

# Response of chironomids to late Pleistocene and Holocene environmental change in the eastern Bolivian Andes

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**Abstract** We present the first palaeolimnological investigation of chironomid larval assemblages from the Bolivian Eastern Cordillera. Taxonomic diagnoses are provided for the 10 chironomid taxa (subfamilies: Chironominae, Orthocladiinae and Tanypodinae) identified in the lake sediments. We compared changes in the chironomid assemblage from two Andean sites with previously reported palynological, charcoal and geochemical data, and highlight the potential of chironomid analysis to provide additional insights into environmental change in this region of high biodiversity over the last 18,000 years. At Lake Challacaba (17°33.257'S, 65°34.024'W; 3,400 m asl), the chironomid and geochemical data indicate

periodic desiccation and hypersalinity of the basin *c.* 4,000–3,460 cal year BP. Increased abundance of *Chironomus* sp. at *c.* 1,000 cal year BP suggests a change in human activity, supporting inferences from the pollen and spore records, which indicate elevated pastoral agriculture at this time. The greatest assemblage change in the chironomid record from Laguna Khomer Kocha Upper (17°16.514'S, 65°43.945'W; 4,153 m asl) occurred at *c.* 6,380 cal year BP, concomitant with an increase in marsh woodland taxa, wetter conditions and a rising lake level at the end of a Holocene dry event. There is no apparent response in the chironomid assemblage to burning, however, at the onset of this dry event (*c.* 10,000 cal year BP), which is the major transformative agent of the terrestrial vegetation. This study shows that chironomid assemblages in the tropical Andes responded to regional and local environmental changes, and in particular, that they were sensitive to adjustments in net moisture balance (water level fluctuations and salinity) and anthropogenic impacts (nutrient input). This suggests that within-lake processes are more important as drivers of chironomid assemblage composition than terrestrial vegetation or fire regime. Nevertheless, the full potential of subfossil chironomid analysis will only be realised once more modern autecological data are available.

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Salinity

## Introduction

Owing to their high chitin content, head capsules of chironomid larvae (Insecta, Diptera, Chironomidae) are well preserved within lake sediments (Walker 2001). Chironomids regularly represent the most abundant group of macroinvertebrates in fresh- and brackish-water habitats. They have a worldwide distribution, exploiting large ranges in elevation and temperature (Armitage et al. 1995). Previous studies of fossil chironomid assemblages have highlighted their potential as indicators of a broad range of environmental changes. These include anthropogenic land disturbance (Woodward and Shulmeister 2005), hydrology (Hofmann 1998), lake pH (Brodin and Gransberg 1993), lake trophic status, (Brodersen and Quinlan 2006), oxygen regime (Quinlan and Smol 2001), salinity (Chen et al. 2009), substrate type (Verschuren et al. 2000) and water and air temperatures (Brooks and Birks 2001; Lang et al. 2010).

Despite the proven value of subfossil chironomids in palaeoenvironmental reconstruction, a paucity of modern ecological and taxonomic research in South America remains a serious limitation to any palaeoecological investigation in this area. The most significant progress in using chironomids for palaeoenvironmental reconstruction has been made in the Patagonian region of Chile and Argentina (Verschuren and Eggermont 2006). Recent ecological and palaeoecological studies of chironomids have highlighted the improvements possible in resolving taxonomic difficulties when a research focus exists (Massaferro et al. 2008, 2009). Nowhere else in South America is there an equivalent intensity of research effort and the central Andes (Bolivia/Peru) in particular remains deficient in studies. Chironomids are poorly known in the region and the only inventory of aquatic Diptera from modern lakes in Bolivia-Peru was collected during the 1978 Catherwood Expedition (Roback and Coffman 1983). A detailed modern ecological investigation of Lake Titicaca, and the smaller, separate Lake Umayo, revealed the presence of only nine species of Orthoclaadiinae and six species of Chironominae (Roback and Coffman 1983). Elsewhere in the Bolivian Eastern Cordillera, taxa from streams and lakes have also been identified, but their ecology is largely unknown (Navarro and Maldonado 2002).

This study represents the first investigation of subfossil chironomids in the Eastern Cordillera of

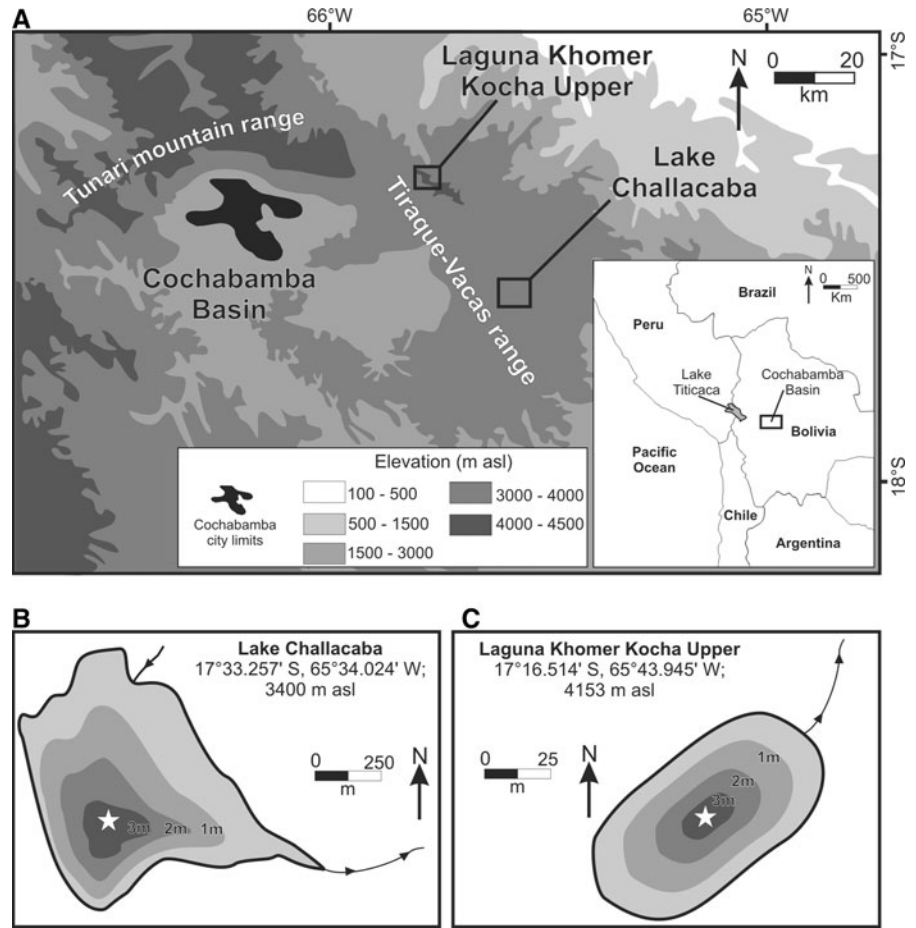
Bolivia. We present the chironomid assemblages from two sediment cores collected in the Cochabamba region. The records extend back 4,000 and 18,000 years. These data provide new insights into the chironomid taxa present above 3,200 m above sea level (m asl), and changes in their distribution and abundance during the late Pleistocene and Holocene. We first provide taxonomic notes to standardise approaches in future investigations and test the utility of chironomid remains as independent indicators of changing environmental conditions in the eastern Bolivian tropical Andes. Then, with reference to previously published palynological, charcoal, geochemical and physical analyses (Williams et al. 2011a, b), we explore the relationship between turnover in the chironomid taxa and the impacts of climate change and pre-Columbian societies. By comparing the scale and timing of changes in the chironomid assemblage to previously identified changes in local vegetation and fire regime, we establish the relative importance of changes in climate and within-lake variables in determining the composition of chironomid assemblages.

## Regional setting and study sites

The eastern slopes of the tropical Andes, where high precipitation is caused by the collision of moist, westerly Amazonian air with the Andean mountain chain, is one of the most biologically diverse areas on Earth (Killeen et al. 2007). Increasing human occupation of the Andes and predicted future climate changes mean the biodiversity is highly vulnerable (Malcolm et al. 2006). Situated within the Eastern Cordillera forethrust zone of the Bolivian Orocline, the Cochabamba Basin is a Plio-Pleistocene valley formed after 5.33 Ma, and includes large volumes of Quaternary sedimentary deposits (McQuarrie 2002). This inter-Andean montane valley is limited on the northern and western sides by the Cordillera del Tunari, and on the east by the mountain range of Tiraque-Vacas (Fig. 1a). Although the specific geology of this surrounding high ground is not known in detail, the bedrock material is mainly of Ordovician-age (488.3–443.7 Ma) quartzite, lutites and sandstone, with some granite intrusions (Kessler 2002; McQuarrie 2002).

At the heart of the central valley, the city of Cochabamba (17°40S, 66°14 W/2,500 m asl) has a

**Fig. 1** The study location within Bolivia.  
**a** Cochabamba Basin showing altitudes, current city extent and study sites. *Inset map* locates Cochabamba Basin within Bolivia. **b** Lake Challababa (also know as Pilawitu). Bathymetry shown in metres. Coring location marked (*asterisk*). **c** Laguna Khomer Kocho Upper. Bathymetry shown in metres. Coring location marked (*asterisk*)



modern population of ~600,000. Owing to the fertile Quaternary deposits, the Cochabamba valleys are a major region of food production, and were a location of pre-Columbian agriculture and trading beginning more than 3,000 years ago (Hensen 2002; Williams et al. 2011a). This was intensified during Tiwanaku (c. 1,500–900 year BP) and Inca (c. 650–550 year BP) rule, when a road network was developed to connect the Cochabamba Valley to both upland and lowland areas (Higuera 1996; Janusek 2008; Stanish et al. 2010).

Regional climate, particularly precipitation, is controlled by several climate systems including movement of the Intertropical Convergence Zone (ITCZ; Leduc et al. 2009), variability of the South American summer monsoon (SASM; Zhou and Lau 1998), and inter-annual variation of the El Niño-Southern Oscillation (ENSO; Chiang 2009). Changes in precipitation are predicted to be the predominant feature of future climate changes (Urrutia and Vuille 2009).

Topographic and climatic variation place the Cochabamba region at the confluence of four Tropical Andean ecoregions: the Bolivian Yungas, the Bolivian montane dry forests, the central Andean Puna and the central Andean dry Puna (Olson et al. 2001). Locally, several species of endemic birds, mammals, amphibians and plants occur (Young 2007), and the Cochabamba Basin is recognised as an important conservation area for the protection of high-elevation *Polylepis* woodlands (Fjeldså and Kessler 1996). High biodiversity and narrow vertical species ranges in sites of complex topography, means even small variations in temperature and precipitation can cause considerable species turnover. As a result, the fauna and flora of the region are highly sensitive to change in environmental conditions.

Remnants of a large water body that existed within the Cochabamba Basin during the Quaternary, together with smaller lakes created by local glaciation features in the surrounding mountain ranges, provide

opportunities to obtain palaeolimnological records. In this study, two lake systems north and east of the main Cochabamba Basin were investigated.

#### Lake Challacaba (Vacas Lake District)

The Vacas Lake District, situated 60 km east of the city of Cochabamba (Fig. 1a), is a system of six lakes located within a cold (7.2–11.3 °C) and seasonally dry (2.6 mm/month June–August, 114 mm/month January–March), high-elevation (>3,000 m asl) valley (Hijmans et al. 2005; Ritter 2000). The Vacas Lake District is positioned within the biogeographic regions of the “northern Puna/semi-humid” and the “sub-humid/Puna and Punean woodlands of the Tunari” (Ibisch et al. 2003; Navarro and Maldonado 2002). Today, however, the area is dominated by cultivation of potatoes and other tubers, and has also been heavily impacted by grazing. Farther from the agricultural districts, and more typical of the natural vegetation of the Cordillera of Tiraque–Vacas, are a variety of grassland, shrubland and woodland types.

Within the Vacas Lake District, Lake Challacaba is a small, ~1.5-km<sup>2</sup>, freshwater system, 2.5 km from the settlement of Vacas (17°33.257'S, 65°34.024'W; 3,400 m asl; Fig. 1b). Lake Challacaba is fed at its northernmost point by a stream from the surrounding mountains and drained via an outflow at the southeast end (Fig. 1b). At the time of coring in June 2007, water depth was 3 m, conductivity was 332 µS/cm, pH was 9.45 and Secchi depth was 0.58 m. Today Lake Challacaba is surrounded by actively worked agricultural land, much of which is inundated by water during the wet months. *Myriophyllum* (Haloragaceae) was the dominant component of the aquatic vegetation in Lake Challacaba, and many of the other Vacas lakes, and is an important food source for cattle during the dry season (Ritter 2000). Other important aquatic vegetation of the Vacas Lake District includes *Lemna* (Lemnaceae), *Schoenoplectus* (Cyperaceae), *Zanichellia* and *Potamogeton* (Potamogetonaceae) (De la Barra 2003).

Since at least early Incan times (650–550 cal year BP), the Vacas municipality was significant for regional transportation routes. The current road passing through the Vacas lake district was once a principal route linking the main Cochabamba Valley and the archaeological sites of Inca Rakay in the west, to those in the southeast such as Inkallajta and Mizque

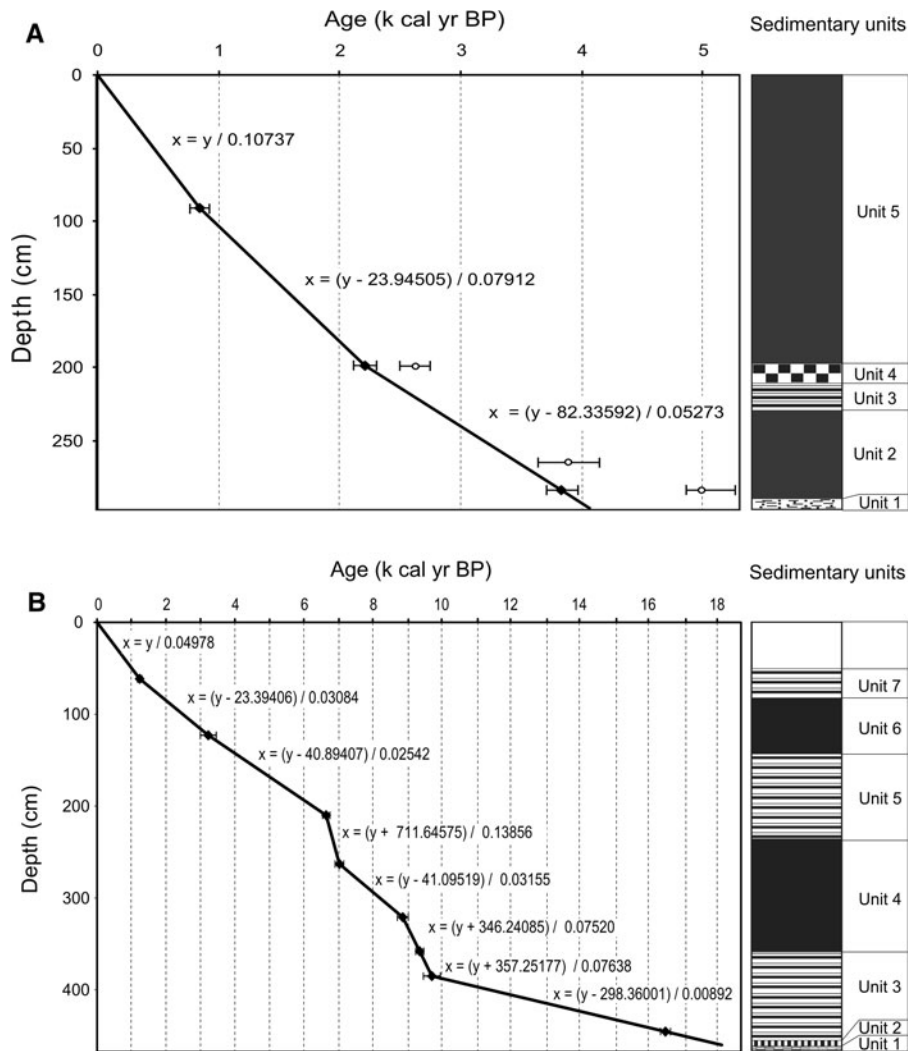
(Higuera 1996). Given the importance of camelid pastoralism and caravans for pre-Columbian peoples (Lynch 1983), and the movement of Tiwanaku and Inca traders between the main valley and the Mizque enclave (Janusek 2008), it seems likely that many groups of people would have had direct contact with the Vacas lakes.

#### Palaeoecological summary

A 297-cm-long sediment core from Lake Challacaba provides a continuous record of the last c. 4,000 years (Fig. 2a). The full sediment lithology, chronological data and palaeoecological assemblages are detailed in Williams et al. (2011a). Previous analyses of pollen, charcoal, geochemical and geophysical properties of the lake sediments revealed the sensitivity of the site to changes driven by humans as well as climatic factors (Williams et al. 2011a). Fluctuations in drought-tolerant pollen taxa (Amaranthaceae and Caryophyllaceae) and calcium carbonate (CaCO<sub>3</sub>) indicate two periods of reduced net moisture (c. 4,000–3,370 and c. 2,190–1,020 cal year BP) with wetter episodes between c. 3,370–2,190 and c. 1,020 cal year BP-present (Fig. 4c). Lake formation and moisture fluctuations broadly correlate to the end of the Holocene dry event (HDE) and broad variations in El Niño/Southern Oscillation activity reported elsewhere in the Andes (Moy et al. 2002). The HDE lasted from c. 8,000–5,000 year BP, but appears to be spatially age-transgressive. High charcoal abundance from c. 4,000–2,000 years ago suggests human presence and implies continuous use of the ancient road network. A decline in charcoal, an increase in landscape destabilisation, and the presence of an invasive species (*Ludwigia*) and dung fungus (*Sporormiella*) from c. 1,340–1,210 cal year BP, suggests changes in human cultural activity, particularly increased camelid herding, were a major factor in shaping the modern landscape (Williams et al. 2011a). This change in human activity correlates with major cultural transitions seen in the Tiwanaku archaeological record (Janusek 2008).

#### Laguna Khomer Kocha Upper (Cordillera el Ronco)

Situated on the eastern slopes of the Cordillera el Ronco, Laguna Khomer Kocha Upper is located above



**Fig. 2** Age-depth curves and sediment stratigraphy of sediment cores. **a** Lake Challacaba. Sedimentary units: 1 Greenish-grey sandy clay, 2 dark gyttjas with irregular brownish bands, 1–3 cm thick, 3 gyttjas with alternating dark and pale bands, 4 dark mottled gyttjas, and 5 pale to medium-gray gyttjas with progressively higher quantities of clays. **b** Laguna Khomer Kocha Upper. Sedimentary units: 1 Greenish-gray sandy clay, 2 pale brown coarse sand, 3 dark brown gyttjas with some bands

of sandy material, 4 dark brown gyttjas, 5 very dark brown gyttjas, with some strong banding evident, 6 dark brown gyttjas, and 7 very dark brown gyttjas, with some strong banding evident. Sediments upwards of 47 cm were not retrieved due to their extremely fluid nature. Rejected <sup>14</sup>C dates shown by open circles. Detailed results of <sup>14</sup>C dates previously published (Williams et al. 2011a, b)

the tributaries of the Rio San Mateo, a valley that descends >2,000 m in elevation over <10 km. Laguna Khomer Kocha Upper is 45 km west of Cochabamba city and 35 km north of the Vacas Lake District (Fig. 1a). Laguna Khomer Kocha Upper is a small, ~0.1-km<sup>2</sup>, glacially formed lake and its maximum depth at the time of fieldwork in June 2007 was 3.6 m (17°16.514'S, 65°43.945'W; 4,153 m asl; Fig. 1c). During the same fieldwork season, water transparency

was 3.2 m, conductivity was 28 μS/cm and pH was 7.38. The lake is fed by runoff from the surrounding slopes and drains via an outflow channel at the northeast end (Fig. 1c).

At Laguna Khomer Kocha Upper, dry season (June–August) precipitation averages 13 mm/month and increases to 138 mm/month during the wet season (January–March). Additional humidity is contributed, even during the dry season, by clouds that ascend from

the valleys to the northwest and deposit large quantities of moisture on the sparsely vegetated slopes (Kessler 2002). Mean temperature varies from 4.5 °C in the wet season to 7.6 °C in the dry season (Hijmans et al. 2005) and the local lapse rate is estimated to be ~4.5 °C/1,000 m (Williams et al. 2011b).

Laguna Khomer Kocha Upper lies in a region of rapidly changing vegetation, associated with the steep elevation gradients present in the valley of San Mateo. The lake lies in the sub-humid Puna and transitional Punean woodlands that split the Puna and Yungas zones along the Cochabamba section of the Eastern Cordillera (Ibisch et al. 2003; Navarro and Maldonado 2002). Today the local landscape immediately surrounding the lake is dominated by Andean tussock-forming grassland, within which are pockets of woodland dominated by *Polylepis* (Rosaceae). A low (<2 m) glacial moraine separates the lake from an area of flat, waterlogged ground, which is probably an in-filled lake of similar size. Today there is minimal sign of human impact at Laguna Khomer Kocha Upper and examination of the *Polylepis* woodland patches surrounding the lake revealed no indications of exploitation.

#### *Palaeoecological summary*

A 413-cm sediment core was extracted from the deepest point of Laguna Khomer Kocha Upper. The chronology for the succession was derived from <sup>14</sup>C AMS dating of three bulk sediment samples and five samples comprised of picked charcoal fragments (Fig. 2b). A full description of the sediment structure, chronological and palaeoecological data has already been published (Williams et al. 2011b). The sedimentary succession starts at c. 18,100 cal year BP and indicates that fire regime, governed by climate variation, has long been a transformative agent in eastern Andean ecosystems (Williams et al. 2011b). The fossil charcoal record from Laguna Khomer Kocha Upper demonstrates that before c. 14,500 cal year BP, fire was virtually absent from the landscape surrounding the lake. Deglacial warming (c. 18,000–14,500 cal year BP), coupled with relatively moist conditions that were free from fire, allowed locally growing high-Andean *Polylepis* woodland to expand. Between c. 14,500 and 10,000 cal year BP burning was minimal, but still quickly began to transform the local vegetation, as woodland was probably restricted to

areas naturally protected from fire, such as steep scree slopes and gullies surrounding the lake. A major increase in burning 10,000–6,400 cal year BP almost completely removed high-Andean woodland from around the lake. The increase in fire was probably a function of region-wide aridity (the HDE), which although spatially variable in timing, peaked c. 8,000–5,000 cal year BP. Increased aridity at Laguna Khomer Kocha Upper also caused lake water levels to fall. A sharp decline in burning at c. 6,400 cal year BP and an increase in marsh woodland (*Alnus*) marked the termination of the HDE at Laguna Khomer Kocha Upper and a return to wetter conditions. *Polylepis* woodland expanded from the small, fire-protected stands to which it was formerly limited during the height of the aridity, suggesting that fire, led by climate, was critical in determining the niche space available for woodland growth.

As well as recording an environmental history of local vegetation dynamics, long-distance transport of pollen into Laguna Khomer Kocha Upper via upslope winds provides a background signal of vegetation changes in the lower montane forests. Simultaneous changes in both Andean and lowland taxa suggest that vegetation dynamics were primarily controlled by climate. There is no evidence in the sediment record to indicate that human activity had any impact on the local landscape 18,000–1,000 cal year BP (Williams et al. 2011b).

#### **Materials and methods**

Two sediment cores from each site (Challacaba B and C and Khomer Kocha Upper A and B) were recovered from the deepest point of each lake using a cam-modified Livingstone piston corer in June 2007. Staggered, overlapping starting depths below the sediment–water interface ensured that a continuous record was recovered despite some sediment loss from the core-tube ends. All sediment cores were recovered in aluminum tubes (50 or 38 mm diameter) and sealed on site. The sediment–water interface was recovered, where possible, using a Perspex surface sample tube, attached to coring rods. The sediments collected by the surface sampler (top 50 cm) were extruded and bagged in the field. All recovered sediment was transferred to The Open University, Milton Keynes, UK, and stored at 4 °C. The sediment cores were split and the sediment divided using a fine strand of wire.

Core chronology was established for the sites using accelerator mass spectrometry (AMS)  $^{14}\text{C}$  dates on bulk gyttja, macrofossil plant remains and picked charcoal fragments. Full details and discussion of the age-depth model are provided by Williams et al. (2011a, b).

Analysis of the chironomid head capsules was conducted on subsamples of  $1\text{ cm}^3$ . Following the procedure described by Brooks et al. (2007), samples were deflocculated in 10 % KOH, heated to  $70\text{ }^\circ\text{C}$  for 5 min, sieved and separated into two size fractions (90 and  $212\text{ }\mu\text{m}$ ). Head capsules were picked by hand from a sorting tray under a binocular microscope (Olympus SZX12) at  $12.5\text{--}25\times$  magnification and progressively dehydrated. Depending on size and fragmentation of head capsules, between 1 and 5 were mounted ventral side up under 6-mm-diameter coverslips onto a microscope slide. Identification was subsequently achieved using a Nikon *Eclipse 50i* microscope at  $400\times$  magnification and relevant keys (Brooks et al. 2007; Dieffenbacher-Krall et al. 2008; Rieradevall and Brooks 2001; Wiederholm 1983). Stratigraphic diagrams were plotted using the program C2 (Juggins 2003). Procedures for radiocarbon, palynological, charcoal, geochemical and physical analysis followed standard protocols that were described in full by Williams et al. (2011a, b).

Stratigraphic diagrams were zoned by optimal sum of squares partitioning (Birks and Gordon 1985) using the software ZONE v. 1.2 (Lotter and Juggins 1991). The broken-stick model (Bennett 1996; Birks 1998) was used to identify significant zones using the software BSTICK v. 1.0 (Line and Birks 1996). Rate of change analysis was calculated from the Euclidean distance between adjacent sample scores (from the ordination axes), divided by the inter-sample time (Urrego et al. 2009).

## Results

### Taxonomic notes

#### *Chironomus* (Fig. 3a I)

**Diagnostic features** Mentum with trifold median tooth; 6 lateral teeth; 4th lateral shorter or equal to 5th. Ventromental plates large, with smooth outer margin; prominent striations at base. Mandible with 3 inner teeth. This taxon differs from *C. plumosus*-type

(Brooks et al. 2007), which has a long 4th lateral tooth on the mentum, and from *C. anthracinus*-type, which has two inner teeth on the mandible. Occurrence: Found in Lake Challacaba. Description based on 216 specimens.

#### *Parachironomus* (Fig. 3a II)

**Diagnostic features** Mentum with single median tooth, often up to twice as broad as the 1st lateral tooth; 7 lateral teeth; 7th lateral often tiny and sometimes difficult to distinguish on worn specimens. Ventromental plates large, triangular and with scalloped outer margin; striations often visible. This species can be distinguished from *P. varus*-type described by Brooks et al. (2007) in which the mentum is less convex, 6th lateral tooth is long and ventromental plates more scalloped. Occurrence: Found in Lake Challacaba. Description based on 10 specimens.

#### *Tanytarsus* (Fig. 3a III)

**Diagnostic features** Mentum with single notched median tooth; 5 pairs of lateral teeth evenly spaced. Short, broad, blunt spur on antennal pedestal. Post-occipital plate large and darkly pigmented, but only present in final instar larvae. Mandible with 3 inner teeth, single dorsal tooth, no surficial teeth. Premandible with three apical teeth. Differs from *T. mendax*-type (Brooks et al. 2007), which has no spur on the pedestal spur. Occurrence: Found in both Lake Challacaba and Laguna Khomer Kocha Upper. Description based on 278 specimens.

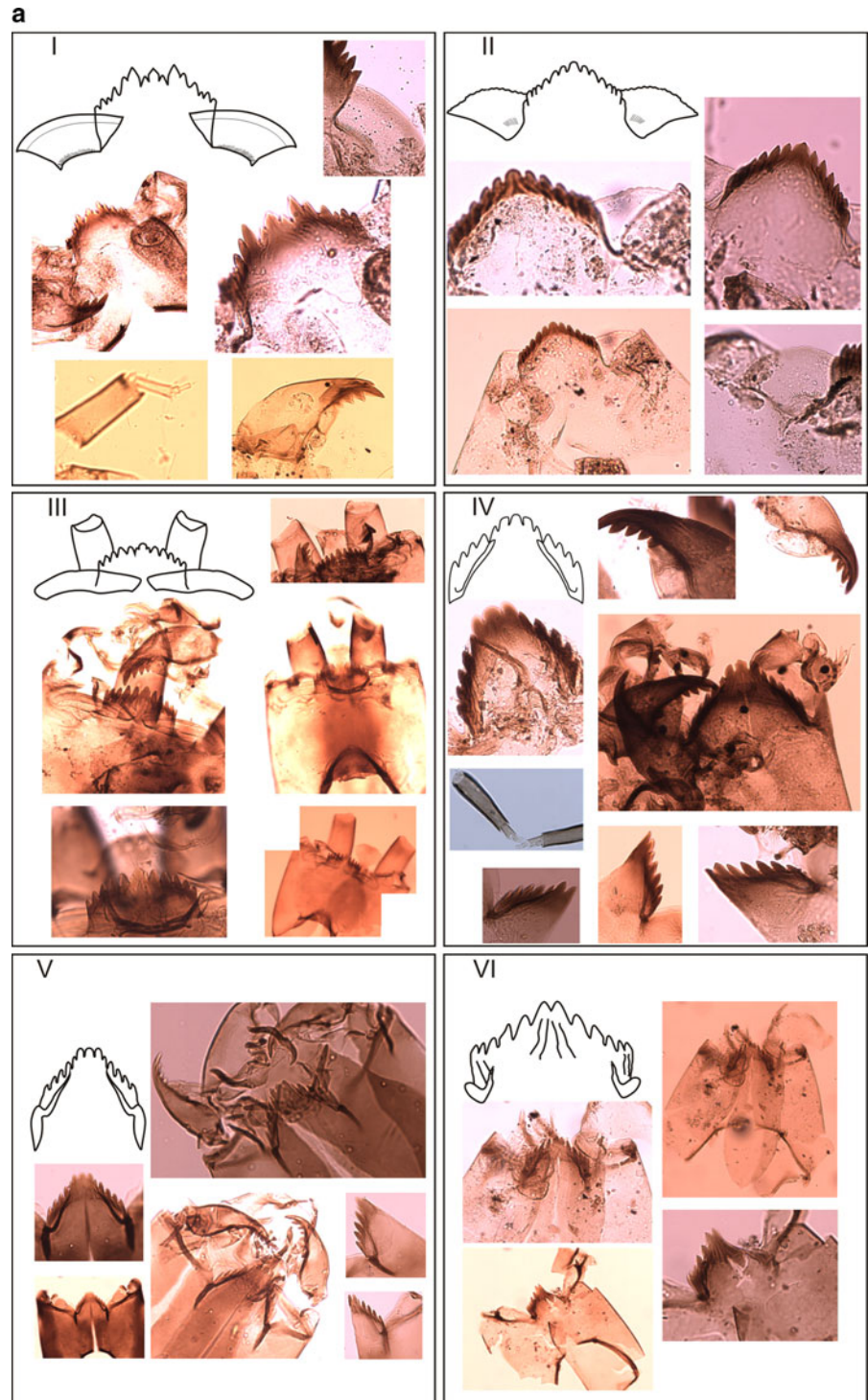
#### *Cricotopus/Orthocladius* type I (Fig. 3a IV)

**Diagnostic features** Mentum with single median tooth; median tooth about same width and equal to or slightly taller than 1st lateral tooth; 6 lateral teeth; 2nd lateral often shorter than 3rd with gap between 2nd and 3rd. Narrow ventromental plates. Mandible with 3 inner teeth and small indentations visible on outside edge. Occurrence: Found in Lake Challacaba. Description based on 418 specimens.

#### *Cricotopus/Orthocladius* type II (Fig. 3a V)

**Diagnostic features** Mentum with single median tooth; 6 lateral teeth; 2nd lateral narrow and often

**Fig. 3** Line drawings and photographs of key fossil chironomid head capsules from Lake Challacaba and Laguna Khomer Kotcha Upper. **a** I *Chironomus*, II *Parachironomus*, III *Tanytarsus*, IV *Cricotopus/Orthocladius* type I, V *Cricotopus/Orthocladius* type II, V *Limnophyes/Paralimnophyes*. **b** I *Paracricotopus*, II *Smittia/Parasmittia*, III *Pseudosmittia*, IV *Apsectrotanypus*

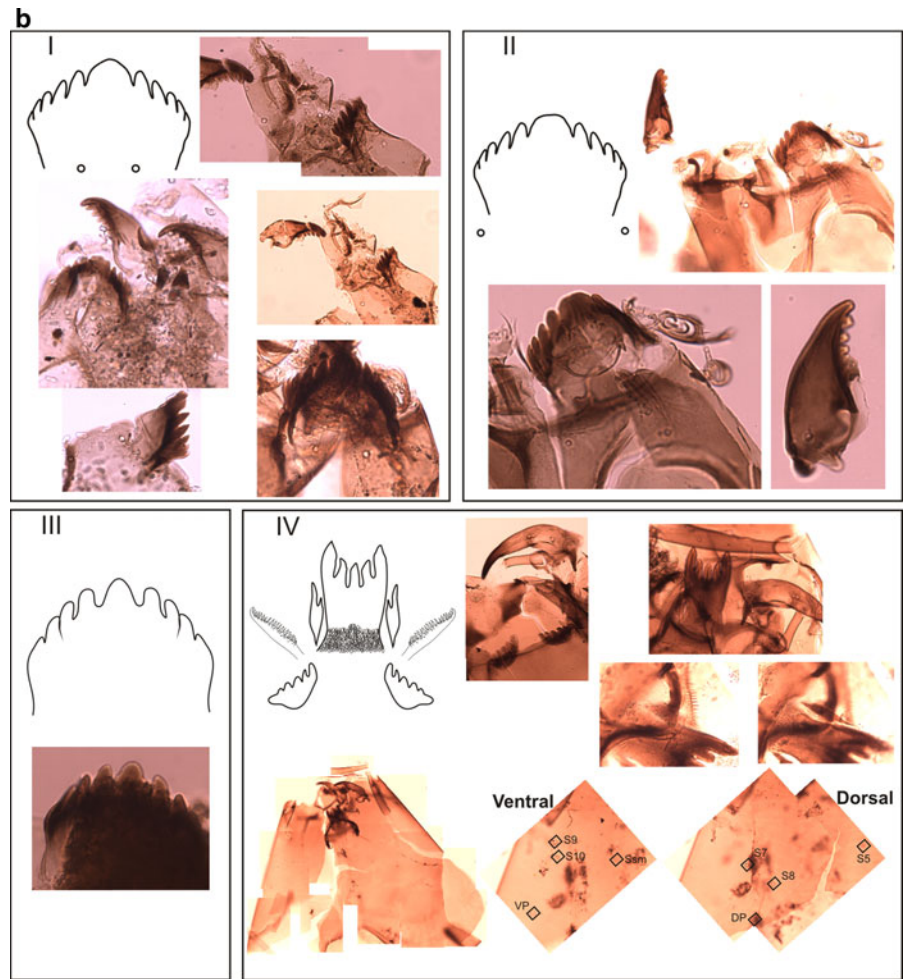


shorter than 3rd with gap between 2nd and 3rd. Narrow ventromental plates. Mandible with 3 inner teeth. Differentiated from *Cricotopus/Orthocladius*

type I by 2nd lateral tooth width, which is narrower and positioned closer to the 1st lateral tooth in *Cricotopus/Orthocladius* type II. Occurrence: Found



**Fig. 3** continued



in Laguna Khomer Kocha Upper. Description based on 240 specimens.

*Limnophyes/Paralimnophyes* (Fig. 3a VI)

**Diagnostic features** Mentum with one pair of median teeth, and five lateral teeth. Teeth decrease in size, although the outer two are of similar size; outer edge of 5th lateral distinctly inwardly curved; banding can often be seen, particularly in the median region; rounded projections below outer teeth of mentum. No specimens with mandibles or premandibles were found. Occurrence: Found in both Lake Challacaba and Laguna Khomer Kocha Upper. Description based on 3 specimens.

*Paracricotopus* (Fig. 3b I)

**Diagnostic features** Mentum with single, broad median tooth; 5 lateral teeth; outer edge of 5th lateral distinctly inwardly curved. Setae submenti positioned centrally below mentum. Occurrence: Found in Lake Challacaba. Description based on 8 specimens.

*Smittia/Parasmittia* (Fig. 3b II)

**Diagnostic features** Mentum with single, broad median tooth; 5 lateral teeth; 5th lateral often tiny and sometimes difficult to distinguish on worn specimens; outer edge of 5th lateral distinctly inwardly curved. Setae submenti positioned near to

base of ventromental plates. Occurrence: Found in Laguna Khomer Kocha Upper. Description based on 1 specimen.

*Pseudosmittia* (Fig. 3b III)

**Diagnostic features** Mentum with single, broad median tooth; 4 lateral teeth; outer edge of 4th lateral distinctly inwardly curved. Occurrence: Found in Lake Challacaba. Description based on 2 specimens—both heavily worn.

*Apsectrotanypus* (Fig. 3b IV)

**Diagnostic features** Large head capsule. Ligula with 5 teeth; central tooth shortest, outer teeth longest. Bifid paraligula. 5 dorsomental teeth. Pecten hypopharyngis with ~15 small teeth. Ventral setation: S9 and S10 positioned close together; VP lateral to S9 and S10. Dorsal setation: S7 positioned above S8. Occurrence: Found in Laguna Khomer Kocha Upper. Description based on 211 specimens.

Zonation and chironomid stratigraphy

No statistically significant chironomid zones were identified from either site and so the chironomid assemblages are discussed with reference to previously established zones identified from either pollen (Lake Challacaba) or charcoal (Laguna Khomer Kocha Upper) composition. Zone boundaries are shown in Figs. 4 and 5. As previously discovered (Walker 1987), this study supports the conclusion that Orthoclaadiinae head capsules are more prone to splitting than those of other subfamily groups. In this study, however, we found that counting split head capsules as half (0.5) or whole (1) had little effect on the final results.

*Lake Challacaba*

Twenty-two samples were analysed from the c. 4,000-year sedimentary succession of Lake Challacaba, at an average sampling resolution of 200 years (median: 189). Three samples (76, 284 and 295 cm) contained no head capsules (Fig. 4a, b). Of the remaining samples, the average head capsule concentration was 40 per gram (hc/g), the maximum was 156 hc/g at 215 cm (c. 2,520 cal year BP), and the minimum was

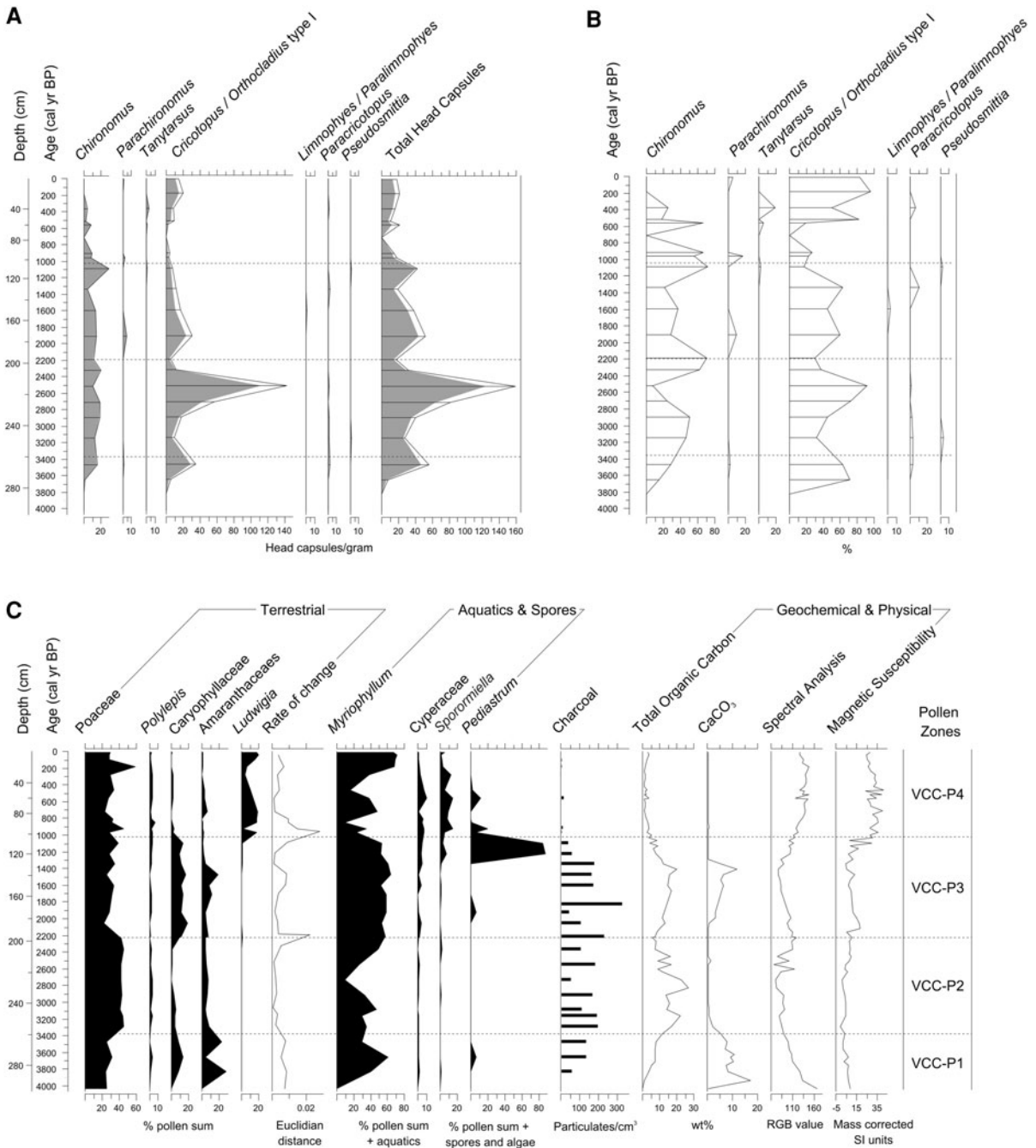
7 hc/g at 275 cm (c. 3,650 cal year BP). In total, seven chironomid taxa were identified from this site: *Chironomus*, *Parachironomus*, *Cricotopus/Orthocladus* type I, *Limnophyes/Paralimnophyes*, *Paracricotopus*, *Pseudosmittia* and *Tanytarsus* (Fig. 3a, b).

The chironomid record from Lake Challacaba is dominated by *Chironomus* and *Cricotopus/Orthocladus* type I, which together constitute 75–100 % of the taxa in each sample (Fig. 4b). As other taxa were at low abundances, the percentage plot highlights only the fluctuation in the dominance between these two taxa, so the data are also presented as head capsule concentrations (Fig. 4a). *Chironomus* concentration is relatively stable from 265 to 150 cm (c. 3,460–1,590 cal year BP) at abundances of 11–20 hc/g. Above 130 cm (c. 1,340 cal year BP) concentration is reduced (<9 hc/g), except for a maximum (30 hc/g) at 110 cm (1,090 cal year BP) and a sample containing no head capsules at 76 cm (c. 710 cal year BP). At some point between 370 and 190 cal year BP, *Chironomus* disappears entirely from the record and is absent in the two uppermost samples.

The *Cricotopus/Orthocladus* type I concentration curve peaks (142 hc/g) at 215 cm (c. 2,520 cal year BP). From 175 cm (c. 1,910 cal year BP), *Cricotopus/Orthocladus* type I displays a gradually decreasing trend in concentration from 30 to 4 hc/g, terminating at 76 cm. After this sample, which is devoid of all head capsules, concentration increases (>15 hc/g) towards the most recent sample. Concentrations of other taxa remain very low throughout the core (<3 hc/g, <18 %), although there is a peak in *Parachironomus* at c. 960 cal year BP (100 cm), and a sporadic occurrence of *Tanytarsus* from c. 560 cal year BP (60 cm) to the top of the sequence.

*Laguna Khomer Kocha Upper*

Chironomid analysis was conducted on 23 samples from the c. 18,000-year Laguna Khomer Kocha Upper record, with an average sampling resolution of 767 years (median: 633). Head capsule concentration varied from 1 hc/g at 453 cm (c. 17,350 cal year BP) to 215 hc/g at 413 cm (c. 12,858 cal year BP), with a core average of 33 hc/g (Fig. 5a, b). Five chironomid taxa were identified: *Apsectrotanypus*, *Cricotopus/Orthocladus* type II, *Limnophyes/Paralimnophyes*, *Smittia/Parasmittia* and *Tanytarsus* (Fig. 3a, b).

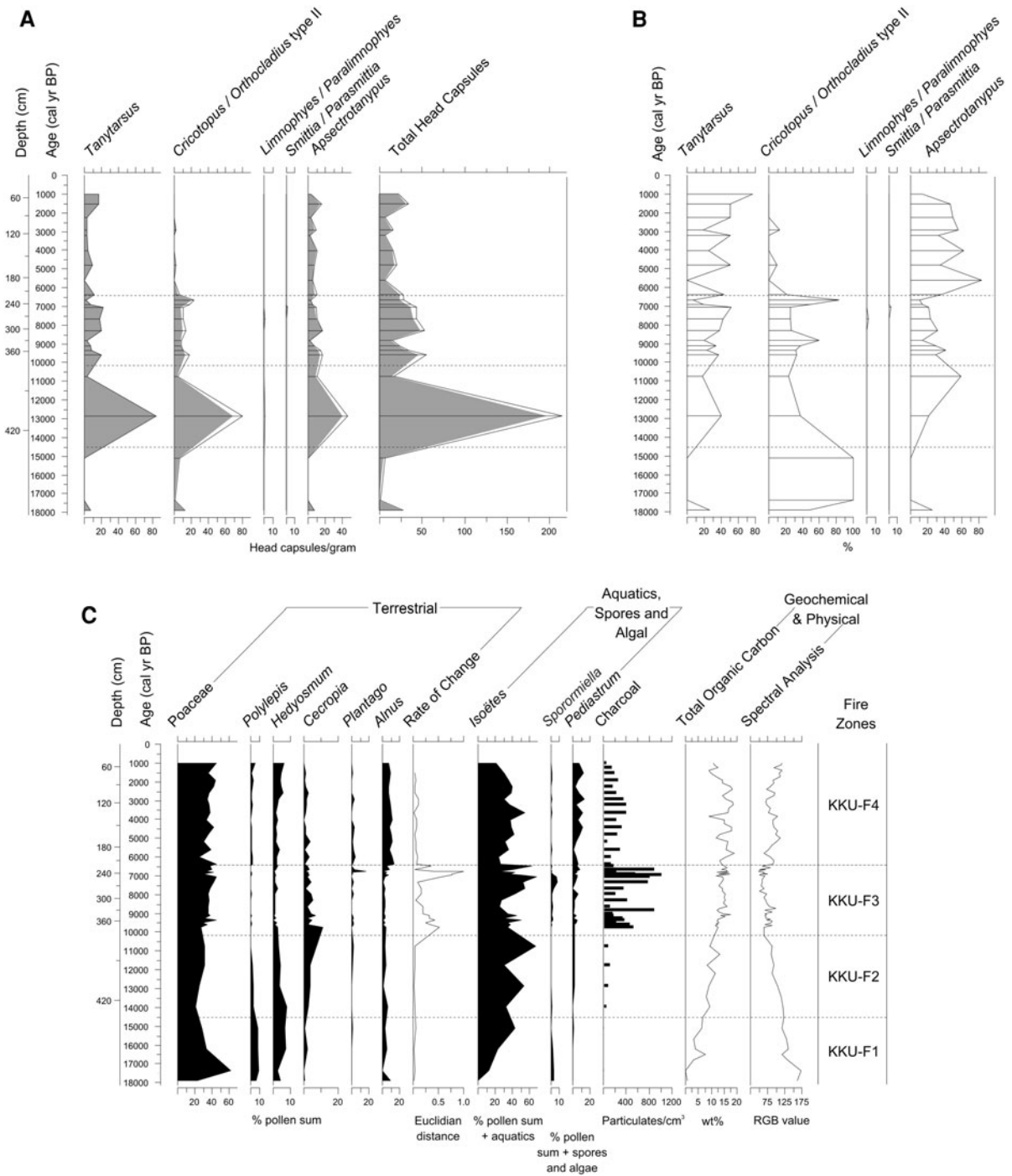


**Fig. 4** Palaeolimnological data from Lake Challacaba. *Horizontal lines* represent sample points. *Dashed horizontal lines* indicate the position of Lake Challacaba pollen zones (VCC-P 1–4). **a** Fossil chironomid concentration data for Lake Challacaba, counting half head capsules as one. *Inner grey shaded area*

marks concentrations when counting half head capsules as half. **b** Fossil chironomid percentage data for Lake Challacaba. **c** Summary pollen, spore, algal, charcoal, geochemical and physical data from Lake Challacaba (Williams et al. 2011a)

The subfossil chironomid record at Khomer Kocha Upper is dominated by 3 taxa, *Apsectrotanypus*, *Cricotopus/Orthocladus* type II and *Tanytarsus*,

representing >90 % in all samples (Fig. 5a, b). The major feature of the sequences is a peak in concentration in all three taxa at c. 12,858 cal year BP, which



**Fig. 5** Palaeolimnological data from Laguna Khomer Kocha Upper. *Horizontal lines* represent sample points. *Dashed horizontal lines* indicate Laguna Khomer Kocha Upper fire zones (KKU-F 1–4). **a** Fossil chironomid concentration data from Laguna Khomer Kocha Upper, counting half head capsules

as one. *Inner grey shaded area* marks concentrations when counting half head capsules as half. **b** Fossil chironomid percentage data for Laguna Khomer Kocha Upper. **c** Summary pollen, spore, algal, charcoal, geochemical and physical data for Laguna Khomer Kocha Upper (Williams et al. 2011b)

occurs after a 5,000-year period of generally low concentrations (0–25 hc/g). From 394 cm (*c.* 10,700 cal year BP), concentrations of *Apsectrotanypus*, a carnivorous genus, remain at relatively stable, medium to low values (2–17 hc/g). For the same time period, *Tanytarsus* concentrations are less than 11 hc/g, with higher values (17–20 hc/g) observed at 376, 303–263 and 71–51 cm. From 10,700 to 6,380 cal year BP, *Cricotopus/Orthocladus* type II concentrations range between 5 and 23 hc/g. After 203 cm (6,380 cal year BP), *Cricotopus/Orthocladus* type II values decrease (<2 hc/g) and are absent from six of the nine uppermost samples. Concentrations of the other taxa (*Limnophyes/Paralimnophyes* and *Smittia/Parasmittia*) remain very low throughout the core (<1 hc/g, <3 %).

## Discussion

### Lake Challacaba

The 4,000-year record from Lake Challacaba spans a complicated period of changes in moisture balance and human occupation. These changes resulted in shifts in the abundance of dry-tolerant plants and aquatic plants, as well as nutrient and sediment input to the lake (Fig. 4). Although dominated by only two taxa, the chironomid assemblage from the sediments of Lake Challacaba provides insights into the response of lake biota to environmental change, which was determined by previous analysis (Williams et al. 2011a, b).

#### *Lake establishment and moisture/lake level fluctuations*

The complete absence of chironomid head capsules in samples prior to *c.* 3,650 cal year BP supports the previous interpretation that the early basal sediments from the site represent a period of lake formation. Pollen preservation and organic sediment indicate that a permanent lake was present at Challacaba from *c.* 3,820 cal year BP. It was not until *c.* 200 years later, however, that chironomids were preserved within the lake sediments. In addition, very low concentrations (<7 hc/g) of chironomid head capsules before 3,460 cal year BP suggest that conditions for chironomids were poor. Chironomids are known to be rapid

colonisers of water bodies (Ruse 2010), so this 400-year period of minimal chironomid abundance in a permanent lake is intriguing. Chironomids tolerate a wide range of salinities (Armitage et al. 1995) and have been used to quantify lake salinity (Chen et al. 2009). Larval numbers, however, have been shown to decline with increasing salinity (Ólafsson et al. 2000) and chironomids are absent from poly- to hypersaline lakes in Africa (Verschuren and Eggermont 2006). Therefore, it is plausible that exceptionally low water levels at Challacaba before *c.* 3,460 cal year BP, possibly with periodic desiccation, resulted in a hypersaline lake. This interpretation is supported by high CaCO<sub>3</sub> concentrations in the sediments (Fig. 4c), which are known to precipitate preferentially under high salinity (Baker et al. 2001).

A peak in the abundance of *Cricotopus/Orthocladus* type I (60–140 hc/g) at *c.* 2,700–2,520 cal year BP, coincides with a decrease in abundance of *Myriophyllum* pollen (Fig. 4c). *Myriophyllum* can form dense populations, especially in shallow waters 0.4–4 m deep, but not in hypersaline conditions (Ritter and Crow 1998; Ybert 1992). As lake level increases *Myriophyllum* moves further from the lake centre (the site of core extraction) and is restricted to the shallows, thus becoming a less dominant component of the sediment pollen record. If the decrease in *Myriophyllum* were a response to increased salinity, it is likely that a peak in the salt-tolerant Amaranthaceae would be observed, as at other sites (Bush et al. 2010). As this does not occur at Challacaba, and there are no other indications of decreased water level and thus increased salinity (e.g. CaCO<sub>3</sub>), it seems likely that an increase in water level caused the decreased *Myriophyllum* abundance.

The more than doubling of *Cricotopus/Orthocladus* type I concentration, whilst *Chironomus* shows a marginally decreasing trend, therefore appears to have been a response to lake deepening. The observation that the head capsule concentrations of the two dominant chironomid types show different patterns at this point supports an interpretation that this increase in *Cricotopus/Orthocladus* type I is not an artefact of lake basin processes, such as decreased sedimentation rate, as this should have had a similar effect on the head capsule numbers of all taxa. Lake deepening and the likely associated drop in salinity, and possibly temperature, appears to be favourable to *Cricotopus/Orthocladus* type I.

### Human impacts

The first significant occurrence of fungal dung spores (*Sporormiella*) at *c.* 1,280 cal year BP, together with increased landscape erosion (as indicated by magnetic susceptibility and spectral analysis) and a marked rise in the abundance of green algal remains (*Pediastrum*) between *c.* 1,280 and 1,090 cal year BP, indicates increased trading and pastoralism at Lake Challacaba (Fig. 4c; Williams et al. 2011a). The chironomid record provides further evidence for this change in cultural practice, signified by a peak in abundance of *Chironomus* at *c.* 1,090 cal year BP. Although the temperature tolerance of *Chironomus* appears to vary between hemispheres (warm-tolerant in the north, cold-resistant in the south) and is still unresolved within South America, the taxon does appear able to survive in highly disturbed systems (Massaferro et al. 2009). Above all, its tolerance of increased lake nutrients (eutrophication) is well documented (Brodersen and Quinlan 2006; Massaferro et al. 2008). At Lake Challacaba the peak in *Chironomus* abundance is therefore likely to be a response to an initial increase in nutrient input caused by the arrival of substantial numbers of domesticated herbivores (camelids) at the lake site, as indicated by the rise in *Sporormiella* spores (Fig. 4c). Increased herbivore numbers leads to landscape destabilisation and erosion by both the action of animal hooves and by removal of vegetation, further increasing the in-wash of material as recorded by an increase in the magnetic susceptibility of the sediments (Fig. 4c.) A change in lake trophic status is supported by the maximum in *Pediastrum*, which has been shown at other sites to respond to increased nutrient in-wash (Woodward and Shulmeister 2005).

After the possible lake desiccation or onset of a shift to hypersalinity, which leads to the elimination of chironomids at *c.* 710 cal year BP, abundances of both *Chironomus* and *Cricotopus/Orthocladius* type I recover, albeit to relatively low levels. It remains unclear what changes in local terrestrial or aquatic conditions may have brought about the disappearance of *Chironomus* from the record in the last 250 years.

### Laguna Khomer Kocha Upper

Sediments from Laguna Khomer Kocha Upper provide an important record of deglacial and Holocene environments on the wet, eastern slopes of the Andes. The

pollen and chironomid records recovered from Khomer Kocha Upper reveal relatively stable environmental conditions for much of the period 18,000–1,000 cal year BP. However, comparison of changes in the abundance of the three dominant chironomid taxa with other environmental indicators, does provide valuable insights into the response of high-elevation chironomids to environmental change, from what is thought to be a site of minimal human disturbance.

The largest and most significant shift in the chironomid record occurs after *c.* 6,380 cal year BP when *Cricotopus/Orthocladius* type II becomes almost completely absent. In Patagonia, *Cricotopus* has been interpreted as a warm-tolerant taxon (Massaferro et al. 2009), but the disappearance of this taxon at Laguna Khomer Kocha Upper at 203 cm does not appear to correlate to any temperature changes detected in the other palaeoenvironmental indicators. This decline, however, does coincide with a major shift in the overall terrestrial pollen taxa, as shown by higher values in the rates of change (ROC) analysis, and is associated with a marked rise in the percentage abundance of *Alnus* (Andean Alder) pollen. *Alnus* is a pioneer taxon, growing in marsh and riparian transitional Puna woodland habitats (Navarro and Maldonado 2002), so the increase at this time indicates local environmental conditions became wetter. This interpretation is supported by a sharp decline in burning and suggests an early ending of the influence of the HDE, which at other sites appears to have continued until *c.* 5.0 ka BP (Williams et al. 2011b). Increased net moisture caused a reduction in fire, created an expansion of regional marsh habitat, and also appears to have increased water depth at Laguna Khomer Kocha Upper. This is apparent from a decline in the abundance of *Isoetes*, an aquatic plant typical of cool waters <4 m deep (Navarro and Maldonado 2002; Urrego et al. 2011). The decline in *Cricotopus/Orthocladius* type II with increased water depth contrasts with the results from Lake Challacaba, where a peak in abundance was observed in *Cricotopus/Orthocladius* type I when the lake deepened. Although we cannot rule out the effect of other controlling factors, the contrasting responses of these two taxa to increased water depth supports our interpretation that these two *Cricotopus/Orthocladius* types (see taxonomic notes) represent distinct species that respond differently to environmental conditions.

Intriguingly, the chironomid record from Laguna Khomer Kocha Upper does not show any response to

the onset of burning, which was such a dominant driver of terrestrial vegetation at the onset of a HDE at *c.* 10,000 cal year BP (Fig. 5). Rates of change analysis reveal this is also a period of major turnover in local vegetation, as woodland patches are severely reduced in size. Although there is a slight decline in concentrations of all chironomid taxa at that time, it is probably related to the increase in sedimentation rate. The peak in head capsule concentration of all taxa at *c.* 12,858 cal year BP is also likely to be a result of lake basin processes (i.e. decreased sedimentation rate), which caused a simultaneous increase in the head capsule concentration of all taxa in the sediment record. The low sampling resolution in this section of the core precludes further interpretation.

#### Chironomids as environmental indicators in the tropical Andes

The current paucity of modern autecological data inhibits the use of chironomids as an independent environmental proxy in central Andean palaeolimnological investigations. Only by reference to other palaeolimnological data (e.g. pollen and charcoal) can the chironomid data be interpreted in a meaningful way. Although the average abundance of chironomid head capsules per sample in this study was low (<40 hc/g) and there is low diversity, shifts in the assemblage can be interpreted in terms of response to environmental change. The reduction in diversity with increasing elevation, is in general agreement with observations elsewhere, which show a “hump-shaped” relationship between taxon richness and elevation, with low species richness at the elevation extremes (Bigler et al. 2006). With such low taxon richness, use of percentage data to represent changes through time should be done with caution, as they can easily be misinterpreted. For example, in the Laguna Khomer Kocha Upper record, the percent data for *Apsectrotanypus* show increased abundance after *c.* 6,500 cal year BP, whereas the concentration data reveal that no significant change occurred (Fig. 5a, b).

#### Conclusions

Investigation of subfossil chironomid assemblages in the sediments of Lake Challacaba and Laguna Khomer Kocha Upper, the first study of its kind in the central

Andean region, demonstrated the sensitivity of chironomids to long-term ecosystem changes over the last 18,000 years. Our results demonstrate that there are chironomid assemblages in the sediments of tropical, high Andean lakes above 3,200 m asl, albeit at relatively low abundances and diversity.

This study demonstrated that chironomid assemblages at high-elevation sites are responsive to regional and local environmental change. As part of a multi-proxy investigation that includes pollen, spore, charcoal, and geochemical analyses, changes in the dominant chironomid taxa offer valuable insights into environmental adjustments of the late Pleistocene and Holocene. Although preliminary, this research revealed that chironomids are sensitive to changes in net moisture balance and associated water-level fluctuations and salinity. In addition, it is apparent that at sites with a known history of severe human impact, such as Lake Challacaba, changes in chironomid assemblages can be related to anthropogenic disturbances such as increased nutrient input and changes in herding activity.

Before chironomids can fulfill their full potential as useful indicators of palaeoenvironmental change in this region, further work is required to refine and standardise chironomid larval taxonomy and to increase our understanding of the ecological responses of these taxa. Nevertheless, our work demonstrated that chironomids can be a useful part of a regional multi-proxy study by providing complementary data on changing environmental conditions through the late Pleistocene and Holocene.

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