Late Pleistocene (OIS 3) paleoenvironmental reconstruction for the Térapa vertebrate site, northcentral Sonora, Mexico, based on stable isotopes and autecology of ostracodes

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ABSTRACT

The Térapa fossil vertebrate site, northcentral Sonora, Mexico, provides a rare opportunity to study the paleoenvironmental conditions present in northeastern Mexico during mid-Oxygen Isotope Stage (OIS) 3. Ostracode faunal assemblages and stable oxygen (δ18O) and stable carbon (δ13C) isotope values from ostracode calcite were used to reconstruct the seasonality of precipitation and vegetation cover at Térapa at 40–43 ka. The ostracode fauna was a non-analogue mix of temperate and tropical ostracode species composed of 13 species from 12 genera. The neartic ostracodes Fabaeformiscandona caudata, Physocypria pustulosa, Cypridopsis vidua and the cosmopolitan ostracode Darwinula stevensoni dominate the assemblage. Two tropical ostracode genera, Chlamydotheca arcuata and Stenocypris sp., were present throughout the deposit and indicate that mean monthly summer temperatures were probably no more than 4°C to 6°C cooler than at present, based on available ecological information. Winter precipitation dominated the hydrologic cycle as evidenced by low than at present, based on available ecological information. Winter precipitation dominated the hydrologic cycle as evidenced by low

INTRODUCTION

Absolutely dated vertebrate fossils sites that provide late Pleistocene paleoenvironmental information for northern Mexico are rare, and their distribution is highly fragmentary (Metcalfe et al., 2000; Arroyo-Cabrales et al., 2010; Ferrusquia-Villafranca et al., 2010). The majority of such sites are located in the central and southern parts of the country and the resulting paleoenvironmental information displays a similar geographic bias (Ferrusquia-Villafranca et al., 2010). Late Pleistocene fossil sites from Sonora only comprise about 2% of all known Mexican localities (Arroyo-Cabrales et al., 2002; Ferrusquia-Villafranca et al., 2010). The Térapa fossil vertebrate site, located in northcentral Sonora, Mexico, near the towns of San Clemente de Térapa and El Llano (hereafter Térapa; Figure 1), contains an exceptional and extensive array of Late Pleistocene aquatic and terrestrial faunal remains (Mead et al., 2006, 2007; Hodnett et al., 2009; Steadman and Mead, 2010; Oswald...
A preliminary ostracode faunal assemblage for Térapa was reported in Mead et al. (2006). This study expands on those results by reporting several additional ostracode species, and reconstructs in greater detail the paleoenvironment at Térapa through the use of the ostracode assemblage and stable isotope (δ18O and δ13C) analysis of ostracode valve calcite. The ostracode δ18O values provide insight into the seasonality of peak surface discharge, assuming that the water temperature at the time of calcification can be reasonably estimated. The ostracode δ13C values can provide insight into the vegetation community growing around the site because respired CO₂ from plant roots contributed to the dissolved inorganic pool of the streams and wetland that deposited the Térapa sediments. In 2010, Nunez et al. (2010) described the ostracode assemblage and stable isotope (δ18O and δ13C) analysis of ostracode valve calcite. The ostracode δ18O values suggested that a strong C ₄ plant component was present. Our ostracode δ18O and δ13C data provide an excellent opportunity to compare paleoenvironmental interpretations for a single deposit that are derived from two very different and commonly used archives – aquatic ostracode calcite and terrestrial tooth enamel. To our knowledge, this is the first time such a comparison has been attempted. We demonstrate that seasonality of precipitation and ecologic variables must be considered when reconstructing paleohydrology from different stable isotopic archives, especially in environments that experience marked differences in the seasonality of precipitation and vegetation cover. Our results provide an important, albeit brief, absolutely dated record of paleoenvironmental conditions in northeastern Sonora at a time when biotic communities and their associated environmental gradients were considerably different than today.

SITE DESCRIPTION AND BACKGROUND

The town of Térapa (29°41’ N; 109°39’ W; Figure 1) is located in the Moctezuma River valley, in the northwestern portion of the Sierra Madre Occidental, at an elevation of 605 meters above sea level (m a.s.l.). The vegetation community at Térapa is classified as foothill thorn-scrub (Van Devender et al., 1997; Martin et al., 1998). Oak and oak-pine woodlands dominate at higher elevations (> 1,400 m a.s.l.) and the vegetation below about 600 m a.s.l. is classified as Sonoran Desert (Búrquez et al., 1992; Orvis, 1998).

The Moctezuma Valley is located between the Oposura Mountains (max. elevation ~ 1,800) to the west and the Sierra La Madera (max. elevation ~ 2,300 m a.s.l.) and another lower (max. elevation ~ 1,800 m a.s.l.) unnamed range to the east (Figure 2). The local geology consists of Lower Cretaceous fossiliferous limestone, granites, Eocene to Miocene-aged ignimbrites, Miocene and Pliocene-aged basin fill, and Quaternary-aged basalts of the Moctezuma Volcanic Field (Paz-Moreno et al., 2003).

The mean annual temperature (MAT) and mean annual precipitation (MAP) at Térapa are approximately 22°C and 58 cm·yr⁻¹, respectively (Figure 3). Average minimum monthly temperatures do not fall below 4°C and average maximum monthly temperatures approach 40°C in the summer (Figure 3). Monsoon rainfall during just two months (July-August) accounts for nearly 50% of the total annual precipitation (Figure 3). Winter precipitation is derived from Pacific storms that pass over the area as the polar jet stream and the associated storm track shift southward during the winter (Magaña et al., 2003; Nicholas and Battisti, 2008).
The $\delta^{18}$O value (VSMOW) of precipitation at Térapa is not monitored, but modeled values range from about -12‰ in the winter to -6‰ in the summer, with an average annual value of -7 ± 2‰ (Bowen, 2014; Figure 3). In contrast to modeled values, limited seasonal precipitation collections (2003-2004) at two stations within 50 km of Térapa (Figure 1) produced average $\delta^{18}$O values for winter (November-May) and summer (June-October) precipitation that were -7 ± 1‰ and -3 ± 2‰, respectively (n = 4; Figure 3; C. Eastoe, unpublished data). The winter precipitation $\delta^{18}$O value falls near the modeled value, but the summer precipitation $\delta^{18}$O value is much higher. The $\delta^{18}$O value of summer and winter precipitation in the southwestern U.S. varies by several per mille from year to year (Wright et al., 2001; Eastoe and Dettman, 2016). This variability likely explains the discrepancy between the modeled $\delta^{18}$O value for summer precipitation and the limited seasonal measurements near Térapa (Figure 3).

The fossiliferous sedimentary sequence at Térapa was deposited in a roughly 1 km × 2 km-wide basin along the eastern edge of the Tonibabi lava flow (Figure 2). The basin was created when the Tonibabi lava flow spilled southward from its vent and down the Río Moctezuma Valley (Figure 2). The Tonibabi lava flow blocked and altered the course of the Río Moctezuma and many small tributaries. Blocking of these tributaries caused water and sediments to be impounded along the edges of the flow (Mead et al., 2006).

The source of the water and sediments that inundated the Térapa basin has not been conclusively identified (Mead et al., 2006). Given the overall fine grain size of the sediments and the orientation of the modern stream network, the water and sediments were most likely derived from several small washes that are sourced from small catchments in the eastern highlands (Figure 2; Mead et al., 2006). The basin at Térapa was two orders of magnitude smaller than its upstream source area, making it sensitive to changes in effective moisture in the eastern mountains.

The sedimentology and age of the Térapa fossil deposit is covered in detail in Mead et al. (2006) and Bright et al. (2010). Briefly, the entire sediment package is about 11 m thick (Figure 4). The basal 0.5 m of sediment (units A$_1$ and A$_2$) is comprised of coarse-grained sands that are deposited directly on the Tonibabi lava. Unit A$_3$ is overlain by about 1.5 m of silty clay (Unit A$_s$). A well-sorted wedge of sand (Unit A$_s$) occurs within Unit A$_s$. The basal A-series sediments are overlain by roughly 1.5-2 m of blocky fossiliferous clays (Unit B$_p1$), which are in turn overlain by about 4 m of faintly bedded sandy silt (Unit B$_c$). A fairly prominent oxidized sorted sand occurs near the top of Unit B$_c$, which here is denoted B$_c$-s (“s” for sand). Unit B$_c$ is overlain by another blocky fossiliferous unit that is about 1.5 m thick (Unit B$_c$). Coarse pebble-armored stream channel deposits are formed into Unit B$_p2$ (Figure 4). Abruptly on top of both Unit B$_p2$ and the Tonibabi basalt are 2 to 4 m of coarse cobbles and sands of Unit C. Unit C likely represents coarse alluvial valley fill that spread across the valley floor after the Térapa basin was completely filled in with sediment. The Térapa locality has been dated, using multiple geochronological techniques, to about 40–43 ka, or to mid-marine Oxygen Isotope Stage (OIS) 3 (Bright et al., 2010).

Figure 2. Satellite image of Térapa, Sonora, Mexico (white star) and its location in relation to the town of Moctezuma (white square), the Río Moctezuma, the Tonibabi lava flow and its vent (white circle), the Moctezuma Volcanic Field, and the surrounding highlands. Image modified from Google Earth.
Figure 3. Climate data for Térapa, Sonora, Mexico. Average monthly precipitation totals in mm (gray columns); average monthly air temperatures (°C) (red line); average minimum and average maximum monthly air temperatures (°C) (red shading); and δ¹⁸O values of summer (June-October, warm colored horizontal lines) and winter (November-May, cool colored horizontal lines) precipitation collected at the towns of Huasabas and Mazocahui (see Figure 1) from 2002-2004. Dashed black line shows model-predicted δ¹⁸O values in Térapa precipitation from http://www.waterisotopes.org. Temperature and precipitation data are from http://smn.conagua.gob.mx/climatologia/normales/estacion/son/NORMAL26251 at the time of writing. Period of record, 1971-2000.

Figure 4. Stylized composite stratigraphic column for the Térapa deposit (modified from Mead et al. (2006)). Uncorrected ostracode calcite δ¹⁸O and δ¹³C values (‰, VPDB) are displayed in stratigraphic context. Black diamonds - Fabaeformiscandona caudata; red circles - Ilyocypris bradyi; green squares - Eucypris meadensis. Unit designations and sample names are the same as in Table 2 and Figure 6.
RESULTS

Ostracode fauna

The fossil ostracode fauna at Térapa currently consists of 13 species from 12 genera (Table 1). The nearctic ostracodes Fabaeformiscandona caudata, Physocypria pustulosa, Cypridopsis vidua, and the cosmopolitan ostracode Darwinula stevensoni (Figure 5) were encountered most frequently (Table 1). Pelocypris cf. tuberculatum, Cypridopsis okeechobei, Chlamydotheca arcuata, Limnocythere paraornata, and Heterocypris incongruens (Figure 5) are species not previously reported in Mead et al. (2006). The ostracode fauna is generally similar and consistent throughout the deposit (Table 1).

δ¹⁸O and δ¹³C values from ostracode valve calcite

The δ¹⁸OOST and δ¹³COST values (VPDB) range from about -4‰ to -8‰ and from about -1‰ to -9‰, respectively (Figures 4 and 6; Table 2). With the exception of 2 outliers, Ilyocypris bradyi valves have the lowest δ¹⁸O and δ¹³C values (Figures 4 and 6; Table 2). The average δ¹⁸O and δ¹³C values from I. bradyi valves are -8 ± 0‰ and -8 ± 1‰, respectively (n = 12). The average δ¹⁸O and δ¹³C values from F. caudata valves are -6 ± 1‰ and -4 ± 2‰, respectively (n = 25). The two E. meadensis valves produced δ¹⁸O and δ¹³C values of about -8‰ and -6‰, respectively (Figures 4 and 6; Table 2). The δ¹⁸OOST and δ¹³COST values are positively correlated (r = 0.74), although the low δ¹⁸O and δ¹³C values from I. bradyi control much of the correlation (Figure 6a). Excluding the I. bradyi values reduces the correlation considerably (r = 0.37).

DISCUSSION

Paleohydrology reconstruction

Ostracodes indicative of flowing-water settings (I. bradyi, E. meadensis) are sometimes found intermixed with ostracodes indicative of vegetated, more wetland-like conditions (H. incongruens, C. vidua, C. arcuata). The mixing of flowing- and stagnant-water ostracodes suggests environmental heterogeneity or possibly post-mortem reworking of the valves. Infrequent occurrences of C. okeechobei and E. meadensis may be indicative of spring discharge. The presence of C. arcuata and an unidentified Stenocypris species (Figure 5) is notable. Both Chlamydotheca and Stenocypris have circumtropical distributions (Tressler, 1949). At Térapa, these two tropical ostracode species are frequently found in association with F. caudata, an ostracode with a range that is currently restricted to the continental United States and Canada (Forester et al., 2005).

The fossil ostracode fauna at Térapa is indicative of a persistent freshwater setting. The majority of the fossil ostracode species have upper total dissolved solids (TDS) limits generally <1,000 mg L⁻¹, and both F. caudata and L. paraornata commonly inhabit water with TDS values between about 200 and 600 mg L⁻¹ (Forester et al., 2005). To date, no ostracode species indicative of chemically evolved water, such as Limnocythere staplini or Limnocythere sappaensis, has been recovered at Térapa even though they were common in Late Pleistocene-aged closed-basin lakes from the southwestern U.S. and northern Mexico (e.g., Palacios-Fest et al., 2002; Wells et al., 2003; Allen et al., 2009; Chávez-Lara et al., 2012). The persistent low-TDS ostracode fauna suggests that the Térapa impoundment was through-flowing. Over-spilling or leakage through the Tonibabi basalt are also reasonable mechanisms that would have suppressed evaporative chemical enrichment and maintained a freshwater environment.

The presence of P. pustulosa, C. arcuata, and the unidentified Stenocypris species are key warm-water indicators at Térapa. Physocypris pustulosa requires at least 2 consecutive months with water temperatures above 20°C to complete its lifecycle (Forester et al., 1987). Chlamydotheca and Stenocypris are both considered circumtropical genera (Tressler, 1949). Chlamydotheca and Stenocypris have both been reported in the continental United States, but reports are typically from southern and Gulf-coast states or from warm (geothermal) spring settings (Furtos, 1933; Hoff, 1944; Ferguson, 1962, 1964, 1966; Bowen, 1976; Davis, 1980; Forester, 1991, 1999; Ourso and Horing, 2000; Curry and Baker, 2000). Being tropical genera, Chlamydotheca and Stenocypris are probably unable to survive cold winter temperatures (e.g., Addo-Bediako et al., 2000; Sunday et al., 2011). Uncontrolled experiments have shown that water temperatures below about 20°C are lethal to C. arcuata (Forester, 1991). Both of the tropical ostraco-
des at Térapa undoubtedly required optimal water temperatures that were much warmer than 20°C. For example, Bowen (1976) reported that *Stenocypris* sp. would only appear in a pond in South Carolina when the minimum water temperature exceeded 28°C, and Forester (1991) recovered *Chlamydotheca* from several springs in the western U.S. and northern Mexico where water temperatures were between 25°C and 32°C.

The water temperature requirements of the tropical ostracode species at Térapa provide insight into summer temperatures in northeastern Mexico at 40–43 ka. A modern shallow lake in north-central Sonora (Lake El Yeso; Figure 1) has mean monthly lake water temperatures that are, on average, about 3°C cooler than the mean monthly air temperatures (Palacios-Fest and Dettman, 2001). Using the water and air temperature relationship at Lake El Yeso as an analog, the mean summer air temperature at Térapa during OIS 3 could not have been more than 5°C cooler than today (Figure 4) in order to support the tropical ostracode taxa. This estimate seems reasonable based on temperature reconstructions for the last glacial period from southern California, southern Arizona, and southern Texas that collectively suggest a reduction in annual temperatures of about 4°C to 6°C, with associated errors of ± 0.5°C to ±1.1°C depending on the study (Stute et al., 1992; Anderson et al., 2002; Holmgren et al., 2006; Kulongoski et al., 2009).

To our knowledge, the Térapa locality is only the third reported fossil occurrence of *F. caudata* in northern Mexico, with the other two being from Late Pleistocene sediments deposited in Laguna Babicora, Chihuahua (Figure 1; Palacios-Fest et al., 2002), and juvenile valves that have been reported from extensive but undated sediments at Comarca Lagunera (Paleolake Irritia) of Durango and Coahuila (Czaja et al., 2014). The modern distribution of *F. caudata* is confined to Canada and the continental United States (Forester et al., 2005) where it lives in water with optimal and maximum temperatures of about 6°C to

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Table 1. Fossil ostracode species presence (P) or absence (-) listed by sample and stratum, Térapa, Sonora, Mexico.

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**Occurrence** 29 24 24 19 10 9 8 6 5 5 3 2

Fc – *Fabaeformiscandona caudata*; Pp – *Phyocypria pustulosa*; Cyp – *Cypridopsis vidua*; Ds – *Darwinula stevensoni*; Ib – *Ilyocypris bradyi*; Pot – *Potamocypris* sp.; Em – *Eucypris meadensis*; Stn – *Stenocypris* sp.; Cha – *Chlamydotheca arcuata*; Hi – *Heterocypris incongruens*; Lp – *Limnocythere paraornata*; Pt – *Pelocypris* cf. *P. tuberculatum*. * Samples processed by N.A.U. Laboratory of Paleoeology and screen washed at 300 μm. b Species used for stable isotope analysis. c Includes several valves of *Cypridopsis okeechobei.*
Figure 5. Digital images of the fossil ostracode fauna at Térapa, Sonora, Mexico. Group a) *Fabaeformiscandona caudata*; i - male right valve, ii- male left valve, iii- female right valve, iv - female left valve. Group b) *Cypridopsis vidua*; i - right valve, ii- left valve. Group c) *Cypridopsis okeechoebi*; i- right valve, ii- left valve. Group d) *Darwinula stevensoni*; i- right valve, ii- left valve. Group e) *Limnocythere parornata*; i- male right valve, ii- male left valve, iii- female right valve, iv- female left valve. f) *Potamocypris* sp., left valve. Group g) *Stenocypris* sp.; i - right valve, ii- left valve. Group h) *Ilyocypris bradyi*, right valve; Group i) *Physocypris pustulosa*; i- right valve, ii-left valve. j) *Heterocypris incongruens*; right valve. k) *Eucypris meadensis*; right valve. l) *Chlamydotheca arcuta*; right valve. m) *Pelocypris* cf. *P. tuberculatum*; left valve. All images are external lateral views taken under transmitted light using an Olympus SXZ-12 binocular microscope fitted with an Olympus DP71 digital camera. Images were modified in Photoshop CS3 for contrast and clarity.
Figure 6. Uncorrected δ18O and δ13C values (%o, VPDB) from ostracode calcite preserved at Térapa, Sonora, Mexico. a) Cross-plot of individual δ18O and δ13C values grouped by ostracode taxon and sedimentary unit. Sedimentary unit and sample names are as in Figure 4. Box-and-whisker plots of uncorrected δ18O values (blue boxes) and δ13C values (green boxes) from Fabaeformiscandona caudata and Ilyocypris bradyi valves. Thick black line – median value, colored box – 1st to 3rd quartile range, open circles – outliers. Individual δ18O and δ13C values from two Eucypris meadensis valves are plotted as small black boxes.

Surface water δ18O reconstruction and seasonality of precipitation

Correcting ostracode δ18O values for vital effects

Ostracodes molt eight or nine times over the course of their life cycle and calcify their new valves within a few hours to at most a few days after molting (Turpen and Angel, 1971; Chivas et al., 1983). Rather than providing a continuous isotopic record over weeks to years like mollusk shell or tooth enamel, the calcite in ostracode valves provides a “snapshot” of the δ18O composition of the host water at the time the ostracode molted.

Unlike inorganic calcite, the oxygen isotope value in ostracode calcite (δ18Oost) does not appear to be in isotopic equilibrium with the surrounding water; for a given water temperature and δ18O value, δ18Oost is usually more positive than the expected equilibrium value (e.g., Pérez et al., 2013), partially because of the presence of a poorly understood “vital effect” (e.g., von Grafenstein et al., 1999). The δ18O vital effect in ostracodes is species specific, but is probably relatively similar within any given genus (von Grafenstein et al., 1999). Numerous natural calibration studies on a variety of Fabaeformiscandona species report vital effects of about +2‰ to +3‰ (e.g., von Grafenstein et al., 1999; Keatings et al., 2002; Belmecheri et al., 2002; Wetterich et al., 2000). Xia et al. (1997) reported a slightly lower vital effect of about +1‰ from laboratory cultured F. rawsoni. However, the ostracode valves from this experiment were less massive than the valves of naturally occurring F. rawsoni and this vital effect may not be accurate. We favor correcting the F. caudata δ18O values using vital effects of +2‰ and +3‰ because of the larger naturally calibrated data set.

Correcting the I. bradyi δ18O results (δ18Obr) is more problematic because a vital effect for Ilyocypris has not been clearly established. Published vital effects for various species of Ilyocypris are as high as about +2‰ (Develle et al. 2010) and as low as about +0.2‰ (Schwalb et al. 2002; Belis and Ariztegui, 2004; Mischke et al., 2008; Lawrence et al., 2008). For the purposes of this paper we corrected the I. bradyi δ18O values using vital effects of 0‰ and +2‰.

To our knowledge, there are no data on vital effects specifically for E. meadensis calcite. Li and Liu (2010) demonstrated that there is no vital effect in cultured E. mareotica at 10°C and a small negative vital effect at both 15°C and 19°C. Based on our optimal water temperature estimate (see below), the E. meadensis δ18O values were not corrected for any vital effect.

The δ18O value of ostracode calcite (δ18Oost) is dictated by the water temperature and the δ18O value of the water (δ18Osw) in which the ostracode calcified its valves (von Grafenstein et al., 1999). Our δ18OOST (VPDB) values were converted to surface water δ18O values (δ18Osw; VSMOW) using the calcite-water fractionation data of Friedman and
δ1.5‰ VSMOW range in the reconstructed 2°C range in optimal water temperatures will produce about a 6°C range in modern water temperature constraints for F. caudata (Curry, 1999), which was the most common ostracode in the Térapa sediments (Table 1) and comprised the bulk of the δ18O results (Figures 4 and 6; Table 2). The 6°C range in optimal water temperatures will produce about 1.5‰ VSMOW range in the reconstructed δ18O estimates, which is sensitive enough for the purpose of this study.

Reconstructing surface water δ18O values at Térapa

The ostracode-based surface water δ18O reconstruction for Térapa (δ18OSW-OST, VSMOW), using the optimal temperature range for F. caudata (6°C to 12°C) and assuming vital effects of 0‰ for both Ilyocypris and Eucypris and +2‰ to +3‰ for F. caudata, is -10 ± 1‰ (Figure 7). Increasing the temperature of calcification to the upper temperature limit for F. caudata (18°C) increases the δ18OSW-OST estimate to about -8 ± 1‰, with one maximum value of about -6‰ (Figure 7). More negative δ18OSW-OST estimates of about -12‰ at water temperatures of 6°C to 12°C and about -10‰ at water temperature of 18°C are produced when the δ13C values are corrected for a +2‰ vital effect.

The reconstructed δ18OSW-OST values for Térapa at 40–43 ka (Figure 7) indicate that the isotopic composition of the Térapa impoundment was dominated by winter precipitation and runoff. This result agrees with other speleothem (Szabo et al., 1994; Wagner et al., 2010; Asmerom et al., 2010) and numerous paleolake/paleowetland studies in the southwestern U.S. and northwestern Mexico (Ortega-Guerrero et al., 2010) and numerous paleolake/paleowetland studies in the southwestern U.S. and northwestern Mexico (Ortega-Guerrero et al., 2010; Asmerom et al., 2010; Allen et al., 2009; Pigati et al., 2009, 2011; Roy et al., 2010, 2012; Garcia et al., 2014; Reheis et al., 2015) that suggest increased winter moisture at about 40-45 ka, the time the Térapa sediments were deposited.
Comparing ostracode-based and tooth enamel-based surface water δ¹⁸O reconstructions for Térapa

We also compared our δ¹⁸O.subst with both bulk and serial δ¹⁸O values from herbivore tooth enamel (δ¹⁸O.ETM) previously recovered from Térapa (Nunez et al., 2010). Enamel δ¹⁸O values are often used to reconstruct paleo-water δ¹⁸O values (e.g., Wigda et al., 2010; Metcalfe et al., 2011; Pérez-Crespo et al., 2012), and Térapa affords the opportunity to compare δ¹⁸O.subst reconstructions from the same site based on two commonly used archives; ostracode calcite and tooth enamel. The δ¹⁸O.subst values (VPDB) from Nunez et al. (2010) were converted to surface water values (δ¹⁸O.subst-EN VSMOW) using the equations provided in their results section.

Several studies have demonstrated that the δ¹⁸O.subst values from large herbivores are strongly positively correlated with δ¹⁸O.subst (Huertas et al., 1995; Kohn et al., 1996; Hoppe et al., 2004). The strength of the correlation between δ¹⁸O.subst and δ¹⁸O.subst increases with the body size of the herbivore because larger animals are preferentially obligate drinkers (e.g., Bryant and Froelich, 1995; Hoppe et al., 2004). Smaller herbivores are better able to meet their water requirement through the food that they eat which weakens or eliminates the correlation between δ¹⁸O.subst and δ¹⁸O.subst in small animals (Huertas et al., 1995). Instead, the δ¹⁸O.subst in small herbivores correlate better with humidity as it relates to evaporation and water stress on vegetation (Huertas et al., 1995). Leaves, especially in arid environments, can have δ¹⁸O values as much as 20‰ higher than the water absorbed at the plant root ( Förstel, 1978; Kohn et al., 1996).

In order to generate the best comparison, we excluded the bulk tooth δ¹⁸O.subst data from two small herbivores (peccary; +0.9‰; caypbara, -5.3‰; Nunez et al. (2010)) and a very high outlier from a llama (+4.4‰; Nunez et al. (2010)). This produced an average bulk δ¹⁸O.subst estimate of about -4 ± 3‰ ( n = 19). This value is dominated by the results from numerous horse teeth that cluster with consistently high δ¹⁸O.subst values (-3 ± 3‰; n = 10). Nunez et al. (2010) produced serial δ¹⁸O.subst values from a bison and a horse tooth that captured 1 and 2 years of hydrologic information, respectively. When converted to δ¹⁸O.subst values, the serial bison and horse teeth results are also on the order of -4‰ to +2‰. We recognize that both the bulk and serial horse δ¹⁸O.subst values may be slightly too high because of a potential offset between δ¹⁸O.subst and δ¹⁸O.subst that has been reported for modern horses (Hoppe et al., 2004), but that does not change the observation that the majority of δ¹⁸O.subst estimates at Térapa are roughly 4‰ to 12‰ higher than the δ¹⁸O.subst estimate (Figure 7).

The dissimilarity between δ¹⁸O.subst and δ¹⁸O.subst at Térapa was unexpected and intriguing. The δ¹⁸O.subst and δ¹⁸O.subst values lead to very different paleohydrologic interpretations; the δ¹⁸O.subst estimate favors winter-derived moisture, whereas the δ¹⁸O.subst estimate favors significant amounts of monsoon-derived moisture or possibly a very evaporative environment. If we assume that the δ¹⁸O.subst estimate is correct, then to generate the measured δ¹⁸O.subst values would require either the absence of any vital effects and calcification in 18–20°C water, or the presence of vital effects and calcification in >28°C water. Both of these options seem unreasonable based on the available literature regarding δ¹⁸O isotope systematics in ostracode calcite (e.g., von Grafenstein et al., 1999) and the ecological tolerances of the ostracodes used in this study (Forster, 1991; Curry, 1999) which are admittedly skewed towards ostracode occurrences at higher latitudes than Térapa. Diagenetic alteration of the δ¹⁸O values is not a likely cause for the discrepancy because alteration typically changes δ¹⁸O by about ±1‰ (Kohn et al., 1999), which is much less than the offset between the δ¹⁸O.subst and δ¹⁸O.subst values reported here. The most likely explanation for the offset is that the ostracodes consistently calcified their valves during the spring or early summer when the runoff feeding the impoundment was still dominated by winter precipitation. Additionally, the high δ¹⁸O.ETM values from the large mammals may suggest that the animals consistently drank from evaporated water sources (e.g., Hoppe et al., 2004; Wigda et al., 2010) or incorporated a higher than expected proportion of evaporated leaf-water in their diet (e.g., Feranec and MacFadden, 2006; Zanazzi and Kohn, 2008; Pérez-Crespo et al., 2016), or perhaps the animals (especially the horses) migrated through the Térapa area. If the large herbivores are migrants then their δ¹⁸O.subst values may include contributions from non-local water sources (e.g., Pérez-Crespo et al., 2012).

Ostracode δ¹⁸O values and paleovegetation reconstruction

The δ¹⁸O.value in ostracode calcite (δ¹⁸O.subst) faithfully records the δ¹⁸O.value of dissolved inorganic carbon (δ¹⁸O(CO₂)) of the water the ostracode calcified its valves in (von Grafenstein et al., 1999). The isotopic fractionation of carbon between aqueous carbon dioxide (CO₂) and inorganic calcite produces a calcite δ¹⁸O value that, over the range of 10°C to 25°C, is approximately +12‰ higher than the δ¹⁸O.value of the dissolved CO₂ in the host water (Romaneck et al., 1992).

Figure 7. Comparisons of (a) reconstructed δ¹⁸O.subst values (‰, VSMOW) of surface/meteoric water based on ostracode calcite and herbivore tooth enamel (open circles), and (b) the range of δ¹³C values in ostracode calcite and herbivore tooth enamel (open circles) at Térapa, Sonora, Mexico, during mid-OIS 3. Open circles in (a) and (b) are values derived from bulk and serial analysis of enamel from the teeth of large herbivores collected throughout the deposit (Nunez et al., 2010). Finest dashed vertical line and faint blue box in (a) are the mean and 1σ standard deviation, respectively, of δ¹⁸O.subst values calculated from all ostracode calcite samples corrected for various vital effects and calculated on the preferred water temperature range of 6°C to 12°C. Medium dashed vertical line and faint orange box in (a) are the mean and 1σ standard deviation, respectively, of δ¹³C.subst values calculated from all ostracode calcite samples corrected for various vital effects and calculated at the maximum water temperature estimate of 18°C. Coarsest dashed vertical line in (a) is the highest reconstructed δ¹⁸O.subst value (see text for discussion). Medium dashed vertical line and grey box in (b) are the mean and 1σ standard deviation, respectively, of δ¹³C values from all ostracode calcite samples.
In this study, we are interested in using δ13COST values from *Ilyocypris bradyi*, an ostracode with a strong affinity for streams and flowing water (Curry, 1999; Quade et al., 2003), to reconstruct the δ13C DIC value of the streams feeding the Térapa impoundment, and from that, broadly estimating the relative proportion of paleovegetation types present in the Térapa watershed at 40–43 ka.

**Variables that influence ostracode δ13C values**

The δ13C DIC value of springs and streams is largely derived from respirated soil CO2 (δ13C DIC), which itself is derived from the surrounding plant community, although contributions from water-rock interactions, for instance the dissolution of marine carbonate bedrock (δ13C = 0‰), may be present in groundwater as well. Terrestrial vegetation can be subdivided into C3, C4 and Crassulacean Acid Metabolism (CAM) groups, with each group having a representative range of δ13C values. Grasses and other plants that use the C4 photosynthetic pathway generally have higher δ13C values (-13 + 2‰) than woody plants and shrubs that use the C3 photosynthetic pathway (-28 ± 3‰; O'Leary, 1981). Plants that use the CAM photosynthetic pathway (e.g., cactus, agave, yucca) have intermediate δ13C values (-13‰ to -27‰; O'Leary, 1981) that overlap with C3 and C4 plants. Obligate CAM plants have δ13C values closer to C3 plants, whereas facultative CAM plants tend to have δ13C values that are closer to C4 plants (Griffiths, 1992). Thus, the δ13C value of CAM plants overlaps those of C3 and C4 plants, rendering them isotopically invisible as a group. As a result, our discussion of plant communities is restricted to an estimate of the apparent abundances of C3 and C4 plants, recognizing that the C2 category may contain contributions from facultative CAM plants and that the C4 category may contain contributions from obligate CAM plants. And finally, aquatic vegetation typically has very low δ13C values (-25 to -30‰; Keeley and Sandquist, 1992).

Further complicating the issue is the fact that some ostracode species live within the top few cm of sediment (epifaunal; Decoury et al., 2012) and may calcify their valves within the sediment. Epifaunal species may record the δ13C DIC value of sediment pore water rather than the overlying water body (Decoury et al., 2012). Consequently, δ13COST of epifaunal ostracodes may be lower than expected because the valves were calcified in an environment where decaying organic matter often leads to pore water that is enriched in respired 13C (e.g., Keeley and Sandquist, 1992; Decoury et al., 2011).

**Reconstructing ground cover at Térapa**

The modern flora of the Sonoran Desert consists of roughly 50% annuals and 50% perennials (e.g., Venable and Pake, 1999). The winter annual flora is populated exclusively by C4 plants whereas the summer annual flora is dominated by C3 plants (summer annual C3:C4 = 35:65; Mulroy and Rundel, 1977). Perennials are comprised mostly of C3 and CAM plants (Drennan and Nobel, 1997). Packrat middens dating to the last glacial period (60 to 13 ka) indicate that much of the Sonoran Desert landscape between about 300 and 1,300 m a.s.l. was dominated by pinyon-juniper-oak woodlands and chaparral (Van Devender, 1990). Similar packrat midden studies and the isotopic analysis of megaherbivore e.g. mammoth, bison, horse) tooth enamel have suggested that seasonal monsoon precipitation supported C3 grasslands throughout much of the southwestern U.S. and northern Mexico during the last glacial period (e.g., Connin et al., 1998; Holmgren et al., 2006, 2007).

The average δ13C value (VPDB) for *I. bradyi* (δ13C ILY) is about -8‰ (Figure 6; Table 2). Reducing this value by 12‰ (e.g., Romanek et al., 1992) produces a δ13C value (VPDB) for dissolved aqueous CO2 of about -20‰. Subtracting an additional 4‰ for the kinetic fractionation of CO2 in soil profiles (Cerling, 1984) the δ13C DIC value could have been derived from a landscape with a δ13C DIC value of about -24‰.

The C3 and C4 vegetation at Térapa was assigned end member values of -28‰ and -13‰, respectively, based on previous studies in similar desert environments (Mooney et al., 1989; Biedenbender et al., 2004). If Térapa had a δ13C DIC value of about -24‰ then that would suggest ground cover with a C3:C4 ratio of about 75:25.

**Comparing ostracode-based and tooth enamel-based paleovegetation reconstructions for Térapa**

At face value, a C3-dominated flora surrounding Térapa at 40–43 ka contrasts with the enamel results of Nunez et al. (2010), where they concluded that C4 grasses and perhaps obligate CAM plants were abundant around Térapa and comprised a significant portion of the diet of even typically obligate browsing herbivores (i.e., Odocoileus; Figure 7). The discrepancy between our C3- and C4-dominated interpretation (Nunez et al.’s 2010) C3-rich interpretation (Figure 7) may be explained by several factors. First, the δ13C ILY and δ13C DIC values are derived from two very different processes. The δ13C DIC values likely reflect the averaged composition of the surrounding watershed during the season that the ostracodes preferentially calcified their valves, whereas the δ13C DIC values undoubtedly incorporate a selective dietary preference for each animal (e.g., Feranec and MacFadden, 2006). Second, the δ13C DIC values suggest a winter-dominated precipitation regime. If so, then the δ13C DIC of runoff was probably dominated by a winter vegetation signal that would have been skewed towards C4 plants. Similarly, we suspect that the streams that fed the Térapa impoundment drained the highlands to the east (Figure 2) and may have had δ13C DIC values that were skewed towards the low values typical of a woodier C3-dominated mountainous ecosystem. And finally, *I. bradyi* may have calcified in 13C-enriched microhabitats such that their δ13C values would be lower than the bulk stream value. This would suggest that additional factors that should have increased the δ13C DIC value, such as the absorption of atmospheric CO2 (δ13C ≈ -6.7‰; Köhler et al., 2010) or the decay of C3 organic material that might have washed into the streams, were outweighed by the decay of aquatic vegetation within the streams. A combination of these seasonal and habitat-specific factors likely produced δ13C DIC values that significantly underestimated the abundance of C4 plants on the landscape. In spite of their aquatic origin and likely seasonal bias, the δ13C DIC values still require about 25% input from C4 plants, suggesting that C4 plants were perhaps abundant near Térapa, as Nunez et al. (2010) concluded.

**CONCLUSIONS**

A fossil ostracode fauna and stable isotope (δ18O and δ13C) analyses have been used to reconstruct the paleoenvironment during the deposition of a unique megaflora vertebrate assemblage at Térapa, Sonora, Mexico, during mid-OIS 3 (about 40–43 ka). The fossil ostracode fauna was comprised of 12 genera and 13 species. Species that reflect flowing water and more quiescent conditions were found intermixed. Most of the ostracode species are common, wide-spread temperate species, but two, *C. arcuata* and *Stenocypris* sp., have tropical affinities. The mix of temperate and tropical ostracode species mirrors the mix of temperate and tropical vertebrate fossils recovered from the site. Based on the presence of tropical ostracode species, summer temperatures at Térapa at 40–43 ka were at most ~5°C cooler than at present. The fresh-water ostracode fauna and low δ18O OILT values suggest that the water body at Térapa was through-flowing. Our ostracode-based TDS estimate for the impoundment is on the order of 200–600 mg L−1.

The δ13C DIC and δ13C DIC values from throughout the deposit suggest that winter precipitation dominated the hydrologic cycle and that the surrounding vegetation community was dominated by C4 plants. The
δ¹⁸O⁰SW-OST estimate for Térapa at 40-43 ka was approximately -10 ± 2‰ VSMOW, indicating that increased winter precipitation dominated the surface runoff. This finding is consistent with other paleoclimatic studies from the south-western U.S. and northern Mexico at 45–40 ka. The δ¹⁸O⁰SW-OST Estimate is roughly 4‰ to 12‰ lower than the δ¹⁸O⁰SW-EN estimates derived from teeth of large herbivores collected from the same site, however. The δ¹⁸C⁰ values suggest that C₃ plants dominated the landscape (perhaps 75%), although associated herbivore tooth enamel suggests a strong C₄ (i.e., grass) component was present. Because of the season and aquatic setting in which the ostracode valves were likely calcified, the δ¹³C⁰ values probably underestimate the proportion of C₃ plants that were on the landscape.

The Térapa vertebrate site is an excellent example of how different isotopic archives can produce very different paleoenvironmental interpretations from the same deposit. Térapa provides a cautionary example of how using a single isotopic archive to reconstruct desert paleohydrology may be misleading. When used individually, the ostracode and enamel δ¹⁸O and δ¹³C values suggested opposing precipitation and vegetation regimes. The ostracode results favor a winter-dominated hydrology and a C₃-rich vegetation community whereas the tooth enamel results favor a summer-dominated or more evaporative hydrology and a C₄-rich vegetation community. A more complete interpretation emerged when both datasets were used together. Interpretive differences arose because the processes that produced the δ¹⁸O and δ¹³C values in the ostracode calcite and herbivore enamel captured paleoenvironmental information at different spatial, temporal, and seasonal scales.

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