A CHIRONOMID-BASED RECONSTRUCTION OF LATE HOLOCENE CLIMATE CHANGE IN SOUTHERN COSTA RICA

By

JIAYING WU

ABSTRACT

The modern distribution of sub-fossil chironomids in Costa Rica is described making use of a fifty-four lake calibration set. The relationship between modern chironomid distribution and the measured limnological variables indicated that surface water temperature (SWT) accounts for a statistically significant amount of variance in the chironomid communities. A chironomid-based inference model for SWT, developed using weighted-averaging partial least squares, was applied to sub-fossil midge assemblages from Laguna Zoncho, Costa Rica, to reconstruct late Holocene thermal variability. The major findings of this study are: (1) SWT between1750 and 3100 cal yr BP was higher than the late Holocene average, (2) southern Costa Rica was characterized by below average temperatures during the Little Ice Age, and (3) Laguna Zoncho experienced very low lake levels, possibly reflecting drought, during the Medieval Climate Anomaly. This study pioneers the use of sub-fossil chironomid remains to develop quantitative estimates of Holocene thermal variability in Central America.

INDEX WORDS: Paleoclimate; Temperature; Chironomid; Holocence; Costa Rica; Little Ice Age.

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By

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DEDICATION

This thesis is dedicated to my dearest Mum and Dad, who have always supported me, to my boyfriend, Yihuan Zhang, who accompanies me whenever I need to, and to my advisor, Dr. David Porinchu, who has been patient to me all the time and teach me to never give up.

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CHAPTER 1

INTRODUCTION

Evidence of increasing mean global temperature has been well documented (ACIA, 2005; IPCC, 2007; Stern Report, 2007). The Intergovernmental Panel on Climate Change (IPCC) has identified that the average global temperature of the land and ocean surface has increased ~0.74℃ between 1906 and 2005 (IPCC, 2007). Warming induced sea level rise and altered precipitation have also been documented (Lu et al., 2007). To fully understand the interactions between climate and vegetation, and to improve our predictions of future climate conditions, requires a longer-term perspective than that offered by the instrumental record (Bradley, 1999). Multi-proxy paleoclimate reconstructions have provided rich evidence of quasi-periodic variations in climate (Sachs et al., 1977; Cook et al., 1995; Briffa and Melvin, 2008) during the Quaternary (Bradley, 1999), and have also helped in identifying the causal factors responsible for present climate variability (Kutzbach, 1976; Bradley, 1999). Development and continued refinement of multi-proxy approaches to paleoenvironmental reconstruction can contribute much in furthering our understanding of climate and ecosystem response to on-going climate forcing (Bauch et al., 2001; Birks and Birks, 2006; Goman et al., 2010).

Central America will be greatly affected by climate change (Bundschuh et al., 2007). Therefore, the longer-term perspective afforded by paleoclimatology is quite useful in placing existing climate variability in Central America in a broader temporal context. Environmental reconstructions based on neo-tropical lake and swamp sediments have clearly demonstrated that significant fluctuations in precipitation (pattern, volume) and temperature characterized the late Quaternary in Central America (Hodell et al., 2008; Bush et al., 2009). This recent work has led to the rejection of earlier assumptions of tropical climate stability during the late Quaternary (Horn, 2007). Multiple lines of evidence indicate that temperatures during the Last Glacial Maxima (LGM) in the tropics were lower than present (Thompson et al., 1997; Farrera et al., 1999; Pinot et al., 1999; Broccoli, 2000; Hostetler and Clark, 2000; Thompson et al., 2000; Clark et al., 2002; Ballantyne et al., 2005; Roy and Lachniet, 2010), and that the Holocene itself was a time of considerable climatic variability (Horn, 2007). Re-evaluated CLIMAP ocean temperatures derived from marine sediments also support the interpretation of notable variability in SSTs during Holocene (Bush et al., 2001).

Costa Rica, which is located in the Central American Isthmus, has been a focus of intensive paleoclimate and paleoenvironmental research with numerous, multi-proxy lake and bog-based paleoclimate studies undertaken during recent decades (Hooghiemstra et al., 1992; Horn, 1993; Islebe et al., 1995; Islebe, 1996; Rodgers and Horn, 1996; Islebe and Hoogheimstra, 1997; Orvis and Horn, 2000; League and Horn, 2000; Clement and Horn, 2001; Lachniet and Seltzer, 2002; Haberyan et al., 2003; Lane et al., 2004; Haberyan and Horn, 2005). The results from these studies have provided important insights into the nature of tropical climate and landscape change during the late Pleistocene and Holocene. For example, the pollen spectrum in La Chonta bog suggests that the region surrounding the bog was characterized by a treeless Páramo vegetation with the upper limit of forest 600-700 m lower relative to modern timberline and temperature 7-8℃ lower than present between ~36,000 and 15,000 cal yr BP (Horn, 2007). The termination of the most recent glacial was characterized by an increase of 4.6^{o}C in annual temperature, and increases in annual precipitation and timberline elevation (Horn, 2007). Post-glacial climate amelioration was briefly interrupted by an event correlative with the Younger Dryas (12,900-11,600 cal yr BP). A decrease of 2-3^{o}C in mean annual temperature is inferred to have occurred between 12,300-11,200 cal yr BP in the Cordillera de Talamanc in central Costa Rica (Islebe et al., 1995; Horn, 2007). Pollen evidence from La Chonta bog and Trinidad bog, Costa Rica indicate that the early to mid-Holocene (10,700 and 5200 cal yr BP) in this region was characterized by higher effective moisture and temperature conditions that were similar to modern (Horn, 1993; Horn, 2007). Charcoal records developed from Laguna Zoncho provide evidence of increasing fire frequency and human modification of the landscape during the late Holocene in the southern highlands of Costa Rica (Clement and Horn, 2001; Lane et al., 2004; Haberyan and Horn, 2005). Paleoenvironmental reconstructions conducted on sediment recovered from glacial lakes, Morrenas and Lago Chirripó, reveal that the late Holocene was generally drier than present (Horn, 2007).

Much of what is known about late Holocene climate and environmental change in southern Costa Rica comes from detailed analyses of lake sediment cores recovered from Laguna Zoncho. Laguna Zoncho is located in the Diquís subregion, one of three least known archaeological zones in the country (Snarskis, 1981). The Diquís subregion, known as the Greater or Gran Chiriqí, spans southern Costa Rica and western Panama. Clement and Horn (2001) analyzed the pollen and charcoal from a 5.9 m lake-sediment core recovered from Laguna Zoncho and developed 3000 year record of indigenous settlement, forest clearance, maize cultivation and fire. This study also constrained the timing of the oldest maize (*Zea mays*) cultivation in southern Costa Rica. A diatom-based study by Haberyan and Horn (2005) illustrated that Laguna Zoncho may have experienced an interval of low lake levels and pH between ~1020 to 460 cal yr BP and high lake levels between 460 cal yr BP and 1997 AD. The diatom results together with the previous pollen and charcoal analyses, suggest that the dry conditions that characterized the late Holocene may have been driven by the southward migration of the Intertropical Convergence Zone (Thompson et al., 1997). In addition to the climate inferences, Lane et al. (2007) made use of stable isotopes (C, N), pollen and charcoal to assess the role that humans played, through forest clearance and crop cultivation, in modifying the landscape surrounding Laguna Zoncho during the late Holocene. It is important to note that the downcore interpretation of paleoenvironmental proxies at Laguna Zoncho, e.g. diatoms and pollen, is heavily reliant on an extensive regional training set which was developed to improve our knowledge of modern relationship between these proxies and the contemporaneous environment (Haberyan et al., 2003).

Although numerous proxy-based reconstructions describing various aspects of late Holocene environmental change have been developed for Laguna Zoncho, Costa Rica, the degree to which thermal conditions contributed to observed landscape change remains poorly described. Chironmids have been used to reconstruct late Holocene thermal conditions in a variety of environments including the alpine and arctic regions of North America (Porinchu and Cywnar, 2002; Porinchu and MacDonald, 2003; Porinchu et al., 2009a); however, little to no sub-fossil midge analysis has been undertaken in Costa Rica.

Lakes are very effective archives, capturing and accumulating sediment, which in turn can be analyzed for multitude of proxies. As a result, lakes serve as excellent “sentinels”, documenting changes in the function and composition of aquatic ecosystems in response to climate and environmental changes (Williamson et al., 2009). Proxy-based paleolimnological studies make use of the physical, chemical and biological information preserved in sediments, to assess the sensitivity of lacustrine ecosystems to climate and environmental change (e.g. Smol et al., 1995; Pienitz et al., 1999; Pienitz et al., 2004; Bennion and Battarbee, 2007). For example, diatoms and chironomids, which are well preserved in lake sediments, provide detailed information on the nature of the linkages, both direct and indirect, between biotic communities and limnological and climatic variables (e.g. Smol et al., 1995; Bradley, 1999; Pienitz and Lotter, 2009).

Paleolimnological reconstructions of climate and environmental history are dependent on three basic assumptions: (1) a linear response exists between the aquatic organism of interest and the contemporaneous environment, (2) a sufficient number of identifiable subfossil remains can be recovered, and (3) the sediment can be dated (Smol et al., 1995; Birks, 1998).

Quantitative paleolimnological studies typically consist of two, discrete, but related steps: (1) establishing the modern distribution of the proxy of interest and modeling the relationship between the proxy and specific abiotic variables using transfer functions or inference models; and (2) applying inference models (developed in step 1) to biotic assemblages to derive reconstructions of past climate or environmental change (Moser et al., 1996). The development of a training or calibration set requires collecting surface sediment (uppermost 1 cm) from a suite of lakes and characterizing the abiotic and biotic environment of the lakes. The lakes sampled for inclusion in the training set should be chosen to maximize environmental variation within the region of interest (Moser et al., 1996). Typically, in palaeolimnological studies, the number of lakes, taxa and environmental variables sampled varies between 30–300, 30–500, and 10–40, respectively (terBraak, 1995; Birks, 1998). The biotic assemblages, comprised of q samples of fossil data with r taxa, should share their taxa (r) plentifully enough with taxa (m) in the training set to enable meaningful downcore reconstructions (Maddy and Brew, 1995; Birks, 1998).

Developing the environmental dataset to be used in the calibration set analyses requires: 1) measurement of physical and limnological variables, and 2) collection of water samples for laboratory chemical analyses. Physical and limnological variables that are typically measured in the field during surface sediment collection include surface water temperature, lake depth, pH, Secchi depth, conductivity, salinity and dissolved oxygen. Water samples are analyzed in the laboratory for the trace metal concentrations, ions, dissolved organic carbon, chlorophyll a and nutrients (Moser et al., 1996; Moser, 2004). In addition, complementary data such as lake size, composition of regional vegetation, pedology, geology and local climate data (Moser et al., 1996; Haberyan et al., 2003) are incorporated into the environmental dataset. The relationship between specific environmental variables and the distribution of the biotic proxy of interest can be established using ordination analyses. The assumption that a linear response exists between the aquatic organism and a specific environmental variable enables the development of transfer functions (mathematical equations that estimate environmental variables from community composition) for specific environmental variables (Birks 1998).

In studies of lake sediments, subfossil chironomids have proven to be valuable in paleoclimate reconstruction (Porinchu and MacDonald, 2003; Potito et al., 2006; Reinemann et al., 2009). Numerous studies have provided evidence that variations in chironomid assemblages correspond to the temperature, depth and vegetation gradients that exist in the northeastern United States, north-central and eastern Canada, Fennoscandia, Russia and the Swiss Alps (Walker et al., 1991a; Cwynar and Levesque, 1995; Walker and MacDonald, 1995; Olander et al., 1997; Lotter et al., 1997; Brooks et al., 1997; Olander et al., 1999; Porinchu and Cwynar, 2000; Porinchu et al., 2009b). Compared to pollen, chironomids appear to be a more sensitive indicator of past temperature and offer great potential in providing independent estimates of regional climate conditions during intervals of transition (Cwynar and Levesque, 1995; Brooks et al., 1997; Porinchu et al., 2003). Many midge-based paleolimnological studies have identified strong, statistical significant correlations between midge distribution and average July or summer air temperature (Dieffenbacher-Krall et al., 2007; Luoto, 2009; Porinchu et al., 2009a; Porinchu et al., 2010), and between the distribution of chironomids and summer surface water temperature (Walker et al., 1991a; Olander et al., 1997; Walker et al., 1997, Olander et al., 1999; Brooks and Birks, 2001; Porinchu et al., 2007; Porinchu et al., 2009a). Application of the inference models developed in these studies has enabled researchers to obtain detailed, quantitative paleotemperature reconstructions for arctic and sub-arctic North America, the northeastern and western United States and northwest Europe spanning the Pleistocene-Holocene transition (Walker et al., 1991b; Levesque et al., 1993; Wilson et al., 1993; Levesque et al., 1994; Cwynar and Levesque, 1995; Levesque et al., 1997; Brooks and Birks, 2000; Brooks and Birks, 2001; Heiri, 2003; Porinchu et al., 2003) and western Norway, France and northern Sweden during the Holocene (Brooks and Birks, 2000; Larocque and Hall, 2004; Heiri and Millet, 2005).

My research project, which aims to take advantage of the midge-temperature relationship and centers on reconstructing late Holocene paleoclimate conditions in southern Costa Rica, has three main objectives:

1) Describe the modern distribution of sub-fossil midges in Costa Rica, identify limnological variables that account for a significant amount of variance in the distribution of midges, and model the relationship between midges and specific variables using transfer functions;

2) Apply the inference model to sub-fossil midges identified in the Laguna Zoncho sediment core to develop a quantitative reconstruction of late Holocene paleoclimate for the southern highlands of Costa Rica;

3) Compare this newly developed reconstruction to existing terrestrial and adjacent marine records to determine if correlations exist between late Holocene climate in Costa Rica and the tropical Pacific Ocean and Caribbean Sea.

CHAPTER 2

STUDY AREA

Geology

Costa Rica is situated in the Central American isthmus (Figure 2.1). The rocks that comprise the batholithic basement of Costa Rica consist primarily of Palaeozoic-Paleogen sedimentary rocks, Cenozoic volcanic rocks and Neogene-Holocene sedimentary rocks (Weyl, 1980). The complex tectonic-induced geomorphology of Costa Rica is a mirror for historical Cenozoic volcanism and upper-plate deformation in southern Central America (Gardner et al., 1987; Coates and Obando, 1996). The terrestrial connection between Costa Rica and Panama was presumptively formed as the result of initial oceanic plate subduction and following frequent volcanism from ~15 Ma to 3 Ma BP (Escalante, 1990; Bundschuhet al., 2007). Recent fault activities have changed the North Panama deformed belt into the Central Costa Rica deformed belt (Bundschuh et al., 2007). Thirteen volcanoes are located along a northwest to southeast trending axis; nine of those volcanoes, including Irazú (3432 m asl), are still active (Wyk De Vries et al., 2007; Bundschuh et al., 2007). High annual rainfall, a wide array of basin forming geomorphic activities and human processes have created ~ 652 observed water bodies in Costa Rica. These water bodies are distributed throughout the country and scattered from lowlands in the coastal region to highlands near volcanic craters (Horn and Haberyan, 1993; Haberyan et al., 2003). The 54 lakes that were incorporated into the training set were formed through volcanic, fluvial, glacial or hillslope processes and include lakes formed from artificial impoundments (Horn and Hyberyan, 1993; Haberyan et al., 2003). The late Holocene downcore sediment was extracted from Laguna Zoncho, a small natural lake (0.8 ha, 2.6m deep) in the southern highlands of Costa Rica that was possibly formed by faulting or large-scale slumping, or by damming behind slumped debris (Haberyan et al., 2003).

Climate

Due to its location and restricted latitudinal range (8°N-12°N), the modern day climate of Costa Rica, which can be considered tropical, is characterized by wet summers and dry winters (Bundschuh et al., 2007). The climate of Costa Rica is primarily influenced by two factors, warm ocean currents and seasonal shifts in atmospheric pressure (Clawson, 1997). High temperature and relatively low humidity along the Pacific coast of Costa Rica mainly results from the northward flowing Equatorial Current; whereas, high temperature and humidity along the Caribbean coast are influenced by the Atlantic North Equatorial Current and the Gulf Stream (Winograd et al., 2000). Distinct wet summers and dry winters are produced by the shift in the position of equatorial low pressure and subtropical high pressure over Central America in response to the seasonal migration of the sub-solar point and Intertropical Convergence Zone (ITCZ). Generally, the wet season begins in May when the ITCZ shifts northward and ends in October when the ITCZ migrates southward. The onset of the winter dry season starts in November when subtropical high pressure exerts control (Bundschuh et al., 2007). Situated within the ITCZ, Costa Rica is subject to intense tropical cyclonic storms, which often lead to heavy precipitation in southern Costa Rica and severe damage in to fruit plantations (Martinson, 1993; Clawson, 1997; Bundschuh et al., 2007; Vasquez, 2009).

The amount and spatial distribution of precipitation is also strongly influenced by topography (Clawson, 1997; Bundschuh et al., 2007). The presence of elevated highlands and the resultant orographic effect are very pronounced on the eastern side of the Cordillera Central in Costa Rica (Clawson, 1997). The Cordillera de Talamanca lifts maritime air masses (northeasterly trade winds) along the east slope of the mountains, yielding decreasing rainfall totals from east to west (George et al., 1998; Winograd et al., 2000). As a result, annual rainfall totals vary from 3000-4000 mm in the southeast windswept slope of the Cordillera de Talamanca occupied by evergreen cloud forest, to 1500- 2000 mm in the northwest Pacific lowlands dominated by seasonal dry forests and savannas (Horn and Hyberyan, 1993; George et al., 1998; Bundschuh et al., 2007; Horn and Haberyan, *in press*). Orographic induced lifting and cooling of air masses result in very high amounts of precipitation falling in the central Costa Rican Highlands (Winograd et al., 2000). Meteorological data indicates that the annual precipitation reaches up to 7555 mm in the Cordillera Central, but precipitation in the northeastern lowlands is 2000 mm less (Winograd et al., 2000; Bundschuh et al., 2007). Temporally, there is little difference between annual mean temperature in January (AJAMT) and in July (AJUMT) for the lowlands. Spatially, AJAMT and AJUMT both decrease with increasing elevation. For example, AJAMT ranges from 26℃ in the coastal region to 6.25℃ in the Cordillera de Talamanca area (3820 m a.s.l) (Winograd et al., 2000; Bundschuh et al., 2007).

Glacial History

Geomorphological evidence for the existence of glaciers during late Quaternary in Costa Rica exists in the Highlands, although there are no glaciers in Central America today (Seltzer, 1994; Benn and Gemmell, 1997; Kaser and Osmaston, 2002). Talamanca Cordillera contained the most extensive glaciers in Costa Rica during the late Quaternary (Orvis and Horn, 2000). The rapid rise of the Talamanca Cordillera, beginning ~1 million years ago, formed peaks high enough (> 3300 m) to exceed equilibrium line altitudes (ELAs, where steady-state glacier mass balance is zero) facilitating glacier development (Orivis and Horn, 2000; Lachniet and Seltzer, 2002; Lachniet, 2007). Chirripó National Park (Chirripó N.P.) contains some of the best evidence of past glacial extents in the Talamanca Cordillera. Moraine limits and glacial geomorphology in Chirripó N.P. have been used to determine the spatial extent of glaciers during late Quaternary for this region. Glaciers mainly existed above 3300 m asl (Weyl, 1956; Hastenrath, 1973) with the upper glacial limit located at 3700 m asl and the lower ice limit extending down to the U-shaped or V-shaped valleys at transition zones in Chirripó N.P. and valleys surrounding Cerro Chirripó (3842 m asl, the summit in Chirripó, N.P., also the highest peak in Costa Rica) (Orvis and Horn, 2000; Lachnient and Seltzer, 2002). The glaciated areas in Chirripó N.P., outside of Chirripó N.P. and Cerro de la Muerte, and around Cerro Kámuk are estimated to be ~35 km^2, ~5 km^2, ~5 km^2, ~ 2 km^2 respectively (Van Uffelen, 1991; Lachnient and Sltzer, 2002) during the late Quaternary.

The glacial history of Costa Rica has also been inferred from studies reconstructing ELAs using changes in the position of treeline and through the analysis of lake sediment records. The estimated ELA in Costa Rica today is 5000 ± 200 m; whereas, during the late Quaternary the ELA was 3500 m. The decrease in ELA of 1500 ± 200 m is assumed to be the result of an 8.1

±1.1 ^{o}C temperature decrease in the Highlands during the late Quaternary (Hooghiemstra et al., 1992; Bundschuh et al., 2007). Glacial expansion in Chirripó N.P. during the LGM is indicated by a decrease in timberline at ~18,000 ^{14}C cal yr BP (Hooghiemstra et al., 1992; Lachniet and Seltzer, 2002). However, evidence of glacial expansion in Chirripó N.P. during the Younger Dryas (12,900 to 11,600 cal yr BP) is inconclusive. A temperature reduction of 2-3^{o}C, inferred from a montane pollen profile, appears to provide evidence of limited cooling during the Younger Dryas (Orvis and Horn, 2000; Islebe and Hooghiemstra, 1997); however, lake sediments from tarns in Morrenas valley, Costa Rica clearly indicate that glaciers retreat to above 3500 m asl prior to 10,140 ± 120 ^{14}C cal yr BP (Horn, 1990; Horn, 1993).

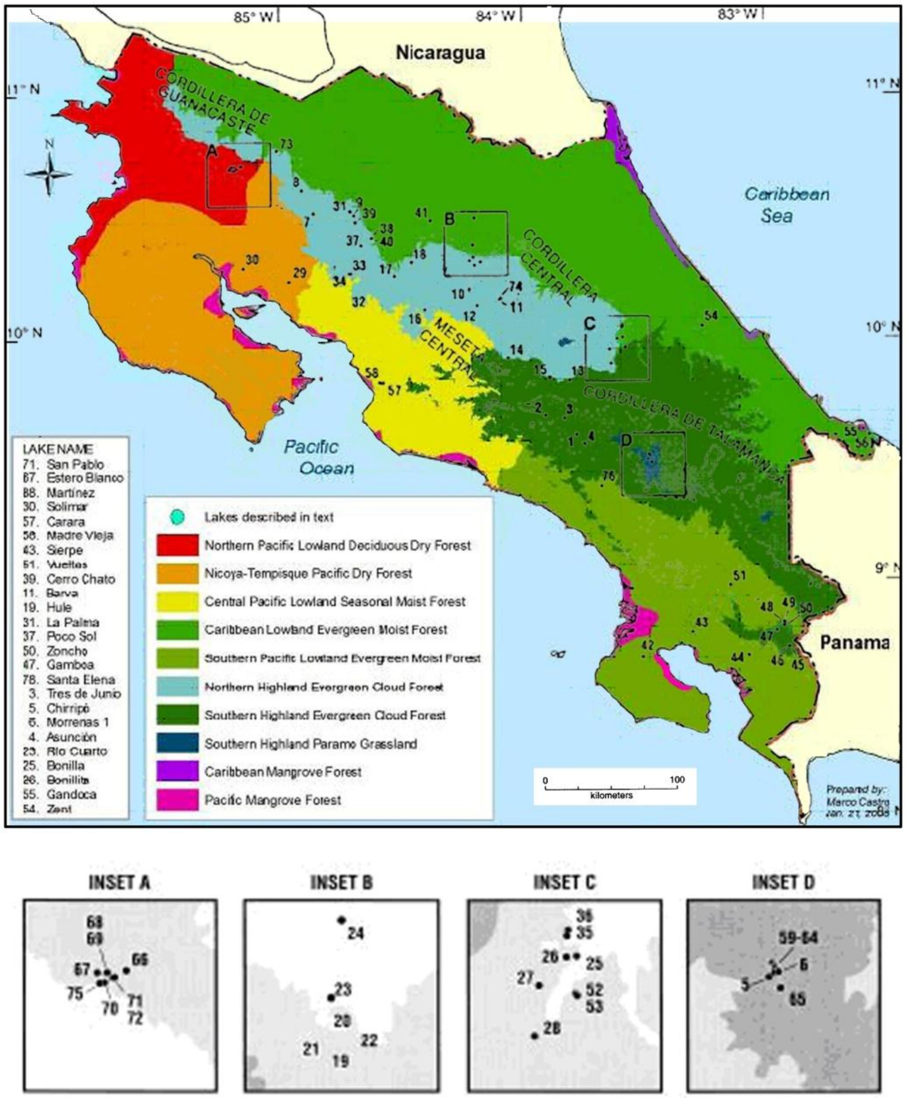

Figure 2.1 Location of lakes in the fifty-four Costa Rican lake calibration set and regional vegetation types (Haberyan et al., 2003; Horn and Haberyan, in press; modified by Wu).

Vegetation

Relying on Holdridge et al. (1971) and Tosi (1969), Costa Rica is divided into ten vegetation-based zones: (1) mangrove swamp, (2) tropical dry forest, (3) derived savanna, (4) tropical moist forest, (5) tropical wet forest, (6) lowland freshwater swamp, (7) premontane rain forest, (8) montane rain forest, (9) montane bog, and (10) páramo (Rodgers and Horn, 1996). Common vegetation types in Costa Rica include black mangrove (*Laguncularia racemosa*), leguminous trees, dwarf bamboos, palm species, tree ferns, woody vines, African grasses (*Hyparrhenia rufa*) and herbaceous epiphytes (Hartshorn, 1983; Rogers and Horn, 1996).

The fifty-four lakes documented in the training set are scattered in seven vegetation zones based on the classification of Horn and Haberyan (*in press*) (Figure 2.1). Located near central Costa Rica, the northern highland evergreen cloud forest, the southern highland evergreen cloud forest and the southern highland Paramo grassland are dotted with the greatest number of lakes in this study, with nine, twelve and nine lakes respectively (Horn and Haberyan, *in press*). There are eight recorded lakes in the deciduous dry forest in the north, two in the Nicoya-Tempisque dry forest in the northwest and three in the seasonal moist forest of the Pacific lowlands in the west. These forests covering northwestern Costa Rica generally have annual precipitation less than 2000 mm. (Horn and Haberyan, 1993; Haberyan et al., 2003; Horn and Haberyan, *in press*).

Settlement History

Costa Rica is situated in an archaeological region, known as the Intermediate Area or the "Chibchan-Chocoan Cultural Area", which covers both lower Central America and northwestern South America (Cooke and Ranere, 1992; Lange, 1992; Fonseca, 1993). Evidence from archaeology, genetics and linguistics suggests that the indigenous groups living in southern

Costa Rica and western Panama reflect thousands of years of continuous human occupation and cultural tradition. Laguna Zoncho, is found within a region of the Chibchan-Chocoan Cultural Area known as Greater Chiriquí. The Greater Chiriquí encompasses a significant portion of southern Pacific Costa Rica and western Panama. Laguna Zoncho lies in one of the Greater Chiriquís subregions --- Diquís subregion.

Research in the Greater Chiriquí has identified the existence of three discrete periods relating to human occupation of the Greater Chiriquí: (1) Aguas Buenas Period ~300 BC – 700 AD (Blanco and Mora, 1994); (2) Chiriqui Period (pre-contact period) 800 AD — 1500 AD (Quilter and Blanco, 1995; Baudez et al., 1996; Corrales, 2000); (3) Conquest Period 1500 AD – onward.

Aguas Buenas represents a time of widespread communication, evidenced primarily by common modes of decoration on pottery, and during this period, communities became smaller and more dispersed (Lange, 1996). However, the timing and the nature of the agricultural conditions that existed during the Aguas Buenas phase remain controversial (Linares and Sheets, 1980). For example, Linares and Sheets (1980) argue that the population of Costa Rica expanded during the Aguas Buenas period in response to the introduction of maize cultivation to the Diquís subregion in the latter half of the first millennium BC; whereas, Hoopes (1996) suggests that increase in population and the development of social complexity during the Chiriquí phase coincided with the introduction of maize in southern Costa Rica at ~700 AD (Hoopes, 1996). Furthermore, Drolet (1988) argues that in southern Costa Rica Aguas Buenas peoples were more likely dependent on wild food instead of cultivated maize, and Correles et al. (1988) point out that manioc, not maize, was mainly planted by village horticulturalists in the Diquís subregion between 1500 and 300 BC.

More recent paleoecological studies, focusing on documenting the timing of maize cultivation in the Diquís subregion, have revealed evidence for the presence of maize in this region for over 3,000 years (~1300 BC – 1950 AD). Clement and Horn (2001) report the presence of maize pollen in lake sediment recovered from Laguna Zoncho in the southern highlands of Costa Rica dating back to approximately 3000 cal yr BP. Behling (2000) documents the existence of maize pollen in Laguna Volcán, located in the western highlands of Panama, dating back to 1800 cal yr BP (150 AD). Conclusions from these palaeoecological studies prove that cultivation of maize occurred in southern Costa Rica and western Panama before the Aguas Buenas Period and also substantiate the claim that maize cultivation existed in both the Diquís and Greater Chiriquí regions during the Aguas Buenas and Chiriquí cultural phases (Anchukaitis and Horn, 2005).

In the Chiriquí phase, material culture in Greater Chiriquí experienced a significant change as evidenced by more elaborate and distinctly different ceramics than the Aguas Buenas phase. Settlements and settlement patterns indicate that communities became larger and more complex (Corrales et al., 1988; Drolet, 1992). Widely planted maize implies great growth in population. The increasing importance of maize production may have contributed to the dissolution of traditional societal linkages and to a transition to more hierarchical organization and ranked societies (Corrales et al., 1988; Drolet, 1992).

The Chiriquí phase ended with the arrival of the Spanish in the early 16th century. In 1502 AD, Christopher Columbus explored the Caribbean coast of Costa Rica during his fourth voyage. In 1519 AD, Juan de Castañeda and Hernan Ponce de Leon arrived at the Golfo Dulce on the southern Pacific coast near Golfito (Corrales et al., 1988). Juan Vásquez de Coronado’s expedition in 1562–1563 AD involved invading a large indigenous village, Coctú, in the Rio

Térraba- Coto Brus Valley (Fernández-Guardia, 1913). During the expedition, Coronado documented the presence of large cultivated maize, beans and fruit trees in the region, as well as the occurrence of widespread warfare over territory and property between territorial chieftains (Fernández-Guardia, 1913).

During the Spanish conquest and more recent European colonization of the region, indigenous settlement survived, though the native population dropped dramatically due to war and introduced disease (Masing, 1964). European ceramics and glass discovered in indigenous cemeteries near Paso Real (Quintanilla, 1986) and Potrero Grande (Corrales, 1986) suggest some degree of co-existence between Spanish colonists and post-Contact Diquís subregion groups (Corrales et al., 1988). Southern Pacific Costa Rica remained only lightly settled into the 20th century (Hall, 1985) even after the local arrival of Italians, but only limited demographic data is available for this period.

CHAPTER 3

METHODOLOGY

Calibration Set Development

The midge-based inference model to be developed in this study was based on a fifty-four lake calibration set (Table 3.1; Figure 3.1). The lakes in the calibration set range from 0 m a.s.l to 3520 m a.s.l. The majority of the limnological data used in this study, available in Haberyan et al. (2003), were collected in July 1991 and July 1997 with additional measurements made in March 1998, March 1999 and March 2000. Water samples were typically collected near the middle of the lakes but a few were obtained near the shore due to weather and other constraints.

Most basic geographic information, including names, locations, elevations, and surface area of the fifty-four lakes (Table 3.1, Figure 3.1) were identified using topographic maps (1:50 000 scale*) and complementary aerial photography (1:14 000 scale) for glacial lakes in Chirripó N.P. (Figure 2.1) (Haberyan et al., 2003). Those lakes that failed to be identified in topographic maps or aerial surveys were named based on advice from local villages and lake size was estimated (Horn et al., 1999). The fifty-four lakes were classified as being surrounded by one of ten vegetation types according to Horn and Haberyan (in press) (Table 3.1, Figure 2.1).

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*Published by the Instituto Geográfico Nacional de Costa Rica

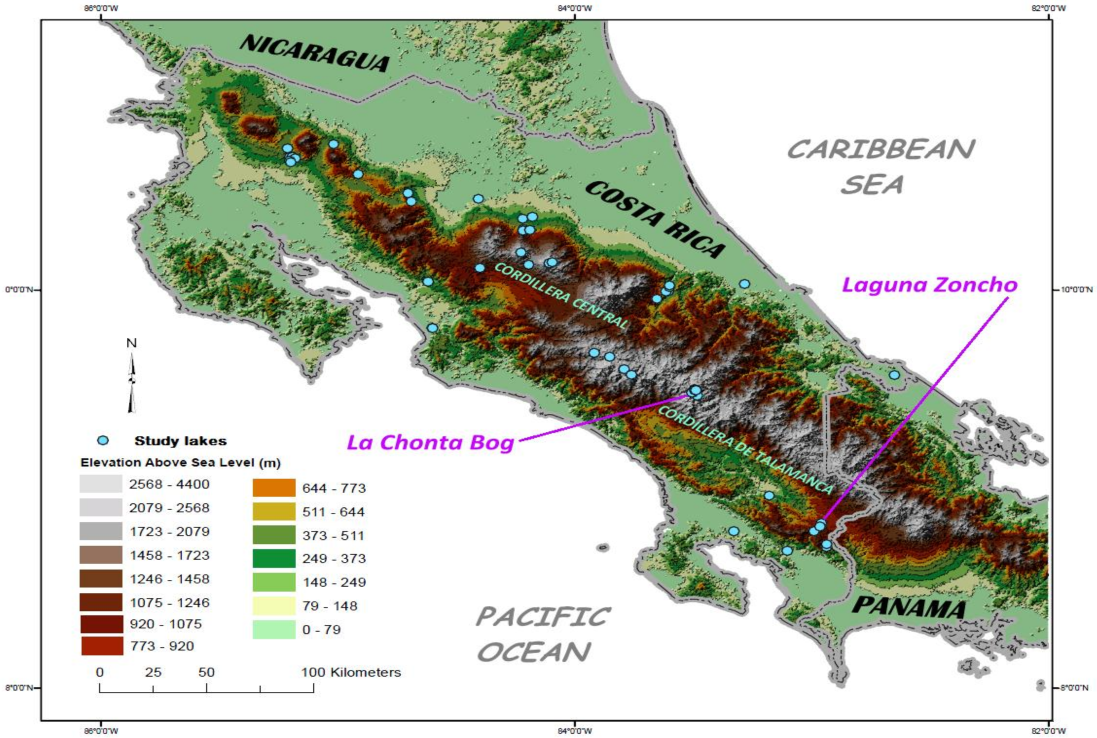

Figure 3.1 Location of La Chonta bog and the lakes incorporated in the Costa Rican calibration set (Clement and Horn, 2001; modified by Wu).

Physical parameters such as water temperature, oxygen, pH, conductivity and transparency, were measured by YSI model 55, Oakton pHW, Hanna HI 8733 and a Secchi disk, respectively (Haberyan et al., 2003). Carbon dioxide was analyzed immediately following sample collection and alkalinity was measured within five hours in the field using LaMotte tests. Water samples collected in 1991 and 1997 were filtered; whereas, water samples obtained in 1998, 1999 and 2003 were not. Sealed samples were returned for additional chemical analyses, including concentration of Ca^{+2}, Mg^{+2}, K^{+}, Na^{+}, Si, and Cl^{-} (Table 3.1) (Haberyan et al., 2003). Monthly mean air temperature for the past ten years (1997-1988 AD) was based on interpolated data from NOAA NCEP CPC GHCN_CAMS gridded Air Temperature database and applied in development of inference model.

Late Holocene Lake Sediment

Laguna Zoncho (8.813°N, 82.963°W) is a small (0.75 ha) lake located near the southern border of Costa Rica. Laguna Zoncho (1190 m asl) lies on the eastern slope of the mountain Fila Costeña in the Greater Chiriqí archaeological region, with Coto Brus Valley and the town of San Vito located down valley (Figure 3.2, Figure 3.3) (Snarskis, 1981; Clement and Horn, 2001). Laguna Zoncho is situated in Tertiary volcanic rocks and Barú tephra (Behling, 2000; Clement and Horn, 2001).

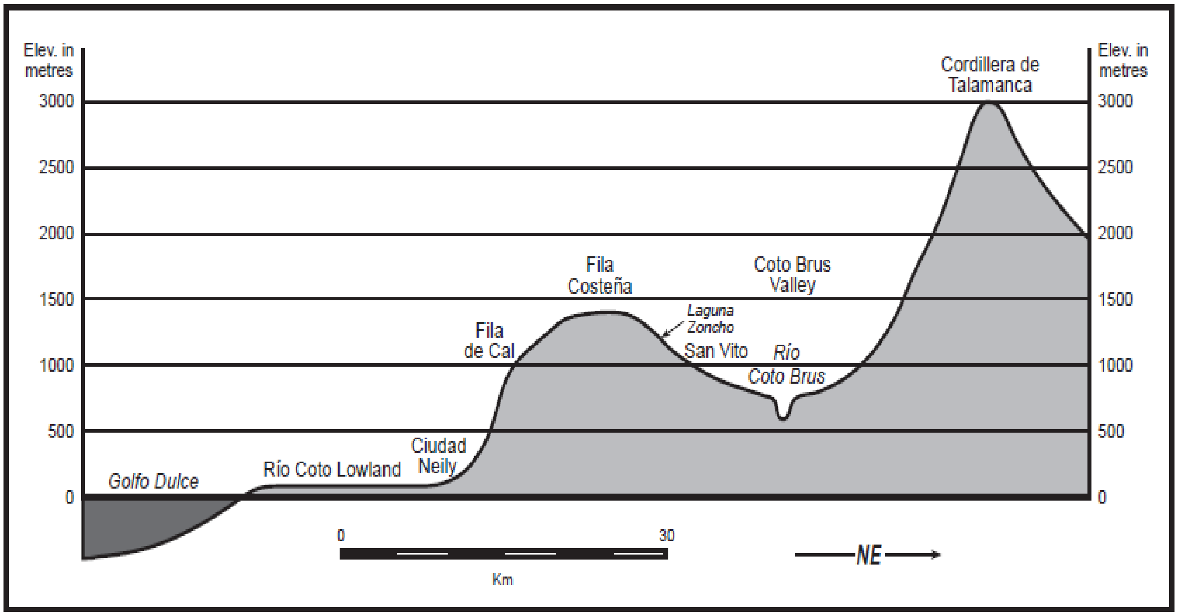

Figure 3.2 Profile across part of southern Costa Rica illustrating the topographic setting of Laguna Zoncho and other locations mentioned in text (Clement and Horn, 2001).

Figure 3.3 A photo of Laguna Zoncho (Picture by Sally P. Horn, 1997).

In 1997 a 6 m lake sediment core was recovered from the center of Laguna Zoncho, a small natural lake (0.8 ha, 2.6m deep) (Hayberan et al. 2003). Laguna Zoncho was possibly formed by faulting or large-scale slumping, or by damming behind slumped debris (Haberyan et al., 2003). Flocculent surface sediment (upper 1.13 m) and deeper sediment were recovered using a plastic tube sealed by a fitted rubber piston and Colinvaux locking piston corer, respectively. The sediment cores were tagged, and wrapped with plastic film and aluminum foil before being sent to University of Tennessee for storage at a constant temperature of 4 ^{o}C (Clement and Horn, 2001; Haberyan and Horn, 2003; Lane et al., 2004; Haberyan and Horn, 2005). To facilitate comparison with the previous studies of pollen, diatom, charcoal and stable isotope ratios in Laguna Zoncho (Clement and Horn, 2001; Lane et al., 2004; Haberyan and Horn, 2005), the midge study will focus on the upper lacustrine section (0-290 cm) which spans the interval from ~3100 cal yr BP to 1997 AD. Chronologic control is provided by three AMS radiocarbon dates on wood and charcoal, seeds and leaf fragments, and the tephra associated with the eruption of Volcán Barú** at 500±60 cal yr BP (Behling, 2000). Further details regarding the Laguna Zoncho chronology are available in Clement and Horn (2001).

Laboratory Analyses

Chironomid samples were analyzed following standard procedures as outlined in Walker (2001). Identification of the subfossil chironomid remains extracted from the surface sediments and Zoncho lake sediments relied primarily on Epler (2001), with Brooks et al. (2007) and Eggermont et al. (2008) providing additional diagnostic information. Reference material from the western United States, stored at the Department of Geography, The University of Georgia was also relied upon.

The stratigraphy and color of the sediments were determined by visual inspection and the use of a MUNSELL soil color chart. The sediment was treated with 5% KOH solution to facilitate the break-up of colloidal matter (Figure 3.4). A known volume (usually 0.5-2 ml) of sediment was placed in a beaker with 50 ml of 5% KOH and heated at 50°C for approximately

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** 35 km east of Laguna Zoncho near northwest boundary of Panama

30 minutes. The deflocculated sediment was washed through a 95 μm mesh using distilled water and the material retained on the mesh was backwashed into beaker. A dissection microscope at 50X and a Bogorov plankton counting try was used to separate the chironomid head capsules from the sediment matrix. The midge remains were permanently mounted on slides in Entellan for identification. Taxonomic identification, done at 400X, is typically to genus (Figure 3.4). Midge samples from the Laguna Zoncho were analyzed at a 2 cm resolution (~ 25 yr/ sample).

Figure 3.4 Procedure for extracting and identifying subfossil midge remains. (A) Sediment is treated with an 8% KOH solution and heated at 50°C for ~30 minutes to facilitate the break-up of colloidal matter. (B) A dissection microscope at 50X and a Bogorov plankton counting tray are used to separate the chironomid head capsules from the sediment matrix. (C) The chironomid remains are permanently mounted on slides in Entellan for identification. (D) Chironomid head capsules prepared for making permanent slides. (E) A photograph of a *Chironomus* head capsule at 400x.

Statistical Analyses

Quantitative reconstructions of paleoenvironmental change include a number of steps: (1) describing the general patterns in the modern distributions of midges in the fifty-four lake training set and determining the type of direct ordination analysis, (2) evaluating the relationship existing between modern chironomid assemblages and measured limnological environmental variables, (3) developing an inference model for a specific environmental variable and assessing the robustness of the model, (4) applying the transfer function or inference model to downcore assemblages to reconstruct environmental change (Birks, 1995; Porinchu and MacDonald, 2003).

The first step, which involved detrended correspondence analyses (DCA), a form of indirect gradient analyses, was used to identify patterns of variation in the distribution of chironomids in the surface training set and the length of the environmental gradients captured by the training set to determine whether the following constrained ordinations should be based on a linear or unimodal response models (terBraak and Prentice, 1988; Pienitz et al., 1995; terBraak and Verdonschot, 1995). The length of DCA axis 1 and axis 2 were 3.27 and 3.15 standard deviation units, respectively. The eigenvalues of the first two axes in DCA were 0.44 and 0.26, indicating these two axes captured 70% of the variance in the chironomid assemblages. The results of the DCA indicate that the midges in the calibration set are responding in a unimodal fashion to the underlying environmental gradient. The form of direct gradient analysis most appropriate to assess relationships between midge distribution and environmental variables when long environmental gradients have been sampled is canonical correspondence analysis (CCA) (terBraak and Verdonschot, 1995; Birks 1995).

The second step, evaluating the correspondence between midge distribution and measured limnological variables, was achieved using canonical correspondence analysis (CCA). A series of CCAs, constrained to individual predictor variables, i.e. environmental variables, was implemented to determine a subset of the environmental variables that explain a statistically significant amount of variation ($P \leq 0.05$) in the chironomid distributions using Monte Carlo permutation tests (499 permutations). Four variables were identified as accounting for a statistical significant amount of variance: SWT, JMAT_10, AMAT_10 and SATA_10. This subset of predictor variables was analyzed for variance inflation factors (VIFs) and variables with high VIFs were removed at one time, until the VIFs of the remaining variables were less than 20x (Birks 1998), leaving SWT and SATA_10. The amount of statistically significant and independent variance captured by SWT and SATA_10 was determined using a series of partial CCAs.

All numeric analyses were undertaken on chironomid taxa that were present in at least two lakes with a relative abundance of 2% in at least one lake; taxa that did not meet this criterion were removed from further analysis. The relative abundance of the chironomid taxa were square-root transformed to optimize the ‘signal’ to ‘noise’ ratio and stabilize the variance in the chironomid data (Prentice, 1980). In all DCAs and CCAs, rare taxa were downweighted. CANOCO 4.5 (ter Braak and Šmilauer 2002) was used to implement all ordination analyses.

In the third step, a midge-based transfer function or inference model for temperature was created using statistical approaches commonly used in quantitative paleolimnology such as, weighted- averaging (WA), weighted-averaging partial least squares (WA-PLS) and partial least squares (PLS). Transfer functions can be considered: reliable if > 90% of the subfossil taxa used in the reconstruction occur in modern calibration set; and very reliable if > 95% of the taxa are present in the training set (Birks, 1998). The second method used to assess the reliability of an inference model is jackknifing (Birks, 1998). Jacknifing is a form of cross validation that is used to estimate the bias and standard error (variance) of a statistic in statistical inference.

The midge-based SWT transfer function developed from the modern calibration set was applied to the late Holocene sediment core recovered from Laguna Zoncho in the southern highlands of Costa Rica to reconstruct the past fluctuations in the lake surface water temperature (from ~3100 cal yr BP to 1997 AD). The Holocene chironomid percentage diagram, using square-root transferred taxa data, was plotted and zoned by C2 (Juggins, 2003). The zonation is based on a constrained incremental sum of square cluster-analysis implemented using ZONE and BSTICK (Bennett 1996). Each sample contained a minimum of 50 identified midge head capsules with the exception of the samples between 136 and184cm where an insufficient number of head capsules were recovered and did not meet the screening criterion. The midge-based temperature reconstructed for Laguna Zoncho was compared to existing paleoenvironmental data from Laguna Zocho which includes pollen, diatom and stable carbon isotope ratios (Clement and Horn, 2001; Lane et al., 2004; Haberyan and Horn, 2005).

Table 3.1 Geographic and limnological data for the fifty-four Costa Rican lakes calibration set (Horn, 1990; Horn, 1993; Horn and Haberyan, 1993, in pressing; Horn, 2007). Units of concentration for O_2, CO_2, Alk, Ca^{+2}, Mg^{+2}, K^+, Na^+, Si, Cl^- are mg/L.

#	Name	Lat (°N)	Lon (°W)	Ele (m)	Depth (m)	T ℃	PH	Conduct ($\mu S\,cm^{-1}$)	O_2 ($mg\,l^{-1}$)	CO_2 ($mg\,l^{-1}$)	Alk ($mg\,l^{-1}$)	Ca^{+2} ($mg\,l^{-1}$)	Mg^{+2} ($mg\,l^{-1}$)	K^+ ($mg\,l^{-1}$)	Na^+ ($mg\,l^{-1}$)	Si ($mg\,l^{-1}$)	Cl^- ($mg\,l^{-1}$)
1	Quebr	9.603	83.790	3040	2	13.2	6.7	0	6.4	4	23	2.14	0.42	0	2.9	9.05	1.48
2	Canon	9.685	83.916	2480	1.3	21.3	5.6	0	4.1	6	5	7.83	0.61	1.07	1.51	1.85	2.61
3	Tres	9.666	83.851	2670	0.7	15	5.2	30	5.8	12	3	1.68	0.33	5.2	7.28	0.36	9.38
4	Asun	9.575	83.759	3340	1	12.3	4.9	0	6.9	3	0	0.76	0.17	1.13	3	0.72	9.43
5	Chi1	9.484	83.498	3520	22	12.8	5.4	0	5.2	3	8	1.23	0.17	0	0.81	0.93	0.42
6	Moren1	9.494	83.489	3477	8.3	14.6	7.3	0	6.6	3	10	1.86	0.2	0.57	1.37	1.84	1.27
8	Cote	10.583	84.913	650	11	25.1	7.2	20	8.3	3	26	2.38	0.94	1.21	3.85	4.62	7.55
10	Botos	10.188	84.225	2600	5	13.8	4.4	30	7.3	6	1	2.68	0.6	2.5	2.2	2.4	6.51
11	Barva	10.135	84.107	2840	7.9	11.7	7.5	60	8	4	9	0.63	0.32	1.39	7.41	0.84	9.49
12	Fraij	10.127	84.193	1650	6.2	21	7.3	90	8.8	4	69	8.51	3.84	4.35	8.17	7.96	9.51
16	Seraf	10.111	84.399	1140	0.7	21.3	6.7	100	6.2	15	100	12.91	3.94	1.78	5.13	26.91	3.39
19	Hule	10.296	84.216	740	19.9	21.1	6.5	78	9.2	5	60	7.88	2.48	1.47	3.97	13.47	2.82
20	Congo	10.306	84.216	740	14.6	25.7	6.5	60	6.8	3	3	0.91	0.26	0	0.94	2.8	9.52
21	Bosqu	10.299	84.217	740	4	24.9	6.4	60	10.4	0	11	6.7	1.71	0.9	5.05	12.71	8.66
22	Maria	10.302	84.187	770	6.9	25.1	5.7	60	6	6	12	4.68	1.14	1.71	4.24	7.57	9.14
24	Sisab	10.369	84.177	160	3	28	6.4	20		5	12	1.51	0.5	0.98	3.96	3.66	9.54
25	Bonla	9.994	83.604	380	27	27.4	7	139	6.7	4	97	8.6	5.16	2.84	4.9	16.45	1.7
26	Bonta	9.993	83.614	450	20	23.9	7	19	5.8	5	23	2.36	1.16	1.13	2.1	3.78	1.6
27	Azul	9.956	83.652	630	2		7.2	240		13	174	18.96	3.94	5.24	31.7	4.82	9.44
31	LaPalma	10.488	84.702	570	10.8	25.7	8.2	293	11.3	6	130	21.64	17.21	2.82	15.02	25.53	10.68
35	LanctAb	10.015	83.598	330	16.9	25.3	7.2	246	8.5	6	81	12.6	6.24	2.74	6.48	20.48	2.77
36	Lanar	10.023	83.598	430	2	22.4	6.9	108	4.8	21	64	8.25	4.13	1.6	6.28	15.45	2.69
38	Cocor	10.043	84.618	520	1	29.8	7.4	114	7.8	6	19	1.76	0.74	0.86	2.46	5.42	2.6
39	C.Chato	10.444	84.689	1050	17.9	21.2	7.2	28	7	3	8	0.3	0.1	0	1.2	0.3	2
40	SanFran	10.458	84.405	90	2.5e	25.9	8	144	6.8	6	72	10.8	5	1.6	6.5	22	3.5
43	Sierpe	8.789	83.327	16	2.2	33	7.1	102	6.6	6	48	8.9	3.5	0	4.4	9.9	2.6
44	Fost	8.690	83.102	40	1.5	30.4	7.8	89	9.1	6	159	53.83	2.43	0	4.87	11.61	0.7
45	CamDo	8.710	82.937	1036	1.5	26.2	7	54	6.5	9	39	5.69	0.94	0	1.64	6.31	0.3
46	CampoTr	8.723	82.935	1097	2.6		7	44	4.6	10	31	4.2	0.7	0	1	4.5	0.4
47	Gamboa	8.788	82.988	1460	2	21.8	6.9	17	2.8	14	16	0.6	0.3	0	0.6	0.9	0.4
48	Sjoaq	8.830	82.958	976	1	24.4	6.3	41	4.2	17	26	3.9	1.31	0	1.47	4.87	0.7
50	Zonch	8.813	82.963	1190	2.6	24.6	7.4	16	7.1	3	12	0.66	0.2	0	0.84	0.69	0.1
51	Vuelt	8.967	83.178	270	3	29.9	8.7	233	10.1	0	125	21.72	8.43	3.86	7.02	20.95	1.5
54	Zent	10.030	83.282	17	2	29.7	7.5	383	1	18	188	56.24	6.04	1.34	7.28	10.65	5.6
56	SanMigue	9.573	82.648	10	2	31	7	148	2	9	61	15.5	2	2.8	8	5.1	6
57	Carar	9.810	84.600	16	3.5	30.8	8	362	4.4	12	169	35.33	9.24	5.37	18.85	15.05	4.7
58	Madre	9.809	84.598	16	3	32.9	7.6	412	0.6	27	202	44.01	15.05	3.17	12.2	18.38	2
59	MorR	9.503	83.493	3450	1	14.8			4.7			12.25	1.16	0	2.76	6.2	0.19
60	Moren0	9.492	83.485	3496	3	15.6			4.9			2.28	1.98	0.13	1.38	1.74	0.06
61	Moren2	9.495	83.490	3475	1.3	16			4.9			3.79	0.5	0.14	1.55	2.96	0.07
63	Mor4	9.500	83.489	3466	3	17.2			5.2			4.86	0.59	0.08	1.45	2.92	0.03
65	Ditkebi	9.470	83.482	3493	7							4.59	1.33	0.06	1.11	2.27	0.08
67	EstBlanc	10.668	85.201	430	2.8	28.8	7.9	214	7.6	6	75	18.1	6.39	4.63	11.69	15.07	4.47
69	Los Jun	10.668	85.191	440	1.7	30.8	7.5	119	10.7	4	56	9.25	3.36	8.46	7.62	11.11	5.94
71	Spabl	10.662	85.179	450	2.5	29.1	9.5	176	12		95	17.72	2.37	6.46	15.71	28.33	7.24
73	Ramir	10.732	85.017	570	2.5							4.71	1.68	2.45	3.36	8.7	3.16
74	Copey	10.139	84.093	2460	2							0.2	0.2	1.1	0.3	0.7	8.7
75	Brisa	10.649	85.201	390	3	25.9	6.2		3.4	46		11.75	4.02	4.75	8.52	10.02	1.53
79	Chi2	9.483	83.501	3495	4	14.2						3.87	0.19	0	0.9	0.65	0.1
80	Chi3	9.484	83.504	3457	4	13.9						5.69	0.42	0	2.66	1.55	0.1
81	Mor3a	9.497	83.491	3494	0.3	16.9						2.08	0.2	0.14	1.15	1.85	0.18
82	Mor3c	9.497	83.487	3492	1.5	14.8						0.34	0.11	0	0.58	1.37	
87	Sorpr	10.711	85.211	570	0.8	27.6	6.7	145	0.6	23	60	8.91	2.7	4.11	12.21	3.96	5.4
88	Martg	10.642	85.197	330	3.6	25.5	6.4	45				28.02	8.87	5.7	24.54	33.32	4.81

Table 3.2 Ten-year (1988-1997) mean air temperature for Costa Rica extracted from the NOAA NCEP CPC GHCN_CAMS gridded air temperature data (at 0.5° longtitude x 0.5° latitude of spatial resolution). The three types of air temperature used in this study are SATA_10 (summer air temperature average for the interval of 1988-1997), AMAT_10 (annual mean air temperature for the interval of 1988-1997) and JMAT_10 (July mean air temperature for the interval of 1988-1997). (http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.CPC/.GHCN_CAMS/.gridded/.deg0p5/.temp/).

Lon(W)	Lat(N)	SATA_10	AMAT_10	JMAT_10
-87.25	12.75	28.4	27.9	27.7
-86.75	12.75	26.3	25.9	25.2
-86.75	12.25	27	26.7	26.2
-86.25	12.75	24.1	24	23.7
-86.25	12.25	26.5	26.4	25.7
-86.25	11.75	27.5	27.1	26.1
-85.75	12.75	24.1	24	23.3
-85.75	12.25	25.9	25.7	24.7
-85.75	11.75	26.1	26	25.8
-85.75	11.25	27.2	27.1	26.8
-85.75	10.75	27	26.6	26.5
-85.75	10.25	29.4	28.6	28.1
-85.25	12.75	23.9	24	23.6
-85.25	12.25	25.2	25.1	24.5
-85.25	11.75	26.7	26.5	26
-85.25	11.25	26.6	26.4	26.3
-85.25	10.75	27.8	27.4	27.2
-85.25	10.25	28.5	27.7	27.3
-85.25	9.75	29.6	28.7	28.1
-84.75	12.75	24.1	24.3	24
-84.75	12.25	25.2	25.2	25
-84.75	11.75	26.2	26	25.8
-84.75	11.25	26.4	26.2	26.2
-84.75	10.75	28.2	27.6	27.4
-84.75	10.25	28	27.4	27.1
-84.75	9.75	28.1	27.4	27
-84.25	12.75	25.5	25.8	26.3
-84.25	12.25	25.4	25.9	26.3
-84.25	11.75	26.3	26.4	26.9
-84.25	11.25	26.8	26.7	27
-84.25	10.75	25.6	25.3	25.5
-84.25	10.25	24.7	24.3	24.4
-84.25	9.75	24.6	24	24.1
-84.25	9.25	25.6	24.9	24.7
-83.75	12.75	26.5	27	27.9
-83.75	12.25	26.5	27.1	28
-83.75	11.75	26.2	26.7	27.5
-83.75	11.25	27	27.3	27.9
-83.75	10.75	25.1	25.1	25.5
-83.75	10.25	21.9	22.4	22.8
-83.75	9.75	20.9	21.3	21.5
-83.75	9.25	22.7	22.3	22.4
-83.75	8.75	25	24.4	24.2
-83.25	10.25	25.4	26	26.3
-83.25	9.75	23.8	24.3	24.5
-83.25	9.25	23.1	23.3	23.4
-83.25	8.75	22.5	22.3	22.4
-83.25	8.25	26.5	26	25.6
-82.75	9.75	23.6	24.3	24.6
-82.75	9.25	21.4	21.8	22.1
-82.75	8.75	21	21.1	21.5
-82.75	8.25	27.8	27.3	26.8
-82.25	9.25	22.2	22.6	23.1
-82.25	8.75	22.8	23	23.3
-82.25	8.25	28.1	27.7	27.3
-81.75	8.75	24.7	24.8	25
-81.75	8.25	26.6	26.1	26
-81.75	7.75	28.3	27.5	27.3
-81.25	8.75	25.1	25.1	25.2
-81.25	8.25	26.3	25.9	25.8

Air Temperature Data Estimation

Air temperature measurements were not made during surface sediment collection. Air temperature estimates were obtained from a gridded terrestrial air temperature dataset and extracted using ArcGIS (see Porinchu et al. 2009a; 2010). The raw data extracted from the NOAA NCEP CPC GHCN_CAMS gridded air temperature dataset (at 0.5° longitude x 0.5° latitude of spatial resolution) is provided in Table 3.2 and Figure 3.5. In tropical environments the uppermost lake sediment (1-2 cm) represents approximately 5-10 years of deposition. Therefore, we computed the ten years (1988-1997) mean air temperature for: (1) annual mean air temperature (AMAT_10), (2) July mean air temperature (JMAT_10), and (3) summer air temperature (SATA_10) from the extracted air temperature data and plot the interpolated AMAT_10 and SATA_10 in Figure 3.6 and Figure 3.7. These three variables (AMAT_10, JMAT_10, SATA_10) were included in the environmental environmental dataset used in the direct ordination analysis.

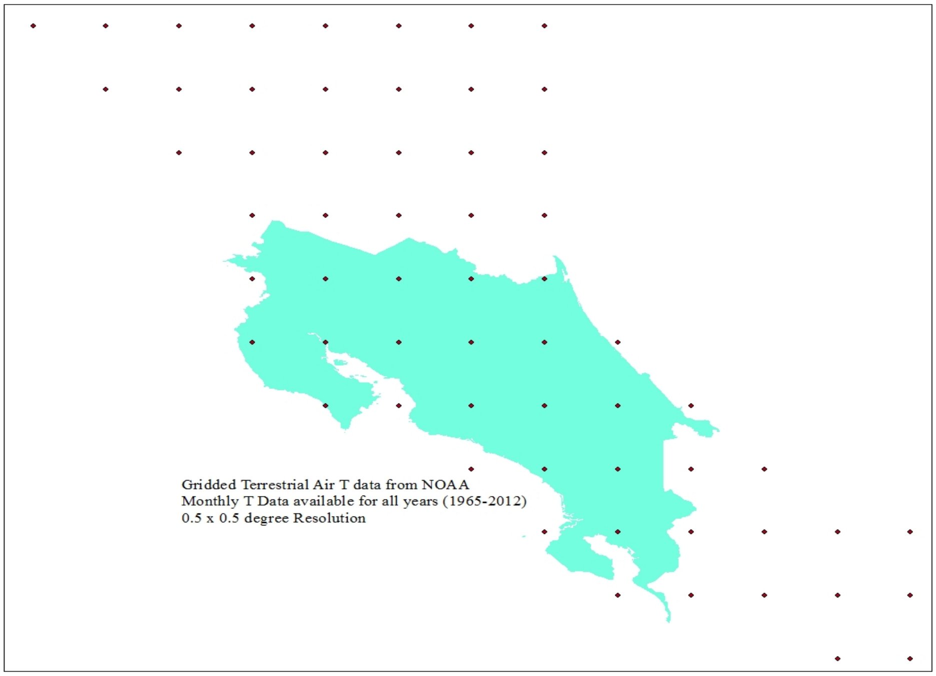


Figure 3.5. Map of grid points associated with gridded air temperature datadaset.

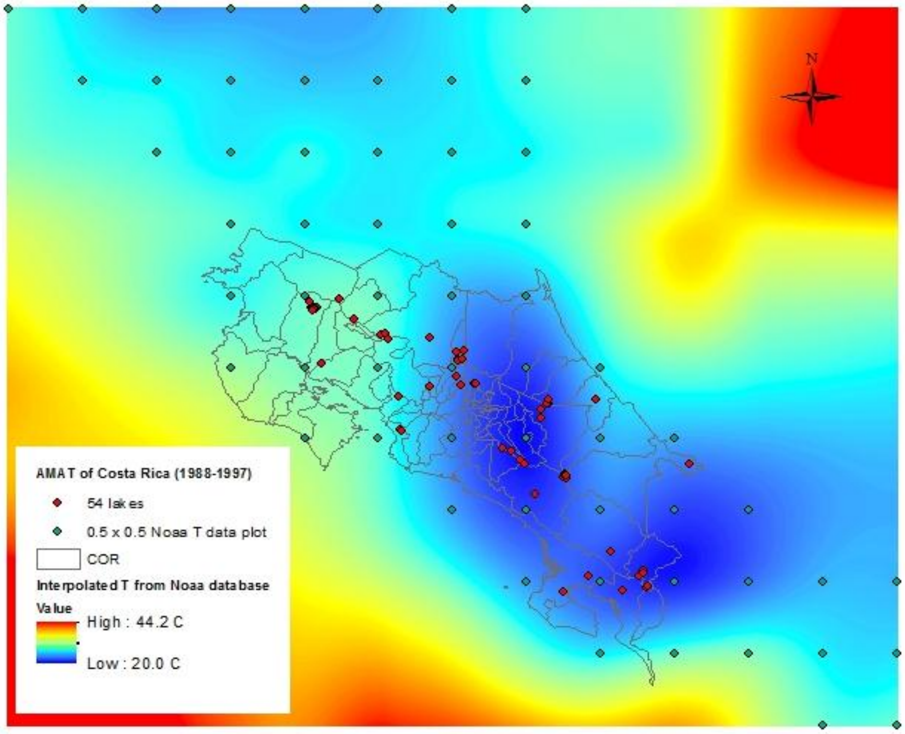


Figure 3.6 Interpolated annual mean air temperature (AMAT_10) from NOAA database (1988-1997). Green dots are the 0.5 x 0.5 grid points, red dots represent the location of the fifty-four lakes included in the calibration set.

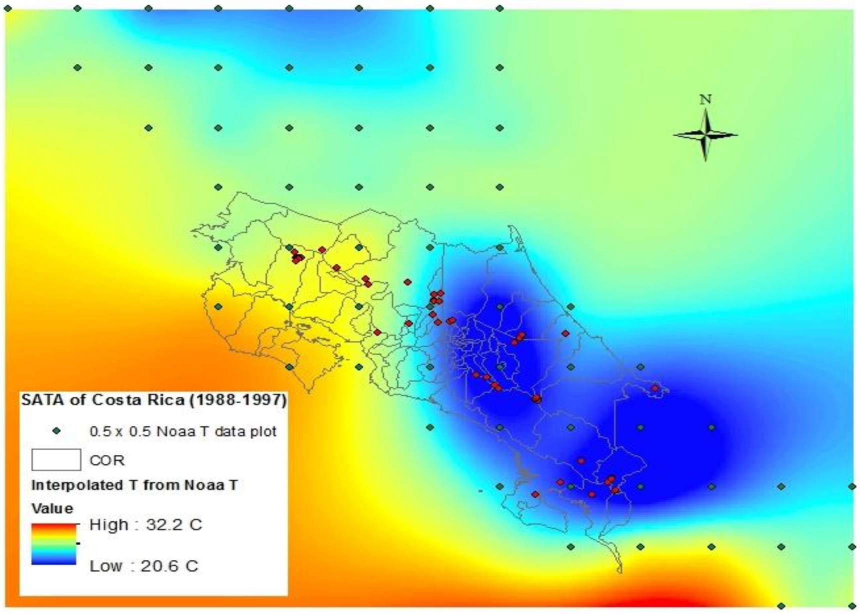


Figure 3.7 Interpolated summer air temperature average values (SATA_10) from NOAA database (1988-1997). Green dots are the 0.5 x 0.5 grid points, red dots represent the location of the fifty-four lakes included in the calibration set.

CHAPTER 4

RESULTS

Modern Distribution of Midges

A total of 62 chironomid taxa, including 4 unknown types, were identified in the fifty-four surface sediment samples. Of the 62 chironomid taxa, 54 taxa met the initial data screening criteria. These 54 taxa accounted for between 96.4% and 100% of the total chironomid remains enumerated per sample. The taxa that were identified in the fifty-four lake calibration set have been displayed in the appendix (Figures A.1-A.3).

The chironomid percentage diagram reveals a strong relationship between elevation and midge distribution. It is important to note that a strong inverse relationship exists between elevation and SWT (see Figure 4.1). For example, Orthocladiinae, such as *Psectrocladius*, *Cricotopus* and *Chaetocladius*, are most abundant in the high elevation lakes with low SWT, but are absent in the lower elevation lakes (Figure 4.2). Chironominae, such as *Cladopelma*, *Geoldichironomus, Beardius resis* type and *Polypedilum* type N occur predominately in low elevation lakes with high SWT. Other Chironominae taxa, i.e. *Chironomus, Micropsectra* and *Tanytarsus*, appear to be eurythermic, with these taxa distributed across the broad elevation and SWT ranges. Tanypodinae such as *Procladius* have a large SWT tolerance, while *Labrundinia* is restricted to warmer lakes found in mid- to low elevations.

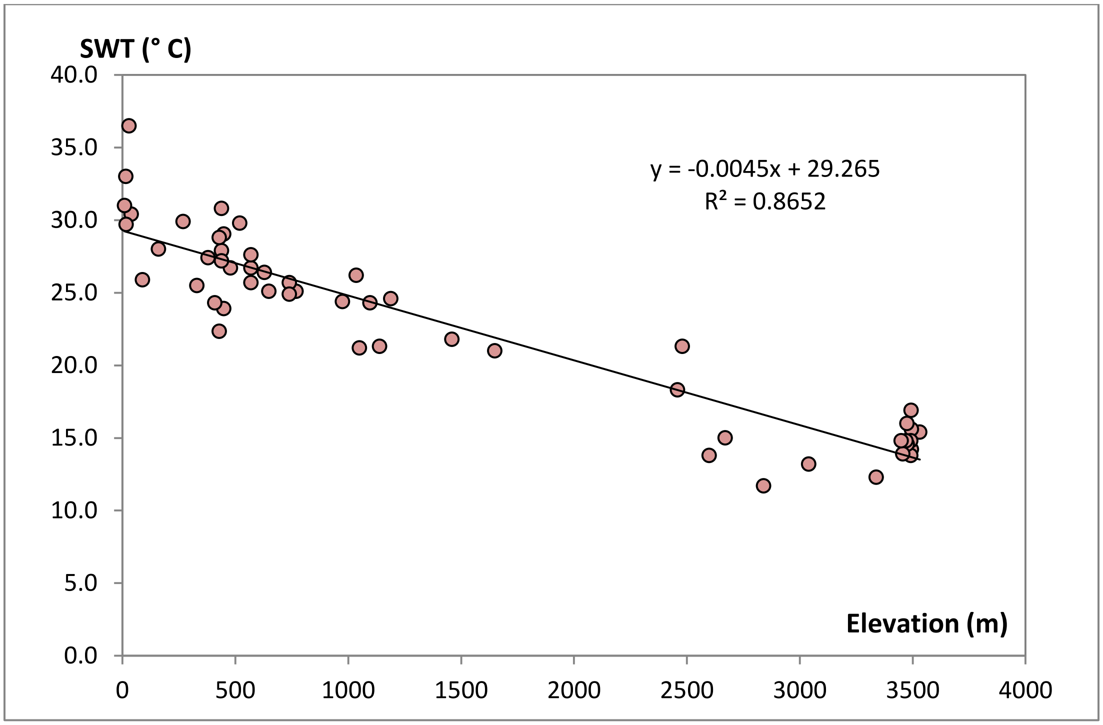


Figure 4.1 Relationship between measured SWT and elevation for the fifty-four lakes in the Costa Rican calibration set.

Table 4.1 Thirty-nine lakes with the full suite of limnological and climate data used in direct gradient analyses. Units of elevation (Ele) and depth (Dep) are meter (m), SWT (ºC) and Condct (µS/cm) are short for surface water temperature and conductivity respectively.

Name	Ele(m)	Depth(m)	SWT	PH	Conduct	O_2	CO_2	Alk	Ca^{+2}	Mg^{+2}	K^+	Na^+	Si	Cl^-	AMAT_10	JMAT_10	SATA_10
Moren1	3477	8.3	14.57	7.29	0	6.6	3	10	1.86	0.2	0.57	1.37	1.84	1.27	22.25	22.39	22.51
Asun	3340	1	12.3	4.93	0	6.9	3	0	0.76	0.17	1.13	3	0.72	9.43	21.46	21.63	21.56
Quebr	3040	2	13.2	6.71	0	6.4	4	23	2.14	0.42	0	2.9	9.05	1.48	21.45	21.62	21.43
Barva	2840	7.9	11.7	7.45	60	8	4	9	0.63	0.32	1.39	7.41	0.84	9.49	23.21	23.45	23.29
Tres	2670	0.7	15	5.23	30	5.8	12	3	1.68	0.33	5.2	7.28	0.36	9.38	21.5	21.69	21.39
Botos	2600	5	13.8	4.39	30	7.3	6	1	2.68	0.6	2.5	2.2	2.4	6.51	24.04	24.23	24.44
Canon	2480	1.3	21.3	5.61	0	4.1	6	5	7.83	0.61	1.07	1.51	1.85	2.61	21.75	21.93	21.68
Fraij	1650	6.2	21	7.3	90	8.8	4	69	8.51	3.84	4.35	8.17	7.96	9.51	23.72	23.93	23.12
Gamboa	1460	2	21.8	6.91	17	2.8	14	16	0.6	0.3	0	0.6	0.9	0.4	21.41	21.66	24
Zonch	1190	2.6	24.6	7.37	16	7.1	3	12	0.66	0.2	0	0.84	0.69	0.1	21.35	21.61	21.47
Seraf	1140	0.7	21.3	6.7	100	6.2	15	100	12.91	3.94	1.78	5.13	26.91	3.39	25.09	25.14	21.34
CampoT	1097	2.6	24.6	7.01	44	4.6	10	31	4.2	0.7	0	1	4.5	0.4	21.39	21.65	25.72
CChato	1050	17.9	21.2	7.24	28	7	3	8	0.3	0.1	0	1.2	0.3	2	27.17	26.99	21.51
CamDo	1036	1.5	26.2	7.01	54	6.5	9	39	5.69	0.94	0	1.64	6.31	0.3	21.43	21.69	27.91
Sjoaq	976	1	24.4	6.33	41	4.2	17	26	3.9	1.31	0	1.47	4.87	0.7	21.33	21.59	21.64
Maria	770	6.9	25.1	5.68	60	6	6	12	4.68	1.14	1.71	4.24	7.57	9.14	23.96	24.18	21.21
Congo	740	14.6	25.7	6.47	60	6.8	3	3	0.91	0.26	0	0.94	2.8	9.52	24.11	24.32	24.33
Bosqu	740	4	24.9	6.41	60	10.4	0	11	6.7	1.71	0.9	5.05	12.71	8.66	24.09	24.3	24.49
Cote	650	11	25.1	7.18	20	8.3	3	26	2.38	0.94	1.21	3.85	4.62	7.55	27.81	27.54	24.45
Azul	630	2	24.6	7.22	240	6.7	13	174	18.96	3.94	5.24	31.7	4.82	9.44	21.72	21.98	28.37
LaPalma	570	10.8	25.7	8.16	293	11.3	6	130	21.64	17.21	2.82	15	25.53	10.7	27.28	27.1	21.57
Sorpr	570	0.8	27.6	6.72	145	0.6	23	60	8.91	2.7	4.11	12.2	3.955	5.4	27.5	27.24	28.09
Cocor	520	1	29.8	7.35	114	7.8	6	19	1.76	0.74	0.86	2.46	5.42	2.6	26.53	26.35	27.93
Cuipilap	480	2	26.7	7.06	94	7	7	47	12.08	5.38	2.15	7.34	23.81	5.1	27.58	27.3	27.31
Bonta	450	20	23.9	6.98	18.5	5.75	5	23	2.355	1.16	1.125	2.1	3.78	1.6	21.99	22.25	28.03
Spabl	450	2.5	29.05	9.5	176	12	7	95	17.72	2.37	6.46	15.7	28.33	7.24	27.57	27.28	21.9
LosJunF	440	1.8	27.9	6.76	136	9.3	7	78	6.19	3.33	7.04	7.67	12.26	4.92	27.55	27.27	28.03
LosJun	440	1.7	30.8	7.53	119	10.7	4	56	9.25	3.36	8.46	7.62	11.11	5.94	27.55	27.27	28.01
Lanar	430	2	22.35	6.89	107.5	4.8	21	64	8.25	4.125	1.595	6.28	15.45	2.69	22.17	22.44	28.01
EstBlanc	430	2.8	28.8	7.9	214	7.6	6	75	18.1	6.39	4.63	11.7	15.07	4.47	27.53	27.25	22.14
Bonla	380	27	27.4	6.98	138.5	6.7	4	97	8.6	5.16	2.84	4.9	16.45	1.7	22.09	22.36	28.03
Vuelt	270	3	29.9	8.72	233	10.1	0	125	21.72	8.43	3.86	7.02	20.95	1.5	22.43	22.53	28.03
Sisab	160	3	28	6.43	20	6.7	5	12	1.51	0.5	0.98	3.96	3.66	9.54	24.01	24.25	22.2
SanFran	90	2.5	25.9	7.97	144	6.8	6	72	10.8	5	1.6	6.5	22	3.5	25.44	25.52	24.33
Fost	40	1.5	30.4	7.83	89	9.1	6	159	53.83	2.43	0	4.87	11.61	0.7	21.92	22.09	26.21
Osa1	30	1.5	36.5	7.08	40	6.5	5	22	0.71	0.53	3.08	0.73	2.28	1.4	23.45	23.38	22.32
Zent	17	2	29.7	7.47	383	1	18	188	56.24	6.04	1.34	7.28	10.65	5.6	24.92	25.14	23.98
Sierpe	16	2.2	33	7.09	102	6.6	6	48	8.9	3.5	0	4.4	9.9	2.6	22.54	22.61	24.26
SanMig	10	2	31	7.01	148	2	9	61	15.5	2	2.8	8	5.1	6	23.04	23.38	22.79

Table 4.2 The ratios of the eigenvalues (λ) of the 1st (constrained) CCA axis to the eigenvalues of the 2nd (unconstrained) CCA axis based on the thirty-nine lake dataset.

Environmental Variable	λ1	λ2	λ1/λ2	% variance	P
SWT	0.246	0.289	0.85	6.4	0.002
AMAT_10	0.121	0.356	0.34	3.8	0.04
JMAT_10	0.12	0.355	0.34	3.7	0.04
SATA_10	0.12	0.356	0.34	3.7	0.044

Table 4.3 Summary of partial CCAs based on chironomid assemblages from the thirty-nine lake training set.

Environmental Variable	Co-variable (s)	λ1	λ2	% Variance	P
SWT	None	0.256	0.441	6.4	0.002
	SATA_10	0.225	0.437	5.9	0.002
	All	0.22	0.43	6.1	0.002
	Lake chemistry	0.197	0.369	7.1	0.008
	Other physical	0.076	0.42	2.1	0.8

All = remaining forward selected variables (JMAT_10, AMAT_10, SATA_10); Lake chemistry = pH, conductivity, O^2, CO^2, Alk, Ca^{2+}, Mg^{2+}, K^+, Na^+,Si, Cl^-; Other physical = depth and elevation.

Constrained ordination analysis was applied to each of the 17 environmental variables individually to determine which of the measured environmental variables could account for a statistically significant amount of variance ($P \leq 0.05$) in the distribution of chironomids in the surface training set. The CCA was based on the covariance matrix of the square-root transformed species data with 99 unrestricted Monte Carlo permutation tests. The number of lakes in the surface training set was reduced from fifty-four to thirty-nine due to the missing values of some environmental variables (Table 4.1). Among the 17 variables, thirteen were removed because of their great collinearity and because they did not account for a statistically significant amount of variance. The variables that were removed were: elevation, depth, Ph, conductivity, O_2, CO_2, alkalinity, Ca^{+2}, Mg^{+2}, $K^{+,}$ Na^+, Si, Cl^-. The explanatory variables remaining in the analysis were: surface water temperature (SWT), annual mean air temperature of 1988-1997 (AMAT_10), July mean air temperature of 1988-1997 (JMAT_10) and summer air temperature average of 1988-1997 (SATA_10). The eigenvalues of the first axis and second axis of a CCA constrained to these four variables was 0.266 and 0.103, respectively. These two axes counted 8.3% of the variance in the dataset. However, the variance inflation factors (VIFs) for AMAT_10, JMAT_10 and SATA_10 were greater than 20X, which indicates that these three environmental variables are highly correlated. JMAT_10 and AMAT_10 were removed one at a time from further analyses until the remaining variables had VIFs below 20X. Therefore, SWT and SATA_10, where identified as the minimal subset of the remaining variables that explained the largest statistically significant amount of variance in the thirty-nine lake calibration set. A CCA with SWT and SATA_10 as the sole constraining environmental variables provided eigenvalues of 0.255 for axis 1 (λ_1) and 0.057 for axis 2 (λ_2) (Table 4.7 and Table 4.8). The total variance in chironomid communities captured by these two axes was 6.40% (Table 4.2) and the species-environment correlations for the first two axes were 84.3% and 60.6% respectively. This suggested that the remaining subset of environmental variables (SWT and SATA_10) still capture a large amount of variance in the chironomid distributions of surface calibration set (Table 4.3). Both axes were statistically significant ($P \leq 0.02$) based on the Monte Carlo permutation tests (499 unrestricted permutations).

A CCA bi-plot with fifty-four samples, 54 taxa and 2 environmental variables is depicted in Figure 4.4 and Figure 4.5. Chironomid species are represented by blue dots, corresponding to their approximate environmental optima (Figure 4.4). Lakes are classified by elevation (Figure 4.5). SWT and SATA_10 are represented by arrows with arrow pointing the the direction of the maximum rate of change (ter Braak, 1987; ter Braak and Prentice, 1988; ter Braak and

Verdonschot, 1995). The length of the arrow represents relative importance of the each environmental variable (ter Braak, 1987; ter Braak and Verdonschot, 1995).

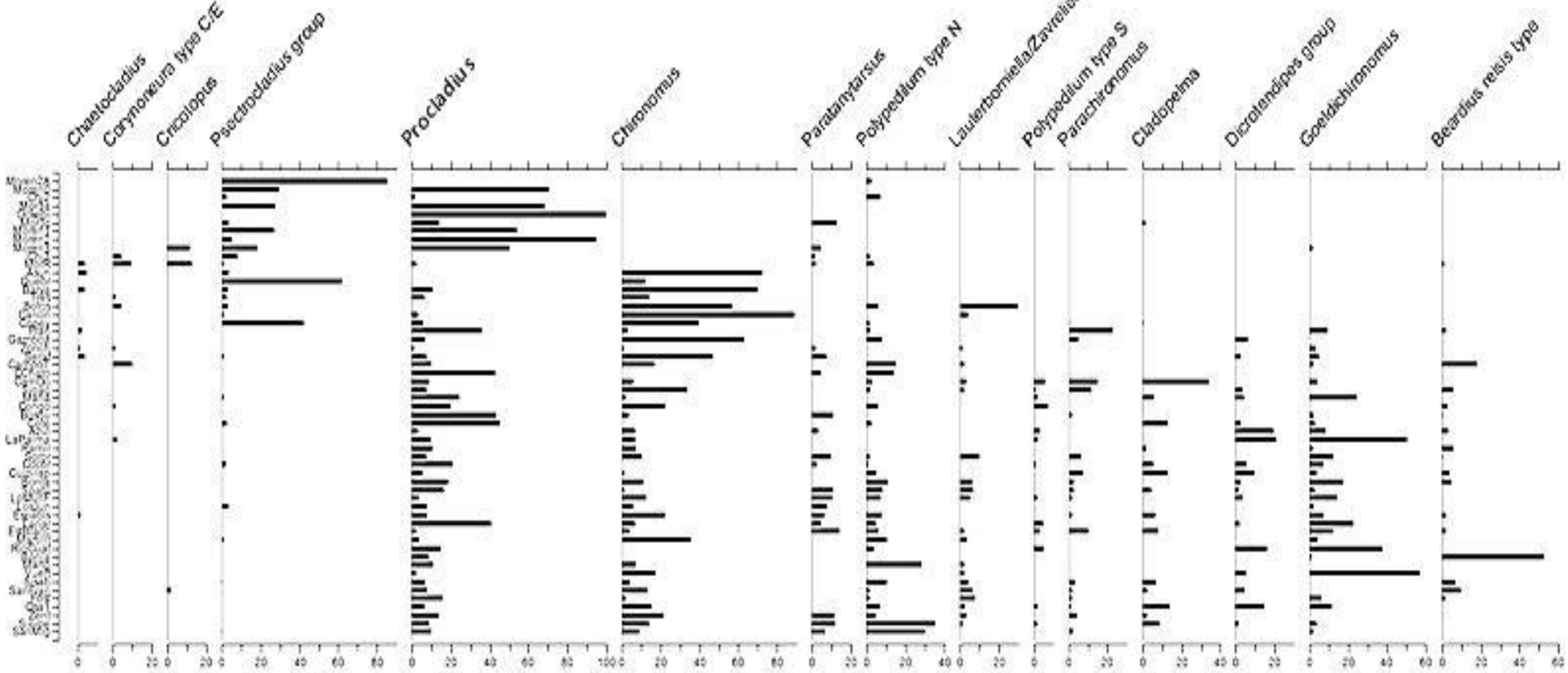
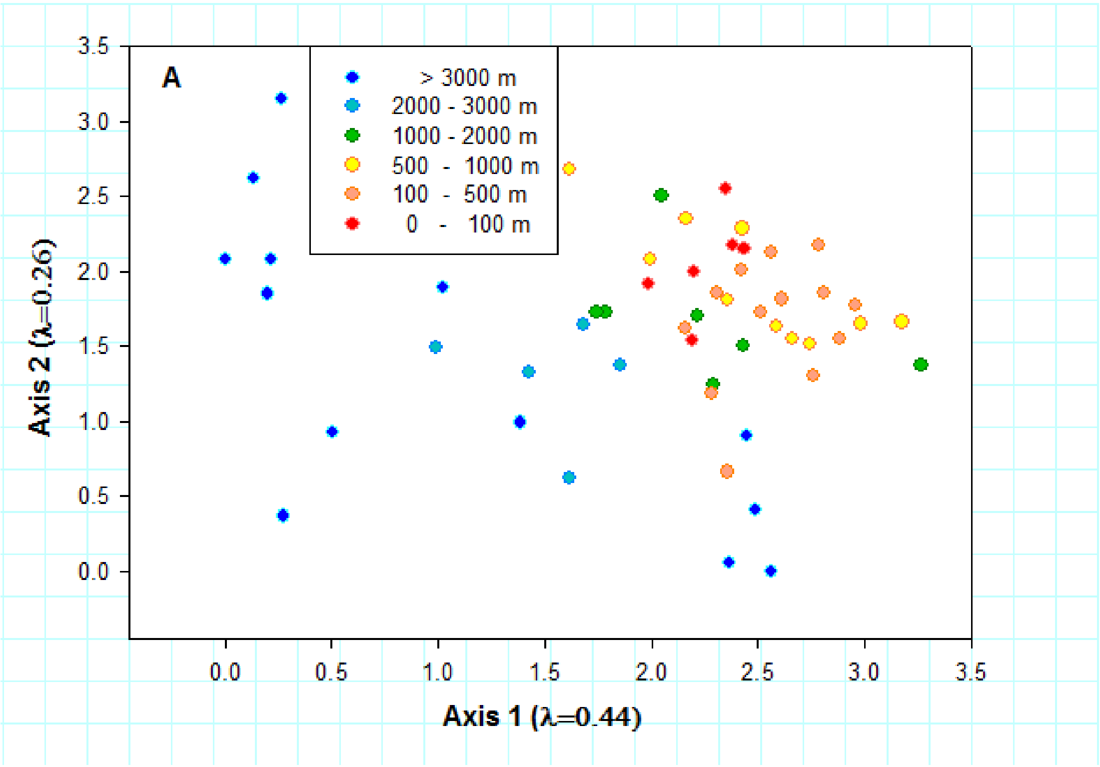
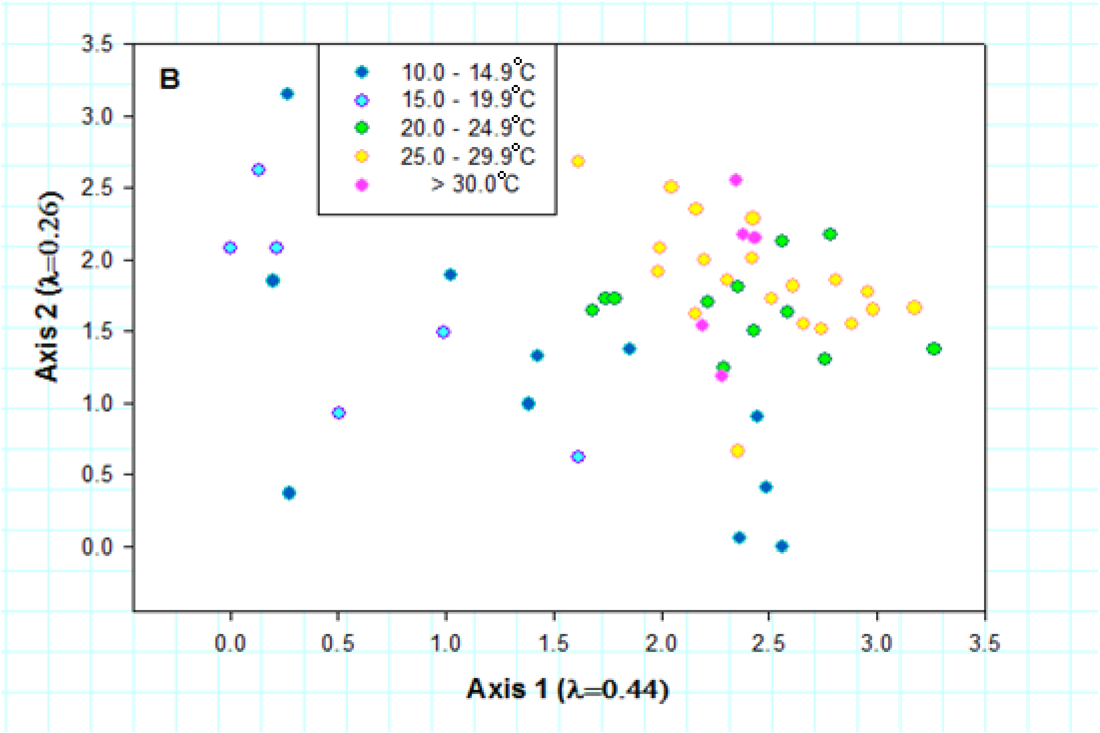


Figure 4.2 Modern distribution of chironomids in 54 lakes training set along the elevation range.


A
> 3000 m
2000 - 3000 m
1000 - 2000 m
500 - 1000 m
100 - 500 m
0 - 100 m
Axis 2 (λ=0.26)
Axis 1 (λ=0.44)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5


B
10.0 - 14.9°C
15.0 - 19.9°C
20.0 - 24.9°C
25.0 - 29.9°C
> 30.0°C
Axis 2 (λ=0.26)
Axis 1 (λ=0.44)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5

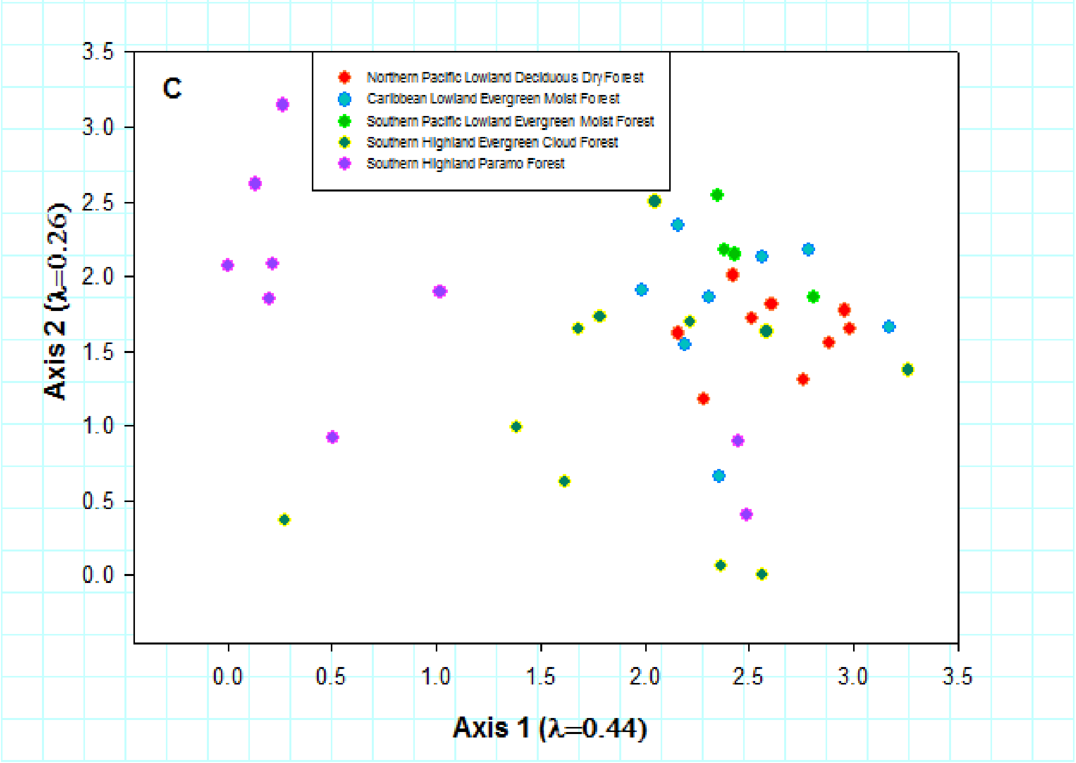


Figure 4.3 DCA sample score biplots of the fifty-four lakes classified by: (A) elevation, (B) SWT, and (C) vegetation.

In the CCA biplot of midge taxa (Figure 4.4), *Corynoneura* type *C/E*, mostly found in the lakes located at around 2000 m a.s.l, is separated from *Cryptochironomus*, which is most abundant in warm lakes. The CCA illustrates that *Symposiocladius, UKii* and *Smittia/Pseudosmittia* (lower right quadrant) strongly favor lakes with low SATA_10 and SWT; whereas, taxa such as *Tribelos*, *Tanypus, Tanytarsus type KR* and *Tanytarsus type NZ* are found in the upper left quadrant and associated with high SATA_10 and SWT. Certain taxa, such as *Tanypodinae type LP*, *Limnophyes, Fittkauimyia, Psedochironomus and Synorthocladius* are associated with lakes that have low SATA_10 but moderately high SWT. These taxa, squeezed in the cluster near the origin of the coordinates in the diagram, suggest that the inter-lake variation in chironomid communities in the lakes with moderate SWT and SATA_10 is low, while inter-lake variation in lakes with high summer air temperature (high SATA_10) but cool surface water (low SWT) is much greater, reflected by the cluster with more scattered points in upper right quadrant of the diagram, representing taxa, such as *Doithrix, Chaetocladius*, *Psectrocladius*, *Cricotopus*, *Brundiniella, Orthocladius* and *Parametriocnemous*. However, *Chironomus* is positioned near the centroid, indicating that it is most abundant in lakes near the middle of the temperature (SWT and SATA_10) range captured by the training set.

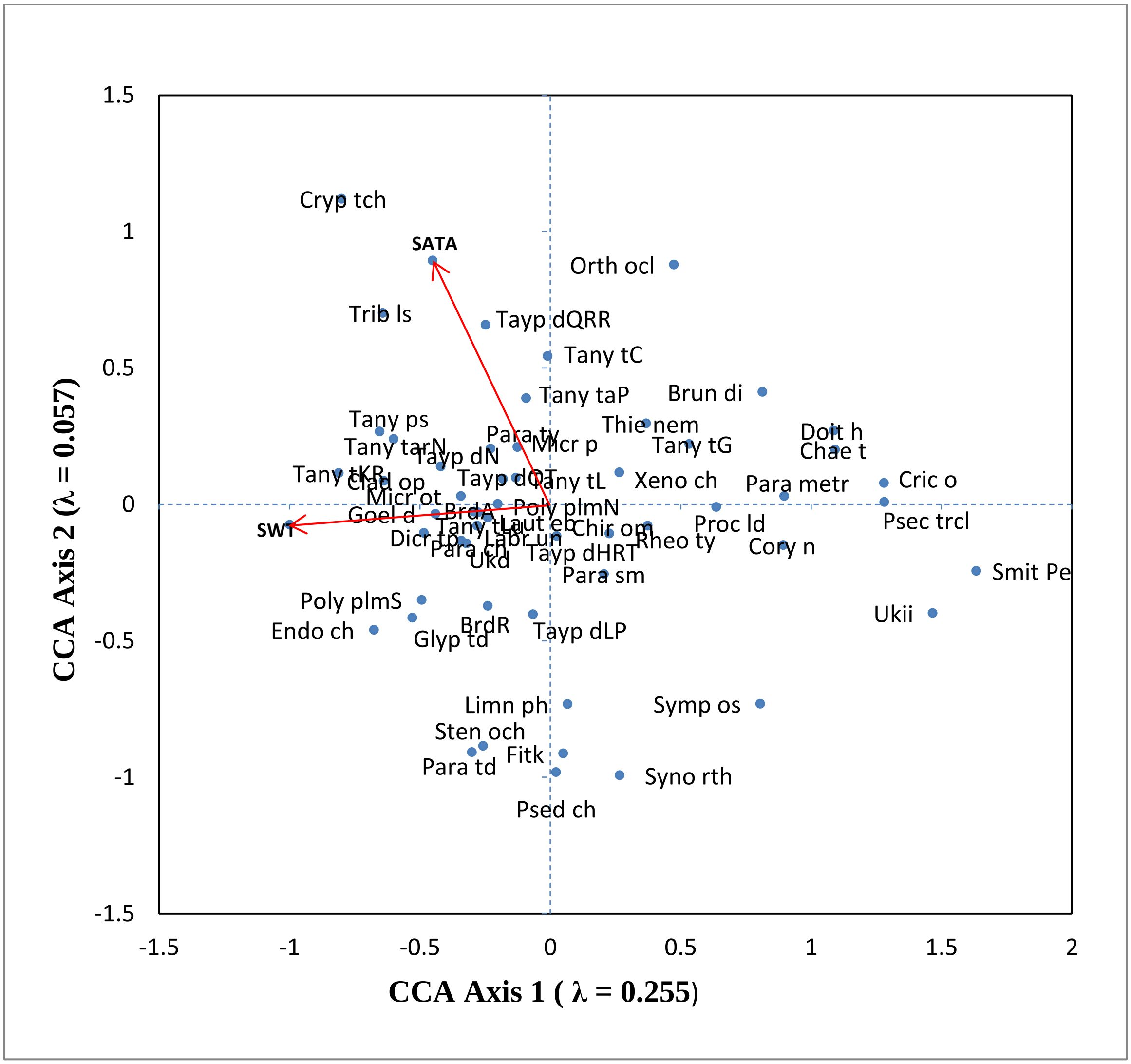


Figure 4.4 CCA correlation bi-plots illustrating the relationships between the fifty-four chironomid taxa and the two forward selected variables (SWT and SATA_10). SWT = surface water temperature; SATA_10 = 10 years' summer air temperature average. Abbreviations for chironomid taxa: Chaet = *Chaetocladius*; Coryn = *Corynoneura type C/E*; Crico = *Cricotopus*; Doith = *Doithrix*; Limnph = *Limnophyes*; Orthocl = *Orthocladius;* Parametr = *Parametriocnemus*; Parasm = *Parasmittia*; Psectrcl = *Psectrocladius group*; SmitPe = *Smittia/Pseudosmittia (SS);* Sympos = *Symposiocladius(SC);* Synorth = *Synorthocladius (SY);* Thienem = *Thienemanniella clavicornis;* BrdA = *Beardius type A*; BrdR= *Beardius reissi type*; Chirom = *Chironomus;* Cladop = *Cladopelma;* Cryptch = *Cryptochironomus*; Dicrtp = *Dicrotendipes*; Endoch = *Endochironomus;* Goeld = *Goeldichironomus*; Lauteb = *Lauterborniella/Zavreliella*; Micrp = *Micropsectra*; Microt = *Microtendipes;* Parach =

Parachironomus; Paraty = *Paratanytarsus;* Paratd = *Paratendipes*; PolyplmN = *Polypedilum type N;* PolyplmS = *Polypedilum type S*; Psedch = *Pseudochironomus;* Rheoty = *Rheotanytarsus*; Stenoch = *Stenochironomus;* Tanyps = *Tanypus;* Tany tC = *Tanytarsus type C*; Tany tG = *Tanytarsus type G;* Tany tL= *Tanytarsus type L*; Tany tLu=*Tanytarsus type LU*; TanytarN = *Tanytarsus type NZ*; Tany taP = *Tanytarsus type P*; Tany tKR = *Tanytarsus KR sp;* Tribls = *Tribelos*; Xenoch = *Xenochironomus*; Brundi = *Brundiniella;* Fitk = *Fittkauimyia;* Labrun = *Labrundinia*; Procld= *Procladius*; TaypdHRT = *Tanypodinae type HRT;* TaypdLP = *Tanypodinae type LP;* TaypdN = *Tanypodinae type N*; TaypdQRR = *Tanypodinae type QRRS*; TaypdOT = *Tanypodinae other*; Ukii = *Unknown ii.*

The CCA identified two distinct groups of lakes (Figure 4.5), which matched the results of the DCA (Figure 4.3). The first group, in the right half of the diagram, represented by light blue and dark blue points, includes: Moren2, Quebr, Botos and Barva. These lakes are located above 2500 m a.s.l. and their SWTs range between 11^{o}C and 15 °C. The second group is illustrated by orange, pink and red points clustered in the left half of the diagram, though there are green points mixed in the transitional part that are close to the origin of the coordinates. Lakes in this group are found in the elevation range of 0 m -1000m with an average SWT of 26 °C and span a smaller temperature range. Bonla (380 m a.s.l, 27.4 °C, 27 m) is notable due to its depth and ion concentration.

Covariance analyses from partial CCAs demonstrate that amount of variance captured by SWT independent of the effect SATA_10 and all the three air-temperature variables (JMAT_10, AMAT_10, SATA_10) is 5.9% and 6.1% , respectively (Table 4.3). Covariance between SWT and lake chemistry and other physical variables was also assessed. The amount of variance captured by SWT independent of lake chemistry and other physical variables is 7.1% ($P \geq 0.05$).

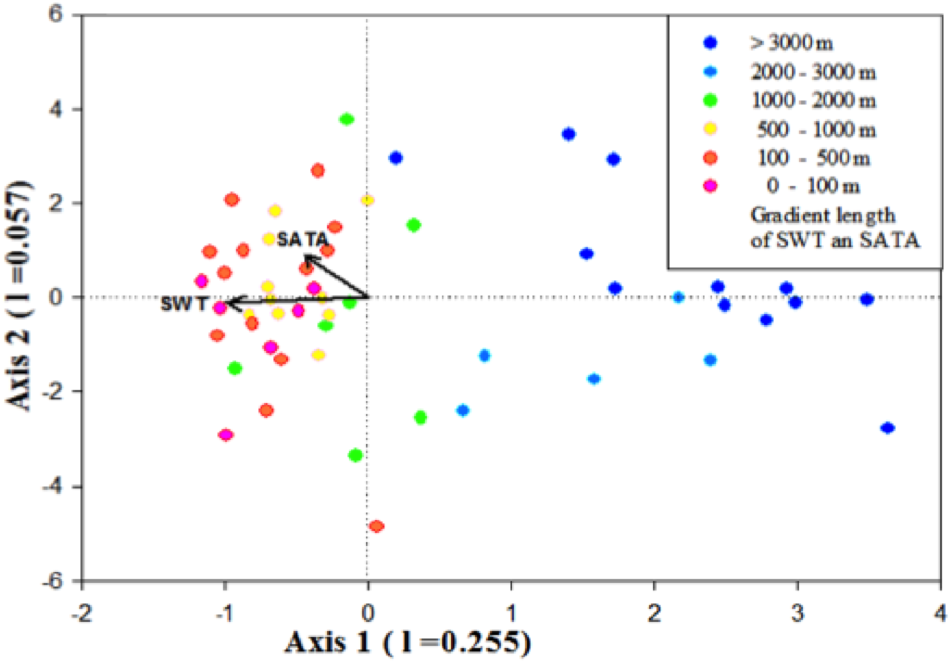


Figure 4.5 CCA correlation bi-plots illustrating the relationship between the fifty-four sites classified by elevation and SWT and SATA_10.

Quantitative Inferene Model Development

Weighted averaging and WA-PLS (leave-one-out cross validation) were identified as the two ‘best’ models based on the coefficient of determination (r^2_{jack}), RMSEP and maximum bias. Three lakes (Mor3C, Botos, Osa1) were removed from the inference model due to their absolute residuals being greater than one standard deviation of the observed SWT. The r^2_{jack}, RMSEP and the maximum bias are 0.63, 3.61°C and 4.78 °C, respectively, using a WA approach. The performance statistics for a one-component WA-PLS model (leave-one-out) are $r^2_{jack} = 0.63$, RMSEP=3.60°C and maximum bias = 4.54 °C. Graphs of the observed surface water temperature (SWT) and the predicted SWT for both models are plotted in Figure 4.6 and Figure 4.7. The residuals (predicted – observed SWT) for both models are depicted in Figure 4.8 and Figure 4.9, respectively. No obvious trend is identified in the residuals.

Table 4.4 Performance statistics for the five different midge-based inference models for surface water temperature (SWT).

Inference model	Apparent		Cross-validation		
	RMSE (°C)	r^2	RMSEP (°C)	r^2	Maximum bias (°C)
WA_{tol} (Leave one out)	2.62	0.8	3.61	0.63	4.78
WA_{tol} (Bootstrapping)	2.62	0.8	3.97	0.62	4.78
WA (Leave one out)	2.62	0.8	3.61	0.63	4.78
WA (Bootstrapping)	2.62	0.8	3.97	0.62	4.78
WA-PLS (Leave one out)	2.63	0.8	3.6	0.63	4.54
WA-PLS (Bootstrapping)	2.63	0.8	3.98	0.62	4.54

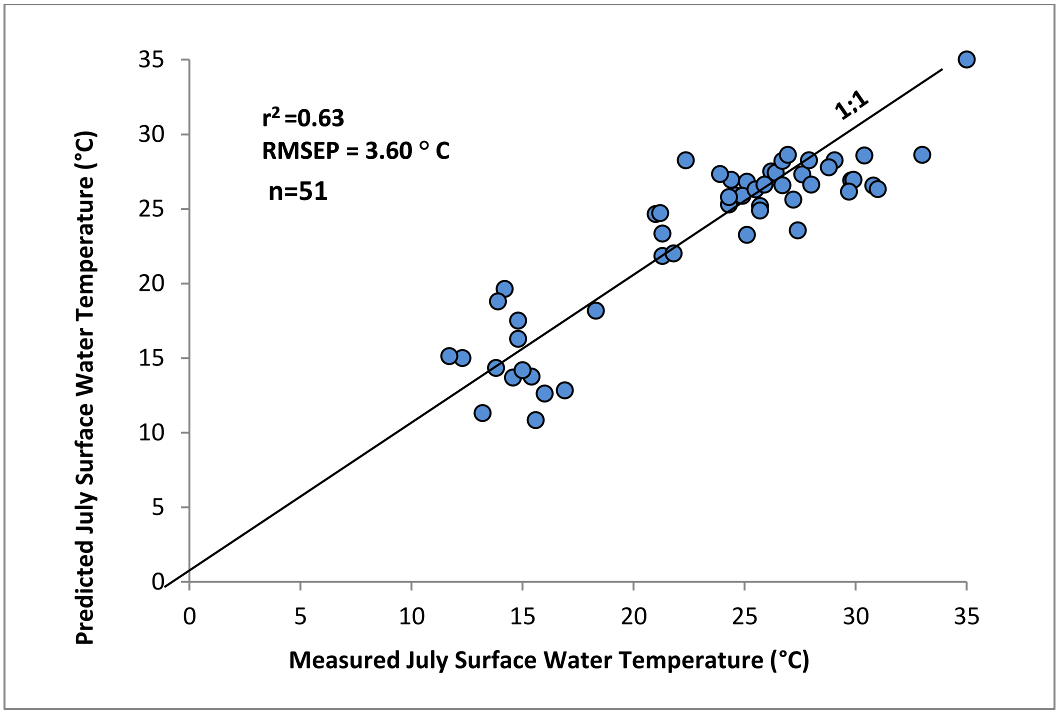


Figure 4.6 Relationship between observed and midge-inferred (jack-knifed) summer water temperature based on WA-PLS

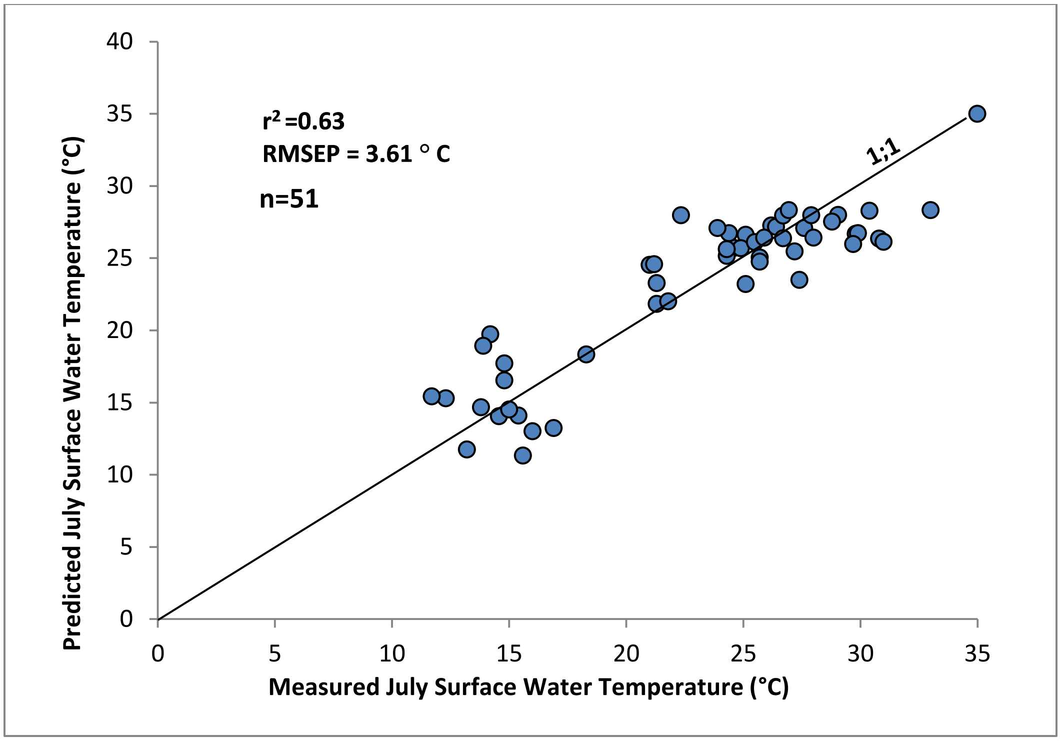


Figure 4.7 Relationship between observed and predicted (jack-knifed) summer water temperature based on WA.

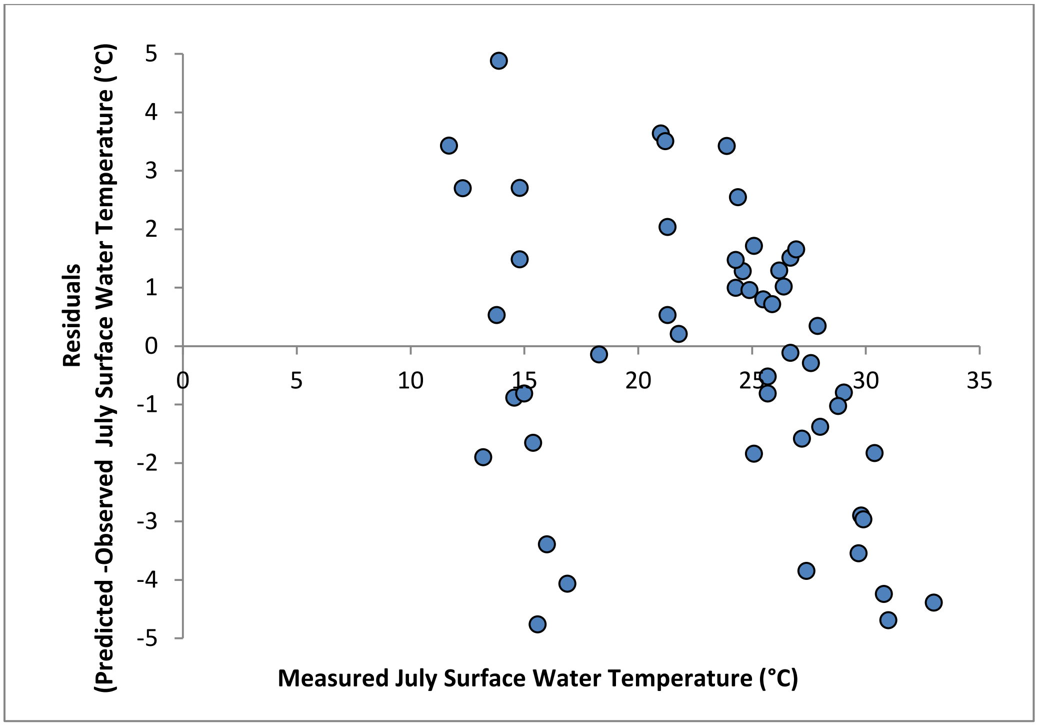


Figure 4.8 Residuals (predicted – observed) for SATA_10 based on WA-PLS.

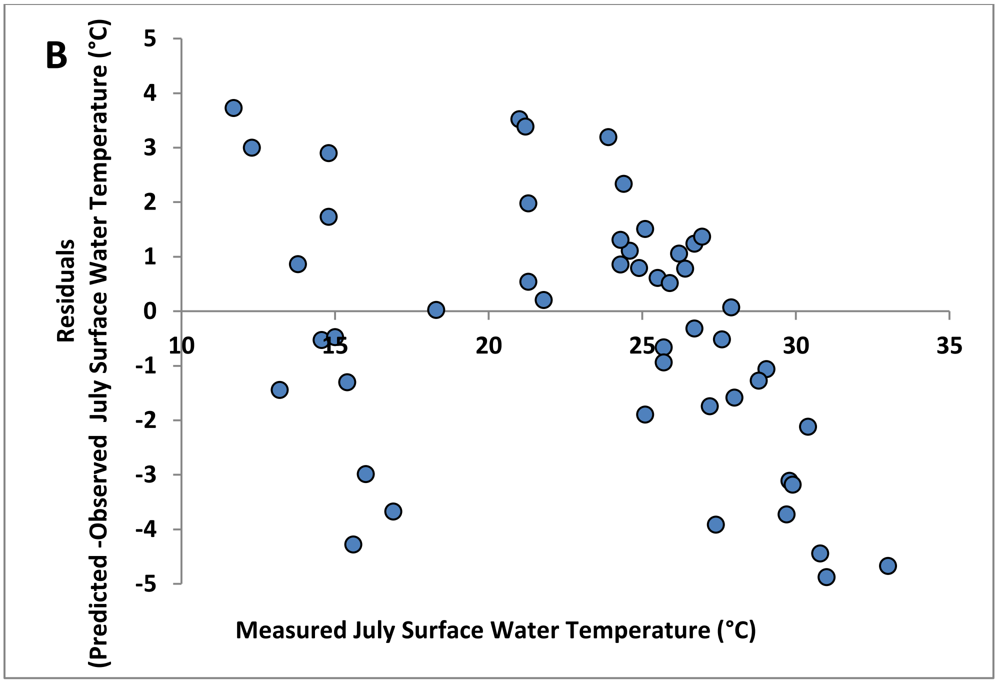


Figure 4.9 Residuals (predicted – observed) for SATA_10 based on WA.

Age-depth Modeling

The age depth model for Zoncho Lake was determined using *Clam* (Blauuw 2011) (Figure 4.10). Average accumulation rates at Laguna Zoncho varied between 3.2 cm/100 yr from 500 cal yr BP-1997 AD, 10 cm/100 yr from 2000-500 cal yr BP and 20 cm/100 yr from 3100-2000 cal yr BP. Sediment accumulation decreases towards the present. Sediment accumulated nearly six times faster during the early part of the record (3100-2000 cal yr BP) relative to the later portion of the record (600 cal yr BP-1997 AD). *Clam* calculates an age-depth model through the ^{14}C dates associated with their depths and appears to provide reasonable approximations of the true (simulated) accumulation history (black line). However, a limited number of ^{14}C dates results in poor smooth spline fit, showing that the modeled sedimentation rate has a linear relationship with the ^{14}C derived ages.

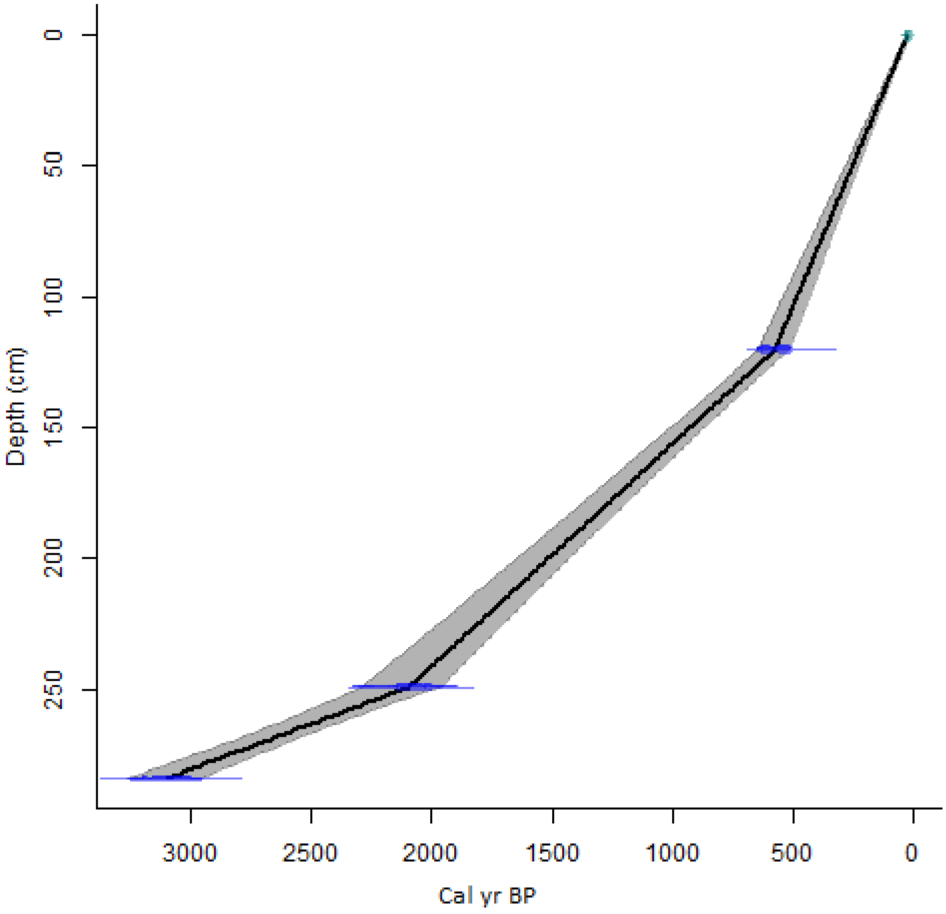


Figure 4.10 ^{14}C age depth model (blue blocks show 95% hpd ranges) of the Lake Zoncho sediment record, developed using an R-project based age-depth model *(Clam*) (error-weighted with smoothness set at the default of 0.3; grey envelopes show 95% confidence intervals).

Late Holocene Midge stratigraphy, Laguna Zoncho

The chironomid percentage diagram is divided into four zones (Figure 4.11). Zone LZ-1 (~3100-3000 cal yr BP; 288-287 cm) with taxon richness of 4, is dominated by *Chironomus*, a eurythermic taxon. Three taxa, considered to be thermophilous based on their modern distribution, *Beardius* type A (3%), *Cladopelma* and *Goeldichironomus*, were also present in LZ-1 (Figue 4.11). No cold water taxa were present in this zone. Zone LZ-2 (~3000 and 1450 cal yr BP; 287-184 cm) is characterized by a very diverse midge community, with the taxon richness reaching 27. In this zone, the midge assemblage is dominated by *Chironomus*; however, lesser amounts of taxa such as *Micropsectra*, *Parachironomus*, *Paratanytarsus* and *Polypedilium nubifer* type are also present. Warm water taxa including *Cladopelma*, *Dicrotendipes*, *Microtendiptes*, *Goeldichironomus* and *Tanytarsus type KR* are also present in this zone. *Corynoneura type C* and *Procadius*, taxa associated with cool water temperature, are present in LZ-2. A break in the sub-fossil midge stratigraphy occurs between 136 cm and 184 cm (1450-850 cal yr BP) with an insufficient number of head capsules recovered in the samples from this layer. LZ-3 (850-600 cal yr BP; 136-94 cm) is characterized by the disappearance of some warm water taxa (e.g. *Tanyarsus type N*, *Microtendipes, Tanytarsus type KR*) and an increase in cool water taxa such as *Cricotopus*, *Rheotanytarsus* and *Stenochironomus*. *Chironomus* (50%) still dominates this zone with lesser amounts of *Parachironomus* also present. A relatively high abundance of *Beardius ressi type* and *Labrundinia*, which are reflective of moderate surface water temperature, also characterizes zone LZ-2. Taxon richness decreases to 17 in this zone. LZ-4 (600 cal yr BP or 1350 AD to 1997 AD; 94 -0 cm), is characterized by an increase in both cold water taxa and temperate water taxa. *Chironomus* dominated the midge community in LZ-4. A high relative abundance of *Procladius, Labrundinia*, *Parachironomus*, *Corynoneura type C/E* and *Cricotopus group* also characterizes this zone and is associated with the disappearance of warm condition indicators, e.g. *Beardius resis* type, *Microtendipes, Tanytarsus type N*, *Tanytarsus type KR*. Taxon richness recovered and reached the a core maximum of 28.

To determine if the composition of sub-fossil chironomid assemblages in Laguna Zoncho are well-represented in the Costa Rican training set, subfossil chironomid assemblages were passively plotted against the modern training set samples using CA (correspondence analysis) (Figure 4.12). The black crosses plotted near the center of the CA diagram illustrates how the composition of the midge sub-fossil midge assemblages at Laguna Zoncho over the 3000 year record compare to the midge assemblages captured by the modern calibration set. The CA diagram also reflects that the subfossil assemblages are most similar to the midges communities found today in lakes with moderate surface water temperature. However, it appears that no abrupt changes in terms of water temperature occurred in the lake during the past 3000 years. Generally, from 3100 cal yr BP to 1750 cal yr BP (crosses plotted at left half quadrants), Laguna Zoncho experienced a relatively warmer water condition; during the time period of 600 cal yr BP – the present (1997 AD) (crosses plotted at right half quadrants), the surface water temperature in Laguna Zoncho decreased and became more similar to those in high elevation lakes.

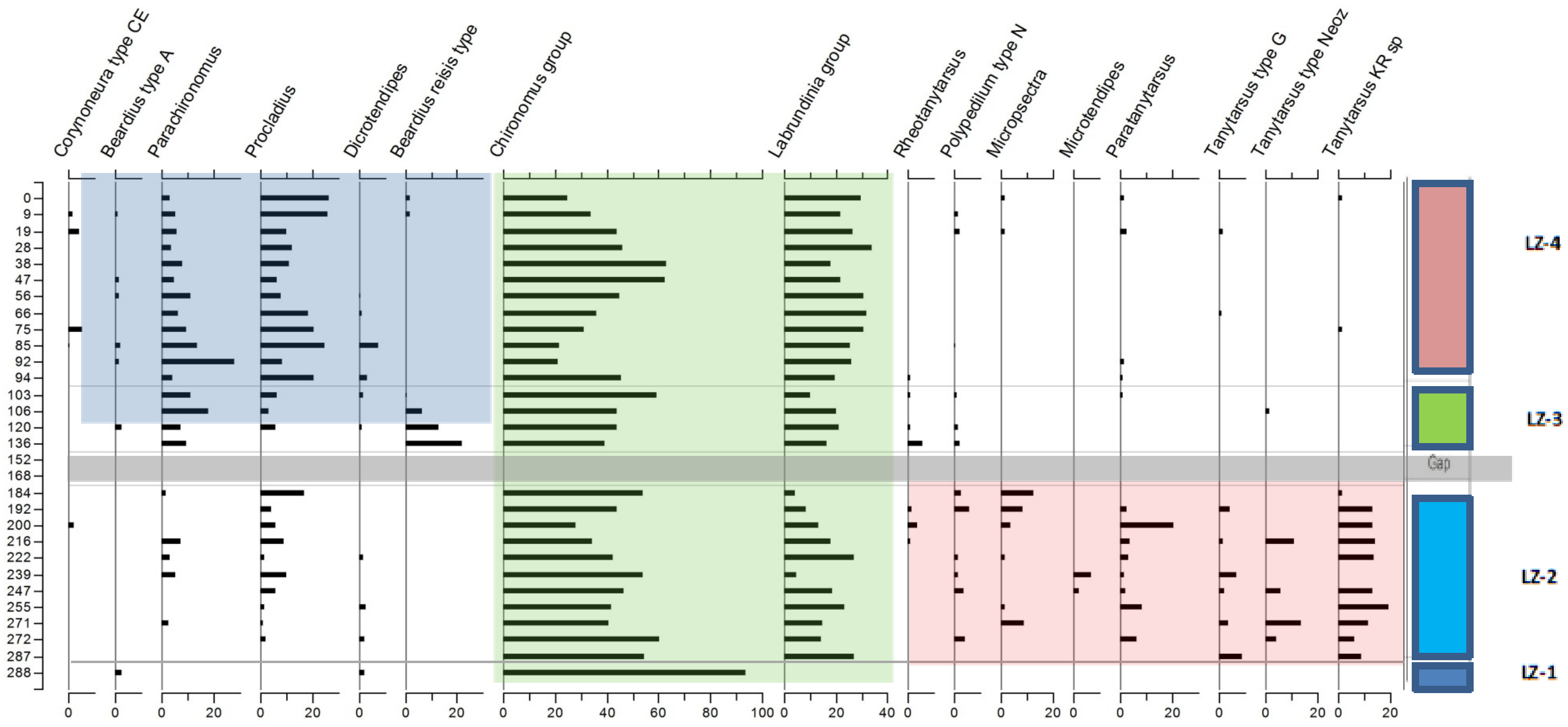


Figure 4.11 Subfossil distribution of Chironomid in thirty layers of the down-core sediment from Laguna Zoncho.

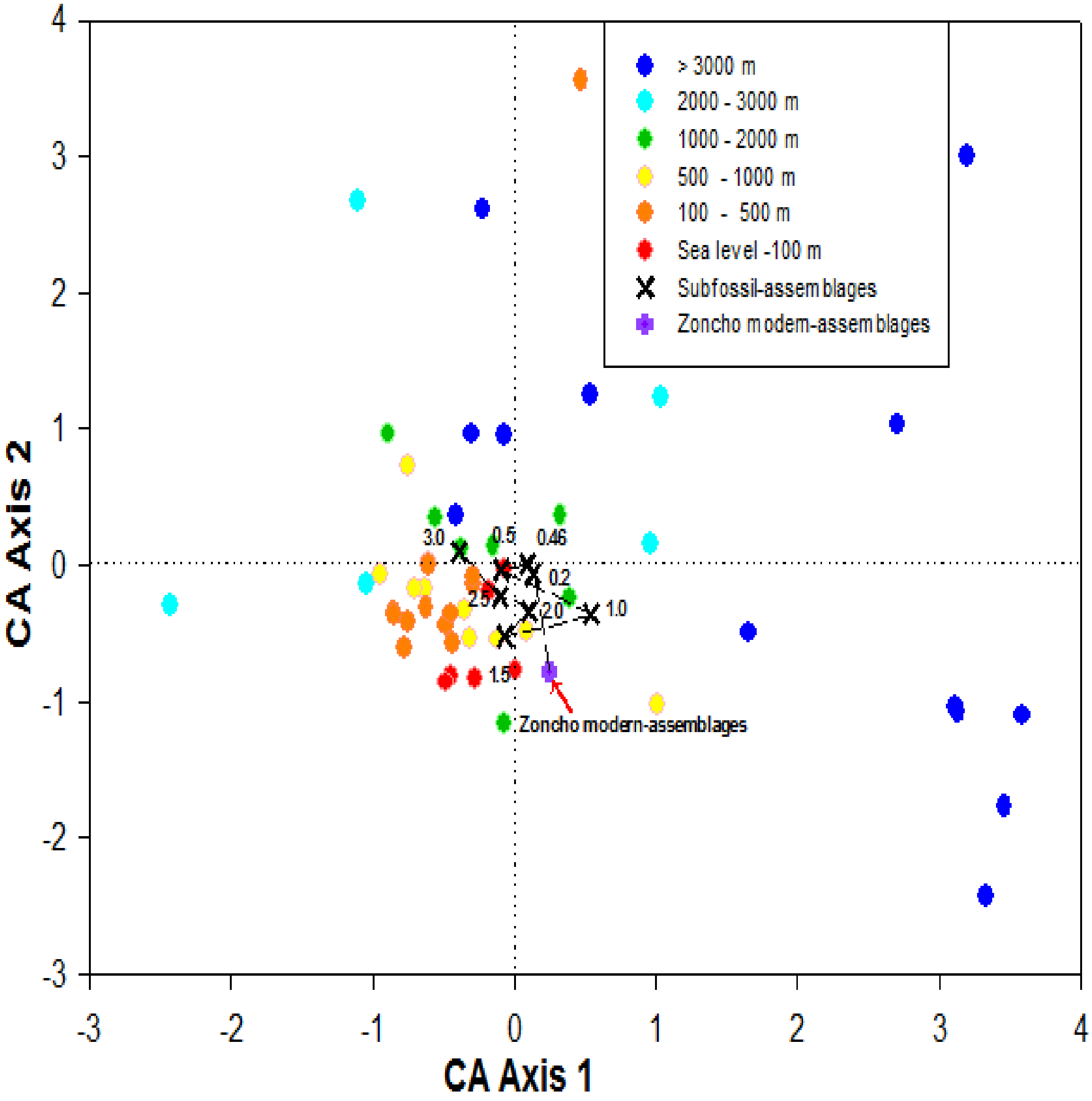


Figure 4.12 Time-trend CA biplot comparing fossil chironomid assemblages from Laguna Zoncho with fifty-four lake calibration data-set from Costa Rica. Calibration dataset are clustered based on measured surface water temperature. Numeric values near the black crosses of subfossil assemblages in the diagram represent ~0.5 k year interval (cal yr BP).

Application and Performance of Midge-based SWT Inference Model

The subfossil midge taxa present in Laguna are well represented in the fifty-four lake calibration set. Of the thirty-seven chironomid taxa recovered from the Laguna Zoncho sediment, only one taxon (*Stempellina*) is absent from the surface calibration set. *Stempellina* is present in three samples at a low relative abundance (range= 0.8 -3.7%, mean = 2.1%). According to Birks (1998) quantitative reconstructions can be considered robust if (1) > 90% of the subfossil taxa used in the paleotemperature reconstruction occur in modern calibration set, and (2) very reliable if > 95% of the taxa were present in the training set (Birks, 1998). A one-component WA-PLS model provides the most robust performance statistics for the surface water temperature (SWT) inference model. This model was applied to the chironomid stratigraphy from Laguna Zoncho and used to develop a quantitative reconstruction of surface water temperature spanning the late Holocene. The average midge-inferred SWT is 24 °C and ranges from 21.5°C to 27.2°C (Figure 4.13). The interval between 1997 AD and 600 cal yr BP (1350 AD) was characterized by surface water temperature (average SWT =23.2°C) lower than the 3000-year average. Between 600 cal yr BP and 850 cal yr BP, surface water temperature increased to 26.0°C; however, the lack of midge remains between 136 and 184 cm precludes our ability to develop an estimate of SWT between 850 cal yr BP and 1450 cal yr BP. Elevated temperature characterized the early 2nd millennium but this is only based one sample. Surface water temperature remained below average between 1350 AD and 1997 AD.

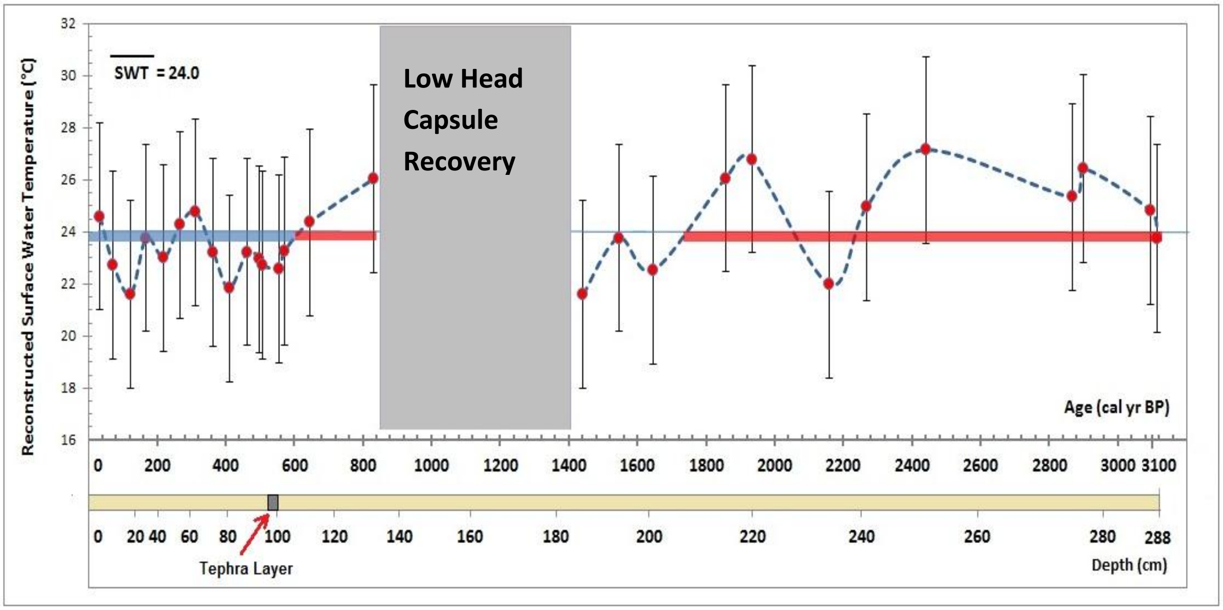


Figure 4.13 Reconstructed July water surface temperature based on a 1-component WA-PLS model. Vertical gray bar represents the portion of the Zoncho core (136-184 cm in depth) with low head capsule recovery. Blue bars represent the below-average SWT, red bars indicate the above-average warmth. Points represent reconstructed SWT with error bars.

CHAPTER 5

DISCUSSION

Extensive studies have been undertaken assessing the relationship between the modern distribution of sub-fossil midges and physical and chemical conditions in freshwater ecosytems in Canada, the Northeast U.S., the Swiss Alps, Fennoscandia, Scotland, the western U.S. and Eurasia (Walker and Mathews 1989; Walker et al., 1991a, 1997; Wilson et al., 1993; Olander et al., 1997, 1999; Lotter et al., 1997; Porinchu and MacDonald, 2001; Porinchu et al., 2002; Porinchu et al., 2007; Nazarova et al., 2011, Self et al. 2011). These studies have identified that summer surface water temperature can account for an independent and statistically significant amount of variance in the distribution of chironomids across broad geographic regions. To date, this is the first study that has quantified the contemporaneous relationship between chironomid distribution and limnological and climatic parameters and to develop an inference model relating midge distribution to SWT in Central America.

It has been recognized for some time that thermal conditions (air and water) influence the composition of midge communities (Brundin 1949; Brundin 1956). Developmental rates, emergence and voltinism of chironomid larvae are influenced by water temperature (Brundin 1949; Walker and Mathewes, 1989; Menzie 1981; Ward and Cummings, 1987; Mackay 1997). For example, the influence of water temperature was documented in a study identifying temperature dependent-timing of the main occurrence of adult chironomids in Lake Stigsholm (Lindegaard and Borodersen, 2000). Strong correlations between surface water temperature and modern chironomid communities have been found in a number of regions including the Sierra Nevada, California (Porinchu et al., 2002) and the Great Basin of the western United States (Porinchu et al., 2010) and many other regions including arctic, temperate and tropical areas (Walker and Cwynar, 2006; Eggermont and Heri, 2012). In this study, CCA indicated that SWT and SATA_10 were significantly correlated to distributions of chironomids in the Costa Rica training set. Of these two variables, SWT explained the greatest amount of variance in the chironomid communities, agreeing with results from calibration sets developed in arctic, sub-arctic and alpine environments (Olander et al., 1999; Barley et al., 2006; Porinchu et al., 2010).

The lake sample scores depicted in the CCA biplots diagram of sample scores suggests that the fifty-four lakes in the training set can be classified in to two distinct groups (Figure 4.5), agreeing with the results of the DCA (Figure 4.3). One group includes most of the low elevation lakes (0 -1000 m) with relatively high surface water temperature and air temperature. For example, surface water temperatures of Lake Cote (650 m a.s.l), Lake EstBlanc (430 m a.s.l) and Lake Sierpe (16 m a.s.l) are 25.1°C, 28.8°C and 33°C separately. The averages of surface water temperature and summer air temperature for the low elevation lakes (n=29) are 27.6°C and 25.3°C, respectively. Having a maximum depth of 27 m (the deepest lake in the training set), Lake Bonla is not located near the group of low elevation lakes in the CCA biplot, suggesting the limnology and/or the midge community of Lake Bonla are distinct from the lakes in this group. It is likely that depth and thermal stratification play a role in influencing the distinctive midge community in Lake Bonla. The second group consists of high elevation lakes (2000-4000 m a.s.l) with low surface water temperatures and summer air temperatures. The average of SWT and SATA_10 for this group (n=18) are 15.0°C and 22.5°C, respectively. It is notable that surface water temperature decreases rapidly with increasing elevation; whereas, air temperature only drops ~3°C along the elevation range (2000 m) spanned by the high elevation lake group. Green points, reflecting lakes at mid-elevations (1000-2000 m a.s.l), are scattered in the central area of the diagram. The average SWTof this group (n=7) is 22.9°C and summer air temperature is 23.4°C, respectively. Laguna Zoncho (SWT = 24.6°C, SATA_10 = 21.34°C), located at 1190 m a.s.l, is found in this mid-elevation group. Lower surface water temperature than summer air temperature in the low-elevation lakes is reasonable because the great heat capacity of water can slow down the increase of surface water temperature in the daytime. Thus, air temperature at high elevations is expected to be lower than SWT. However, NOAA database based interpolated air temperature for the middle and high elevation lakes that are generally higher than surface water temperature is not reasonable. It is possibly due to the inaccuracy of extracted air temperature data based on interplotated method.

The CCA biplot diagram of species scores (Figure 4.4), reveals that *Cryptochironomus, Triboles, Tanypus, Tanytarsus* spp., Tanypodinae, *Cladopelma, Microtendipes, Geoldichironomus, Beardius* and *Dicrotendipes* are associated with high surface water temperature and summer air temperature. Among these species, *Dicrotendipes* and *Microtendipes* were identified as the taxa that are predominantly found in forested regions and sites south of treeline respectively in studies conducted in Canada (Oliver and Roussel, 1983) and Northeast Siberia, Russia (Porinchu and Cwynar, 2000). The results of this study are consistent with earlier work reporting that *Microtendipes* and *Dicrotendipes* are thermophilous genera (Walker and Mathewes, 1989; Walker and MacDonald, 1995). Taxa such as *Orthocladius, Brundiniella, Doithrix, Parametriocnemus* and *Chaetocladius,* favor lakes with low surface water temperature and mild air temperatures. Taxa such as *Limnophyes, Parasmittia, Fittkauimyia, Psedochironomus* and *Synorthocladius* are likely to prefer low summer air temperature but temperate surface water environment. In the lower right quadrant, *Corynoneura type C/E*, *Psectrocladius, Unknown ii* and *Symposiocladius* are found to dominate lakes at high elevations (2000-3000 m) with low surface water temperature and summer air temperatures. In our study, *Psectrocladius*, *Symposiocladius* and *Unknown ii* are restricted entirely to cold lakes and can be considered cold stenotherms, although Walker and Mathewes (1989) identified *Psectrocladius* as a common constituent of low-elevation lakes in British Columbia.

This is the first report of *Psectrocladius*, which occurred solely in high-elevation lakes, in Costa Rica. Two additional taxa – *Chaetocladius and Symposiocladius* – identified in this study are also not found in the existing checklists of Central American Chironomidae (Watson and Heyn, 1992; Spies et al., 1996). These three Chironomidae taxa (Figure 5.1) are restricted to lakes with very low water temperature (Figure 4.4). These taxa may be absent from the existing checklists due to a limited number of midge surveys being conducted alpine environments (Watson and Heyn, 1992; Spies et al., 1996), with most sampled lakes located below 2000 m a.s.l. In this study *Psectrocladius* is most abundant in lakes 2000-4000 m a.s.l.

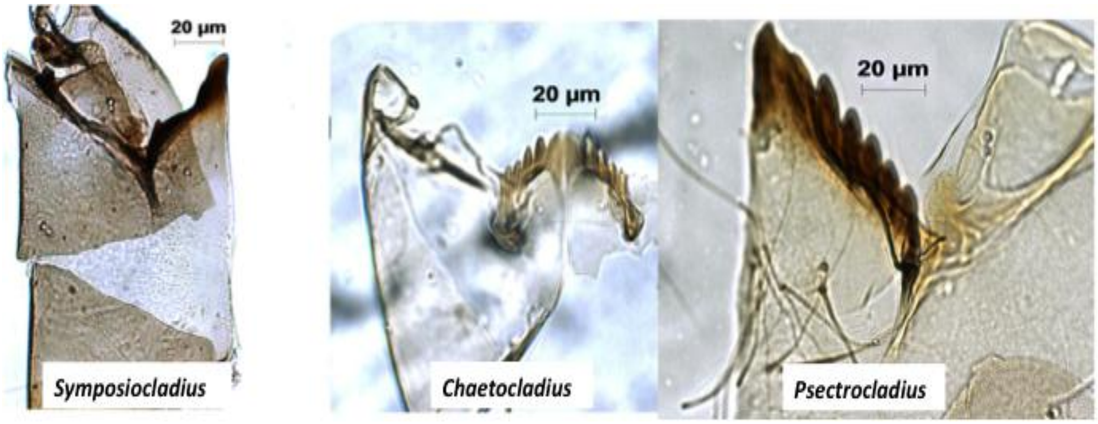


Figure 5.1 Three chironomid taxa reported first time in this study. (A) *Symposiocladius,* (B) *Chaetocladius,* (C) *Psectrocladius.*

Chironomids have long been used as bio-indicators of lake trophic status (Thienemann, 1921; Brundin, 1985); however, the relationship between nutrient status, lake productivity and midge distribution can not be assessed using this dataset since no measures relating to lake nutrient status were made during surface sediment collection. In many calibration sets dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total organic carbon (TOC), total nitrogen-unfiltered (TN-UF), total phosphorus-unfiltered (TP-UF) and chlorophyll a (CHLA) are measured (Olander et al., 1999; Porinchu et al., 2002; Barley et al. 2006; Porinchu et al., 2009). These variables are considered indicators of lake productivity and nutrient status. However, none of the above parameters were determined during surface sediment collection making it difficult to assess the relationship between midge assemblages and trophic status. Other issues surrouding the development of the training set include:

(1) **The calibration set contains a limited number of lakes with expansive limnological data**. In this study, sub-fossil midges were extracted and identified for the fifty-four lakes in the calibration set, but a full suite of limnological data was only available for thirty-nine of these lakes, reducing the limnological and faunal diversity present in the training set.

(2) **Lake Ontogeny.** The calibration dataset includes oxbow lakes, wetland lakes, artificial lakes (reservoirs), lava- and lahar-dammed lakes, landslid^{e} lakes, crater lakes and glacial lakes (Haberyan et al. 2003). The physical and chemical limnology of lakes will vary greatly due to their mode of formation and their geographical location (Horn and Haberyan, 1993; Haberyan et al., 2003). For example, Lake La Palma and Lake Cocor are located at 570m a.s.l and 520m a.s.l, respectively, however, the ontogeny of each lake is different; Lake La Palma was formed by volcanism and Lake Cocor is a reservoir

(Haberyan et al., 2003). The physical and chemical limnology of each lake is distinct. Lake LaCocor is a shallow (1 m), warm (29.8°C) lake characterized by low ion concentration relative to Lake La Palma (10.8 m, 25.7°C) (Table 3.1). The diversity of lakes in this datset complicates interpretation and establishment of midge-environment relations.

(3) **A single point sample of may not be fully representative of limnological conditions.** In this study, for the majority of lakes in the training the faunal assemblages were compared to a single point measure of the physical and chemical limnology of each lake. This is the approach that is employed in most training sets developed in remote environments (Olander et al. 1999; Barley et al. 2006; Porinchu et al 2009b), however these single point measures may not adequately capture intra-lake variabililty in limnology.

Table 5.1 Comparison of the existing chironomid-based inference models for lake surface water temperature.

Study	Study area	# of lakes	# of taxa	Model	r^2_{jack}	RMSEP (°C)	Range of Gradient (°C)	RMSEP as % of range	Max bias (°C)
Walker et al. (1997)	Eastern Canada	39	34	WA-PLS (2 component)	0.88	2.26	21	10.76	2.4
Olander et al. (1999)	Northern Finland	53	38	MAT (6 matches)	0.43	1.48	9.3	15.91	1.9
Brooks and Birks (2000)	Western Norway	44	81	WA-PLS (1 component)	0.3	2.22	12.4	19.9	5.29
Brooks and Birks (2001)	Svalbard, Norway	111	119	WA-PLS (3 component)	0.86	2.13	22.7	9.83	2.84
Porinchu et al. (2002)	Sierra Nevada, USA	44	44	WA (classical)	0.73	1.2	8.5	14.1	0.9
Francis et al. (2006)	Eastern Canada	68	44	$WA_{inverse}$	0.88	2.22	24.3	8.2	4.01
Larocque et al. (2006)	Western Quebec	52	64	PLS	0.59	2.24	10.6	21.1	-
Porinchu et al. (2009a)	Central Arctic	77	50	WA-PLS (1 component)	0.75	1.39	10.6	13.1	2.33
Wu et al. (this study)	Southern Costa Rica	54	54	WA-PLS (1 component)	0.63	3.6	24.8	14.52	4.54

The midge-based inference model developed in this study has the highest RMSEP and max bias compared to previously developped chironomid-based SWT inferrence models (Walker et al., 1997; Olander et al., 1999; Brooks and Birks, 2000; Brooks and Birks, 2001; Porinchu et al., 2002) (Table 5.1). However, the range of surface water temperature captured in the Costa Rica training set is 24.8°C, resulting in the RMSEP being relatively small when reported as a percentage of the SWT range. The existence of such a large surface water temperature gradient increases the biological and environmental heterogeneity in the training set and may confound estimates of midge taxa optima and tolerances (Olander et al. 1999; Porinchu et al., 2002). In addition, the lakes included in the training set were not evenly distributed by elevation. For example, of the fifty-four lakes in the training set, twenty-nine lakes are located between 0 and 1000 m a.s.l, with only seven lakes sampled between 1000 and 2000 m asl. The poor representation of mid-elevation lakes in the existing training set may limit our ability to develop accurate downcore reconstructions for midge stratigraphies from mid-elevation lakes.

Although the majority of the limnological measurements and surface sediments provided by Dr. Horn and her colleagues were collected in July 1997, it is also important to note that the lake sediments used in this study were collected as part of an on-going research program that spanned twelve years (1991-2003). The upper sediment (0-2 cm) was assumed to represent approximately 5-10 years worth of deposition. The midge assemblages extracted from these surface sediments was calibrated to various temperature measures using a 10-year average (1988-1997). However, sediment accumulation varies for a number of reasons including lake productivity (authochtonous inputs) and changes in land-use (allochtonous inputs) and the 10-year calibration window may not be appropriate for all lakes. In addition, the poor performance statistics of the air temperature inference model may reflect the relatively low spatial resolution of the gridded temperature dataset that was used to derive air temperature estimates for each lake.

The time-trend CA biplot illustrates the development trajectory of the chironomid community in Laguna Zoncho over the last 3000 years (Figure 4.12). The 500-year sample score averages, clustered near the centroid of the CA biplot, indicate that surface water temperature changed abruptly at various times during the 3000 years. The modern chironomid assemblage represented by a purple cross at the lower right to the subfossil cluster reflects the rapid faunal turnover that has occurred during the last 2000 years. The recently deposited sediment is dominated by *Tanytarsus Other types*, taxa that are associated with warm water; however, these taxa are not present prior to the LIA.

The midge-based surface water temperature reconstruction indicates that Laguna Zoncho experienced two warm phases with higher than average SWT: (1) 600-850 cal yr BP and (2) 1750 - 3100 cal yr BP. The interval from 1997 AD to 1350 AD (600 cal yr BP) was characterized by below average SWT. Zone LZ-4 (1350 AD – 1997 AD) was characterized by large fluctuations in midge community composition with decreases in the relative abundance of warm water taxa and increases in the relative abundance of cold water indicators such as *Procladius, Polypedilum type S*. Surface water temperature decreased to a late Holocene minimum of 21.6°C (2.4°C lower than the 3000-year average) at ~1750 AD. Diatom and pollen data suggest that Laguna Zoncho lake levels increased and that regeneration of forest occurred in the catchment surrounding the lake starting at 460 cal yr BP (Clement and Horn, 2001; Lane et al., 2004). Taken together, this research indicates that Laguna Zoncho likely experienced a cold and wet climate rather than cold and dry climate during the LIA. In fact, a number of studies do suggest that the LIA in Central America was characterized by increased effective moisture. For example, a diatom-study indicates increased lake level and effective moisture at Lake La Yeguada, Panama (Bush et al., 1992) and speleothem records from the Vaca Plateau in western Belize indicate higher rainfall during the LIA (Webster, 2000). However, the inference of a cool and wet LIA is not supported by the Haug et al. (2003) Cariaco Basin Titanium (Ti) record. Haug et al. (2003) argued that the low Ti concentrations found in Cariaco Basin between 600 cal yr BP and 200 cal yr BP are indicative of decreased rainfall and concomitant occurrence of widespread droughts in Central America, resulting from the southern migration of the Intertropical Convergence Zone (ITCZ). It has been suggested that the combined effects of an extended drought, together with the arrival of the Spanish lead to the collapse of the population of the indigenous groups living near Laguna Zoncho during the LIA (Haberyan and Horn, 2005).

The midge community in Zone LZ-1(~3100-3000 cal yr BP) is de-pauperate with only four midge taxa present. The appearance of *Dicrotendipes*, *Tanytarsus type NZ* and *Beardius type A*, indicators of moderate to high SWT, suggest that the basal portion of the core could reflect an temperate interval. Lending support to the midge-based inference of SWT of 23.7°C for this interval, which is close to the 3000 year average SWT (23.9 ≅ 24.0°C). The corresponding records of diatom, pollen and charcoal concentration likely reflect drier, and possibly warmer, conditions (Clement and Horn, 2001; Lane et al., 2004; Haberyan and Horn, 2005). The diatom flora at the base of the record is dominated acidophilous and/or benthic taxa such as *Pinnularia braunii*, *Eunotia*, *Encyonema* and *Staurosira construens venter*, indicating increasing acidification and shallowness of Laguna Zoncho between ~3100 and 3000 cal yr BP. The high abundance of *Poaceae* and *Cyperaceae* reflects the deforestration of the surrounding catchment (Clement and Horn, 2001; Haberyan and Horn, 2005). High charcoal concentrations and more enriched δ^{13}C values suggest increased fire and/or local agricultural activities (Lane et al., 2004).

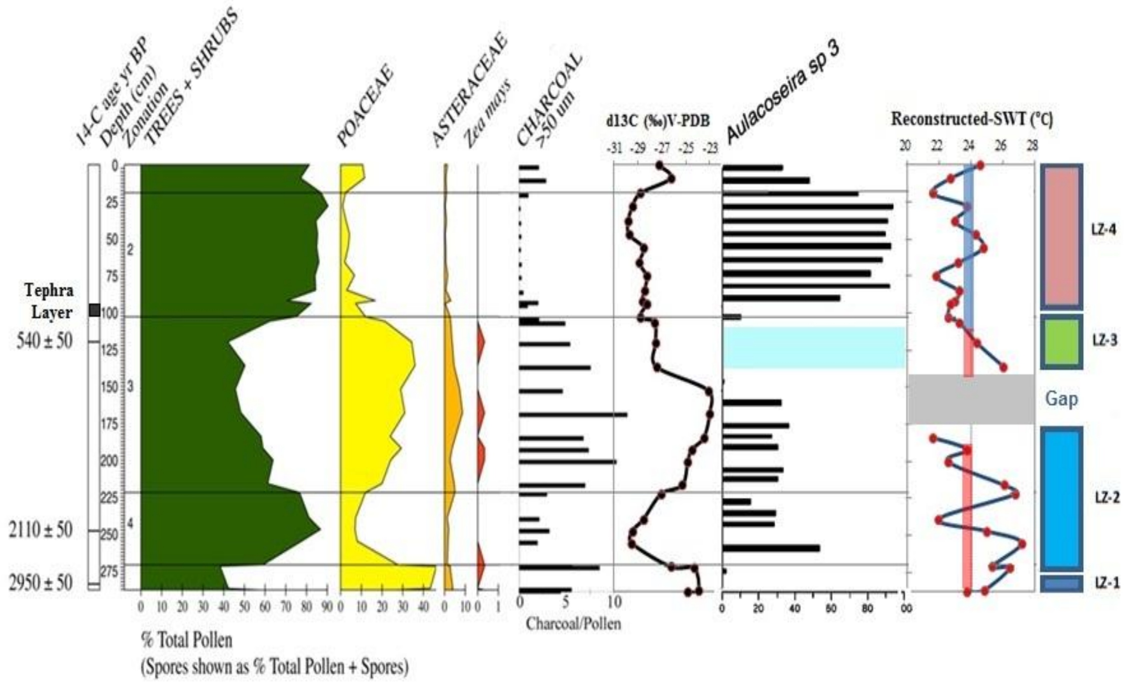


Figure 5.2 Summary diagram depicting pollen abundance for select taxa, charcoal content, δ^{13}C values and the midge-based surface water temperature reconstruction (Clement and Horn, 2003; Lane et al., 2007; modified by Wu).

LZ-2 zone (184 cm-287 cm, 3000-1450 cal yr BP) is characterized by an abrupt increase in the number of chironomid taxa, particularly thermophilous taxa such as *Dicrotendipes*, *Goeldichironomus*, *Microtendipes*, *Tanytarsus type NZ*, *Fittkauimyia* and *Micropsectra*, *Parachironomus*, *Partanytarsus*, *Polypedilum type N* and *Labrundinia* with only two cold water taxa, *Cricotopus* and *Procladius*, present. In the interval between ~3000 cal yr BP and 1750 cal yr BP, climate is inferred to be warm based on the chironomid assemblages, and Laguna Zoncho is characterized by a diatom-inferred increase in lake depth and more acidic lake water (Haberyan and Horn, 2005). Consistenly, the pollen and charcoal data illustrate that the catchment surrounding Laguna Zoncho experienced reforestation, greatly decreased human activity, and possibly increased effective moisture during this interval (Clement and Horn, 2001; Lane et al., 2004).

The midge stratigraphy between ~1400 cal yr BP and 850 cal yr BP (184-136 cm) is characterized by a hiatus with chironomid head capsules absent or found in very limited numbers. Zone LZ-3 spans the interval between approximately 850 cal yr BP and 600 cal yr BP (1350 AD). In LZ-3, the diversity of the midge community increases with a mix of thermophilous chironomids, such as *Beardius resis type*, *Parachironomus, Polypedilum type N* and *Labrundinia*, and cold water taxa, such as *Cricotopus*, *Rheotanytarsus, Stenochironomus and Procladius* present in this zone. The diatom flora in this zone is also very diverse, with the presence of *Eunotia minor, Encyonema lunatum, Gomphonema gracile* and *Pinnularia braunii*, indicating a decreasing lake-levels (Haberyan and Horn, 2005). Of note is the absence of a planktonic diatom taxon, *Aulacoseira sp 3,* in LZ-3 (Figure 5.2). The pollen, charcoal and $\delta^{13}C$ records are consistent with the diatom data. A high number of charcoal fragments were found between 184 cm and 136 cm, corresponding to the hiatus in chironomid record (1450-850 cal yr BP) and a decrease in tree pollen abundance. The increase in *Zea mays* abundance at this time suggests that catchment surrounding Laguna Zoncho may have experienced an increase in the intensity of human activities such as deforestation and cultivation (Clement and Horn, 2001; Lane et al., 2004; Haberyan and Horn, 2005). Comparing the midge abundance data to the records of vegetation and human occupation, reveals that poor chironomid head capsule recovery was limited to between 1450 and 850 cal yr BP (136-184 cm), the period of the greatest intensity of human activity. There are a number of possible explanations that can account for the near absence of midges between 1450 and 850 cal yr BP at Laguna Zoncho. The midge community could have been indirectly affected by human activities and/or climate change. For example, the clearance of forest and increased cultivation may have led to increased erosion and sediment input to the lake, which in turn may have altered habitat and food availability for the midges. Thus, human activities may not only affect the forest coverage surrounding Laguna Zoncho and diatom communities in the lake (Clement and Horn, 2001; Brenner et al., 2002; Lane et al., 2004; Haberyan and Horn, 2005), but may have also influenced chironomid communities. Alternatively, it is also possible that a decrease in effective moisture between 1450 and 850 cal yr BP caused the lake to shallow sufficiently that only a limited pool of standing water remained or lake became more swamplike, both of which would decrease the midge diversity and abundance. The inference of dry condition at this time is also supported by the existence of enriched $\delta^{13}C$ and a peak in charcoal abundance.

The vegetation surrounding Laguna Zoncho between 1400-600 cal yr BP and 3100-3000 cal yr BP was compositionally similar. This, taken together with the increased midge-infered SWT, suggest that these two periods were characterized by warm and dry conditions, possibly facilitating the growth of C_4 plants. The higher temperature during the latter interval (1450-600 cal yr BP) is possibly linked to the Medieval Climate Anomaly (MCA), which is widely observed in circum-Caribbean (Malaizé et al., 2011; Lane et al., 2011). The hiatus in the subfossil midge remains also support the occurrence of a significant drought during this time period.

A decrease in temperate taxa such as *Parachironomus, Partanytarsus* and *Polypedilum type N* between 600 cal yr BP (1350 AD) and 1997 AD (LZ-4), and an increase in cool water chironomids, i.e. *Corynoneura type C/E, Cricotopus* and *Procladius*, indicates that surface water temperature of Laguna Zoncho fluctuated notably during the last ~500 years. The chironomid-based SWT reconstruction is highly correlated to the pollen, charcoal and $\delta^{13}C$ records. Average

SWT declined to 22.0°C during this interval, which also saw regeneration of forest and decreased human activity (Clement and Horn, 2001; Lane et al., 2004). The decline in indigenous populations and forest recovery may have been the result of the decimation of native people by diseases brought by the Spanish, the eruption of Volcán Barú (~ 500 cal yr BP) and climate change (Clement and Horn, 2001; Haberyan and Horn, 2005).

Linkage to Little Ice Age

The Little Ice Age (LIA), a period of cold and highly variable climate and glacial readvance following the Medieval Climate Anomaly (MCA), spanned the 14th to late 19th century (Matthes, 1939). Evidence of LIA has been found in mid-to-high latitudes in both the Northern Hemisphere and Southern Hemisphere. For examples, studies have identified the development of snow bank and glacierets in the Canadian Arctic, Norway and in the Alps (Bradley and Miller, 1972; Grove, 1988), an increase in snowfall frequencies and quantities in New England (Conover, 1967), a decrease in the length of the growing season in central England (Davis, 1972), an increase in sea-ice cover in the Baltic (Davis, 1972), an increase in the number of frozen rivers in China (Hsieh, 1976) and low temperatures in New Zealand (Wilson et al., 1979).

More recently, it has been questioned whether the LIA is manifested globally (Matthews and Briffa 2005). Bradley and Jones (1995) pointed out that "The last 500 years was a period of complex climatic anomalies, the understanding of which is not well-served by the continued use of the term 'Little Ice Age'… the period experienced both warm and clod episodes and these varied in importance geographically. There is no evidence for a worldwide synchronous and prolonged cold interval to which we can ascribe the term of 'LIA'." However, an obvious cool episode (1400-1900 AD) with water temperature lower than the 3000-year average has been

been identified in midge-based surface water reconstruction from Laguna Zoncho in the southern highlands of Costa Rica. Evidence of LIA cooling has been found in the circum-Caribbean, though the expression of the event differs intra-regionally. Sea surface temperatures (SSTs) in Puerto Rico during the LIA are ~ 2-3 °C lower than present (Winter et al., 2000). A die-off of coral reefs, growing along the Pacific coast of Costa Rica and Panama, between 1750-1600 AD may have resulted from exposure to relatively cool water during the latter part of the Little Ice Age (Glynn et al., 1983). The magnesium/calcium (Mg/Ca) ratio of a coral skeleton collected from the southwest Caribbean coast of Puerto Rico reflects that SSTs during the LIA were approximately 2°C lower than present with the sea surface salinity (SSS) showing greater seasonal changes (Watanabe et al., 2001). Carbon isotope data from a sclerosponge in Pedro Bank, Jamaica reflects a decrease in SSTs between 1550 and 1700 AD (Böhm et al., 2002). Evidence from oxygen isotope composition in the ice core records extracted from the tropical Andes, suggests a marked cooling occurred between 1400 AD and 1900 AD (Thompson et al., 2006). A cold LIA was also documented in geomorphological and sedimentary records in the Andean highlands (Markgraf et al., 2000; Polissar et al., 2006; Rabatel et al., 2008).

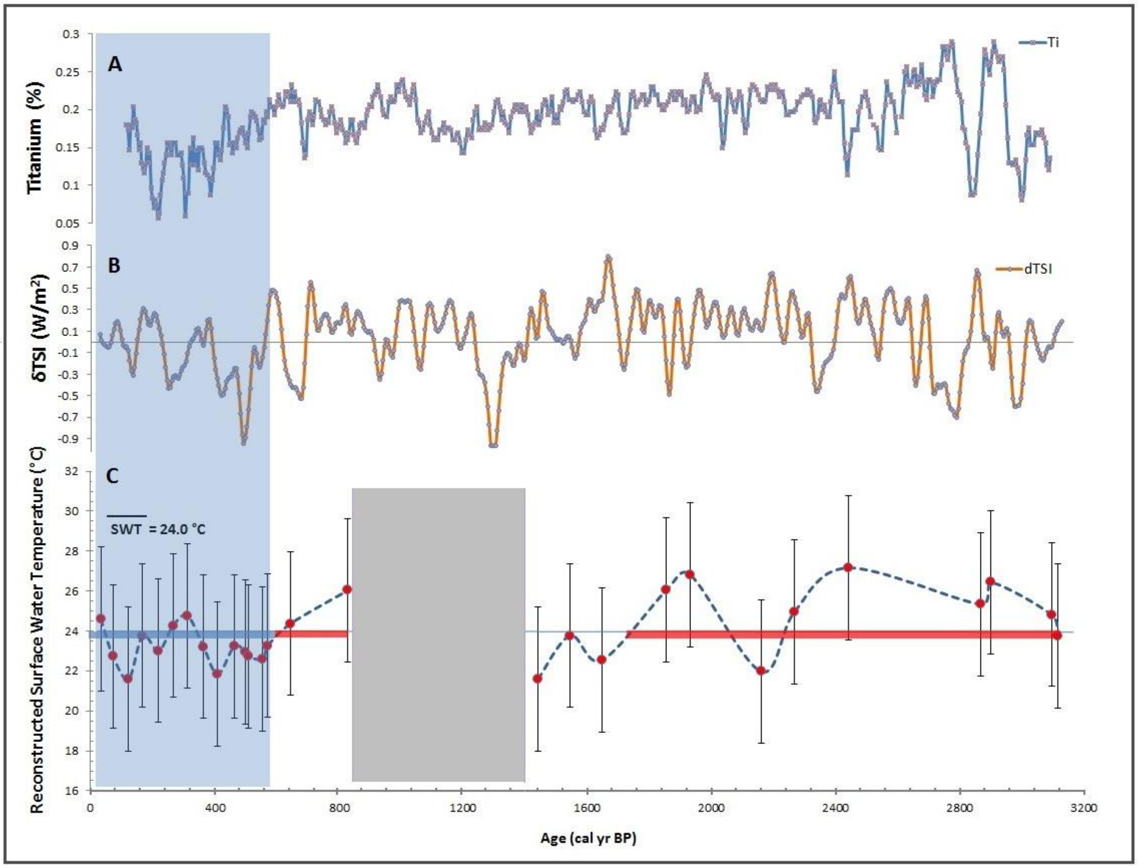


Figure 5.3 Combined records of titanium concentration, solar radiation fluctuation and midge-based surface water temperature for the past 3000 years. (A) Titatinium (Ti) concentration history from Cariaco Basin, Venezuela (Haug et al., 2001), (B) Total solar radiation between 3000 cal yr BP to the present , δTSI represents the difference of total solar irradiance from the value of the ***PMOD composite during the solar cycle minimum of the year 1986 AD (1365.57W/m^2), unit of δTSI is watts per square meter (Frohlich, 2009; Steinhilber et al., 2009), (C) Midge-based water surface temperatures at Laguna Zoncho, Costa Rica (in this study).

***PMOD- The Davos Physical Meteorological Observatory. It is a private institution to investigate sunlight and its properties, built in 1907 in Sweden. http://www.davos.ch/en/services/davos-city-of-research/pmod.html.

general atmospheric circulation (Lamb, 1969). A portion of the observed climatic flactuation of the twentieth century may be attributable to a variation of output energy source of the Sun (Lamb, 1969). Over the most recent 22-year solar cycle, measurements of the solar constant show a variation of only 0.1% around the mean (Crowley and Kim, 1993) (Figure 5.3); hwoever, during the LIA period, the variation of the solar constant exceeded 0.25% relative to the present. Modeling studies suggest that reduction in the solar constant of 0.50% would lead to decrease in global temperature of of ~ 0.50^{o}C (Rind and Overpeck, 1993). Thus the changes in solar forcing may have played a critical role in large-scale temperature decrease on the earth that helps to explain the cooling in LIA episode. Another theory pertaining to atmospheric transparency indicates that the effects of incoming radiation from the sun may have been moderated by changes in the atmospheric composition of the Earth, such as the particulates from volcanic dust emission (Chester, 1988). The presence of dust in the atmosphere could increase the backscattering of incoming radiation and further reduce atmospheric temperature (Lamb, 1970; Bluth et al., 1993). An increase in volcanic eruptions would lead to an increase in the optical thickness of the atmosphere, which can reduce the amount of insolation reaching the Earth's surface, with the impact lasting about 1-3 years. Long-term records of volcanic aerosol deposition measured in ice cores (Zielinski et al., 1994) provide a 2000-year history of volcanic events. This work indicates that an intermediate number of volcanic eruptions occurred between 600 AD and 1300 AD (~ MCA) and that greater number of eruptions occurred between 1400 AD and 1985 AD (~ LIA). The volcanic eruption induced atmospheric transparency reduction may have contributed the observed impacts of associated with the LIA. In addtion, it is important to note that the depressed global temperatures that characterize the LIA may also be due, in part, to increased drawdown in atmposheric $CO_{2\ t}$resulting from the regeneration of Neotropical forest following Spanish conquest (Dull et al., 2010).

In our study, a tephra layer, found between 99 cm and 100.5 cm (red layer in the chronology bar, Figure 5.2) at Laguna Zoncho, indicates that the nearest volcano (Volcán Barú, located 35 km east of Laguna Zoncho) erupted at ~1350 AD (600 cal yr BP) based on the Accelerator Mass Spectrometry (AMS) dating (Clement and Horn, 2001). The disease introduced by the Spanish may have directly leaded to a collapse in the native population in the regions surrounding Laguna Zoncho and thereby may have indirectly contributed to reduce cultivation and support forest regeneration in the Laguna Zoncho catchment. The presence/absemce of a heavily forested catchment influences lake temperatures by affecting the amount of direct radiation incident on the lake surface and though evaporative cooling associated with evapotranspiration, as a result the regeneration of the forest surrounding Laguna Zoncho may decrease the surface water temperature. We conclude that the evidence of the LIA found in the midge-based reconstruction of SWT in the southern highlands of Costa Rica may result from the combined effects of a decrease in solar irradiance, an increase in global volcanic activity, the post-Columbian carbon sequestration event, the eruption of Volcan Barú and re-forestation of the Laguna Zoncho catchment between 1400 AD and AD 1900 AD.

The existence of severe drought during the LIA comes from the Yucatán Peninsula (Islebe et al., 1996; Curtis et al., 1998; Webster, 2000; Haug et al., 2001, 2003; Leyden, 2002; Rosenmeier et al., 2002; Wahl et al., 2006; Polk et al., 2007; Webster et al., 2007), La Chonta Bog, Lago Chiripó and Morrenas Lake 1 in central Costa Rica (Horn and Sanford, 1992), Lake Chichancanab in Mexico (Hodell et al., 1995), Wodehouse Lake in western Panama (Bush and Colinvaux, 1994) and the Caribbean slope of the Cordillera Central, Dominican Republic (Lane et al., 2011). It has been propsed that the mechanism responsible for the LIA drought in Central America is a southern displacement of the Intertropical Convergence Zone (ITCZ), which would result in reduced precipitation through much of the northern tropics (Haug et al., 2001). This finding is based on the high-resolution titanium (Ti) stratigraphy in a marine sediment core that was extracted from Cariaco Basin, Venezuela (Haug et al., 2001; Figure 5.3). A number of studies have supported this hypothesis (Hodell et al., 2004; Brown and Johnson, 2005; Polissar et al., 2005; Lozano-García et al., 2007; Russell and Johnson, 2007; Russel et al., 2007; Lane et al., 2011).

However, vegetation reconstructions conducted at sites that were strongly disturbed by human activities, like La Yeguada Lake and Garún Basin (Bush et al., 1992; Grimm et al., 2001) in the central Panama and Laguna Volcán (Cordillera de Talamnca) in eastern Panama (Behling, 2000) suggest that Central America during the past 3000 years. Laguna Zoncho is located in Costa Rican archeological site-Diquis subregion. Pollen, $\delta^{13}C$ and charcoal based vegetation reconstruction around Laguna Zoncho indicate that this small lake basin has been disturbed by humans for over 3000 years. Similarly, little connection has been observed between the proxy records and the Late Holocene droughts (Clement and Horn, 2001) and the diatom stratigraphy between 1900 AD and 1400 AD even supports possible higher lake level or wet climate (Haberyan and Horn, 2005). Possibly, the wet condition, indicated by diatom-based higher lake level during the LIA at Laguna Zoncho, may be explained by reduction of agricultural irrigation. Because of the Spanish invasion, population dropped greatly at Laguna Zoncho region, which would directly reduced the intensity of agricultural activities (e.g. such as irrigation). Furthermore, Reducing lake water for agricultural use might be the reason that water level of Laguna Zoncho rised. However, providing additional detail history of land-use at this site is necessary for future research, and long-term records of precipitation from other sites that are isolated from human impact will also help to interpret whether our observation only represent regional signal.

CHAPTER 6

CONCLUSION

Modern Chironomid Communities

This is the first attempt at quantifying the modern relationship between chironomid distribution and limnological and climatic parameters in Costa Rica. Direct gradient analyses, i.e. CCA, indicated that surface water temperature and average summer air temperature (1988-1997 AD) were strongly related to the distribution of midges in Costa Rica. Of the two variables, surface water temperature explained the greatest variance in the chironomid communities, which agrees with the conclusions in most existing trainig sets.

This research pertaining to modern distribution of chironomids in fifty-four Costa Rican lakes produced the following specific findings:

(1) Fifty-four lakes in the training set can be clearly classified in to two distinct groups based on midge assemblages (Figure 4.4). The first group includes most low elevation lakes (0 -1000 m asl) with high surface water temperature and summer air temperature. The second group contains all the high elevation lakes (2000-4000 m a.s.l) with low surface water temperature and summer air temperature.

(2) *Cryptochironomus, Triboles, Tanypus, Tanytarsus group, Tanypodinae* group, *Cladopelma, Microtendipes, Geoldichironomus, Beardius* and *Dicrotendipes*are indicators of warm surface water temperature and summer air temperature in Costa Rica.

(3) *Doithrix, Parametriocnemus* and *Chaetocladius, Limnophyes, Parasmittia, Fittkauimyia, Psedochironomus*, *Synorthocladius*, *Corynoneura type C/E, Psectrocladius* and *Symposiocladius* are mainly found in high elevation lakes (2000-3000 m asl) with low surface water temperature and summer air temperatures.

(4) *Psectrocladius, Chaetocladius and Symposiocladius* have been reported for the first time in Costa Rica and can be used as cold water indicators.

(5) No chemical variables have been identified as a significant factor to drive the chironomid distributions. This may be due to limited number of lakes in the training set that have a full suite of limnological data and the absence of measures of lake nutrient conditions

(6) Diverse ontogenies make physical and chemical features vary greatly among Costa Rican lakes. This indirectly results in high heterogeneity in the abiotic and biotic characteristics of the training set; however, the influence of lake ontogeny is difficult to remove.

(7) The RMSEP and the maximum bias for the best the midge-based inference for SWT, based on a one-component WA-PLS approach, are 3.61°C and 4.78 °C, respectively.

(8) The SWT inference model developed in this study has a higher RMSEP and max bias than most of existing chironomid-based SWT inference models (Walker et al., 1997; Olander et al., 1999; Brooks and Birks, 2000; Brooks and Birks, 2001; Porinchu et al., 2002). This may be due to the great heterogeneity of the biological and environmental condition in the training set.

Late Holocene Midge Community Change

The subfossil chironomid assemblage based SWT reconstruction in this study pioneers the quantitative assessment of surface water temperature in Central America using chironomid remains. Our results indicate that surface water temperature during the past 3000 years in Laguna Zoncho, Costa Rica is characterized by large fluctuations, with a notable decrease in SWT during the LIA, which corresponds to previous research in the tropics (Markgraf et al., 2000; Brown and Johnson, 2005; Thompson et al., 2006; Polissar et al., 2006; Rabatel et al., 2008).

CA species scores of Laguna Zoncho at every 0.5 kyr interval are depicted in a group near the center of the CA coordinates, indicating that in general the midge assemblages did reflect large magnitude changes during the 3000 years. However, interpreted from the WA-PLS based reconstructed surface water temperatures with higher temporal resolution, there are two main phases of higher than average SWT at Laguna Zoncho: (1) ~600 cal yr BP to 850 cal yr BP ($\overline{\text{SWT}}$ =25.2°C) and (2) 1750 cal yr BP to 3100 cal yr BP ($\overline{\text{SWT}}$ =25.3°C). During the period from 1850 AD to 1350 AD, Laguna Zoncho generally experienced an extended cold interval with surface water temperature that was lower than the long-term average. Particularly, the SWT averages for the sub-interval, 1350 AD – 1900 AD, are as low as 22.8°C.

The interval between ~3100 cal yr BP and 1750 cal yr BP, was generally warm (indicated by chironomid assemblages). This inference is supported by the diatom, which suggesting decrease in lake water pH and lake depth at Laguna Zoncho (Haberyan and Horn, 2005). However, the pollen and charcoal data suggest that reforestation and decreased human activity, possibly associated with wet and cold climate during the same time interval (Clement and Horn, 2001; Lane et al., 2004), characterizes this time period.

Between ~1450 cal yr BP and 850 cal yr BP, a hiatus is identified in the downcore sediment layers (184 cm-136 cm) with chironomid head capsules rarely found. Beginning at 1450 cal yr BP, chironomid taxa reappeared with a mixture constituent of thermophilous chironomids, such as *Beardius* resis type, *Parachironomus*, *Polypedilum type N* and *Labrundinia*, and cold water species, such as *Cricotopus, Rheotanytarsus, Stenochironomus* and *Procladius*, indicating a temperate period. Interestingly, the low number of chironomid head capsules found during this window of time, are associated with the synchronous increase in the intensity of human activity. Human activities may not only affect the forest coverage surrounding Laguna Zoncho and diatom communities in the lake (Clement and Horn, 2001; Brenner et al., 2002; Lane et al., 2004; Haberyan and Horn, 2005), but also bring an impact to chironomid assemblages in the freshwater system. However, indicated by the high concentration of charcoal and more enriched $\delta^{13}C$ during the gap period, the gap in chironomid communities may also possibly be due to a decrease in effective moisture that shallowened Laguana Zoncho sufficiently to limit chironomid habitat.

A decrease in temperate taxa such as *Parachironomus, Partanytarsus* and *Polypedilum type N* between 420 cal yr BP and 1997 AD and an increase in cold water chironomids, i.e.*Corynoneura* type C/E, *Cricotopus* and *Procladius*, indicate that surface water temperature of Laguna Zoncho fluctuated during the last two millennia. Decreasing surface water temperature is associated with regeneration of forest and a decline in the intensity of human activities (Clement and Horn, 2001; Lane et al., 2004). It likely supports that indigenous population decline of and forest recovery may have been the comprehensive result of the decimation in native people by diseases brought by the Spanish colonies and cold climate accompanied with contribution from the eruption of Volcán Barú around ~500 cal yr BP (Clement and Horn, 2001; Haberyan and Horn, 2005).

The signal of so-called Little Ice Age (LIA) of the 15th to 19th centuries is apparent in the chironomid-based SWT reconstruction between ~1350 and 1900 AD (Figure 18). Combined with the disappearance of shallow water indicators of diatom and occurrence of regeneration of forest (Clement and Horn, 2001; Lane et al., 2004), the watershed of Laguna Zoncho appeared to experience a wet and cold, rather than cold and direr, climate during the LIA, though this result is not supported by Haug et al., 2003. Southern migration of Intertropical Convergence Zone (ITCZ) has been identified as the possible cause of potential droughts occurred throughout the circum-Caribbean region in LIA. However, increasing studies have been conducted to show "A wet Central America during LIA (Bush et al., 1992; Webster, 2000; Haberyan and Horn, 2005). Thus, reconstructed surface water temperature and the multi-evidence of wet condition, perhaps can conclude a cold and wet LIA in Costa Rica.

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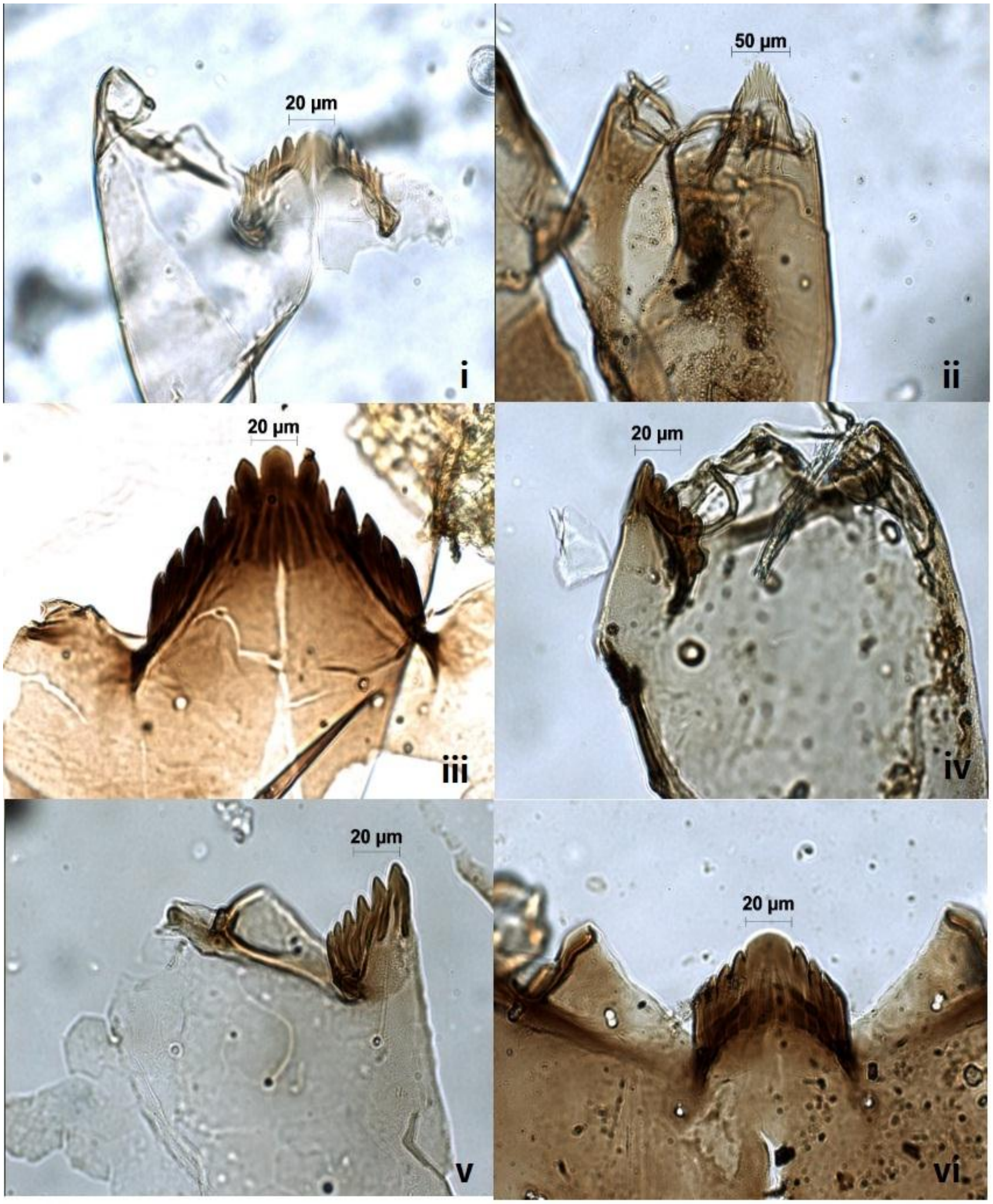
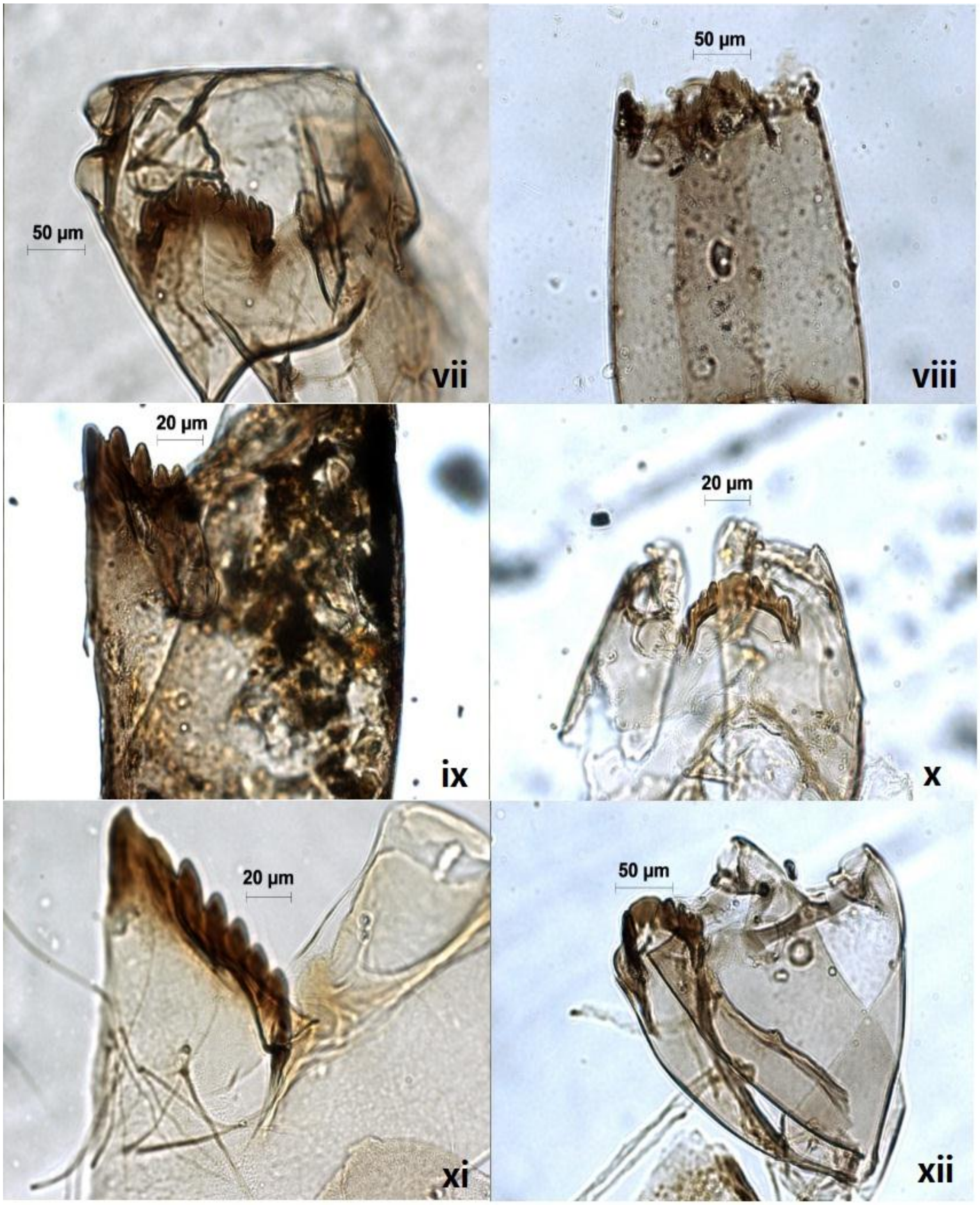
Changes: facts and figures (http://www.grid.unep.ch/glaciers/pdfs/cover.pdf)

APPENDIXES

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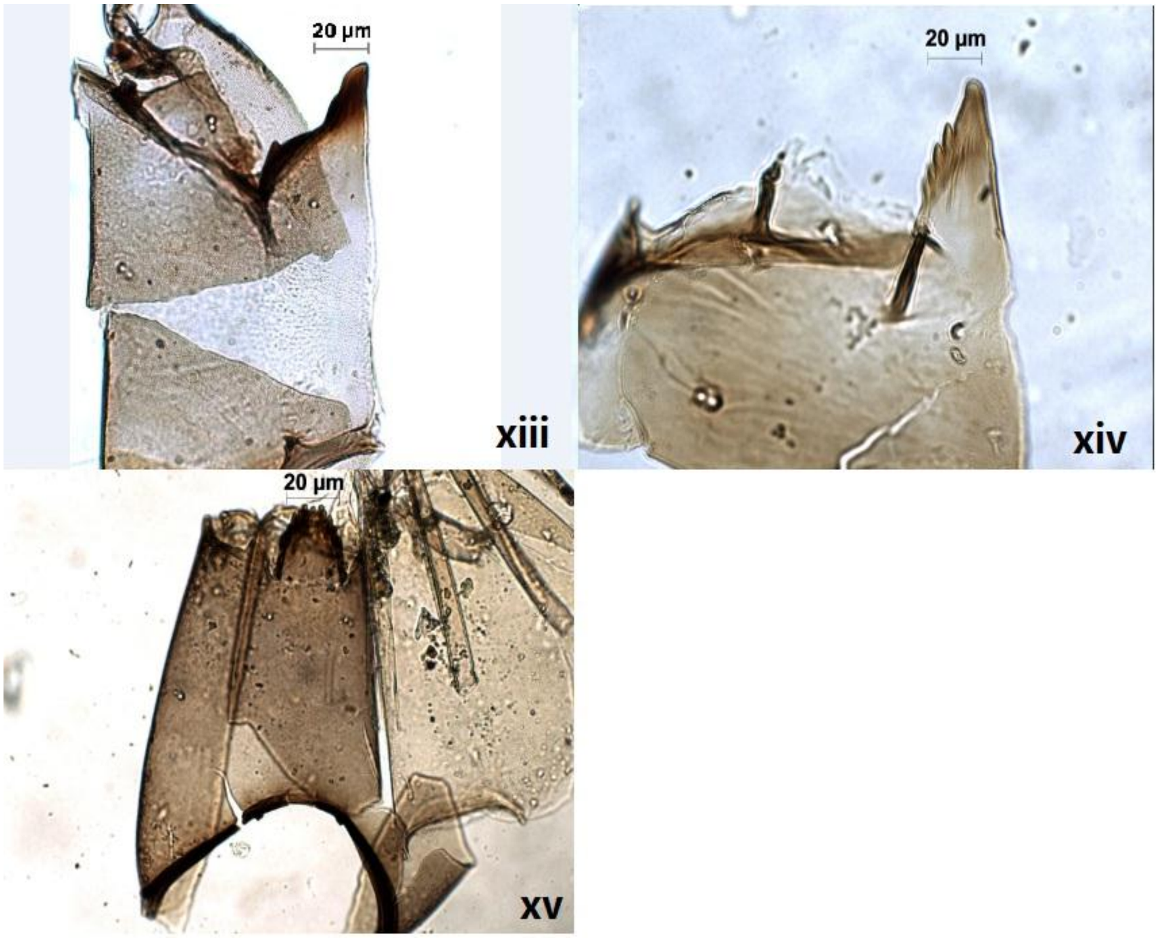
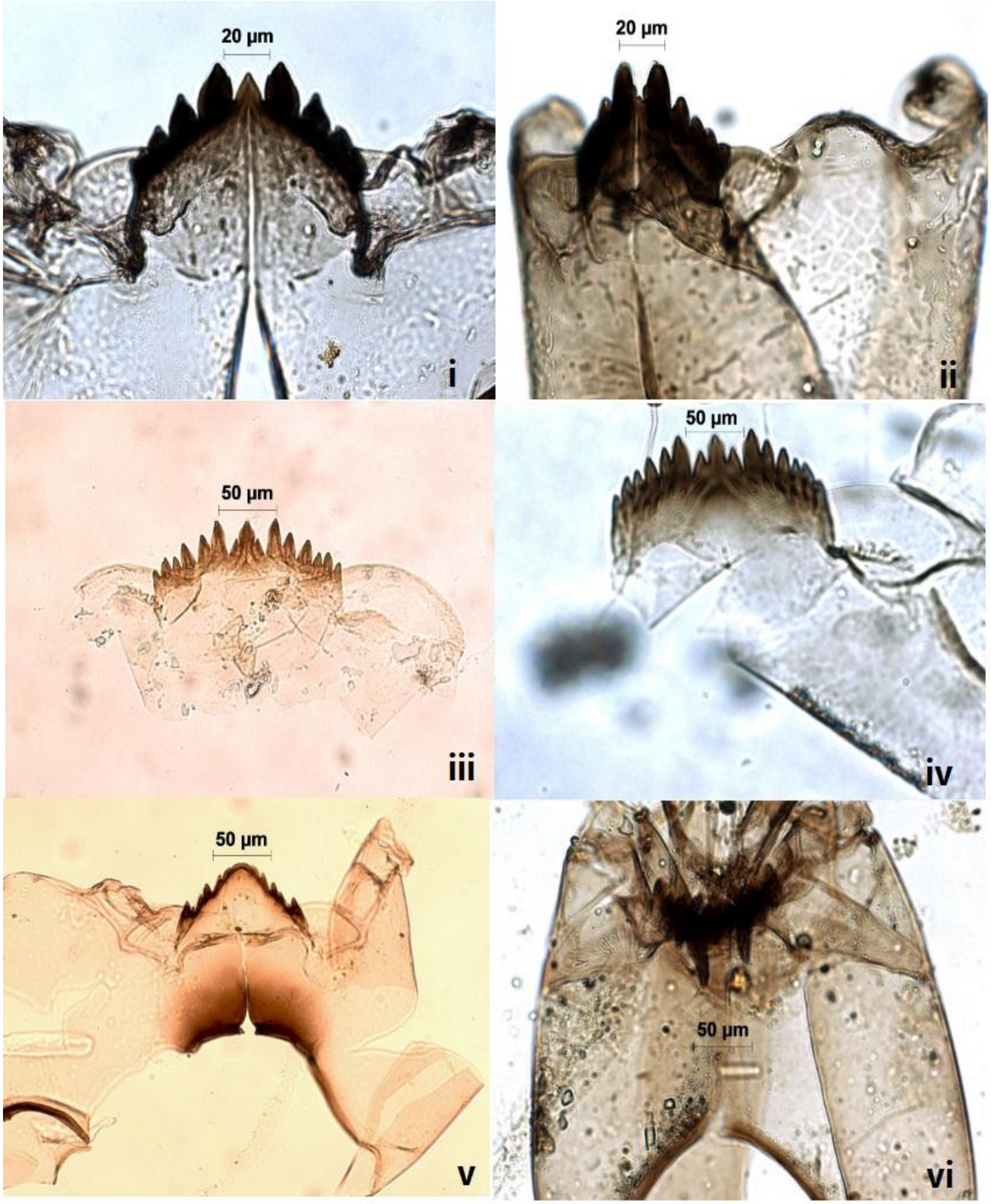


Figure A-1 Orthocladiinae taxa identified in Costa Rica: (i) *Chaetocladius*, (ii) *Corynoneura*, (iii) *Cricotopus*, (iv) *Doithrix*, (v) *Eukiefferiella claripennis*, (vi) *Eukiefferiella fittkaui*, (vii) *Limnophyes*, (viii) *Orthocladius*, (ix) *Parametriocnemus*, (x) *Parasmittia*, (xi) *Psectrocladius*, (xii) *Pseudosmittia*, (xiv) *Symposiocladius*, (xiv) *Synorthocladius*, (xv) *Thienemanniella*.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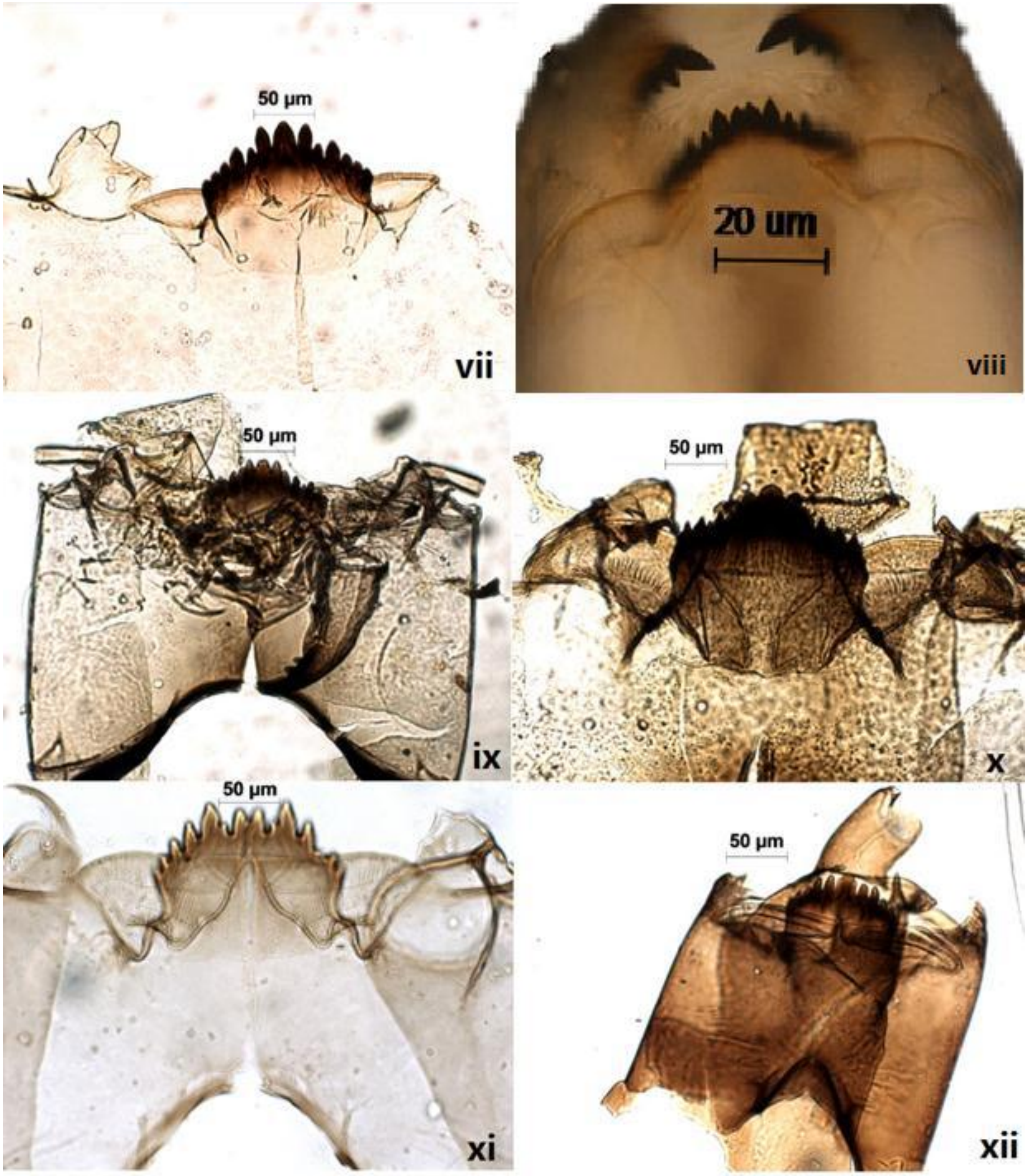
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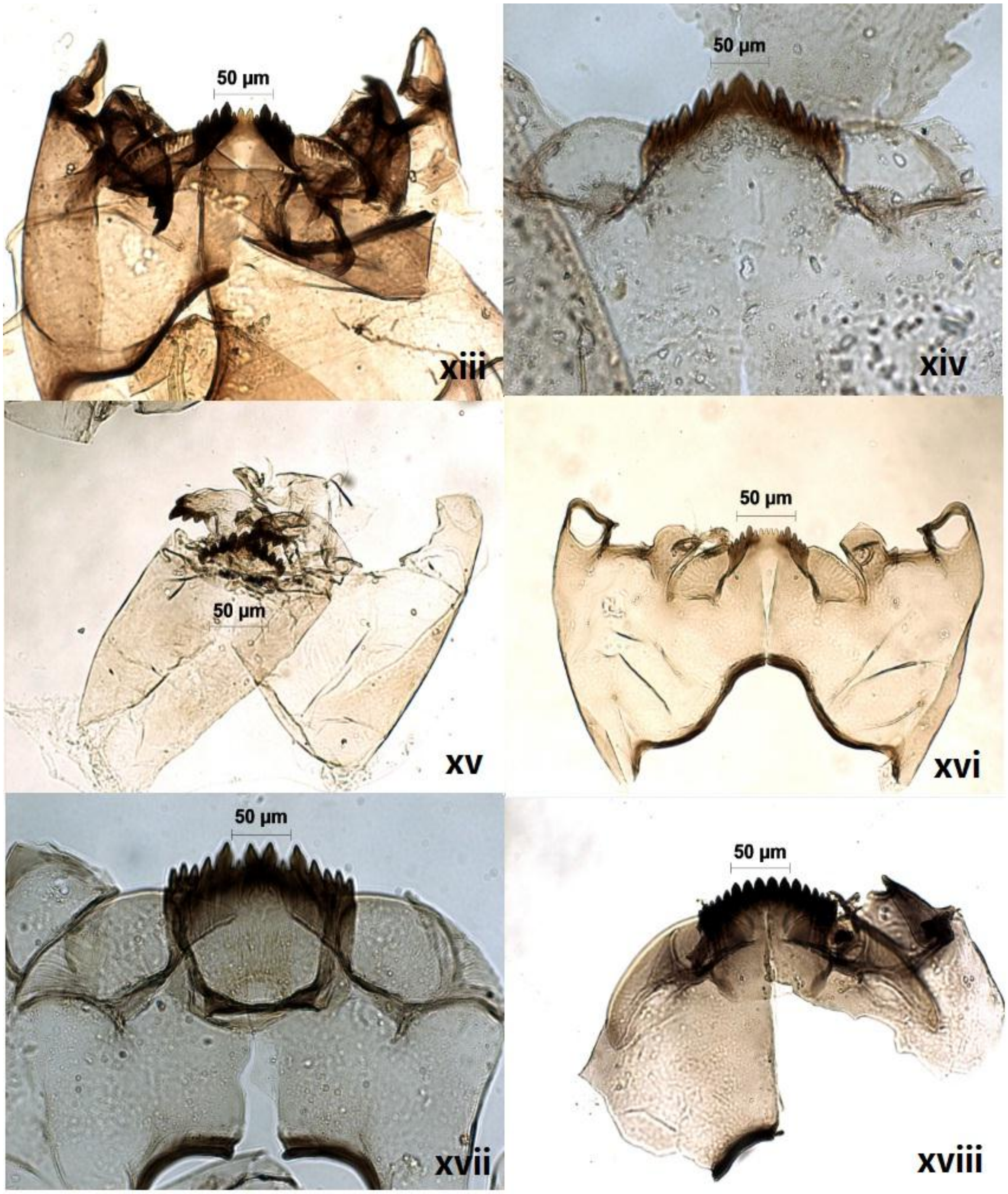
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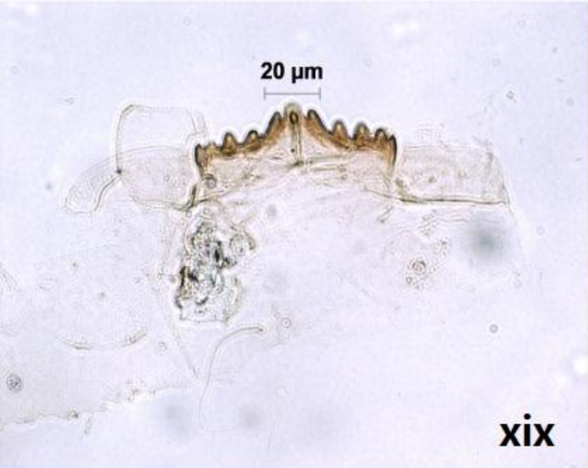
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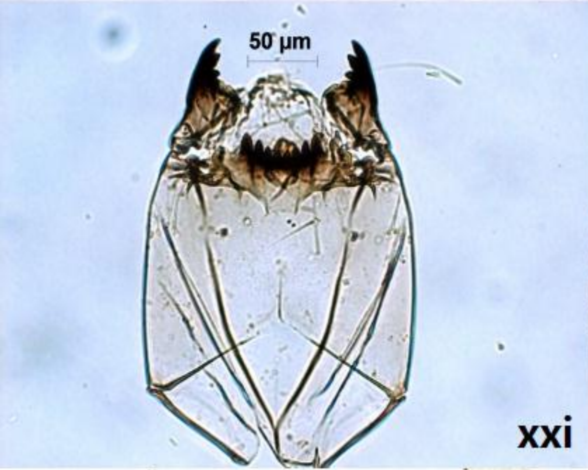
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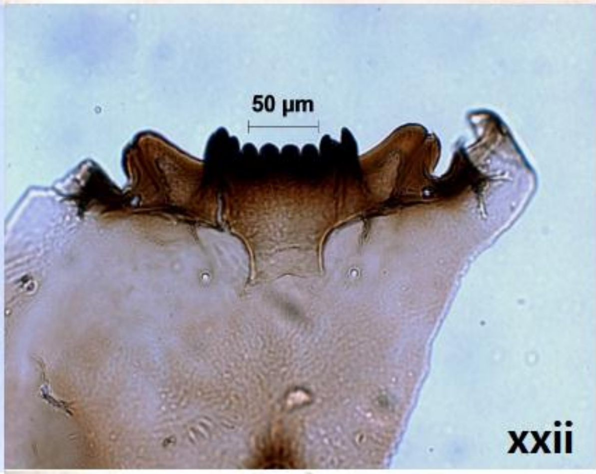
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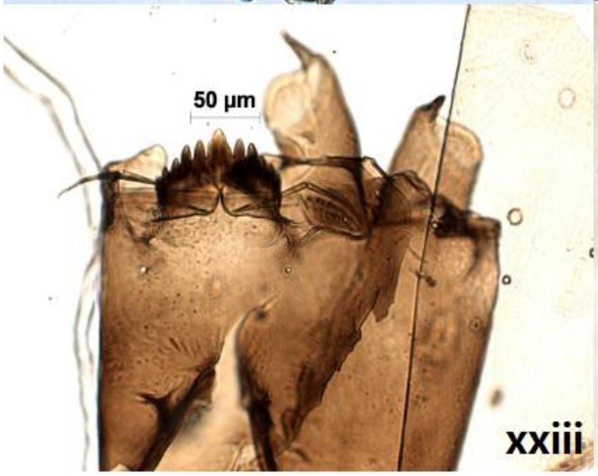
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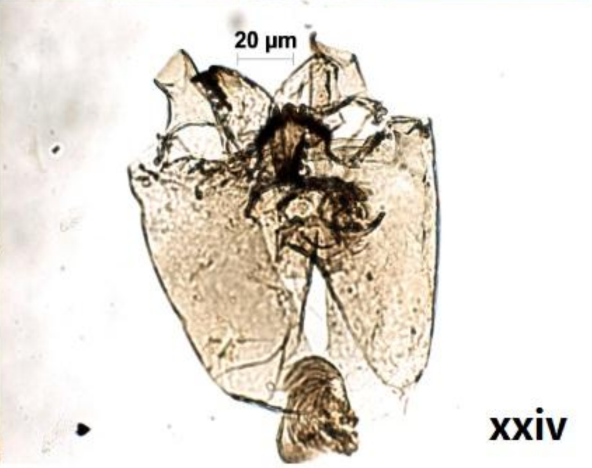
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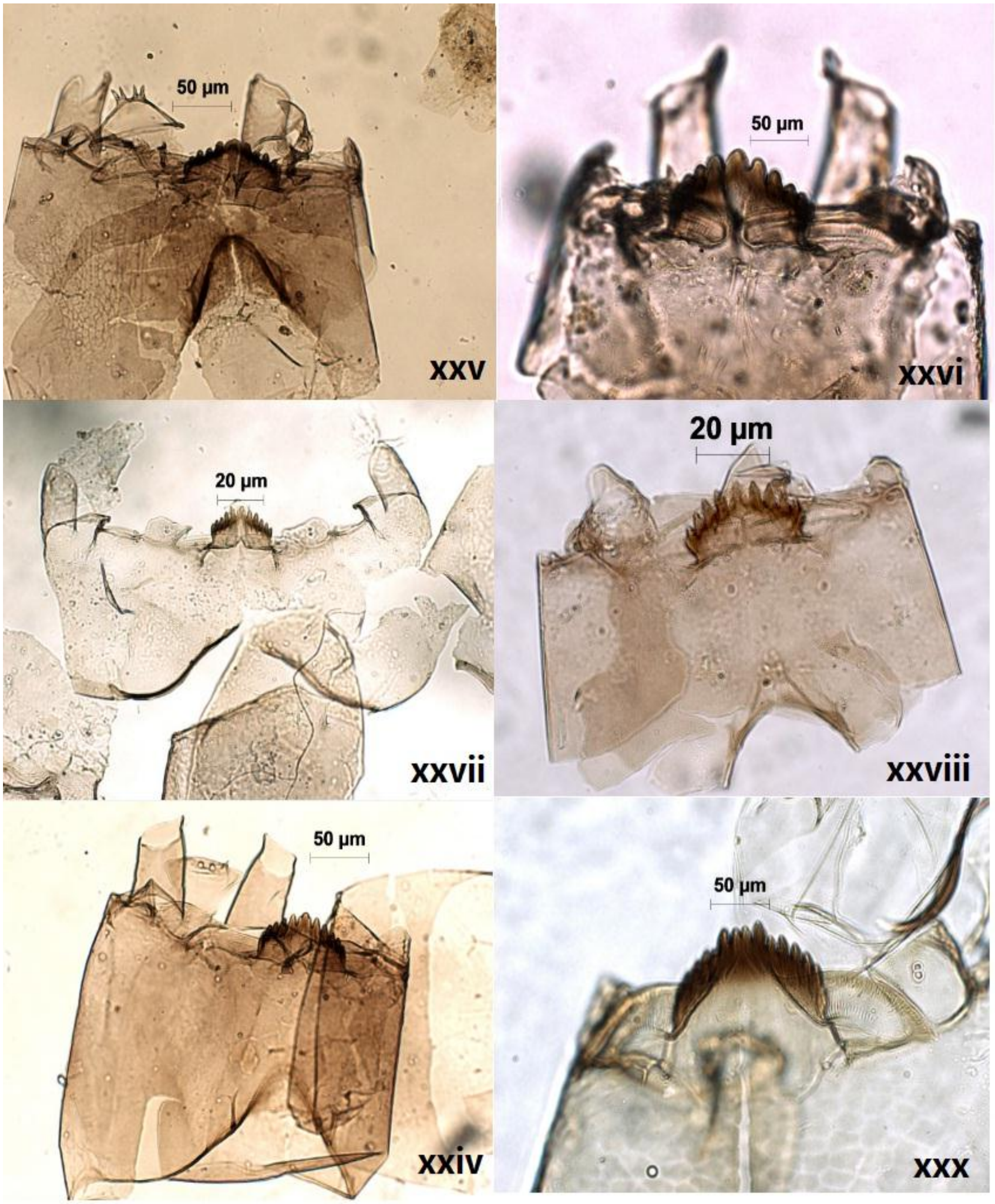
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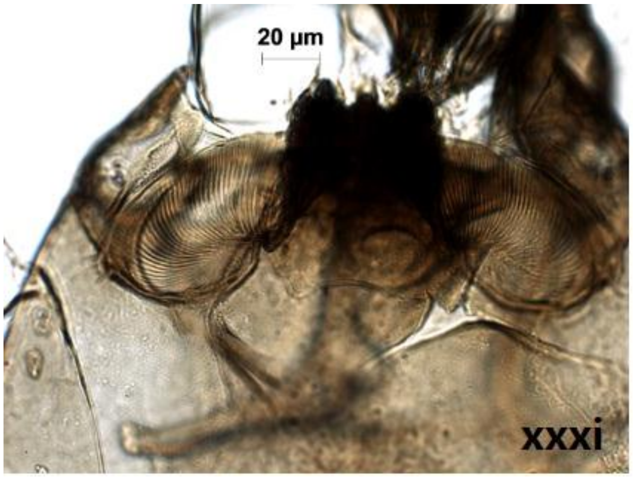
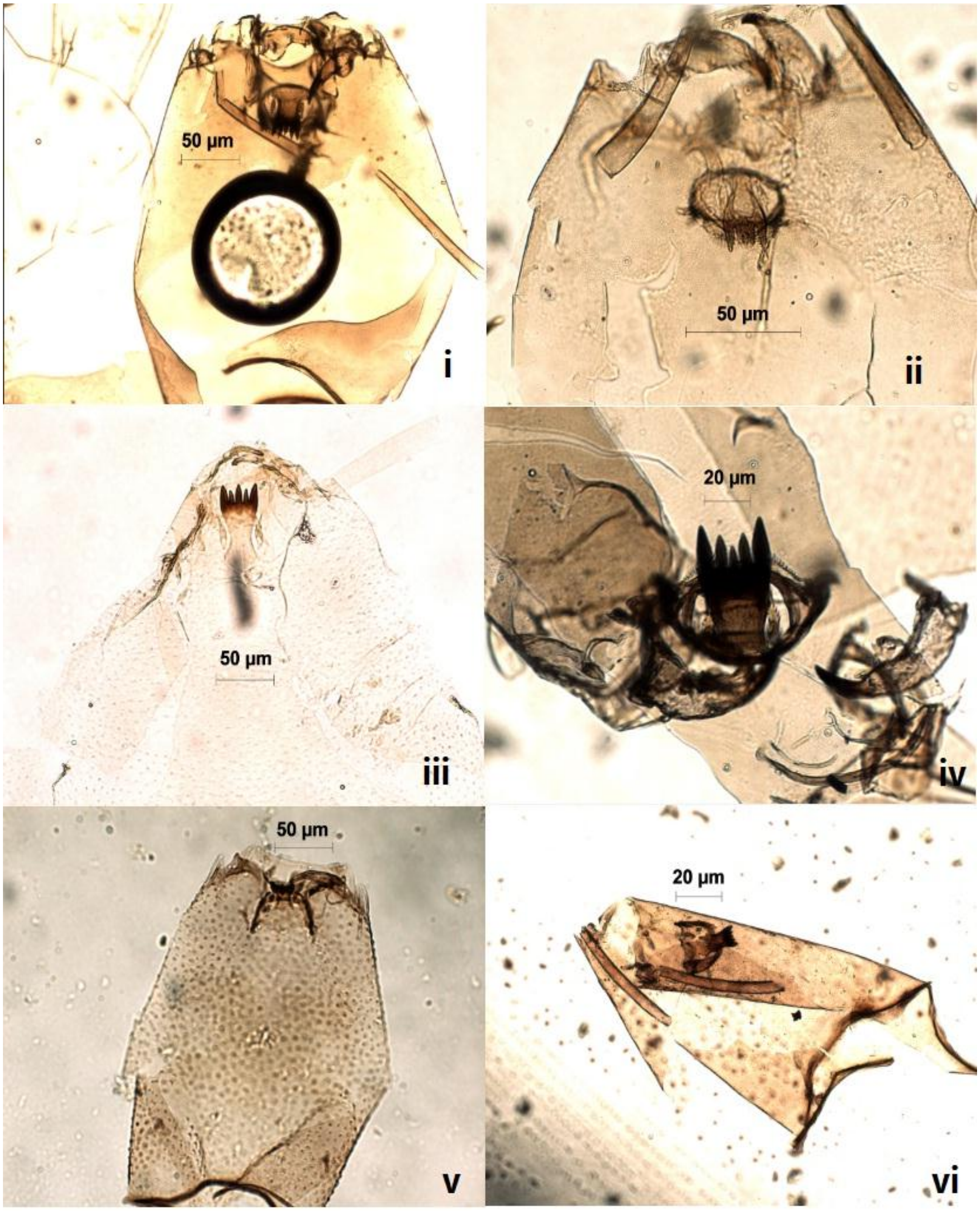


Figure A-2 Chironominae taxa found in Costa Rica: (i) *Beardius resis type*, (ii) *Beardius type A*, (iii) *Chironomus anthracinus*, (iv) *Chironomus plumosus*, (v) *Cladopelma*, (vi) *Cryptochironomus*, (vii) *Dicrotendipe*s, (viii) *Endochironmomus*, (ix) *Glyptendipes*, (x) *Geoldichironomus*, (xi) *Lauterborniella/ Zavreliella,* (xii) *Micropsectra*, (xiii) *Microtendipes,* (xiv) *Parachironomus,* (xv) *Paratanytarsus*, (xvi) *Paratendipes,* (xvii) *Polypedilum nubifer,* (xviii) *Polypedilum sorderns,* (xix) *Pseudochironomus*, (xx) *Rheotanytarsus*, (xxi) *Stenochironomus* (whole head), (xxii) *Stenochironomus mentum*, (xxiii) *Tanytarsus type C,* (xxiv) *Tanytarsus type G*, (xxv) *Tanytarsus type KR*, (xxvi) *Tanytarsus type L*, (xxvii) *Tanytarsus type LU*, (xxviii) *Tanytarsus type NZ,* (xxix) *Tanytarsus type P*, (xxx) *Tribelos,* (xxxi) *Xenochironomus*.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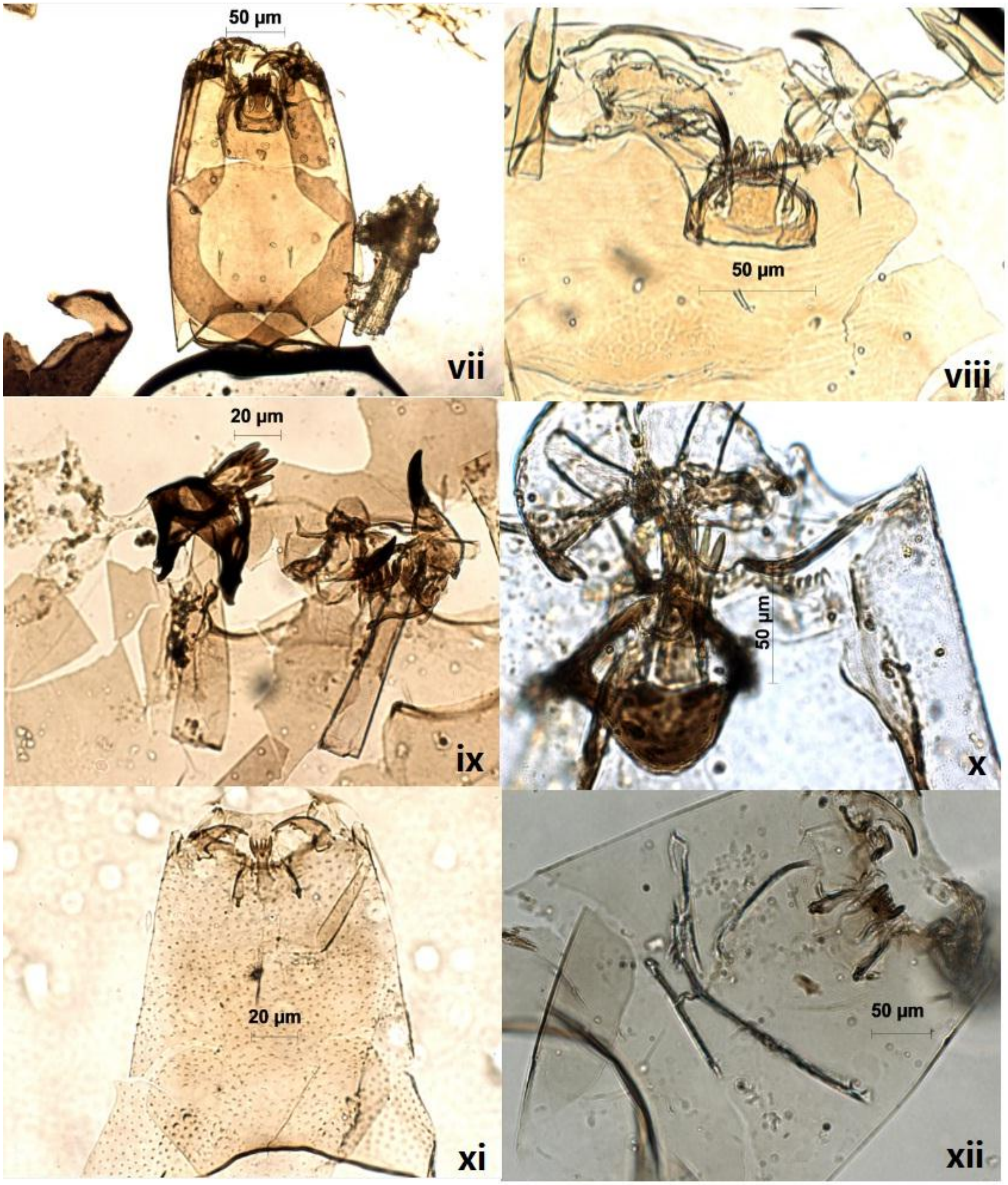
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Figure A-3 Tanytardinae taxa found in Costa Rica: (i) *Brundiniella*, (ii) *Fittkauimyia*, (iii) *Labroundinia*, (iv) *Procladius*, (v) *Tanypodinae type H*, (vi) *Tanypodinae type LP*, (vii) *Tanypodinae type R*, (viii) *Tanypodinae type T* (*Apsectrotanypus*), (ix) *Tanypus*, (x) *Tanypus mentum*, (xi) *Tanypodinae type QRRS*, (xii) *Tanypodinae other taxa1*, (xiii) *Tanypodinae other taxa2*,(xiv) *Tanypodinae other taxa3*, (xv) *Tanypodinae other taxa4*.