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ORIGINAL PAPER

An ostracod-based record of paleoecological conditions during MIS6 and MIS5, from Lake Chalco, Basin of Mexico

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Abstract A sediment record from Lake Chalco, Basin of Mexico, revealed the presence of two endemic ostracod species during the latter part of Marine Isotope Stages (MIS) 6 (146–130 ka) and MIS5 (130–72 ka), namely *Candona alchichica* and *Limnocytherina axalapasco.* Higher abundance of *C. alchichica* was found during MIS6, when prevailing conditions were cold, lake waters were fresh, and relatively deep bottom waters were anoxic. The species is typically associated with saline environments today, consistent with its presence in MIS5 sediments. The Chalco record, however, reveals that it coexisted with freshwater diatom species during MIS6. Thus, we suggest that *C. alchichica* had a wider salinity tolerance, ranging from freshwater to more saline environments. Examination of MIS5 substages provides further insights into ostracod species responses to changing lake conditions. During MIS5e, the lake water level declined and salinity and dissolved oxygen in the water column increased, thereby favouring *L. axalapasco* productivity, whereas *C. alchichica* productivity decreased. Enhanced runoff and lower than average evaporation during MIS5d coincided with the increasing abundance of *C. alchichica*, suggesting a period of relatively high lake level and more dilute waters. These environmental conditions, however, changed during MIS5c when lake stage dropped once again and *L. axalapasco* abundance increased. Shallow conditions during this substage were optimal for *L. axalapasco*. Subsequently, as the lake level continued to decline during MIS5b, both ostracod species disappeared from the sediment record. Finally, during MIS5a, runoff increased and both ostracod species reappeared in the record, with *L. axalapasco* dominating, suggesting another period of lake level recovery. Increased evaporation rates during the last part of this substage (75–72 cal ka BP) may have led to disappearance of ostracods from the sediment record. Overall, during MIS5, we detected higher *L. axalapasco*, which represent relatively shallow lake conditions.

Keywords Lake Chalco · Glacial–interglacial · North America · Ostracods · *Candona alchichica* · *Limnocytherina axalapasco*

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Introduction

During the last 2.5 Ma, glacial–interglacial cycles, which have been clearly identified in marine and ice-core records, have been linked mainly to insolation changes such as the 100-ka eccentricity cycle (Raymo 1992; Schmidt and Spero 2011). In southwest North America and Central America, climate responses during the Marine Isotope Stage (MIS) 6 and MIS5 transition, ca. 130 ka, have been identified in several lake sediment records (Kaufman et al. 2009; Macario-Gonzalez 2017; Cárdenes-Sandí et al. 2019). Lake Chalco is considered a key continental record because its sediments preserve a history of paleoclimate in the Basin of Mexico that spans the last 400 ka, and because it lies between the Neotropical equatorial zone and the Northern Hemisphere temperate region (Lozano-García et al. 2017; Brown et al. 2019). Moreover, 23-ka cyclicity for the Intertropical Convergence Zone (ITCZ) mean latitudinal migration during the last 350 ka has been reported in $\delta^{18}O$ marine records from the Caribbean Sea (Schmidt and Spero 2011). Additionally, a recent study on spectral analysis of Ti data from Lake Chalco sediments as a runoff indicator, also identified a 20-ka ($\pm$2 ka) cycle, suggesting that precessional forcing could have been the driving mechanism for past runoff variations in the Chalco region (Martínez-Abarca et al. 2021). Several studies suggest that ITCZ migration was caused mainly by changes in the energy balance, determined by summer insolation, particularly at 65° N (Lachniet et al. 2014; Schneider et al. 2014; Bosmans et al. 2015). Over short timescales (Holocene), however, other factors also may have influenced the ITCZ mean position (currently 6° N), such as Pacific and Atlantic sea surface temperatures (SSTs), solar irradiance and teleconnections (Pacific Decadal Oscillation, El Niño Southern Oscillation) (Magaña et al. 2003; Knight et al. 2006; Metcalfe et al. 2015).

Previous studies suggested that during MIS6, wet conditions prevailed in temperate regions, whereas dry environments existed in tropical areas (Kaufman et al. 2009; Bogotá et al. 2011; Cárdenes-Sandí et al. 2019). Lake Chalco's runoff record suggests overall wet conditions punctuated by drier episodes (143 ka), as well as a tendency toward sudden increases in runoff (132 ka), with a clear dry episode at the end of MIS6 (Martínez-Abarca et al. 2021). These findings may be compared with the precipitation distribution model proposed by Metcalfe et al. (2015) for the MIS2 to MIS1 transition. Those results suggest that at the end of MIS2, the ITCZ was in a more southerly location, thereby depriving southern Mexico and Central America of moisture, whereas the southwestern United States and northern Mexico records exhibit greater precipitation, associated with strong Pacific westerly activity. Martínez-Abarca et al. (2021) proposed that a contrasting set of conditions may have occurred during 134–130 ka, leading to increased runoff at Lake Chalco during the MIS6 and MIS5 transition. During MIS5, coastal marine records, such as ODP 1239 and the Cariaco Basin, exhibited sudden changes in terrestrial input, particularly during the MIS5e and MIS5c periods (Yarincik et al. 2000; Rincón-Martínez et al. 2010). Similar to Lake Chalco, other continental records also display evidence of increasing runoff during MIS5e. Runoff responses, however, show a delay compared to equatorial records, although they are still consistent with the proposed ITCZ migration mechanism (Martínez-Abarca et al. 2021).

Previous Lake Chalco studies characterised paleoclimate conditions during the last 150 ka, using inorganic geochemical proxies such as magnetic susceptibility and mineralogy (e.g., Lozano-García et al. 2015; Torres-Rodríguez et al. 2015; Ortega-Guerrero et al. 2017, 2020; Martínez-Abarca et al. 2019, 2021). Moreover, biological proxies such as pollen and diatom assemblages have played an important role in deciphering paleoenvironmental conditions in the Chalco region (Bradbury 1989; Lozano-García et al. 1993; Avendaño et al. 2018; Caballero et al. 2019). In this work, we present paleoenvironmental inferences based on ostracods in the Lake Chalco sediment record during the latter part of MIS6 (146–130 ka) and MIS5 (130–72 ka). In addition, we consider the MIS5 substages proposed by Lisiecki and Raymo (2005).

Ostracods respond to climate and environmental changes such as precipitation variability, described above. Furthermore, changes in the abundance and diversity of ostracods in lacustrine sediments can be used to infer past shifts in physico-chemical and other ecological conditions in a lake, including such characteristics as water chemistry, salinity, conductivity and temperature (Forester 1986; Pérez et al. 2013), especially when compared with other proxies such as diatoms (Ortega-Guerrero et al. 2020). Therefore, the ostracod record has the potential to reveal the biochemical responses of Lake Chalco to precipitation changes driven by migration of the ITCZ and local climate forces during MIS6 and MIS5.

Study site

The Lake Chalco sub-basin is located in the Trans-Mexican Volcanic Belt (TMVB), in central Mexico (Fig. 1). This endorheic basin, which covers an area of ~ 240 km^2, was formed by volcanic activity in the Sierra Chichinautzin Mountain range during the Early Pliocene (Mooser and Molina 1990; Arce et al. 2003). The remnant lake is surrounded by volcanic and volcaniclastic deposits, including lava and pyroclastic flows (Lozano-García et al. 1993). The nearest meteorological station, Tlahuac (19° 15′ 46″ N; 93° 00′ 13″ W; 2240 masl; Fig. 1), provided mean monthly temperature and precipitation data from 1981 to 2010 CE (Source: Servicio Meteorológico Nacional, Mexico), recording an average annual temperature of ~ 18 °C. The region experiences a maximum monthly temperature of 20 °C during May and a low monthly temperature of 15 °C in December and January (Fig. 1). Average annual precipitation is ~ 462 mm and has a unimodal distribution, with most (~ 425 mm) falling between May and October, and the maximum in July, when the ITCZ is at its most northerly position (Fig. 1). Precipitation during the rest of the year is only 37 mm, with frontal systems bringing occasional rain in the winter months. Modern-day vegetation in the region consists of ~ 26% woodland, including pine, cypress and eucalyptus plantations, and sacred fir (*Abies religiosa*), which is highly exploited. Halophilic grasslands, adapted to high-alkalinity soils represent ~ 13% of the vegetation cover, especially in areas modified for agriculture. Finally, shrubland occurs to a lower extent and is dominated by the genera *Baccharis* and *Senecio*. The remaining land area is urbanised (Source: Gobierno de Chalco, Mexico).

Materials and methods

A 122-m sediment core (CHA08) was collected in 1.0-m sections, using a Shelby corer. Core sections were stored in 10-cm-diameter PVC tubes. An additional 10 cm from each drive was collected from the drilling shoe. Initial measurements and core descriptions were carried out at the LacCore Facility (Continental Scientific Drilling Facility), University of Minnesota, Minneapolis, MN. Detailed litho-stratigraphic and physical properties, such as magnetic

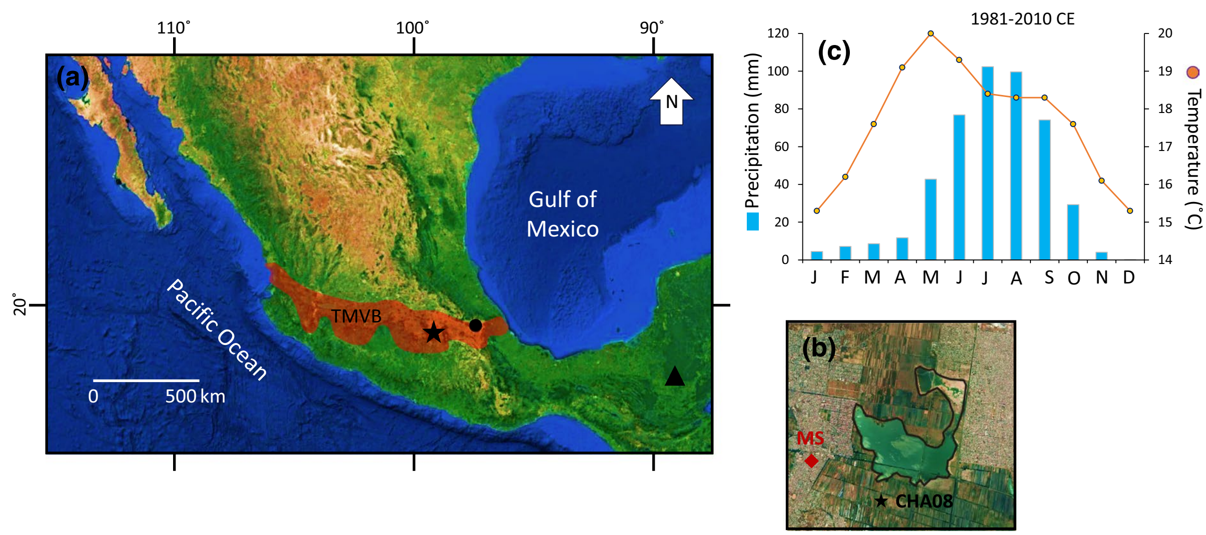

Fig. 1 **a** Lake Chalco (star) and Lake Alchichica (circle) are located along the Transmexican Volcanic Belt (TMVB) in the central part of Mexico, whereas Lake Petén Itzá (triangle) is located on the Yucatán Peninsula. **b** The sediment profile CHA08 (star) was collected to the southwest of modern-day Lake Chalco, and the nearest meteorological station (MS), Tlahuac, provides **c** mean monthly temperature and precipitation data from 1981 to 2010 CE

susceptibility and density of the CHA08 sequence, are reported in Ortega-Guerrero et al. (2017), who identified seven litho-stratigraphic units based on stratigraphic features, diatoms, tephras and magnetic susceptibility. Sediments from Unit 7 (122.4–106.0 m) were composed primarily of sets of rhythmic light/dark laminae. Light laminae are diatom oozes dominated by *Stephanodiscus niagarae* and *S. oregonicus*, whereas dark laminae are silts with minor calcareous components. Sediments from Unit 6 (106.0–57.5 m) included dark greyish-brown sandy silt, light olive-brown to dark olive-grey laminated diatomaceous silt and diatom ooze, dark olive-brown to pale yellow clayey silt, dark olive-grey clayey silt, olive-brown sandy silt and very dark greyish-brown to dark reddish-brown sandy silt. More information about litho-stratigraphy and facies characteristics can be found in Ortega-Guerrero et al. (2017, 2020).

In this study, we utilised the age model (Fig. 2) developed by Ortega-Guerrero et al. (2017), using Bayesian calculations with R-Studio software and the Bacon package (Blaauw and Christen 2011; R Core Team, 2018). For the upper 35 m, 14 radiocarbon ages, calibrated using the IntCal13 curve (Reimer et al. 2013) were used for the chronology, along with the ages of two tephra deposits recognised in the Basin of Mexico, the Upper Toluca Pumice and the Tutti Frutti Pumice (Arce et al. 2003; García-Palomo et al. 2002; Sosa-Ceballos et al. 2012). In addition, the age model included a U/Th date on a zircon from 63.5 m depth (Torres-Rodríguez et al. 2015) and an age of 130 ka at 106 m, based on the assumption that stratigraphic and diatom transitions at that depth (Avendaño et al. 2018) represent the MIS6 termination (Lisiecki and Raymo 2005) (Table 1).

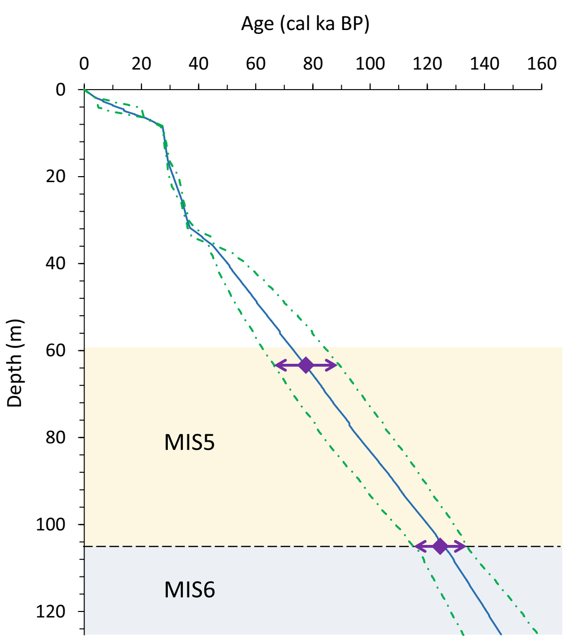

Fig. 2 The calibrated age model of the CHA08 sediment sequence from Lake Chalco is based on 14 radiocarbon ages, two tephra deposits, a zircon U/Th age and an assumed correlation with the termination of MIS6 (Table 1). Modified from Ortega-Guerrero et al. (2017, 2020)

A total of 59 samples, taken at intervals of ~ 1 m from Units 7 (122.4–106.0 m) and 6 (106.0–57.5 m) from the CHA08 sediment sequence, were processed for ostracod analyses. Each sample (~ 3 g) was oven-dried to determine dry weight, then soaked in tap water for 1–2 days prior to sieving at 240 and 53 µm. Sieve residues were oven-dried and examined under a Zeiss stereomicroscope (Stemi 508) to determine species abundances, following Cohuo-Durán et al. (2014, 2017). Lake Chalco sediments preserve *Candona alchichica* valves. This species exhibits morphological characteristics similar to those of *C. patzcuaro* Tressler 1954, and the main features used to distinguish the two taxa are present in soft parts, which are rarely preserved in sediment records. Cohuo-Durán et al. (2017), however, described some key valve differences, in that *C. alchichica* valves tend to be more compressed and have dorsal margins that are slightly rounded, whereas *C. patzcuaro* valves are more elongated and possess straighter dorsal margins, which is especially the case for females. The very rounded dorsal margin in females (Fig. 3c, d) is a key feature for identification of *C. alchichica* in Chalco sediments. For a visual comparison of valves from these two species, and more detailed information about how they can be distinguished, see Cohuo-Durán et al. (2017).

Total ostracod abundance is reported as the number of adult and juvenile valves of all species in 1 g of dry sediment (valves/g). Adult male and female valves of each species in dry sediment were quantified, and they are presented in terms of relative abundance (as a percentage of the total including juveniles), to gain insights into changes in these endemic species through time. The paleoecological inferences presented in this study are based solely on adult counts, as the final ostracod moult would have taken place during optimal environmental conditions (De

Table 1 Dates included on Bayesian age model of CHA08 sedimentary sequence from Lake Chalco

Lab code or parameter	Depth (m)	Radiocarbon date (BP ± 1σ)	Material dated	References
Beta-347500	0.47	4830 ± 30	Pollen	Ortega-Guerrero et al. (2017)
Beta-347502	1.36	7220 ± 30	Ostracods	Ortega-Guerrero et al. (2017)
Beta-347503	1.37	2780 ± 40	Pollen	Ortega-Guerrero et al. (2017)
Beta-347501	1.76	8490 ± 40	Pollen	Ortega-Guerrero et al. (2017)
UTP date	2.53	10,445 ± 90	n.a.	Arce et al. (2003) and García-Palomo et al. (2002)
PTF date	4.88	14,065 ± 500	n.a	Sosa-Ceballos et al. (2012)
Beta-359187	6.35	17,180 ± 60	Pollen	Ortega-Guerrero et al. (2017)
Beta-359191	9.25	23,180 ± 90	Pollen	Ortega-Guerrero et al. (2017)
Beta-359189	10.25	23,450 ± 100	Pollen	Ortega-Guerrero et al. (2017)
Beta-359190	11.03	23,720 ± 110	Pollen	Ortega-Guerrero et al. (2017)
Beta-344189	15.41	24,760 ± 100	Pollen	Ortega-Guerrero et al. (2017)
Beta-344190	25.63	29,970 ± 180	Pollen	Ortega-Guerrero et al. (2017)
Beta-344191	29.47	31,840 ± 230	Pollen	Ortega-Guerrero et al. (2017)
Beta-344192	30.46	31,940 ± 210	Pollen	Ortega-Guerrero et al. (2017)
Beta-347499	35.18	40,460 ± 520	Ostracods	Ortega-Guerrero et al. (2017)
U/Th*	63.50	76,700 ± 4700	Zircons	Torres-Rodríguez et al. (2015)
MIS5–6*	106	130,000 ± 3000	n.a.	Avendaño et al. 92018) and Lisiecki and Raymo (2005)

Asterisk (*) represents ages not obtained by AMS ^{14}C

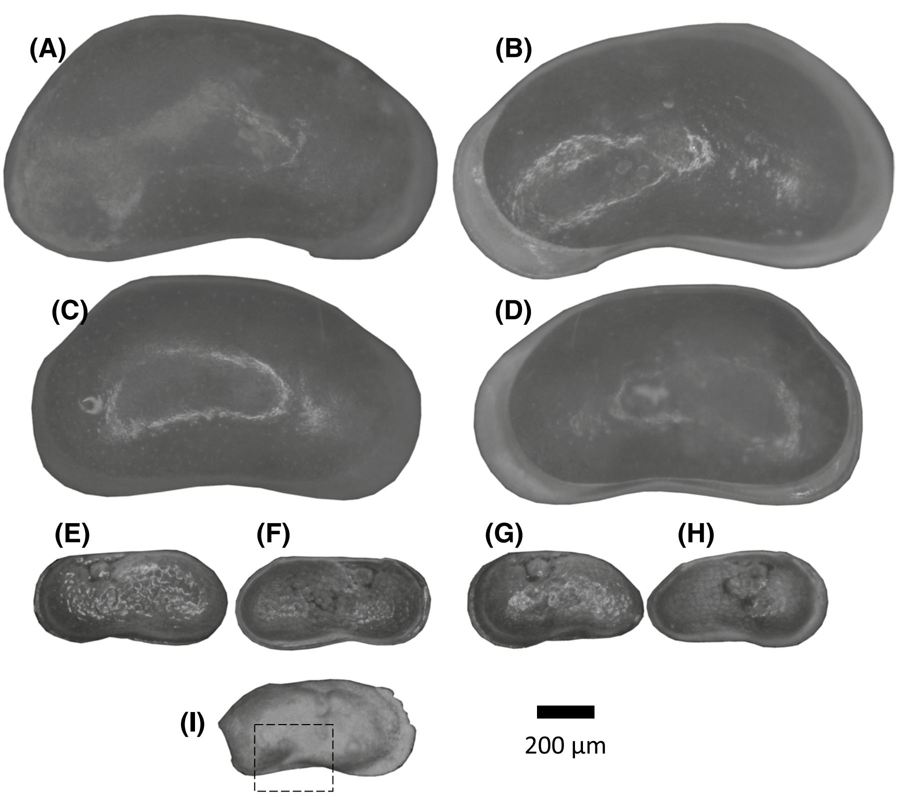

Fig. 3 Sediments in Units 7 and 6 from Lake Chalco preserve *Candona alchichica* (**a** male external view, **b** male internal view, **c** female external view, **d** female internal view) and *Limnocytherina axalapasco* (**e** male external view, **f** male internal view, **g** female external view, **h** female internal view, **i** female external view with bump and covered with authigenic carbonates) ostracod valves

Deckker 2002). Moreover, low abundance and presence of only juvenile instars of one species can lead to inaccurate taxonomic identification. Adult valves were extracted and stored in 25-ml glass vials. Images of the ostracod valves were captured with a Zeiss Axiocam ERc 5 s.

Results

Only two ostracod species were present as adults and juveniles in Units 7 and 6 of the Lake Chalco sediment sequence (Fig. 3). Most of the shells were well-preserved, but some were coated with authigenic carbonate and diatoms. As reported by Ortega-Guerrero et al. (2017), some sediments also contained ostracod fragments. The first identified species, *Limnocytherina axalapasco*, belongs to the genus *Limnocytherina* Negadaev-Nikonov, 1967, which was originally described as a subgenus of *Limnocythere* Brady, 1868, but subsequently was raised to genus status by Martens (1996, 2000). The second identified species, *C. alchichica*, belongs to the genus *Candona* Baird, 1845. Figure 4 summarises the total ostracod (adult and juvenile instars) abundances (valves/g) and relative abundances (%) of both species (only adult instars) from Units 7 and 6. Total ostracod abundance ranged from 0 to 518 valves/g. Sediments from Unit 7 (122.4–106.0 m) contained as many as 95.4 valves/g, whereas sediments from Unit 6 (106.0–57.5 m) had up to 518 valves/g. Sediments at depths of 87.4 m and 80.4 m possessed the highest total abundances in the record, with 312 and 518 valves/g, respectively. Adult relative abundance reached a maximum of 57%. Sediments at depths of 114.5 m and 109.9 m exhibited the highest adult abundances, at 50% and 57%, respectively. *Limnocytherina axalapasco* was only preserved in sediments from Unit 7, with abundance of up to 40%. Sediments from depths of 88.1 m and 65 m had the highest *L. axalapasco* abundances, with 29% and 40%, respectively. On the other hand, *C. alchichica* was present in both sediment Units 6 and

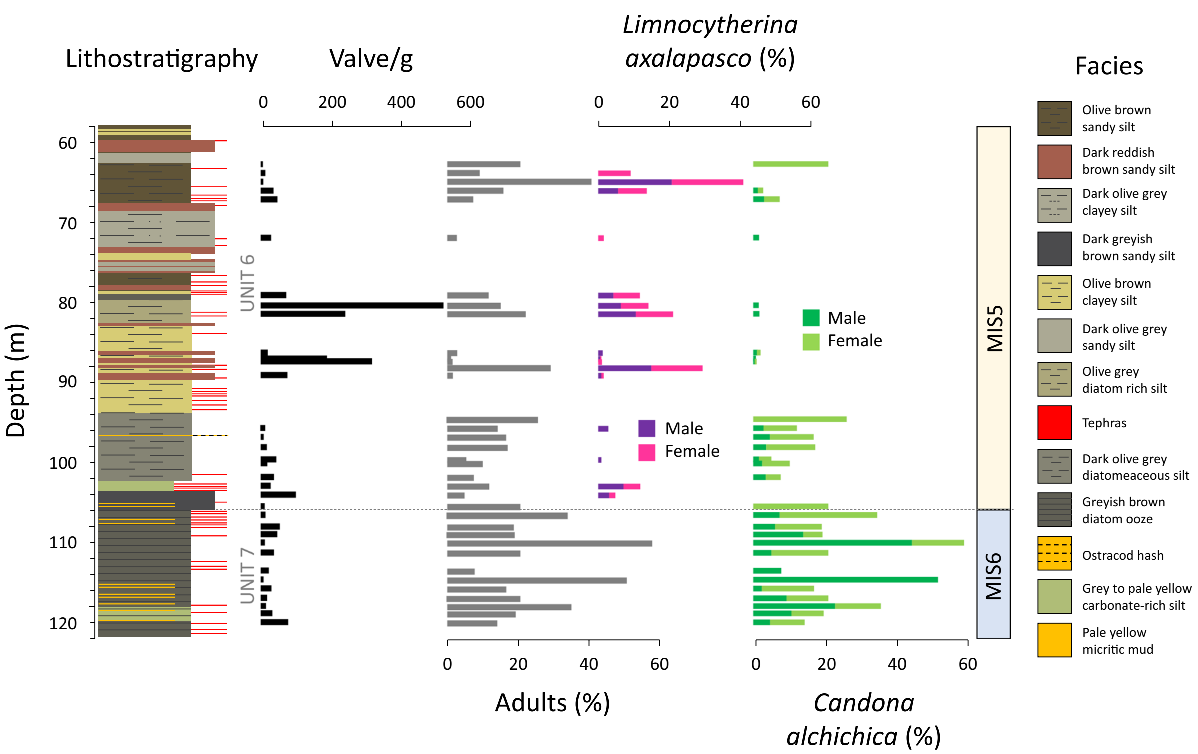

Fig. 4 Total ostracod abundance as valves/g and the relative abundances of adults, and of *Limnocytherina axalapasco* and *Candona alchichica* by gender, in sediments from Units 7 and 6 of Lake Chalco. Relative abundances of males and females do not add to 100% because juvenile instars are not reported

7, with relative abundances of up to 57%. Sediments at depths of 114.5 m and 109.9 m had the highest *C. alchichica* abundances, with 50% and 57%, respectively. In general, remains of *C. alchichica* males were more abundant than females in sediments from Unit 7 (Fig. 4), whereas *C. alchichica* females dominated in sediments from Unit 6, especially at depths of 94.6 m and 62.8 m, with relative abundances of 25% and 20%, respectively.

Discussion

We found only two ostracod species in the Chalco sediment record, *L. axalapasco* and *C. alchichica*, which we consider surprising, given that previous environmental inferences using Chalco sediments indicated well-established lake conditions during MIS6 and MIS5. We propose that our core sampling location may account for the low number of ostracod taxa we encountered. For example, modern ostracod species distribution in Lake Petén Itzá (Guatemala) is influenced mainly by water depth, followed by other physico-chemical characteristics such as temperature, dissolved oxygen concentration and sediment type (Pérez et al. 2010). Lake Petén Itzá occupies a closed basin at ~110 masl, and is one of the largest (~100 km^2) and deepest water bodies in the lowland Neotropics (Fig. 1). Moreover, the ostracod record from Lake Petén Itzá, representing the last ~85 ka of accumulation, also displays very low abundances in sediments older than 50 ka (Pérez et al. 2021).

Limnocytherina axalapasco and *C. alchichica* are thought to be endemic species from central Mexico and little is known about their ecological preferences. *Limnocytherina axalapasco* has been found in alkaline waters (pH 8.9–9.3) dominated by Cl^- or HCO_3^- and Na^+ or Mg^{2+}, with temperatures between 19.1 and 20.3 °C, total dissolved solids (TDS) ranging from 0.5 to 9 g/L and dissolved oxygen concentrations of 5.0 to 6.5 mg/L (Cohuo-Durán et al. 2014). Moreover, the species seems to favour deep areas, e.g., at 64 m depth in saline Lake Alchichica (Alcocer et al. 1998). On the other hand, *C. alchichica* can be found in alkaline waters (pH 8.9–9.6) dominated by Cl^- and Na^+, with temperatures between 14.4 and 24.9 °C, TDS of 8.9 g/L and dissolved oxygen concentrations from 0 to 12.3 mg/L (Cohuo-Durán et al. 2017). The ostracod record from Lake Chalco sediments reveals changes in ecological and physico-chemical conditions during MIS6 and MIS5. In Fig. 5, we present changes in total ostracod

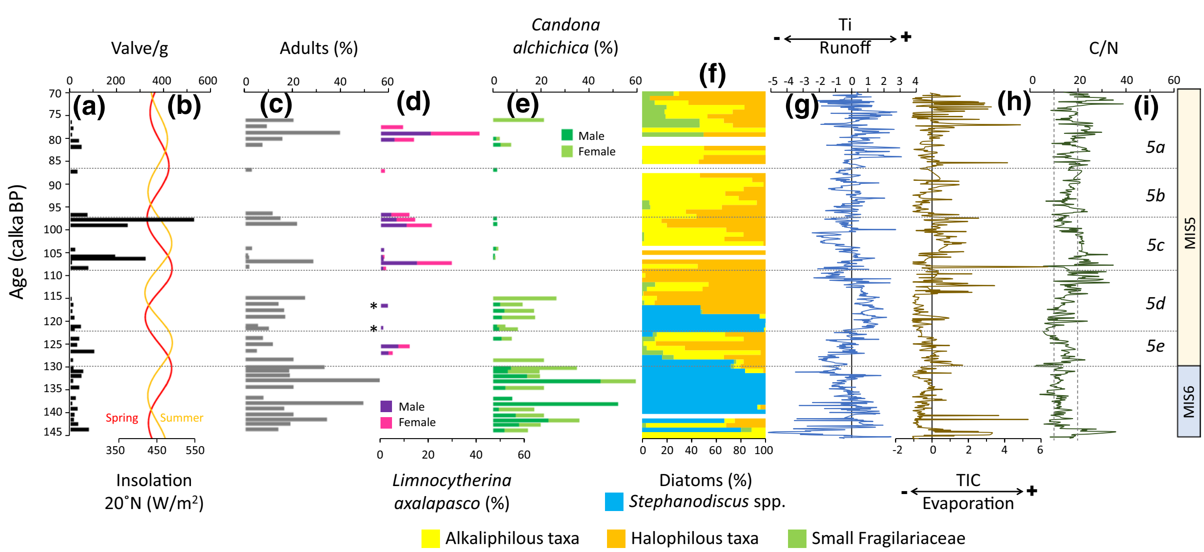

Fig. 5 Comparison through time of **a** total ostracod abundance as valve/g, **b** spring and summer insolation at 20° N as W/m^2, and relative abundances of **c** total adults, **d** *L. axalapasco*, **e** *C. alchichica* and **f** diatom assemblage (Ortega-Guerrero et al. 2020) as percentages (%) with other environmental proxies, previously published by Martínez-Abarca et al. (2021), such as **g** standardised Ti as an indicator of runoff, **h** standardised total inorganic carbon (TIC) as the evaporation rate and **i** organic matter source based on the C/N ratio. Asterisks represent the presence of *L. axalapasco* with developed nodes

abundance, as well as *L. axalapasco* and *C. alchichica* relative abundances through time, and compare these results with previously published paleoenvironmental proxies, such as runoff inferred from Ti concentration, evaporation rate based on total inorganic carbon (TIC) concentration and organic matter source based on the C/N ratio. For detailed information about the use of these paleoenvironmental proxies, fire activity and pollen in Chalco sediments, see Martínez-Abarca et al. (2021). We also compare ostracod results with the summary diatom record presented by Ortega-Guerrero et al. (2020), considering relative abundances (%) of main taxa groups. Based on the principal component analysis (PCA) presented in Fig. 6, we discuss inferred paleoecological conditions during the sub-stages of MIS6 and MIS5 and link them to regional climate forcings. We also discuss the possible origins and ecological preferences of these two endemic ostracod species, which coexist today in Lake Alchichica, a volcanic lake in central Mexico.

Paleoecological inferences

Marine Isotope Stage 6 (146–130 ka)

Previous studies in Lake Chalco suggested cold, low-runoff, and low evaporation rates during MIS6, which favoured a relatively deep, freshwater lake with anoxic bottom waters (Avendaño et al. 2018; Ortega-Guerrero et al. 2020; Martínez-Abarca et al. 2021). The diatom record indicates the presence of *S. niagarae* and *S. oregonicus* (Avendaño et al. 2018). The ecology of these two diatom species is well characterised and they are considered to be planktonic, with a tolerance for high nutrient concentrations and a preference for cool to cold waters (Theriot and Stoermer 1981, 1984; Brugam 1983; Fritz et al. 1993; Bradbury 1997; Julius et al. 1998; Avendaño et al. 2021). Avendaño et al. (2021) analysed the modern ecological distribution of *S. niagarae* in central Mexico, revealing that the diatom prefers temperate, subhumid climate conditions, and is found in freshwater lakes with [Mg^{2+}]–[Ca^{2+}]–[HCO_3^-] ionic dominance and high turbidity, which are mesotrophic to hypertrophic. Reduced fire activity in the Chalco region during MIS6, inferred from the charcoal record, is likely related to lower spring insolation and to the establishment of an open forest with abundant non-arboreal vegetation, which led to low fuel availability (Martínez-Abarca et al. 2021).

The ostracod record reveals relatively low total abundance, between 0 and 73.3 valves/g, and there are very few *C. alchichica* in Chalco sediments during MIS6. However, this species had higher relative abundance (up to 57.1%) during that stage. This alkaline species apparently tolerates a wide range of temperatures (14.4–24.9 °C) and dissolved oxygen concentrations (0–12.3 mg/L), and today is found in saline waters with TDS as high as 8.9 g/L (Cohuo-Durán et al. 2017). The reported freshwater diatom

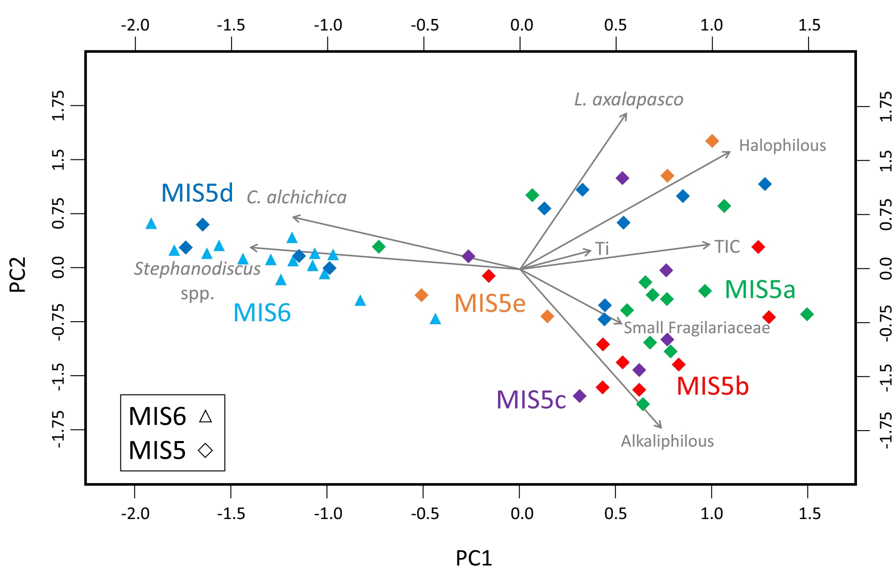

Fig. 6 Principal component analysis (PCA) of *L. axalapasco*, *C. alchichica*, diatom assemblage (*Stephanodiscus* spp., alkaliphilous taxa, halophilous taxa and small Fragilariaceae) and geochemical proxies such as Ti and TIC. Samples from MIS6 are presented as triangles, and samples from MIS5 are shown as diamonds. Sub-stages of MIS5 are marked by different colours. (Color figure online)

assemblage, with the presence of *S. niagarae* and *S. oregonicus* (TDS 0.5–3.0 g/L), appears to be at odds with the presence of this saline ostracod species. There exists, however, evidence of ostracod species such as *Cyprideis australiensis*, which can tolerate high salinity, coexisting with oligohaline diatom species (Edwards et al. 2006). We suggest that cold and anoxic conditions were the main factors for dominance of *C. alchichica* over *L. axalapasco*, which is completely absent from that part of the record. During 146–145 ka, runoff was at its lowest in the record, whereas evaporation rate was high, perhaps leading to very concentrated waters. These factors account for the absence of *C. alchichica* and the presence of alkaliphilous diatom taxa, including *Cyclotella meneghiniana*, *Nitzschia amphibia* and *Surirella peisonis*. Optimal conditions for *C. alchichica* were recorded between 143.5 and 130.2 ka, and the data reveal dominance of males over females during 142–141, 138–137 and 133–132 ka. These intervals coincide with relatively higher runoff and the highest *Stephanodiscus* spp. relative abundances. These findings suggest that males better tolerated freshwater conditions than did females. There are, however, multiple factors that influence the adult sex ratio (ASR) in Ostracoda, including differences in time of emergence between the sexes, age at maturation, reproductive lifespan, dispersal and migration patterns, and the mortality rate of young and adults (Székely et al. 2014; Kappeler 2017; Fernandes-Martins 2019). The most accepted cause for sex ratio variations in non-marine taxa is differential mortality of the sexes, linked to environmental conditions (Martens 1998), with evidence from fossil (Namiotko and Martins 2008) and experimental work (Rossi et al. 2013). This hypothesis was examined in more detail by analysis of responses to environmental changes during MIS5.

Marine Isotope Stage 5e (130–122 ka)

During MIS5, Lake Chalco water level declined and the waterbody became shallower, more saline, carbonate-rich and oxic, with relatively higher organic matter input to the sediments from macrophytes. Total diatom abundance decreased because of lower productivity during drier times that led to higher lake salinity. Relative abundances of alkaliphilous taxa (e.g., *C. meneghiniana*, *N. amphibia* and *S. peisonis*) and halophilous taxa (e.g., *Anomoeoneis costata*, *A. sphaerophora* and *Camphylodiscus clypeus*) increased (Ortega-Guerrero et al. 2020). The surrounding terrestrial ecosystem changed considerably during MIS5e, with forest expansion and greater fire activity (Martínez-Abarca et al. 2021). Total ostracod abundance increased from 0 to 95.4 valves/g. *Candona alchichica* abundance, however, decreased significantly, with males becoming completely absent during 128–125 ka. We suggest that the climate and environmental changes that led to more saline waters affected *C. alchichica* productivity, as the lake level declined during this sub-stage. Moreover, complete absence of *C. alchichica* males at 128 ka could indicate comparatively better female adaptation to increasingly saline conditions. Nevertheless, males of many ostracod species are suspected of having different maturation times and shorter lifespans compared to females (Cohen and Morin 1990). Shorter lifespans may be a consequence of males engaging in more active and riskier mating behaviour (Kamiya 1988). Higher predation risk in males has been observed, but this pattern is not always consistent across taxa (Abe 1983, 1990; Kamiya 1988; Rivers and Morin 2008; Speiser et al. 2013). Subsequently, females also disappeared from the sediment record during the interval 127–125 ka. This occurred at a time of higher dominance of alkaliphilous and halophilous diatom taxa (TDS > 6 g/L) and with the appearance of *L. axalapasco* in the sediment record. As mentioned, this ostracod, which prefers alkaline waters, tolerates a wide range of salinity (0.5 to 9.0 g/L). It also requires a dissolved oxygen concentration greater than ~ 5.0–6.5 mg/L. We posit that the shallower and oxic conditions in Lake Chalco triggered greater *L. axalapasco* productivity during this sub-stage. By the end of MIS5e, increasing runoff and low evaporation rates might have diluted the lake water, as *C. alchichica* (males and females) and *Stephanodiscus* spp. reappeared in the sediment record at 123.7 ka.

Marine Isotope Stage 5d (122–109 ka)

During MIS5d, runoff increased and fire activity in the Chalco region decreased, as did insolation. The ostracod record shows *C. alchichica* relative abundance increasing up to 25%, with the clear dominance of females over males (3:1) during 122–115 ka. This occurred during a period of lower than average evaporation and lower spring and summer insolation.

Moreover, *Stephanodiscus* spp. abundance also increased, indicating dilute waters. We suggest these relatively dilute water conditions favoured the increasing abundance of *C. alchichica*. On the other hand, *L. axalapasco* abundance was very scarce (0–2.3%) at 120 ka and 116 ka, but the few that were present had developed nodes, or "bumps" (Fig. 3i), as Cohuo-Durán et al. (2014) described for this endemic species. Environmental factors associated with the development of this morphology in *L. axalapasco* valves are not yet understood. Nevertheless, it has been observed that the valves of species in the sub-family Limnocytherinae display nodes or hollow protrusions during times of high salinity. Both the number of 'noded' valves and the number of nodes per valve appear to increase with rising salinity, suggesting that node formation is related to hydrological changes and consequent shifts in salinity and/or alkalinity (McCormack et al. 2019). The Lake Chalco sediment record, however, indicates less saline conditions during 122–115 ka, when nodes in *L. axalapasco* valves were observed. Therefore, we suggest that changes in pH could have triggered the morphological changes in *L. axalapasco*, and that pH values ranged between 9.3 and 9.6 during that period, based on the currently established pH ranges of *L. axalapasco* and *C. alchichica*. Nevertheless, among the species that develop these nodes is *C. torosa*, which is presumed to produce both more nodes and more prominent nodes with decreasing salinity (Keyser 2005; Frenzel et al. 2012). We recognise that valve numbers with this feature were very low, so experiments should be carried out to test this hypothesis. By the end of MIS5d, during the interval 114–109 ka, both *L. axalapasco* and *C. alchichica* were absent from the sediment record. As other paleoenvironmental proxies indicate, it was a period of decreasing runoff, enhanced evaporation and greater spring insolation. Moreover, increasing concentrations of alkaliphilous and halophilous diatom taxa, as well as the low presence of small Fragilariales, indicate shallower conditions. We therefore suggest that shallower and more concentrated lake waters inhibited the growth of both ostracod species. Caballero et al. (2019) presented diatom-based transfer functions for environmental conditions, using a training set that included data from 40 sites across central Mexico, including Lake Chalco. Their results indicated that salinity is the most important variable explaining diatom distribution in the dataset, followed by precipitation and temperature. We therefore suggest that these same environmental factors also affected ostracod occurrence.

Marine Isotope Stage 5c (109–97 ka)

MIS5c represents the period with the greatest total ostracod abundance, up to 518 valves/g, and is marked by the dominance of *L. axalapasco* (up to 28.6%) over *C. alchichica* (up to 1.5%). Moreover, the sub-stage is characterised by greater abundance of alkaliphilous diatom taxa. Increasing runoff and relatively low evaporation during 109–104 ka might have restored the lake environmental conditions that are optional for ostracod productivity, especially for *L. axalapasco*. However, during 103–100 ka, i.e., the period with the highest MIS5 summer insolation values, both ostracod species are absent from the sedimentary record. Therefore, we suggest that more concentrated water conditions, and possibly increasing water temperatures, prevented production of both species. Subsequently, by the end of MIS5c, inferred increased runoff coincided with increased *L. axalapasco* abundance, ca. 100–97 ka.

Marine Isotope Stage 5b (97–87 ka)

During MIS5b, total ostracod abundance was the lowest found in the record; *C. alchichica* and *L. axalapasco* relative abundances were 0–1.1% and 0–12%, respectively. Moreover, the relative increase in abundance of small Fragilariales and the alkaliphilous and halophilous diatom taxa dominate the record. Runoff remained below average and the evaporation rate decreased, consistent with the decline in summer insolation. We infer that diminished runoff led to low lake levels and saline conditions, which in turn inhibited ostracod productivity, with environmental conditions very similar to those at the end of MIS5d.

Marine Isotope Stage 5a (87–72 ka)

During MIS5a, total ostracod abundances range from 0 to 42 valves/g, and both species reappeared in the sediment record. *L. axalapasco* represents the dominant species, with relative abundances up to 40%, whereas *C. alchichica* had abundances up to 20%. As in earlier times, *C. alchichica* females were more common than males (2:1). Moreover, the increasing abundance of small Fragilariales among the alkaliphilous and halophilous diatom taxa reflects shallow and saline conditions. Overall, proxy environmental variables indicate enhanced runoff during MIS5a, consistent with increasing values for summer insolation, alongside high, but variable, evaporation rates. During the interval 87–83 ka, both ostracod species were absent from the sediment record. We suggest that this gap represents a period of rising lake level, as runoff increased and the evaporation rate remained low. Subsequently, shallow, but otherwise optimal conditions for both ostracods (similar to those described for MIS5c) might have been reached in the interval 82–76 ka. Finally, during the last part of MIS5a (75–72 ka), both ostracod species disappeared. This period was characterised by enhanced evaporation rates and greater variability, although both spring and summer insolation were relatively low. We suggest increasingly saline conditions reduced ostracod productivity during the time period 75–72 ka, as the evaporation rate was higher. However, ostracod analysis from the upper sediment unit will be necessary to yield a more detailed evaluation of the transition from MIS5 to MIS4.

Regional changes

Ostracod changes in the Lake Chalco sediment record seem to have been driven mainly by shifts in water salinity, and they coincide with changes in diatom assemblages, as illustrated in the PCA diagram (Fig. 6). Moreover, transfer functions based on diatoms in the Chalco region (Caballero et al. 2019) indicate that salinity is the most important variable explaining diatom distribution, followed by precipitation and temperature. We suggest salinity changes in the water column, mainly driven by the precipitation to evaporation ratio, were of primary importance in determining ostracod occurrence. Martínez-Abarca et al. (2021) suggested that precipitation changes around Lake Chalco were influenced mainly by precessional forcing, resulting in the migration of the ITCZ during MIS6 and MIS5. This contrasts with the precipitation distribution model presented by Metcalfe et al. (2015) for the MIS2–MIS1 transition (Martínez-Abarca et al. 2021). Model simulations by Roberts et al. (2017), however, suggest that the relationship between the ITCZ and atmospheric heat transport is different during abrupt climate changes, such as during glacial–interglacial transitions, and that the Hadley Circulation is not the main factor influencing precipitation in tropical areas, as other regional factors might also be involved. Sediments from Lake Petén Itzá, representing the last ~ 85 ka (MIS4–MIS1), suggest that ostracod communities responded rapidly to climate and environmental changes (Pérez et al. 2021). Similar to Lake Chalco, however, the Lake Petén Itzá sediment record possesses very low abundances in deposits older than 50 ka. We therefore posit that sediments from the upper stratigraphic units of Lake Chalco might reveal a more diverse ostracod community than was encountered in MIS6 and MIS5, thus improving our understanding of long-term climate changes in the Chalco region.

Origins and ecological preferences of *Candona alchichica* and *Limnocytherina axalapasco*

In modern settings, *C. alchichica* and *L. axalapasco* are endemic ostracods that coexist in Lake Alchichica, located ~ 200 km east (19° 24.7′ N, 97° 24.0′ W, Puebla, Mexico; Fig. 1) of Lake Chalco. That lake formed during the Pleistocene–Holocene transition. It has a surface area of ~ 2.4 km^2 and a maximum depth of 64 m (Alcocer 2021). It is an alkaline (pH 8.7–9.2), closed-basin maar lake with 8.5 ± 0.52 g/L salinity, 13 ± 0.5 mS/cm conductivity and water dominated by chloride >> carbonate, sodium >> magnesium ions (Vilaclara et al. 1993; Alcocer et al. 2000; Sigala et al. 2017). Moreover, it has a diatom ensemble of up to 40 species, including alkaliphilous and halophilous species such as *C. meneghiniana* and *Nitzschia frustulum* (Alcocer 2021), which were also present in the Chalco record during warm intervals (Caballero et al. 2019). The Chalco sediment record shows that *C. alchichica* was abundant in MIS6 when waters were relatively fresh, but persisted under more saline conditions in MIS5. Therefore, we suggest that Chalco sediments may have recorded a wider range of ecological preference for *C. alchichica*, which tolerates freshwater conditions (Lake Chalco MIS6) to saline environments such as those found today in Lake Alchichica. On the other hand, *L. axalapasco* is abundant in Chalco sediments from MIS5. This species dwells in the deepest areas of Lake Alchichica at ~ 64 m, where sand with a low percentage of silt is its preferred substrate (Alcocer et al. 1998). In the Chalco sediment record, however, there is a relatively higher *L. axalapasco* abundance during times of relatively shallow conditions (MIS5a, MIS5c and MIS5e). Today, neither *C. alchichica* nor *L. axalapasco* is present in Lake Chalco, and we hypothesise that Chalco could have been the site of origin for these two endemic ostracod species: *C. alchichica*, which subsequently adapted to saline conditions, and *L. axalapasco*, which subsequently adapted to deep-water areas such as those in Lake Alchichica. Ostracod analysis in the upper sediment units of the Chalco record should enable evaluation of this hypothesis, and help us understand why these species disappeared from Lake Chalco. Moreover, *in vitro* ecological studies could provide more information about *C. alchichica* ecological tolerances, and preference differences between males and females, than we can learn from the Lake Chalco sediment record.

Conclusions

The Lake Chalco sediment record possesses two endemic ostracod species during MIS6 and MIS5, *C. alchichica* and *L. axalapasco.* Overall, shifts through time in the ostracod record coincide with changes identified in sedimented diatom assemblages. We suggest that salinity was the main factor that influenced the ostracod community. *Candona alchichica* was most abundant during MIS6, when waters were fresh and cold, and deep, bottom waters were anoxic. During MIS5, the lake level declined, and salinity and bottom-water dissolved oxygen increased. These conditions favoured *L. axalapasco*, which appears in the record during MIS5e, whereas *C. alchichica* abundance decreased, especially among male specimens. During MIS5d, a general trend of increasing runoff and lower than the average evaporation rates coincided with increasing abundance of *C. alchichica* (mainly females), indicating increasingly higher lake levels and more dilute waters. During MIS5c and MIS5b, the lake level declined. MIS5c appears to have provided optimal shallow-water conditions for *L. axalapasco*, whereas conditions became too shallow for either ostracod species during MIS5b. Finally, during MIS5a, water level in Lake Chalco recovered with increased runoff, and both ostracod species reappeared in the record, with *L. axalapasco* dominant. Increasing evaporation rate during the last part of this period (75–72 ka), however, resulted in absence of ostracods in the sediment record.

In modern settings, these two ostracod species are typically found in saline environments and coexist in Lake Alchichica. This is contrary to what is seen in the Chalco record, where the highest *C. alchichica* abundances were recorded in MIS6 sediments, deposited during a time when the deep basin held cold fresh water, and possessed anoxic bottom waters. The ostracod was also present during MIS5, albeit with lower abundances, when salinity was high. Thus, we suggest that *C. alchichica* might have a greater range of salinity tolerance, and could be found from freshwater to saline settings. Similarly, we detect higher *L. axalapasco* abundances during periods of relatively shallow conditions (MIS5a, MIS5c and MIS5e), although at present this species is abundant in deeper (~64 m) areas of Lake Alchichica. Ostracod analysis from more recent sediment units should reveal when and why these two ostracod species disappeared from the record and provide insights into why they have not returned to modern-day Lake Chalco. Moreover, these upper sediment units might also reveal a more diverse ostracod community, thereby improving our understanding of past climate influences in the Chalco region.

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