LATE-QUATERNARY PALAEOECOLOGY OF CHIRONOMIDAE (DIPTERA: INSECTA) FROM LAKE SEDIMENTS IN BRITISH COLUMBIA

by

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ABSTRACT

Chironomid (midge) fossils were analyzed from sediments of three small lakes of moderate depth (5 to 6.5 m) in southwestern British Columbia. Fossil stratigraphy reveals a similar postglacial succession among lakes. Cold–stenothermous taxa, requiring well–oxygenated, oligotrophic habitats, were common in the late–Pleistocene (*ca.* 12,000 to 10,000 yr B.P.), but were mostly rare or absent during Holocene time (10,000 yr B.P. to present). The similar timing of these changes among lakes, and correlation with independent palynological evidence for climatic change, suggests that climate was the ultimate cause. Similar late–glacial/early Holocene faunal changes are evident across North America and Europe. Subsequent Holocene changes are less consistent among lakes, and are time–transgressive. These changes are not clearly climatically related, and may be attributed to gradual shallowing of each lake, or other local factors.

A core analyzed from a much shallower lake, on the Queen Charlotte Islands, includes a eurytopic fauna throughout. Little evidence of climatic change or trophic succession is apparent in this maritime environment. Although the successional pattern is unlike that documented in southern British Columbia, it resembles an arctic Alaskan sequence.

Surficial sediment samples were analyzed from 30 lakes distributed across an altitudinal gradient in western Canada. The cold–stenothermous taxa recorded from late–glacial southwestern British Columbia lakes are common at high elevations, particularly in the Rocky Mountains, and in deep profundal waters of low–elevation oligotrophic lakes. Many taxa presently common at low elevations do not occur above timberline. These low–elevation taxa are also very rare, or absent, in arctic regions.

Although the climatic effects upon chironomid faunas may be mostly indirect, chironomid succession is, in part, climatically related, especially around the late–glacial/Holocene transition.

DEDICATION

To Ma and Pa

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CHAPTER 1

INTRODUCTION[1]

The Chironomidae compose a family of true flies (Diptera) which as larvae constitute the most abundant bottom–dwelling macro–invertebrates of freshwater aquatic systems. Long viewed with importance by limnologists, they have proven valuable as indicators of lake productivity, and have been instrumental in the development of modern lake trophic classification (Brinkhurst, 1974; Sæther, 1979). Remains of dead larvae, and exuviae produced during each of four larval moults, occur abundantly as fossils in lake sediments, and are recognized as important palaeoecological tools (Crisman, 1978; Frey, 1964, 1976; Hofmann, 1986; Walker, 1987).

The influence of lake productivity, acidity, and salinity upon chironomid faunas has already proven useful in palaeolimnological research (Walker, 1987). As yet, little work has focused upon the direct and indirect effects of climate on chironomids (Danks, 1971a, b, c, 1981; Oliver, 1968). However, the direct influence of temperature, and indirect climatic regulation of lake productivity may have important consequences for chironomid faunal composition. Indeed, Andersen's (1938) pioneering results in this area depict the ability of midge communities to respond rapidly to known Danish late–Pleistocene climatic variations.

Little research regarding either the ecology, or palaeoecology, of these invertebrates has been conducted in the Pacific Northwest of North America. Garrett's (1925) Dipteran studies may be the earliest investigation of British Columbia Chironomidae. Rawson (1942, 1955) and Ricker's (1952) surveys of benthos in large Cordilleran lakes suffer from poor taxonomic resolution. More recently, Hamilton (1965) has provided a detailed account of

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[1] This chapter is partially adapted from three published articles (Walker, 1987; Walker and Mathewes, 1987a, b).

Chironomidae inhabiting Marion Lake, near Maple Ridge, British Columbia. Similarly Sæther (1970) and Sæther and McLean (1972) have conducted several recent surveys of large lakes occupying the Okanagan Valley. The littoral faunas of both saline lakes (Cannings, 1975a, b; Cannings and Scudder, 1978; Topping, 1969, 1971; Wiederholm, 1980) and marine (Morley and Ring, 1972a, b; Parkinson and Ring, 1983) habitats have been addressed. In addition, the present and very recent fossil faunas of Lakes Washington, and Sammamish, near Seattle, Washington were described by Thut (1969) and Wiederholm (1976, 1979). Most recently, Roback (1984) has examined the Tanypodinae of Afognak and Kodiak Islands, Alaska. Many other records are scattered through the literature (e.g. Cranston, 1982a; Hansen and Cook, 1976; Kangasniemi and Oliver, 1983; Sæther, 1969, 1976, 1977).

Consequently, the investigations reported in this manuscript contribute to the limited, but growing knowledge of Pacific Northwest Chironomidae. Three questions fundamental to chironomid biology are addressed: 1) Which genera are represented in lacustrine sediments of the Pacific Northwest?; 2) How are these taxa distributed in space and time?; 3) How did their present patterns of distribution originate?

Literature Review

Chironomids and lake classification

The roots of limnology as a modern science may be traced to the work of August Thienemann and Einar Naumann, contemporaries who both sought to develop a classification for lakes (Sæther, 1979). Borrowing terms which Weber (1907) had coined for nutrient supply to bogs, Naumann (1919) categorized lakes according to their phytoplankton productivity, providing the basis for our present lake trophic classification. Naumann (1919) described two basic lake types, the highly productive or "eutrophic"

Baltic lakes and the unproductive or "oligotrophic" north European lakes. Hansen (1962) also credits Naumann (1917, 1918, 1920) with introducing the "dystrophic", humic or brown-water lake as a sub-type of the north European lakes.

Thienemann (1918, 1921) derived similar conclusions through his attempts to classify lakes on the basis of dominant components in their benthic fauna. Thienemann (1921), accepting Naumann's (1919) terminology, described oligotrophic *Tanytarsus* v.d.Wulp lakes, eutrophic *Chironomus* Meigen lakes, and humic lakes in which both *Chironomus* and *Corethra* Meigen (=*Chaoborus* Lichtenstein, Chaoboridae) were prominent.

Brinkhurst (1974) provides an excellent review of subsequent attempts to refine Thienemann's typology. The scheme of Brundin (1949, 1956, 1958) describes several classes of temperature stratified lakes: arctic *Heterotrissocladius subpilosus* (Kieffer) lakes (ultraoligotrophic), subarctic and high boreal *Tanytarsus*–*Heterotrissocladius* Spärck lakes, boreal and montane *Tanytarsus lugens* Kieffer lakes (oligotrophic), *Stictochironomus rosenscholdi* (Zetterstedt)–*Sergentia coracina* (Zetterstedt) lakes (a transitional "mesotrophic" type between oligotrophy and eutrophy), *Chironomus anthracinus* Zetterstedt and *C. plumosus* (Linnaeus) lakes (eutrophic), and *C. tenuistylus* Brundin (dystrophic) lakes. Furthermore, Brundin (1951) argued that oxygen microstratification at the mud-water interface was a major determinant of the profundal fauna. Larger chironomid taxa, commonly associated with more productive lakes, could better cope with a micro-layer of O_2-depleted water at the mud-water interface. Also, such larvae (e.g. *Chironomus*) frequently possess hemoglobin. Because lakes with higher productivity generally display greater profundal oxygen deficiencies, a correlation was perceived among lake productivity, oxygen deficit, and benthic fauna.

As Rodhe (1969) has emphasized, trophic categories are abstract entities with overlapping ranges. A continuum of lakes among all of those described probably exists.

This is apparent in Sæther's (1975a, 1979, 1980a) recent re–evaluation of benthic lake typology. He describes 15 trophic categories, ranging from ultra–oligotrophy to extreme eutrophy, in addition to the mesohumic and polyhumic types. Sæther's (1975a, 1979) analysis extends European benthic lake typology to North America. He also describes a trophic range for each of many chironomid taxa. Warwick (1975) and Sæther (1979) suggest that apart from the more eutrophic lakes, food may be more critical than oxygen microstratification in determining the profundal fauna of lakes.

Sæther's studies (1975a, 1979, 1980a) correlate the occurrence of characteristic benthic faunas with total phosphorous, epilimnetic chlorophyll *a*, and lake depth. The total phosphorous and chlorophyll *a* relationships with benthic fauna confirms the importance of chironomids as indicators of lake productivity. This relationship however varies with lake depth (Sæther, 1980a) such that an increase in lake productivity would have to be much greater in a deep lake, than a shallow lake to yield a similar change in profundal fauna. Thus, the faunas of shallow stratified lakes are much more responsive to productivity changes than those of deep lakes.

Chironomids and palaeoecology

The attribute of chironomids as lake trophic indicators, and the abundance of chironomid remains in lake sediments has stimulated much palaeolimnological research (Walker, 1987). Although some investigations have dealt with the response of chironomids to changes in salinity or lake acidity (e.g. Brodin, 1986; Paterson and Walker, 1974), most have addressed natural and man–induced variations in lake productivity.

According to Frey (1964), the earliest report of the chitinous sedimentary remains of Chironomidae may be attributed to Ekman (1915). Numerous subsequent reports (e.g. Lundbeck, 1926; Gross, 1937; Brehm *et al.*, 1948) have since been compiled by Frey (1964) who considers the earliest attempt to interpret such remains in terms of past conditions to be that of Gams (1927). Gams (1927) was able to demonstrate that *Eutanytarsus* Thienemann & Bause, abundant in interstadial sediments of Lunzer Obersee, was later replaced by *Bezzia* Kieffer (Ceratopogonidae) and *Chironomus*. Such a sequence could be interpreted as indicating a natural increase in lake productivity. This was contrary to the original speculation of Naumann (1919) that lakes should gradually become less productive as a consequence of constant leaching of catchment soils.

Deevey (1942) described evidence that an early *Tanytarsus* fauna at Linsley Pond was first succeeded by *Endochironomus* Kieffer and *Glyptotendipes* Kieffer, and subsequently by *Chironomus*. Frey (1955) reported *Eutanytarsus* as initially abundant in Längsee, Austria, but with *Chaoborus* (Chaoboridae) arriving later. In contrast to Naumann's (1919) concept, these results contributed to the perception that "eutrophication", a gradual increase in lake productivity, was a dominant, if not universal process (Whiteside, 1983).

However, Livingstone *et al.* (1958) suggested, on the basis of large concentrations of chironomid remains [principally Tanytarsini, including *Corynocera* Zetterstedt (as *Dryadotanytarsus* Andersen)] and other microfossils, that Eight Lake in arctic Alaska may have experienced an early eutrophic stage, becoming less productive as the lake tended to dystrophy. At Myers Lake, Indiana (Stahl, 1959), an early *Sergentia* Kieffer dominated fauna declined as *Chaoborus* increased. Stahl (1959) argued that even in its early stages this lake may have experienced "moderate severe oxygen depletion", and that subsequent changes arose from a reduction in hypolimnetic volume rather than an increase in productivity.

Bryce (1962) also presented contrary results, indicating an early dominance by *Chironomus* at his Malham Tarn Moss site. Bryce (1962) argued that marl deposition may have reversed the ontogenetic process, causing the site to become more oligotrophic. Stahl

(1969) finds this conclusion unsubstantiated.

In southern Finland, Alhonen and Haavisto (1969) noted an early eutrophic stage subsequent to a lake's isolation from the sea. Hofmann (1971a, 1979) indicates that the eutrophic north German *Chironomus* lakes were formerly oligotrophic *Tanytarsus lugens* lakes. Lawrenz (1975) suggested that Green Lake, Michigan, had always remained oligotrophic, although the fauna did respond to a variety of factors including changes in sediment type, water level, and climate. Stark's (1976) results imply an early oligotrophic phase, but eutrophic conditions thereafter.

The above results suggest that broad generalizations regarding lake ontogenetic patterns may be unwarranted. The oligotrophic phase suggested in early lake sediments often relates to cold climatic conditions prevailing during the late–Pleistocene. Indeed, if the timing of the described changes is considered, the relevance of climate is readily apparent.

In addition, Hofmann (1971a: p.55, 1980) notes that Thienemann's (1915) *Tanytarsus* lakes were originally characterized by a misidentified species, later placed in *Lauterbornia* Kieffer, and now recognized to belong to *Micropsectra* Kieffer. Since few palaeoecologists have been able to distinguish among several Tanytarsini genera (including *Micropsectra*), the genus *Tanytarsus* has been employed in a broad sense incorporating taxa not characteristic of profundal oligotrophic environments. Similarly, although *Chironomus anthracinus* and *C. plumosus* are important indicators of eutrophy, some *Chironomus* species may be abundant in dystrophic, or even oligotrophic situations.

Stahl (1969) has noted that chironomid palaeoecological investigation sites have included unstratified lakes. The system of benthic lake typology conceived by Thienemann (1915, 1918, 1921) and Brundin (1956) was intended only for stratified lake environments. Nevertheless, Warwick (1975) and Sæther (1979) have argued that, apart from the more eutrophic lakes, food may be more important than O_2 microstratification in determining the benthic fauna. If true, benthic lake typology may be applicable to shallow polymictic lakes. Unfortunately, many of the best oligotrophic and mesotrophic indicators are cold stenotherms restricted to profundal habitats at temperate latitudes.

Chironomids, trophic status, and climate

Climate has had a tremendous impact upon the development of lakes. This point is not obvious within a small geographical area (the "local scale" at which most limnologists conduct their work). At this scale differences in geology of catchments, and size of lakes and watersheds are more important. However, on a continental scale the role of climate dominates (Brylinsky and Mann, 1973). This is dramatically depicted by the distribution of lake types in western Canada (Northcote and Larkin, 1963). In British Columbia the dilute unproductive ("oligotrophic") lakes of the humid coast contrast with the more saline and often more productive ("mesotrophic" to "eutrophic") lakes of the dry interior. Similarly, the saline lakes of southern Alberta and Saskatchewan share few characteristics with those present on similar bedrock in northern Alberta. Differences in nutrient concentrations, temperature, and phytoplankton density are also readily apparent in Moore's (1978) survey of benthos across the arctic – subarctic transition.

Although the relationships between chironomids, lake trophic state, and climate have attracted little recognition, these effects are implicit in the early benthic lake classifications. Thienemann's (1918) *Chironomus* lakes were low elevation Baltic sites, but his *Tanytarsus* lakes are described as sub-Alpine. Similarly, Brundin (1949, 1956, 1958) described the ultraoligotrophic *Heterotrissocladius* lakes as principally arctic whereas *Tanytarsus lugens* lakes were common in boreal and montane climates. In warmer climates, *Chironomus* lakes are common. Furthermore, Brundin states (1958: p.289), "In a lake type system of the world the ultraoligotrophic lake indicates one extreme of a climatically based type–series, where the ultraeutrophic equatorial lowland lake forms the other extreme." *Heterotrissocladius* is a characteristic taxon of the cold, ultraoligotrophic lakes, whereas *Chironomus* prevails in eutrophic lakes. Brundin's (1958) views portray the fact that climate, lake trophic state, and chironomid faunas are related. Lakes in warm climates have higher temperatures in both epilimnetic and hypolimnetic regions (Barton and Smith, 1984), receive more radiant energy, and via chemical weathering profit from a greater nutrient supply. Thus, "all low–altitude tropical lakes are eutrophic and all arctic lakes are oligotrophic by accepted standards regardless of basin morphometry" (Lawrenz, 1975).

Chironomids have evolved adaptations necessary to cope with the full range of conditions prevailing across this gradient. Arctic lacustrine chironomids must cope with very low temperatures, short emergence periods, silty substrata, and low "food" supplies, but benefit from abundant oxygen in all lakes of moderate or greater depth. Chironomids adapted to conditions prevailing in warm climates may benefit from abundant food, but must cope with higher water temperatures as larvae, higher air temperatures during emergence, and the extremely low oxygen concentrations prevalent in hypolimnetic sediments of eutrophic lakes. It is therefore not surprising that the factors influencing chironomid faunal changes frequently escape simple explanations.

In general terms, the chironomid subfamilies Podonominae, Diamesinae, Prodiamesinae, and Orthocladiinae are cold–stenothermous oligotrophic taxa with distributions centred in temperate and montane to polar and alpine climatic regions (Oliver, 1971). In contrast, the Tanypodinae and Chironominae tend to be most abundant at low elevation and latitude (Oliver, 1971).

The preceding discussion indicates that a relation between chironomids, lake trophic state, and climate exists. Thus the Chironomidae may have potential, as yet little exploited, for indicating rapid climatic changes such as those conceived for the late–Pleistocene. Although the climatic control of chironomid faunas is unlikely to be as closely defined as that regulating terrestrial vegetation, chironomid palaeoecological studies might prove useful where equivocal climatic interpretations exist. Thus, in addressing the ecology and palaeoecology of Pacific Northwest Chironomidae, I shall focus particularly on this possibility.

The main text of this thesis is arranged into 5 chapters. This introduction and literature review, the first chapter, have introduced several major concepts which are central to subsequent discussions. Chapter 2 reports a first exploratory look at chironomid stratigraphy in one British Columbia lake, Marion Lake, in the University of British Columbia Research Forest. Ideas developed during the Marion Lake research, regarding the influence of climate upon postglacial chironomid succession, were tested with subsequent cores from Mike and Misty Lakes (Chapter 3). Chapter 4 reports exploratory chironomid stratigraphic work at Hippa Lake, on the biogeographically intriguing Queen Charlotte Islands. Finally, to better appreciate the role of climate in shaping chironomid faunas, fossil head capsules were analyzed from surficial sediment of a lake series, spanning an altitude gradient. This study is reported in Chapter 5. These chapters are arranged in chronological order, which best reflects the progression of thought through my studies. As much as possible each chapter is arranged as an independent paper.

CHAPTER 2

MARION LAKE STRATIGRAPHY[1]

As a first exploratory look at the chironomid stratigraphy in a British Columbia lake, Marion Lake in the University of British Columbia Research Forest was selected for study. This initial investigation would allow a comparison of chironomid successional patterns in British Columbia with those documented elsewhere in North America and Europe.

Extensive ecological (Efford and Hall, 1975; Hall and Hyatt, 1974) and palaeoecological (Mathewes, 1973; Mathewes and Heusser, 1981; Wainman and Mathewes, 1987) research has been conducted at Marion Lake. The extant chironomid fauna is well documented (Hamilton, 1965), and the lake is of comparable size to other North American sites from which detailed postglacial chironomid stratigraphic records have been obtained (Lawrenz, 1975; Walker and Paterson, 1983). The faunas of small lakes are likely to be most responsive to climatic changes. Also, a complete postglacial sediment core was available for study. The lake is unusual in having large stream and spring-water inputs.

Study Area

Located about 50 km east of Vancouver, British Columbia, in the University of British Columbia Research Forest (Fig. 2.1), Marion Lake (49° 19'N, 122° 33'W) occupies a valley depression in the Coast Mountains at 304 m above sea level. The area is exposed to a mediterranean type climate. Although summer precipitation is similar to that in much of southern Canada, summer temperatures are slightly cooler, and winter is

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[1] This chapter is largely adapted from a previously published account (Walker and Mathewes, 1987a).

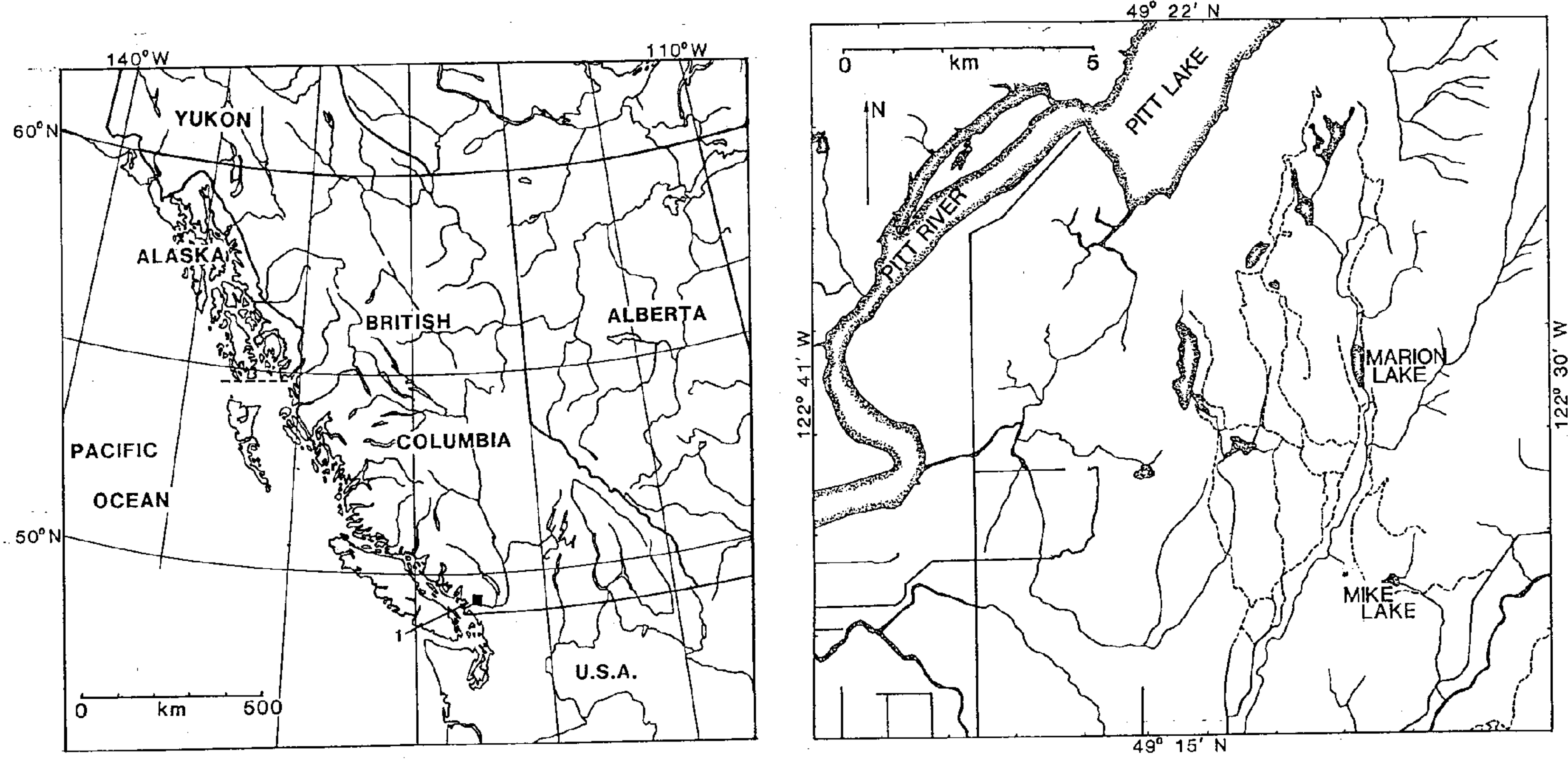

Figure 2.1 Location of Marion Lake in the University of British Columbia Research Forest, near Maple Ridge, British Columbia, Canada.

comparatively warm and wet (Table 2.1). The lake has an area of 13.3 ha and maximum depth of approximately 6 m (Hamilton, 1965). The catchment encompasses 15 km², with tributary streams extending to at least 500 m above lake level. Perhaps owing to the rapid flushing of Marion Lake following frequent rains, little stratification of the water column is apparent. Temperatures at 5.0 m depth can exceed 17° C during summer, whereas winter temperatures approach 2° C (Hamilton, 1965). Efford (1967) notes, however, that water as cold as 9.5° C can be found during summer over one large spring in the lake bottom. As a result of the high precipitation (2500 mm) and base-poor plutonic bedrock (Roddick, 1965), Marion Lake is a weakly-acidic to circum-neutral (pH 5.9 to 7.4), oligotrophic, softwater lake, typical of those along British Columbia's mainland coast.

The conifer-dominated forests of the (wetter) coastal Western Hemlock Zone (Krajina, 1969) that surround the lake have been extensively disturbed by fires and logging. The present forest consists primarily of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* Donn.), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), and red alder (*Alnus rubra* Bong.).

Palynological investigations (Fig. 2.2) reveal the postglacial forest history of Marion Lake's catchment (Mathewes, 1973). Climatic interpretations are available as established by pollen/climate transfer functions (Mathewes and Heusser, 1981). The earliest sediment (≥12,000 yr B.P.; ≥8.85 m) is dominated by clay and contains a significant non-arboreal pollen component including willow (*Salix* L.) and soapberry (*Shepherdia canadensis* (L.) Nutt.). Forests were then rapidly established at the site. All subsequent sediments, excluding the Mazama volcanic ash layer (6800 yr B.P.: Bacon, 1983), are highly organic, containing much allochthonous plant debris. Early forests (12,000 - 10,000 yr B.P.) included lodgepole pine (*Pinus contorta* Dougl.), balsam fir (*Abies* Mill.), spruce (*Picea* A.Dietr.), mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) and alder, suggesting a

Table 2.1. Climatic summary (1951-1980) for Loon Lake (49°18'N, 122°35'W; 354 m elev.), University of British Columbia Research Forest, Haney, British Columbia.

Mean Daily Temperature	
Coldest Month (Jan)	0.5°C
Warmest Month (Jul)	16.3
Precipitation	
Rain: Annual	2459.1 mm
Wettest Month (Dec)	343.3
Driest Month (Jul)	86.7
Snow: Annual	195.2 cm
Frost-free Period	199 d
Degree-days	
Above 0°C	3092.7°C·d
Above 5°C	1633.7

(Environment Canada, 1982)

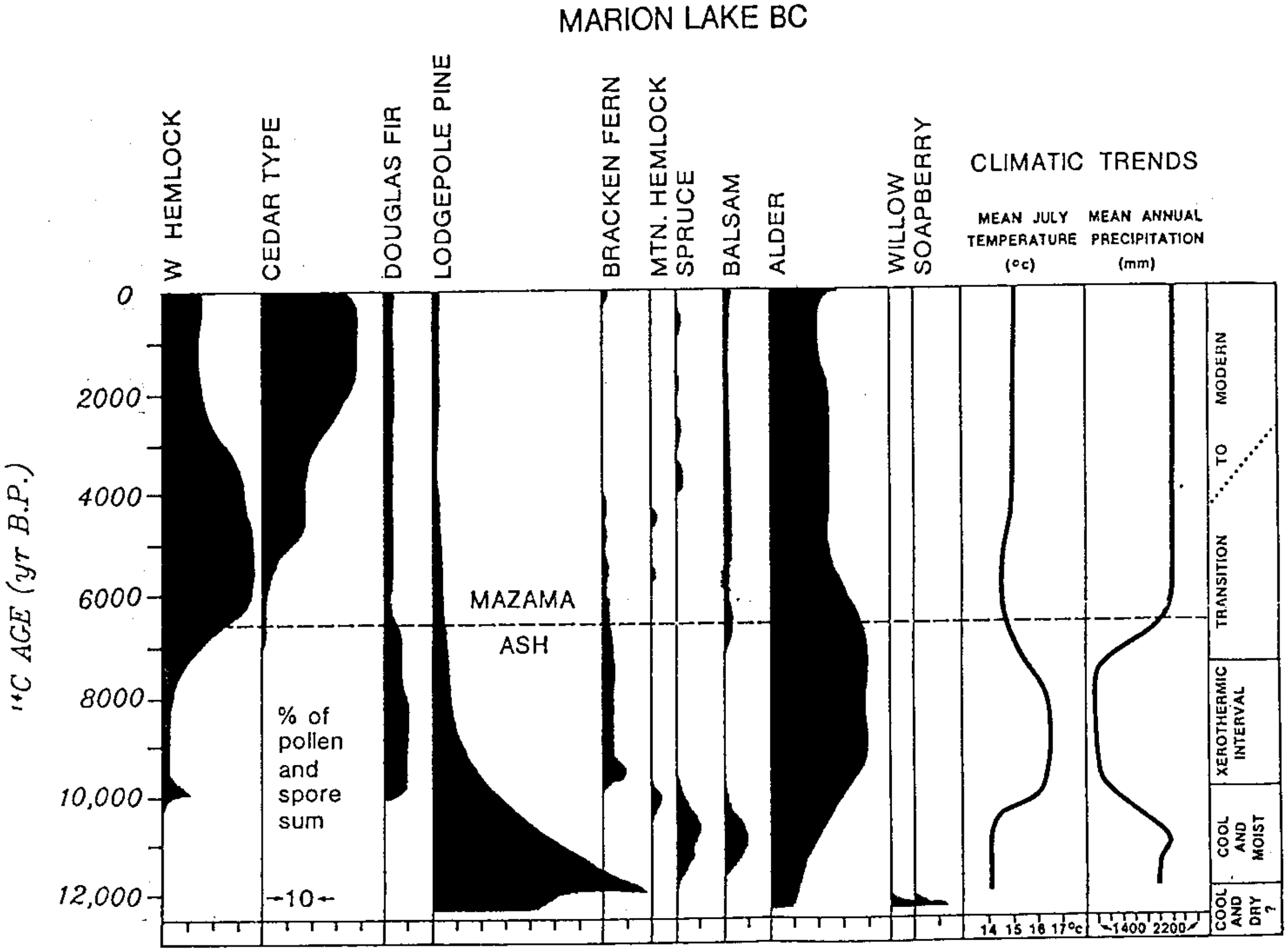

Figure 2.2 Summary diagram of postglacial pollen stratigraphy at Marion Lake, B.C. (adapted from Mathewes, 1985).

cool moist climate. Maximum proportions of Douglas-fir, alder, and bracken (*Pteridium aquilinum* (L.) Kuhn.) palynomorphs between 10,000 and 7000 yr B.P. imply a warm dry climate, described as a xerothermic interval (Mathewes and Heusser, 1981) with increased fire frequency (Mathewes, 1985). Post-Mazama maximum frequencies of western hemlock and western red cedar indicate a shift towards the present cooler and wetter climate. These patterns of forest development and the climatic inferences accord well with evidence from other sites in the same region (Mathewes, 1985).

Methods

A 5-cm-diameter sediment core was collected at the point of maximum depth (*ca.* 6 m) in Marion Lake using those methods described by Mathewes (1973). Because this core was taken close to one previously studied palynologically (Mathewes, 1973) the stratigraphy of this 8.95-m core is identical to that described by Mathewes (1973). A reliable stratigraphic correlation of the two records is therefore possible.

One millilitre samples of sediment were normally used for chironomid analysis. Larger samples (≤30 mL) were occasionally necessary, especially for the basal clay (≥8.85 m). The samples were spaced at approximately 1.0 m intervals, except in sediments below 8.0 m and near the Mazama ash (6.1 m) where rapid faunal changes were expected. In these instances, samples were more closely spaced. Samples were deflocculated in hot 10% KOH and sieved through a .075 mm mesh. The sediment retained in the sieve was washed into a beaker and later examined in a Bogorov counting tray (Gannon, 1971) at a magnification of 50X for fossil chironomids. All fossil Chironomidae were mounted on microscope slides in Permount® and retained for identification. Counts per sample averaged 91.6 ±12.2 (S.E.) chironomid head capsules, with a minimum of 25.5 and maximum of 203.5.

Head capsules were identified principally with reference to the work of Hamilton (1965), Oliver and Roussel (1983a) and Wiederholm (1983). Nomenclature follows Wiederholm (1983). Because most appendages were separated from the head capsules, it was not possible to provide all identifications at the generic level and few at the species level. Thus, several broader taxonomic categories (e.g. *Corynoneura* Winnertz/*Thienemanniella* Kieffer, *Cricotopus* v.d.Wulp/*Orthocladius* v.d.Wulp/*Paratrichocladius* Santos Abreu, *Tanytarsus* s.lat.) have been designated. Details regarding the identification of individual taxa, including diagnostic characters, illustrations, and species likely to be included in each group are provided as an appendix to this thesis.

The chironomid diagrams were been plotted using the pollen-plotting package MICHIGRANA developed by R. Futyma and C. Meachum. Head capsule influx estimates were calculated assuming constant sedimentation rates between radiocarbon-dated levels. Zonation of the diagrams is subjective.

Results

The counts of head capsules are presented as percentages[2] (Fig. 2.3), as well as total influx[3] (Fig. 2.4). Although ideally representing the abundance of individual taxa, interpretation of influx data is limited by the possibility of sediment focusing (Davis *et al.*, 1984) concentrating littoral head capsules in the less turbulent sublittoral region (Iovino, 1975). Thus total influx values are presented, but not influx estimates for individual chironomid taxa.

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[2] For individual samples, the proportion of each taxon has been calculated as a percentage, of the total number of chironomid head capsules.

[3] Total influx refers to the rate at which head capsules of all chironomid species are being deposited and preserved in the sediments. Influx is reported as the number of head capsules deposited per cm^2 per year ($hc \cdot cm^{-2} \cdot yr^{-1}$).

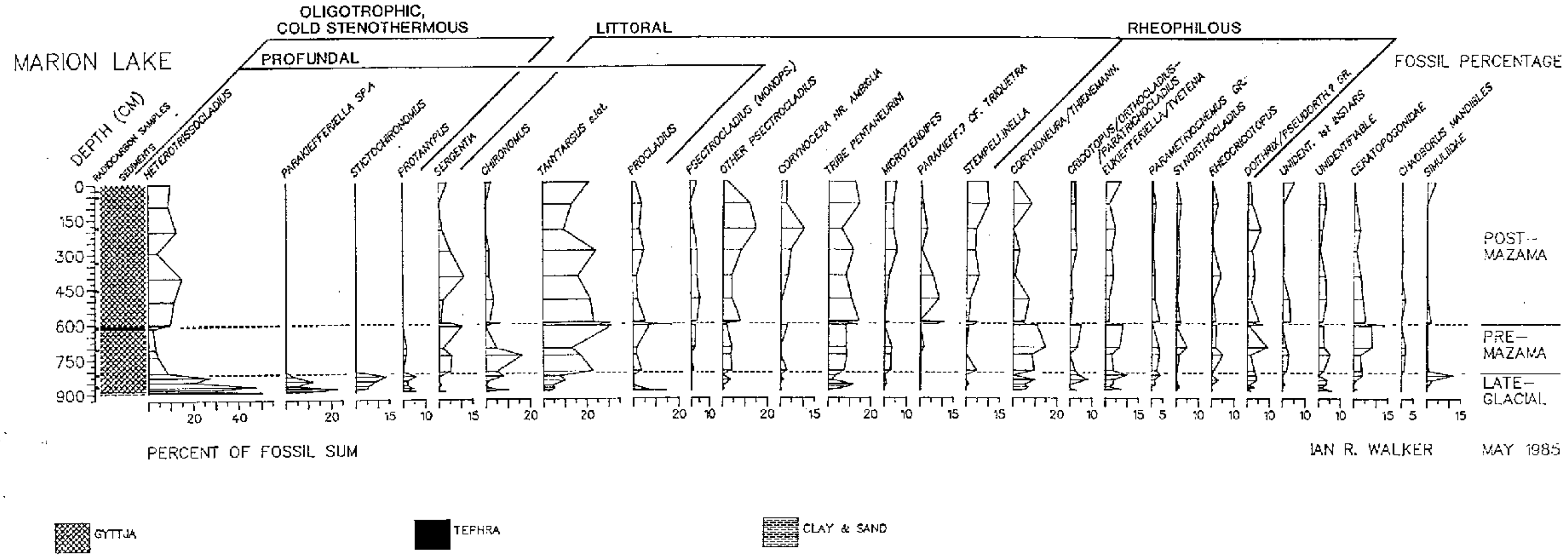

Figure 2.3 Percentage (of total number of chironomid head capsules at each sample level) diagram representing stratigraphy of common Chironomidae at Marion Lake, B.C. (Several rare taxa, including *Pseudodiamesa* Goetghebuer have been excluded.)

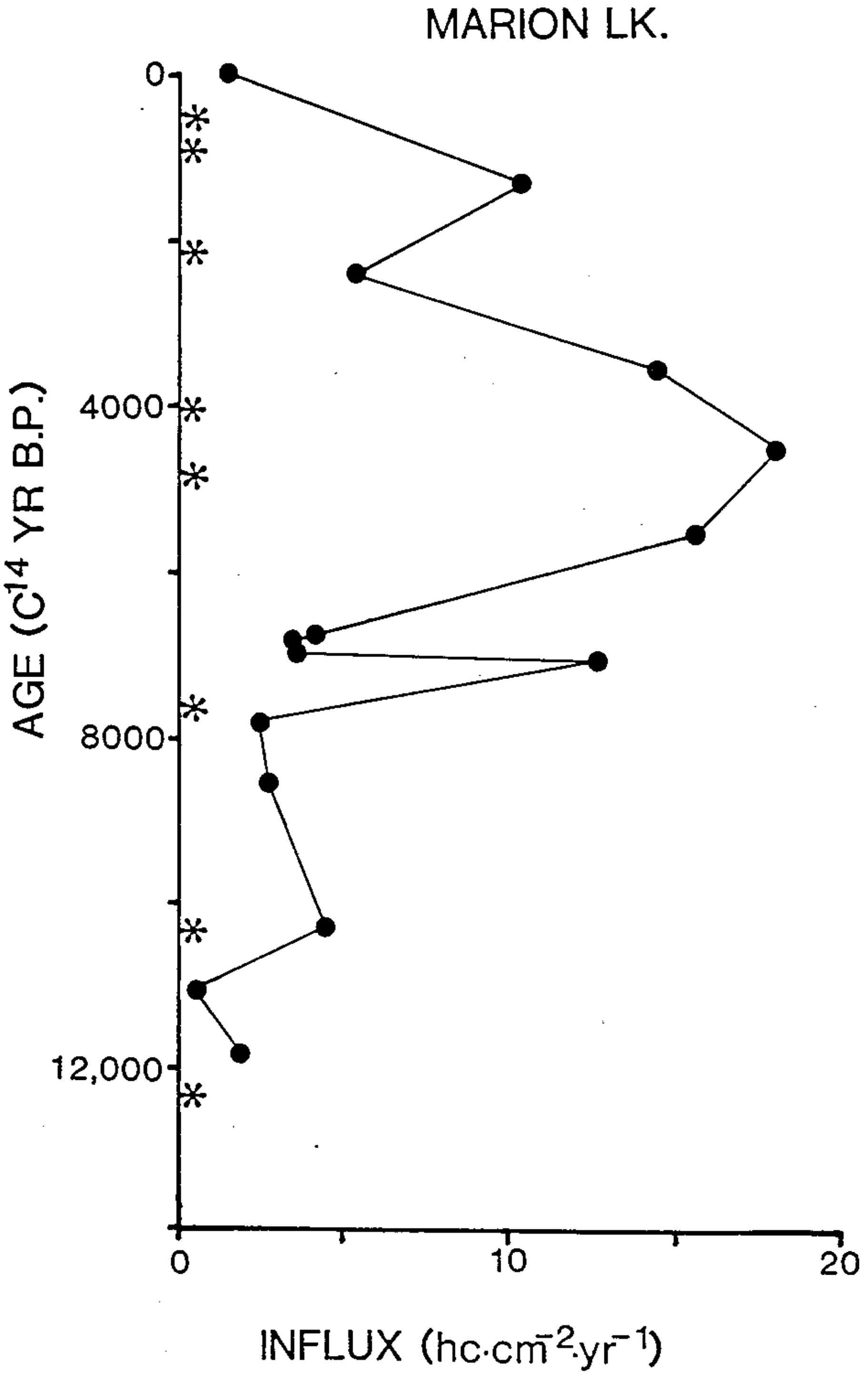

Figure 2.4 Total chironomid influx at Marion Lake, B.C. (*–indicate ^{14}C–dated levels – from Mathewes, 1973).

Chironomid taxa have been assigned to ecological groups, but given the broad ecological range of most genera, these designations must be considered approximate. The "cold–stenothermous" taxa are commonly regarded as profundal species at temperate latitudes, but may extend into shallower habitats at high elevation or latitude. For example, *Stictochironomus rosenscholdi*, considered a temperate profundal midge (Sæther, 1979), has been collected emerging among macrophytes in arctic Alaskan lakes and ponds (Butler *et al.*, 1981; Hershey, 1985a). Those taxa designated as "rheophilous" were not recorded as common components of Marion Lake's extant fauna (Hamilton, 1965), and are known to be associated with stream habitats in other regions (Coffman and Ferrington, 1984; Wiederholm, 1983). *Cricotopus/Orthocladius/Paratrichocladius* is the only taxon of the "rheophilous" group commonly recorded as a fossil in British Columbia lakes with no significant stream input (see chapter 5).

Most of the remaining chironomids are common in littoral environments. Only *Chironomus decorus* Johannsen, *C. rempelii* Thienemann, *Procladius* sp.A, *Psectrocladius* (*Monopsectrocladius*) sp.B, and *Sergentia* sp.A were noted by Hamilton (1965) as being most common in deep–water areas of Marion Lake, suggesting a preference for profundal environments. Both *Chironomus* and *Sergentia* are well known as profundal inhabitants of other lakes.

The fossil chironomid record may be divided into 3 zones. The lowermost zone (8.95 – 8.20 m) encompasses the late–glacial sediments deposited between *ca.* 12,000 and *ca.* 10,000 yr B.P. (Mathewes and Heusser, 1981). The second zone (8.2 – 6.1 m) was deposited between 10,000 and 6800 yr B.P. The third zone, containing sediments above the Mazama ash (6.1 to 0.0 m), spans the period from 6800 yr B.P. to the present day.

Late-glacial assemblages

Chironomid assemblages in the late-glacial sediments are distinguished by low influx[4] (*ca.* 2.0 $hc \cdot cm^{-2} \cdot yr^{-1}$) (Fig. 2.4) and by the prevalence of ***Heterotrissocladius*, *Parakiefferiella*** sp.A, ***Protanypus*,** and ***Stictochironomus*** (Fig. 2.3). Although the clays forming the base of this zone bear lower concentrations of head capsules, they have not yielded a distinctive fossil fauna.

Heterotrissocladius and ***Protanypus*** Kieffer are cold-stenothermous taxa which at temperate latitudes are mostly restricted to the profundal sediments of deep, oligotrophic lakes (Sæther, 1975b, c). At higher latitudes they may become more common in shallow waters. ***Stictochironomus*** Kieffer is also a resident of northern lakes (Hershey, 1985a, b; Moore, 1978, 1980; Danks, 1981) and a common deep-water component of temperate oligotrophic and mesotrophic water (Sæther, 1975a, 1979). Although some ***Stictochironomus*** species do occur in warm waters, the common species in British Columbia is restricted to cold environments (see Chapter 5).

Parakiefferiella sp.A is probably identical to Sæther's (1970) "genus near *Trissocladius*". This taxon presently inhabits the deep-water sediments of two large lakes in British Columbia's Okanagan Valley (Sæther, 1970; Sæther and McLean, 1972). It appears identical to larvae collected by M. Ouellet from Manicouagan Reservoir, a large oligotrophic lake in northern Québec, and to larvae collected by S. Mozley from the Alaskan north slope (D.R. Oliver, pers. comm.). Hare (1976) reports this taxon as abundant in the deep, oligotrophic waters of Parry Sound, Lake Huron, and as inhabiting several small lakes at alpine and subalpine sites in Banff National Park, Alberta.

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[4] The abbreviation "hc" is used throughout this thesis as an alternative to "head capsules".

A rare but significant taxon in the late–glacial sediments is *Pseudodiamesa* Goetghebuer. Like the preceding taxa, it is characteristic of very cold, waters, including ponds on glacier surfaces, oligotrophic lakes, and alpine streams (de March *et al.*, 1978; Elgmork and Sæther, 1970; Minns, 1977; Oliver, 1976). *Pseudodiamesa* is principally distributed in arctic and alpine regions (Downes, 1964), although Beck (1980) provides one record from Tennessee. D.R. Oliver (pers. comm.) notes the occurence of *Pseudodiamesa* in Ontario springs.

Local extinction of *Parakiefferiella* sp.A and *Stictochironomus* appears to have occurred in the interval encompassing the 8.1 and 8.3 m depths, dated approximately 10,000 yr B.P. *Heterotrissocladius* and *Protanypus* occur above 8.1 m, but constitute a much reduced faunal element.

Holocene assemblages

Unlike the late–glacial fauna, the Holocene fauna bears a high proportion of *Tanytarsus* s.lat. remains. Although I divide the Holocene with a zone boundary at the Mazama Ash, the gradual changes in the Holocene do not provide a marked distinction between the fauna immediately above and below the ash. However, this boundary does facilitate description of observed faunal changes.

Some taxa appear relatively more abundant in the pre–Mazama sediments. The high pre–Mazama proportion of rheophilous taxa, including *Corynoneura/Thienemanniella*, *Eukiefferiella* Thienemann/*Tvetenia* Kieffer, *Orthocladius* (*Symposiocladius*) *lignicola* Kieffer, *Parametriocnemus* Goetghebuer group and *Stilocladius* Rossaro, may reflect low production of lake Chironomidae, rather than a higher influx of chironomids from the in–flowing stream (Figs. 2.3, 2.4).

Littoral taxa (e.g. *Corynocera* nr. *ambigua* Zetterstedt, *Pagastiella* cf. *ostansa* Webb, *Parakiefferiella*? cf. *triquetra* (Chernovskii), *Psectrocladius* Kieffer, *Stempellinella* Brundin, *Tribelos* Townes) are more abundant in sediments above the Mazama ash. Although abundant between 4.0 m and 1.0 m, *Corynocera* nr. *ambigua* is rare in pre–Mazama sediments, as well as being absent from the present lake (Hamilton, 1965). The influx of head capsules increases sharply (Fig. 2.4) in post–Mazama sediments. In part this may reflect greater chironomid production as the lake shallowed and littoral habitat increased. On the other hand, head capsules may be concentrated at sublittoral sites by offshore displacement of head capsules. Head capsules resuspended from the turbulent littoral environment can be transported to deeper water (Iovino, 1975).

The deposition of Mazama ash does not appear to have had great effect upon the chironomid fauna. Perhaps, such a response would be evident at another lake where laminated sediments provide greater time resolution. Curiously however, Simuliidae (blackfly) larval remains are abundant, on a relative basis, during three periods in which soil disturbance and consequently stream sediment loads may have been great. These periods include the late–glacial (solifluction, incomplete forest cover), the period subsequent to ash deposition, and the recent settlement era (logging and increased fire frequency). Unfortunately, because this is a relative increase, and because it is difficult to accurately assess the rate of sediment deposition, it is not clear whether the apparent abundance of Simuliidae is real, or is instead caused by a decrease in total chironomid influx.

Discussion

To what factors might these variations in the chironomid fauna be attributed? For those changes occurring at or near the Pleistocene/Holocene boundary, two explanations are possible, temperature changes and trophic alterations. Subsequent Holocene changes may have resulted largely from the gradual shallowing of Marion Lake. It is the possible influence of the late–Pleistocene climatic amelioration which will constitute the focal point of this discussion.

Chironomidae, to date, have been employed principally as indicators of the trophic status of lakes. *Chironomus* characterizes the deep–water benthic communities of eutrophic waters; *Heterotrissocladius*, associated with several Tanytarsini, is considered indicative of oligotrophic conditions. It is, however, important to note that the "*Heterotrissocladius*" fauna[5] includes cold–stenothermous types, such as *Protanypus*. Although typically residents of very deep water at temperate latitudes, some members of the *Heterotrissocladius* community may inhabit shallower waters in arctic, subarctic, and alpine lakes (Hershey, 1985a; Hofmann, 1971a, 1983a; Moore, 1978; Sæther, 1975b, c).

Was the demise of the late–glacial *Heterotrissocladius* fauna a result of increasing summer water temperatures? Was its demise associated with an increase in lake productivity? Both events are likely to have occurred, and both may have contributed to this faunal change.

During Marion Lake's earliest development (>12,000 yr B.P.), cold water temperatures may have been maintained by meltwater from persistent valley glaciers. After *ca.* 12,000 yr B.P., sediments suggest low inorganic sediment influx, indicating disappearance of local ice and stabilization of adjacent slopes by forest vegetation. Subsequently, summer water temperatures would have increased with ameliorating climate. Warmer water, after *ca.* 10,000 yr B.P., would have restricted cold–stenothermous organisms to the deepest portions of the lake (if thermally stratified) and to the vicinity of cold springs. However, considering the rapid flushing which occurs at Marion Lake

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[5] In this manuscript, the "*Heterotrissocladius*" fauna will be considered to include *Heterotrissocladius*, *Parakiefferiella* sp.A, *Protanypus*, and *Stictochironomus*. It is probably a regional analogue to the fauna in Brundin's (1958) "*Heterotrissocladius subpilosus*" lakes.

(Efford, 1967), it is debatable whether or not a stable, cold, hypolimnetic environment ever persisted throughout the summer.

Given the lake's large littoral extent, and essentially polymictic nature, most fossil Chironomidae deposited at the coring site are probably from littoral areas subject to warm summer temperatures. Present summer temperatures near the maximum depth attain 17° C (Hamilton, 1965). Sæther (1975b) reports that in Europe, ***Heterotrissocladius marcidus*** (Walker), the most warm-adapted member of the genus, is restricted to waters colder than 18° C. Clearly, Marion Lake provides marginal conditions. Increased water temperatures would also promote colonization by warm-adapted species. Thus warm water would produce a relative decline in the ***Heterotrissocladius*** fauna by restricting the cold-stenothermous species to those limited regions of the lake where cold spring water or bottom water prevailed throughout the summer, and by facilitating colonization by other chironomids and competitor organisms.

Trophic changes must also have occurred, but most likely in response to rising summer temperatures. By regulating growth rates and other biological processes, temperature can directly influence both autochthonous and allochthonous productivity. Analyzing data from 55 International Biological Program studies, Brylinsky and Mann (1973) concluded that primary production, at the global scale, depends mostly upon latitude, altitude, length of growing season, and mean air temperature. In addition, the nutrient supply and hence production is regulated by nutrient release from the catchment. Higher temperatures facilitate more rapid chemical weathering of parent materials, releasing scarce nutrients such as phosphorus.

Therefore, temperature, through both direct effects upon organisms and indirect regulation of lake productivity, could account for the observed Pleistocene to Holocene faunal changes. Indeed, pollen/climate transfer functions (Mathewes and Heusser, 1981) indicate a rapid climatic warming at Marion Lake spanning the Pleistocene/Holocene boundary. Although significant water level fluctuations might produce faunal changes of the sort involved here, neither the present study nor Mathewes' (1973) study suggest water level fluctuations sufficient to explain these changes.

At this point comparison of these results with earlier reports is instructive (Fig. 2.5). Most early investigations (e.g. Goulden, 1964; Megard, 1964; Stahl, 1959) of postglacial chironomid stratigraphy suffer from inadequate dating and poor taxonomic resolution, so they are of little use in this analysis. Most recent, detailed investigations (Günther, 1983; Hofmann, 1971a, 1983a; Lawrenz, 1975; Schakau and Frank, 1984; Walker and Paterson, 1983) document ***Heterotrissocladius*** at maximum abundance during the late Pleistocene, when cold air and water temperatures are thought to have prevailed at each study site. ***Heterotrissocladius*** is extremely rare or entirely absent during postglacial time. It is compelling, therefore, to invoke climate as the principal factor regulating occurrence of the ***Heterotrissocladius*** community.

In a recent analysis of succession in a shallow North German lake, Hofmann (1983a) suggests that changing trophic conditions do not alone account for the observed successional patterns. Climatic conditions were also likely to be involved. Similarly, Brodin (1986) states, "The reasons for the almost complete elimination of cold-stenothermal species and the marked dominance of eutrophic species characteristic of the temperate climate zone in all shallow lakes at the beginning of the postglacial period seem to be mainly the distinctly warmer climate and an intrinsic capacity for highly productive conditions in these lakes, ..." I also believe climatic variations are necessary to account for the early chironomid succession in Marion Lake. When I consider the strong similarity of chironomid profiles within a restricted geographic area, as in Germany (Günther, 1983; Hofmann, 1971a, 1983a) or New Brunswick (Walker and Paterson, 1983) it is clear that the lake faunas are not reacting independently. A regional influence,

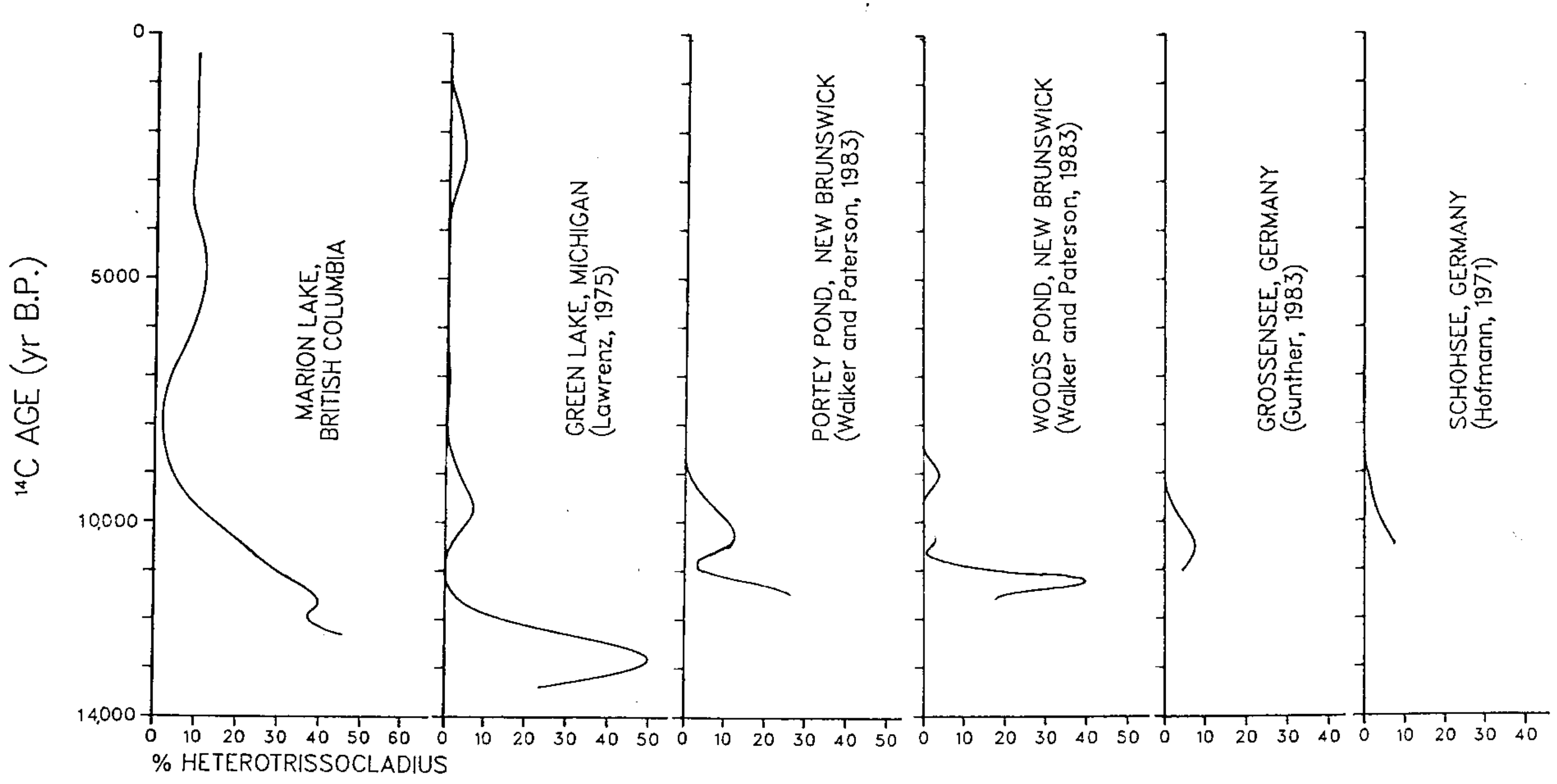

Figure 2.5 Holarctic trends in the postglacial abundance of *Heterotrissocladius* in temperate lakes.

probably climate, is being exerted upon these faunas. This stimulus does not coincide with the arrival of forest, but may precede forest development as in New Brunswick, or follow, as at Marion Lake. Because those sites where a late–glacial ***Heterotrissocladius*** community has been recorded are widely separated, the evidence suggests a widely distributed ***Heterotrissocladius*** fauna in lakes near the ice margins. With rising temperatures this fauna retreated to its present distribution in arctic–alpine regions and to the deep–waters of large oligotrophic temperate lakes.

As described above, the large temperature changes inferred near the Pleistocene/Holocene boundary probably account for the major faunal changes. Subsequent Holocene succession is not clearly climatically related. However, ***Heterotrissocladius*** declines to minimum numbers at Marion Lake during the inferred xerothermic interval (10,000 to 7000 yr B.P.: Mathewes and Heusser, 1981; Mathewes, 1985). The subsequent post–Mazama increase in ***Heterotrissocladius*** could also record a palaeoclimatic response. ***Corynocera***, another element often associated with cool waters (Fjellberg, 1972; Moore, 1978), and late–glacial climates (Andersen, 1938; Hofmann, 1978, 1983a, b; Schakau and Frank, 1984) is also prominent in the post–Mazama sediments.

One might argue that a gradual oligotrophication of Marion Lake occurred through the Holocene, yet Marion Lake is so dependent upon allochthonous and littoral (epipelic algal and macrophytic) production (Efford and Hall, 1975) that planktonic photosynthesis may have little relevance. Littoral production would not have decreased as the lake shallowed. Also, given that Marion Lake's sediments are predominantly (by volume) allochthonous organic tissues, sedimentation rates may reflect allochthonous inputs. The radiocarbon chronology provided by Mathewes' (1973) indicates relatively rapid post–Mazama sedimentation. This rapid sedimentation would indicate greater allochthonous inputs following 6800 yr B.P. Such an effect would not explain the observed Holocene chironomid succession.

It should be noted, however, that both *Heterotrissocladius* species presently inhabiting Marion Lake (*H. marcidus* and *H. latilaminus* Sæther: Sæther, 1975b) belong to the more warm-adapted *H. marcidus* group. The more cold-stenothermal *H. subpilosus* group is often associated with *Parakiefferiella* sp.A (Sæther, 1970; Sæther and McLean, 1972; Hare, 1976). Günther (1983) records only *H. subpilosus* in the late-glacial of his German site. Thus the late-glacial and Holocene faunas of Marion Lake may not include the same *Heterotrissocladius* species.

CHAPTER 3

MIKE AND MISTY LAKE STRATIGRAPHY[1]

Although the chironomid stratigraphic results obtained from Marion Lake, discussed in the preceding chapter, and those of several earlier investigations (Andersen, 1938; Günther, 1983; Hofmann, 1983a, b, 1985) suggest a climatic control upon chironomid faunas, a more rigorous test of this hypothesis is desirable. Without the ability to experimentally manipulate climate, it is necessary to examine other fossil evidence from critical periods of rapid climatic change. This process Deevey (1969) dubbed "Coaxing history to conduct experiments."

It would be expected, if climate is directly or indirectly responsible for the late-Pleistocene faunal changes at Marion Lake, that similar changes should be evident, synchronously, at other lakes within the same region. Thus two lakes, Mike Lake and Misty Lake in southwestern British Columbia were selected for study. These are small, low-elevation lakes of comparable depth to Marion Lake.

Study sites

Mike lake (225 m elev.; 49° 16.5'N, 122° 32.3'W) is located 3 km south of Marion Lake, in Golden Ears Provincial Park. Because it lies farther from the mountains and at lower elevation (Fig. 3.1), the climate at Mike Lake is probably slightly warmer and drier. Forests surrounding the lake are placed within the drier subzone of the Coastal Western Hemlock zone (Klinka, 1976). These distances, elevation differences, and expected climatic discrepancies are slight however. Although two University of British Columbia Research Forest weather stations in the area near Marion and Mike Lakes

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[1] A manuscript adapted from this chapter has been submitted to Journal of Paleolimnology.

Published in modified form, 1989 (Journal of Paleolimnology 2: 1-14)

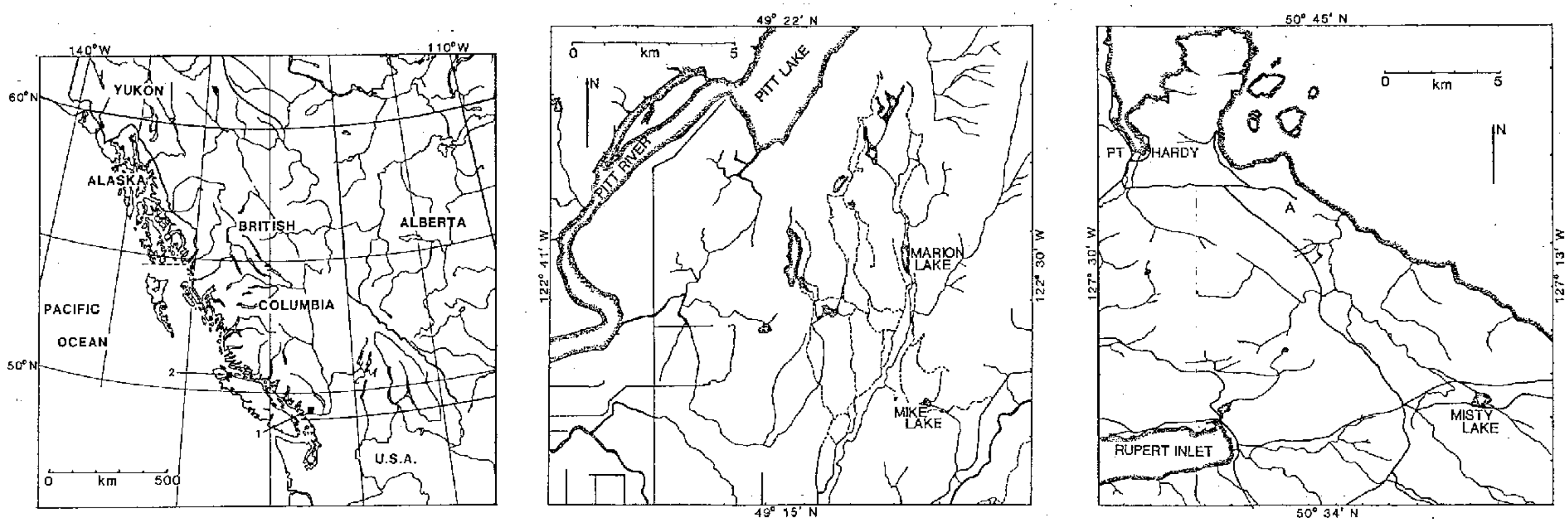

Figure 3.1 Locations of Mike and Misty Lakes in southwestern British Columbia, Canada. (1–indicates Mike Lake study area; 2–indicates Misty Lake study area)

(Table 3.1) are separated by 211 m elevation, mean temperatures differ by less than 1° C. Annual precipitation is about 16% less at the lower site. Consequently, a very similar climatic regime must also exist for Marion and Mike Lakes, now and in the past. This, it was expected, would be reflected in the chironomid record.

With a surface area of 4.5 ha and maximum depth of 6.5 m, Mike Lake's catchment extends to at least 200 m above lake level. Owing to the limited, 1.7 km^2 catchment, inflowing streams are small. During summer a distinct thermal stratification is apparent. On August 22, 1987, the upper 3.0 m of water ranged from 19 to 21.5° C, but waters below 5.0 m varied from 12.5 to 10° C. The lake is surrounded, and presumably underlain by a thick morainal blanket (Klinka, 1976). Bedrock beneath the lake and catchment consists of base-poor crystalline plutonic rocks, diorite, of the coast mountain complex (Roddick, 1965). The surrounding forests are similar to those at Marion Lake.

Misty Lake (70 m elev.; 50° 36.3' N, 127° 15.7' W) is situated 360 km northwest of Marion and Mike Lakes, near Port Hardy on northern Vancouver Island (Fig 3.1). Despite the great distance separating this site from Marion and Mike Lakes, the similar vegetation and climate also place this site (Farley, 1979) within the Coastal Western Hemlock biogeoclimatic unit (wetter subzone). Port Hardy (Table 3.2) is drier than the southern stations, receiving 1700 $mm \cdot yr^{-1}$ as rain. Although Port Hardy is warmer in winter, its summers are cooler. Differences in the forest cover are evident. Although western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) dominate at mesic sites, the low relief and cool summer climate have allowed extensive paludification (Hebda, 1983). Thus bog forest complexes are prominent throughout the area. According to Hebda (1983) Douglas-fir (*Pseudotsuga meneziesii*) is uncommon, restricted to xeric sites, and trees typical of higher elevations near Vancouver (e.g. *Chamaecyparis nootkatensis* (D.Don) Spach) are more widespread.

Table 3.1. Climatic summary (1951-1980) for Loon Lake (49°18'N, 122°35'W; 354 m elev.), and Administration (49°16'N, 122°34'W; 143 m elev.), University of British Columbia Research Forest, Haney, British Columbia.

	Loon Lk	Administration
Mean Daily Temperature (°C)		
Coldest Month (Jan)	0.5	1.4
Warmest Month (Jul)	16.3	16.8
Precipitation		
Rain (mm): Annual	2459.1	2059.3
Wettest Month (Dec)	343.3	306.3
Driest Month (Jul)	86.7	65.5
Snow (cm): Annual	195.2	81.6
Frost-free Period (d)	199	198
Degree-days (°C·d)		
Above 0°C	3092.7	3445.7
Above 5°C	1633.7	1882.1

(Environment Canada, 1982)

Table 3.2. Climatic summary (1951-1980) for Port Hardy Airport (50°41',127°22'W; 22 m elev.), northern Vancouver Island, British Columbia.

Mean Daily Temperature	
Coldest Month (Jan)	2.4°C
Warmest Month (Aug)	13.8
Precipitation	
Rain: Annual	1705.8 mm
Wettest Month (Dec)	260.3
Driest Month (Jul)	52.0
Snow: Annual	72.1 cm
Frost-free Period	177 d
Degree-days	
Above 0°C	2931.2°C·d
Above 5°C	1350.0

(Environment Canada, 1982)

With a surface area of 36 ha and maximum depth of 5.2 m, Misty Lake's catchment extends to approximately 100 m above lake level, encompassing 10 km^2. Although an extensive stream system enters the lake, the core was taken near the maximum depth, distant from the inflow. The lake and catchment are underlain by Mesozoic rocks. To the northeast side are Cretaceous sedimentary rocks consisting largely of shales, sandstones, siltstones, and conglomerates, with some coal. Southwestward, Triassic rocks, including both sedimentary (limestone and dolomite) and volcanic units (andesite, basalt, and rhyolite), are exposed (Prov. of B.C., undated).

Methods

The methods used in the stratigraphic study of Mike and Misty Lakes differ little from those described for Marion Lake in the preceding chapter. A 5–cm–diameter sediment core, 6.43 m long, was obtained from the centre of Mike Lake, Golden Ears Provincial Park, at a water depth of 6.47 m. At Misty Lake, 7.53 m of sediment were removed near the lake centre, in 5.2 m of water. For Mike Lake, the 1.0–m–long piston core segments were stored intact, but Misty Lake sediments were bagged as smaller units. For Misty Lake, the upper 7.00 m of sediment were cut into 0.10 m sections, which were individually sealed in plastic bags. To allow closer sampling of the late–glacial deposit, sediment below 7.00 m was packaged as 0.05 m slices. During analysis sediment subsamples of 1.0 to 2.0 mL were examined at 0.80 m intervals throughout most of both cores. Closer sampling was necessary to characterize changes within the late–glacial sediments and, for Mike Lake, near the Mazama volcanic ash.

The sediment subsamples were deflocculated in warm 6% KOH and then sieved (.075 mm mesh). The coarse matter retained was later manually sorted, at 50X magnification in Bogorov counting trays. Fossil chironomids were mounted in Permount®

and identified, principally with reference to Hamilton (1965) and Wiederholm (1983). Diagnostic features used for identification of specific taxa are reported in the Appendix. Percentage diagrams were plotted using the computer program MICHIGRANA developed by R. Futyma and C. Meachum.

Results: Mike Lake

The basal sediments (6.40 – 6.43 m) of Mike Lake are inorganic (Fig. 3.2), composed mostly of grey clay with little, if any, sand or coarser matter. A mottled grey-brown clay-gyttja was subsequently deposited (6.32 – 6.40 m), grading into organic gyttja above (6.275 – 6.32 m). This progression to more organic-rich sediments is interrupted by a thin compact clay layer between 6.26 and 6.275 m. Subsequent sediments, above 6.26 m, consist of a rather uniform-looking organic dy or gyttja, except for the Mazama ash at 4.25 to 4.28 m. Although organic matter and water compose much of the sediment bulk, mineral matter constitutes, by weight, approximately 70 to 80% of the dry residue from 6.1 to 3.0 m. Above 3.0 m, sediments are only slightly less inorganic (*ca.* 60%).

Radiocarbon dates have been obtained on sediments from the lower half of the Mike Lake core, as summarized in Table 3.3. Basal organic-rich sediment at 640 cm dates to 12,910 yr B.P. Thus the timing of deglaciation at Mike Lake is very similar to that at Marion Lake. Dates of 10,350 and 10,360 yr B.P., on sediments near 5.9 m, approximately define the Pleistocene/Holocene boundary.

Although a detailed palynological investigation of Mike Lake's sediments is not yet complete, preliminary data, provided by R. Mathewes, suggest a vegetation history similar to that evident at Marion Lake. As at Marion Lake, the basal sediments (>6.40 m; >12,000 yr B.P.) are a clay in which two shrubs, willow (*Salix*) and soapberry

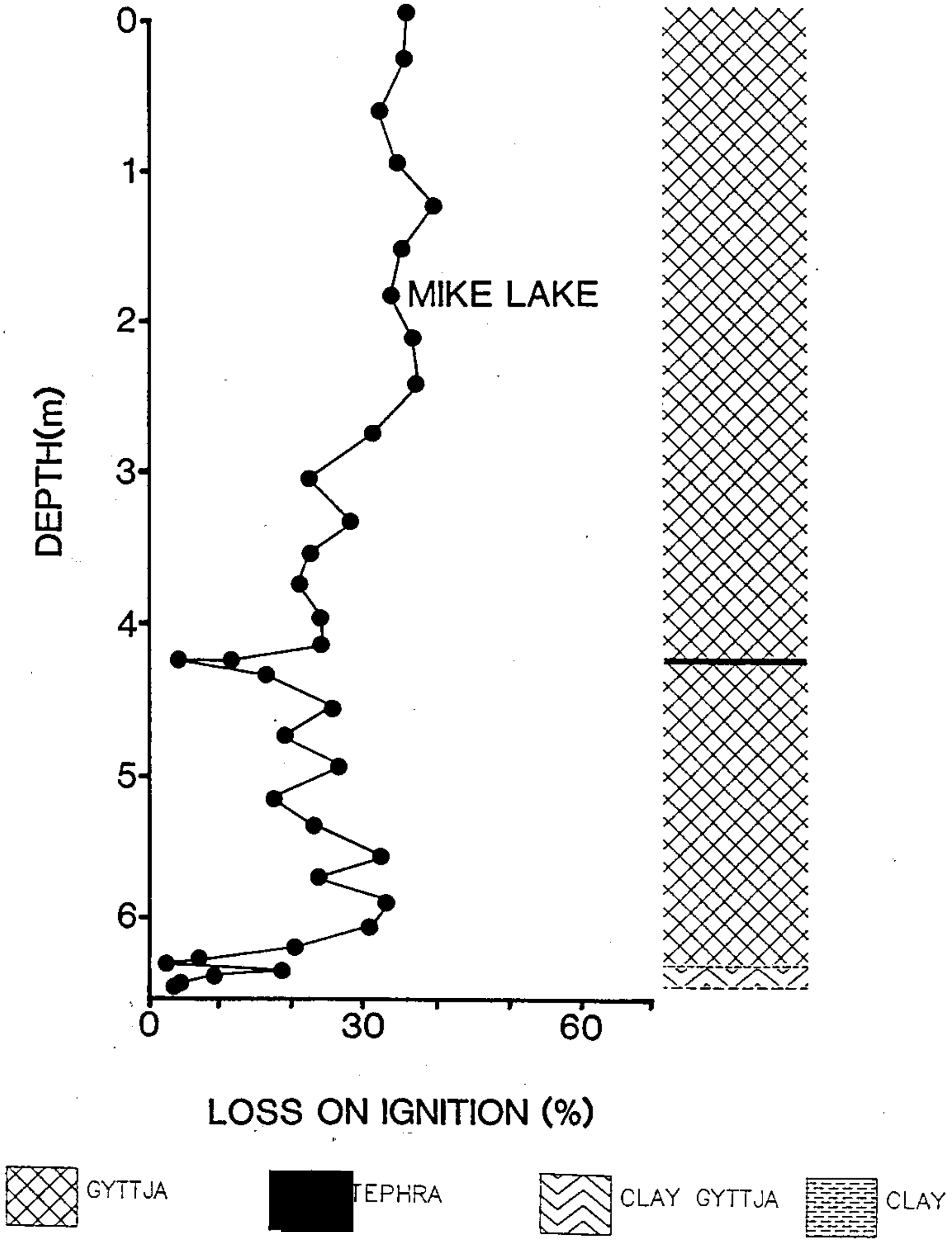

Figure 3.2 Sediment lithology and loss on ignition diagram for dry sediments of Mike Lake, B.C.

Table 3.3. Radiocarbon age for Mike and Misty Lake sediments, British Columbia, Canada.

Sample Depth	Material Dated	Laboratory Reference No.	$\delta^{13}C$*	Age (corrected)
<u>Mike Lake</u>**				
425 cm	Sediment	RIDDL-647	-25	7040±110 yr B.P.
425-428	Mazama Ash	(Bacon, 1983)		6845±50
428	Sediment	RIDDL-648	-25	7500±110
589	Sediment	RIDDL-649	-25	10,350±100
598	Sediment	RIDDL-650	-25	10,360±110
628	Sediment	RIDDL-651	-25	11,850±170
640	Sediment	RIDDL-653	-25	12,910±160
<u>Misty Lake</u>				
90-100	Sediment	BETA-16582	-25	1760±80
290-300	Sediment	BETA-16583	-25	2860±80
490-500	Sediment	BETA-16584	-25	5720±90
590-600	Sediment	BETA-16585	-25	6960±110
705-710	Sediment	BETA-16586	-25	10,180±130
735-740	Sediment	GSC-4029	-25	12,100±130

*-assumed

**-Mike Lake dates are Accelerator Mass Spectroscopy dates, on sediment following KOH, HCl, and HF treatment

(*Shepherdia canadensis*) are prominent, as well as pine (*Pinus* L.). Subsequent forest establishment is marked by the sharp increase in sediment organic content and a preponderance of lodgepole pine (*Pinus contorta*) pollen. Pollen evidence also suggests the presence of balsam fir (*Abies*), spruce (*Picea*), and poplar or cottonwood (*Populus* L.). The thin clay band between 6.26 and 6.275 m (Fig. 3.2) is apparently not distinguished by a distinctive fossil spectrum. Lodgepole pine pollen continues to dominate the sediments through late–glacial time (6.40 to *ca.* 5.90 m; *ca.* 12,000 to 10,000 yr B.P.) with the proportion of balsam, spruce, and alder (*Alnus* Hill) being greater above the clay band.

Western hemlock and mountain hemlock (*Tsuga mertensiana*) are relatively abundant near the Pleistocene/Holocene boundary (*ca.* 5.90 m; 10,000 yr B.P.). Early Holocene sediments (above 5.85 m) include a high proportion of Douglas–fir suggesting a xerothermic interval. However, the renewed abundance of western hemlock pollen (above *ca.* 5.2 m), arrival of western red cedar at *ca.* 3.5 m, and corresponding decline in Douglas–fir indicate, thereafter, a gradual Holocene shift towards the moist climate presently extant in the lower Fraser Valley.

The chironomid record at Mike Lake is in many respects comparable to that at Marion Lake. The results have been portrayed both as percentage data (Fig. 3.3) and total influx (Fig. 3.4). Since the chironomid records do appear similar, the Mike Lake profile will also be discussed in terms of 3 zones. As at Marion Lake, the lowermost zone (6.43 to 5.90 m) encompasses late–glacial sediments deposited prior to 10,000 yr B.P. The second, pre–Mazama zone (5.90 to 4.28 m) was deposited between *ca.* 10,000 yr B.P. and 6800 yr B.P. The third zone, comprising sediments above the Mazama ash (4.25 to 0.0 m), spans the period from 6800 yr B.P. to the present.

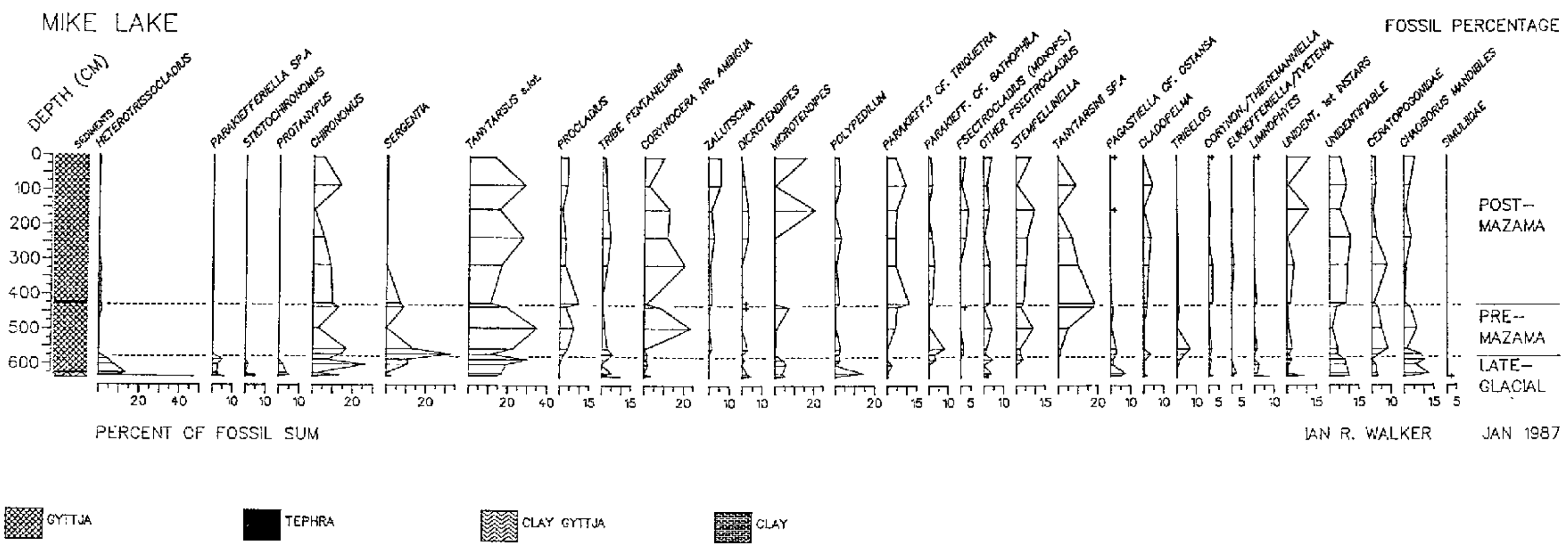

Figure 3.3 Percentage (of total number of chironomid head capsules at each sample level) diagram representing stratigraphy of common Chironomidae at Mike Lake, B.C. (Several rare taxa have been excluded; "+" indicates presence in small numbers).

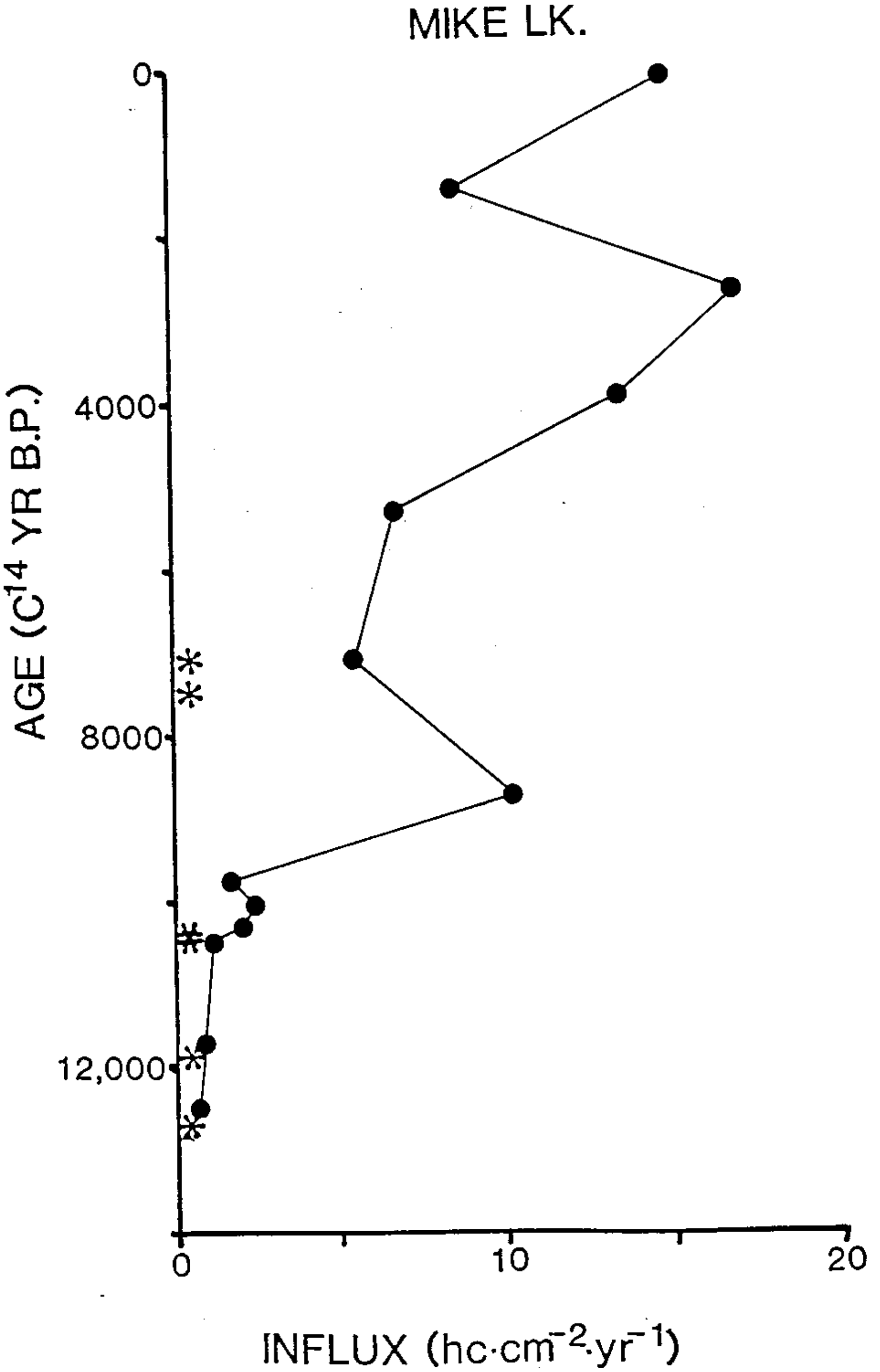

Figure 3.4 Total chironomid influx at Mike Lake, B.C. (*–indicate ^{14}C–dated levels).

Late-glacial assemblages

Late-glacial head capsule influx was low, *ca.* 1.0 $hc{\cdot}cm^{-2}{\cdot}yr^{-1}$ (Fig. 3.4). Prominent late-glacial taxa at Mike Lake included each of the oligotrophic, cold-stenothermous elements recorded at Marion Lake, apart from *Pseudodiamesa*[2] (ie. *Heterotrissocladius*, *Parakiefferiella* sp.A, *Protanypus*, and *Stictochironomus*). Many other taxa (e.g. *Chironomus*, *Corynocera* nr. *ambigua*, *Microtendipes* Kieffer, *Pagastiella* cf. *ostansa*, *Psectrocladius*, *Sergentia*, *Tanytarsus* s.lat.) are also represented. Although, as compared to Marion Lake, the cold-stenothermous taxa at Mike Lake constitute a smaller proportion of the total fauna, the late-glacial trend is distinctly similar. This cold element persists throughout the late-glacial to essentially disappear at 5.7 to 5.85 m, near the Pleistocene/Holocene boundary. *Heterotrissocladius* is the only genus of this group represented in later sediments.

Holocene assemblages

The Holocene is characterized by gradually increasing chironomid influx, rising from near 1.0 $hc{\cdot}cm^{-2}{\cdot}yr^{-1}$ during the earliest Holocene to 17.0 $hc{\cdot}cm^{-2}{\cdot}yr^{-1}$ for modern sediments (Fig. 3.4). A marked separation between early and late Holocene faunas is not evident.

Apart from a single record of *Heterotrissocladius* just below the Mazama ash, the late-glacial cold-stenotherms are absent from pre-Mazama Holocene sediments. *Corynocera* nr. *ambigua* occurs abundantly. Although *C. ambigua* is often regarded as a cold-stenotherm, it is recorded as a littoral resident, occurring throughout Scandinavia, and in the temperate lowlands of north Germany (Fitkau and Reiss, 1978; Mothes, 1968). Its northern limit is in the low arctic (Danks, 1981).

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[2] *Pseudodiamesa* has been found in the late-glacial sediments of Marion Lake since Walker and Mathewes' (1987a) account.

At Mike Lake, *Sergentia* is very abundant in the earliest Holocene sediments, rapidly declining in later deposits. As a common profundal inhabitant of northern oligo–mesotrophic waters (Brundin, 1958; Sæther, 1979), *Sergentia* is probably intolerant of warm water (Pinder and Reiss, 1986), but has survived elsewhere in low–elevation profundal environments of the Pacific Northwest (Wiederholm, 1976: as *Phaenopsectra coracina* (Zetterstedt)). However, the increasing productivity, and reduction in hypolimnetic volume, as Mike Lake shallowed, would have adversely affected this relatively O_2–sensitive taxon. In mid–to late Holocene deposits *Sergentia* disappears from the fauna.

In contrast to Marion Lake, *Heterotrissocladius* is rare in post–Mazama deposits of Mike Lake. The presence of cold lake–bottom springs is likely responsible for the greater abundance of cold–stenotherms at Marion Lake. *Corynocera* nr. *ambigua* is no more abundant during the late–Holocene than during the early Holocene. Thus, no evidence suggestive of cooler or more oligotrophic late Holocene conditions is noted. Although some littoral taxa (e.g. *Dicrotendipes* Kieffer, *Microtendipes, Zalutschia* Lipina) appear more abundantly in post–Mazama sediments, the palaeoecological significance of such minor changes remains obscure. Gradual shallowing of the lake and expansion of littoral habitats are likely to be important influences.

A conspicuous difference between the Mike and Marion Lake profiles is the rarity of rheophiles ("stream–loving" taxa) at Mike Lake. With a much smaller stream input (catchment area of 1.7 km^2, vs 15 km^2 for Marion Lake), this feature was not unexpected.

Results: Misty Lake

Inorganic sediments were also encountered at the base of the Misty Lake core on northern Vancouver Island. This clay deposit, extending from 7.53 to 7.40 m includes sand and pebbles as minor constituents. Thereafter, throughout the remaining late–glacial and Holocene deposits, the sediment is a uniform dark brown dy or gyttja, averaging *ca.* 55% mineral matter on a dry weight basis (Fig. 3.5).

Radiocarbon dates have been obtained throughout the core, as summarized in Table 3.3. Basal, organic–rich sediments (7.35 to 7.40 m) date to 12,100 yr B.P. A date of 10,180 yr B.P. at 7.05 – 7.10 m approximately defines the Pleistocene/Holocene boundary. This indicates a rather thin, 0.45 m late–glacial deposit. Slow sedimentation continued through the early Holocene, but increased towards the present day.

A detailed palynological record is, not yet, available for Misty Lake. R. Mathewes has provided preliminary data on major changes. Lodgepole pine pollen dominates throughout the late–glacial sediments. Balsam, spruce, and mountain hemlock also occur. Western hemlock is first evident at 7.20 – 7.25 m (*ca.* 11,000 yr B.P.). The beginning of the Holocene is marked by the first occurrence of Douglas–fir pollen (6.90 – 7.00 m).

In contrast to Marion and Mike Lakes, Douglas–fir pollen is not abundant during the early Holocene. Instead, western hemlock and spruce prevail from 7.0 to *ca.* 4.0 m (*ca.* 10,000 to *ca.* 4000 yr B.P.). This suggests a wetter and perhaps cooler early Holocene climate than existed at the two southerly sites. The gradual Holocene climatic deterioration and paludification of adjacent forests is marked by the prevalence of skunk cabbage (*Lysichiton americanum* Hultên & St.John) pollen above 6.0 m, and later occurrence of burnet (*Sanguisorba* L.) and Douglas' Gentian (*Gentiana douglasiana* Bong.). Above 4.0 m, western hemlock and Cupressaceae (probably western red cedar) dominate,

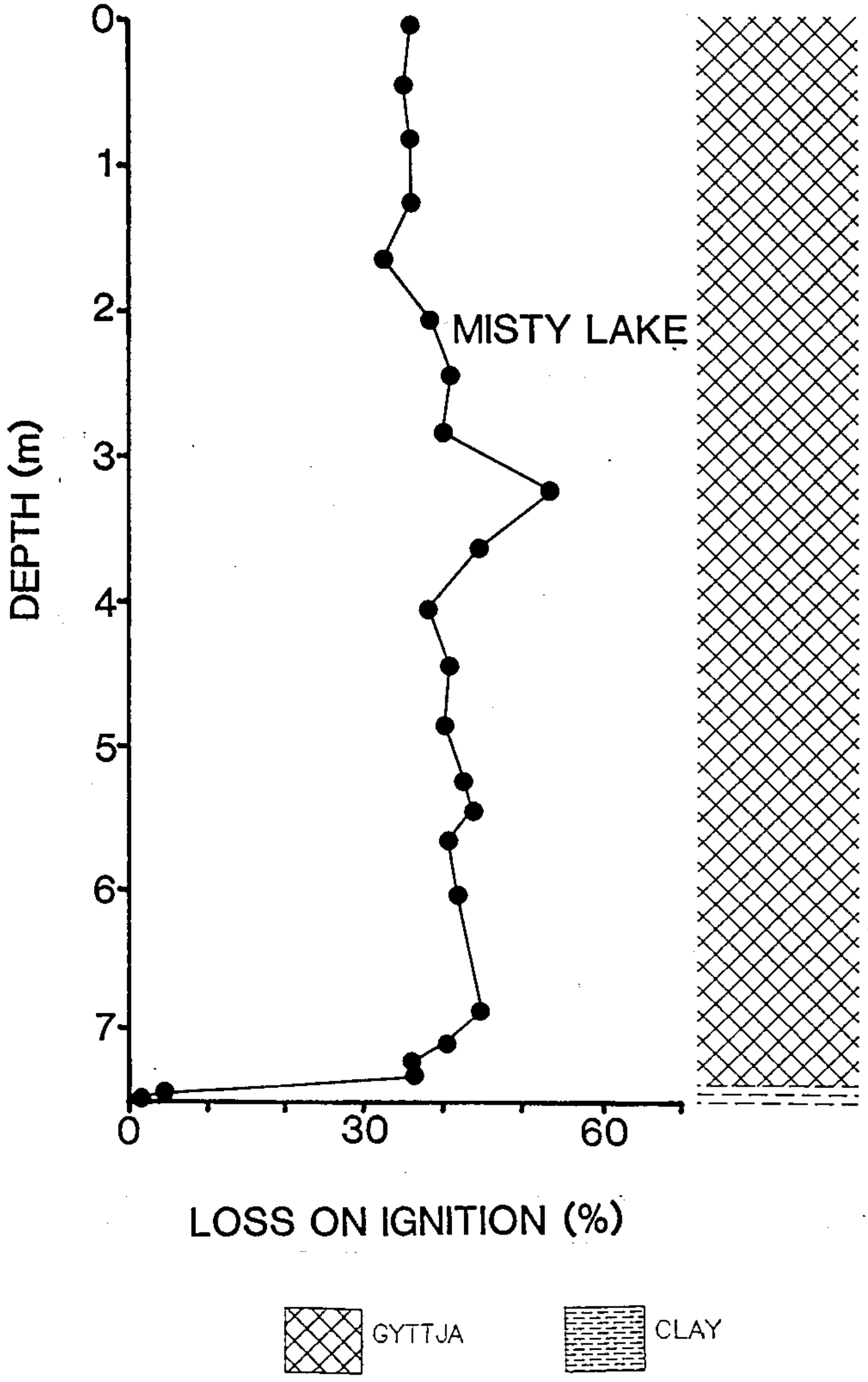

Figure 3.5 Sediment lithology and loss on ignition diagram for dry sediments of Misty Lake, B.C.

as they do today.

Correlation of the late–glacial/early Holocene pollen record with Hebda's (1983) Bear Cove Bog profile, 18 km northwest of Misty Lake, has proven difficult. The dates on Bear Cove Bog imply the arrival of Douglas–fir and decline in mountain hemlock around 8000, and not 10,000 yr B.P. In this report, I assume the Misty Lake dates to be correct. Roots penetrating deeper peat from above could have contaminated Bear Cove radiocarbon samples, making them too young.

The major chironomid changes at Misty Lake are also best described in terms of 3 zones, the late–glacial, early Holocene, and late Holocene (Fig. 3.6). The late–glacial (≥7.00 m) is represented by the lowermost 0.45 m. A division between early and late Holocene deposits is possible at a marked decline in *Sergentia* abundance, *ca.* 4.40 m (about 5500 yr B.P.).

Late– glacial assemblages

At Misty Lake, the influx of chironomid head capsules was initially low, about 1.0 hc·cm^{-2}·yr^{-1} (Fig. 3.7). The cold–stenothermous element is represented by *Heterotrissocladius*, *Protanypus*, and *Stictochironomus* (Fig. 3.6). The two latter taxa are present in very small numbers, and only in the two lowermost samples. As at Mike Lake, the cold–stenothermous elements have essentially disappeared by 10,000 yr B.P.

Several other taxa also occur in the late–Pleistocene sediments. Particularly intriguing is the presence of *Corynocera* nr. *ambigua* in the late–glacial, but not in subsequent Holocene sediments. As expressed earlier, *C. ambigua* has occasionally been regarded as a cold–stenotherm. It is frequently recorded in European late–glacial deposits (e.g. Andersen, 1938; Fjellberg, 1972), but its littoral habitat and geographical distribution also suggest its occurrence in warm waters.

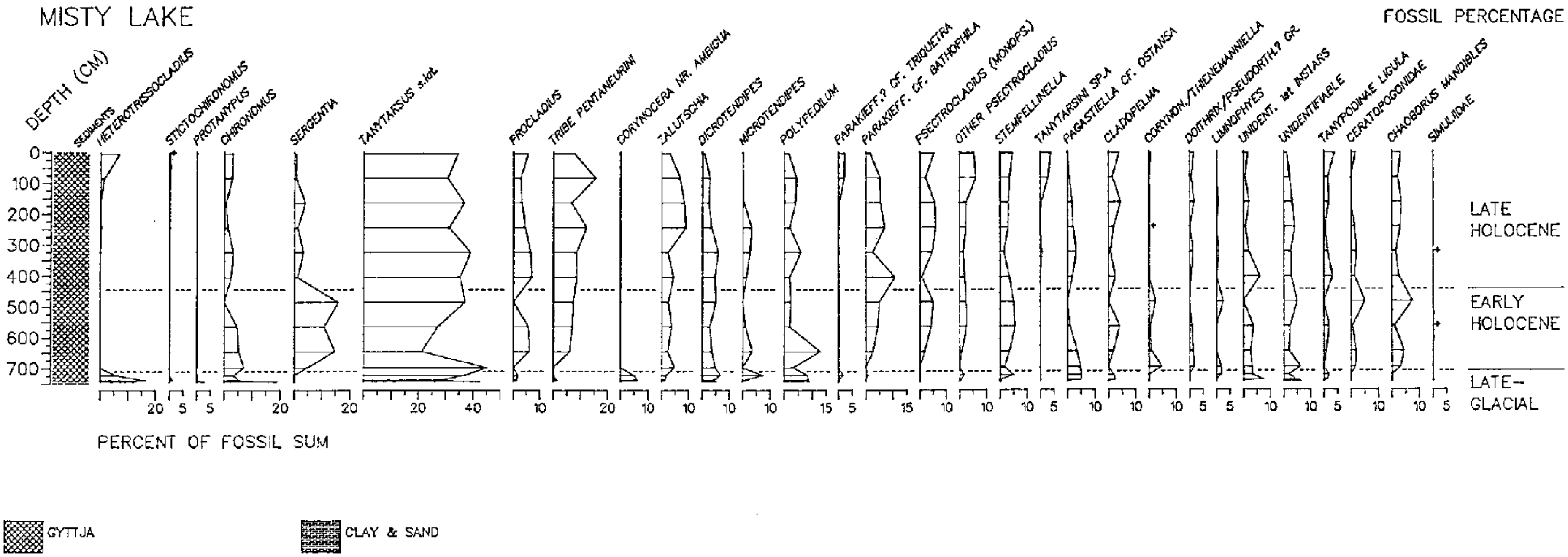

Figure 3.6 Percentage (of total number of chironomid head capsules at each sample level) diagram representing stratigraphy of common Chironomidae at Misty Lake, B.C. (Several rare taxa have been excluded; "+" indicates presence in small numbers).

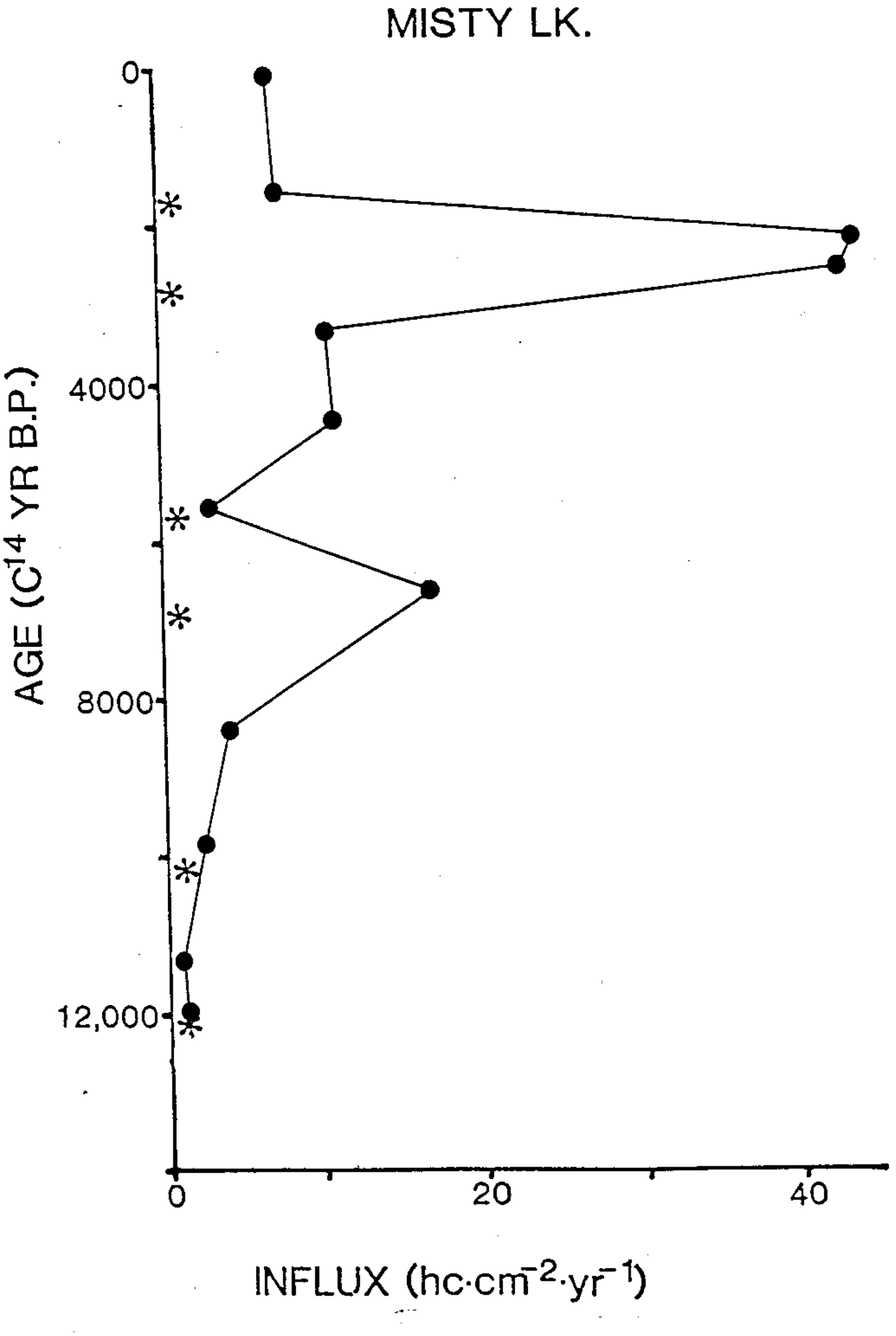

Figure 3.7 Total chironomid influx at Misty Lake, B.C. (*–indicate ^{14}C–dated levels).

Apart from the lowermost sample, the late–glacial faunal diversity is close to that in Holocene deposits. However, this may not be unusual, even for a subarctic lake. Most Canadian chironomid genera occur north to tree–line (Oliver *et al.*, 1978; Oliver and Roussel, 1983a; Wiens *et al.*, 1975), although many are not known from the arctic (Danks, 1981).

Holocene assemblages

Chironomid influx at Misty Lake gradually increases throughout much of the Holocene. Peak influx may exceed 40 hc·cm^{-2}·yr^{-1} at about 2500 yr B.P. (*ca.* 2.0–m–depth) (Fig. 3.7). Interpretation of influx profiles is complex, owing in part to the possible concentration of head capsules in sublittoral environments.

The Holocene faunal changes at Misty Lake illustrate few trends. Most striking is the early Holocene prominence of *Sergentia*, which abruptly declines in abundance *ca.* 5000 yr B.P. An explanation for this distinct shift is not readily apparent. However, the gradual infilling of Misty Lake would have slowly reduced the available cool, relatively well–oxygenated profundal habitat.

In the uppermost sediments, three taxa which had been present during the late–glacial again appear, *Heterotrissocladius*, *Parakiefferiella*? cf. *triquetra*, and *Stictochironomus*. Since two of these taxa, *Heterotrissocladius* and *Stictochironomus* seem to be associated with cool, oligotrophic environments in British Columbia, their presence could indicate a recent trend to cooler or more oligotrophic conditions. The mid to late–Holocene deterioration of Pacific Northwest climate (neoglaciation) has been well documented through other evidence (Clague, 1981; Mathewes, 1985).

As at Mike Lake, few rheophiles were identified from the core. Although Misty Lake receives significant stream input, the coring site was distant from this supply.

Discussion

The above results are largely in accord with the hypothesis that climatic changes were responsible for the late–glacial faunal changes. In Marion, Mike and Misty Lakes, a pronounced oligotrophic, cold–stenothermous element is evident through the late–glacial, but is much less common in subsequent Holocene sediments. Thus, global climatic change may have had an important bearing upon chironomid succession.

This pattern is similar to that in New Brunswick (Walker and Paterson, 1983) and Germany (Hofmann, 1971a, 1983a) where late–glacial chironomid faunal changes appear to occur with similar timing among lakes. This implies that the lakes and their faunas are not reacting independently. A regional influence, like climate, appears to be directing late–glacial change.

Local watershed characteristics would seem to be less important. There is no change in sediment composition evident in the British Columbia lakes at the Pleistocene/Holocene boundary. Chironomids do not appear to be responsive to the late–glacial/early Holocene pH and alkalinity variations noted elsewhere (Walker and Paterson, unpublished data).

There is a possibility that terrestrial vegetation could influence chironomid faunal composition, perhaps through the detritus food chain, or through biogeochemical pathways within the watershed. The problem of distinguishing vegetation's possible role is not trivial in British Columbia. Since full–glacial and late–glacial refugia for common trees probably existed within a few hundred kilometres of southern British Columbia (Barnosky, 1984; Heusser, 1972; Tsukada, 1982), I have assumed that late–glacial vegetation was in equilibrium or near equilibrium with climate. Migration lags for major tree species, apparently a major influence on early postglacial vegetation in eastern North America (Davis, 1984), were probably of short duration in southern British Columbia. Thus, floristic changes should provide reliable evidence for climatic change.

Linkages between the terrestrial and aquatic environments should not be ignored. However, any demonstration that the late–glacial faunal changes in British Columbia were independent of terrestrial vegetation changes, and were instead climatically dependent requires that climate change with little indication of a vegetation response. At each British Columbia site, the decline in pine pollen, and arrival of Douglas–fir, *ca.* 10,000 yr B.P., indicates a shift in forest composition. This forest change occurs over the same time interval throughout southwestern British Columbia, and thus is probably climatically induced. Forest vegetation can influence lake and stream biogeochemistry, including both nutrient and allochthonous organic inputs (Likens and Bormann, 1974). However, the earlier shift from a non–forested to a forested environment should have had more dramatic consequences for lake biota than a shift in coniferous forest composition.

Despite these concerns there is little evidence that many chironomid distributions are influenced significantly by terrestrial vegetation. It is pertinent that despite a continuously changing forest composition at Portey Pond, in New Brunswick, the chironomid fauna has changed little in 9000 yr (Walker and Paterson, 1983). In Portey and Wood's Ponds, the major late–glacial chironomid faunal change is not accompanied by a marked change in either terrestrial vegetation or sediment type.

A pronounced late–glacial climatic warming could have had both direct and indirect effects upon chironomids. Lethal warmth would have eliminated cold–stenotherms from littoral habitats. However, summer stratification is evident at Mike Lake today. Thus, a cool hypolimnetic region must also have existed in the deeper late–glacial/early Holocene basin. Survival of cold–stenotherms should have been possible in the profundal zone. Consequently, increased Holocene productivity, and the resultant hypolimnetic O_2–deficit must have contributed to the faunal change. The summer O_2 profile of Mike Lake (Fig.

3.8) illustrates the hypolimnetic O_2 demand. This profile is typical for mesotrophic lakes (Wetzel, 1975).

A similar explanation could account for early faunal changes at Elk Lake, Minnesota (Stark, 1976). Despite being isolated from the direct influence of climate by 30 m of water, the Elk Lake chironomid faunal changes parallel palynological evidence for climatic amelioration (Walker and Mathewes, 1987b).

It is significant that in Marion, Mike, and Misty Lakes the faunal changes are gradual. The abundance of cold-stenothermous oligotrophic taxa gradually decreases through the entire late-glacial interval. This differs from the temperature record provided by Mathewes and Heusser (1981). They indicate a rapid warming between 11,000 and 10,000 yr B.P. However, the pollen record on which it is based (Mathewes, 1973) indicates a more gradual floristic shift. Similar gradual patterns are suggested at Saanich Inlet, Squeah Lake, and Surprise Lake (Heusser, 1983; Mathewes, 1973; Mathewes and Rouse, 1975). Thus the late-glacial amelioration may have been less abrupt than the pollen/climate transfer functions indicate. The retreat of Cordilleran ice is evidence that a full-glacial climate no longer existed. However, cold, catabatic winds from persistent interior British Columbia ice, directed eastward by valleys and a major continental anticyclone (Broccoli and Manabe, 1987), could have maintained cooler conditions locally.

Subsequent Holocene changes cannot be correlated among lakes. The similarities of successional pattern are more subtle and time-transgressive. Consequently, it is difficult, or perhaps impossible, to justify a climatic cause.

Sergentia is common in the early Holocene sediments of Mike and Misty Lakes, but much less common through the late Holocene. Many littoral taxa are abundant in recent sediments. As suggested earlier, these changes may relate to the gradual shallowing of the lakes. The similarity of successional pattern among the lakes may correspond to

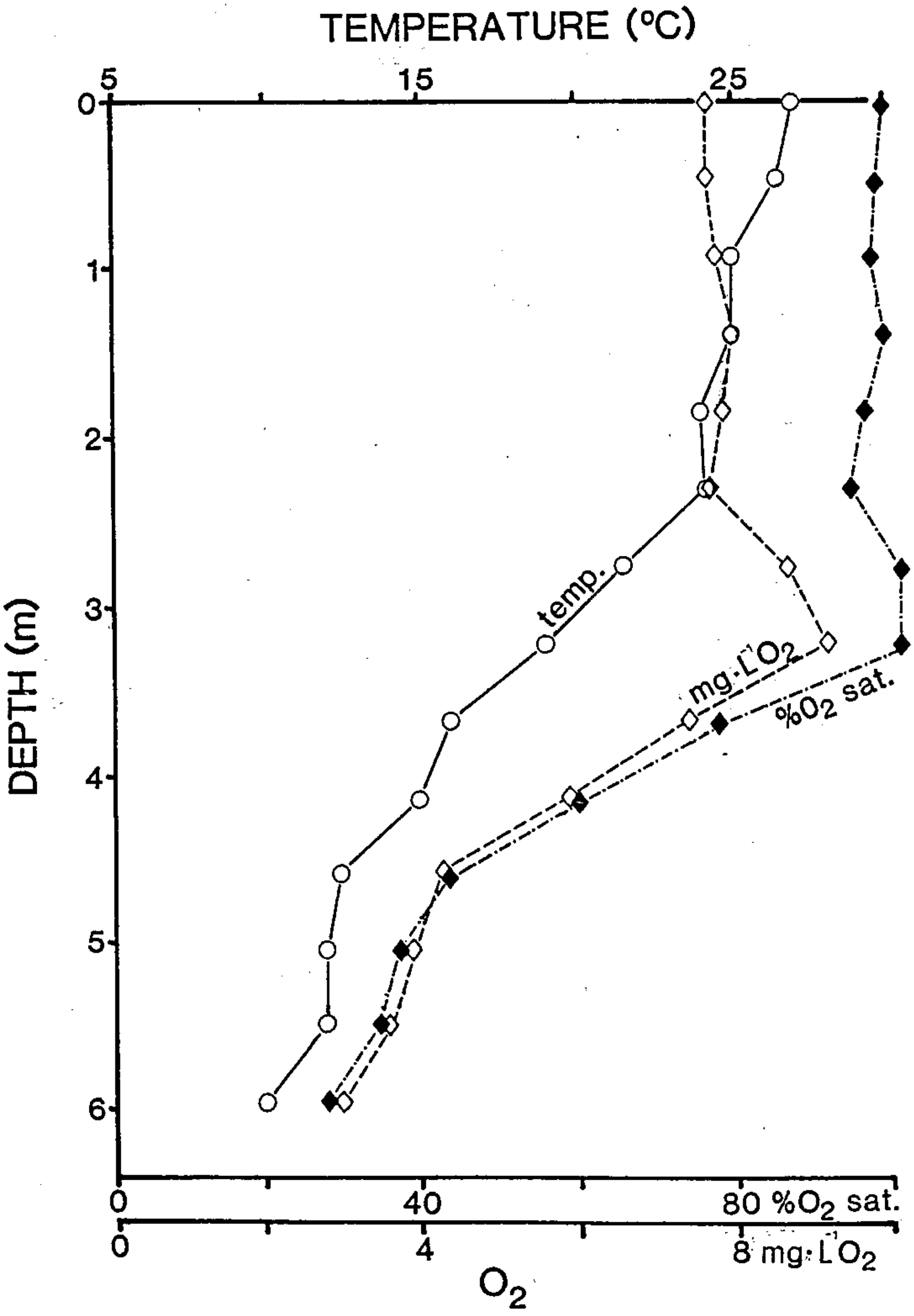

Figure 3.8 Late summer oxygen and temperature profile of Mike Lake, B.C. (late afternoon September 7, 1987).

the similarity of the lakes' depths throughout postglacial time. If constant surface levels are assumed, the initial depths of Marion, Mike and Misty Lakes were, repectively, 15.0, 12.9, and 12.7 m. Their present depths vary from 6.5 to 5.2 m. As Mike and Misty Lakes shallowed the smaller hypolimnetic volume was expressed partly as decreased O_2 concentrations. Deevey (1955a) and Sæther (1980a) have, respectively, noted the importance of hypolimnetic volume to lake trophic state and benthic fauna.

The late Holocene increase of *Corynocera* nr. *ambigua*, and *Heterotrissocladius* at Marion Lake, and recent reappearance of *Heterotrissocladius* and *Stictochironomus* at Misty Lake, could relate to the cooler or more oligotrophic late Holocene conditions. However, no similar trend is evident at Mike Lake. The trends are too inconsistent among lakes, and through time to define a clear pattern.

It is interesting to compare the rates of chironomid head capsule deposition among Marion, Mike and Misty Lakes (Fig. 3.9). In each case a late–glacial influx of *ca.* 1.0 to 2.0 $hc{\cdot}cm^{-2}{\cdot}yr^{-1}$ is evident. After 10,000 yr B.P. a trend to greatly increased chironomid influx exists. Peak influx values range from 17 to 43 $hc{\cdot}cm^{-2}{\cdot}yr^{-1}$. Recently, at Mike and Marion Lakes, influx declined.

The influx records probably reflect complex changes within the lakes. Late–glacial chironomid populations may have been low, owing to deep water and low productivity. However, late–glacial transport of littoral head capsules to the core sites may have been limited by the less turbulent waters of the deepwater environment. Within a lake, chironomid production is typically greater in the shallower waters (Brinkhurst, 1974). Thus, the Holocene trend to greater influx may relate to higher productivity (partly a function of climate, and lake depth), decreasing depth, and the influence of "head–capsule focusing". Separation of these effects is not yet possible. Influx profiles from lakes of greater and lesser depths could prove interesting. For example, the influence of water

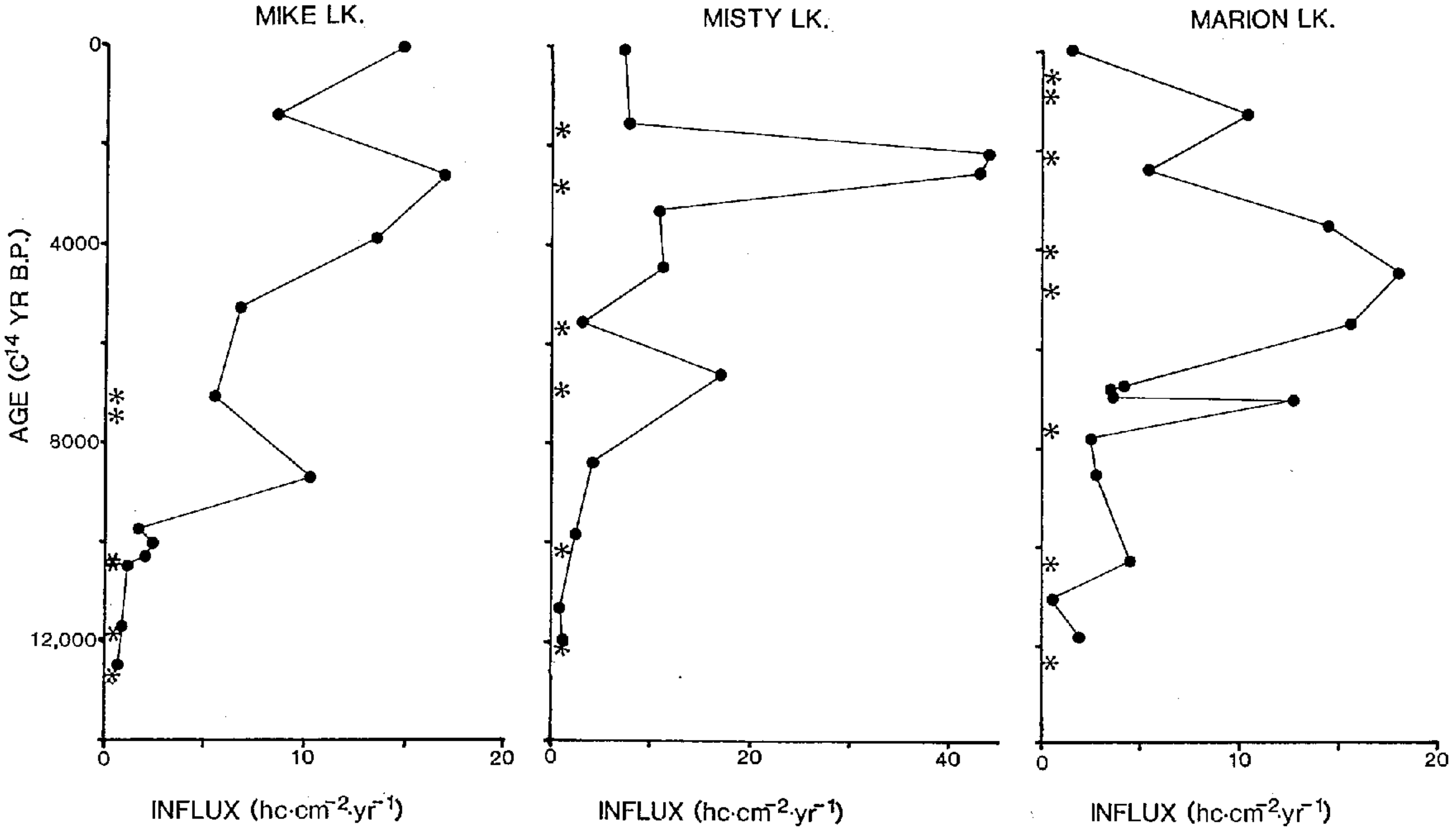

Figure 3.9 Comparison of total chironomid influx among Mike, Misty, and Marion Lakes, southwestern British Columbia. (*–indicate ^{14}C–dated levels).

depth and focusing should be minimal in a deep lake which, morphometrically, has not changed greatly through postglacial time.

Although postglacial succession has not been examined in any of the deep lakes of British Columbia, late–glacial/early Holocene faunal changes would probably parallel those of the shallow lakes presently studied. The influence of a great hypolimnetic volume would likely be evident, however, with the faunal changes being much less dramatic in the deeper lakes. Such an investigation would be a valuable extension to the present research.

CHAPTER 4

HIPPA LAKE STRATIGRAPHY[1]

Biologists have long been fascinated by the flora and fauna of islands. In Canada, the Queen Charlotte archipelago has been a site of special interest. Although recent studies have demonstrated that few vascular plant species are truly endemic (Pojar, 1980), curious biogeographic relationships still provide a research focus for botanists (e.g. Schuster and Schofield, 1982; Vitt and Schofield, 1976), entomologists (Kavanaugh, 1984), ichthyologists (Moodie and Reimchen, 1976), and especially palaeoecologists (Hann and Warner, 1987; Hebda and Mathewes, 1984; Warner, 1984; Warner and Chmielewski, 1987; Warner *et al.*, 1984).

The unique Queen Charlotte biota has been regarded as evidence for a glacial refugium. However, proof of a continuously ice–free refugium remains elusive. Radiocarbon chronologies can trace the advance of local Queen Charlotte ice after 27,500 yr B.P. (Warner *et al.*, 1984). The unusually early glacial retreat, which began prior to 16,000 yr B.P., in parts of eastern Graham Island, is also documented (Clague *et al.*, 1982; Mathewes *et al.*, 1985; Warner *et al.*, 1982). However, no terrestrial or freshwater record spans the interval of maximum glaciation to prove refugial status (Warner, 1984).

I have examined a fourth British Columbia site, situated on an island off the western coast of Graham Island, in the Queen Charlotte archipelago. This site, Hippa Lake, provides the longest complete late–glacial/Holocene lacustrine sequence as yet available for the archipelago. The record spans the interval 11,000 yr B.P. to the present. The lake's shallow basin, isolated setting and hyperoceanic climate represents a previously unstudied situation, contrasting with my earlier chironomid stratigraphic study sites in

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[1] A manuscript, largely adapted from this chapter, has been submitted to <u>The Canadian Entomologist</u>.

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southwestern British Columbia.

Study area

The Queen Charlotte Islands are separated from other coastal islands nearer mainland British Columbia by Hecate Strait. Hecate Strait varies in width from *ca.* 50 to *ca.* 130 km along the length of the archipelago. Although fifty or more islands compose the Queen Charlotte archipelago (Fig. 4.1), Graham and Moresby Islands include most of the islands' mass. Many smaller islands lie scattered off the eastern shore of Moresby Island, but the western Queen Charlotte shoreline is abruptly defined by the Queen Charlotte Islands fault (Sutherland Brown, 1968).

Hippa Island (4.9 km^2) is one of the few small islands lying beyond Graham Island's western flank (Fig. 4.1). Lying 0.7 km offshore, climate at this study site is dominated by proximity to the Pacific Ocean. Weather stations at Langara Island and Cape St. James (Table 4.1), with similar settings to Hippa Island, suggest mean August temperatures averaging *ca.* 13.5° C near sea level. Corresponding January temperatures approach 3° C. Although the Langara and Cape St. James stations record *ca.* 1500 $mm \cdot yr^{-1}$ as rain, neither station is susceptible to the additional orographic precipitation that should be evident near Hippa Lake. For example, Tasu Sound receives 4173 $mm \cdot yr^{-1}$ as rain. However, sheltered from the direct Pacific influence, records at Tasu Sound reflect a more continental temperature regime. The temperature regime inferred for Hippa Lake is not unlike that for the Misty Lake area at present, but given the isolated setting of Hippa Lake, the possible importance of sea level fluctuations (Clague, 1981), and late–glacial outflow winds to Misty Lake's past climate, there is no assurance that this situation has existed throughout postglacial time.

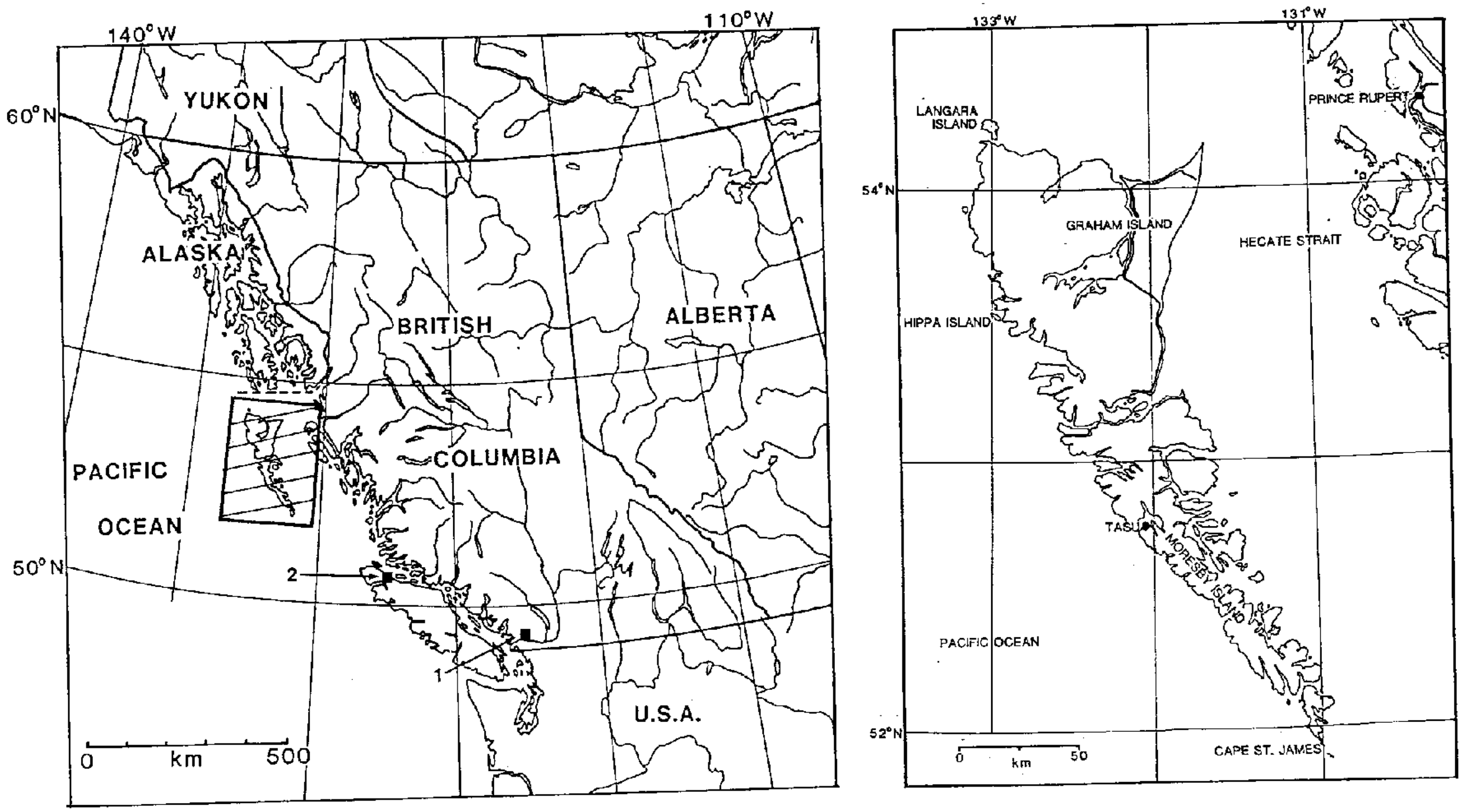

Figure 4.1 Location of Hippa Island, Queen Charlotte Islands, British Columbia, where Hippa Lake is located. (Arrows indicate location of earlier chironomid stratigraphic study sites – 1) Marion and Mike Lakes; 2) Misty Lake)

Table 4.1. Climatic summary (1951-1980) for Cape Saint James (51°56'N,131°01'W; 89 m elev.), Langara (54°15'N,133°03'W; 41 m), and Tasu Sound (52°46'N,132°03'W; 15 m elev.), western Queen Charlotte Islands, British Columbia.

	Cape St. James	Langara Island	Tasu Sound
Mean Daily Temperature (°C)			
Coldest Month (Jan)	3.9	2.3	2.8
Warmest Month (Aug)	13.8	13.2	14.6
Precipitation			
Rain (mm): Annual	1481.1	1658.1	4172.7
Wettest Month	197.5 (Oct)	193.2 (Nov)	596.1 (Oct)
Driest Month	58.4 (Jul)	80.1 (Jul)	123.9 (Jul)
Snow (cm): Annual	51.3	101.4	75.7
Frost-free Period (d)	265	242	217
Degree-days (°C·d)			
Above 0°C	3102.7	2767.8	3039.0
Above 5°C	1397.7	1180.3	1441.5

(Environment Canada, 1982)

Hippa Lake (53° 31.9'N, 132° 58.4'W), the only lake on Hippa Island, is small (3.2 ha) and shallow (1.1 m). Situated at an elevation of 230 m, no permanent inflowing streams are apparent although local relief extends to 450 m, defining a 0.4 km^2 catchment. The lake, and most of the island are underlain by Tertiary basalt and rhyolite of the Masset Formation (Sutherland Brown, 1968). Quartz diorite and diorite of Jurassic age are exposed on the island's eastern flank.

The island has been placed in the Coastal Cedars-Pine-Hemlock Biogeoclimatic Zone (Banner *et al.*, 1983) which includes low elevation forests of the western Queen Charlotte Islands slopes. Forest inventories (Prov. of B.C., 1967) indicate western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) , and yellow cedar (*Chamaecyparis nootkatensis*) to be prominent trees of Hippa Island forests. Lodgepole pine (*Pinus contorta* var. *contorta*) is also present, and mountain hemlock (*Tsuga mertensiana*) can be abundant in forests of adjacent Graham Island.

Methods

The methods employed for stratigraphic studies at Hippa Lake differ little from those employed at Marion Lake.

A sediment core 3.55-m-long was obtained from a *Nuphar lutea* (L.) Sibth. & Sm. bed in the centre of Hippa Lake in 1.1 m of water by R.W. Mathewes and B.G. Warner. The core was cut into 5 cm slices, which were individually sealed in plastic bags. Sediment subsamples (1.0 to 5.0 mL) were retained for chironomid analysis. Samples were examined at 40 cm intervals throughout most of the core. Closer sampling was used to characterize late-glacial changes.

Sediment was deflocculated in hot 6% KOH and sieved (.075 mm mesh). Coarse matter retained by the sieve was later sorted wet, at 50X in a Bogorov counting tray. Head capsules recovered from the sediments were mounted in Permount® on microscope slides and identified, with reference mostly to Hamilton (1965) and Wiederholm (1983). Stratigraphic results were plotted using the computer program MICHIGRANA developed by R. Futyma and C. Meachum.

Results

The Hippa Lake basal sediments (3.47 to 3.55 m) consist of grey, pebbly clay with very low loss on ignition (Fig. 4.2). Light-tan coloured gyttja characterizes the remaining late-glacial deposits, between 3.20 and 3.47 m. Subsequent Holocene sediments are a coarse brown detritus gyttja including a rather small organic fraction. The organic fraction constitutes 20 to 30% by weight of the dry sediment (Fig. 4.2).

Radiocarbon dates have been obtained throughout the Hippa Lake core, as summarized in Table 4.2. Basal organic-rich sediment (3.40 to 3.47 m) is dated at 11,100 yr B.P. The late-glacial/Holocene transition *ca.* 9780 yr B.P. occurs at 3.20 to 3.25 m. This implies very slow sedimentation during the late-glacial. Although subsequent Holocene sedimentation was more rapid, the implied rates may be unrealistically high for the 1.70 to 2.65 m interval. The two dates defining this interval, although separated by 0.90 m, indicate a deposition time of less than 300 years. This raises questions as to the two dates' validity. For this reason I will not present chironomid influx estimates.

A detailed palynological study of Hippa Lake's sediments has not yet been completed. R. Mathewes has provided a preliminary outline of major changes in pollen stratigraphy. The pollen of early mineral-rich sediments (>346 cm) suggests a sparse herbaceous-type vegetation, perhaps similar to tundra. Coincident with the shift to an

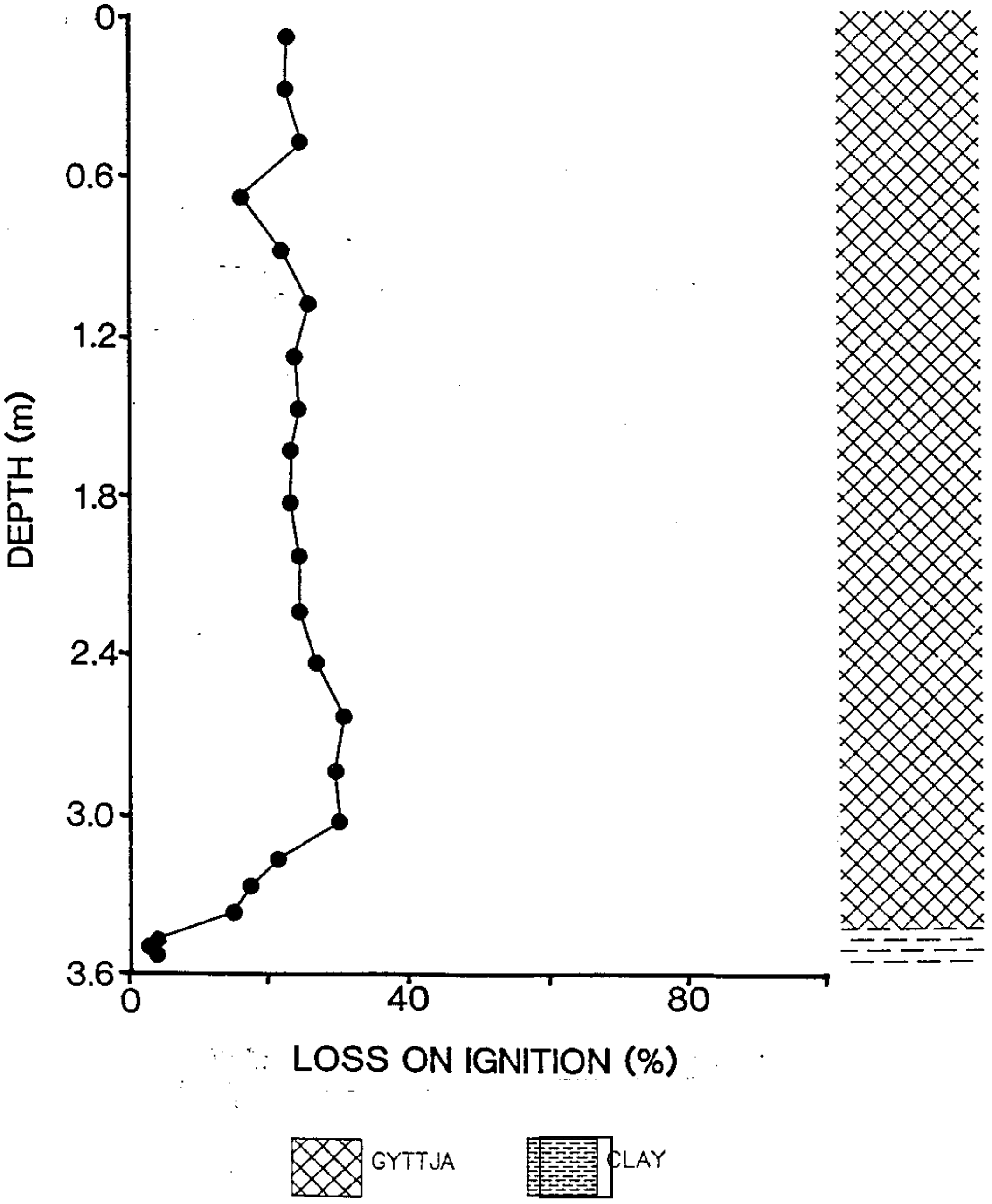

Figure 4.2 Sediment lithology and loss on ignition diagram for dry, postglacial sediments of Hippa Lake, Queen Charlotte Islands, B.C.

Table 4.2. Radiocarbon age for Hippa Lake sediments, Queen Charlotte Islands, British Columbia, Canada.

Sample Depth	Material Dated	Laboratory Reference No.	$\delta^{13}C$	Age (corrected)
80-85 cm	Sediment	BETA-16579	-25*	4860±140 yr B.P.
170-175	Sediment	BETA-16580	-25*	6760±130
260-265	Sediment	BETA-16581	-25*	7020±250
320-325	Sediment	GSC-3773	-25.7	9780±110
340-347	Sediment	GSC-3760	-24.2	11,100±220

*-assumed

organic-rich sediment, lodgepole pine pollen becomes very abundant. The decreased mineral-fraction probably reflects stabilization of adjacent slopes by vegetation.

As in southwestern British Columbia (e.g. Mathewes, 1973), lodgepole pine pollen predominates throughout the late-glacial organic-rich sediments. During the latter part of the late-glacial, spruce becomes abundant along with alder (*Alnus*) and ferns (Polypodiaceae).

The end of the late-glacial is marked by the arrival of western hemlock at 3.15 to 3.20 m. Spruce and western hemlock pollen, with some alder, dominated the subsequent early and mid-Holocene pollen rain. Cupressaceae pollen, presumably western red cedar, is also very common in more recent sediment (≤4000 yr B.P.).

This pollen record suggests a late-glacial/early Holocene warming trend, similar to that in southwestern British Columbia. However, there is little evidence of a warm, dry xerothermic interval. This feature may reflect the northern setting of the Queen Charlotte Islands, and the high precipitation along the archipelago's western margin. The pollen record at Hippa Lake is broadly similar to that described by Warner (1984) for the islands' eastern lowlands.

Chironomid stratigraphy

Very low chironomid numbers were recovered from the basal, mineral-rich sediments of Hippa Lake. Unfortunately, the samples retained for chironomid analysis were not sufficient to provide statistically meaningful results (Table 4.3). However, these results do indicate the very early arrival of *Corynocera* nr. *ambigua*, *Dicrotendipes*, *Heterotanytarsus* cf. *perennis* Sæther, *Heterotrissocladius*, *Microtendipes*, *Psectrocladius*, and *Tanytarsus* s.lat.

Table 4.3. Chironomid taxa recovered from the basal sediments (≥11,000 yr B.P.) of Hippa Lake, Queen Charlotte Islands, British Columbia, Canada. (Number of head capsules per sample).

Depth(cm)	347-349	351-353	Basal?
Corynocera nr. ambigua Zetterstedt	4		19
Dicrotendipes Kieffer	1		1
Heterotanytarsus cf. perennis Saether		0.5?	1
Heterotrissocladius Sparck	0.5	2.5	1.5
Microtendipes Kieffer	2		1
other* Psectrocladius Kieffer	0.5		0.5
Tanytarsus v.d.Wulp s.lat			1
Volume examined (mL)	5.0	5.0	5.0

*-"other Psectrocladius" includes all species of this genus, apart from subgenus Monopsectrocladius Laville.

Most of these early taxa belong to widely-distributed, eurythermic genera. However, three genera have restricted distributions in arctic-alpine environments (Danks, 1981). Although Moore (1978) records *Microtendipes*, at or just beyond tree-line in the Canadian arctic, it is not known elsewhere in North American arctic or alpine environments (Danks, 1981). *Dicrotendipes* also occurs at, or just beyond, tree-line (Moore, 1978). One species, *D. lobiger* (Kieffer), although rare, is recorded for Barrow, Alaska (Butler *et al.*, 1981). *Heterotanytarsus* Spärck has not been found in arctic habitats (Danks, 1981; Fitkau and Reiss, 1978; Sæther, 1975d). *Heterotanytarsus* seems to be most common in northern, oligotrophic waters (Sæther, 1975d). However, its known Nearctic distribution is limited to Marion Lake, B.C. (*H. perennis*), Ontario (*H. nudalis* Sæther), and New Brunswick (Sæther, 1975d; Walker *et al.*, 1985). Although a cooler climate than that of today possibly existed, late-glacial arctic conditions seem unlikely at Hippa Lake.

The lowermost organic-rich sample provided a tremendous concentration of head capsules, 690·mL^{-1} (Fig. 4.3). This sample contained 13 taxa, but *Corynocera* nr. *ambigua* accounted for 72% of the total fauna. Other common taxa included *Dicrotendipes*, *Microtendipes*, *Procladius* Skuse, *Psectrocladius*, and *Tanytarsus* s.lat.

Subsequent late-glacial and Holocene deposits yield smaller concentrations, averaging 136 head capsules·mL^{-1}. The initial faunal composition appears unstable (Fig. 4.4) with rapid changes in the abundance of several common taxa (e.g. *Corynocera* nr. *ambigua*, *Heterotrissocladius*, *Tanytarsus* s.lat.). Head capsules similar to *Corynocera oliveri* Lindeberg were also noted (see Appendix), but included with *Tanytarsus* s.lat. *C. oliveri* has been reported from Greenland sediments (Hofmann, 1983b), but not elsewhere in North America (Pinder and Reiss, 1983). The total number of Holocene taxa is low relative to other British Columbia sites. On average 11 to 12 taxa were recorded per sample at Hippa Lake, whereas 19 to 20 were typical for Mike Lake, near Vancouver.

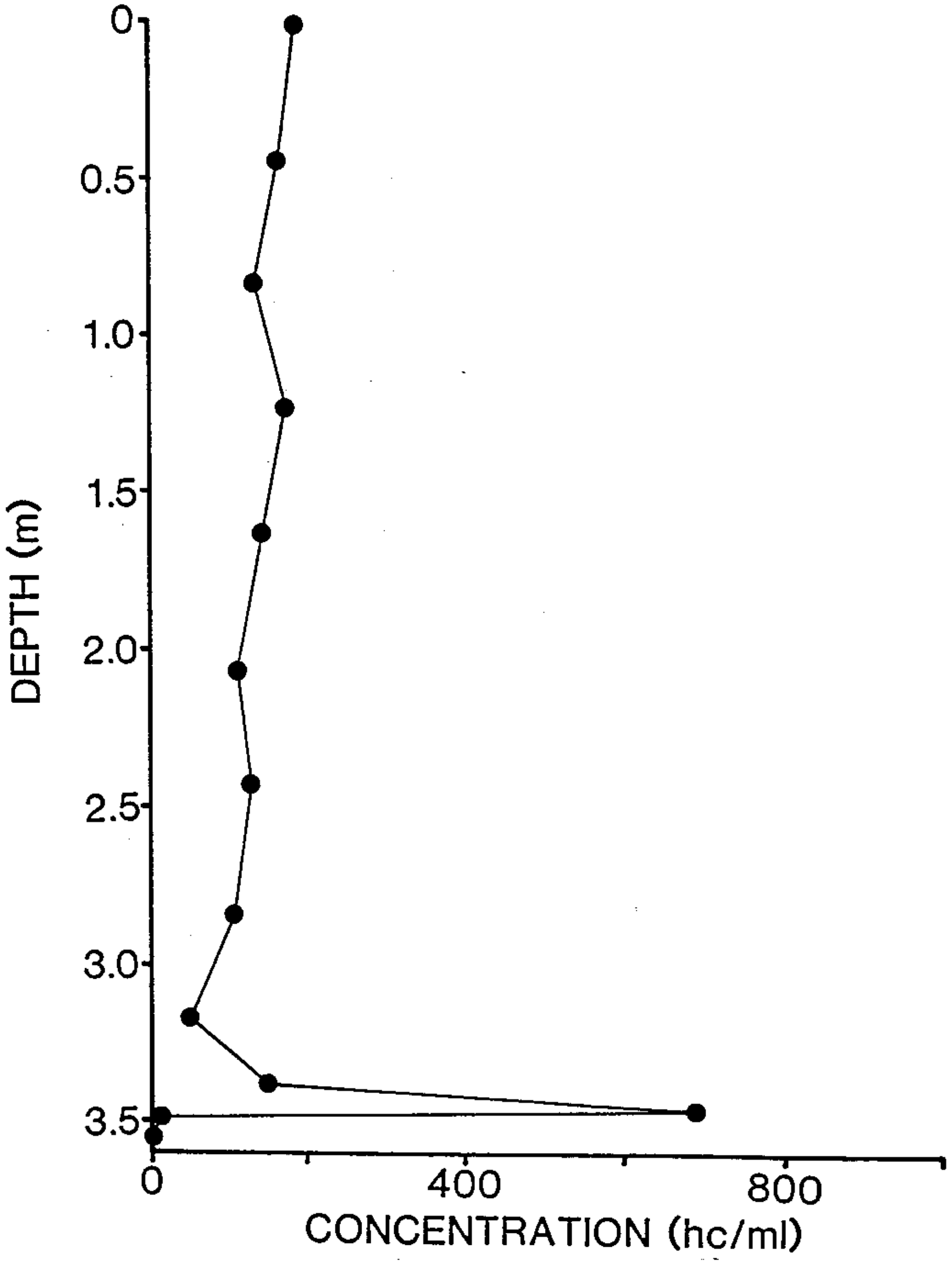

Figure 4.3 Chironomid head capsule concentrations in postglacial sediments of Hippa Lake, Queen Charlotte Islands, B.C.

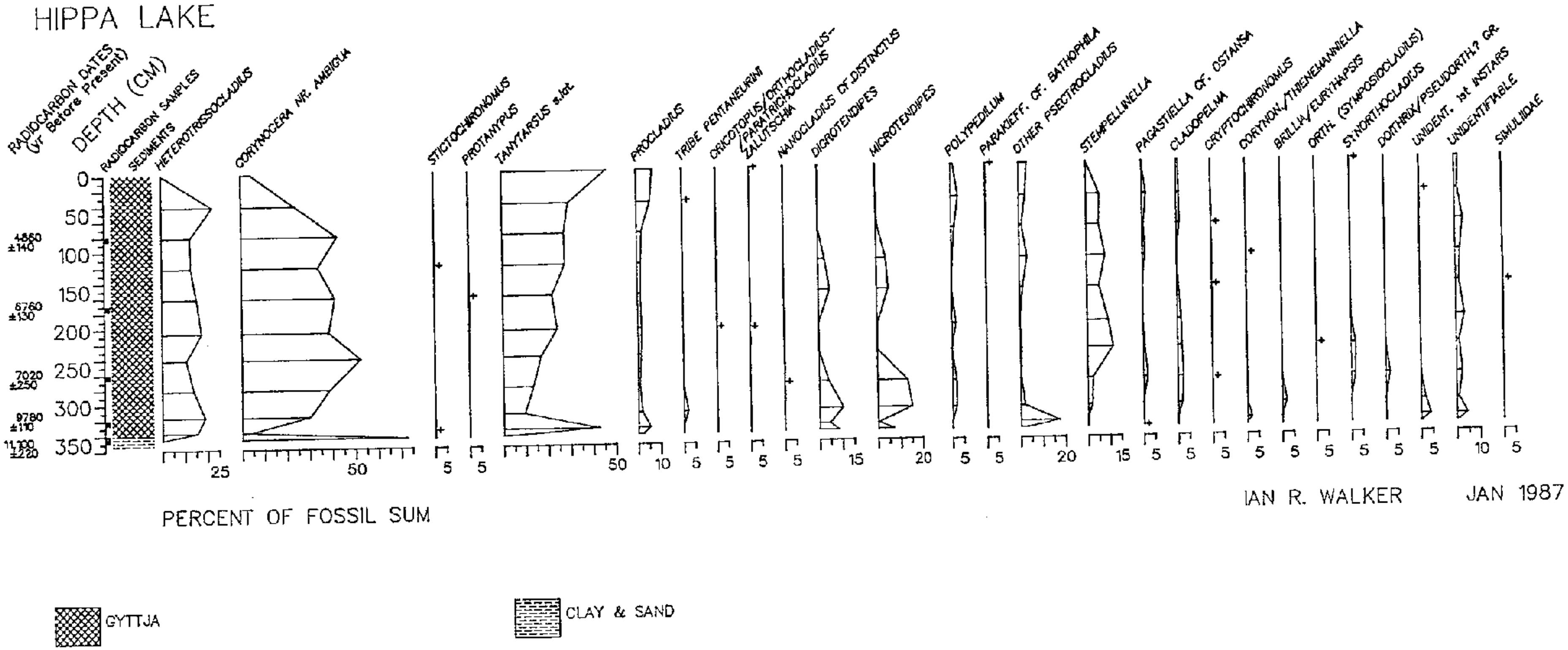

Figure 4.4 Percentage (of total number of chironomid head capsules at each sample level) diagram representing stratigraphy of Chironomidae at Hippa Lake, Queen Charlotte Islands. ("other *Psectrocladius*" refers to all species of the genus, apart from subgenus Monopsectrocladius; "+" indicates presence in small numbers).

The fauna of Hippa Lake has not changed markedly through postglacial time. However, the prevalence of ***Dicrotendipes*, *Microtendipes***, and ***Psectrocladius*** in early sediments is striking. Also significant is the absence of a distinct late-glacial fauna. Of the postglacial chironomid taxa, only ***Heterotanytarsus*** has not been recorded north to tree-line. Most of the postglacial chironomid taxa have been reported from shallow low-elevation lakes or streams in the Vancouver area (Cranston, 1982a; Hamilton, 1965; Sæther, 1969, 1977; Walker and Mathewes, 1987a; this study-Chapter 5). To my knowledge only *Stictochironomus* has not been collected from such sites near Vancouver.

Heterotrissocladius remains occur throughout the Hippa Lake core. ***Protanypus*** and ***Stictochironomus*** are very rare, but both are recorded from mid-Holocene deposits.

Discussion

The results for Hippa Lake are not readily comparable to those of southwestern British Columbia. Hippa Lake has probably never exceeded 5.7 m depth and is exposed to the Pacific Ocean, and isolated from mainland glacial refugia. While nutrients supplied to my other British Columbia sites are likely to reflect weathering of local bedrock and surficial materials, Hippa Lake probably receives large nutrient inputs as marine aerosols (ie. "sea-spray").

Taxa considered typical of oligotrophic, cold-water environments (ie. *Corynocera* nr. ***ambigua*, *Heterotrissocladius***) are evident throughout the core. ***Protanypus*** and ***Stictochironomus*** are rare, but also occur as mid-Holocene elements. This pattern suggests that the cooler, oceanic summer climate may provide refuge to these taxa. Another species frequently associated with these taxa, *Parakiefferiella* sp.A is absent.

Indeed, the Queen Charlotte Islands' climate allows many "high elevation plants" (e.g. mountain hemlock, yellow cedar) to occur near sea level. Calder and Taylor (1968: p. 87) remark that the ability of montane species "to become well established at low elevations is partly due to the uniform climate in the mountainous ranges at low and high altitudes." On the other hand, some southern low-elevation plants (e.g. Salal: *Gaultheria shallon* Pursh) benefit from the mild winters, and may occur abundantly on the islands, near the northern limits of their ranges. Many other taxa requiring warm, dry summers do not occur on the Queen Charlotte Islands (e.g. Douglas-fir: *Pseudotsuga menziesii*). A similar mix of northern and southern elements is evident along Newfoundland's coast, also a hyper-maritime environment (Damman, 1965).

However, cold-stenotherms could also cope if cold spring water feeds the lake. No inflowing streams are apparent, but water does percolate through surrounding talus seeps to the lake (R. Mathewes, pers. comm.). Also, the cold-stenothermous element at Hippa Lake may differ significantly in species composition from that apparent during the late-glacial of southwestern British Columbia. The late-glacial fauna of the deeper southern British Columbia sites is a profundal community, similar to that extant in deep, oligotrophic waters, like Parry Sound, Lake Huron. In Lake Huron, this deepwater fauna includes *Heterotrissocladius oliveri* Sæther (*H. subpilosus* group), *H. changi* Sæther (*H. marcidus* group), *Parakiefferiella* sp.A, *Protanypus ramosus* Sæther, and an unidentified *Stictochironomus* species, as well as several other taxa (Hare, 1976).

Since this "*Heterotrissocladius*" fauna is restricted to oligotrophic waters, its late-Pleistocene survival in small, southern British Columbia lakes reflects extremely low late-glacial productivity, probably limited by a cold climatic regime. During the late-glacial the southern British Columbia sites probably exceeded 10 m depth. However, data for Canadian Rocky Mountain national parks (D.B. Donald, pers. comm.), demonstrates that the fauna of shallow lakes (< *ca.* 5.0 m), often differs from that of deeper waters, even in glacial lakes where temperature, oxygen concentrations, and substrate are uniform, regardless of depth. Assuming a constant surface level, Hippa Lake would never have exceeded 5.7 m depth. Many shallow lakes, even in arctic climates, experience severe oxygen depletion beneath winter ice (Hobbie, 1973). Thus, a profundal community, similar to that at our southwestern British Columbia sites, cannot be expected.

On the basis of ecological information obtained elsewhere (Sæther, 1975b), the common *Heterotrissocladius* at Hippa Lake is probably *H. marcidus* or *H. latilaminus.* Both of these taxa occur in the shallow waters of Marion Lake today (Sæther, 1975b). I believe *H. oliveri* may have been the characteristic late–glacial species in southern British Columbia, and elsewhere in North America. Günther (1983) reports *H. subpilosus,* a very closely related species, from European late–glacial sediments. Donald's (pers. comm.) results indicate that *H. oliveri* may not occur in shallow waters, even in glacial lakes.

The isolated location of Hippa Island poses a biogeographic problem. As previously indicated, the fauna is less diverse than that of southern British Columbia sites. The number of chironomid species is known to decrease with increasing latitude. However, some virtually ubiquitous taxa (e.g. *Chironomus*) were not recorded at Hippa Lake. The ability of chironomids to cross Hecate Strait, or to survive in a Queen Charlotte Island refugium is an important consideration. The "instability" of the late–glacial fauna may reflect an extended colonization phase, resulting from Hippa Lake's isolated setting. As yet little knowledge exists as to what habitats, if any, were available in a Queen Charlotte refugium. Geologists have been willing to concede a few ice–free nunataks, or coastal headlands, but many doubt the existence of more extensive habitat (Banner *et al.*, 1983; Calder and Taylor, 1968; Sutherland Brown, 1968). Because most lakes have been formed through glacial scour, lakes are not common in unglaciated areas.

Although the Hippa Lake record is not comparable to my other British Columbia sites, it is strikingly similar to one reported in arctic Alaska. Livingstone *et al.* (1958) found *Corynocera* (as *Dryadotanytarsus*) and other Tanytarsini (as Calopsectrini) head capsules to be abundant in sediments of Eight Lake, in the Brooks Range. *Corynocera* occurred throughout the sediment column, and probably occurs there today. Extremely high chironomid head capsule concentrations were reported in the basal sediments, $8000 \cdot mL^{-1}$! This concentration stands as the world's record (Frey, 1964; Walker, 1987). Although it is tempting to attribute this high concentration to high early postglacial productivity, low sedimentation rates are possibly important.

Indications of climatic change are not readily apparent at Hippa Lake. Most of the taxa occur at arctic tree–line, and also at low elevations near Vancouver (Oliver *et al.*, 1978; Wiens *et al.*, 1975). Although late–glacial species diversity is low at Hippa Lake, this is also true throughout the Holocene sediments. Biogeographic isolation may have been more important than climate in regulating chironomid diversity at Hippa Lake. Although *Corynocera* seems to be most common in cold, oligotrophic lakes and ponds (Fjellberg, 1972; Pinder and Reiss, 1986), it does occur in temperate north German lakes. The larva and pupa of *C. ambigua* are supposed to be cold stenothermic, but eggs survive the temperate summer period (Berglund and Digerfeldt, 1970; Mothes, 1968). Emergence occurs in waters at *ca.* 8° C (Fjellberg, 1972).

Since cold–stenothermous chironomids tend to emerge during the spring – early summer thaw, when temperatures are still cool, larvae inhabiting littoral areas may be more susceptible than adults to the direct effects of temperature. Thus, it is intriguing that the littoral fauna of Hippa Lake does not suggest evidence of a climatic effect. Similarly, at Marion, Mike, and Misty Lakes in southwestern British Columbia, it is the profundal fauna, not the littoral fauna, that is most suggestive of climatic change. This leads to an ironic conclusion – that the littoral fauna of north temperate lakes, most exposed to climate, may be less responsive than the profundal fauna. Consequently, the effects of different north temperate climates upon chironomid communities may be mostly indirect.

The same situation is not apparent at tree-line. Although most Canadian chironomid genera occur north through temperate and boreal regions, many are not known from the Canadian arctic (Danks, 1981; Oliver and Roussel, 1983a). This pattern implies that littoral chironomids may be useful in distinguishing arctic palaeoclimates from warmer situations, but not so useful for describing recent Holocene changes, within the north temperate zone.

There is also little evidence to support a trophic interpretation of Hippa Lake's record. The initial high head capsule concentrations imply high productivity, as Livingstone *et al.* (1958) suggested. However, late-glacial organic sedimentation was very low. This low rate is also evident as very high pollen concentrations in the lowermost organic sediments (R. Mathewes, pers. comm.). Thus high chironomid concentrations are more likely a reflection of low sediment inputs, and perhaps some focusing of near-shore sediments and fossils to the main basin.

Palaeoecology and ecology of Corynocera

Remains similar to *Corynocera ambigua* are abundant at Hippa Lake. This taxon has always fascinated palaeoecologists. The larva was first described as *Dryadotanytarsus edentulus* Andersen, a subfossil in European late-glacial deposits. Deevey (1955b) found another subfossil species, *D. duffi* Deevey, in New Zealand sediments. Two years after the discovery of *Dryadotanytarsus* as an Alaskan subfossil (Livingstone *et al.*, 1958), *Dryadotanytarsus edentulus* was discovered emerging from a Finnish lake. Hirvenoja (1960, 1961) noted that adults had previously been described as *Corynocera ambigua* Zetterstedt (1838).

C. ambigua is extant in Ireland (Murray, 1983), Germany, Poland, the Soviet Union (both east and west of the Ural Mountains), Scandinavia (Fjellberg, 1972; Mothes, 1968; Fitkau and Reiss, 1978), and the Canadian low arctic and subarctic (Downes, 1962; Moore, 1978; Wiens *et al.*, 1975). Late–Quaternary records of *C. ambigua* group fossils also include Alaska, Scotland (Livingstone *et al.*, 1958), Switzerland (Hofmann, 1983b, 1985), and British Columbia. Fossils from the upper 20 cm of McDougal Lake (46° 3.2'N, 60° 25.8'W), Cape Breton Island, provide the only eastern North American record of the *C. ambigua* group (D.A. Livingstone *pers. comm.*). Tertiary fossils from Greenland, identified by W. Hofmann, record its more northerly presence, during a warmer time (O. Bennike, pers. comm.).

The early occurrence at Hippa Lake of *C.* nr. *ambigua* fossils is especially fascinating since the known adults of *Corynocera* species cannot fly (Fjellberg, 1972; Lindeberg, 1970). Instead, the brachypterous adults swarm by "whirling about on the surface of lakes" (Lindeberg, 1970). The early arrival of *Corynocera* at Hippa Lake attests either to its survival in a glacial refugium, an amazing ability to disperse with little apparent means, or the existence of a previously unknown species in the North American Cordillera, with well–developed wings.

The possible existence of a new species cannot be discounted. The British Columbia material differs from subfossils collected near Yellowknife, N.W.T. by having a darker, more variable mentum. A small, but distinct, apical projection is evident on the antennal pedestal in British Columbia collections, but not those from the Yellowknife area. Livingstone (1953) noted that the Alaskan subfossils are closer to *C. duffi* (Deevey) than *C. ambigua*. Downes (1962) claims the existence of an undescribed species in southern Alberta.

If *Corynocera* nr. *ambigua* is brachypterous, and is dispersed as readily as its early occurrence in Hippa Lake would suggest, it is difficult to imagine postglacial chironomid colonization as ever being significantly dispersal-limited. The dispersal abilities of *C. ambigua* are impressive. In Europe, it is among the first immigrants to lakes, following glacial retreat (Andersen, 1938; Berglund and Digerfeldt, 1970; Brodin, 1986; Hofmann, 1978, 1983a, b; Schakau and Frank, 1984). How it accomplishes this is not clear. It may "hitch" rides on waterfowl. Perhaps the species can be carried long distances by thermal convection and turbulent air masses. Active flight is not a prerequisite for aerial dispersal. Similar dispersal difficulties have not prevented the postglacial spread of trees across the same or similar barriers (Green, 1987). Records, albeit rare, even exist for fish and amphibians having fallen from the skies (Maguire, 1963). With regard to insects, Danks (1981: p. 369) notes "... many groups - including some that are wingless - although once believed to disperse little, in fact travel long distances in aerial plankton ...".

The unusual structure of the *C. ambigua* group's larval mentum suggests a unique feeding strategy. It has been suggested (Livingstone *et al.*, 1958) that larvae crush giant cells of characeous macroalgae, sucking out their contents. According to Fjellberg (1972), *C. ambigua* is often associated with Characeae. He notes that Characeae and *Corynocera* also occur together in several fossil localities (Andersen, 1943; Berglund and Digerfeldt, 1970; Deevey, 1955b). Late-glacial plant and animal fossils from Lobsigensee, Switzerland, also illustrate this relationship (Hofmann, 1983b, 1985; Tobolski, 1985). The one exception seems to be the Alaskan sequence. Livingstone *et al.* (1958) suggest that an obligate relationship does not exist.

A *Corynocera*-Characeae relationship could resolve *C.* nr. *ambigua*'s inconsistent fossil distribution in British Columbia. It occurs throughout the fossil record at Mike and Marion Lakes near Vancouver, and at Hippa Lake. In Marion Lake it is more abundant in late-Holocene sediments. In Misty Lake, northern Vancouver Island, it is restricted to late–glacial deposits.

To examine this hypothesis (an obligate dependence of *C.* nr. *ambigua* on Characeae) in greater detail, fossil Characeae and *Corynocera* distributions were compared. At present, such data are available in British Columbia for Marion, Misty, and Hippa Lakes (Fig. 4.5). A strong correlation is evident at Misty Lake. Also, at Hippa Lake, both *Corynocera* nr. *ambigua* and Characeae fossils are distributed throughout the core. However, despite the late Holocene abundance of *Corynocera* nr. *ambigua* at Marion Lake, only one Characeae oospore was found, at 260–270 cm (N. Wainman, pers. comm.). Unfortunately, taphonomic (decomposition, deposition, and preservation) processes clearly interfere with these results. Wainman (pers. comm.) reports *Nitella* Agardh oospores as abundant in Marion Lake surface samples, collected near a large spring. Since none of these were found at the core site, the oospores are not being evenly distributed throughout the lake. Thus, the test results are inconclusive. Characeae may or may not play an important role in regulating the occurrence and abundance of *Corynocera* nr. *ambigua*.

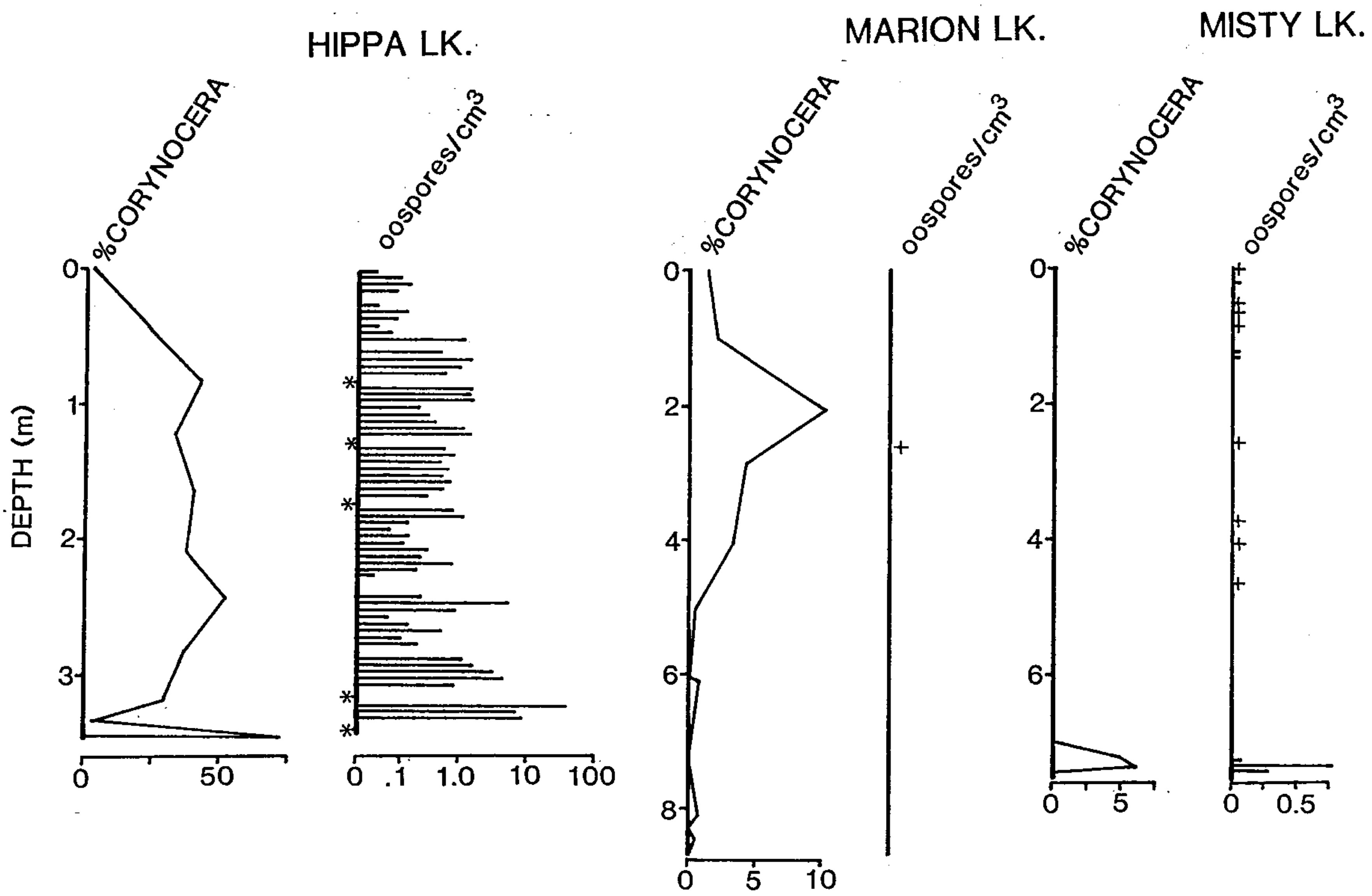

Figure 4.5 Comparison of fossil *Corynocera* nr. *ambigua* and Characeae oospore records for Marion, Misty, and Hippa Lakes, British Columbia. (*–indicate missing samples at Hippa Lake, mostly used for ^{14}C–dating; "+" indicates presence in small numbers; Note: log(x+1) scale used for Hippa Lake oospore record).

CHAPTER 5

SURFACE SAMPLES

One of the major impediments to palaeoecological research is the dearth of ecological information for many fossil organisms. Although "descriptive" research is no longer in vogue, palaeoecologists often wish more professional naturalists, like Darwin, Dawson, Ganong, and Richardson, were surveying our flora and fauna today. A tremendous volume of chironomid ecological data is scattered through the literature, yet isolating the pertinent facts for palaeoecological reconstructions is a laborious process. Fortunately, a few recent synthetic articles compile this information for the holistic ecologist (e.g. Brinkhurst, 1974; Danks, 1981; Fitkau and Reiss, 1978; Sæther, 1979).

This information must be used cautiously by palaeoecologists. The fossil assemblage, isolated by palaeoecologists, is not the same as the fauna perceived by ecologists. Benthic ecologists often sample the summer fauna, ignoring winter inhabitants. The methods of separating benthos vary widely (e.g. Ankar *et al.*, 1979; Flannagan, 1973). On the other hand, taphonomic (factors relating to decomposition, deposition, and preservation of fossils) processes regulate which organisms will be preserved, in what numbers, and where. Fortunately, taphonomic considerations are not as severe an influence upon chironomid fossils (Iovino, 1975; Walker *et al.*, 1984), as with some other groups of organisms.

To avoid, or at least to partially circumvent such problems, palynologists and diatomists have increasingly relied upon recent "fossil" assemblages available in the surficial sediments of lakes (e.g. Davis and Anderson, 1985; MacDonald and Ritchie, 1986). Analysis of surficial sediment samples across environmental gradients, such as pH, climate, or concentrations of specific nutrients, can reveal the influence of each factor. No comparable chironomid analyses have yet been published.

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To examine how climate influences chironomid faunal composition, as perceived by the palaeoecologist, I have collected surficial sediments from lakes distributed across an altitudinal gradient. This gradient is not entirely comparable to a horizontal climatic gradient, but offers a first approximation.

Study sites

Thirty surface samples were collected primarily in the Pacific Northwest, from lakes near Vancouver, Canada, and the adjacent Mount Baker area of Washington State, U.S.A. Several samples were also collected in Yoho and Banff National Parks, in the Canadian Rocky Mountains. These parks straddle the British Columbia - Alberta border. Also included is one Queen Charlotte Island location, and surface records from each of my four British Columbia stratigraphic study sites (Chapters 2, 3, and 4). The locations of each of these sites are summarized in Table 5.1. Several of the lake names are informal designations (placed in quotation marks), since no formal names have yet been assigned. Some observations concerning the lakes' characteristics, at the time of sampling are summarized in Table 5.2.

The lakes are distributed from near sea level to alpine situations. Complete forest cover surrounds most of the low elevation lakes, whereas no trees are present at the highest elevations. Heikkinen (1984b, 1985) notes that the coastal timberline zone is exceptionally broad, spanning elevations from 1400 to 1750 m on Mount Baker, Washington (near Vancouver, B.C.). Although in many regions timberline is primarily regulated by temperature, the great snow accumulations in coastal British Columbia persist long into summer. Patches of persistent snow are likely responsible for the great breadth of the upper subalpine woodland-meadow mosaic (Brooke *et al.*, 1970; Heikkinen, 1984b, 1985) on Pacific coastal mountains. Although trees were common on the south side of

Table 5.1. Locations of the Cordilleran lakes sampled for surficial sediments.

Park and District Codes:

AL=Alice Lake Provincial Park
B=Banff National Park, Alberta
DL=Duffey Lake area
G^1=Garibaldi Provincial Park, near Elfin Shelter
G^2=Garibaldi Provincial Park, near the Black Tusk
G^3=Garibaldi Provincial Park, near Singing Pass
GE=Golden Ears Provincial Park
MB=Mount Baker National Forest, Washington, U.S.A.
MS=Mount Seymour Provincial Park
QCI=Queen Charlotte Islands
S=Sasquatch Provincial Park
URF=University of British Columbia Research Forest
VI=Vancouver Island
W=Whistler area
Y=Yoho National Park

	Elevation	Longitude	Latitude	Park or District
<u>Banff and Yoho Nat. Pk</u>				
Ptarmigan Lk.	2330 m	116°04.5'W	51°29.0'N	B
Hidden Lk.	2270	116°06.5'	51°29.1'	B
Opabin Lk.	2270	116°18.7'	51°20.4'	Y
Hungabee Lk.	2240	116°19.1'	51°20.5'	Y
Lk. Annette	1970	116°12.5'	51°19.3'	B
Mud Lk.	1600	116°10.5'	51°26.3'	B
<u>Southwestern B.C.</u>				
"Chlorine" Lk.	2090	122°09.2'	50°20.5'	DL
"Aqua incognito"	1970	122°10.2'	50°20.4'	DL
Russet Lake	1870	122°51.9'	50°01.4'	G^{3}
Black Tusk Lk.	1750	123°01.6'	49°57.6'	G^{2}
Helm Lk.	1720	123°01.4'	49°58.0'	G^{2}
Mimulus Lk.	1720	123°01.8'	49°57.5'	G^{2}
"Coleman Pd"	1680	121°44.0'	48°48.6'	MB
"N." Elfin Lk.	1480	122°59.2'	49°47.2'	G^{1}
"S." Elfin Lk.	1480	122°59.2'	49°47.1'	G^{1}
Hayes Lk.	1460	121°43.3'	48°51.5'	MB
Highwood Lk.	1250	121°40.5'	48°51.9'	MB
Mystery Lk.	1140	122°56.0'	49°22.5'	MS
Goldie Lk.	990	122°56.1'	49°22.3'	MS
Lost Lk.	690	122°56.1'	50°07.7'	W
Marion Lk.	300	122°33.0'	49°19.0'	URF
Mike Lk.	220	122°32.3'	49°16.5'	GE
Stump Lk.	200	123°07.3'	49°47.3'	AL
Alice Lk.	180	123°07.3'	49°46.7'	AL
Misty Lk.	70	127°15.7'	50°36.3'	VI
Hicks Lk.	60	121°42.0'	49°20.5'	S
Deer Lk.	60	121°40.5'	49°22.0'	S
Great Central Lk.	25	125°05.0'	49°20.0'	VI
<u>Queen Charlotte Islands</u>				
"Hermit Thrush Pd"	550	131°54.4'	52°41.3'	QCI
"Hippa Lk."	230	132°58.4'	53°31.9'	QCI

Table 5.2. Characteristics of lakes and ponds from which surface samples were collected for chironomid analysis. (Temperature and pH values are for surface water.)

Lake	Depth of Sample	pH	Temperature at Sampling	Date
<u>Banff and Yoho Nat. Parks</u>				
Ptarmigan	8.5 m	7.9	6°C	4/9/86
Hidden	13.5	8.2	5	4/9/86
Opabin	6.0	7.9	5	3/9/86
Hungabee	2.5	7.6	7	3/9/86
Annette	13.0	8.2	4	2/9/86
Mud	7.0	8.3	10	5/9/86
<u>Southwestern B.C.</u>				
"Chlorine"	3.5	6.6	2	3/8/86
"A. Incognito"	3.	6.9	2	3/8/86
Russet	14.5	8.4	9	13/8/86
Black tusk	13.	7.4	8	17/8/86
Helm	9.5	7.3	1	17/8/86
Mimulus	1.0	7.4	12	17/8/86
"Coleman"	12.	6.1	4	13/9/86
"N." Elfin	4.	5.5	7	27/7/86
"S." Elfin	5.5	5.5	4	27/7/86
Hayes	17.	7.3	15	24/7/86
Highwood	6.5	6.6	7	19/6/86
Mystery	6.5	-	FROZEN	2/86
Goldie	1.	-	FROZEN	2/86
Lost	11.	7.3	-	10/5/86
Marion	6.	-	-	6/82
Mike	6.5	-	-	2/86
Stump	16.	-	FROZEN	2/86
Alice	10.5	-	FROZEN	2/86
Misty	5.	-	-	18/8/86
Hicks	17.	6.5	-	5/4/86
Deer	5.	6.7	-	5/4/86
Great Central	123.	-	-	1/11/88
<u>Queen Charlotte Islands</u>				
"H. Thrush"	2.	5.7	-	20/7/84
"Hippa"	1.	-	-	14/7/83

subalpine "Hermit Thrush Pond", on the Queen Charlotte Islands, trees were scattered and stunted on adjacent, slightly higher slopes. Timberline is higher and better defined in the Rocky Mountains. The alpine–subalpine transition is evident near 2200 m in Banff National Park (Mayhood and Anderson, 1976).

Although timberline is lower on the coast, including the Queen Charlotte Islands and Coast Ranges, mean annual temperatures are lower at timberline in the Rockies. Mean annual temperatures below 0° C occur at some lower subalpine sites in the Rocky Mountains, but may exceed 0° C near coastal timberline (Heikkinen, 1984b; Prov. of B.C, 1980). However, snow accumulation is greater on the coast, and may remain longer to produce a short growing season, similar to that inland. Climatic summaries are provided in Table 5.3 for several locations near my study sites.

Most of the lakes sampled, in the Coast Mountains near Vancouver, including those in Alice, Garibaldi, Golden Ears, and Mount Seymour Provincial Parks, the Duffey Lake area, and the University of British Columbia Research Forest, are underlain by base–poor plutonic rocks of the Coast Mountain complex. However, other volcanic rocks, and some sedimentary exposures, are scattered throughout the Coast Mountains (Prov. of B.C., undated). Those lakes sampled near the Black Tusk in Garibaldi Provincial Park, and at Mount Baker in Washington, lie in areas of recent Pleistocene volcanic activity. Thus intact or finely fragmented basaltic rocks may dominate in the bedrock and derived soils. Palaeozoic and Mesozoic sedimentary rocks prevail within Sasquatch Provincial Park, and at Misty Lake on Vancouver Island.

In contrast, the Canadian Rocky Mountains are mostly composed of sedimentary materials. The main ranges, in which all of the sampled lakes lie, are composed principally of Cambrian carbonates and quartzitic sandstone (Rutter, 1972).

Table 5.3. Climatic summaries for weather stations near the surface sample collection sites. (southwestern British Columbia - Vancouver Harbour and Hollyburn Ridge; Queen Charlotte Islands - Tasu Sound; Rocky Mountains - Boulder Creek, Yoho National Park).

	Vancouver Harbour	Hollyburn Ridge	Tasu Sound	Yoho Nat. Pk (Boulder Ck)
Latitude	49°18'	49°22'	52°46'	51°23'N
Longitude	123°07'	123°12'	132°03'	116°32'W
Elevation (m)	0	951	15	1219
Mean Daily Temperature (°C)				
Coldest Month	3.4	-2.3	2.8	-10.9
Warmest Month	17.6	13.2	14.6	15.3
Annual	10.3	5.0	8.2	2.9
Precipitation				
Rain (mm):				
Annual	1482.3	2134.3	4172.7	308.6
Snow (cm):				
Annual	60.0	820.2	75.7	323.1
Frost-free Period (d)	270	126	217	90
Degree-days (d·°C)				
above 0°C	3838.3	2008.4	3039.0	2102.5
above 5°C	2092.0	919.2	1441.5	1109.4

(Environment Canada, 1982)

Intrusive Mesozoic crystalline rock, dissected by mafic dykes, is exposed at "Hermit Thrush Pond" in the Queen Charlotte Islands. Volcanic rocks, including basalt and rhyolite, are common near "Hippa Lake" (Sutherland Brown, 1968).

Methods

Surface samples were collected with an Ekman grab, deployed from a small inflatable raft. Collections were usually made near the centre of the lakes, although practical considerations including safety, winds, and sampling difficulties occasionally interfered with my best intentions. Sampling depths are summarized in Table 5.2. About 250 mL of sediment, within the top 10 cm of the grab sample, were retained. These sediments probably represent the last 50 to 100 years of deposition. These were refrigerated upon my return from field trips.

Analysis of this sediment proceeded largely as described for earlier core investigations. Head capsule concentrations usually permitted small aliquots (1 or 2 mL), to be analyzed. However, some samples, particularly those obtained from glacial lakes required more elaborate treatments. For those samples, larger aliquots, up to 93 mL, were occasionally analyzed.

To achieve acceptable head capsule "concentrates" from glacial lakes unusual chemical treatments were necessary. These frequently included the HF and HCl acid treatments commonly employed by palynologists, as well as the usual KOH and sieving techniques. Best results for clay samples were obtained using the following treatment series:

1) Sediment washed in .075 mm sieve; backwash material retained by sieve into centifuge tube.

2) Centrifugation of material at moderate speeds for about 5 minutes; decant water

3) Wash with 10% HCl

4) Centrifuge and decant acid

5) Wash with cold concentrated HF (let stand overnight)

6) Centrifuge and decant acid

7) Wash with HCl

8) Centrifuge and decant

9) Wash with warm 6% KOH

10) Collect and wash concentrate in .075 mm sieve with water

11) Backwash concentrate into 50 mL beaker for later examination in Bogorov counting cells (Gannon, 1971)

Although the HF treatment is unusual for chironomid stratigraphic work, it is commonly employed by palynologists to dissolve silicates. HF has little apparent effect on organic tissues. Palynologists regularly discover chitinous remains on their slides, including insect and fungal fragments, even where acetolysis (a more severe treatment to remove organic matter) has been employed. Without the HCl and HF treatments analysis of glacial lake sediments for chironomids would usually have been impossible.

Results

A summary of the surface sample results is presented in Figure 5.1. It was readily apparent that many species common at low elevations were absent at higher elevations, particularly in the alpine or upper subalpine. A few taxa were common at all altitudes, and another group was most abundant at the highest locations. Diversity figures (Figure

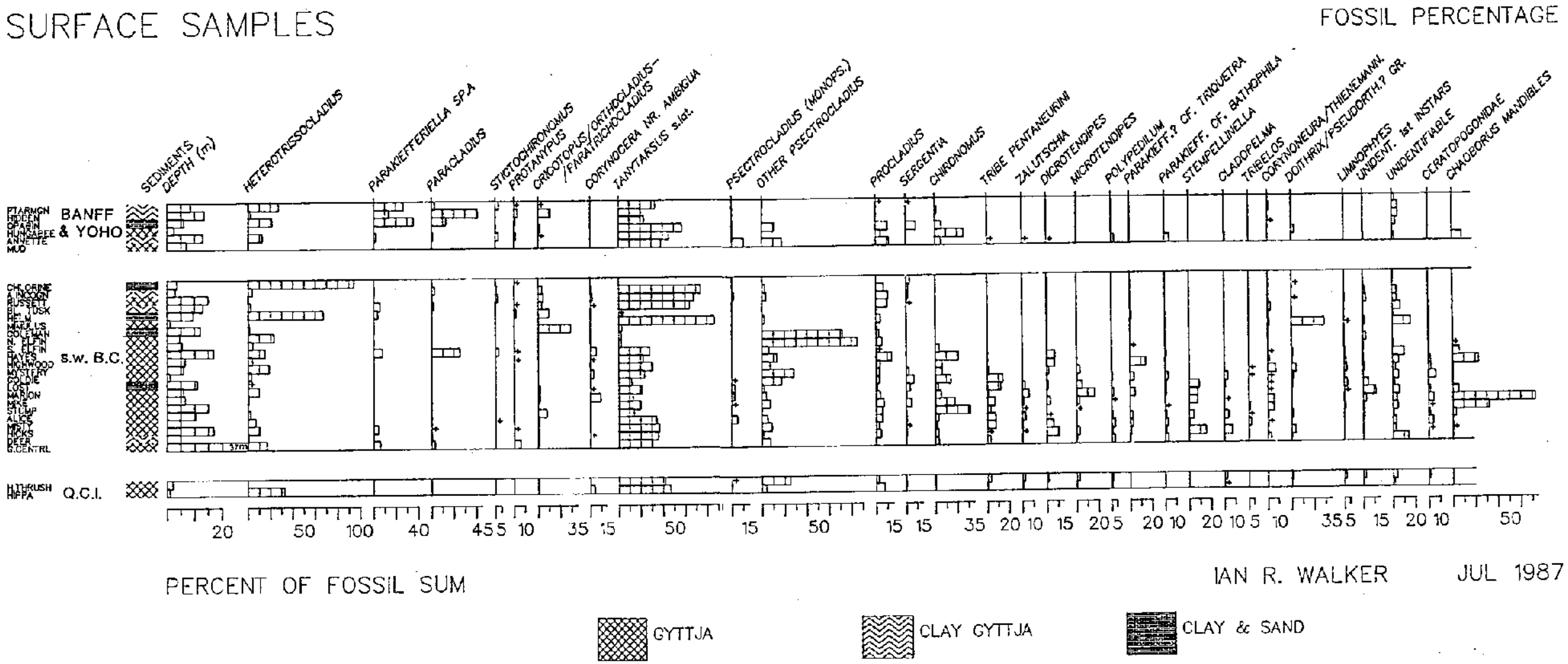

Figure 5.1 Percentage (of total number of chironomid head capsules at each sample site) diagram representing altitude distribution of common chironomid taxa from surface samples in the Cordillera of southern Canada, and adjacent United States.
(Several rare taxa, including *Pseudodiamesa* have been excluded; "+" indicates presence in small numbers). Samples are arranged as in Tables 5.1 and 5.2 – ie. 1) Samples from different regions are separated; 2) Within a region the samples are organized by altitude.

5.2) indicate complex faunas at all sites lower than the subalpine, but a sharp decrease in diversity occurs in the coastal upper subalpine zone (*ca.* 1400 to 2000 m). To effectively summarize these results, I have divided the total fauna into three groups:

1) *Low to mid-elevation taxa* - Few chironomid genera completely disappeared from the samples at elevations below the lower subalpine, however many were rare or entirely absent from higher sites, including the alpine and upper subalpine. Prominent low to mid elevation taxa included many of the Chironomini (e.g. *Cladopelma* Kieffer, *Cryptotendipes* Lenz, *Dicrotendipes*, *Lauterborniella* Thienemann & Bause/*Zavreliella* Kieffer, *Microtendipes*, *Pagastiella* cf. *ostansa*, *Paratendipes* Kieffer, *Polypedilum* Kieffer, and *Tribelos*), but some representatives of the Tanytarsini, Orthocladiinae, and Tanypodinae also fall within this category. For example, *Stempellinella*, Tanytarsini sp.A, *Parakiefferiella* cf. *bathophila* (Kieffer), *Zalutschia*, and the Pentaneurini were never recorded higher than the lower subalpine lakes. Most Ceratopogonidae and *Chaoborus* seem to be similarly distributed. In addition, several taxa common at low altitudes were much less common at the higher sites, although they did occur. *Chironomus*, *Parakiefferiella*? cf. *triquetra*, and *Psectrocladius* (including *Monopsectrocladius* Laville) clearly portray this pattern of distribution. *Psectrocladius* was exceptionally abundant in two upper subalpine lakes, but rare or absent at other high altitude stations. These two sites, "North" and "South" Elfin Lakes were the most acidic lakes sampled (pH near 5.6). *Psectrocladius* is often common in acidic conditions (e.g. Henriksson *et al.*, 1982; Mossberg and Nyberg, 1979; Walker *et al.*, 1985). *Corynocera* nr. *ambigua* could also be included with the low to mid-elevation group. However, *C.* nr. *ambigua* was most abundant at mid-elevations, and rare at the highest and lowest lakes.

2) *High elevation taxa* - None of the taxa are truly restricted to high elevation sites, since all occur either in the benthos of low-elevation arctic waters, the profundal of

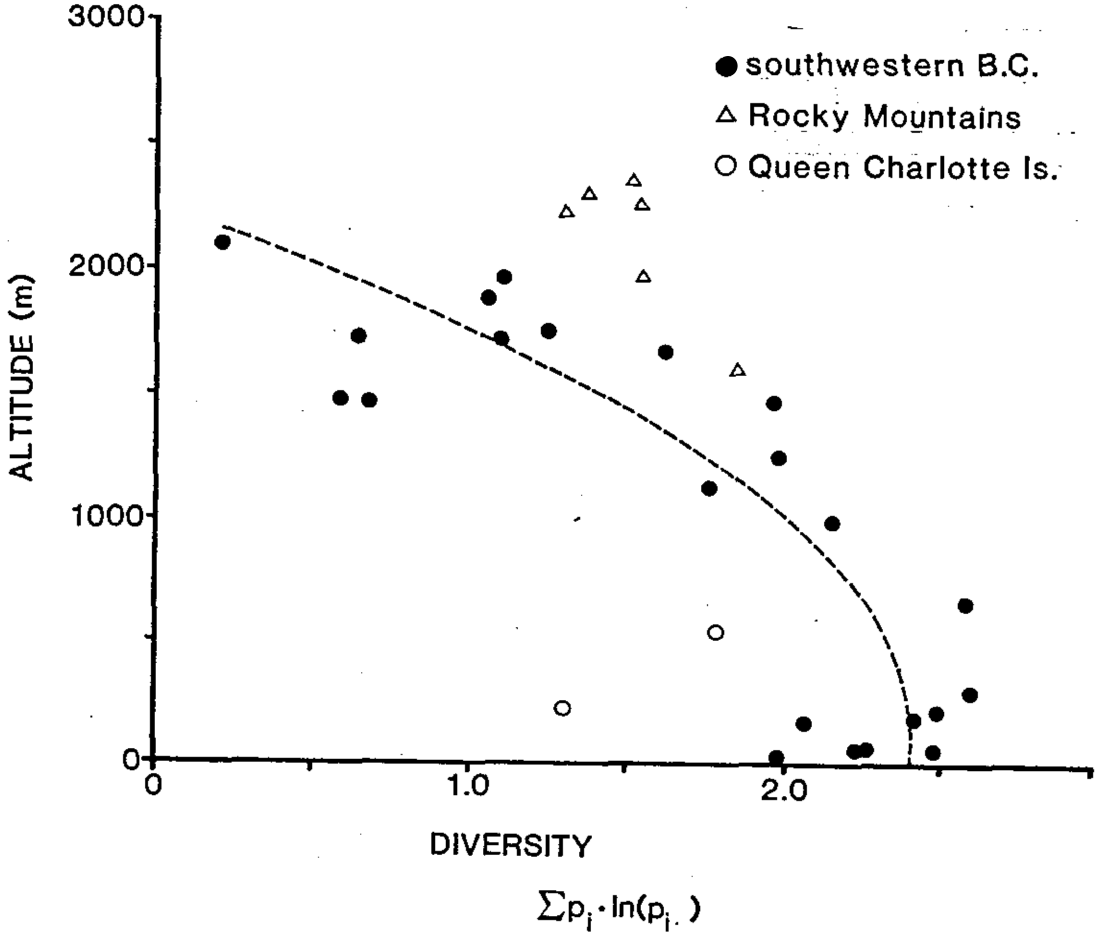

Figure 5.2 Shannon–Wiener diversity of surface–sample chironomid taxa versus elevation in the Cordillera. (Closed circles=sites in southern, coastal British Columbia; Open circles=Queen Charlotte Islands sites; Triangles=sites in Banff and Yoho National Parks). Curve is based upon data for southern, coastal British Columbia only. The transition from subalpine forest to open meadows spans ca. 1400 to 2000 m on the southern coast. Timberline is close to 600 m on the Queen Charlotte Islands, and 2250 m in Banff and Yoho National Parks.

deep, temperate, oligotrophic lakes, or both. All of the "high-elevation" taxa, except *Paracladius* Hirvenoja, have been recorded in low-elevation, late-Pleistocene sediments at Marion Lake. Thus, this "high-elevation" group is equivalent to the regional "*Heterotrissocladius*" fauna described in Chapter 2. The larvae are probably cold-stenotherms. Emergence at low-elevations and temperate latitudes probably occurs in early spring when cool weather prevails. Representatives of this group include *Heterotrissocladius*, *Parakiefferiella* sp.A, *Paracladius*, *Protanypus*, *Pseudodiamesa*, and *Stictochironomus*.

Heterotrissocladius is the most common and widely distributed of these taxa. Although it is uncommon at low elevation sites, it still occurs there, even in shallow waters. This broad range probably incorporates the distribution of several *Heterotrissocladius* species which have not been distinguished. *H. marcidus* and *H. latilaminus* may account for most of the low elevation records. *H. oliveri* may be common at the highest elevations.

The distributions of the other "high-elevation taxa" are more restricted, making them the better indicators. These were most common in the alpine samples from the Canadian Rocky Mountains. I suspect each is represented by a single species in this study. Below the subalpine *Parakiefferiella* sp.A and *Paracladius* were collected only at two sites, Hicks Lake, and Great Central Lake. These are two of the three largest and deepest low-elevation lakes sampled. *Protanypus* and *Stictochironomus* were never very common. Their remains occurred sporadically, being most frequent in lakes at lower subalpine or higher elevations.

Pseudodiamesa was a common chironomid in sediments of "Coleman Pond" and rare at Mimulus Lake. *Pseudodiamesa* may occur in either lakes or streams. I suspect most of the remains, at both locations, are derived from inflowing streams. There is little indication of a lacustrine fauna in the "Coleman Pond" sample. Ice from the previous winter was still partially covering the lake in September, 1985. The entire surrounding landscape bears little vegetation. I believe a permanent snowfield occupied "Coleman Pond" until at least this century. Very large volumes of sediment had to be sorted to find any chironomid remains. Heikkinen (1984a, b, c, 1985) reports an expansion of subalpine forest and glacial retreat on Mount Baker during the last century, probably a response to increased warmth and decreased precipitation.

Most of the "high elevation" taxa occur together in the deeper and most oligotrophic lakes of the Okanagan Valley (Sæther, 1970, Sæther and McLean, 1972), and in Parry Sound, Lake Huron (Hare, 1976). [*Paracladius* and *Parakiefferiella* sp.A are respectively reported as *Cricotopus* "*Paratrichocladius*" and "genus near *Trissocladius*" by Sæther (1970) and Sæther and McLean (1972)]. Sediment from Chilko Lake, a large oligotrophic, high-elevation lake in the coast mountains, has been collected by J. Stockner. Although this material only included 6 chironomid head capsules, both *Paracladius* and *Stictochironomus* were represented[1]. *Heterotrissocladius*, *Paracladius*, *Parakiefferiella* sp.A, and *Protanypus* also occur in Hicks and Great Central Lakes, near sea level. Thus summer air temperatures have little direct relevance to the distribution of these taxa. Cool, oligotrophic waters in the profundal of deep, low-elevation lakes offer refuge. Although they are most common at high elevations, they are mostly absent from the shallowest lakes, even at high altitudes.

3) *Widely distributed taxa* - Few taxa were widely distributed at all elevations, although rheophilous chironomids, and taxa characteristic of shallow timberline lakes and ponds appear to fall mostly within this category.

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[1] Other taxa collected from Chilko Lake, included *Corynocera* nr. *ambigua*, *Corynoneura/Thienemanniella*, *Limnophyes* Eaton, and *Tanytarsus* s.lat.

The most widely distributed group is *Tanytarsus* s.lat. This group is certain to include representatives of several genera and species which could not be reliably distinguished. The individual species would have narrower ecological ranges. The same situation may be true for other taxa within this category.

Procladius and *Sergentia* are also common in lakes at all elevations. *Procladius* may occur in both littoral and profundal regions. Although *Sergentia* is a common profundal taxon in temperate climates, at high elevations it was more common in the shallowest lakes and ponds. *Sergentia* seems to occupy similar shallow habitats in the arctic (Andersen, 1937, 1946: as *Pentapedilum coracina* Zetterstedt and *P. coracinum* Zetterstedt).

The groups *Corynoneura/Thienemanniella*, *Cricotopus/Orthocladius/Paratrichocladius*, *Doithrix* Sæther & Sublette/*Pseudorthocladius* Goetghebuer? group, and *Limnophyes* Eaton are also widely distributed. Each of these taxa may be common in soils or streams. *Corynoneura/Thienemanniella*, *Cricotopus/Orthocladius/Paratrichocladius*, and *Limnophyes* may also occur in lakes. *Cricotopus/Orthocladius/Paratrichocladius* includes three large and widely distributed genera, together including at least 150 species in the Holarctic region (Coffman *et al.*, 1986).

Discussion

The trends apparent along my altitude transect parallel the known distribution of chironomids along horizontal climatic gradients. Although most Canadian chironomid genera are present north to tree–line (Table 5.4), many Chironominae and Tanypodinae genera are not known from the Canadian arctic (Danks, 1981; Oliver and Roussel, 1983a). In contrast, at least 2/3 of the Canadian Orthocladiinae genera have been reported in the arctic.

Table 5.4. Number of chironomid taxa in major Canadian regions. HA=high arctic; LA=low arctic; Y&sNWT=Yukon and sw. Northwest Territories (north of 60°N, but south of treeline); W=sw Canada (British Columbia to Manitoba), E=se Canada (Ontario to Newfoundland).

SUBFAMILY OR TRIBE	NUMBER OF GENERA				
	HA	LA	Y&s.NWT	W	E
CHIRONOMINAE					
Chironomini	3	8	26	29	27
Pseudochironomini	-	-	1	1	1
Tanytarsini	3	6	9	10	8
DIAMESINAE	5	5	5	4	3
ORTHOCLADIINAE*	21	22	33	35	36
PODONOMINAE	1	1	1	3	3
PRODIAMESINAE	-	1	2	2	3
TANYPODINAE	1	7	16	18	22
TELMATOGETONINAE	-	-	-	1	-

Compiled with reference to Danks (1981), Oliver (1981), and Oliver and Roussel (1983a).

*-A list compiled by D.R. Oliver (pers. comm.) includes 35 arctic Orthocladiinae genera. Figures for other subfamilies and tribes differ only slightly (±1 or 2 genera).

Lakes inhabited by oligotrophic, cold-stenothermous taxa, including *Heterotrissocladius oliveri, Paracladius, Parakiefferiella* Thienemann, *Protanypus, Pseudodiamesa, Stictochironomus,* and Tanytarsini are not uncommon in the North American arctic (Bliss, 1977; de March *et al.*, 1978; Hershey, 1985a, b; Nyquist and LaPerriere, 1973; Oliver, 1963, 1964, 1968, 1976). The above taxa, however, are largely absent from the shallowest high-elevation and arctic lakes and ponds, where *Chironomus, Corynoneura, Cricotopus, Orthocladius, Procladius, Psectrocladius, Sergentia,* and Tanytarsini may be abundant (Andersen, 1946; Butler *et al.*, 1981; Danks and Oliver, 1972a, b; this study). Danks and Oliver (1972b) indicate "There is little overlap in species between the two types of habitat" (arctic lakes vs. arctic ponds). In the shallow lakes and ponds all or most of the bottom may freeze in winter. The long arctic and alpine winters also contribute to anoxia in shallow waters (Hobbie, 1973). During summer the ponds are much warmer than larger, and deeper lakes nearby. Ice scouring disrupts the littoral fauna of large arctic lakes (Andrews and Rigler, 1985).

The following taxa, recorded only at low-elevations in my southern British Columbia studies, are not known from the North American arctic (Danks, 1981; D.R. Oliver, pers. comm.) - *Labrundinia* Fittkau, *Nilotanypus* Kieffer, *Glyptotendipes, Cladopelma, Cryptotendipes, Cyphomella* Sæther/*Harnischia* Kieffer/*Paracladopelma* Harnisch, *Lauterborniella/Zavreliella*[2], *Nilothauma* Kieffer, *Omisus* Townes, *Pagastiella* cf. *ostansa, Paralauterborniella* Lenz, *Paratendipes, Stenochironomus* Kieffer, *Xenochironomus* Kieffer, *Pseudochironomus* Malloch, *Heterotanytarsus* cf. *perennis,* and *Synorthocladius* Thienemann. Several taxa which I have not collected at high elevations are recorded only as rare elements of the low-arctic tundra fauna (e.g. *Dicrotendipes, Microtendipes,*

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[2] Although *Lauterborniella* has been reported from Char Lake, N.W.T. (Welch, 1973), this record is clearly the result of confusion with *Lauterbornia sedna* Oliver (now a *Micropsectra*), which Oliver (1976) described from this lake. Welch's (1973) error has been propogated in several subsequent articles (ie. Andrews and Rigler, 1985; Davies, 1975; Rigler, 1978).

Parachironomus Lenz, *Polypedilum*, *Stempellinella*).

Ceratopogonidae have been reported from the high arctic (Danks, 1981). One *Chaoborus* record, *C.* (*Schadonophasma*) *trivittatus* (Loew), exists for Baffin Island (Danks, 1981). However, Borkent (1979) remarks, "In the Rocky Mountains, the species has not been found above treeline. The single record from Baffin Island is suspect." While many of these taxa may yet be recorded farther north, or at higher elevations, they are obviously rare in cold climatic regions.

The parallels between the chironomid response along a north–south climatic gradient, and an altitude gradient offer some assurance that climate is directly or indirectly influencing faunistic composition. Independent studies by Mayhood and Anderson (1976) for the Canadian Rockies, and by Reiss (1968) in the Alps, portray similar trends. Although Tuiskunen and Lindeberg (1986) report many of the listed genera north of 68° in Europe, their sites appear to be at, or near timberline. A study of the Saskatchewan River Chironomidae (Mason and Lehmkuhl, 1983) indicates that many Chironomini occurring upstream of a reservoir may not occur in the cooler downstream waters.

The disappearance of many chironomid genera at a major vegetation boundary raises suspicion concerning the independence of these insects from terrestrial flora. The distributions of wood–mining chironomids (e.g. *Orthocladius* (*Symposiocladius*) *lignicola*) are certainly limited by the occurrence of trees and shrubs. Also, since aquatic macrophytes are less common in arctic and alpine lakes, chironomids (e.g. *Brillia* Kieffer, *Stenochironomus*) dependent upon either these habitats, or leaves from terrestrial vegetation will be less common. However, such obligate relationships will not explain the disappearance of the majority of chironomids, including many deposit and filter feeders. If trees were important in providing habitat to chironomids, a similar reduction in generic diversity would be apparent at lakes in grassland regions. However, many of the genera absent in the arctic are abundant in grassland lakes and ponds (Driver, 1977; Cannings and Scudder, 1978; Timms *et al.*, 1986; Wiederholm, 1980).

It should be remembered that the horizontal and vertical climatic gradients are not linear functions of altitude or latitude. The Canadian northern limit of trees is defined by the mean summer position of the arctic front (Bryson, 1966). A marked difference of climate exists on either side of this narrow frontal zone. Summer temperatures, and duration of the growing season are significantly reduced north of arctic treeline. G.M. MacDonald (pers. comm.) indicated a pronounced change in ice thickness, and sedimentation rates at lakes on either side of timberline. Treeline also seems to be an important biogeographic boundary for many other insect groups, including the Odonata (Danks, 1981; Downes, 1964). These predaceous aquatic insects have no direct ties to terrestrial vegetation, yet few Odonata species occur on the southernmost arctic tundra (Danks, 1981; Downes, 1964). The Odonata are aquatic as larvae and predaceous both in mature and immature stages.

Although temperature varies gradually with elevation, distinct climatic changes are evident across the subalpine zone. Freezing levels average *ca.* 900 m during winter in southern coastal British Columbia (Peterson, 1969). Thus, snow and ice cover are ephemeral at elevations below *ca.* 900 m near Vancouver, but at higher elevations (the subalpine zone) snow accumulates to several metres depth (Brooke *et al.*, 1970; Bunnell *et al.*, 1985). This produces a sharp reduction in growing season. Lakes within the lower subalpine may thaw in early summer, but upper subalpine lakes could not be sampled before late July and early August during 1986. At this time ice partially covered many coastal upper subalpine lakes. "Coleman Pond" thawed only in September 1985, when early snow began to reappear on adjacent peaks.

With major climatic changes occurring over such short horizontal and vertical distances, it is not surprising that the northern and altitude limits of many groups of unrelated organisms should nearly coincide. Marked limnological changes may also be expected. The reduced growing season limits primary production. Low temperature also slows the chemical weathering of rocks, the ultimate source for many nutrients.

The task of determining precisely why many chironomid genera and species cannot cope with arctic conditions is not easily resolved. Danks (1981), MacLean (1975) and Oliver (1968) provide extensive reviews of physiological and behavioural adaptations which distinguish arctic insects, but the significance of these adaptations requires much further evaluation.

The harsh physical environment of arctic regions, especially in winter, would seem a likely factor. Andrews and Rigler (1985) report that temperate ice rarely exceeds 0.6 m thick, but arctic ice may reach 2.5 m. Alpine ice 1.3 m thick is also reported (Pennak, 1968). Although, by occupying lake environments most chironomids are isolated from the severity of winter, an ability to avoid or tolerate freezing would seem an important adaptation. Danks (1971a, b, c) has carefully studied the winter habits and survival of chironomids. He (Danks, 1971a) notes "... that freezing tolerance is found in nearly every major genus group (except in Tanypodinae)." Many species are noted as freezing tolerant, including an African tropical species, *Polypedilum vanderplanki* Hint. Thus, Danks (1971a) concluded "... that the Chironomidae can probably be considered preadapted to seasonally frigid habitats." However, it should be noted that prolonged freezing at temperatures below −15°C has proven lethal, even to arctic species (Baust and Edwards, 1979; Danks, 1971a, 1981: p. 278–279). Similar temperatures may exist in arctic littoral habitats (Andrews and Rigler, 1985; Danks, 1971b; Livingstone, 1963). Although arctic Chironomidae lack a "metabolic cold adaptation", polar species may have lower activation energies (Lee and Baust, 1982).

The reduced productivity at arctic and alpine sites (Brylinsky and Mann, 1973) is also a potentially important factor, determining the availability of food to benthos. Thus chironomids characteristic of strongly oligotrophic environments prevail in all arctic lakes where oxygen concentrations remain continuously high. All arctic and alpine species will have to tolerate the characteristically low food supplies of cold climates. Moore's (1978) results indicate that P, NO_3–N, and phytoplankton concentrations are all lower in arctic than subarctic environs.

Chironomus plumosus, a temperate midge of eutrophic lakes is certainly poorly adapted to the arctic food supply. Filter-feeding will require much greater effort and is probably not an effective food-gathering mechanism in dilute ultra-oligotrophic arctic lakes. The pronounced diatom blooms which provide emergence cues to *C. plumosus* (Hilsenhoff, 1967) may not occur in arctic waters.

Perhaps most important is the influence of summer temperature. Danks (1971b) notes, "Ecologically significant processes such as growth and development generally involve temperature thresholds below which the processes do not occur (Allee *et al.*, 1949: pp. 110–11)." Although the metabolism of arctic chironomid larvae is not "extraordinary" (Welch, 1976), normal larval activity may occur at lower temperatures than in temperate species. The activity threshold for arctic pond larvae is near 0° C (Welch, 1976). Apparently many Orthocladiinae larvae grow only at temperatures below 5° C (Sæther: according to Hågvar and Østbye, 1973). In contrast the temperate profundal midge *Chironomus plumosus* may not feed below 5° C (Hilsenhoff, 1966).

The pupation threshold of chironomids is generally higher than the activity threshold. For high arctic pond species, this threshold is about 5° C, with emergence occurring only in water 7° C or warmer (Danks, 1971b; Danks and Oliver, 1972b). Emergence from subarctic lakes near Inuvik, N.W.T. is restricted to temperatures greater than 9° C (Chang, 1975). Fjellberg (1972) suggests the pupation threshold of *Corynocera ambigua* to be *ca.* 8° C. One temperate midge, *Chironomus salinarius* Kieffer requires temperatures of 13° C to complete emergence at the northern limit of its range (Koskinen, 1968). Species characteristic of arctic lakes, *Heterotrissocladius subpilosus, Paracladius quadrinodosus* Hirvenoja, and *Pseudodiamesa arctica* (Malloch), emerge through candled ice at Lake Hazen, Northwest Territories (Oliver, 1968), completing their entire life cycle in temperatures near freezing. Temperatures in arctic lakes of moderate depth or deeper are too cold for development of species from adjacent ponds (Danks and Oliver, 1972a).

Flight and egg development are also temperature dependent. Eggs of *Chironomus plumosus* do not hatch below 8° C (Hilsenhoff, 1966). Arctic chironomids are capable of flight at temperatures near 3.5° C (Downes, 1964). Some arctic chironomid species are parthenogenetic, while others may swarm, copulate, or both without flight (Danks, 1981; Fjellberg, 1972; Oliver, 1968; Oliver and Danks, 1972). Thus low summer air and water temperatures may impair the ability of species to complete their life cycles.

The importance of temperature in restricting chironomid distributions has been noted by Moore (1978) across arctic treeline. *Dicrotendipes nervosus* (Staeger) is reported only from a small, warm subarctic lake. Similarly, "... many of the less common species (e.g. *Ablabesmyia janta* (Roback), *Microtendipes* sp., and *Monodiamesa bathyphila* (Kieffer)) clearly reached the northern limit of their distribution in the study area" (Moore, 1978). Other species, *Heterotrissocladius oliveri* and *Micropsectra* cf. *groenlandica* Andersen occurred only in cold water.

Danks and Oliver (1972a) note that the arctic fauna is derived from the "absolute spring species" of farther south. These species overwinter entirely as fully mature larvae, with diapause preventing emergence late in the preceding summer or autumn season

(Danks and Oliver, 1972a). Emergence begins in spring once sufficient degree–days have accumulated, and when the necessary temperature thresholds are achieved. If such conditions are not presented, the arctic species may overwinter again in the pre–pupal stage (Danks and Oliver, 1972a; Oliver, 1968).

The temperatures which restrict the distribution of chironomids will be those in the least favourable years or series of years. In this regard, it is noteworthy that this century has been warmer than the 19th century (Dunbar, 1985). Thus distributions of many arctic organisms may not be in equilibrium with present climatic conditions. According to Livingstone (1963), maximum summer temperatures at Imikpuk Lake near Point Barrow, Alaska, varied from 8 to 12° C between 1951 and 1955 (Brewer, 1958). Livingstone (1963) notes that 75% of the heat supplied to Chandler and Peters Lakes was consumed in melting the ice.

A temperature gradient similar to that evident along a north–south transect occurs in lakes and ponds along my altitude transect. High elevation lakes are much colder than low–elevation sites. Shallow alpine ponds are usually warmer in mid–summer than deeper waters nearby. In Banff National Park, alpine summer temperature for lakes and pond surfaces range from 6° C to 11° C (Mayhood and Anderson, 1976). One lower subalpine pond, 600 m below timberline, was the warmest in their study area with summer surface temperatures of 20° C (Mayhood and Anderson, 1976). Surface water temperatures of 27° C are recorded for Mike Lake, at low–elevation near Vancouver.

Water temperatures are not a simple function of air temperature (Corbet, 1972). The temperature of shallow ponds often exceeds that of the air, particularly where scant cloud cover permits insolation of the pond bottom (Danks, 1971b; Downes, 1964; Thomasson, 1956). Glacial streams often regulate the temperature of arctic and alpine lakes. Since arctic lakes seldom stratify, the great thermal inertia of deep lakes precludes high summer temperatures in littoral, as well as profundal regions.

Although the temperature and habitat requirements of chironomid larvae obviously require further study, I propose the following factors as important future hypotheses which may explain the distribution of chironomids in the arctic and at high elevations.

1) *Low summer temperatures and short growing seasons* probably prevent many temperate species and genera from permanently colonizing arctic and alpine waters. Arctic and alpine pond species also cannot cope with the lower summer temperatures in arctic lakes which either exceed a moderate depth, or receive glacial meltwater.

2) *Winter anoxia* is probably most important in preventing characteristic arctic and alpine lake species from occupying shallower waters.

3) *The availability of cold, well-oxygenated profundal environments* probably limits the southern and lower limits of arctic and alpine lake taxa (e.g. *Heterotrissocladius subpilosus, Paracladius*). A similar relationship may regulate occurrence of *Sergentia coracina*. Perhaps other arctic and alpine pond species can also find southern refuge in springs where temperatures approach the annual mean.

Much further work is necessary to examine the possible role of these factors in regulating chironomid distributions, during each life stage. Danks (1971a, b, c), Danks and Oliver (1972a, b), Oliver (1964, 1968), and Oliver and Danks (1972) provide excellent evidence of chironomid adaptations to arctic environments. However, much more comparative physiological work and experimental research is necessary to reveal how arctic and temperate species differ. Our knowledge of chironomid distributions is still poor in arctic and alpine habitats, especially in a critical region, the Canadian low arctic.

In view of these data it is interesting to re–examine the palaeoecological data from British Columbia and other North American sites. In Marion, Misty, Mike, and Hippa

Lakes, most chironomid genera arrived very quickly following deglaciation. Summer temperatures were not sufficiently low to prevent rapid colonization. Nevertheless, many chironomid taxa, presently more abundant at high elevations, were common during the late-glacial at low-elevations. This probably reflects, in part the greater water depth, but also colder and more oligotrophic conditions, related to a more severe late-glacial climate.

Elsewhere in North America, several chironomids which are or absent in the arctic occur in the early late-glacial sediments [e.g. *Dicrotendipes*, and *Glyptotendipes* at Green Lake, Michigan (Lawrenz, 1975), and *Cladopelma* and *Polypedilum* in New Brunswick, Canada (Walker and Paterson, 1983)]. Palynological evidence suggests that the late-glacial landscape at these sites was not forested, but trees may have been slow to re-colonize these areas. Thus, warm-adapted Chironomidae may have colonized these habitats before trees were able to reoccupy the same regions. The lacustrine climate is not the same as that of terrestrial habitats, but conditions may have been warmer than the tundra landscape palynological evidence implies. While it is too early to provide a precise statement of how late-glacial conditions differed from arctic environs, future chironomid analyses of surficial sediment samples across the arctic - subarctic transition, and improved knowledge of chironomid distribution limits should provide important clues.

CONCLUSIONS

In these concluding pages I will address the major questions posed at the beginning of this thesis: 1) Which genera are represented in lacustrine sediments of the Pacific Northwest?; 2) How are these taxa distributed in space and time?; 3) How did their present patterns of distribution originate?

At least 58 different taxa, representing 5 chironomid subfamilies, were recovered from surface or fossil samples. A list of these taxa, and descriptions of each are provided as an appendix. It is certain, however, that many more taxa are present in British Columbia. Although most chironomid remains were identifiable to the generic level, several closely related genera, and a great many species could not be distinguished. Nevertheless, 5 genera (*Corynocera, Hydrobaenus, Nilotanypus, Omisus, Stilocladius*) are first reported from British Columbia as a part of this research.

My studies of chironomid distributions were mostly limited to coastal British Columbia, although surface samples from the Rocky Mountain national parks were included. Details regarding the distribution of chironomids in other areas were primarily obtained from literature sources.

Many chironomid genera are widely distributed at low-elevations in southern British Columbia, and elsewhere in temperate North America, but the fauna is much less diverse at high elevation (within the upper subalpine and alpine vegetation zones) and north of arctic treeline. In contrast, a few chironomid taxa (*Heterotrissocladius, Paracladius, Parakiefferiella* sp.A, *Protanypus, Stictochironomus*) are more common in the cold waters of arctic/alpine regions, and the profundal waters of the largest and deepest low elevation lakes. These patterns of distribution suggest that water temperature is an important influence limiting the distribution of chironomid taxa.

Stratigraphic analyses indicate that most chironomid taxa rapidly colonized British Columbia following glacial retreat. This rapid colonization suggests that one or more species of most chironomid genera had survived in refugial areas near southern British Columbia, probably in unglaciated regions of the western United States. Although late–glacial temperatures were colder than present conditions, the climate was sufficiently warm to permit the survival of a diverse fauna.

Other refugial areas may have existed along the British Columbia coast. A Queen Charlotte glacial refugium would have permitted *Corynocera* nr. *ambigua* to rapidly colonize adjacent glaciated areas of these islands.

The late–glacial fauna of small low–elevation lakes in southwestern British Columbia included several taxa (*Heterotrissocladius, Parakiefferiella* sp.A, *Protanypus, Pseudodiamesa, Stictochironomus*) which are commonly associated with cold, well–oxygenated waters. These taxa decrease greatly in abundance or completely disappear near the end of the Pleistocene, when palynological evidence suggests a rapidly warming climate. Thus, changing climatic conditions are likely responsible for these changes. Warm temperatures eliminated cold–stenothermous taxa from littoral habitats. Indirect climatic effects, including hypolimnetic oxygen depletion (a product of increased autochthonous and allochthonous organic loading) may have eliminated these taxa from the profundal waters of small lakes.

A very similar pattern of late–glacial chironomid succession is apparent throughout North America and Europe. A cold–stenothermous fauna was common in cold regions adjacent to the retreating continental glaciers. These cold–stenothermous taxa have since survived in the deep profundal waters of the largest and deepest temperate lakes and in arctic/alpine regions.

During the early phases of deglaciation *Chaoborus* (Chaoboridae) and 3 Chironomidae, which are presently common in British Columbia, may have been absent.

These taxa are *Paracladius*, *Psectrocladius* subg. *Monopsectrocladius*, and Tanytarsini sp.A. Future stratigraphic investigations may require revision of this list. Cold late–glacial temperatures may have limited the spread of some of these taxa, but the absence of *Paracladius* fossils from late–glacial sediments is intriguing. At present *Paracladius* appears to be common in cold water, in association with several taxa which had been common in late–glacial times at low–elevation. Since conditions in the low–elevation late–glacial lakes of British Columbia seem to have been suitable for *Paracladius*, this taxon may be a recent immigrant to British Columbia, having survived in a distant glacial refuge. *Paracladius* may have survived in unglaciated areas far to the east, or perhaps in the Beringian refugium.

My studies indicate that climate has had an important bearing upon the past and present chironomid fauna of British Columbia. Although Chironomidae seem less sensitive to climate than terrestrial vegetation, stratigraphic analyses of their fossils may provide important paleoclimatological evidence.

APPENDIX

Notes on the identification and ecology of fossil Chironomidae

The conclusions outlined in the main portion of this thesis depend greatly upon the correct identification of fossil Chironomidae. Apart from the mentum, few structures were consistently preserved and retained with the fossil head capsule. Yet, systematic placement of many larval taxa is best achieved with reference to other body parts (e.g. Wiederholm, 1983).

This appendix provides details regarding fossil identification, including uncertainties which exist for several taxonomic decisions. While the immediate intent is to provide a measure of quality assurance, the organization of the appendix has also a practical goal.

With so little research yet devoted to the chironomid fauna of British Columbia, aquatic ecologists or palaeoecologists may find this record useful for identification of chironomids in British Columbia, and perhaps elsewhere. To assist comparisons, illustrations and remarks concerning similar-looking, closely-related taxa have been placed on the same page, or adjacent pages. Terminology follows that proposed by Sæther (1980c). Length of the ventromental plates is measured parallel to the median axis of the head capsule; their breadth is measured perpendicular to this axis.

Since no major changes in chironomid mouthparts, apart from size, occur during the final larval instars, the key, descriptions and illustrations should be reliable for 2nd, 3rd, and 4th instar remains. Illustrations have been prepared from remains of one of these three instars.

The order of presentation is not alphabetical. The following outline facilitates quick reference to individual taxa. Nomenclature follows Wiederholm (1983), unless otherwise noted.

Key to British Columbia late-Quaternary chironomid remains

1a) Head capsule without ligula; antennae non-retractile;
mentum conspicuous and, in most taxa, darkly pigmented.... 2.

b) Ligula and retracted 1st antennal segment retained in
most fossil head capsules; mentum inconspicuous, weakly
pigmented...........................Subfamily TANYPODINAE. 4. p.129

2a) Mentum concave; ventromental plates vestigial
........................Subfamily CHIRONOMINAE (in part). 7. p.148

b) Mentum convex; or if concave, then ventromental plates
conspicuous... 3.

3a) Ventromental plates very broad, always extending
laterally far beyond the outermost mental teeth; most
taxa with striated ventromental plates
........................Subfamily CHIRONOMINAE (in part). 7. p.148

b) Ventromental plates much smaller, not extending far
beyond the outermost mental teeth (except in
<u>Nanocladius</u> and <u>Stilocladius</u>); ventromental
plates never striated
..Subfamilies DIAMESINAE, ORTHOCLADIINAE and PODONOMINAE. 32. p.175
& 177

SUBFAMILY TANYPODINAE

4a) Median tooth of ligula much longer than adjacent teeth; dorsomental teeth absent.....Tribe Pentaneurini (in part). 5.

b) Median tooth of ligula about as long as adjacent teeth, or shorter, forming a straight or weakly concave distal ligula margin; dorsomental teeth present or absent........ 6.

5a) Lateral margin of head capsule with small, but distinct swelling; several sharp projections scattered over swollen area....................................*Labrundinia* p.129

b) Lateral margin of head capsule without distinct swelling; no sharp projections along lateral margin of head capsule....................................*Nilotanypus* p.129

6a) Dorsomental teeth lacking; head capsule elongate; 1st antennal segment very long and slender....other Pentaneurini p.130

b) Dorsomental teeth present; head capsule broad; 1st antennal segment rather short and broad

..........................Tribe Macropelopiini: *Procladius* p.130

SUBFAMILY CHIRONOMINAE

7a) Ventromental plates bar-shaped, nearly touching at median axis of mentum.................................... 8.

b) Ventromental plates fan-shaped, and (except for *Lauterborniella/Zavreliella*) widely separated; or ventromental plates vestigial........................... 9.

8a) Second lateral teeth of mentum distinctly smaller than adjacent pair; antennae not on distinct pedestals.........Tribe Pseudochironomini: *Pseudochironomus* p.149

b) Second lateral teeth equal in size to 3rd lateral teeth, or fewer than 3 pairs of lateral teeth visible; antennal pedestal of most taxa conspicuous ....Tribe Tanytarsini (in part). 10.

9a) Antennal pedestals conspicuous, with distinct apical projection..........Tribe Tanytarsini (in part). 10.

b) Antennae not placed on distinct pedestals ....Tribe Chironomini. 13.

Tribe Tanytarsini

10a) Ventromental plates bar-shaped, nearly touching at median axis of mentum.............................. 11.

b) Ventromental plates fan-shaped, widely separated...... 12.

11a) Mentum narrow, usually only 3 teeth visible in ventral view; median and lateral mental teeth similarly pigmented.................*Corynocera* nr. *ambigua* p.149

b) Mentum broad, with 11 conspicuous teeth; median tooth of some taxa weakly pigmented......~~*Tanytarsus s. lat*~~. p.148

sub tribe Tanytarsina

12a) Antennal pedestal with distinctly ridged, or
creased apical spur......................Tanytarsini sp.A p.149
b) Spur of antennal pedestal not ridged or creased
....Stempellinella p.149

Tribe Chironomini

13a) Mentum concave.. 14.
b) Mentum weakly to strongly convex..................... 15.

14a) Ventromental plates vestigial; all mental teeth
dark and strongly sclerotized..............Stenochironomus p.155
b) Ventromental plates broad and conspicuous; with
broad, weakly pigmented median tooth.......Cryptochironomus p.155

15a) Outermost teeth (1 or 2 pairs) of mentum
distinctly longer than adjacent teeth.................. 16.
b) Outermost teeth of similar size to adjacent teeth
or smaller... 17.

16a) Median mental tooth broad, only notched near
extreme lateral margins; outermost teeth not much
broader than other lateral teeth............Cryptotendipes p.154
b) Median mental region notched laterally, and often
at apex to form 3 or 4 narrow teeth; outermost pair
(or pairs) of mental teeth much broader than other

lateral teeth....................................<u>Cladopelma</u> p.154

17a) Anterior margin of ventromental plates broadly scalloped; mentum with light pigmentation, and 15 or 16 pointed teeth..........................<u>Parachironomus</u> p.154

b) Anterior margin of ventromental plates not scalloped; mentum with light or dark pigmentation, and 13 to 16 teeth...................................... 18.

18a) Mentum with even number of teeth; or if odd, then median tooth light coloured and shorter than adjacent pair.. 19.

b) Mentum with odd number of teeth; median tooth light or dark-coloured, large and conspicuous........... 28.

19a) Median and 1st lateral pairs of mental teeth more weakly pigmented than other mental teeth; 16 mental teeth..<u>Paratendipes</u> p.152

b) Either all mental teeth weakly-pigmented, or with fewer than 4 weakly-pigmented teeth; 14 to 16 teeth..... 20.

20a) Median pair, and 2nd lateral pair of mental teeth distinctly longer than 1st lateral teeth................ 21.

b) Median pair of teeth shorter, or subequal to length of adjacent pair................................. 24.

21a) Mentum with 16 teeth................................. 22.

b) Mentum with fewer teeth............................ 23.

22a) All mental teeth small, weakly pigmented; lateral extremity of ventromental plates rounded ....Pagastiella cf. ostansa p.151

b) Mental teeth of normal size, brown to black; lateral extremity of ventromental plates pointed ....Polypedilum p.151

23a) Anterior margin of ventromental plates nearly straight, almost meeting at median axis; all mental teeth weakly pigmented..........Lauterborniella/Zavreliella p.151

b) Anterior margin of ventromental plates distinctly convex, separated by 4 or more teeth; lateral teeth more darkly pigmented than median teeth.......Microtendipes p.151

24a) Median pair of mental teeth much smaller than 1st lateral pair...Omisus p.152

b) Median and 1st lateral teeth subequal................ 25.

25a) Ventromental plates separated by 6 or more teeth, distinctly and coarsely striated throughout ....Cyphomella/Harnischia/Paracladopelma p.152

b) Ventromental plates separated by 4 or fewer teeth, distinctly or indistinctly striated............ 26.

26a) Mandible with 4 inner teeth; striae near anterior ventromental margin distinct and widely spaced (adjacent striations are separated by about their apparent length); 3rd lateral teeth of mentum of normal size..................................<u>Sergentia</u> p.150

b) Mandible with 2 or 3 inner teeth; striae near anterior ventromental margin closely spaced, but distinct to absent; 3rd lateral teeth of mentum larger than adjacent pairs in most specimens........... 27.

27a) Mandible with short dorsal tooth and 3 inner teeth; ventromental striae long, easily discernible in anterior and posterior fields; median teeth of mentum distinctly separated.......................<u>Tribelos</u> p.150

b) Mandible with long dorsal tooth, and 2 or 3 inner teeth; ventromental striae indistinct or not discernible, anterior striae very short; median pair of mental teeth fused in some specimens ....<u>Stictochironomus</u> p.150

28a) All mental teeth dark, similarly pigmented; median origin of ventromental plates not associated with median tooth.................................... 30.

b) Median tooth pale, lateral teeth dark or light; ventromental plates projecting forward in median area, having origin associated with median tooth....... 29.

29a) Median tooth very broad, composing <u>ca</u>. 1/3 of mental width; mandible not sickle-shaped; 3 inner mandibular teeth......................Paralauterborniella p.155

b) Median tooth not exceptionally broad, composing ca. 1/5 of mental width; mandible sickle-shaped; 4 inner mandibular teeth.........................Nilothauma p.155

30a) Median tooth distinctly trifid (except when strongly worn), and flanked by 6 lateral pairs; anterior ventromental margin smooth; striae discernible in posterior field only............Chironomus p.153

b) Median tooth often notched laterally, but not distinctly trifid; median tooth flanked by 6 lateral pairs; ventromental plates distinctly striated, with most specimens having finely crenate anterior margin.. 31.

31a) Width of each ventromental plate about as wide, or wider than mentum; mental teeth low, rounded.Glyptotendipes p.153

b) Width of each ventromental plate about 3/4 of mental width; mental teeth long, separated by deep notches................................Dicrotendipes p.153

SUBFAMILIES DIAMESINAE, ORTHOCLADIINAE and PODONOMINAE

32a) Head capsule with numerous long setae (position of setae may be apparent only by their insertions when the setae have been lost from fossils); mentum weakly convex with 2 distinct pairs of lateral teeth..................................<u>Protanypus</u> p.175

b) Head capsule with normal number of setae; if mentum weakly convex, then mentum has 4 or more pairs of distinct lateral teeth........................ 33.

33a) Submental setae set far back on head capsule, (distance of setae from posterior head capsule margin less than, or equal to, distance from setae to mentum)...................................... 34.

b) Submental setae closer to mentum than posterior margin of head capsule................................ 35.

34a) Ventromental plates wholly or partially concealing lateral teeth of the mentum; mentum with one broad median tooth.......................<u>Pagastia</u> p.176

b) Ventromental plates not overlapping or concealing any mental teeth; mentum with even number of teeth, or if mentum has odd number of teeth, then median tooth small and narrow..................<u>Brillia</u>/<u>Euryhapsis</u> p.177

35a) Mentum with 4 or more pairs of lateral teeth......... 36.

b) Mentum with 2 pairs of lateral teeth ....<u>Orthocladius</u> (<u>Symposiocladius</u>) <u>lignicola</u> p.178

36a) Mentum with pronounced bands of greater and lesser sclerotization in lateral regions of mentum; ventromental plates not overlapping mental teeth; head capsule yellowish to brown....Eukiefferiella/Tvetenia p.184

b) Mentum without pronounced sclerotization banding in lateral regions of mentum; ventromental plates may or may not overlap teeth of mentum; head capsule pigmentation transparent to yellowish or brown.. 37.

37a) Median mental tooth with 2 pronounced median points, weakly pigmented; first 2 pairs of lateral teeth lighter in colour than subsequent pairs; lateral teeth with truncated appearance ....Nanocladius cf. distinctus p.183

b) Median mental tooth without pronounced median points, weakly to strongly pigmented; if first 2 pairs of lateral teeth are lighter in colour than subsequent pairs, then lateral teeth without truncated appearance.................................. 38.

38a) Mentum with odd number of teeth; median tooth without median notch and distinctly broader (2x or more) than any lateral tooth....................... 39.

b) Mentum with even number of teeth; or if mentum has odd number of teeth, then median tooth either medially notched, or not distinctly broader than any lateral tooth............................... 47.

39a) Ventromental plates completely overlapping all
pairs of lateral teeth............................<u>Potthastia</u>? p.176

b) Ventromental plates smaller, some lateral
mental teeth extend beyond anterior ventromental
margin of flattened head capsule...................... 40.

40a) Ventromental plates wholly or partially
overlapping some mental teeth, with
approximately straight or weakly concave
antero-lateral margins; median tooth dark;
premandible simple.<u>Psectrocladius</u> subg. <u>Monopsectrocladius</u> p.181

b) Ventromental plates not overlapping mental
teeth; or if wholly or partially overlapping
mental teeth, then either antero-lateral margin
convex, or median tooth with little or no
pigmentation; premandible simple or compound........... 41.

41a) Ventromental plates very broad in submental
region..<u>Stilocladius</u> p.179

b) Ventromental plates not exceptionally broad
in submental region.................................... 42.

42a) Median tooth flanked by 2 pairs of light
coloured lateral teeth
.......<u>Cricotopus/Orthocladius/Paratrichocladius</u> (in part) p.178

b) Median tooth flanked by 1 pair of light coloured lateral teeth; or all lateral teeth similarly pigmented.................................... 43.

43a) Median tooth notched laterally
..........................Parakiefferiella cf. bathophila p.180
b) Median tooth unnotched.............................. 44.

44a) 2nd lateral teeth distinctly smaller than adjacent teeth (but 1st and 2nd lateral teeth absent when mouthparts strongly worn); median tooth as dark as lateral teeth............Parakiefferiella sp.A p.180
b) 2nd lateral teeth of similar size to adjacent pairs; median tooth with light or dark pigmentation.. 45.

45a) Median tooth very broad, and with little, if any pigmentation.. 46.
b) Median tooth less broad, with distinct pigmentation (varying from pale yellow or tan to dark brown)..................Smittia/Pseudosmittia? group p.178

46a) Median tooth strongly arched
..........................Parakiefferiella? cf. triquetra p.180
b) Median tooth weakly arched.................. Paracladius p.179

47a) Mentum with even number of teeth; each median tooth is distinctly broader (1.5 or more x) than the adjacent 2nd lateral tooth........................ 48.

b) Mentum with odd number of teeth; or if mentum has even number of teeth, then median tooth of similar width to 2nd lateral tooth.................... 56.

48a) Mentum with 4 pairs of lateral teeth.....*Synorthocladius* p.185

b) Mentum with 5 or more pairs of lateral teeth......... 49.

49a) Ventromental plates partially overlapping one or more lateral teeth of mentum; most species with a straight or weakly convex antero-lateral ventromental margin; median pair of teeth without accessory teeth; premandible simple...other *Psectrocladius* p.181

b) Ventromental plates smaller; or if ventromental plates overlap some mental teeth, then antero-lateral margin distinctly convex; median pair of mental teeth with or without accessory teeth; premandible simple or compound................. 50.

50a) Ventromental plates with complex layered structure, probably double; 4th lateral teeth of mentum as long, or longer than 3rd lateral teeth ....*Parametriocnemus* group p.183

b) Ventromental plates single, without complex layered structure; 4th lateral teeth of mentum shorter than 3rd lateral teeth........................ 51.

51a) Median pair of teeth weakly separated............... 52.

b) Median pair of mental teeth distinctly separated..... 53.

52a) 1st lateral mental teeth closely appressed to median pair; ventromental plates extend at least to base of outermost lateral tooth............<u>Hydrobaenus</u> p.182

b) 1st lateral teeth distinctly separated from median pair; ventromental plates not extending to base of outermost lateral tooth ....<u>Doithrix</u>/<u>Pseudorthocladius</u>? group p.184

53a) Ventromental plates poorly developed (antero-lateral margin of ventromental plates not extending to base of outermost lateral teeth); median teeth lacking accessory teeth...........<u>Limnophyes</u> p.184

b) Ventromental plates extend at least to base of outermost lateral teeth; median teeth with or without accessory teeth.............................. 54.

54a) Median pair of mental teeth as dark as laterals, and uniformly pigmented; ventromental beard absent; premandible indistinctly bifid ....<u>Heterotrissocladius</u> p.182

b) Median pair of mental teeth in most specimens more weakly pigmented than laterals, and weakly banded; ventromental beard preserved on some specimens; premandible either simple or distinctly bifid.. 55.

55a) Submental setae set close to ventromental plates (distance from setae to ventromental plates less than breadth of plates), and posterior to 3rd or 4th lateral teeth; premandible simple.......<u>Rheocricotopus</u> p.183

b) Submental setae farther from ventromental plates (distance from setae to ventromental plates greater than breadth of ventromental plates), and posterior to 2nd or 3rd lateral teeth; premandible distinctly bifid...............................<u>Zalutschia</u> p.182

56a) Median mental region with concave area formed by median pair of teeth and 1st and 2nd lateral teeth ....<u>Heterotanytarsus</u> cf. <u>perennis</u> p.185

b) Median region of mentum convex...................... 57.

57a) Ventromental plates wholly or partially overlapping most lateral teeth; median tooth and 1st lateral teeth subequal; 6th lateral teeth distinctly longer than adjacent pairs........<u>Pseudodiamesa</u> p.176

b) Ventromental plates not extending to base of lateral mental teeth; median mental region variable; 6th lateral teeth similar to adjacent mental teeth... 58.

58a) Lateral region of mentum very steeply sloping (*ca*. 60°); median 2 or 3 teeth projecting distinctly beyond adjacent mental teeth; mentum with 12 or 13 teeth...........*Corynoneura*/*Thienemanniella* p.177

b) Lateral region of mentum less steeply inclined (*ca*. 45°); median teeth not projecting distinctly beyond adjacent teeth; mentum with 13 or more teeth.... 59.

59a) Mandible with 8 teeth; mentum with 1 median tooth and 7 or 8 pairs of lateral teeth.........*Boreochlus* p.175

b) Mandible with fewer than 8 teeth; mentum with 1 or 2 median teeth, and 6 to 11 pairs of lateral teeth... 60.

60a) Mentum with odd number of teeth; median tooth flanked by 6 or 7 pairs of lateral teeth ....*Cricotopus*/*Orthocladius*/*Paratrichocladius* (in part) p.178

b) Mentum with odd or even number of teeth; median tooth (or teeth) flanked by 7 to 11 pairs of lateral teeth.....................................*Diamesa*? p.175

Notes regarding individual taxa

Subfamily Tanypodinae

Tribe Pentaneurini

Labrundinia Fittkau (Fig. A.1a–c)

The elongate head capsules of *Labrundinia* have two slightly swollen regions, one along either lateral margin, which bear several sharp projections (Fittkau and Roback, 1983). This feature may be unique to *Labrundinia*. The median tooth of the 5–toothed ligula is distinctly longer than the remaining teeth. A similar ligula arrangement is reported for *Nilotanypus* (Fittkau and Roback, 1983). The mandible bears two inner teeth.

Labrundinia has been reported from subarctic to tropical regions (Fittkau and Roback, 1983; Wiens *et al.*, 1975), preferring bogs and still or slow–moving water (Fittkau and Reiss, 1978; Oliver and Roussel, 1983a). *Labrundinia pilosella* (Loew) has been collected at Kaslo, British Columbia (Roback, 1971). In this study, remains of *Labrundinia*, were found in Deer and Stump Lakes only.

Nilotanypus Kieffer (Fig. A.1d–f)

The 5–toothed ligula of *Nilotanypus* is similar to that of *Labrundinia*, having a median tooth which projects distinctly beyond adjacent teeth. This ligula arrangement is not described for other Tanypodinae genera (Fittkau and Roback, 1983). The more rounded lateral margins of the head capsule, and absence of lateral pointed projections, distinguish *Nilotanypus* from *Labrundinia*. The mandible bears two inner teeth.

In North America, *Nilotanypus* is reported from Florida and Arizona, north to the subarctic Northwest Territories, but no previous record is available for British Columbia (Oliver, 1981a; Oliver and Roussel, 1983a; Roback, 1971). The larvae inhabit flowing water (Oliver and Roussel, 1983a). In this study, remains of *Nilotanypus*, were only found in the Holocene sediments of Marion Lake.

other Pentaneurini (Fig. A.2a–c)

The narrow head capsule (cephalic index 0.40 – 0.67: Fittkau and Roback, 1983), long slender basal antennal segment, and absence of dorsomental teeth are important characteristics distinguishing the tribe Pentaneurini from other Tanypodinae. No attempt has been made at further subdivision of this difficult group (apart from distinguishing *Labrundinia* and *Nilotanypus* as described above). Although first instar head capsules with 4 ligular teeth were noted, all other fossil ligulas included 5 teeth. These teeth formed a straight or weakly-concave distal ligula margin. Canadian genera sharing these characteristics include *Ablabesmyia* Johannsen, *Arctopelopia* Fittkau, *Conchapelopia* Fittkau, *Guttipelopia* Fittkau, *Larsia* Fittkau, *Monopelopia* Fittkau, *Natarsia* Fittkau, *Paramerina* Fittkau, *Pentaneura* Philippi, *Thienemannimyia* Fittkau, *Trissopelopia* Kieffer, and *Zavrelimyia* Fittkau (Fittkau and Roback, 1983; Oliver, 1981a; Oliver and Roussel, 1983a).

The Pentaneurini are widely distributed throughout the world, but Oliver and Roussel (1983a) only regard *Arctopelopia* as an arctic genus. Low arctic records also exist for *Ablabesmyia*, *Conchapelopia*, and *Pentaneura* (Danks, 1981). The Pentaneurini are common in both lotic and lentic waters (Fittkau and Reiss, 1978). Hamilton (1965) reports *Ablabesmyia monilis* (Linnaeus), *Larsia acrocincta* (Goetghebuer), *Thienemannimyia*, *Zavrelimyia*, and several undetermined Pentaneurini at Marion Lake.

Tribe Macropelopiini

Procladius Skuse (Fig. A.2d–g)

The broad head capsule of *Procladius* fossils, and presence of dorsomental teeth distinguish this genus from the Pentaneurini. Apart from first instar head capsules, the ligula always has 5 dark teeth. This feature is rare in the tribe Coelotanypodini (Oliver and Roussel, 1983a). The dorsomental plate and dorsomental teeth are distinct and strongly sclerotized. The first antennal segment is relatively short and broad. Members of the tribe Tanypodini have a ligula with convex to straight distal ligula margins, whereas those of the Macropelopiini are concave. The mandibles of Tanypodini have broad bases (Oliver and Roussel, 1983a). No other Canadian Macropelopiini have a ligula with 5 dark teeth (Oliver and Roussel, 1983a).

The genus *Procladius* is widespread, even occurring in shallow high arctic lakes and ponds (Danks and Oliver, 1972a, b). Hamilton (1965) reports four species at Marion Lake, *P. denticulatus* Sublette, *P. freemani* Sublette, *P.* sp.A, and *P.* (*Psilotanypus*) *bellus* (Loew). Roback (1971) indicates that *P. nietus* Roback, *P. culiciformis* (Linnaeus), and *P. ruris* var. *grandis* Roback also occur in British Columbia.

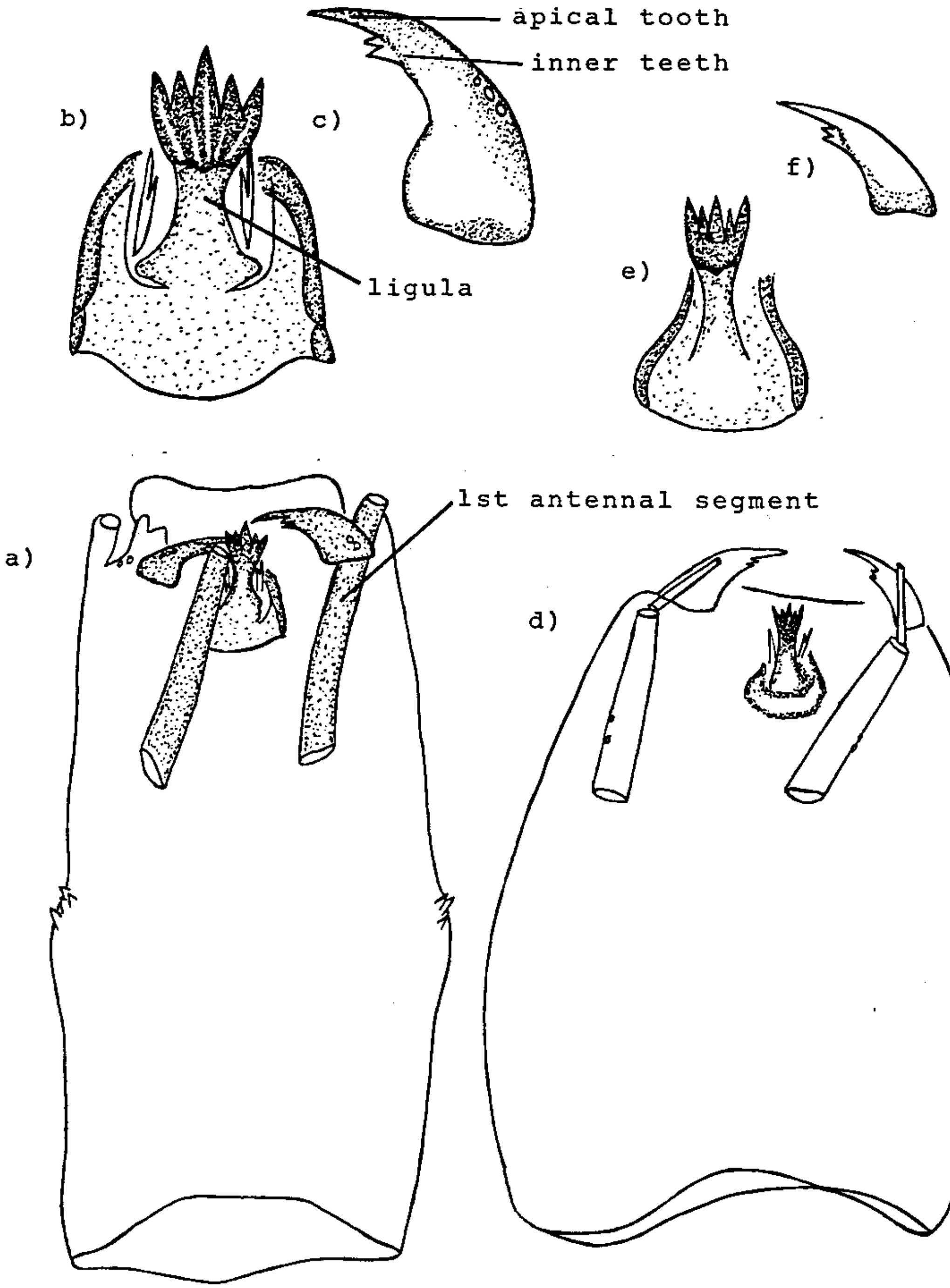

Figure A.1 Tanypodinae: Pentaneurini: *Labrundinia* Fittkau: a) head capsule (340X), b) premento–hypopharyngeal complex (730X), c) mandible (730X) – *Nilotanypus* Kieffer: d) head capsule (610X), e) premento–hypopharyngeal complex (1600X), f) mandible (1600X)

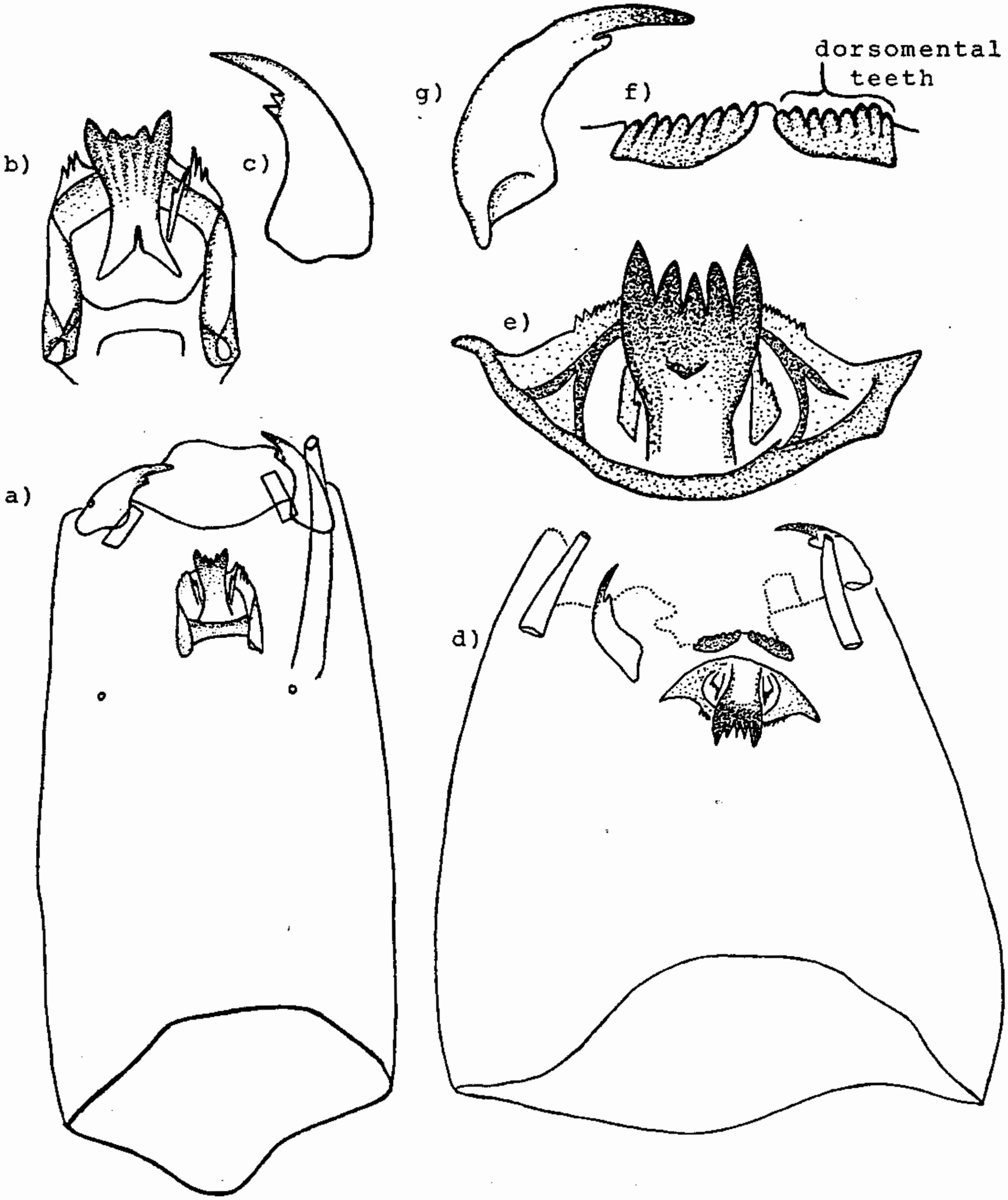

Figure A.2 Tanypodinae: Pentaneurini and Macropelopiini: other Pentaneurini: a) head capsule (310X), b) premento-hypopharyngeal complex (780X), c) mandible (780X) – *Procladius* Skuse: d) head capsule (100X), e) premento-hypopharyngeal complex (280X), f) dorsomentum (280X), g) mandible (280X)

Subfamily Chironominae

Tribe Tanytarsini

Tanytarsus v.d.Wulp s.lat. (Fig. A.3a-g)

Fossils attributed to *Tanytarsus* s.lat. typically included 1 median mental tooth and 5 lateral teeth, although a considerable diversity of form was noted. The median tooth of many fossils was weakly-pigmented. The median tooth of some fossil specimens was notched laterally. The lateral teeth were all similar in size and pigmentation. The striated ventromental plates were bar-shaped, several times broader (laterally) than long. These plates nearly meet at the median axis. Prominent antennal pedestals were noted on most fossil head capsules. The pedestals often included small apical projections, similar to those of many *Micropsectra* Kieffer species. The mandibles normally included 1 dorsal tooth, one dark apical tooth, and 3 inner teeth. In the rare instances when a premandible was retained with the fossil, 3 or 4 distinct apical teeth were usually noted. Thus, most fossils probably belong to *Tanytarsus* s.str. or *Cladotanytarsus*. However, several other genera (e.g. *Micropsectra*, *Paratanytarsus* Thienemann & Bause, and *Rheotanytarsus* Thienemann & Bause) will be included. The presence of fossils (Fig. A.3c&f) with a distinct group of 3 central teeth (the median tooth and 1st lateral pair), flanked by 4 additional pairs of lateral teeth is worthy of note. The mentum and mandible of these specimens resemble that of *Corynocera oliveri* Lindeberg, especially the worn mouthparts illustrated by Hofmann (1985).

The genera possibly included in *Tanytarsus* s.lat. are distributed in lotic and lentic habitats throughout the world, including high arctic regions (Danks, 1981; Pinder and Reiss, 1983). Hamilton (1965) notes the presence of 2 species of *Micropsectra* (as *Lundstroemia* Kieffer) and 4 species of *Tanytarsus* at Marion Lake. *C. oliveri* has not yet been discovered in North America (Pinder and Reiss, 1983), although Hofmann (1983b) reports this species as a subfossil in northwestern Greenland. *C. oliveri* group fossils were noted at "Aqua Incognito", Black Tusk, "Hippa", Mimulus and Russet Lakes. *Corynocera oliveri* group head capsules are possibly the most common chironomid remains in high elevation coastal lakes.

Corynocera nr. *ambigua* Zett. (Fig. A.4a–c)

Corynocera nr. *ambigua* fossils are conspicuous, by virtue of the narrow mentum, typically with 3 teeth visible in ventral view. Other lateral teeth may be present, but would be hidden behind the median tooth and 1st lateral teeth. The broad, bar–shaped ventromental plates nearly meet at the median axis. The teeth of the mandibles were usually indistinct, but this partially results from abrasion of mouthparts. The antennal pedestals are pronounced, including a small, blunt apical projection.

I have examined collections of *Corynocera ambigua* group fossils from the forest–tundra region near Yellowknife, Northwest Territories. Since these differ from the British Columbia material, at least two species may be represented in North America. The British Columbia collections differ by having a darker, more variable mentum. The apical projection of the antennal pedestals could not be distinguished on head capsules from the Yellowknife area. Livingstone (1953) noted that collections from Alaska more closely resembled *C. duffi* (Deevey) than *C. ambigua*. Downes (1962) claims the existence of an undescribed species in southern Alberta.

Corynocera ambigua is widely–distributed in shallow lentic habitats at northern latitudes, and is known from northern Asia, Europe, and northwestern North America, including the low arctic (Danks, 1981; Fittkau and Reiss, 1978). The only record of the *C. ambigua* group from eastern North America, is as a fossil in near surface lake sediments from Cape Breton Island, Nova Scotia (D.A. Livingstone, pers. comm.). Although the genus is previously unknown in British Columbia, it has been recorded in

Alaska, the Northwest Territories, Alberta, and Wyoming (Coffman and Ferrington, 1984; Downes, 1962; Livingstone *et al.*, 1958; Moore, 1978). The genus has also been reported from New Zealand (Pinder and Reiss, 1983).

Stempellinella Brundin (Fig. A.4d–f)

The median tooth and 1st lateral teeth of *Stempellinella* are fused, and flanked by 5 additional pairs of lateral teeth, forming a weakly convex mentum. The broad, fan–shaped ventromental plates are widely separated, and distinctly striated. Mandibles include 1 lightly–pigmented dorsal tooth, a dark apical tooth, and 3 inner teeth. When retained, the premandibles included 3 distinct apical teeth. A long, smooth, and undivided apical projection is a conspicuous feature of the antennal pedestals. The closely–related genus *Zavrelia* is very similar, although the premandible differs slightly in shape, and includes 4 apical teeth (Pinder and Reiss, 1983).

Stempellinella is probably widely–distributed in North American lotic and lentic waters (Bass, 1986; Oliver and Roussel, 1983a; Pinder and Reiss, 1983), but is rare in the arctic. *Stempellinella minor* (Edwards) is reported from Toolik Lake in arctic Alaska (Hershey, 1985a). Hamilton (1965) has described larvae similar to my fossils at Marion Lake. Although he refers to these as *Zavrelia* sp.A, he notes that they belong with *Stempellinella* according to Brundin's (1948) classification. Sæther (1970) also records collections from Okanagan Lake, as *Zavrelia* "Stempellinella" group.

Tanytarsini sp.A (Fig. A.4g–i)

The 1st lateral teeth of Tanytarsini sp.A are closely appressed or fused to the median tooth and accompanied by 5 additional lateral pairs. The mentum is usually weakly convex, although a distinctly concave mentum was apparent with several specimens. Distinct striae are apparent across the widely–separated, fan–shaped ventromental plates.

The teeth of the mandible are dark, including 1 small dorsal tooth, an apical tooth, and two inner teeth. A prominent, distinctly ridged apical projection extends from the antennal pedestals.

The generic placement of these fossils is uncertain. They could belong with *Constempellina* Brundin, *Stempellinella*, *Thienemanniola* Kieffer, or *Zavrelia* Kieffer. The specimens including a concave mentum are suggestive of *Thienemanniola*. Hofmann's (1971b) illustrations of *Thienemanniola* also indicate a similarly ridged apical projection extending from the antennal pedestal. *Thienemanniola*, however, is known only from north-central Europe (Fittkau and Reiss, 1978; Pinder and Reiss, 1986). I have collections of Tanytarsini sp.A remains from Deer Lake, and Holocene sediments of Mike and Misty Lakes.

Tribe Pseudochironomini

Pseudochironomus Malloch (Fig. A.4j-k)

The dark mentum of *Pseudochironomus* includes one median tooth and 6 pairs of lateral teeth. The 2nd lateral teeth are distinctly smaller than adjacent pairs. The broad ventromental plates are bar-shaped, nearly meeting at the median axis, but are not so broad as those of *Tanytarsus* s.lat. remains. The antennal pedestal is short and inconspicuous. Mandibles include an apical tooth, and 3 inner teeth. I have found the reduced 2nd lateral teeth useful for distinguishing fossil head capsules of *Pseudochironomus* from *Tanytarsus* s.lat. remains, although this feature is not shared by all *Pseudochironomus* (Sæther, 1977). The absence of a prominent antennal pedestal is an additional aid to identification.

In this study, remains of *Pseudochironomus*, were found in the surface sediments of Hicks and Lost Lakes, and the Holocene sediments of Marion Lake. The larvae are widely distributed in lotic and lentic habitats throughout North America (Sublette and Sublette, 1965; Pinder and Reiss, 1983), but have not been recorded from arctic sites (Danks, 1981). *Pseudochironomus* larvae have previously been reported from Okanagan Valley lakes (Sæther, 1970; Sæther and McLean, 1972).

Tribe Chironomini

Sergentia Kieffer (Fig. A.5a–b)

In *Sergentia* fossils, the median teeth and 1st lateral teeth are largest and project beyond the remaining 6 pairs of lateral teeth. The median and 1st lateral teeth also separate a pair of broad, fan–shaped ventromental plates. Striations are easily discernible only near the anterior margin of the ventromentum. These striations are coarse and sparsely distributed. Adjacent striation pairs are separated by approximately their apparent length. The mandibles have 1 dorsal tooth, 1 apical tooth, and 4 inner teeth. Pinder and Reiss (1983) note that the presence of four inner mandibular teeth distinguishes *Sergentia* from several similar genera (e.g. *Phaenopsectra* Kieffer, *Tribelos*). Since mandibles were infrequently retained with fossils, the ventromental striation pattern was considered diagnostic. This appears to be reliable for my material, but may not be useful elsewhere.

Sergentia species are reported from profundal and sublittoral zones in lakes, and are considered to be cold–stenothermal (Pinder and Reiss, 1983). The genus is reported principally from northern regions, including the arctic, in both Europe and North America (Danks, 1981; Fittkau and Reiss, 1978; Sublette and Sublette, 1965). Bass (1986) notes its presence in Texas. Hamilton (1965) has reared larvae of *Sergentia* sp.A from Marion Lake.

Stictochironomus Kieffer (Fig. A.5c–d)

The mentum of *Stictochironomus* fossils is similar to that of *Sergentia* in general form, with the median pair of teeth, and 1st lateral teeth projecting distinctly beyond the remaining 6 lateral pairs. The teeth are usually more rounded than for *Sergentia*, although this character may partially result from abrasion in mineral sediments. The median pair of teeth may be indistinctly separated, or completely fused. Ventromental striations, when visible, were short, closely-spaced, and only discernible near the anterior margin of the ventromental plates. Associated mandibles had 1 long dorsal tooth, 1 apical tooth, and 2 or 3 inner teeth. Although the mentum of several genera (ie. *Phaenopsectra*, *Sergentia*, *Tribelos*) may resemble *Stictochironomus*, these genera usually have a shorter dorsal mandibular tooth, and either 3 or 4 inner teeth (Pinder and Reiss, 1983). Since mandibles were infrequently retained with the head capsules, the striation pattern of ventromental plates was normally used for separation from similar-looking genera. This character may not be useful elsewhere. My material may represent a single species.

Stictochironomus species occur in lakes and streams throughout North America and Europe, including the high arctic (Danks, 1981; Fittkau and Reiss, 1978; Pinder and Reiss, 1983; Sublette and Sublette, 1965). In my British Columbia surface collections, it was almost always associated with *Heterotrissocladius*, *Paracladius*, *Parakiefferiella* sp.A, and *Protanypus* in cold, high-elevation waters. Sæther (1970) reports *Stictochironomus* cf. *rosenscholdi* (Zetterstedt) with *Heterotrissocladius oliveri* Sæther (as *H.* near *subpilosus* (Kieffer) in the profundal zone of Skaha Lake, Okanagan Valley, B.C.

Tribelos Townes (Fig. A.5e–f)

In *Tribelos* fossils, like *Sergentia* and *Stictochironomus*, the median pair of teeth, and 1st lateral teeth project slightly beyond other teeth of the mentum. Of the remaining pairs of lateral teeth, the 3rd laterals are largest, distinctly longer than the 2nd lateral pair in most specimens. The ventromental plates bear distinct, closely-spaced striae. Two distinct bands of striations are apparent, one across the median region, and another at the anterior ventromental margin. The mandible includes one dorsal tooth, 1 apical tooth, and 3 inner teeth. *Tribelos* was most reliably separated from *Sergentia* and *Stictochironomus* on the basis of the ventromental striation pattern.

Tribelos is widely distributed in the littoral of lakes from subarctic to subtropical latitudes (Pinder and Reiss, 1983). Although I cannot distinguish *Tribelos* from *Phaenopsectra* s.str., Hamilton (1965) reports *Tribelos protextus* (Townes) at Marion Lake.

Lauterborniella Thienemann & Bause/*Zavreliella* Kieffer (Fig. A.6a)

The lightly-pigmented mentum of *Lauterborniella/Zavreliella* bears 7 pairs of teeth. The median pair, and 2nd lateral teeth are long, projecting distinctly beyond the minute 1st laterals. The broad, fan-shaped ventromental plates are striated. The plates differ from those of most Chironomini by having a nearly straight anterior margin, and by nearly meeting along the median axis. Although the above characters readily distinguish *Lauterborniella* and *Zavreliella* from other genera, I have not distinguished between these two genera. My material is closest to *Lauterborniella* as illustrated, and described by Pinder and Reiss (1983).

In this study, remains of *Lauterborniella/Zavreliella*, were found in Stump Lake, Hicks Lake and Holocene sediments from Mike and Misty Lakes. *Lauterborniella* and *Zavreliella* appear to be widely distributed in North America, south of tree-line (Pinder and Reiss, 1983; Sublette and Sublette, 1965). These genera are normally associated with shallow water vegetation, in both lotic and lentic habitats (Pinder and Reiss, 1983). Although *Lauterborniella* has been reported from Char Lake, N.W.T. (Andrews and Rigler, 1985; Davies, 1975; Rigler, 1978; Welch, 1973), these reports clearly result from confusion of this genus with *Lauterbornia* Kieffer. *Lauterbornia sedna* Oliver (1976) was originally described from Char Lake collections.

Microtendipes Kieffer (Fig. A.6b)

The median mental region of *Microtendipes* is weakly-pigmented, with two long teeth, separated in some specimens by a smaller 3rd tooth at the median axis. The six remaining pairs of lateral teeth are dark. The 2nd lateral teeth are as long, or longer than the median pair, but the 1st lateral teeth are short, and closely-appressed to the 2nd pair. The ventromental plates are distinctly and coarsely striated, and are separated by the median teeth and 1st and 2nd lateral pairs. The arrangement of teeth is similar to *Lauterborniella*, *Polypedilum*, and *Zavreliella*, but the median teeth are more lightly pigmented than the lateral teeth in *Microtendipes*.

Microtendipes larvae are widely-distributed in shallow lotic and lentic habitats south of tree-line. In the Canadian arctic *Microtendipes* has been collected only from the southernmost tundra (Moore, 1978). Hamilton (1965) records *Microtendipes pedellus* (de Geer) from Marion Lake.

Pagastiella cf. *ostansa* Webb (Fig. A.6c)

The mentum of *Pagastiella* cf. *ostansa* includes 8 pairs of small, weakly-pigmented teeth. The median pair and the 2nd lateral teeth are of a similar size and length, but the 1st laterals are minute. Ventromental plates are distinctly striated, and strongly arched, with rounded posterior-lateral margins. The small, light-coloured teeth, and strongly-arched ventromental plates readily distinguish this genus. Only *Pagastiella ostansa* is known from the Nearctic.

Pagastiella Brundin has been collected at Marion Lake (Hamilton, 1965), and is widely-distributed in Canada, south of treeline (Oliver and Roussel, 1983a). The genus is also recorded from Michigan, and Washington states (Oliver, 1981a; Wiederholm, 1976). Bass (1986) reports "*Pagastiella ? ostansa*" from eastern Texas. The larvae inhabit shallow lentic waters (Oliver and Roussel, 1983a; Pinder and Reiss, 1983)

Polypedilum Kieffer (Fig. A.6d)

As in *Lauterborniella*, *Microtendipes*, *Pagastiella*, and *Zavreliella*, the median and 2nd lateral teeth are long in *Polypedilum* fossils. The 1st lateral teeth are distinctly shorter. In total the mentum includes 8 pairs of moderately to strongly-pigmented teeth. The broad, fan-shaped ventromental plates are widely separated. Although the mentum of most early instar head capsules is weakly-pigmented in some specimens, resembling *Lauterborniella*, the shape of the ventromental plates facilitates identification. *Polypedilum* normally has a greater number of mental teeth than either *Lauterborniella* or *Microtendipes*. Although the genus *Polypedilum* is very heterogeneous (Pinder and Reiss, 1983), all of the fossil material conforms to the "normal" type described above. In several known species, the mental teeth are all of approximately equal size (Pinder and Reiss, 1983).

Polypedilum species are very widely-distributed in both lotic and lentic waters, except in arctic and alpine regions (Pinder and Reiss, 1983). The genus has been collected in the southernmost Canadian arctic (Moore, 1978). Hershey (1985a) reports one *Polypedilum* larva at Toolik Lake in arctic Alaska. Three species, *P. nubeculosum* (Meigen), *P. tritum* (Walker), and *P. simulans* Townes are reported from Marion Lake (Hamilton, 1965).

Cyphomella Sæther/*Harnischia* Harnisch/*Paracladopelma* Harnisch (Fig. A.7a-b)

Cyphomella, *Harnischia*, and *Paracladopelma* have similar arrangements of mental teeth and ventromental plates. Although my fossils seem closest to *Paracladopelma* as described by Pinder and Reiss (1983), the correct generic placement is uncertain. The mentum is weakly-arched, including 8 pairs of similarly-pigmented teeth. The median and 1st lateral pairs of mental teeth project slightly beyond the remaining pairs. The fan-shaped ventromental plates are very widely separated, about as wide as the mentum, and taper to an acute lateral margin. These plates are coarsely striated and weakly crenate along the anterior ventromental margin. The premandible includes four teeth. The 2 apical teeth are longer than the 2 inner premandibular teeth. Hamilton (1965) has described a similar larva, which he tentatively associated with *Parachironomus potamogeti* (Townes) (as *Harnischia potamogeti* Townes). This association is probably incorrect. Hamilton (1965) also collected *Paracladopelma galaptera* (Townes) (as *Harnischia galaptera* Townes) adults from Marion Lake.

Harnischia and *Paracladopelma* appear to be widely-distributed in lotic and lentic habitats south of treeline (Oliver and Roussel, 1983a). *Paracladopelma* is considered somewhat cold-stenothermic (Pinder and Reiss, 1983). *Cyphomella* occurs in large rivers of central North America (Oliver and Roussel, 1983a; Sæther, 1977). In this study, remains of *Cyphomella/Harnischia/Paracladopelma*, were found in the late-glacial sediments of Marion Lake, Holocene sediments of Mike Lake, and surface sediment from Deer and Mystery Lakes.

Omisus Townes (Fig. A.7c)

The mentum of *Omisus* fossils includes 8 pairs of dark teeth and a concave median region. The median pair of teeth are short. The 1st lateral teeth are long, projecting distinctly beyond the median pair. Ventromental plates are broad, striated and fan-shaped, separated by the 8 teeth closest to the median axis. The concave median region, formed by 3 pairs of teeth, produces a distinctive mentum. The light-coloured median teeth of the closely-related genus *Paratendipes* provide a reliable distinction.

Omisus fossils were only collected from Misty Lake sediments. This genus has not previously been recorded from British Columbia, but occurs throughout much of eastern North America (Oliver, 1981a; Oliver and Roussel, 1983a). The immature stages are commonly associated with humic waters (Pinder and Reiss, 1983). One species, *O. pica* Townes has been described from North America (Oliver, 1981a).

Paratendipes Kieffer (Fig. A.7d)

The lightly-pigmented median and 1st lateral mental teeth of *Paratendipes*, contrast with the 6 remaining pairs. In the fossils, the median pair of teeth and 1st lateral teeth are of a similar size, but the 2nd laterals are slightly shorter. The 3rd lateral teeth are as long, or longer than the median pair. Broad ventromental plates are separated by the 6 teeth closest to the median axis. *Paratendipes* fossils were infrequently collected, but easily recognized by the lightly-pigmented median and 1st lateral mental teeth.

This genus is widely distributed in lotic and lentic waters south of treeline (Danks, 1981; Oliver, 1981a; Oliver and Roussel, 1983a; Sublette and Sublette, 1965). *Paratendipes* remains were found in "Hermit Thrush Pond", Lost Lake, and Holocene sediments from Marion and Mike Lakes.

Chironomus Meigen (Fig. A.8a-b)

The darkly-pigmented mentum of *Chironomus* has a trifid median tooth and 6 lateral pairs. The median tooth, however, is sometimes very strongly worn in fossils from mineral sediments. The 1st laterals project about as far forward as the median tooth. Broad, fan-shaped ventromental plates are separated by most of the mentum's width. In my material, striations were indistinct, and only discernible as a band on the posterior ventromental region. The mandible includes a prominent dorsal tooth, 1 apical tooth, and 3 inner teeth. A series of radially arranged grooves was noted at the base of several mandibles. These grooves occur only in *Baeotendipes* Kieffer, *Chironomus*, *Einfeldia* Kieffer, and *Fleuria* Kieffer (Pinder and Reiss, 1983). *Fleuria* is reported only from Europe. *Baeotendipes* and some *Einfeldia* larvae are inseparable from *Chironomus*, and may be better placed within this genus (Pinder and Reiss, 1983).

Chironomus larvae are widely-distributed, mostly in standing waters throughout the world, including the high arctic (Danks, 1981; Pinder and Reiss, 1983). Although eutrophic lakes are characterized by the great abundance of certain *Chironomus* species, a few species inhabit oligotrophic waters (Sæther, 1979). Hamilton (1965) reported *C. rempelii* Thienemann and *C. decorus* Johannsen at Marion Lake. *C. vancouveri* Michailova & Fischer (1986) was recently described from collections at Deer Lake, in "Vancouver" (presumably Burnaby). At least 7 other species have been reported in British Columbia (Cannings, 1975a, b; Sublette and Sublette, 1965).

Dicrotendipes Kieffer (Fig. A.8c)

The median mental tooth of *Dicrotendipes* head capsules may be weakly notched laterally, but is never trifid. The 1st lateral teeth are about as long as the median tooth and are closely appressed to the 2nd lateral pair. All mental teeth are darkly-pigmented. The distinctly striated ventromental plates are not much broader (laterally) than long, and have a finely crenate anterior margin in my specimens. The weakly-notched median tooth, closely appressed 1st and 2nd lateral teeth, and narrow ventromental plates provide easily recognizable features, although several genera (e.g. *Einfeldia*, *Glyptotendipes*) share a rather similar mentum.

Dicrotendipes larvae are widely-distributed, mostly in shallow lentic waters, but are rare in arctic regions (Danks, 1981; Pinder and Reiss, 1983). *Dicrotendipes lobiger* (Kieffer) is reported from Barrow, Alaska (Butler *et al.*, 1981). In Canada, *D. modestus* (Say) is reported from the southernmost arctic tundra (Moore, 1978). This species also inhabits Marion Lake (Hamilton, 1965). *D. modestus* and *D. nervosus* Staeger are reported from the Okanagan Valley (Kangasniemi and Oliver, 1983; Sæther, 1970).

Glyptotendipes Kieffer (Fig. A.8d)

The mentum of *Glyptotendipes* fossils is similar to *Dicrotendipes* in form, but the teeth are distinctly shorter, and blunt. The ventromental plates of my specimens were very broad, tapering to acute median and lateral points. These plates are usually finely-crenate along the anterior margin and distinctly striated. Although easily distinguished from most other Canadian genera, *Einfeldia* may include very similar-looking species (Oliver and Roussel, 1983a).

In this study, *Glyptotendipes* was only collected from the surficial sediments of Alice Lake. The genus is widely-distributed in lotic and lentic waters, but has not been reported from the North American arctic (Danks, 1981; Oliver and Roussel, 1983a; Pinder and Reiss, 1983). The larvae are often associated with aquatic plants (Oliver and Roussel, 1983a). *G. barbipes* (Staeger) and *G. lobiferus* (Say) are reported from British Columbia (Sublette and Sublette, 1965).

Cladopelma Kieffer (Fig. A.9a)

The greatly enlarged teeth at the extreme lateral margins produce a distinctive mentum. This feature is also reported for *Cryptotendipes*, *Microchironomus* Kieffer, and some *Paracladopelma* larvae (Pinder and Reiss, 1983). The mentum is mostly darkly-pigmented, although the median tooth or teeth are often lighter in colour. The median tooth appears to be narrower than in *Cryptotendipes* larvae, and in some specimens includes a median notch. The median tooth of *Microchironomus* is distinctly trifid (Pinder and Reiss, 1983). Striations were discernible only near the posterior margin of the ventromental plates.

Larvae of *Cladopelma* are widely-distributed in North American lotic and lentic waters (Oliver, 1981a; Pinder and Reiss, 1983), but are not reported from arctic regions (Danks, 1981). Very similar larvae were collected by Hamilton (1965), and associated with adults of *Cladopelma amachaera* (Townes) (as *Harnischia amachaerus* Townes).

Cryptotendipes Lenz (Fig. A.9b)

Cryptotendipes fossils were characterized by a broad, dome-shaped median tooth, which is notched laterally to form 2 closely appressed accessory teeth. The remaining mental teeth are darker. The 2 outermost pairs of lateral teeth were closely appressed, and somewhat enlarged relative to the lateral teeth. The median tooth is distinctly broader than that of *Cladopelma*. The mentum is also more strongly-arched, having smaller extreme lateral teeth. Striae were only discernible near the posterior region of the broad ventromental plates.

Cryptotendipes fossils were collected at low-elevations in the clay-rich sediments of Deer and Lost Lakes only. The genus is probably widely-distributed in North American lotic and lentic habitats (Bass, 1986; Oliver, 1981a), but is not reported from arctic regions (Danks, 1981).

Parachironomus Lenz (Fig. A.9c-d)

Remains of *Parachironomus* have 15 or 16 weakly-pigmented mental teeth. The median tooth was largest, but most of the lateral teeth are of a similar size. The broad, fan-shaped ventromental plates were indistinctly striated, but were scalloped along the anterior margin. This scalloped ventromental margin is, to my knowledge, unique to *Parachironomus* although it is not shared by all species of the genus (Pinder and Reiss, 1983). The mandibles, which included an apical tooth, and 2 truncated inner teeth were also weakly-pigmented.

Parachironomus is widely distributed in lotic and lentic waters (Oliver, 1981a; Pinder and Reiss, 1983) but is rare in arctic habitats. The genus is reported from Toolik Lake, on the north slope of arctic Alaska (Hershey, 1985a). Several *Parachironomus* species were associated with *Myriophyllum spicatum* L. in Okanagan Valley lakes, including *P. tenuicaudata* (Malloch) (Kangasniemi and Oliver, 1983). Adults of *Parachironomus potamogeti* have been reported from Marion Lake (Hamilton, 1965: as *Harnischia potamogeti*). Hamilton (1965) also describes a larva resembling *Parachironomus* as *Harnischia galaptera*. In both instances the associations between adults and larvae were only tentative, and were probably incorrect. In this study, remains of *Parachironomus*, were found in Lost Lake, and scattered throughout late-Pleistocene and Holocene sediments of Misty Lake.

Cryptochironomus Kieffer (Fig. A.10a-b)

The distinctive concave mentum of *Cryptochironomus* fossils includes one broad, light-coloured median tooth, and 6 dark lateral pairs. The 1st lateral teeth are small, closely-appressed to the median tooth. The 5th and 6th lateral teeth are partially fused. The ventromental plates are striated and very broad, tapering to sharp median and lateral points. The mandibles include 1 long apical tooth and two darker inner teeth. The mandible and mentum of *Cryptochironomus* are very similar to *Demicryptochironomus* Lenz and may be inseparable on the basis of mandible and mentum. However, Pinder and Reiss (1983) indicate 7 lateral mental teeth to be normal for *Demicryptochironomus*.

Hamilton (1965) has collected 2 *Cryptochironomus* species at Marion Lake. The genus is known to be very widely-distributed in lotic and lentic waters, including low arctic regions (Danks, 1981; Oliver, 1981a; Pinder and Reiss, 1983). In this study, remains of *Cryptochironomus*, were found in Lost Lake, Stump Lake, and scattered throughout each of the 4 cores studied.

Stenochironomus Kieffer (Fig. A.10c)

The concave mentum of late-instar *Stenochironomus* fossils includes an even number of dark teeth, but seven distinct teeth were the norm for small remains, presumably derived from early instar larvae. Unlike other Chironomini, the ventromental plates are vestigial structures, indicated by a few indistinct striations adjacent to the mentum. Several small indistinct spines were noted on the adjacent maxillary lobe. *Stenochironomus* differs greatly in structure from all other Chironomini.

The larvae are obligate miners of vegetation, and are widely distributed in lotic and lentic waters (Oliver, 1981a; Pinder and Reiss, 1983). Borkent (1984) notes the occurrence of three species in British Columbia, *S. colei* (Malloch), *S. fuscipatellus* Borkent and *S. hilaris* (Walker). *S. fuscipatellus* is recorded as a miner in wood of *Acer macrophyllum* Pursh and *Alnus rubra* Bong. Borkent (1984) notes that *Stenochironomus* species generally occur only in angiosperm wood of trees and shrubs. In my collections, *Stenochironomus* was only recorded from Alice Lake.

Nilothauma Kieffer (Fig. A.10d–e)

The pale median mental tooth of *Nilothauma* remains is flanked by 6 pairs of lateral teeth, and is broader any lateral tooth, composing about 1/5 of the mental width. The lateral teeth are weakly-pigmented and are of a consistent size throughout. Broad, fan-shaped ventromental plates include a band of fine striae. The weakly-pigmented sickle-shaped mandible includes one apical tooth and 4 small inner teeth. Although I have been unable to discern 4 parts for the median tooth, as described by Pinder and Reiss (1983), the fossils closely resemble a *Nilothauma* species photographed by Oliver and Roussel (1983a), and *Nilothauma babiyi* (Rempel) as illustrated by both Mason (1983) and Simpson and Bode (1980).

Larvae of *Nilothauma* are widely distributed in lotic and lentic waters of North America (Bass, 1986; Mason, 1983; Oliver, 1981a; Sublette and Sublette, 1965). The genus is not known from arctic habitats (Danks, 1981; Fittkau and Reiss, 1978). *Nilothauma* remains were recovered from Lost Lake, Stump Lake, and scattered throughout late–glacial and Holocene sediments from Marion, Mike, and Misty Lakes.

Paralauterborniella Lenz (Fig. A.10f–g)

The broad, pale–coloured median tooth, which composes about 1/3 of the mental width is flanked by 6 pairs of smaller, more darkly pigmented lateral teeth. The mentum is flanked by two very large, broad, and distinctly striated ventromental plates. Mandibles include an apical tooth, and 3 inner teeth. Although the mentum of *Paralauterborniella* resembles *Nilothauma*, the median tooth is much broader. Mandibles of this genus include 3 rather than 4 inner mandibular teeth (Pinder and Reiss, 1983), and are not strongly–arched.

Paralauterborniella is widely–distributed, usually in shallow lentic waters, throughout North America south of treeline (Danks, 1981; Oliver, 1981a; Pinder and Reiss, 1983; Sublette and Sublette, 1965). In my collections, this genus was rare, collected from clay–rich sediments of Deer and Lost Lakes only. *P. nigrohalterale* (Malloch) is reported from 2 Okanagan Valley lakes (Sæther and McLean, 1972).

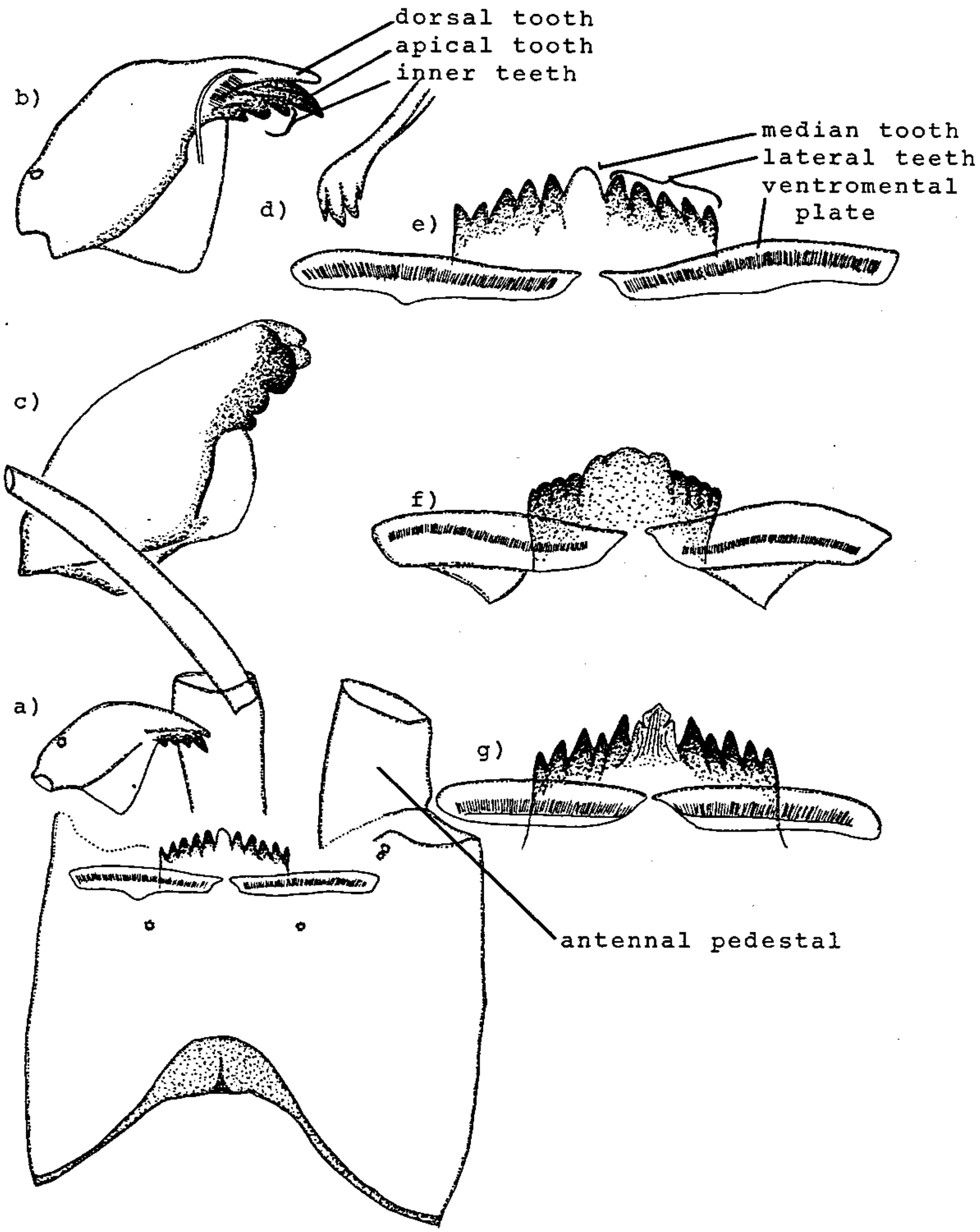

Figure A.3 Chironominae: Tanytarsini: *Tanytarsus* v.d.Wulp s.lat.: a) head capsule (210X), b) mandible (360X), c) mandible (610X), d) premandible (340X), e) mentum (410X), f) mentum (760X), g) mentum (450X)

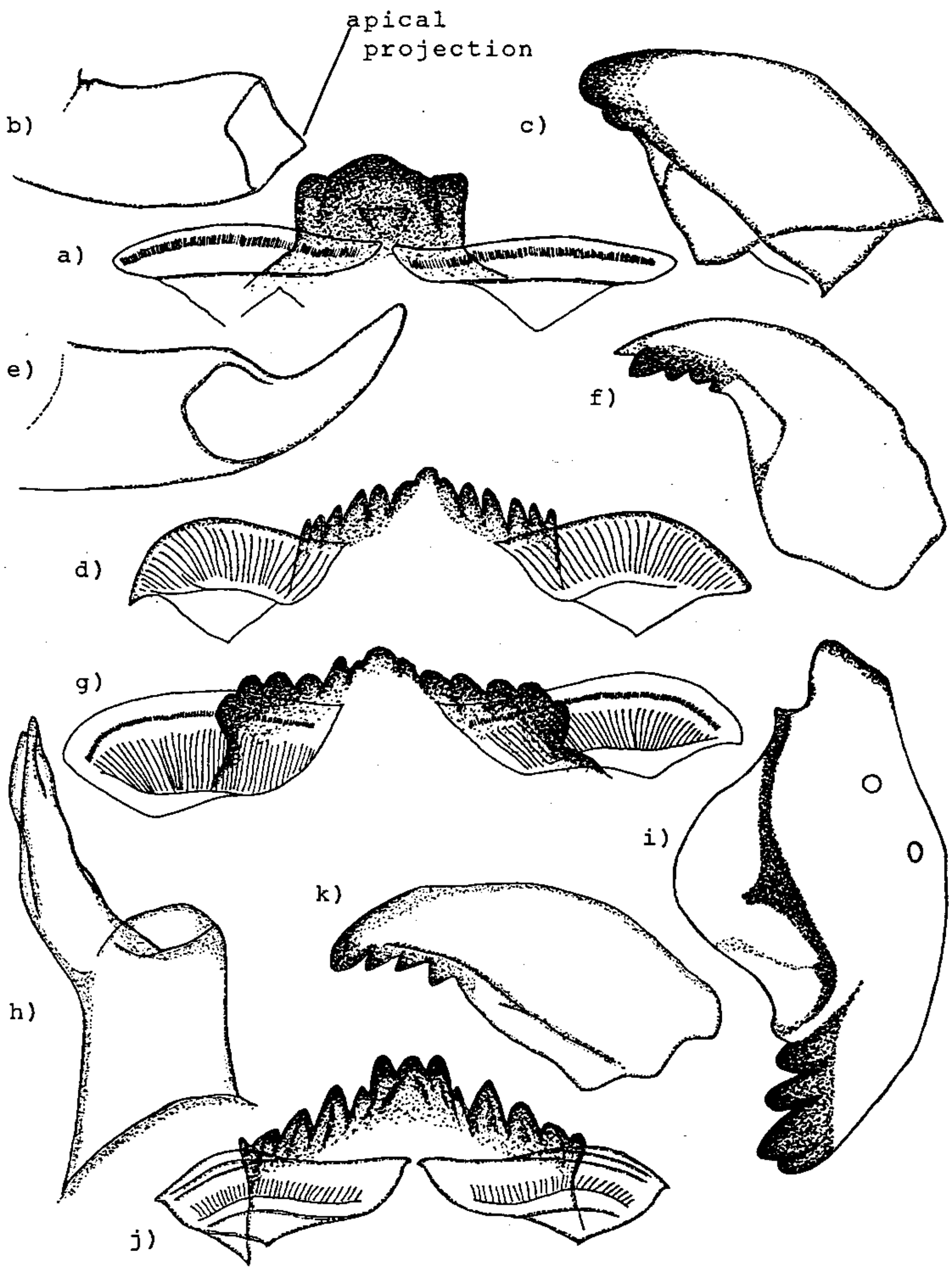

Figure A.4 *Corynocera* nr. *ambigua* Zetterstedt (420X): a) mentum, b) antennal pedestal, c) mandible – *Stempellinella* Brundin (610X): d) mentum, e) antennal pedestal, f) mandible – Tanytarsini sp.A (590X): g) mentum, h) antennal pedestal, i) mandible – Pseudochironomini: *Pseudochironomus* Malloch (560X): j) mentum, k) mandible

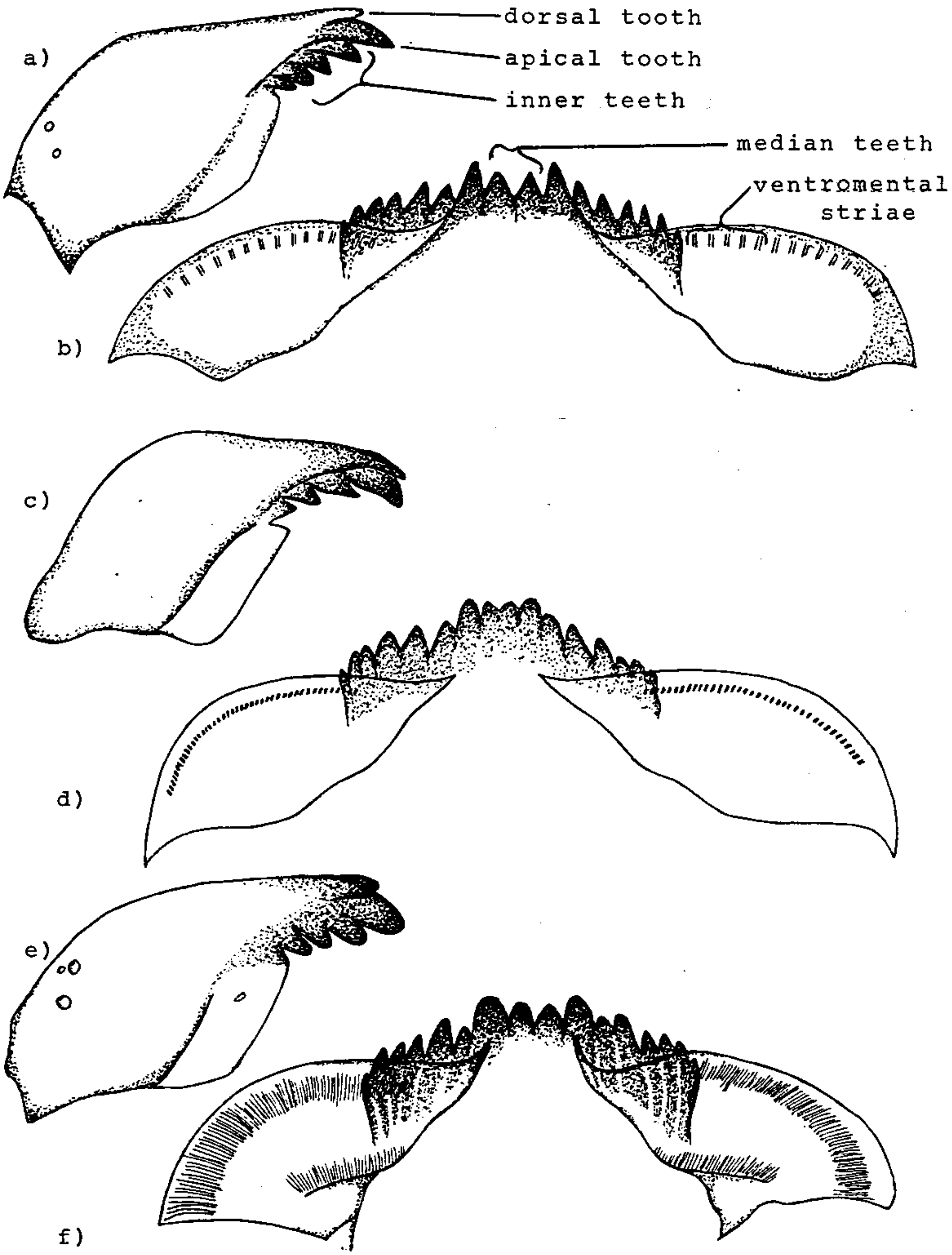

Figure A.5 Chironominae: Chironomini: *Sergentia* Kieffer (520X): a) mandible, b) mentum – *Stictochironomus* Kieffer (350X): c) mandible, d) mentum – *Tribelos* Townes (320X): e) mandible, f) mentum

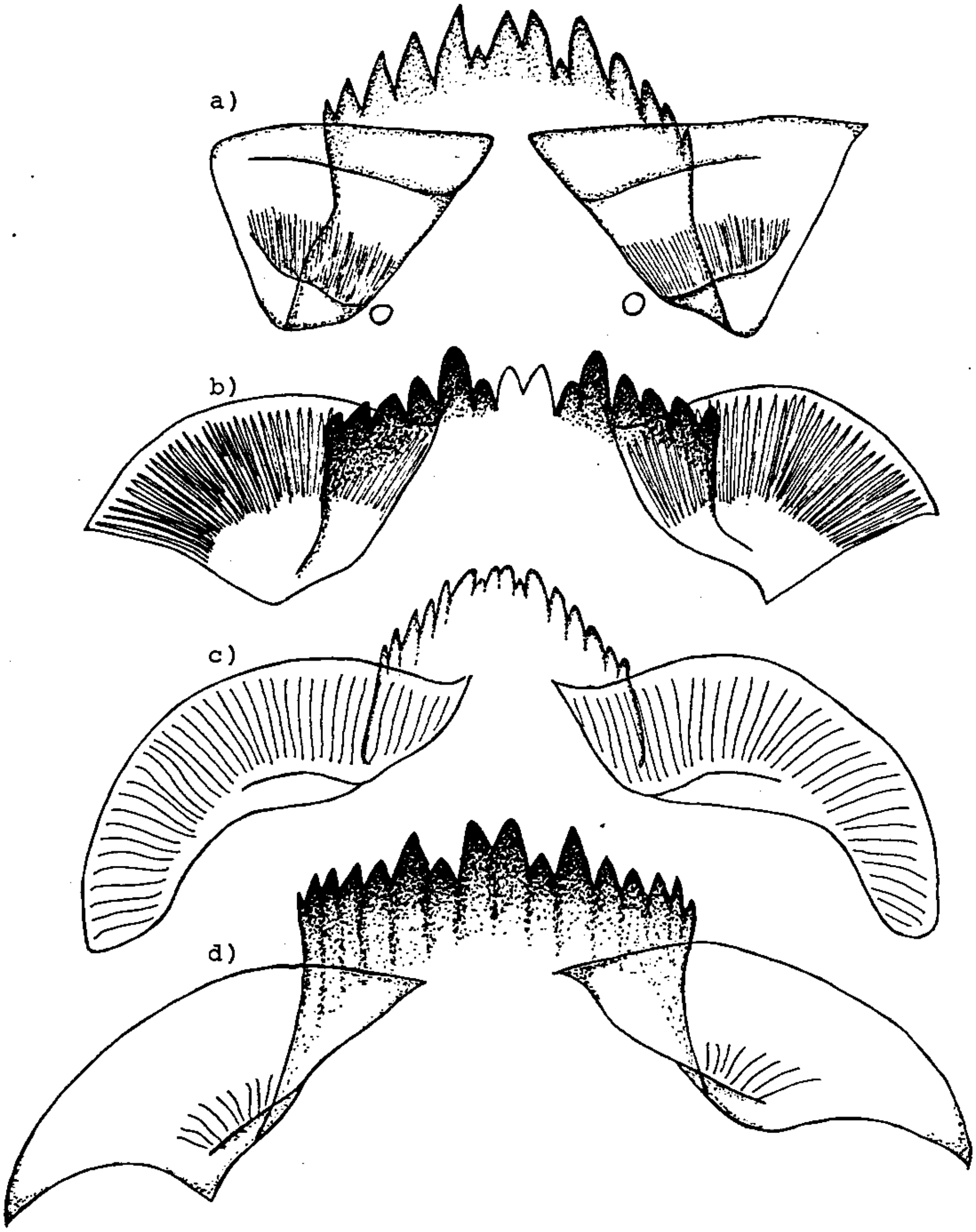

Figure A.6 a) *Lauterborniella* Thienemann & Bause/*Zavreliella* Kieffer mentum (850X), b) *Microtendipes* Kieffer mentum (630X), c) *Pagastiella* cf. *ostansa* Webb mentum (760X), d) *Polypedilum* Kieffer mentum (970X)

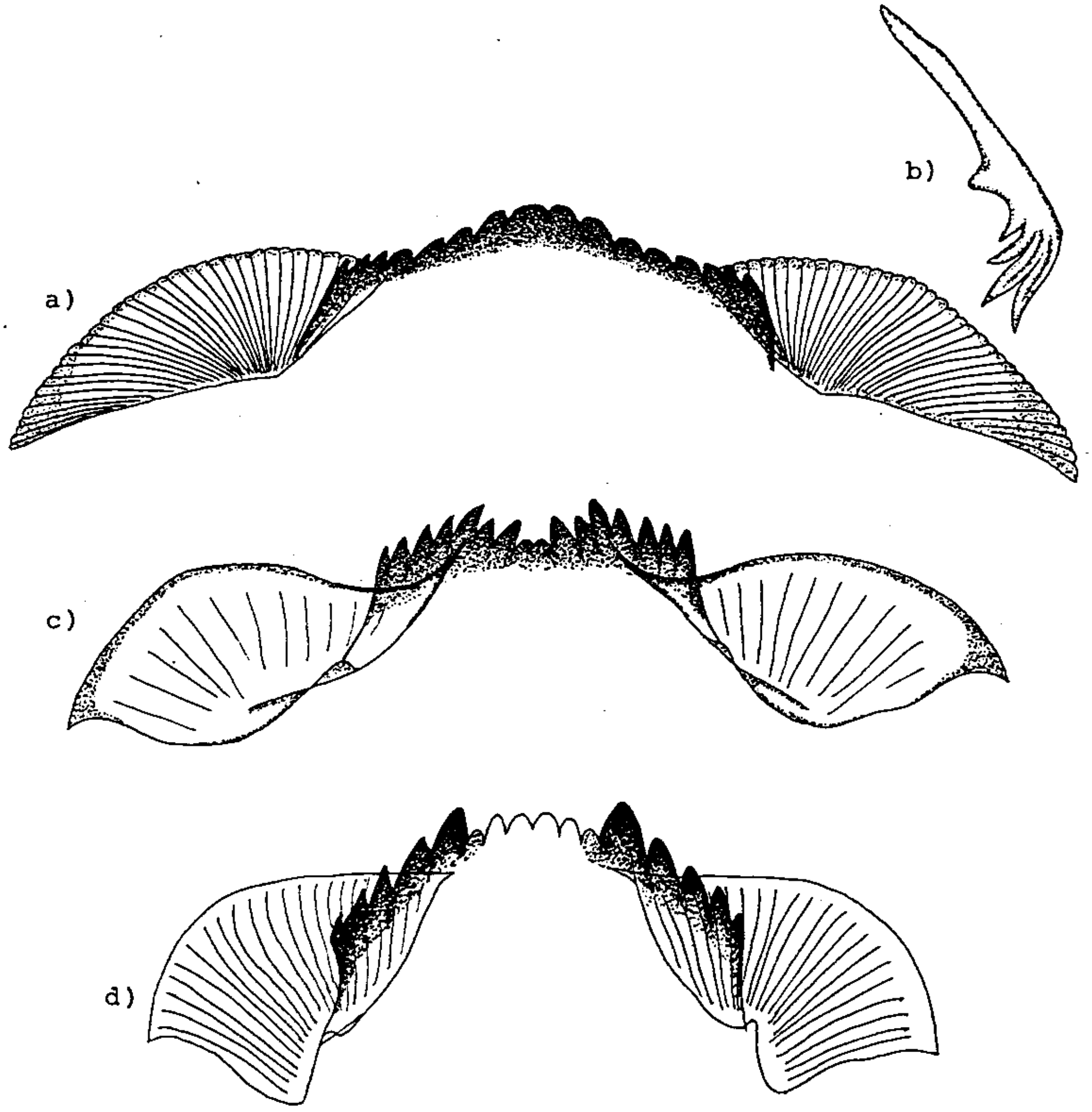

Figure A.7 *Cyphomella* Sæther/*Harnischia* Kieffer/*Paracladopelma* Harnisch (700X): a) mentum, b) premandible – *Omisus* Townes (920X): c) mentum – *Paratendipes* Kieffer (1100X): d) mentum

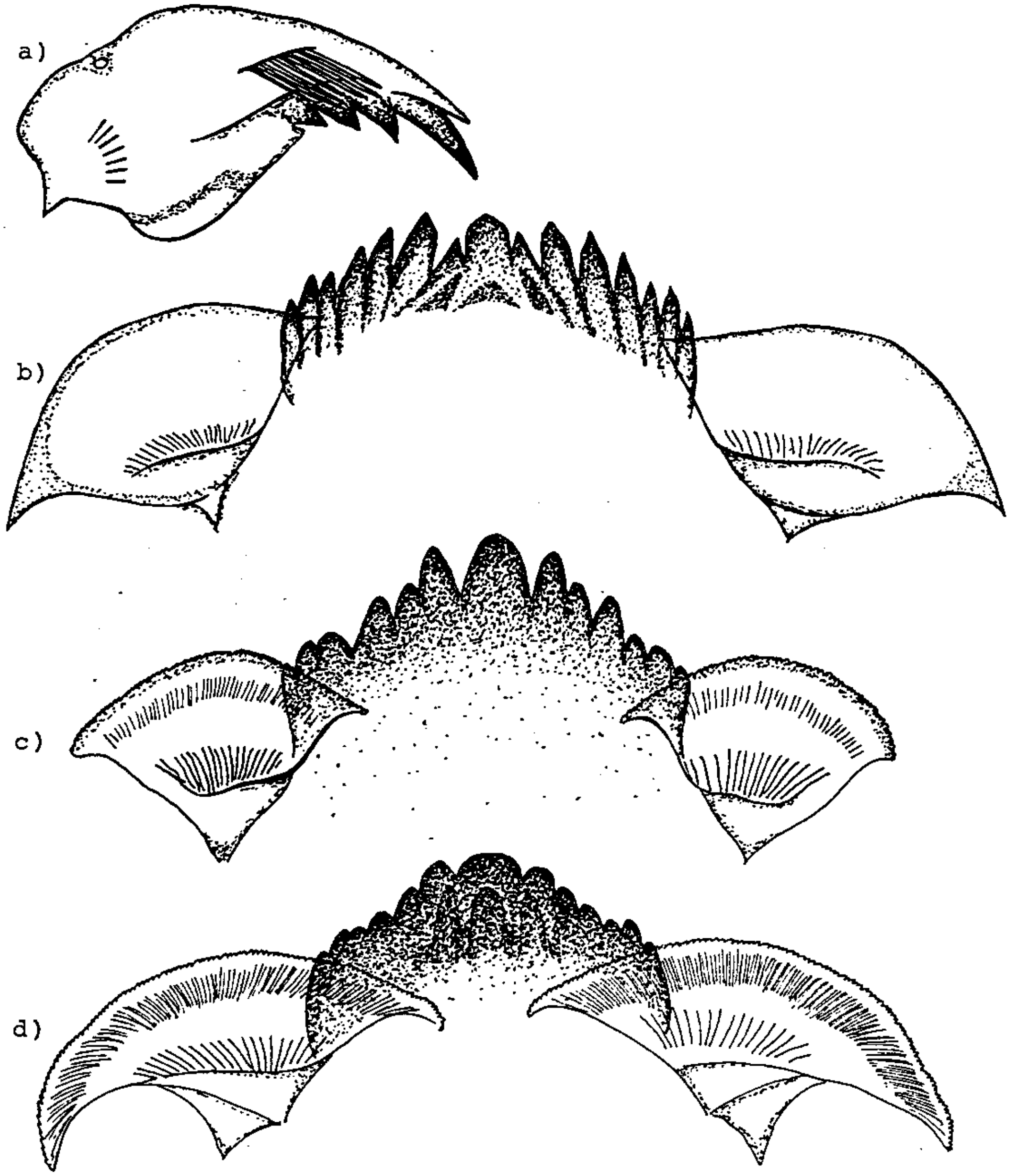

Figure A.8 *Chironomus* Meigen (520X): a) mandible, b) mentum – *Dicrotendipes* Kieffer (400X): c) mentum – *Glyptotendipes* Kieffer (230X): d) mentum

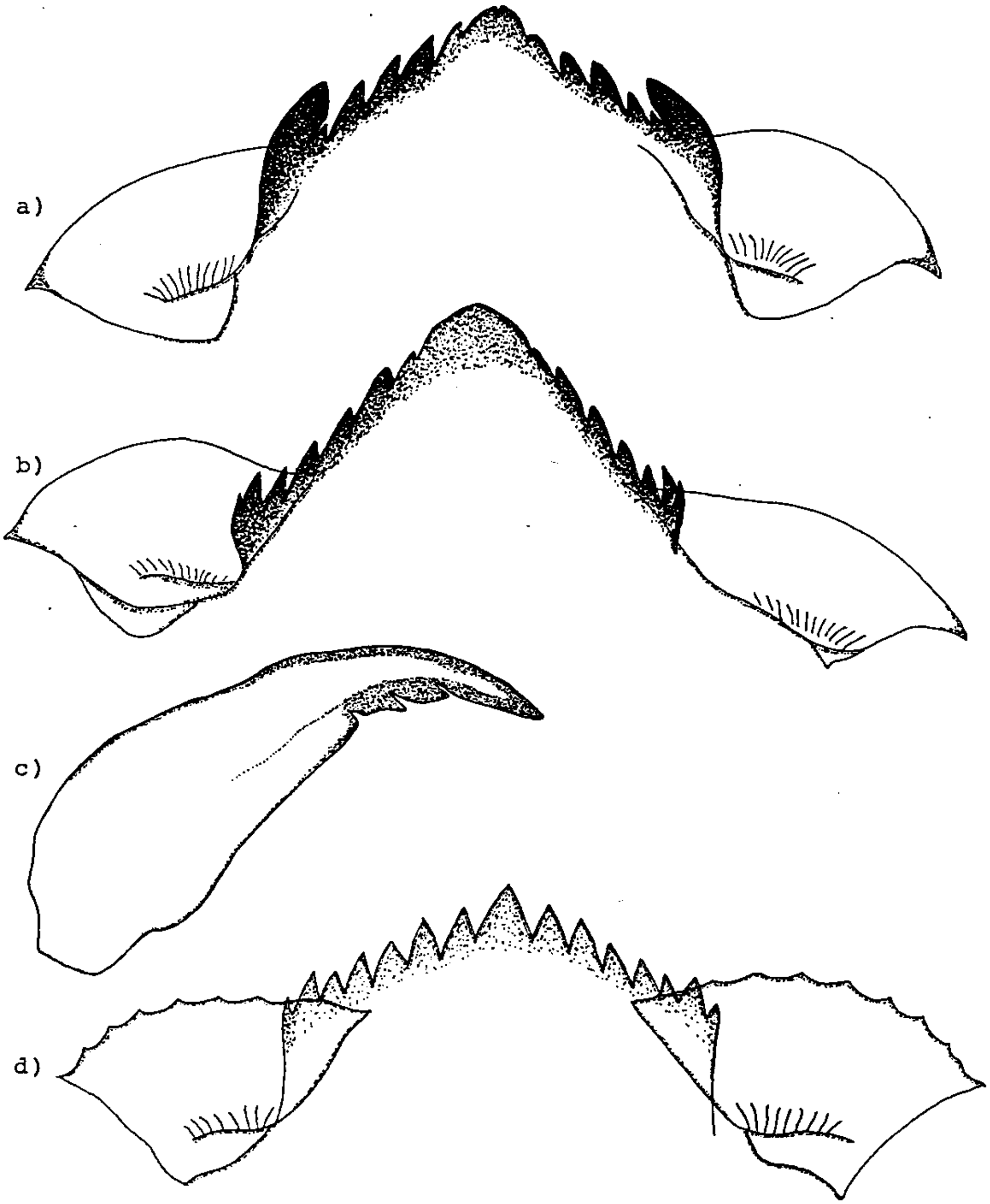

Figure A.9 *Cladopelma* Kieffer (940X): a) mentum - *Cryptotendipes* Lenz (950X): b) mentum - *Parachironomus* Lenz (940X): c) mandible, d) mentum

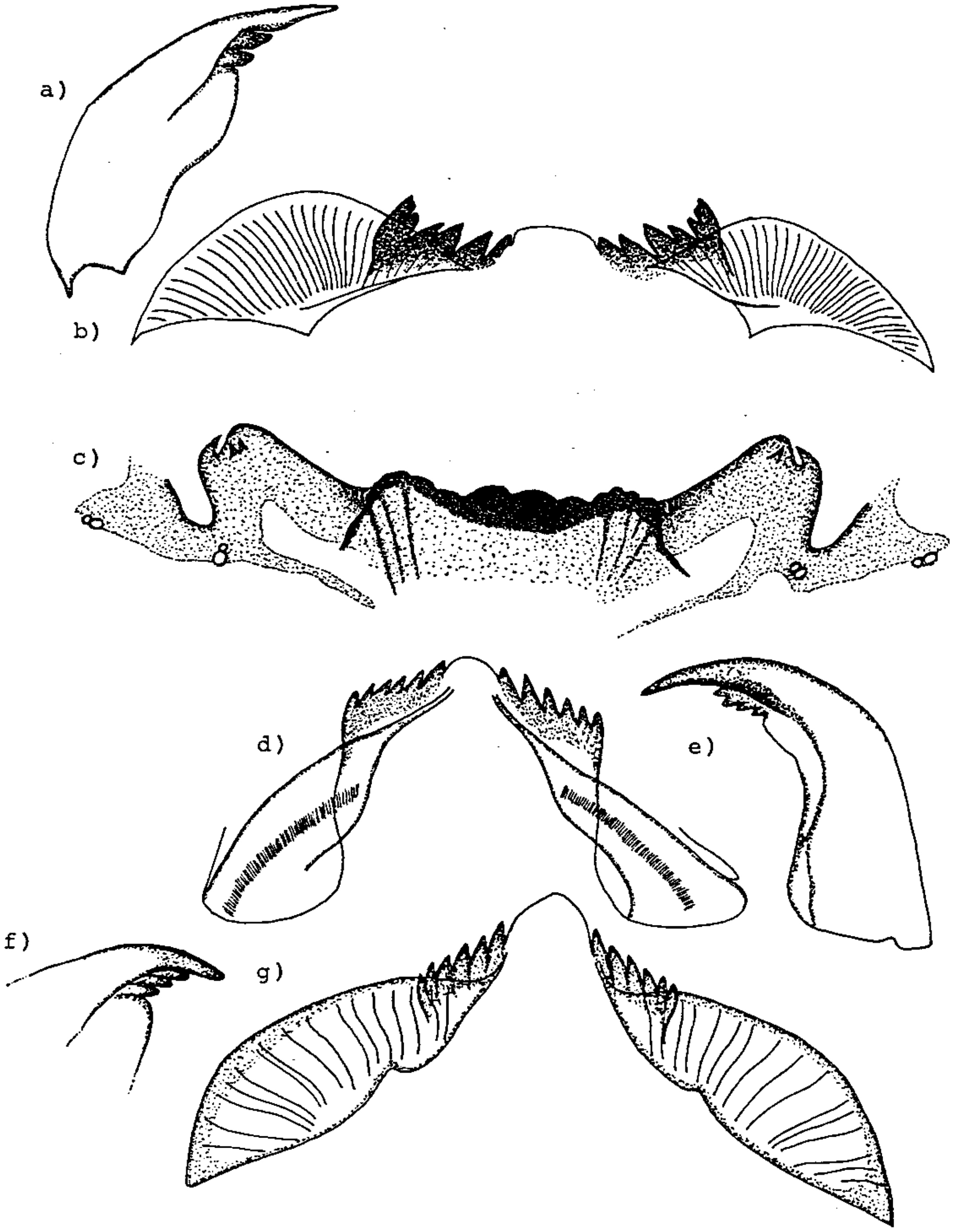

Figure A.10 *Cryptochironomus* Kieffer (870X): a) mandible, b) mentum – *Stenochironomus* Kieffer (370X): c) mentum – *Nilothauma* Kieffer (640X): d) mentum, e) mandible – *Paralauterborniella* Lenz (510X): f) mandible, g) mentum

Subfamily Podonominae

Boreochlus Edwards (Fig. A.11a-b)

A single Podonominae fossil type was discovered, with 15 mental teeth of similar size. The submental setae are separated by a distance about equal to the mental width. The mandible is more distinctive with 8 teeth, including 1 dorsal tooth, 1 large apical tooth, and 6 inner teeth. The second inner tooth is distinctly shorter than the adjacent mandibular teeth.

Although the mentum is similar to that of some Orthocladiinae, the mandible is distinctive among chironomids, apart from Podonominae. The number and arrangement of teeth on the mentum and mandible, as described above, satisfy the generic diagnoses of both *Boreochlus* and *Paraboreochlus* Thienemann (Brundin, 1983). These genera cannot be separated on the basis of labrum, mandible, or mentum (Brundin, 1983).

Boreochlus is reported from much of southern Canada, including British Columbia (Oliver and Roussel, 1983a). Three species (*B. gracilistylus* Brundin, *B. persimilis* (Johannsen), *B. sinuaticornis* Brundin) are reported from adjacent regions of Washington State (Mount Baker area, Olympic Peninsula) (Wirth and Sublette, 1970). One undescribed Nearctic *Paraboreochlus* species is known from the Appalachians (Beck, 1980; Brundin, 1983; Coffman and Ferrington, 1984). Larvae of both genera occur in cool springs and streams among mosses (Brundin, 1983; Oliver and Roussel, 1983a). *Boreochlus* remains were recovered from Black Tusk Lake, and Holocene sediments from Mike and Misty Lakes.

Subfamily Diamesinae

Diamesa Meigen? (Fig. A.11c)

Fossils similar to *Diamesa* were rare in this study, and separated from some Orthocladiinae with difficulty. The mentum is broad, bearing numerous pairs of similar-sized teeth (9 pairs in the example illustrated). Ventromental plates are poorly-developed. The submental setae are near the mentum. Some Orthocladiinae genera (e.g. *Orthocladius*) may include species with characteristics similar to the fossils.

Diamesa are common in cool to cold flowing water and springs, occurring even in the high arctic (Danks, 1981; Oliver, 1983). Four species are known from British Columbia, with 3 additional *Diamesa* species being known from the Mount Baker area of Washington State, U.S.A. (Hansen and Cook, 1976). Remains of *Diamesa*? fossils were found only in "Coleman Pond" and Goldie Lake.

Protanypus Kieffer (Fig. A.11d)

Although the broad, relatively light-coloured median portion of the mentum may be subdivided into several units, creating broad tooth-like divisions, sharp strongly-sclerotized teeth (2 pairs) are confined to the extreme lateral margins of the mentum. Numerous setae are distributed across the head capsule. These characteristics readily distinguish *Protanypus* from all other chironomids.

The larvae occur in cold waters of oligotrophic lakes. The genus is reported from much of Canada, including deep, arctic waters (Oliver, 1964, 1981a; Sæther, 1975c), but only from Washington State, and the Great Lakes region of the United States (Oliver, 1981a; Sæther, 1975c; Wiederholm, 1976; Winnell and White, 1985). A similar northern and high elevation distribution is evident in Europe (Fittkau and Reiss, 1978). The genus is represented by ***Protanypus*** sp.A at Marion Lake today, but ***P. hamiltoni*** Sæther is reported elsewhere in British Columbia (Sæther, 1975c).

Pagastia Oliver (Fig. A.12a–b)

In ***Pagastia*** fossils, a broad light–coloured median tooth separates about 5 pairs of dark lateral teeth. The structure of the mentum is similar to a few Orthocladiinae, and some other Diamesinae. However, the broad ventromental plates overlap the lateral teeth, and the submental setae are distant from the mentum, placed close to the posterior margin of the head capsule. Although no median "ridge–like projections" (Oliver, 1983) were discernible on fossil mental plates, these may have been lost through abrasion.

Pagastia larvae are rheophilous, known from much of northern and western North America, south of treeline (Oliver and Roussel, 1982). I have collected larvae from an upper subalpine stream in the Mount Baker area of Washington State, U.S.A. Oliver and Roussel (1982) report three species in western North America. ***Pagastia*** was noted in sediments from Hayes, Helm, and Mimulus Lakes, during my studies.

Potthastia Kieffer? (Fig. A.12c–d)

Several early instar fossils were similar to ***Potthastia gaedii.*** A broad light–coloured median tooth separates about 5 (perhaps more) pairs of lateral mental teeth in the fossil material. The ventromental plates are well–developed, extending beyond the lateral dorsomental teeth, as also described for ***Pagastia.*** The submental setae are situated close to the mentum.

The above characteristics differ somewhat from the ***Potthastia gaedii*** (Meigen) group as described by Oliver (1983). Some Orthocladiinae genera (e.g. ***Parakiefferiella*** Thienemann) may include species with similar structure, but the broad ventromental plates of the fossils are more similar to those of some Diamesinae.

Potthastia has been reported throughout much of northern Canada, south of treeline (Oliver, 1981a; Oliver and Roussel, 1983a). The *Potthastia longimana* Kieffer group occurs in Lake Okanagan (Sæther, 1970). The larvae of *Potthastia gaedii* are rheophilous (Oliver, 1983). *Potthastia*? was only collected from "Coleman Pond".

Pseudodiamesa Goetghebuer (Fig. A.12e–f)

The median tooth and 1st lateral teeth of *Pseudodiamesa* are subequal, and separate the broad ventromental plates. The ventromental plates wholly or partially conceal the remaining mental teeth. All components of the mentum and ventromental plates are dark (black in the final larval instars). The anterior origin of ventromental plates is apparent at the outer margin of the three median teeth. The 2nd lateral teeth are somewhat appressed to the 1st lateral teeth. The 6th lateral teeth are distinctly longer than adjacent pairs. Submental setae are situated close to the mentum. Mandibles have one prominent apical tooth and four inner teeth. The combined characteristics of the mentum, outlined above, appear to be unique to *Pseudodiamesa*.

The larvae occur in both cold lotic and lentic environments, and are mostly restricted to arctic and alpine habitats (Danks, 1981; Downes, 1964; Oliver, 1983; Oliver and Roussel, 1983a), although Beck (1980) reports one species from Tennessee. *Pseudodiamesa branickii* (Nowicki) and *P. pertinax* (Garrett) are reported from British Columbia (Sublette and Sublette, 1965). In this study, remains of *Pseudodiamesa*, were found in surface sediments from "Coleman Pond", Helm Lake, and Mimulus Lake, and Marion Lake's late–Pleistocene sediments.

Subfamily Orthocladiinae

Brillia Kieffer/*Euryhapsis* Oliver (Fig. A.13a–b)

The submental setae of *Brillia* and *Euryhapsis* larvae are set far back from the mentum, midway between the mentum and the posterior margin of the head capsule. *Pagastia* (Diamesinae) is similar in this regard. Among Orthocladiinae this feature is reported only for *Brillia*, *Euryhapsis*, *Lopescladius* Oliveira, and *Paralimnophyes* Brundin (Cranston *et al.*, 1983). In some species of *Brillia* and *Euryhapsis* the median teeth are separated by a minute third tooth, as illustrated. (Cranston *et al.*, 1983). The outermost 2 pairs of lateral teeth are closely appressed. The ventromental plates are weakly-developed. Although a minute ventromental beard distinguishes the known larvae of *Euryhapsis* (Cranston *et al.*, 1983), this character may be unreliable if the setae are not consistently preserved.

Brillia larvae are often associated with vegetation in both lotic and lentic habitats. *Euryhapsis* is reported from lotic environments (Cranston *et al.*, 1983). Both genera occur north of North American treeline (D.R. Oliver, pers. comm.). *Brillia* is otherwise widely-distributed in North America, but *Euryhapsis* is reported only from the west (Oliver, 1981b). *Brillia retifinis* Sæther is reported from Marion Lake (Oliver and Roussel, 1983b).

Corynoneura Winnertz/*Thienemanniella* Kieffer (Fig. A.13c–d)

The small teeth and steeply sloping margins of the mentum in *Corynoneura* and *Thienemanniella* are distinctive features for fossil identification. The mentum may include 12 or 13 teeth. In the fossil material, the median tooth and the 1st lateral teeth projected distinctly beyond the remaining mental teeth. The mentum was light-coloured with weak sclerotization bands. Ventromental plates are poorly developed. The submental setae are situated near the mentum. Antennal characteristics which allow separation of *Corynoneura* and *Thienemanniella* (Cranston *et al.*, 1983) were seldom available in fossils. Two fossils with intact antennae were distinguished as *Thienemanniella*.

Although *Corynoneura* occurs in both lotic and lentic habitats, *Thienemanniella* is reported only from lotic environments (Cranston *et al.*, 1983). Both genera are widely-distributed throughout the world, and are reported from the Canadian high arctic (Cranston *et al.*, 1983; Danks, 1981).

Smittia Holmgren/*Pseudosmittia* Goetghebuer? group (Fig. A.14a-b)

Fossil head capsules resembling *Smittia* or *Pseudosmittia* were found infrequently and were not readily separable from several other Orthocladiinae genera. Although a considerable diversity of head capsule structure was noted, only one example has been illustrated. The mentum of head capsules assigned to this group had a single, rather broad median tooth, separating 4 or 5 lateral pairs. A medium to dark-brown pigmentation characterized the mental teeth. The ventromental plates varied considerably in size, often being poorly developed. Although mandibles were seldom retained with the fossils, those mandibles examined were similar to those of most Orthocladiinae genera, having 1 apical tooth and 3 distinct inner teeth. The submental setae are set close to the mentum. Fossils of this type may belong to several Orthocladiinae genera, including *Camptocladius* v.d.Wulp, *Cardiocladius* Kieffer, *Chaetocladius* Kieffer, and *Georthocladius* Strenzke, as well as *Pseudosmittia* and *Smittia*.

Those taxa listed are frequently recorded from terrestrial, semi-terrestrial, and lotic environments. Since many of these fossils must have been carried into lakes via streams, or eroded from adjacent soils, mouthparts other than the mentum were seldom retained within the head capsules. The composite distribution of these genera spans most of the world, including the high arctic (Cranston *et al.*, 1983; Danks, 1981).

Cricotopus v.d.Wulp/*Orthocladius* v.d.Wulp/*Paratrichocladius* Santos Abreu (Fig. A.14c,d)

Cricotopus and *Orthocladius* are large genera with diverse mental characteristics. Only one example is illustrated. These genera and *Paratrichocladius* cannot be reliably distinguished as larval fossils. The remains, in this study, were distinguished as having a single median tooth separating 6 lateral pairs. The anterolateral margins of the mentum slope steeply backwards. Ventromental plates are poorly-developed. Submental setae are close to the mentum. In some instances separation of the above taxa from other genera (e.g. *Boreochlus*, *Diamesa*) could be difficult on characters of the mentum alone.

The 3 genera (*Cricotopus*, *Orthocladius*, *Paratrichocladius*) are very widely distributed, occurring in all types of freshwater, with a composite distribution including most of the world (Cranston *et al.*, 1983). Some *Orthocladius* occur in semi-terrestrial habitats (Cranston *et al.*, 1983). *Cricotopus tricinctus* Meigen and *Orthocladius carlatus* (Roback) have been reported from Marion Lake (Hamilton, 1965; Soponis, 1977). Many other species undoubtedly occur in the study areas.

Orthocladius (*Symposiocladius*) *lignicola* Kieffer (Fig. A.14e)

The mentum of *O. lignicola* consists of a broad, strongly-arched median region, separating two pairs of rounded, extreme lateral teeth. The mentum is dark brown to black, being very heavily sclerotized. Ventromental plates are weakly developed. Fossil head capsules of this distinctive species were rare, and invariably had split along the median axis of the mentum. Although this species had been placed in the monospecific genus *Symposiocladius* Cranston (1982a), the pupae and adults are not distinct from *Orthocladius* (Cranston and Oliver, *in press.*; D.R. Oliver, pers. comm.).

According to Cranston *et al.* (1983), the larvae burrow in hardwood submersed in flowing water. This species is widely distributed south of tree-line in both North America and Europe (Cranston, 1982a; Cranston *et al.*, 1983). In this study, remains of *O. lignicola* were found in Holocene sediments from Hippa Lake, and in late-glacial and Holocene sediments from Marion Lake.

Paracladius Hirvenoja (Fig. A.15a–c)

Head capsules of *Paracladius* were common in recent sediments of high elevation lakes. The mentum is weakly arched, with a broad dome-shaped median tooth separating 6 pairs of lateral teeth. The lateral teeth are darker than the median region. Well developed ventromental plates overlap the lateral teeth. The premandible, retained in some fossil head capsules, had a distinct apical notch. These characteristics correspond closely to the published diagnosis of *Paracladius* (Cranston *et al.*, 1983). *Paracladius* larvae had previously been reported from several of my Banff National Park study sites (Mayhood and Anderson, 1976).

Paracladius is known from lakes throughout arctic North America, from high elevation lakes of the Canadian Cordillera, and the profundal of deep temperate lakes in Canada (Danks, 1981; Hare, 1976; Mayhood and Anderson, 1976; Oliver, 1976; Sæther and McLean, 1972), but has only been reported from the Great Lakes and Cordilleran regions of the United States (Coffman and Ferrington, 1984; Oliver, 1981a; Winnell and White, 1985). Older reports are frequently cited as *Cricotopus* (*Paratrichocladius*) cf. *alpicola* (Zetterstedt). The larvae have also been reported from slowly flowing water (Oliver and Roussel, 1983a).

Stilocladius Rossaro (Fig. A.15d)

Fossil material of *Stilocladius* was distinguished by a strongly-arched mentum, and very broad ventromental plates. The broad, light-coloured median tooth may be flanked by 2 small accessory teeth in my material, but these teeth were difficult to resolve. Five subsequent pairs of teeth complete the mentum. The 1st pair is situated at the forward origin of the ventromental plates. The four remaining pairs of lateral teeth are more darkly pigmented. The great breadth of the ventromental plates is an especially distinctive feature. Although no ventromental beard was noted, these setae are rarely preserved.

Stilocladius has previously been recorded only from Carolina streams and Cape Breton Island in North America, and in Europe only from springs and high-elevation streams in the Italian Alps and Apennines (Coffman *et al.*, 1986; Oliver, pers. comm.; Sæther, 1982). The European species, *Stilocladius montanus* Rossaro is a cold stenotherm found in water of 4 to 10° C (Rossaro, 1984). Although confined to cold springs in summer, it occurs in larger streams during winter.

This is the first record for western North America. An undescribed species probably inhabits the western Cordillera. *Stilocladius* remains were collected at "Aqua Incognito", and in late-glacial/early Holocene sediments from Marion and Mike Lakes.

Parakiefferiella? cf. *triquetra* (Chernovskii) (Fig. A.16a-b)

The fossil mentum is strongly-arched with a very large, unpigmented median tooth. Six pairs of small, dark lateral teeth, and well-developed ventromental plates complete the mentum. The lateral teeth are all of similar size. The ventromental plates have a convex lateral margin, which may completely overlap some lateral teeth. The submental setae are separated by a distance approximately equal to the width of the median tooth. The mandible has one long, light-coloured apical tooth, and three inner teeth.

A very similar larva has been described by Pankratova (1970) as *Paratrichocladius triquetra* (Chenovskii), with 5, rather than 6, pairs of lateral teeth. This generic placement is incorrect. The head capsules also correspond to larvae from Marion Lake described by Hamilton (1965). He had tentatively associated the larva with adults of *Parakiefferiella* *nigra* Brundin. Although I have previously accepted this association (Walker and Mathewes, 1987a), a more conservative approach seems justified. The larvae have also been reported from Kalamalka Lake in the Okanagan Valley (Sæther and McLean, 1972: as "Parakiefferiella nigra"). Hare (1975) reports "?*Paratrichocladius* sp. *triquetra* type" from Lake Huron, noting that it may be a *Paracladius* species.

Parakiefferiella cf. *bathophila* (Kieffer) (Fig. A.16c)

The median tooth of the fossil head capsules has a single broad median tooth, flanked by a pair of inconspicuous accessory teeth. The median tooth and accessory teeth are lighter in colour than the remaining teeth of the mentum. The 5 remaining pairs of lateral teeth are all similar to each other in size. The transparent ventromental plates are moderately developed with a convex lateral margin, but seldom completely overlap any lateral teeth. Although some *Psectrocladius* may have a similar mentum, the convex lateral ventromental margins are not common in *Psectrocladius*. The shape of the mentum resembles that of *Parakiefferiella bathophila*, as illustrated by Cranston (1982b), although any median "double hump" was inconspicuous and usually absent. Although neither the mandible nor premandible have been illustrated, a simple premandible was noted with several fossils. Mandibles include a long apical tooth and 3 inner teeth.

I have previously reported this taxon as *Parakiefferiella* sp.B (Walker and Mathewes, 1987a). Although fossil head capsules do occur in surface sediments of Marion Lake, Hamilton (1965) has not reported similar larvae. Hamilton (1965) did collect adults of *Parakiefferiella coronata* (Edwards) and *P. nigra* at Marion Lake. These adults were tentatively associated by Hamilton (1965) with larvae of *Parakiefferiella*? cf. *triquetra* (this study) and *Nanocladius* sp. near *balticus* (Palmén) (Sæther, 1977). Cranston (1982b) described the median tooth of *P. coronata* as "broad and domed", although the larva he described was not reared. *Parakiefferiella* near *bathophila* is listed with Sæther's (1970) exuviae and imagines for Lake Okanagan. Nearctic *Parakiefferiella* species occur in some lotic but mostly lentic habitats in northern and western North America (Coffman and Ferrington, 1984; Oliver, 1981a; Oliver and Roussel, 1983a).

Parakiefferiella sp.A (Fig. A.16d–g)

A broad dark median tooth is flanked by 6 pairs of lateral mental teeth in this fossil. The most distinctive feature is the greatly reduced 2nd lateral pair. The 2nd lateral teeth are usually closely appressed to the 1st lateral teeth. The 3rd, 4th, and 5th lateral teeth are usually of similar size to the 1st lateral pair. The central mental teeth of many fossils from clay sediments were greatly worn. Little evidence of the 1st or 2nd lateral teeth is then apparent. The ventromental plates are moderately well–developed with a convex lateral margin. The mandible includes one rather short apical tooth, and 3 inner teeth. The premandible is distinctly bifid.

Larvae of this type were first described by Sæther (1970) from the profundal of Lake Okanagan as "genus near *Trissocladius*". Hare (1976) reports this larva in Parry Sound, Lake Huron. *Parakiefferiella* sp.A occurs in lower subalpine to alpine lakes of the Canadian Rocky Mountain national parks (D.B. Donald, pers. comm.; Hare, 1976; Mayhood and Anderson, 1976; this study). Collections are available from Manicouagan Reservoir, Québec, and the Alaskan north slope (D.R. Oliver, pers. comm.) and possibly Hazen Camp, Northwest Territories. Warwick (pers. comm.) believes that it may also correspond to his "genus near *Heterotrissocladius*" (Warwick, 1980a, b). A photograph of *Parakiefferiella* sp.A is provided by Oliver and Roussel (1983a: fig. 368).

Psectrocladius subg. (*Monopsectrocladius* Laville) (Fig. A.17a)

One broad median tooth separates 5 pairs of lateral teeth in this group. The median tooth is slightly more weakly pigmented than the remaining teeth. The lateral teeth are arranged in a consistent order of decreasing size. The well-developed ventromental plates have straight or weakly concave anterolateral margins, and may completely overlap one to several lateral teeth. Evidence of a ventromental beard is visible in some remains. The premandible is undivided.

These remains are similar to *P.* (*Monopsectrocladius*) sp. near *calcaratus* Edwards, as illustrated by Cranston *et al.* (1983). *P. calcaratus* is a lentic species reported from Canada, and much of northern Europe (Fittkau and Reiss, 1978; Sæther, 1969), including the low arctic (Oliver, 1964). I have collected similar larvae from bog lakes in New Brunswick and Nova Scotia (Walker *et al.*, 1985). Two larval types from Marion Lake, *Psectrocladius* sp.A and *P.* sp.B (Hamilton, 1965), are similar to my material. Hamilton (1965) has reared *Psectrocladius* sp.A.

other *Psectrocladius* Kieffer (Fig. A.17b–e)

Other fossil material placed with *Psectrocladius* usually had 2 distinct median teeth which were often lightly pigmented, and never had accessory teeth. Five subsequent pairs of dark lateral teeth were arranged in an order of consistently decreasing size. Anterolateral margins of the ventromental plates are usually nearly straight, or weakly concave. Similar plates occur in few other Orthocladiinae genera. The ventromental beard was rarely observed and probably is not consistently preserved. The mandible includes 1 apical tooth and 3 dark inner teeth. The premandible when present was simple. Although most fossils clearly belong to subgenus *Psectrocladius*, rare fossil remains belonging either to *P.* (*Allopsectrocladius* Wülker), or *P.* (*Mesopsectrocladius* Laville), were occasionally found, but not differentiated.

Larvae of these subgenera are common in lakes, but some also occur in temporary ponds, bog pools, and lotic waters (Fittkau and Reiss, 1978). The genus is widely distributed throughout most of the world, including shallow high arctic lakes and ponds

(Cranston *et al.* 1983, Danks, 1981). For Marion Lake, Hamilton (1965) illustrates larvae of *Psectrocladius* s.str., and one larva of either *Allopsectrocladius* or *Mesopsectrocladius*.

Heterotrissocladius Spärck (Fig. A.18a–b)

The broad median pair of teeth in *Heterotrissocladius* fossils are either simple, or flanked by small accessory teeth, similar to those illustrated for *Rheocricotopus* and *Zalutschia*. The 5 pairs of lateral teeth are arranged in a consistent order of decreasing size laterally. In some instances, fossils from clay sediments were strongly worn leaving little indication of the first 3 lateral pairs. Although such a mentum is superficially similar to *Orthocladius lignicola*, the ventromental plates are well-developed with a convex lateral margin. The teeth are always dark, and are black in some final instar head capsules. Although transparent in early instars, the ventromental plates may also be strongly-pigmented in more mature larvae. A light-coloured, weakly-sclerotized region is often evident along the median axis of the submentum (D.R. Oliver, pers. comm.). Head capsules frequently split into 2 equal halves along this zone of weakness.

Although *H. marcidus* (Walker) may occur in relatively warm waters, the larvae of all species are cold stenotherms (Sæther, 1975b). The genus is Holarctic, occurring in lotic and lentic environments, including deep, high-arctic lakes (Oliver, 1976; Sæther, 1975b). In the warmer regions of Europe and North America, the genus is increasingly restricted to cold streams and the deep profundal waters of large lakes (Sæther, 1975b). Few North American records exist outside of Canada and the northern United States (Sæther, 1975b). *H. latilaminus* Sæther and *H. marcidus* occur at Marion Lake today (Sæther, 1975b).

Hydrobaenus Fries (Fig. A.18c)

The median and 1st lateral mental teeth of *Hydrobaenus* fossils are weakly-pigmented and are all of similar length. The two median teeth are broad, rounded and separated by a median notch. The 1st lateral teeth are narrower, about as long as the median teeth in the fossils, but could be considered accessories to the median pair. The remaining 5 lateral pairs are slightly darker and arranged in a consistent order of decreasing size laterally. Ventromental plates are transparent, and moderately to well-developed. The absence of a ventromental beard is consistent with the published diagnosis (Cranston *et al.*, 1983), but this is not a reliable distinction, as I have noted for other taxa in this study. The light-coloured median mental teeth distinguish the fossils from *Heterotrissocladius*. The accessory teeth of *Heterotrissocladius*, *Rheocricotopus*, and *Zalutschia* are distinctly shorter than the median pair.

Although Sæther (1976) does not list a record from British Columbia, Washington, Oregon, or California, the genus seems to be widely distributed throughout much of North America. *Hydrobaenus* is recorded from the high arctic, south to Arkansas, Alabama, and Florida. Sæther (1976) does record one species, *H. fusistylus* (Goetghebuer) from Waterton Lakes National Park, Alberta. The larval mentum of this species is not unlike that of the British Columbia fossils. Although Sæther (1976, 1980b) has distinguished the arctic species *Oliveridia tricornis* (Oliver) with a separate genus, larval head capsules are similar to *Hydrobaenus* (Oliver and Roussel, 1983a). These 2 genera are probably not distinct (D.R. Oliver, pers. comm.). *Hydrobaenus* was collected in sediments from Black Tusk, Helm, Lost, and Mimulus Lakes.

Zalutschia Lipina (Fig. A.18d–e)

The 2 broad median teeth of *Zalutschia* fossils vary greatly in pigmentation, but are usually somewhat lighter in colour than the lateral mental teeth. Accessory teeth are present, and closely appressed to the median teeth. Bands of greater and lesser sclerotization are not conspicuous, but are associated with the median teeth of most specimens. Five additional pairs of lateral teeth, and moderately-developed ventromental plates complete the mentum. The ventromental plates have a convex lateral margin. A distinct ventromental beard was evident on several fossil specimens. The mandible includes 1 apical tooth, and 3 inner teeth. The premandible, although seldom noted, was always bifid. In general form the head capsules resemble ***Heterotrissocladius*, *Hydrobaenus*,** and ***Rheocricotopus*,** but the distinctly bifid premandible and ventromental beard (neither were retained with the illustrated specimen) are important diagnostic characters. ***Psectrocladius*** fossils never have accessory teeth, do not have sclerotization banding on the median teeth, and have undivided premandibles.

Zalutschia is widely distributed throughout much of Canada, including the high arctic. In North America, *Zalutschia* is also known from South Carolina, Florida and the northern United States (Oliver, 1981a; Oliver and Roussel, 1983a; Sæther, 1976). *Zalutschia lingulata* Sæther, collected from Marion Lake (by Hamilton, 1965: reported as *Trissocladius* sp.A), is the only species reported from British Columbia (Sæther, 1976). *Zalutschia* species occur principally in lentic waters, including acid and humic lakes, and occasionally in streams (Sæther, 1976).

Nanocladius cf. *distinctus* (Malloch) (Fig. A.19a–b)

Head capsules placed with *Nanocladius* cf. *distinctus* have a mentum with a broad light coloured median region. The median tooth includes two distinct median projections. Six pairs of lateral teeth were noted, with the first two pairs being weakly pigmented. Subsequent teeth were dark and sometimes indistinct. Transparent, well-developed ventromental plates flank the mentum. Mandibles are distinctive, having a very long, weakly-pigmented apical tooth and three inner teeth.

Apart from *N.* sp. near *balticus*, *N.* cf. *distinctus* is the only member of the genus reported from British Columbia (Sæther, 1977). *Nanocladius* cf. *distinctus* is reported in lakes and streams from much of western Canada, including the Brunette River near

Vancouver (Sæther, 1977). Surface sediments from Alice Lake, and Holocene sediments from Hippa and Marion Lakes, contained remains of *Nanocladius* cf. *distinctus.*

Parametriocnemus Goetghebuer group (Fig. A.19c)

Fossils of the *Parametriocnemus* group include a pair of indistinctly separated median teeth, and five lateral pairs. The median and first lateral teeth are more lightly coloured and have several weak bands of greater sclerotization. The first lateral teeth extend almost as far forward as the median pair. The fourth lateral teeth are about as long as the third pair. The well-developed ventromental plates are complex in structure, probably including two pairs of overlapping plates. The submental setae appear to be set far forward, and are separated from each other by the combined width of the median and first lateral teeth.

The mentum appears very similar to *Parametriocnemus lundbecki* (Johannsen) (Cranston *et al.*, 1983) and to *Paraphaenocladius* Thienemann (Oliver and Roussel, 1983a: fig. 374). Cranston *et al.* (1983) note that *Parametriocnemus, Paraphaenocladius,* and *Psilometriocnemus* Sæther have similar-looking larvae. These genera have a composite Nearctic range including much of northern and eastern North America (Cranston *et al.*, 1983; Oliver, 1981a). Their habitats include soils and cool streams (Cranston *et al.*, 1983).

Rheocricotopus Thienemann & Harnisch (Fig. A.19d)

In my fossils, the light-coloured median teeth are flanked by a pair of much smaller, closely appressed accessory teeth. Several weak bands of greater sclerotization are apparent. The five remaining pairs of lateral teeth are darker. The broad ventromental plates have a distinctly convex lateral margin. In some cases, either the ventromental beard, or the insertions of these setae, could be discerned. The submental setae are always placed close to the ventromental plates, separated by most of the mentum.

Although both *Psectrocladius* and *Zalutschia* can have a similar-looking mentum, the submental setae are more widely separated in *Rheocricotopus.*

Rheocricotopus is widely distributed in streams across Canada, but Oliver (1981a) indicates few records in the United States. *Rheocricotopus pauciseta* Sæther was originally described from a stream near Marion Lake, B.C. (Sæther, 1969).

Eukiefferiella Thienemann/*Tvetenia* Kieffer (Fig. A.20a)

The mentum of *Eukiefferiella* and *Tvetenia* head capsules include considerable diversity of form (Bode, 1983; Cranston *et al.*, 1983). Cranston *et al.* (1983) indicate that the mentum includes 1 or 2 median teeth and 4 to 6 lateral pairs. In this study, the pronounced banding in lateral regions of the mentum, produced by alternating zones of greater and lesser sclerotization were considered to distinguish *Eukiefferiella* and *Tvetenia* larvae from other taxa. The poorly developed ventromental plates, and comparatively strong pigmentation of the head capsule were important secondary characters used for identification.

These two genera have a composite distribution, mostly in flowing waters, including much of the world. Sæther (1969) reports *Eukiefferiella hospita* Edwards from a stream near Marion Lake.

Limnophyes Eaton (Fig. A.20b–c)

The mentum of *Limnophyes* fossils includes one pair of median teeth, and five lateral pairs. The teeth are arranged in a consistent order of decreasing size laterally. Indistinct sclerotization banding can frequently be discerned near the median region. The ventromental plates are poorly developed. Although Cranston (1982b) indicates the presence of small, rounded teeth at the base of the mentum, I interpret these structures to be rounded projections of the ventromental plates. Premandibles were rarely retained with the head capsules. The 3 teeth of the illustrated premandible resemble those portrayed by Cranston *et al.* (1983) in general form. Although *Limnophyes* cannot be reliably distinguished from *Paralimnophyes*, on the basis of these characters, *Paralimnophyes* is known from the Palaearctic only (Cranston *et al.*, 1983).

Limnophyes are widely distributed in soils, streams, and lakes (Cranston *et al.*, 1983; Oliver, 1981a), including those in arctic regions (Danks, 1981). Sæther (1969) has described two species, *L. hamiltoni* Sæther and *L. immucronatus* Sæther, as adults from Marion Lake's shoreline.

Doithrix Sæther & Sublette/*Pseudorthocladius* Goetghebuer? group (Fig. A.20d)

A number of larval Orthocladiinae head capsules were attributed to a *Doithrix/Pseudorthocladius*? group. Although the head capsules include diverse mental characteristics, only one example is illustrated. The mentum of *Doithrix/Pseudorthocladius*? group fossils included an even number of teeth, although the separation of the median pair was usually indistinct. Five lateral pairs of teeth completed the mentum. Ventromental plates were weakly to moderately-developed. The generic placement of many of the head capsules is uncertain, but most are probably attributable to the genera *Doithrix*, *Georthocladius*, *Parachaetocladius* Wülker, and *Pseudorthocladius*. Some may belong to *Bryophaenocladius* Thienemann, *Heleniella* Gowin, or *Gymnometriocnemus* Goetghebuer.

The larva of these genera occur mostly in soils and streams, although some inhabit marginal areas of lakes and ponds (Cranston *et al.*, 1983; Sæther and Sublette, 1983). These genera are poorly known, but are probably widely-distributed. *Doithrix hamiltonii* Sæther & Sublette (1983) is described from adult collections at Marion Lake.

Heterotanytarsus cf. *perennis* Sæther (Fig. A.21a–b)

A concave central region of the mentum is formed by 3 pairs of moderately pigmented teeth in *Heterotanytarsus* Spärck fossils. The 4 remaining pairs of teeth are darker and flanked by well-developed ventromental plates. The mandible bears 1 apical tooth and 3 inner teeth. Among Orthocladiinae, the strongly concave central region of the mentum is unique to *Heterotanytarsus*. Although four species of *Heterotanytarsus* have been described (Cranston *et al.*, 1983; Sæther, 1975d), only *H. perennis* is known from western North America.

Sæther (1975d) notes *Heterotanytarsus* to occur in northern, oligotrophic lakes and streams. *H. perennis* is known only from the type locality, Marion Lake (Sæther, 1975d). *Heterotanytarsus* fossils were collected from late-glacial sediments of Hippa Lake, and Holocene sediments from Marion, Mike, and Misty Lakes.

Synorthocladius Thienemann (Fig. A.21c)

Two very large, lightly pigmented median teeth are indistinctly separated, and flanked by four pairs of small teeth. These lateral teeth define a steeply-sloping lateral margin. A distinct beard was associated with the elongate ventromental plates in some fossil specimens. Several indistinct bands of greater or lesser sclerotization give the median teeth a weakly-striated appearance. The large median teeth and associated small lateral teeth produce an unusual mentum. Most fossil specimens were split along the median axis of the mentum.

Synorthocladius is associated with springs, streams, and littoral areas of lakes (Cranston *et al.*, 1983). Several species occur in North America (Cranston *et al.*, 1983), ranging from tree-line to the southern United States (Bass, 1986; Danks, 1981; Oliver, 1981a; Oliver and Roussel, 1983a).

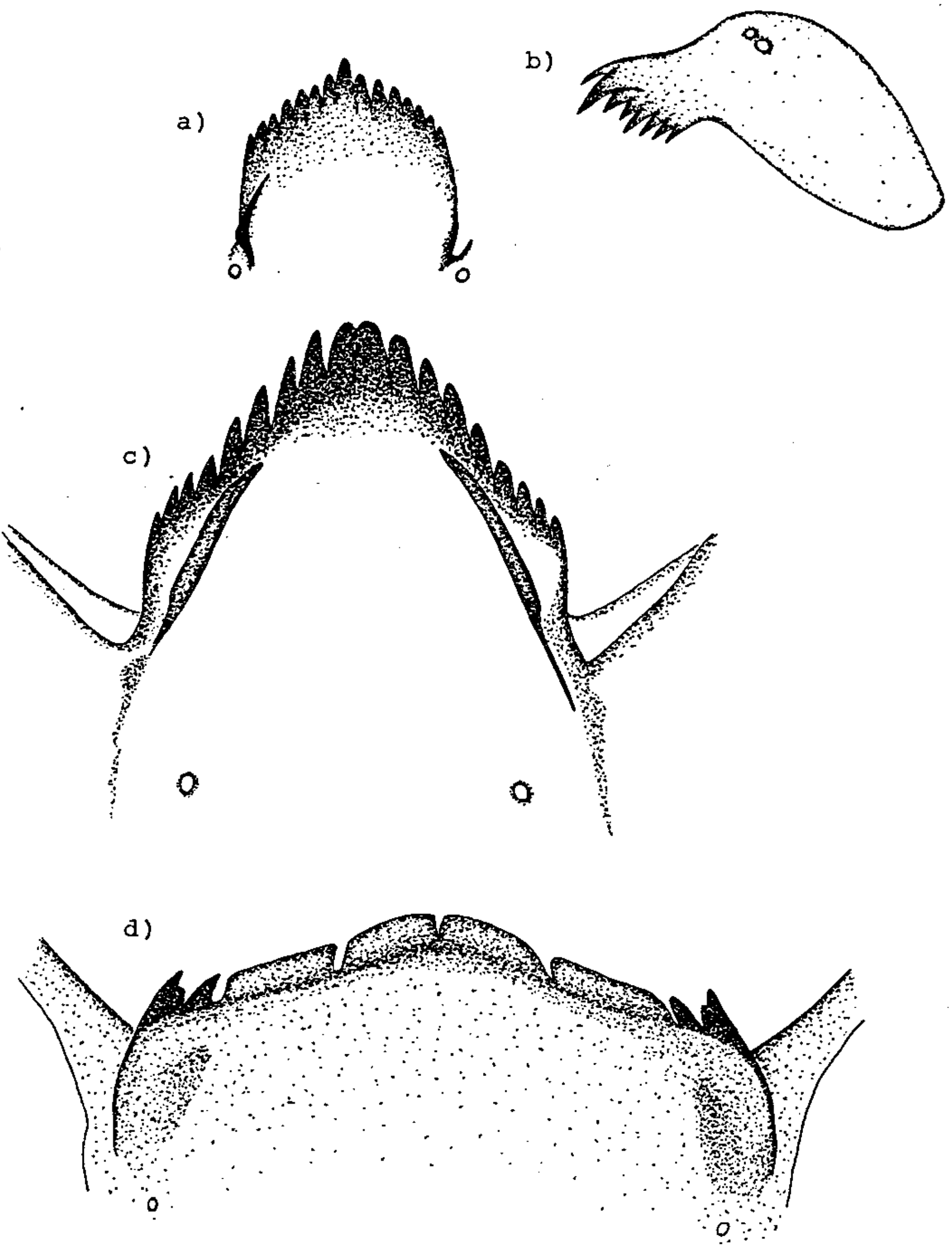

Figure A.11 Podonominae: *Boreochlus* Edwards (690X): a) mentum, b) mandible – Diamesinae: *Diamesa* Meigen? (1400X): c) mentum – *Protanypus* Kieffer (630X): d) mentum

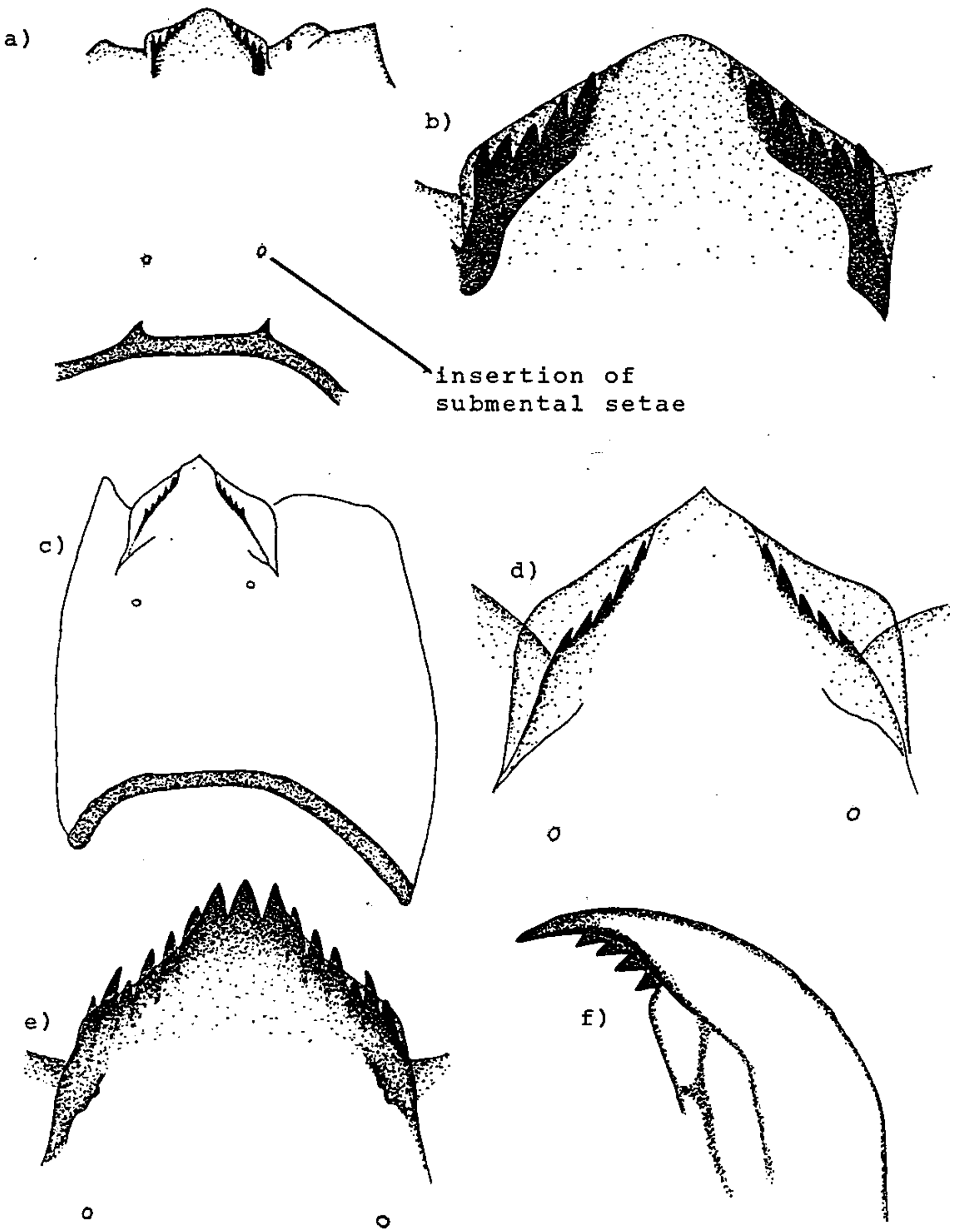

Figure A.12 *Pagastia* Oliver: a) head capsule (270X), b) mentum (1100X)– *Potthastia* Kieffer?: c) head capsule (410X), d) mentum (970X) – *Pseudodiamesa* Goetghebuer (800X): e) mentum, f) mandible

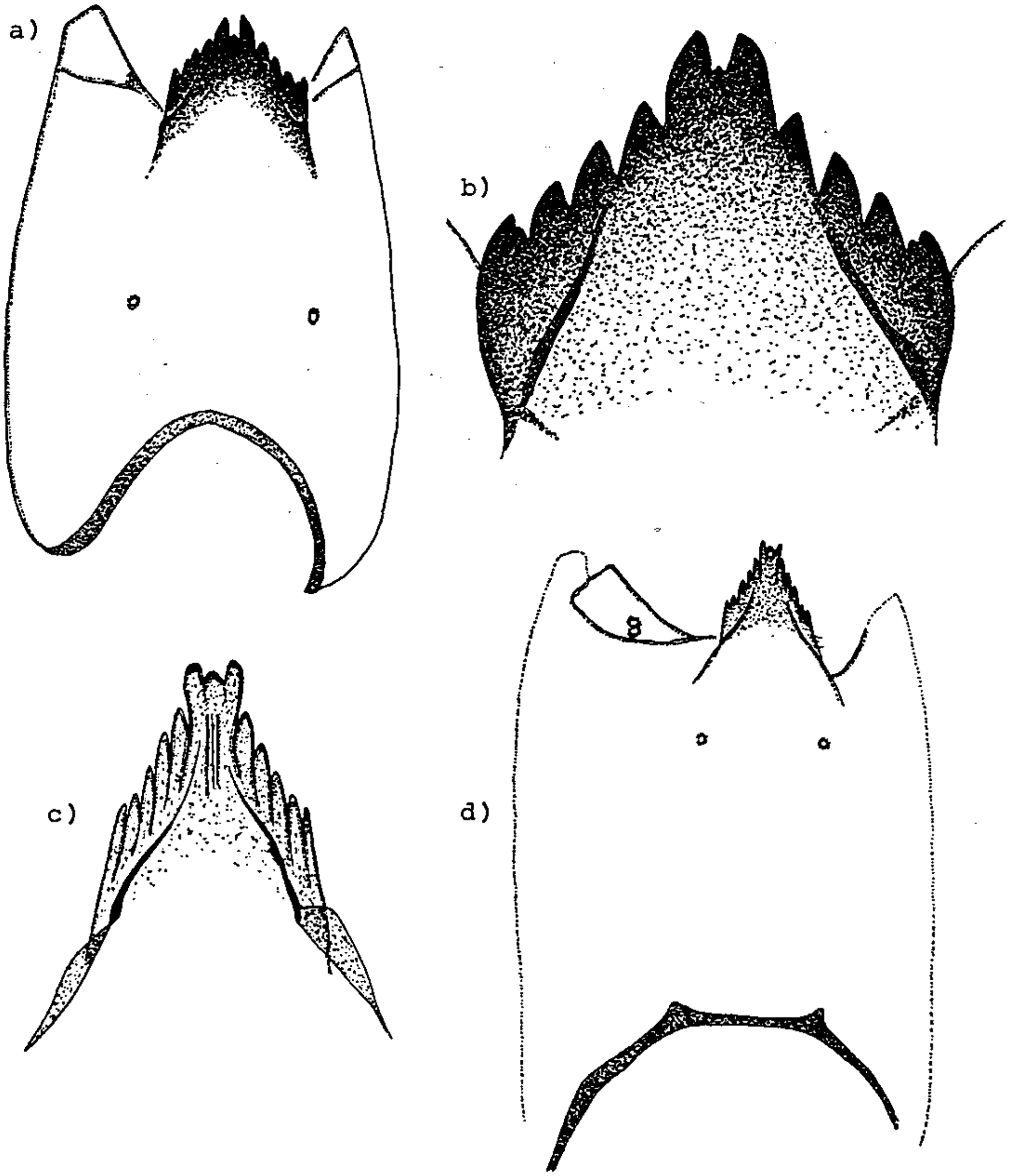

Figure A.13 Orthocladiinae: *Brillia* Kieffer/*Euryhapsis* Oliver: a) head capsule (370X), b) mentum (1100X) – *Corynoneura* Winnertz/*Thienemanniella* Kieffer: c) mentum (590X), d) head capsule (1400X)

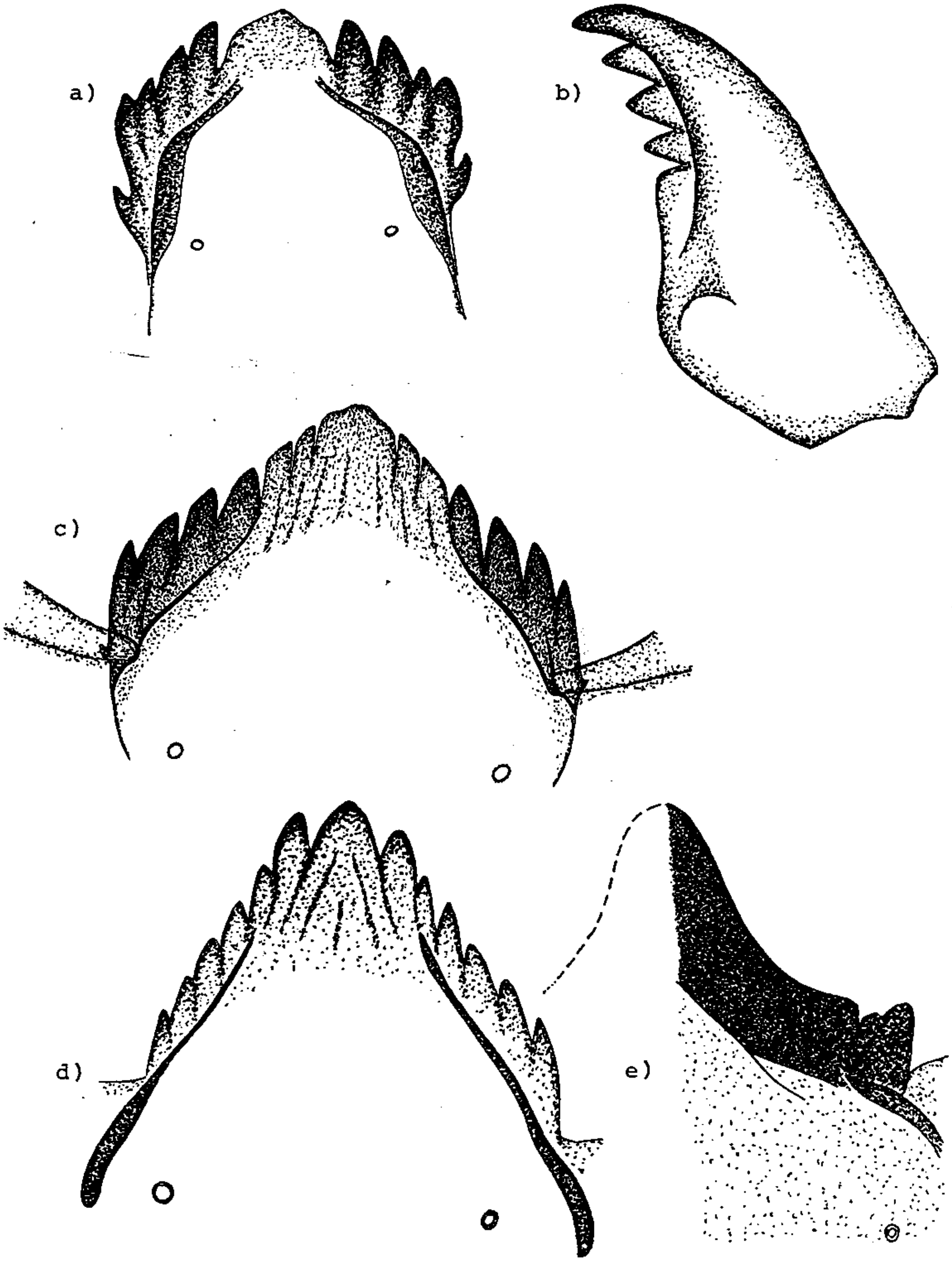

Figure A.14 *Smittia* Holmgren/*Pseudosmittia* Goetghebuer? group (1800X): a) mentum, b) mandible – *Cricotopus* v.d.Wulp/*Orthocladius* v.d.Wulp/*Paratrichocladius* Santos Abreu: c) mentum (990X), d) mentum (820X) – *Orthocladius (Symposiocladius) lignicola* Kieffer (1600X): e) mentum

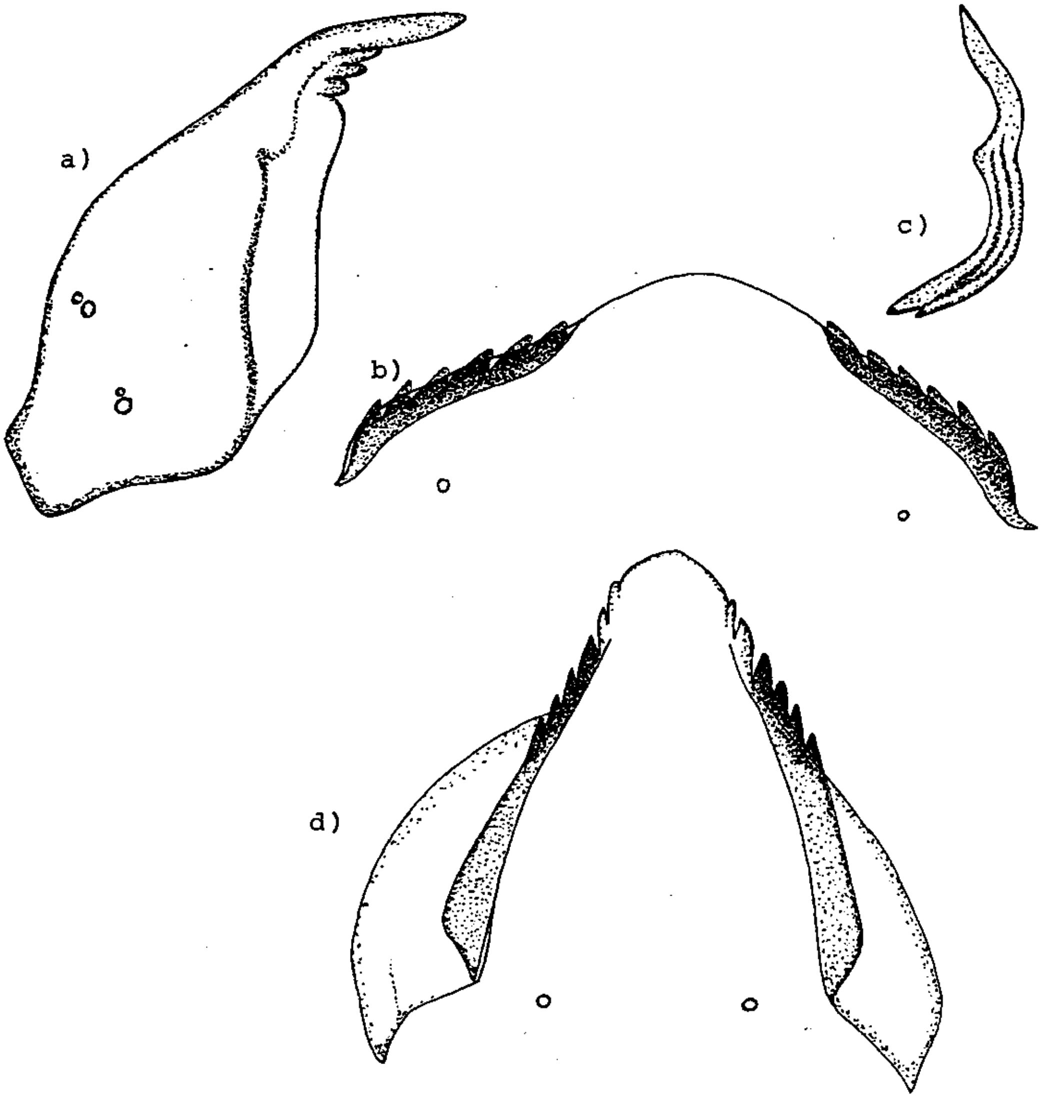

Figure A.15 *Paracladius* Hirvenoja (840X): a) mandible, b) mentum, c) premandible – *Stilocladius* Rossaro (1200X): d) mentum

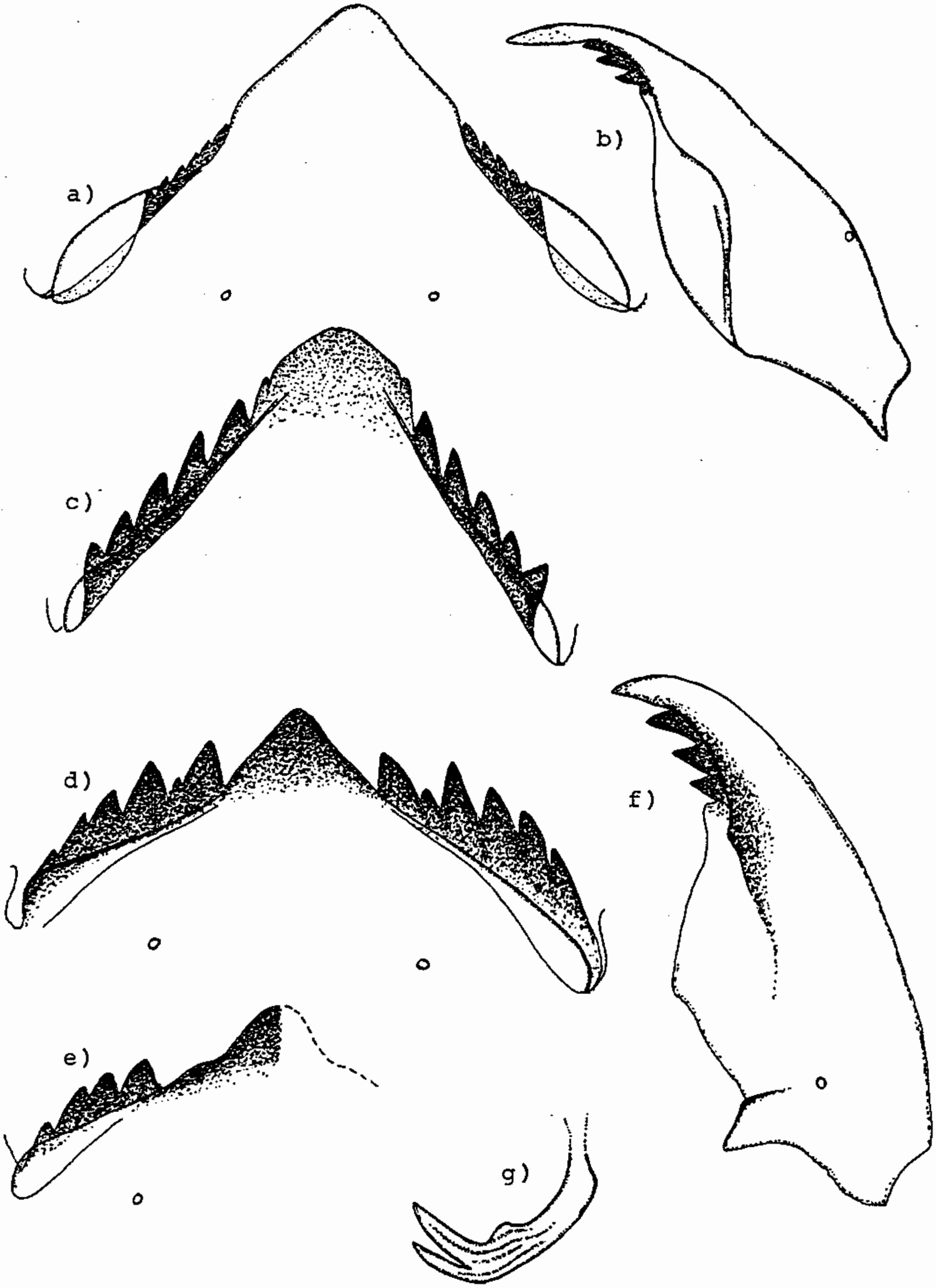

Figure A.16 *Parakiefferiella*? cf. *triquetra* (Chernovskii) (830X): a) mentum, b) mandible, – *Parakiefferiella* cf. *bathophila* (Kieffer) (1400X): c) mentum – *Parakiefferiella* sp.A: d) normal mentum (1200X), e) worn mentum (970X), f) mandible (1200X), g) premandible (1200X)

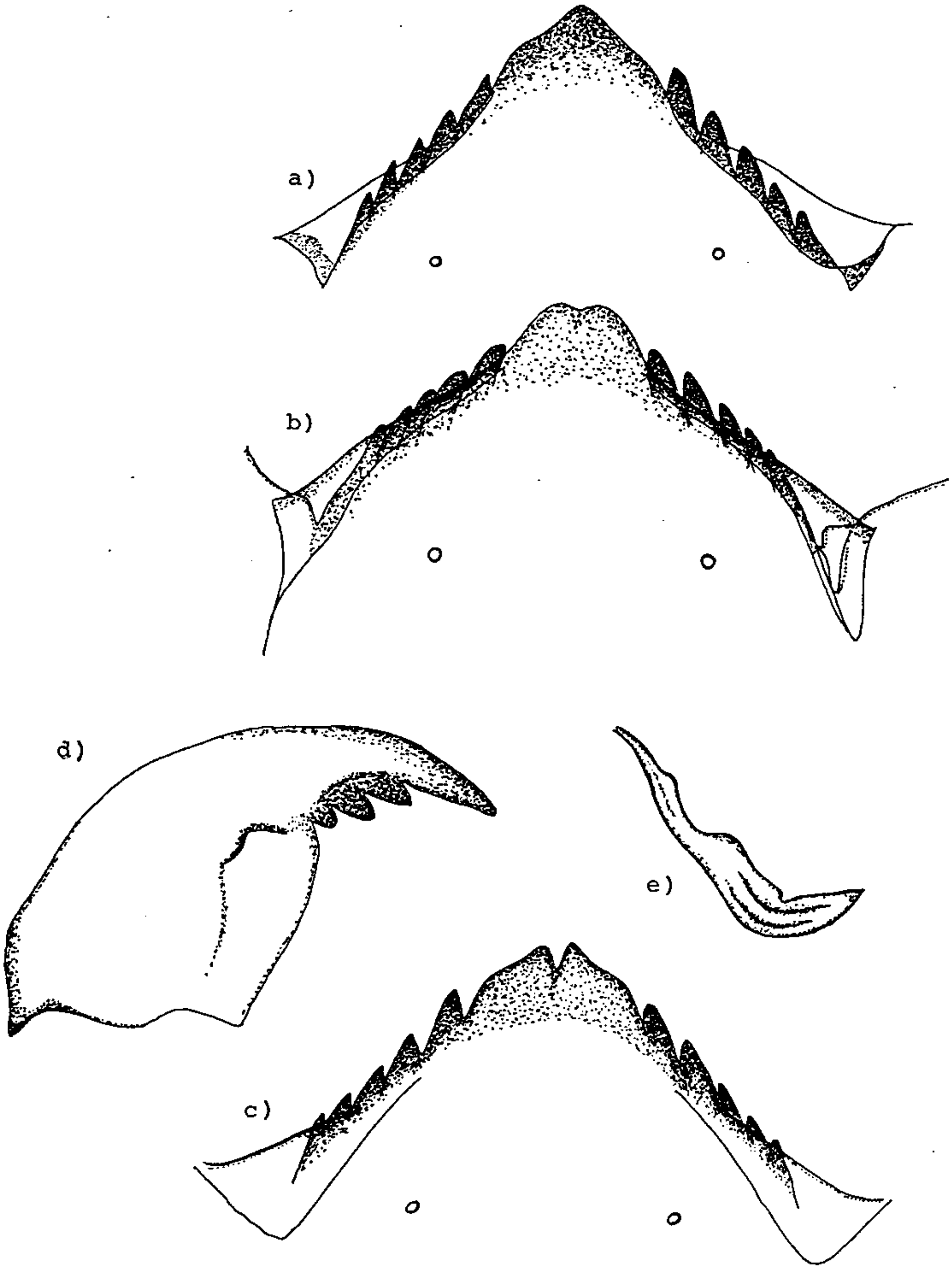

Figure A.17 *Psectrocladius* subg. *Monopsectrocladius* Laville (1400X): a) mentum - other *Psectrocladius* Kieffer: b) mentum (1800X), c) mentum (1540X), d) mandible (1540X), e) premandible (1540X)

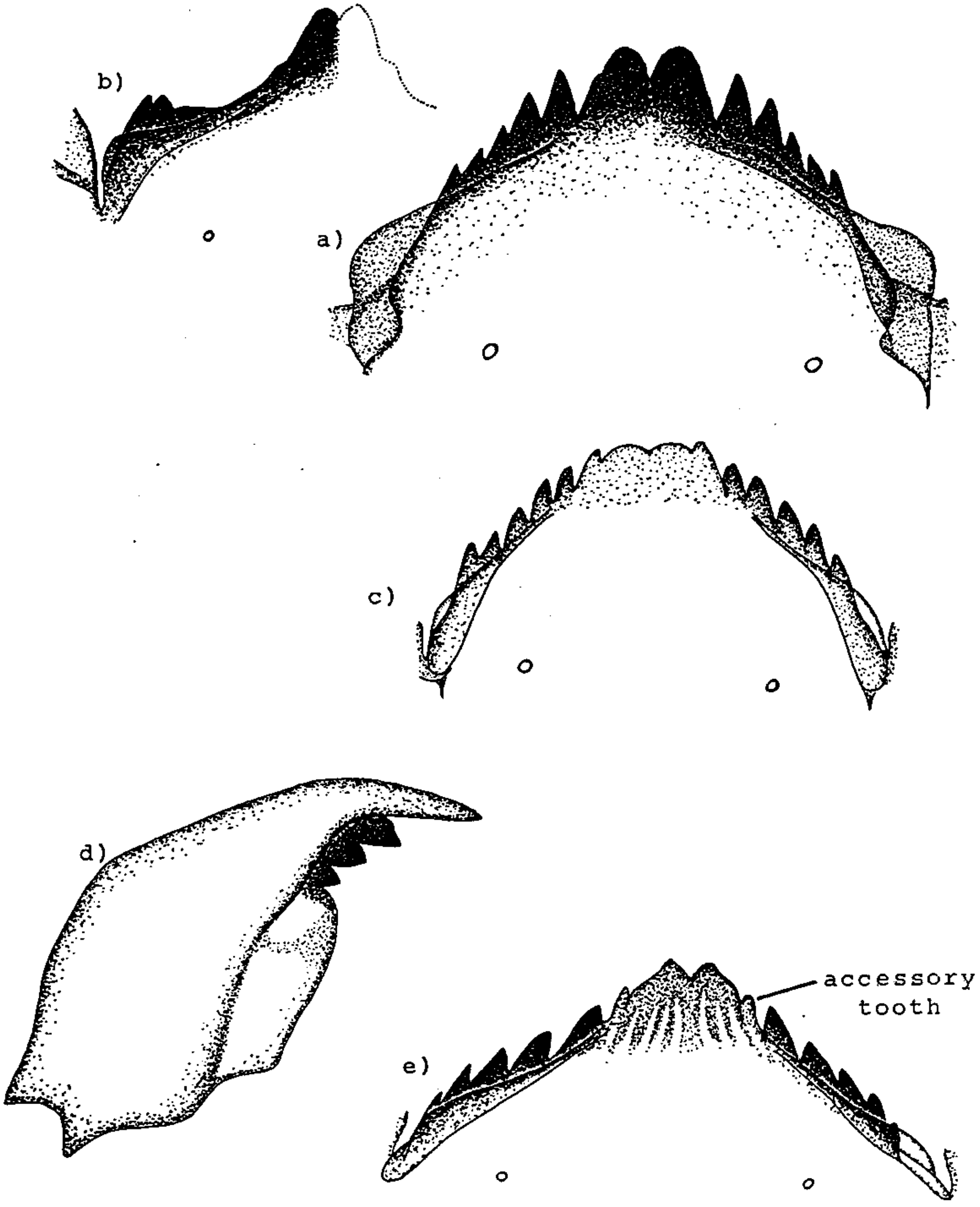

Figure A.18 *Heterotrissocladius* Spärck: a) normal mentum (1300X), b) worn mentum (540X) – *Hydrobaenus* Fries (1700X): c) mentum – *Zalutschia* Lipina (640X): d) mandible, e) mentum

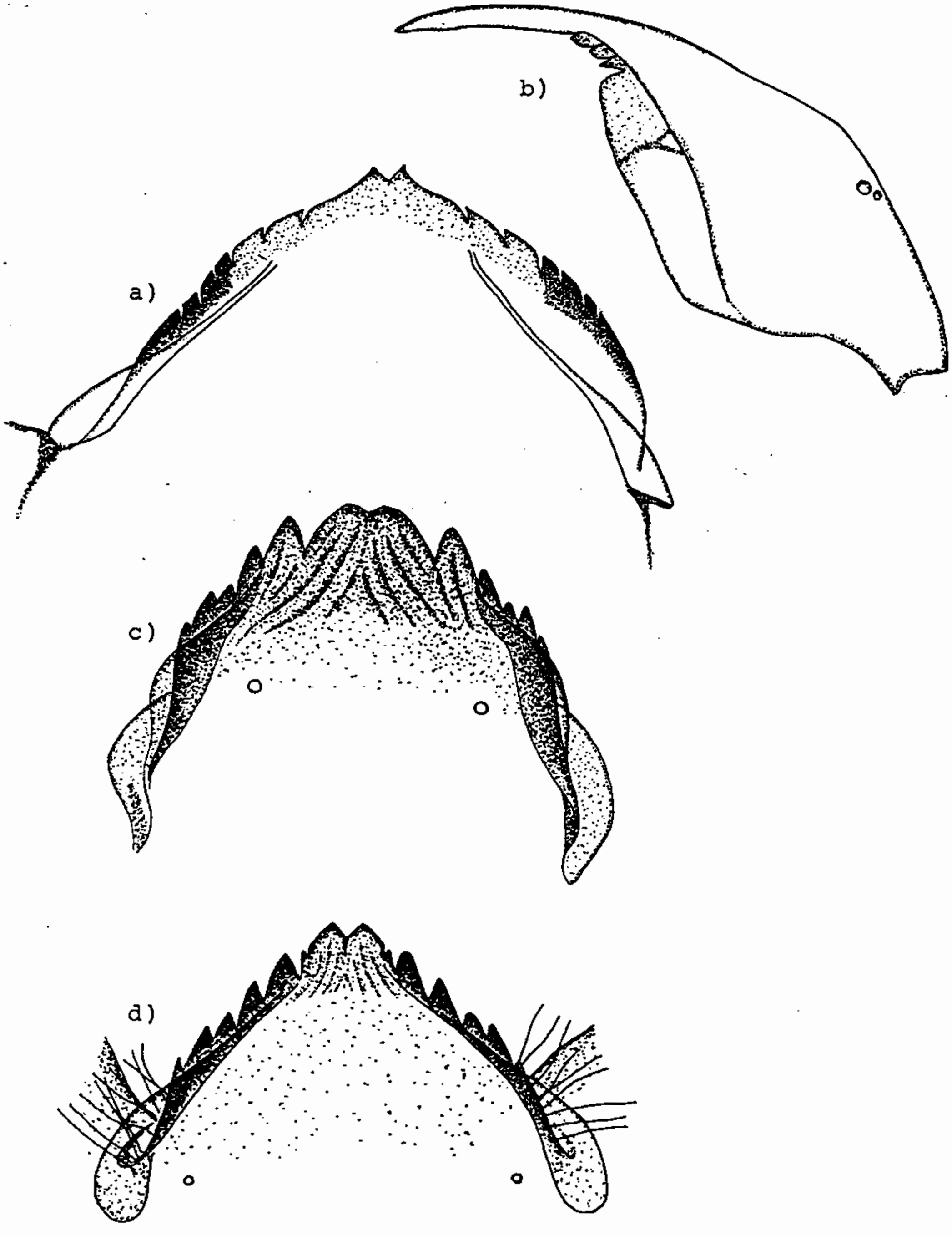

Figure A.19 *Nanocladius* cf. *distinctus* (Malloch) (1400X): a) mentum, b) mandible - *Parametriocnemus* Goetghebuer group (980X): c) mentum - *Rheocricotopus* Thienemann & Harnisch (740X): d) mentum

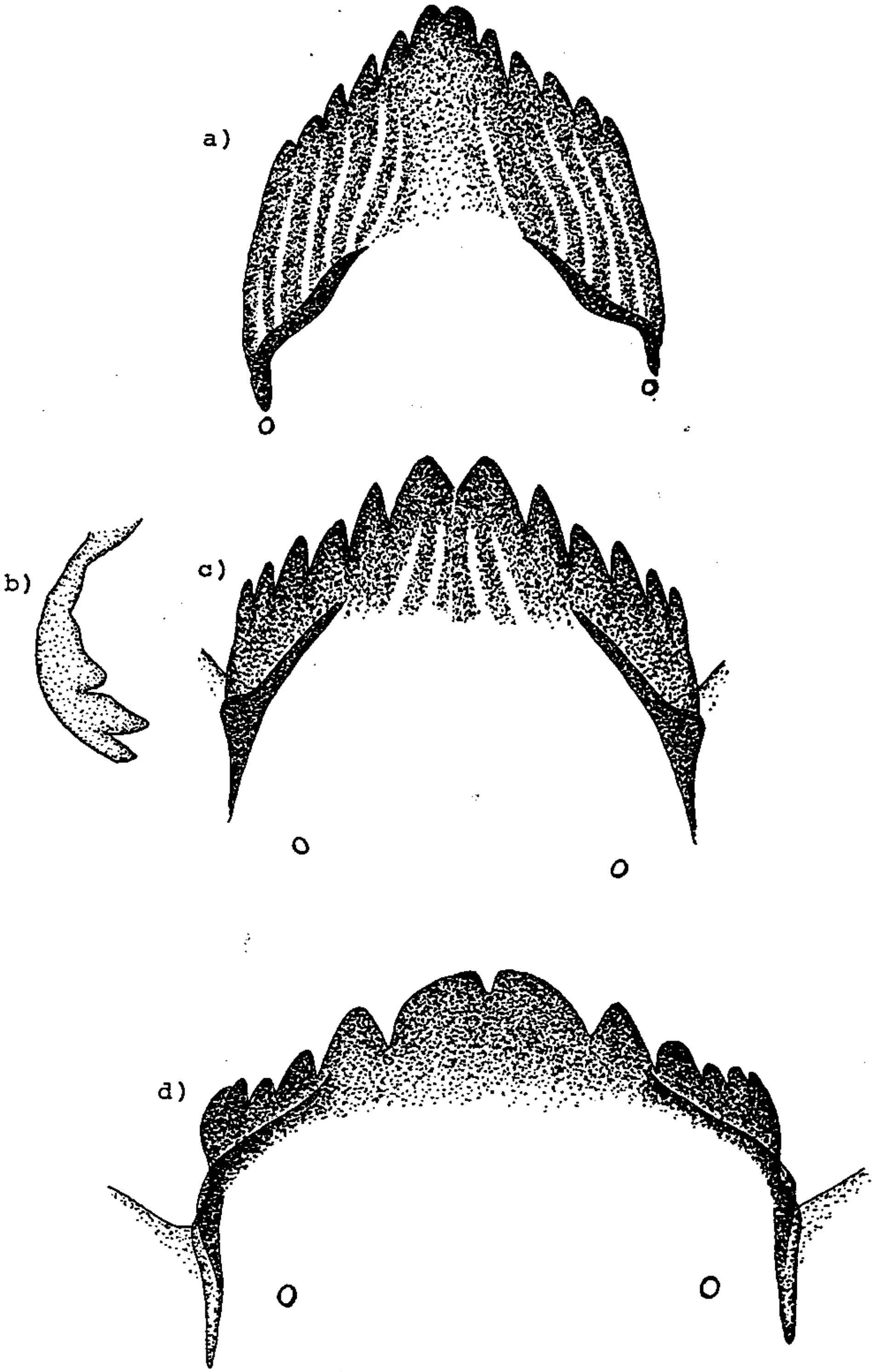

Figure A.20 *Eukiefferiella* Thienemann/*Tvetenia* Kieffer (2100X): a) mentum – *Limnophyes* Eaton (1300X): b) premandible, c) mentum – *Doithrix* Sæther & Sublette/*Pseudorthocladius* Goetghebuer? group (1400X): d) mentum

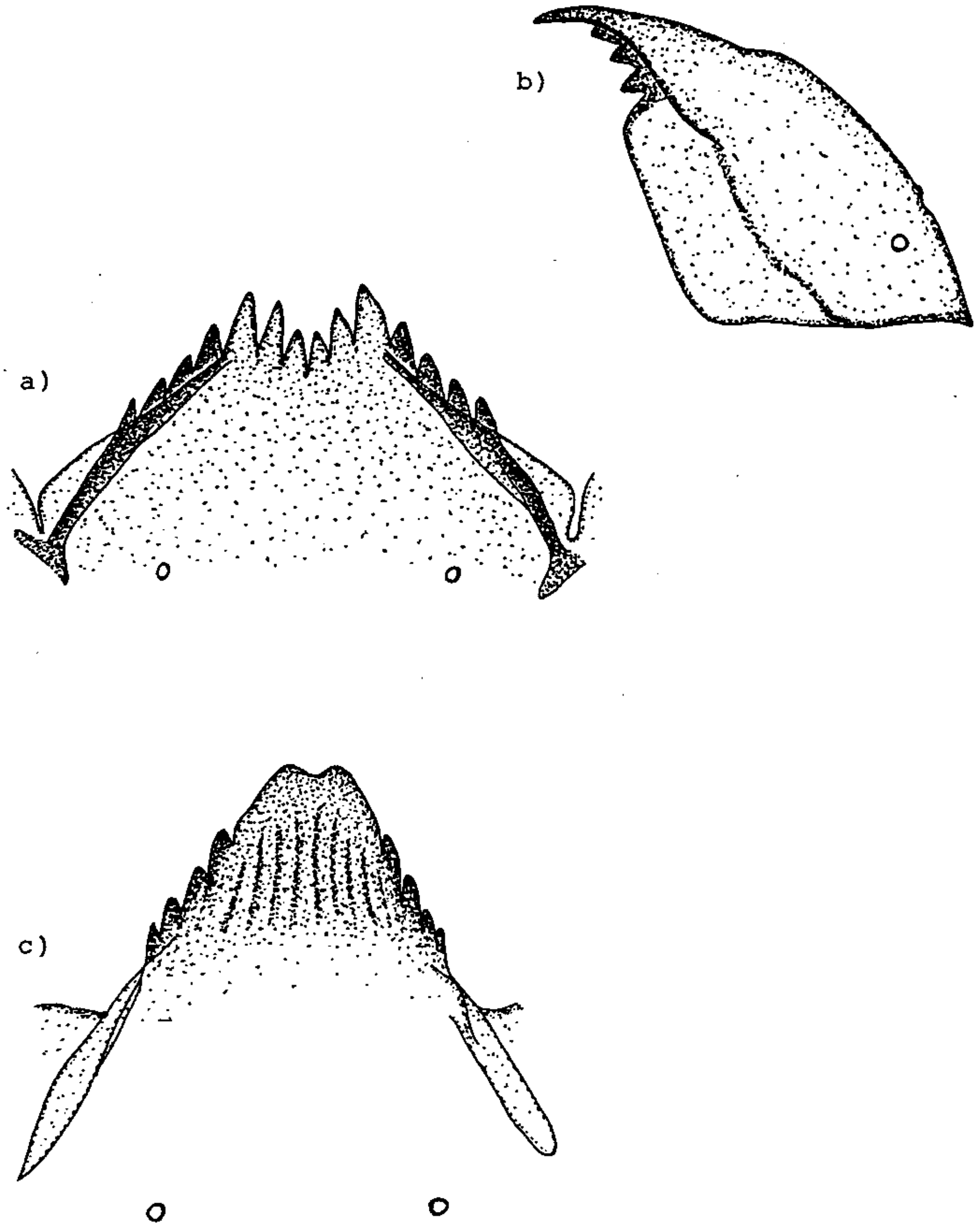

Figure A.21 *Heterotanytarsus* cf. *perennis* Sæther (1400X): a) mentum, b) mandible – *Synorthocladius* Thienemann (940X): c) mentum

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