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## Freshwater midges of the Yukon and adjacent Northwest Territories: a new tool for reconstructing Beringian paleoenvironments?

IAN R. WALKER<sup>1,2,3,6</sup>, ANDRÉ J. LEVESQUE<sup>1,3,5</sup>, REINHARD PIENITZ<sup>2</sup>,  
AND JOHN P. SMOL<sup>4</sup>

<sup>1</sup>Departments of Biology, and Earth and Environmental Sciences, North Kelowna Campus, Okanagan University College, 3333 College Way, Kelowna, British Columbia, Canada V1V 1V7

<sup>2</sup>Centre d'études nordiques and Department of Geography, Université Laval, Québec, Québec, Canada G1K 7P4

<sup>3</sup>Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6

<sup>4</sup>Department of Biology, Queen's University, Kingston, Ontario, Canada K7L 3N6

**Abstract.** Distributions of freshwater midges, including Chironomidae, Chaoboridae, and Ceratopogonidae, were analyzed along a transect of lakes extending north from Whitehorse (Yukon Territory) to the Arctic Ocean (Northwest Territories). *Abiskomyia*, *Mesocricotopus*, *Monodiamesa*, and *Paraccladius* were restricted to arctic tundra lakes, whereas *Chaoborus*, *Pseudochironomus*, *Polypedilum*, and *Glyptotendipes* were clearly associated with forest and forest-tundra environments. Many other taxa were broadly distributed with little apparent regard to latitude or ecoclimatic region. Canonical correspondence analyses revealed that midge distributions were most strongly correlated with total Kjeldahl N, maximum lake depth, pH, and summer surface water temperature. The distribution patterns suggest that subfossil midges may provide valuable proxy evidence for paleoenvironmental conditions in the Beringian region of northwestern Canada and Alaska.

**Key words:** Chironomidae, *Chaoborus*, Yukon, Northwest Territories, Beringia, arctic, paleoecology, paleolimnology.

Relationships among species distributions and environmental factors have long provided a focus for chironomid ecological research. Beginning with the pioneering work of Thienemann (1915, 1921), and later Brundin (1949, 1951, 1958), Sæther (1979, 1980), and Lotter et al. (1998), researchers quickly recognized the importance of hypolimnetic oxygen concentrations and lake trophic state as key factors regulating species distributions. Other factors, such as lake depth, salinity, pH, and dissolved organic C, also influence community composition, and their importance over long gradients has been recognized (Timms et al. 1986, Walker et al. 1985, 1991, 1995, Walker 2001).

The importance of temperature and climate also has been recognized in more recent chironomid studies (Walker and Mathewes 1989, Walker et al. 1991, 1992, Lotter et al. 1997, Olander et al. 1997, 1999, Brodersen and Anderson 2002). Temperature may be the dominant factor regulating midge distributions over broad cli-

matic gradients. Therefore, subfossil remains of these insects can provide means for quantitatively reconstructing past temperatures (Walker 1995, 2001). Battarbee (2000) recently concluded that chironomids were among the best indicators currently available for paleoclimatic research.

We document midge distributions and explore their relationships with environmental variables among 56 lakes in northwestern arctic and subarctic Canada. The lakes span a 1200-km latitudinal transect from Whitehorse, Yukon Territory (YT), to the Mackenzie River delta, Northwest Territories (NWT), adjacent to the Arctic Ocean. This transect encompasses the transition from subarctic boreal forest in the south, to alpine tundra at high elevations in the central YT, and to arctic tundra at sea level along the Arctic coast, NWT (Fig. 1). Walker et al. (1991) conducted an assessment of midge distributions in Labrador, and several comparable studies have since been conducted in Europe (Lotter et al. 1997, Olander et al. 1997, 1999), but no similarly detailed analyses have been published for freshwater lakes in northwestern Canada.

<sup>5</sup> Present address: 2 King's Court, St. Stephen, New Brunswick, Canada E3L 3B2.

<sup>6</sup> E-mail address: iwalker@ouc.bc.ca

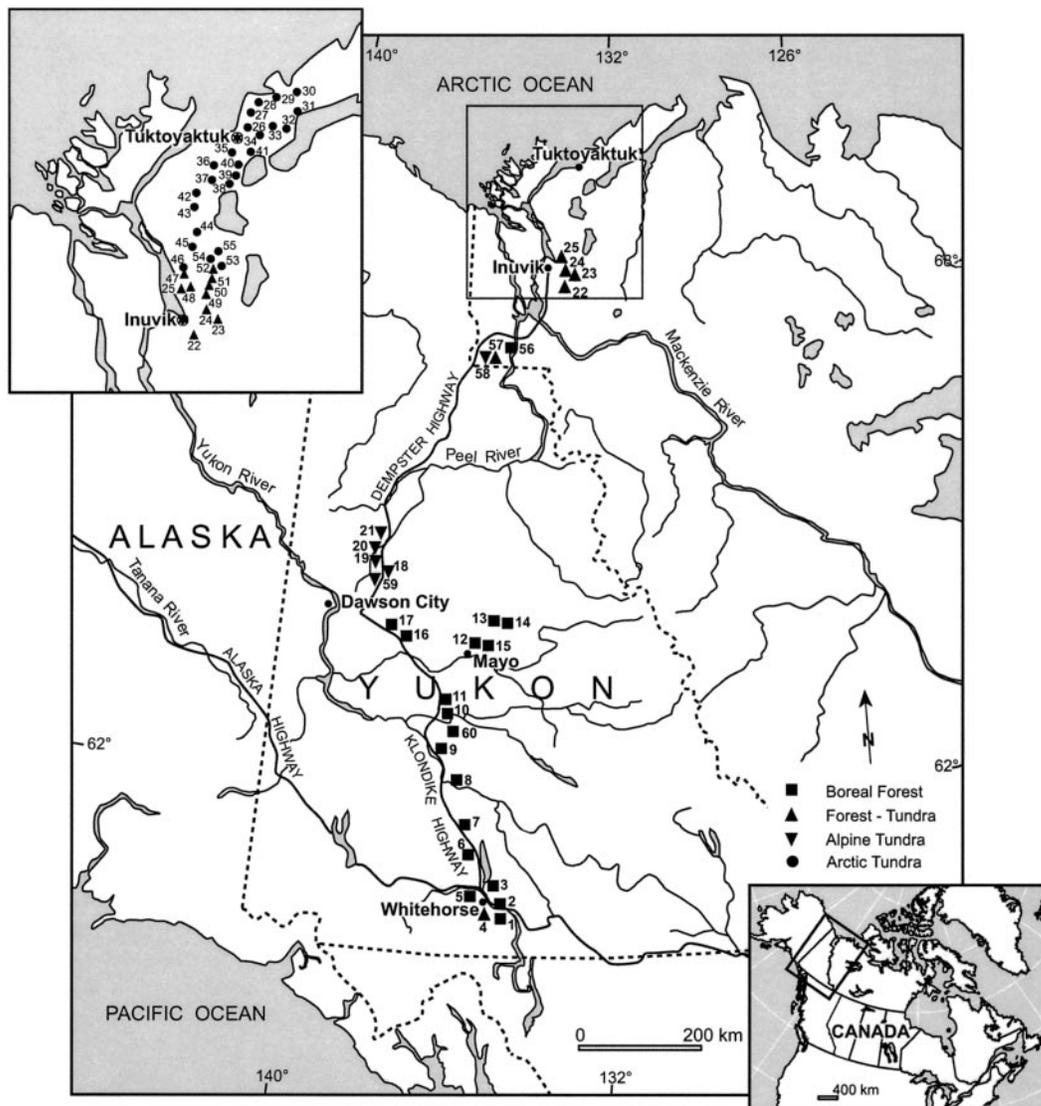


FIG. 1. Location of sampling sites along the transect from Whitehorse, Yukon Territory, to Tuktoyaktuk, Northwest Territories, in northwestern Canada. Lake numbers follow those used in Pienitz et al. (1995, 1997). Top left inset shows detail of transect from Inuvik to Tuktoyaktuk. Lower left inset shows position of study region within Canada.

This assessment of midge distributions will provide a key resource for the interpretation of midge paleoecological research in northwestern Canada and adjacent Beringia. Beringia, the unglaciated land bridge that connected North America and Eurasia through the last glaciation, encompassed much of Alaska, part of the Yukon, and easternmost Siberia. The Beringian

fauna included many large, extinct mammals (e.g., mammoth, mastodon).

Beringia has long been regarded as the most likely avenue for human migration into the Americas. Thus, the nature of Beringian paleoenvironments is a key issue in American paleontological and archeological research. Nevertheless, despite years of research, much con-

troversony concerning the Beringian climate, vegetation, megafauna, and archeological record remains (Cwynar and Ritchie 1980, Guthrie 1985, Colinvaux 1986, Zimov et al. 1995, Elias 2000). Researchers, for example, have long debated details of the glacial climate of Beringia, and whether this climate could have supported a vegetation sufficiently productive to support large populations of grazing mammals (Guthrie 1985, Colinvaux 1986). Similarly, were climatic and vegetation change responsible for the demise of the megafauna, or did human immigrants hunt the fauna to extinction (Martin 1984)?

New indicators are needed to test conflicting hypotheses with respect to past environmental changes in the region. If analyses of fossil Beringian midges can provide reliable means for reconstructing Beringian climate, then they could play a key role in resolving these issues. We evaluate the indicator value of midges for the region.

### Methods

#### *Study sites*

We sampled 56 lakes located between Whitehorse, YT, and Tuktoyaktuk, NWT, ranging from lat 60°37' to 69°35' N and from long 132°04' to 138°22' W (Fig. 1). The lakes spanned a broad climatic gradient; thus, the study area covers 4 major ecoclimatic provinces: Cordilleran, Subarctic Cordilleran, Subarctic, and Arctic (Ecoregions Working Group 1989).

We needed to select lakes similar to those we would later core, to use these data for subsequent interpretation of detailed fossil stratigraphic records. Thus, undisturbed lakes of fairly similar circular shape and simple morphology were selected. Lakes receiving drainage from upstream lakes or rivers were not sampled, to avoid mixed lake and stream assemblages.

Most of the lakes were unnamed and, therefore, they were numbered in consecutive order of sampling. The physiography, geology, vegetation, and soils along the transect are heterogeneous and are described by Pienitz (1993) and Pienitz et al. (1995, 1997).

Lake locations and the physical and chemical conditions of the study sites are also summarized in Pienitz et al. (1997). The water chemis-

try characteristics of the study lakes are diverse. Most are dilute (mean conductivity = 128  $\mu$ S/cm) and slightly acidic to alkaline (pH range 5.9–9.3). Total N (TN) and total P (TPU) vary from 123 to 1585  $\mu$ g/L and 3.0 to 55.1  $\mu$ g/L, respectively. Water transparency is generally lowest within peatland areas of the Forest-Tundra Zone (e.g., sites 23, 24, and 47–52). Many lakes are tea-colored in these areas because of high inputs of humic and fulvic acids from their catchments. Lake altitudes range from 15 m to 1387 m above sea level. Most of the lakes are small to intermediate in size, with surface areas ranging between 1.1 and 547 ha and maximum depths from 1 to 49 m.

The climate of the southern Yukon is subarctic continental, typified by long, cold winters and short, warm summers, large annual day-to-day and daily ranges in temperature, and low-to-moderate and irregular precipitation (Wahl et al. 1987). The mean annual temperature is below freezing in all areas, ranging from near 0°C in the south to  $\sim$ -10°C in the north and at higher altitudes (Pienitz et al. 1997). Mean annual precipitation is generally low ( $\sim$ 200–450 mm) throughout the study area (Environment Canada 1986), mainly as a result of the rain-shadow effect of the coastal mountain barrier in the southwest. The term *subarctic* indicates that, although severe cold spells can develop, the proximity to the Pacific Ocean results in frequent intrusions of mild air in winter. The climate of the northernmost part of the study area, including the Inuvik and Tuktoyaktuk lowland areas, is arctic maritime because it is influenced primarily by weather patterns from the Arctic Ocean. The large central portion of the study area basically endures a cold, continental climate.

Lakes located in the south-central portion of the Yukon are mostly dimictic (Shortreed and Stockner 1986) and were thermally stratified during the summer of 1990 (sites 3, 5–17; Fig. 1). The duration of ice-cover on these lakes extends from October–November to May–June (Canadian National Committee for the International Hydrological Decade 1978). Small (5–10 ha) lakes in the Forest-Tundra Zone near Inuvik are usually ice-free by 15 June and freeze over by 15 October, and ice break-up/freezing events occur roughly 2 wk later and earlier, respectively, in the Arctic Tundra Zone of the study area (Koivo and Ritchie 1978). Large (>50

ha) lakes become ice-free ~2 wk later than smaller ones.

*Chemical analyses, physical measurements, and sediment sampling*

The lakes were sampled from 2 to 23 July 1990. Specific conductance, pH (non-aerated), temperature, and water transparency (Secchi depth) were measured on site, whereas water chemistry determinations (see below) were made from surface-water samples (~50 cm deep) collected from near the center of each lake (Pienitz 1993). Laboratory analyses of nutrients, major ions (except Mg), trace metals, and chlorophyll *a* were performed at the National Laboratory for Environmental Testing (Environment Canada, Burlington, Ontario), following standard methods (Environment Canada 1994).

Lake altitudes were derived from topographic maps, and their surface areas were determined by tracing their perimeters on 1:50,000-scale topographic maps using an HP ScanJet Plus Digitizer. Maximum depths were recorded during repeated sampling for surface sediment and, in a few cases, were based on exploratory sounding transects using a Ray Jeff MX2550 echo sounder. Predominant catchment vegetation was described while in the field.

Surface sediments were sampled near the center of each of the 56 lakes, using a modified Kajak-Brinkhurst gravity corer (Glew 1989) and a Glew (1991) minicorer. The top 2 cm of sediment were collected from each core using a Glew (1988) extruder and stored in Whirlpak® bags. This sample represented an integrated sample (in space and time) of the midge remains that have accumulated over the previous few years. The remains preserved in one sample were used to characterize the fauna in each lake. This sampling strategy focused on interlake variability. Elsewhere, detailed analyses of within-lake variability have been conducted by Iovino (1975) and Walker et al. (1984). Full details of field sampling methods, water chemistry, and other analyses are provided in Pienitz (1993) and Pienitz et al. (1995, 1997).

*Sediment analysis*

Processing of sediment for midge analysis followed the methods outlined in Walker et al. (1991). Sediment was first deflocculated in a

warm solution of 5% KOH, and subsequently sieved on a 95- $\mu$ m mesh. The remaining residue was examined in a Bogorov counting tray at 50 $\times$  magnification for head capsules.

Counting of head capsules followed the standard protocol outlined by Walker et al. (1991). The number of head capsules in each sample varied greatly ( $\bar{x} \pm SD = 278 \pm 109$ , min. = 136, max. = 902), but always exceeded the recommended minimum of 50 (Heiri and Lotter 2001, Quinlan and Smol 2001, Walker 2001).

Picked head capsules were mounted in Entellan® mounting medium and later identified, with reference primarily to Oliver and Roussel (1983), Wiederholm (1983), and Walker (1988). Identifications were rarely possible below the generic level, based solely on a few preserved features of the head capsule. In some cases,  $\geq 2$  genera were lumped to form a single category (e.g., *Cricotopus/Orthocladius*, *Cyphomella/Harnischia/Paracladopelma*). Six groups were separated within the subtribe Tanytarsina: *Corynocera oliveri* type, *Corynocera ambigua* type, *Micropectra* type (with pointed apicomesal projection), Tanytarsina blunt type (with blunt apico-mesal projection), Tanytarsina group SAP (with short antennal pedestal), and other Tanytarsina (normal antennal pedestal and no apicomesal projection).

*Data analysis*

Analysis of the data followed Pienitz et al. (1995) closely. The environmental data consisted of 35 physical, chemical, and biological variables that were measured for each lake and were considered ecologically important. These variables included water chemistry (pH, conductivity [COND], TPU, total dissolved P [TPF], soluble reactive P [SRP], NO<sub>2</sub>, NO<sub>3</sub>, NH<sub>3</sub>, total Kjeldahl N [TKN], TN, particulate N [PN], particulate organic C [POC], dissolved organic C [DOC], dissolved inorganic C [DIC], SiO<sub>2</sub>, Cl, SO<sub>4</sub>, Na, K, Ca, Fe, and Mn), water transparency (TRANSP), surface-water temperature (TEMP), lake surface area (AREA), elevation (ELEV), maximum depth (DEPTH), latitude (LAT), longitude (LONG), and concentrations of uncorrected (CHLaU) and corrected chlorophyll *a* (CHLaC). In addition, the 4 main vegetation zones (Boreal Forest [FOREST], Subarctic Woodland [WOOD; includes both Forest-Tundra and Lichen Woodland], Arctic Tundra [TUNDRA], and Alpine

Tundra [ALPINE]) occurring in our calibration set of lakes were entered as binary variables (value 0 or 1). (Abbreviations correspond to the labels used in the figures and tables.) The positively skewed nature of some of the environmental variables was alleviated by a  $\ln(x + 1)$  transformation, where  $x$  was the environmental variable under consideration (Zar 1984). All ordinations were performed using the computer program CANOCO version 3.12 (ter Braak 1991).

The taxon and environmental data were screened prior to statistical analysis, to identify and eliminate rare taxa, redundant environmental variables, unusual or outlier samples, and environmental variables that did not appear to determine midge distributions (Birks et al. 1990). The taxon data were transformed to square-root % prior to our analyses. Only midge taxa that constituted  $\geq 2\%$  of the fauna in  $\geq 2$  lakes were included. The variables  $\text{NO}_2$ ,  $\text{NO}_3$ ,  $\text{NH}_3$ , and SRP were below their respective detection limits in  $>50\%$  of the lakes, and were therefore eliminated as possible explanatory variables for midge distributions. Environmental variables showing high collinearity in a series of exploratory detrended correspondence analyses (DCA) in which the environmental variables had been regressed onto the DCA axes (ter Braak 1987a) were also deleted. Environmental variables were deleted sequentially, eliminating one variable per DCA run (i.e., deleting the variable with the highest variance inflation factor), until all of the remaining variables had variance inflation factors  $<20.0$ . In total, 7 environmental variables (TN [highly correlated with TKN], PN [highly correlated with POC], ELEV [most strongly positively correlated with LONG, negatively with Cl and LAT], TUNDRA [positively correlated with Cl, negatively with ELEV], COND [strongly correlated with Ca], DIC [strongly correlated with Ca], and LAT [strongly negatively correlated with FOREST, ELEV, and LONG]) were deleted.

Samples were declared outliers and deleted from further analysis if they had an unusual midge assemblage and/or an unusual combination of environmental variables. *Unusual* was defined as samples in which: 1) the sample score fell outside the 95% confidence limits about the sample score means (only on axes reflecting data structure; Gauch 1982) in both the DCA of the taxon data and a principal component anal-

ysis (PCA) of the environmental data in the complete data set (deleted samples 8, 32, and 58); or 2) an environmental variable had extreme ( $>8\times$ ) influence, as detected by leverage diagnostics in canonical correspondence analysis (CCA) (deleted samples 42, 48, 51, 56, 57, and 59) (ter Braak 1990). Following the data-screening procedures outlined above, the surface sample data set used in CCA consisted of 47 samples, 36 midge taxa, and 24 environmental variables (LONG, DEPTH, AREA, pH, TEMP, TRANSP, K, Na, Ca, Fe, Mn, Cl,  $\text{SO}_4$ ,  $\text{SiO}_2$ , TPU, TPE, TKN, POC, DOC, CHLaU, CHLaC, ALPINE, WOOD, FOREST).

Principal patterns of faunistic variation in the data were identified using DCA with detrending via 26 segments. In addition, CCA was used to identify which environmental variables could directly account for variations observed in the midge data. The minimal number of explanatory variables to be included in the CCA, explaining statistically significant ( $p \leq 0.05$ ) proportions of variation in the midge data, were identified using the forward-selection option of CCA, which is analogous to the forward-selection process used in stepwise multiple regression (ter Braak 1990). Monte Carlo permutation tests (with 999 unrestricted permutations) were also used to test the statistical significance of the forward-selected variables and the CCA axes (ter Braak 1990). The taxon scores in all CCAs were scaled to be weighted averages of the site scores. Canonical coefficients (significance judged by approximate  $t$ -tests) and intraset correlations were examined to estimate the relative contributions of the individual environmental variables to the ordination axes (ter Braak 1987a, b).

## Results

A total of 69 midge taxa was recorded from the study sites. Distributions along our transect revealed the geographical range of individual midge taxa in relation to latitude and major vegetation zones (Fig. 2). Taxa that tended to be most abundant in tundra environments included *Abiskomyia*, *Mesocricotopus thienemanni*, *Zalutschia* type 2, *Heterotrissocladius*, *Protanypus*, *Parakiefferiella nigra*, *Micropsectra* type, *Monodiamesa*, *Stictochironomus*, *Paracladius*, and *Tanytarsina* group SAP. Some of the tundra taxa (e.g., *Abiskomyia*, *Mesocricotopus*, *Monodiamesa*, and

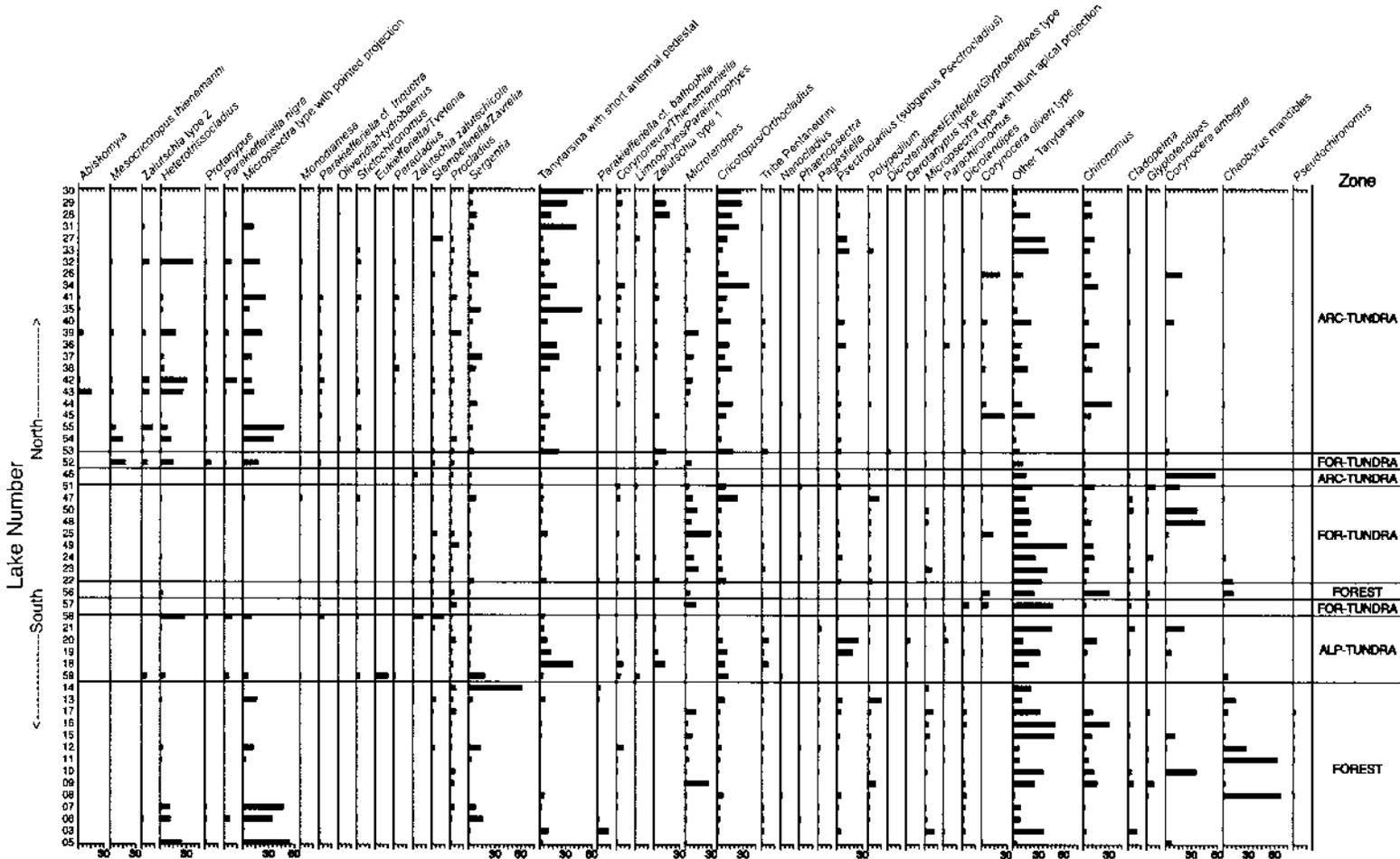


FIG. 2. Percentage diagram depicting the distribution of common midges (i.e., those with an abundance  $\geq 2\%$  in  $\geq 2$  lakes) in the study area. Chironomid head capsule and *Chaoborus* mandible abundances are both expressed as a % of the total identifiable Chironomidae. The lakes are ordered by latitude, with vegetation/ecoclimatic regions indicated at the right of the diagram. ALP = Alpine, ARC = Arctic, FOR = Forest. (Analysis by AJL.)

*Paracladius*) were restricted to Arctic Tundra sites. No taxa, however, were found exclusively at Alpine Tundra sites. Some of the taxa common in tundra lakes (*Heterotrissocladius*, *Protanypus*, *Parakiefferiella nigra*, *Micropsectra* type, and Tanytarsina group SAP) also were abundant in a few deep forest lakes near the southern limit of the transect. A few taxa were clearly most abundant in Forest and Forest-Tundra zones (*Chaoborus*, *Pseudochironomus*, *Polypedilum*, and *Glyptotendipes*), but many (e.g., *Stempellinella/Zavrelia*, *Procladius*, *Sergentia*, *Microtendipes*) were broadly distributed, with little apparent regard to latitude or vegetation type.

#### DCA and CCA

DCA revealed a gradient length of 2.08 SD units, confirming that unimodal ordination methods were best suited for analysis of the taxon data. The patterns revealed by DCA were similar to those evident in CCA, so DCA is not considered further. The overall similarity of the DCA and CCA biplot patterns suggested that the measured environmental variables were useful descriptors of the ecological gradients most important to the midge assemblages.

The CCA sample scores showed a clear separation of sites along the ecoclimatic gradient (Fig. 3A). Low scores on both axes 1 and 2 distinguished Arctic and Alpine Tundra sites from Boreal Forest and Forest-Tundra lakes. Common taxa most clearly associated with Arctic and Alpine Tundra lakes in the CCA included *Abiskomyia*, *Paracladius*, *Parakiefferiella triquetra*, *Stictochironomus*, Tanytarsina group SAP, and *Zalutschia* (Fig. 3B). *Chaoborus*, *Glyptotendipes*, and *Pagastiella* were the common taxa most closely associated with Boreal Forest lake assemblages.

Sites with low axis 1 scores included some of the deepest lakes in each ecoclimatic zone (e.g., 6, 7, 39, 43, 52, 55). These lakes had an abundance of taxa commonly associated with deep, cold, well-oxygenated, or oligotrophic environments (e.g., *Abiskomyia*, *Mesocricotopus*, *Protanypus*, *Parakiefferiella nigra*, *Heterotrissocladius*). Sites with high axis 1 sample scores were mostly comparatively shallow lakes (e.g., 15, 16, 50). Corresponding taxa with high scores on axis 1 included many common littoral taxa (e.g., *Glyptotendipes*, *Cladopelma*, *Polypedilum*).

Five variables (TKN, DEPTH, pH, TEMP, and

ALPINE) accounted for 52% (0.470/0.901) of the explained variance in the taxon data (Table 1). TKN potentially accounted for 22% (0.20/0.901) of the total explainable variance, a greater proportion than any of the 23 remaining variables. Individually, DEPTH, pH, TEMP, and ALPINE, respectively, accounted for 12% (0.11/0.901), 7% (0.06/0.901), 7% (0.06/0.901), and 4% (0.04/0.901) of the total explainable variance (Table 1).

Forward selection provided a useful means for identifying a subset of significant explanatory variables, but the results depended on the variables initially used in the procedure and the order of selection. Therefore, the forward-selection procedure was repeated 1) without deleting any of the collinear environmental variables, and 2) by 1st selecting the 2nd most important variable (DEPTH). In the 1<sup>st</sup> instance (without deletion of collinear variables), the order of selection became TKN>DEPTH>LAT>pH>TEMP>DIC>Mn. Thus, 4 of the initial 5 variables were again identified as potentially important factors controlling midge distributions. A close relationship between lake temperatures and latitude was obviously expected within the study region. The selection of LAT in place of TEMP, therefore, was scarcely a remarkable change in the ordination. In the 2nd instance (i.e., DEPTH selected 1st), the order of forward selection proceeded as follows: DEPTH>TKN>pH>TEMP>ALPINE. Thus, the same environmental variables were identified as in our initial CCA run. The ordination was also re-run with all samples (including outliers) and all variables (including collinear variables) included, to assess the impact of our outlier identification procedure on the ordination. The first 4 variables identified as significant in forward selection were TN>DEPTH>LAT>pH. These results suggested that the outcome of the forward-selection procedure was relatively stable, and served as a useful guide to interpretation of the midge-environment relationships.

Monte Carlo tests confirmed the overall significance of the CCA ( $p < 0.001$ ). All 4 of the ordination axes were also statistically significant (Table 2). The 1st, 2nd, 3rd, and 4th axes, respectively, accounted for 55.5%, 22.9%, 11.2%, and 6.0% of the taxon-environment relation (Table 2). TKN was most closely correlated (positively) with axis 1, whereas DEPTH had a strong negative correlation with this axis (Table 3). TEMP had a strong positive correlation with axis 2, and pH was most closely correlated (neg-

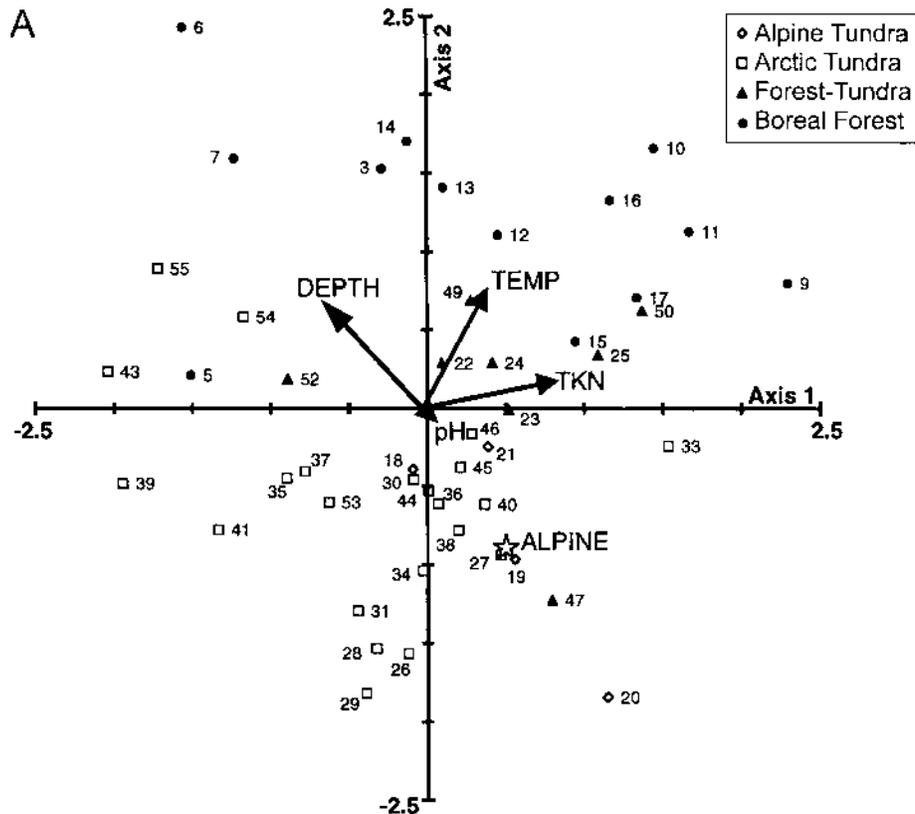


FIG. 3. Canonical correspondence analysis (CCA) output. A.—CCA sample scores depicting the separation of lakes from major vegetation/ecoclimatic regions, and in relation to significant, forward-selected environmental variables. Lake numbers follow those provided in Fig. 1. B.—Taxon scores depicting relationships among midge taxa and significant, forward-selected environmental variables. Abbreviations for midge taxa: Ab, *Abiskomyia*; Ch, *Chironomus*; Cl, *Cladopelma*; CO, *Cricotopus/Orthocladus*; Co, *Corynocera ambigua*; co, *Corynocera oliveri*; CT, *Corynoneura/Thienemanniella*; cU, *Chaoborus*; Di, *Dicortendipes*; Gl, *Glyptotendipes*; Hr, *Heterotrissocladius*; Li, *Limnophyes/Paralimnophyes*; MB, *Micropsectra* type; MP, *Tanytarsina blunt* type; MT, *Mesocricotopus thienemanni*; Mt, *Microtendipes*; Pa, *Pagastiella*; pa, *Paracladius*; pB, *Parakiefferiella* type B; Pc, *Parachironomus*; PE, *Psectrocladius* (subgenus *Psectrocladius*); Pe, Tribe Pentaneurini; PF, *Phaenopsectra* type; pN, *Parakiefferiella nigra*; Po, *Polypedilum*; Pr, *Procladius*; pT, *Parakiefferiella triquetra* type; Py, *Protanypus*; Se, *Sergentia*; Si, *Stictochironomus*; SZ, *Stempellinella/Zaorelia*; Ta, other *Tanytarsina*; TS, *Tanytarsina* SAP type; Z, *Zalutschia* type 1; Z2, *Zalutschia* type 2; Zz, *Zalutschia zalutschicola*.

actively) with axis 3. ALPINE was most closely associated with axis 4.

### Discussion

In general, the fauna (Fig. 2) was similar to that reported for Labrador (Walker et al. 1991, 1997). Taxa not reported in Labrador included *Monodiamesa* and *Corynocera ambigua*. Walker et al. (1991) had misidentified *Mesocricotopus* in their initial research, but it was later discovered

in the material, as subsequently reported by Walker et al. (1997).

*Corynocera ambigua* is common in the western Arctic and subarctic regions (Walker and MacDonald 1995), including many of the southernmost islands of the Arctic Archipelago, but it has never been recorded from Québec/Labrador. Neither this species nor *Abiskomyia* have ever been recorded south of ~60°N in North America, even as subfossils. Thus, these taxa are likely to have spread eastward from a Beringian

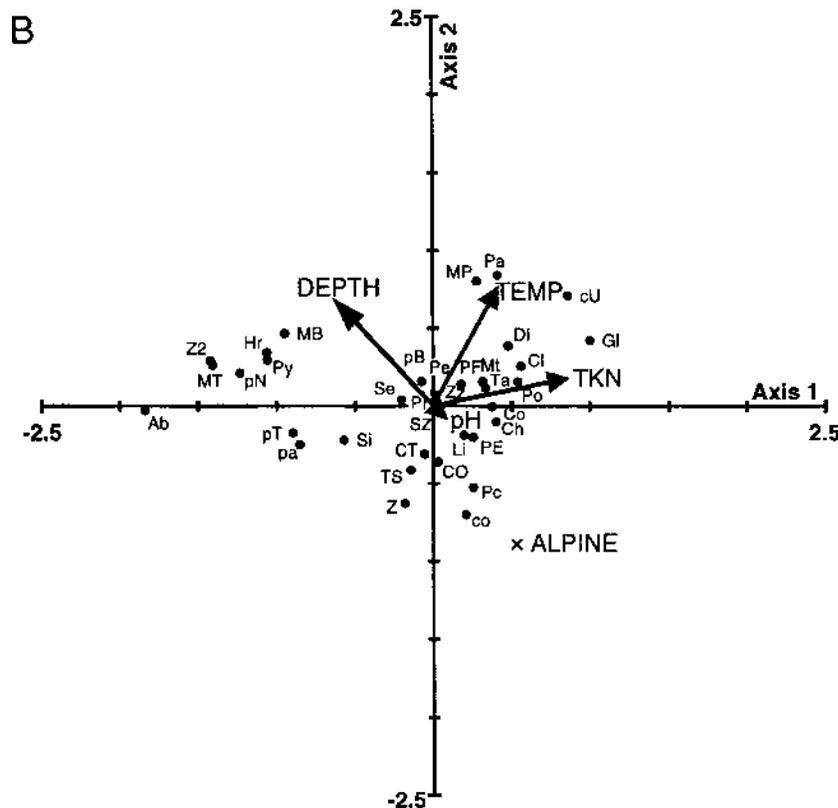


FIG. 3. Continued.

refugium during the Holocene epoch. They may be regarded as Beringian elements in the modern fauna. Nevertheless, *Abiskomyia* and *Corynocera ambigua* have a long history in North America. Both taxa are present in Tertiary sediments from Meighen Island in the Canadian high Arctic (IRW, unpublished data), and *Corynocera ambigua* is also recorded in Plio-Pleistocene deposits from northernmost Greenland (Böcher 1989).

#### TKN and lake productivity

Midge distributions were more highly correlated with TKN than any other variable. TKN provides an indication of nutrient availability and, thus, trophic state. In the CCA data set, TKN was most strongly correlated with TN ( $r = 0.99$ ), DOC ( $r = 0.84$ ), TPU ( $r = 0.70$ ), POC ( $r = 0.68$ ), PN ( $r = 0.65$ ), and DEPTH ( $r = -0.49$ ).

A midge-TKN inference model might be very

useful for reconstructing human impacts on lakes, as well as natural processes, so it would be useful to know whether the nutrient effect was evident within each ecoregion, or only across all ecoregions. This possibility was explored further using a partial CCA. The 1st axis was constrained to represent TKN, and all of the ecoregions were entered as covariables. The result indicated that TKN still explained significant variance in the midge data, independent of ecoregion. A series of CCAs (one for each of the 4 ecoregions) was also performed, with the 1st axis constrained to represent TKN. In each instance, TKN explained significant variation in the midge data. These results indicate that TKN is an important explanatory variable within each ecoregion, and not just across the whole data set.

Chironomids have long been used as indicators of water quality, lake productivity, and hypolimnetic anoxia (Quinlan et al. 1998, Lotter et al. 1998). Therefore, it is surprising that trophic

TABLE 1. Variance explained by environmental variables as added during forward selection in canonical correspondence analysis, as compared to the total variance explainable with all variables included. Variable abbreviations are explained in Methods.

Variable	Total variance potentially explained	Variance explained by variable as added during forward selection	Probability
TKN	0.20	0.20	0.001
DEPTH	0.16	0.11	0.001
TPU	0.15		
DOC	0.14		
POC	0.12		
TEMP	0.12	0.06	0.001
FOREST	0.10		
TPF	0.08		
TRANSP	0.07		
LONG	0.07		
Cl	0.07		
Mn	0.07		
Na	0.06		
Fe	0.06		
CHLaC	0.06		
SiO <sub>2</sub>	0.05		
AREA	0.05		
pH	0.05	0.06	0.001
WOOD	0.04		
Ca	0.04		
ALPINE	0.04	0.04	0.014
CHLaU	0.04		
SO <sub>4</sub>	0.03		
K	0.02		
Total variance explained	0.901	0.470	
Total variance (sum of all eigenvalues in unconstrained ordination)	1.323	1.323	

TABLE 2. Eigenvalues, taxon–environment correlations, cumulative % variance explained, and statistical significance of the 4 canonical correspondence analysis (CCA) axes.

	CCA axis			
	1	2	3	4
Eigenvalue	0.261	0.108	0.053	0.028
Taxon–environment correlations	0.907	0.809	0.704	0.649
Cumulative % variance				
— of taxon data	19.7	27.9	31.9	34.0
— of taxon–environment relation	55.5	78.4	89.6	95.6
Significance (probability) (Overall probability = 0.001)	0.001	0.001	0.004	0.008

TABLE 3. Interset correlations for the forward-selected variables with the canonical correspondence analysis (CCA) taxon axes. Variable abbreviations are explained in Methods.

	CCA Axis			
	1	2	3	4
DEPTH	-0.580	0.556	-0.161	0.149
pH	0.086	-0.074	-0.568	0.284
TEMP	0.384	0.618	-0.157	-0.096
TKN	0.781	0.156	0.160	-0.179
ALPINE	0.143	-0.215	0.131	0.602

measures had not been identified by Walker et al. (1991) as important explanatory variables for midge distributions near arctic treeline in Labrador. The difference between our result and those of Walker et al. (1991) probably reflects the much greater trophic range apparent in our study lakes. Many of the tundra lakes sampled are highly transparent, oligotrophic, or ultraoligotrophic systems, whereas warm shallow lakes in the central Yukon are often nutrient-rich, with pronounced summer algal blooms. Such nutrient-rich systems are rare or absent in Labrador.

Several quantitative models have recently been developed to infer trophic variables from subfossil midge records (Lotter et al. 1998, Quinlan et al. 1998, Brodersen and Lindegaard 1999, Clerk et al. 2000, Brooks et al. 2001, Brodersen and Anderson 2002). A similar model could be developed from our data in relation to TKN, and used for paleolimnological biomonitoring of lake trophic state in northwestern Canada and Alaska.

*Lake depth*

The role of water depth as a key variable regulating midge faunal composition also has been apparent for many years (Sæther 1980), and is well-documented in surface sample surveys similar to the one reported here (Walker et al. 1991, Olander et al. 1997, 1999). It has been suggested that midge remains may yield good proxy records of past water-level changes (Hofmann 1998), and Korhola et al. (2000) have recently developed a quantitative model to infer water depth. Walker (2001) has been critical of the model because the normal amplitude of water-level fluctuations in lakes is too small to be

satisfactorily reconstructed using midges. Although it is technically feasible to develop a depth-inference model from our data, it would rarely be useful.

Water temperature and depth are often significantly correlated in surface sample data sets similar to ours. Shallow lakes tend to be warmer than deep lakes. This effect has the potential to confound midge-temperature reconstructions, especially where sediment accumulations have, over time, greatly reduced a lake's depth. In such situations, it may be difficult to ascertain whether a warming temperature trend, as revealed by midges, was a result of climatic warming, or may instead have been attributable to decreasing lake depth.

*pH*

pH was identified as the 3rd most important explanatory variable for our data set. Our sampling included lakes spanning a broad pH range (5.9–9.3). The pH range in Labrador lakes was narrower (5.8–6.9), which may explain why Walker et al. (1991) did not identify pH as a significant determinant of midge distributions. However, several investigators (Walker et al. 1985, Dermott et al. 1986, Uutala 1986, Johnson and McNeil 1988, Johnson et al. 1990) documented pH-midge relationships in conjunction with earlier acid rain research. Also, Fe was significantly correlated with pH ( $r = -0.58$ ) in the Yukon data set. Walker et al. (1991) identified Fe as an important explanatory variable for midges, with the highest Fe concentrations being reported in shallow, humic lakes of central Labrador.

*Temperature and ecoclimatic zone*

TEMP and ALPINE were the last 2 environmental variables to be identified as significant in forward selection. Midge distributions clearly reflected the strong ecoclimatic gradient across treeline in northwestern Canada, and arctic and alpine lakes are well known to have distinctive assemblages of midge taxa (Walker and Mathewes 1989, Lotter et al. 1997, Palmer et al. 2002). Similar patterns have been documented in Europe (Olander et al. 1997, 1999, Lotter et al. 1999, Larocque et al. 2001), Asia (Porinchu and Cwynar 2002), and elsewhere in North America (Walker et al. 1991, 1997, Walker and

MacDonald 1995, Palmer et al. 2002). This pattern has provided the principal basis for using midges as quantitative paleoclimatic indicators (Walker et al. 1991, 1997, Olander et al. 1997, 1999, Lotter et al. 1999, Palmer et al. 2002).

The importance of the ecoclimatic gradient was certainly expected, and was well-documented in earlier studies. Nevertheless, a detailed assessment of midge distributions across treeline in northwestern Canada was needed as a basis for future midge paleoecological research in the Yukon and adjacent regions. Because the nature of climatic and environmental change in Beringia has long been controversial (Cwynar and Ritchie 1980, Guthrie 1985, Colinvaux 1986, Zimov et al. 1995, Elias 2000), Quaternary paleoenvironmental studies will greatly benefit from the development and application of new paleoenvironmental proxy indicators for the Yukon and adjacent lands.

Much of the Beringian controversy probably arises from over-reliance on Quaternary pollen records as paleoclimatic proxy data. Paleoecologists have long debated whether the full-glacial landscape of Beringia was dominated by tundra or, instead, an extinct biome, the so-called mammoth steppe. Grassland, steppe, and tundra environments are characteristic of very different climatic regions. However, these environments are very difficult to distinguish on the basis of fossil pollen because grass and herb pollen dominate the pollen rain in each of these ecosystems (Guthrie 1985). Furthermore, this problem is exacerbated because pioneer communities in other vegetation belts are similarly dominated by grasses and herbs. Last, it is often difficult to even discern whether trees were, or were not, present because wind-dispersed pollen can be carried long distances beyond treeline. In contrast, the chironomid fauna of tundra environments is markedly different from that characteristic of forest or grassland lakes. There is little danger of larval head capsules being transported long distances between lakes by wind or water.

Our CCA is similar to others in identifying temperature as an important explanatory variable for midge distributions. This result indicates that a midge-temperature inference model can be developed for the Beringian region. Such a model should yield more accurate paleotemperature reconstructions than those currently available for Beringia. These data could play a

key role in resolving Beringian controversies. Nevertheless, we must proceed cautiously in developing and applying such a model. Other environmental variables are also of importance in shaping midge distributions in northwestern Canada. Care must be taken to distinguish the impact of climatic change from changes that might, instead, be attributable to unrelated trophic processes.

We have recently acquired several sediment cores from Beringian lakes, which may span the last glacial cycle. We have also extended our surface sample collections into Alaska and northern British Columbia. We will be using these fossil and surface samples to develop and apply the midge inference models in our ongoing Beringian paleoecological research.

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