitement et représentation des données de la paléoécologie XV ème Symposium de l'Association des Palynologues de Langue Française. Abstracts., pp. 1–31.

Guilizzoni P., Marchetto A., Lami A., Cameron N.G., Appleby P.J., Rose N.L. et al. 1996. The environmental history of a mountain lake (Lago Paione Superiore, Central Alps, Italy) for the last c. 100 years: a multidisciplinary, palaeolimnological study. J. Paleolim. 15: 245–264.

Heiri O. and Lotter A.F. 2001. Effect of low counts on quantitative environmental reconstructions: an example using subfossil chironomids. J. Paleolim. 26: 343–350.

Hofmann W. 1971. Zur Taxonomie und Palöcologie subfossiler Chironomiden (Dipt.) in Seesedimenten. Arch. Hydrobiol. Beih. Ergebn. Limnol. 6: 1–50.

Hofmann W. 1983. Stratigraphy of Cladocera and Chironomidae in a core from a shallow North German lake. Hydrobiologia 103: 235–239.

Hofmann W. 1984. Stratigraphie subfossiler Cladocera (Crustacea) und Chironomidae (Diptera) in zwei Sedimentprofilen des Meerfelder Maares. Cour. Forsch.-Inst. Senckenberg 65: 67–80.

Hofmann W. 1986. Chironomid analysis. In: Berglung B.E. (ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. Wiley & Sons Ltd., Chichester, pp. 715–727.

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). J. Paleolim. 26: 307–322.

Lebart L., Morineau A. and Piron M. 1997. Statistique exploratoire multidimensionnelle. Dunod, Paris, France, 439 pp.

Levesque A.J., Mayle F.E., Walker I.R. and Cwynar L.C. 1993. A previously unrecognized late-glacial cold event in eastern North America. Nature 361: 623–626.

Lindegaard C. 1995. Classification of water-bodies and pollution. In: Armitage P.D., Cranston P.S. and Pinder L.C.V. (eds), The Chironomidae. Biology and Ecology of Non-Biting Midges. Chapman & Hall, London, UK, pp. 385–404.

Livingstone D.M. and Lotter A.F. 1998. The relationship between air and water temperatures in lakes of the swiss Plateau: a case study with palaeolimnological implications. J. Paleolim. 19: 181–198.

Livingstone D.M., Lotter A.F. and Walker I.R. 1999. The decrease in summer surface water temperature with altitude in Swiss Alpine lakes: a comparison with air temperature lapse rates. Arct. Alp. Res. 31: 341–352.

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. J. Paleolim. 18: 395–420.

Lotter A.F., Birks H.J.B., Hofmann W. and Marchetto A. 1998. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. J. Paleolim. 19: 443–463.

Lotter A.F., Walker I.R., Brooks S.J. and Hofmann W. 1999. An intercontinental comparison of chironomid palaeotemperature inference models: Europe vs. North America. Quat. Sci. Rev. 18: 717–735.

Lumley H. 1995. Le grandiose et le sacré. Gravures rupestres protohistoriques et historiques de la région du mont Bego. Edisud, Nice, France, 452 pp.

Magny M. 1995. Une histoire du climat, des derniers mammouths au siècle de l'automobile. Collection des Hesperides. Editions Errance, Paris, France, 175 pp.

Merilaïnen J.J., Hynynen J., Teppo A., Polamäki A., Granberg K. and Reinikainen P. 2000. Importance of diffuse nutrient loading and lake level change to the eutrophication of an originally oligotrophic boreal lake: a palaeolimnological diatom and chironomid analysis. J. Paleolim. 24: 251–270.

Nakagawa T. 1998. Etudes palynologiques dans les Alpes françaises centrals et méridionales: histoire de la végétation Tardiglaciaire et Holocène, Ph.D., Université Aix-Marseille III, Marseille, France 206 pp.

Olander H., Korhola A. and Blom T. 1997. Surface sediment Chironomidae (Insecta: Diptera) distributions along an ecotonal transect in subarctic Fennoscandia: developing a tool for palaeotemperature reconstructions. J. Paleolim. 18: 45–59.

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. Holocene 9: 279–294.

Pellatt M.G., Smith M.J., Mathewes R.W. and Walker I.R. 1998. Palaeoecology of postglacial treeline shifts in the northern Cascade Mountains, Canada. Palaeogeogr. Palaeoclim. Palaeoecol. 141: 123–138.

Pinder L.C.V. 1995. The habitats of chironomid larvae. In: Armitage P.D., Cranston P.S. and Pinder L.C.V. (eds), The Chironomidae. Biology and Ecology of Non-Biting Midges. Chapman & Hall, London, UK, pp. 105–135.

Ponel P., Andrieu-Ponel V., Parchoux F., Juhasz I. and Beaulieu J.L. 2001a. A late-Glacial-Holocene fossil insect succession from Vallée des Merveilles, Lac Long Inférieur, French Alps, and its paleoecological implications. Arct. Alp. Res. 33: 481–492.

Ponel P., Andrieu-Ponel V., Parchoux F., Juhasz I. and Beaulieu J.L. 2001b. Late Glacial and Holocene high altitude environmental changes in Vallée des Merveilles (Alpes-Maritimes, France): insect evidence. J. Quat. Sci. 16: 795–812.

Quinlan R. and Smol J.P. 2001. Setting minimum head capsule abundance and taxa deletion criteria in chironomid-based inference models. J. Paleolim. 26: 327–342.

Reille M. 1990. Leçons de Palynologie et d'analyse pollinique. Editions du CNRS, Paris, France, 206 pp.

Romain O. 1995. Les gravures du Mont Bégo: le secteur des Merveilles et le secteur de Fontanalbe. L'Anthropologie (Paris) 99: 382–392.

Rossaro B. 1982. Chironomidi, 2 (Diptera Chironomidae: Orthocladiinae). Consiglio Nazionale dell Ricerche, Verona, Italy, 80 pp.

Rück A., Walker I.R. and Hebda R. 1998. A palaeolimnological study of Tugulnuit Lake, British Columbia, Canada, with special emphasis on river influence as recorded by chironomids in the lake's sediment. J. Paleolim. 19: 63–75.

Saether O.A. 1968. Chironomids of the Finse area, Norway, with special reference to their distribution in a glacier brook. Arch. Hydrobiol. 64: 426–483.

Saether O.A. 1980. The influence of eutrophication on deep lake benthic invertebrate communites. Prog. Wat. Tech. 12: 161–180.

Schmid P.E. 1993. A Key to the Larval Chironomidae and Their Instars from Austrian Danube Region Streams and Rivers. Part 1. Diamesinae, Prodiamesinae and Orthocladiinae. Wasser und Abwasser Supplement 3. Federal Institute for Water Quality, Wien, Austria, 514 pp.

Schnell O.A. and Willassen E. 1996. The chironomid (Diptera) communities in two sediment cores from Store Hovvatn, S. Norway, an acidified lake. Ann. Limnol. 32: 45–61.

Serra-Tosio B. and Laville H. 1991. Liste annotée des Diptères Chironomidés de France Continentale et de Corse. Ann. Limnol. 27: 37–74.

Smith M.J., Pelatt M.G., Walker I.R. and Mathewes R.W. 1998. Postglacial changes in chironomid communities and inferred climate near treeline at Mount Stoyoma, Cascade Mountains, southwestern British Columbia, Canada. J. Paleolim. 20: 277–293.

Stuiver M., Reimer P.J., Bard E., Beck J.W., Burr G.S., Hughen K.A. et al. 1998. INTCAL98 Radiocarbon age calibration, 24,000 to 0 cal BP. Radiocarbon 40: 1041–1083.

Thioulouse J., Chessel D., Dolédec S. and Oliver J.M. 1997. ADE-4: a multivariate analysis and graphical display software. Stat. Comp. 7: 75–83.

Walker I.R. 1987. Chironomidae (Diptera) in paleoecology. Quat. Sci. Rev. 6: 29–40.

Walker I.R. 1990. Modern assemblages of arctic and alpine Chironomidae as analogues for late-Glacial communities. Hydrobiologia 214: 223–227.

Walker I.R. and Mathewes R.W. 1987. Chironomidae (Diptera) and postglacial climate at Marion Lake, British Columbia, Canada. Quat. Res. 27: 89–102.

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. J. Paleolim. 2: 61–80.

Walker I.R., Smol J.P., Engstrom D.R. and Birks H.J.B. 1991a. An assessment of Chironomidae as quantitative indicators of past climatic change. Can. J. Fish. aquat. Sci. 48: 975–987.

Walker I.R., Mott R.J. and Smol J.P. 1991b. Allerød-Younger Dryas lake temperatures from midge fossils in Atlantic Canada. Science 253: 1010–1012.

Walker I.R., Wilson S.E. and Smol J.P. 1995. Chironomidae (Diptera): quantitative palaeosalinity indicators for lakes of western Canada. Can. J. Fish. aquat. Sci. 52: 950–960.

Walker I.R., Levesque A.J., Cwynar L.C. and Lotter A.F. 1997. An expanded surface-water palaeotemperature inference model for use with fossil midges from eastern Canada. J. Paleolim. 18: 165–178.

Wiederholm T. 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. Ent. Scand. 19 Suppl.: 1–457.