Dietary resource partitioning in the Late Pleistocene horses from Cedral, north-central Mexico: evidence from the study of dental wear

Christian R. Barrón-Ortiz, Jessica M. Theodor, and Joaquín Arroyo-Cabrales

1 Department of Biological Sciences, University of Calgary,
2 Laboratorio de Arqueozoología, Instituto Nacional de Antropología e Historia,
Moneda # 16, Col. Centro, C.P. 06060, México, D.F. Mexico.
* Jrbarron@ucalgary.ca; chbarron45@yahoo.com

ABSTRACT

The Late Pleistocene (late Wisconsinan glacial stage) deposits of the archaeological-paleontological site of Cedral, north-central Mexico, have yielded abundant fossil remains of three horse species: Equus mexicanus, E. conversidens, and E. sp. These horses appear to have been sympatric, not only at this locality but in different sites in Mexico and the southwestern United States, posing the possibility that they partitioned available food resources in order to coexist. In this study, we investigated the feeding ecology of the Cedral horses through the analysis of dental wear (i.e., mesowear and microwear). The extended mesowear and low magnification microwear methods were used to infer the paleodiet of each species. The analysis of mesowear reveals significant differences in cusp shape between E. mexicanus and the other two equid species, with the former showing a higher percentage of rounded cusps and lower percentages of sharp and blunt cusps. These differences are consistent with those reported in a recent study of stable isotopes. Furthermore, the analysis of dental microwear indicates significant differences between the microwear patterns of the three equids. The results of the microwear analysis suggest that each species tended to feed on different foodstuffs with varying physical properties, supporting the hypothesis of dietary resource partitioning. Integrating the results derived from the examination of mesowear and microwear, as well as those gathered from the study of stable isotopes, it is suggested that E. conversidens and E. sp. were predominantly grazers, which may have fed at different feeding heights and/or in different microhabitats. Equus mexicanus also appears to have grazed to a large extent, but possibly with a more generalist dietary behavior.

Key words: paleodiet; mesowear; microwear; Equus; Cedral; Mexico.

INTRODUCTION

Three equid species are currently recognized from the Late Pleistocene deposits of Cedral, San Luis Potosí, Mexico, which have been tentatively identified as: Equus mexicanus Hibbard, 1955; E. conversidens Owen, 1869; and E. sp. (Figure 1c; Alberdi et al., 2003; Melgarejo-Damián and Montellano-Ballesteros, 2008; Barrón-Ortiz et al., 2014).

Three equid species are currently recognized from the Late Pleistocene deposits of Cedral, San Luis Potosí, Mexico, which have been tentatively identified as: Equus mexicanus Hibbard, 1955; E. conversidens Owen, 1869; and E. sp. (Figure 1c; Alberdi et al., 2003; Melgarejo-Damián and Montellano-Ballesteros, 2008; Barrón-Ortiz et al., 2014).

Palabras clave: paleodieta; mesodesgaste; microdesgaste; Equus; Cedral; México.
In this article, we follow these taxonomic designations noting that there is still no consensus regarding to the taxonomy of North American Pleistocene equids (e.g., Winans, 1989; Azzaroli, 1998; Weinstock et al., 2005; Pichardo, 2006; Scott et al., 2010). Nevertheless, regardless of the taxonomic names applied to the Cedral fossil horses, the distinction between the three species is well supported by differences in size (Alberdi et al., 2003; Melgarejo-Damián and Montellano-Ballesteros, 2008; Barrón-Ortiz and Theodor, 2011; Marín Leyva, 2011), metapodial proportions (Melgarejo-Damián and Montellano-Ballesteros, 2008; Marín Leyva, 2011), and features of the occlusal enamel pattern of the cheek teeth (Barrón-Ortiz and Theodor, 2011).

The frequent association of these three equid species in the same stratigraphic levels, not only at Cedral, but in different sites throughout central and northern Mexico as well as the southwestern United States (e.g., Hibbard, 1955; Harris, 1985, 1993; FAUNMAP, 1994; Barrón-Ortiz et al., 2009) suggests that, at least in these regions, they were sympatric. The question therefore arises: did these horses partition the available food resources in order to minimize competition and facilitate coexistence?

In this study, we investigate the paleo diets of the Late Pleistocene (late Wisconsinan glacial stage) horses from Cedral, north-central Mexico, by examining dental wear (i.e., mesowear and microwear), which has been shown to correlate with diet (e.g., Walker et al., 1978; Fortelius and Solounias, 2000; Solounias and Semprebon, 2002). We test for significant differences in dental wear patterns between equid species that would indicate dietary resource partitioning. Thus far, the only other study that has examined the paleo diets of the Cedral horses corresponds to a stable isotope analysis conducted by Pérez-Crespo et al. (2009). Although sample sizes were admittedly reduced, this study hinted at the presence of dietary resource partitioning between *E. mexicanus* and the two other species. The results suggest an isotopically mixed C₃-C₄ diet for *E. mexicanus* and a diet composed largely of C₄ plants for *E. conversidens* and *E. sp.*

**STUDY AREA**

The Cedral archaeological-paleontological site is located in the state of San Luis Potosí, north-central Mexico, at 23°49’ N and 100°43’ W and at an altitude of 1,700 m a.s.l. (Figure 1a). The site was excavated by scholars from the Instituto Nacional de Antropología e Historia (INAH) from 1977 to 1984 (Lorenzo and Mirambell, 1986; Mirambell, 2012). Vertebrate fossil remains were collected from different stratigraphic
levels in sediments that were deposited in a system of springs. A large portion of the equid remains recovered come from sedimentary layers (strata X-XII) that are bracketed by radiocarbon dates of 21,960 ± 540 and 31,850 ± 1,600 14C years before the present (Figure 1b; Alberdi et al., 2003); however, assignment of any particular specimen to a specific stratum cannot be made, as this information is presently missing. Our study, thus, represents a time-averaged assessment of the diets of the Cedral equids at a temporal scale of approximately ten thousand years. The associated mammalian assemblage includes, among other vertebrates, Columbian mammoth (*Mammuthus columbi*), mastodont (*Mammut americanum*), mylodont (*Paramylodon harlani*), glyptodont (*Glyptotherium sp.*), Western camel (*Camelops hesternus*), tapir (*Tapirus haysii*), American lion (*Panthera atrox*), and dire wolf (*Canis dirus*) (Álvarez et al., 2012). The assemblage of herbivore mammals is suggestive of an open habitat with forest patches.

**MATERIAL AND METHODS**

The extended mesowear (Kaiser and Solounias, 2003) and low magnification microwear (Solounias and Semprebon, 2002) methods were used to infer the paleodiet of the Cedral horses. A total of 104 specimens were analyzed (Tables 1A and 2A of the Appendix) all of them housed at the Paleontological Collection of the Archeozoology Laboratory ‘M. en C. Tícuil Álvez Solorzano’, Subdirección de Laboratorios y Apoyo Académico, Instituto Nacional de Antropología e Historia (INAH), Mexico City, catalogued under the acronym DP. Quantification and scoring of the variables investigated were carried out by the first author, as inter-observer error has been shown to be a concern, particularly for low magnification microwear (Mihlbachler et al., 2012). All statistical tests were conducted in PAST 2.17 (Hammer et al., 2001) and STATISTICA v. 9 (StatSoft®, 2009) software packages. The significance level for all tests was set to a p-value of 0.05.

**Extended mesowear method**

We collected mesowear data following the extended mesowear method proposed by Kaiser and Solounias (2003) for teeth in middle stages of wear (i.e., heavily worn as well as little worn teeth were not included in the analysis). The mesowear method was originally developed for the second upper molars (M2) to reconstruct ungulate diets based on the analysis of the buccal cusps (Fortelius and Solounias, 2000). It was subsequently extended in equids by Kaiser and Solounias (2003) to include the last four upper tooth positions: P4, M1, M2, and M3. The variables considered include the degree of relief of the cusps, high or low, and the shape of the sharpest cusp (whether anterior or posterior), which can be scored as sharp, round, or blunt (Figure 2; Fortelius and Solounias, 2000). Ungulates with a browsing diet tend to have molars with low relief and sharp cusps, whereas grazing ungulates tend to show molars with low relief and round/blunt cusps, and mixed feeders tend to present intermediate cusps morphologies.

In this study, digital photographs of the buccal side of each specimen were taken using a Sony Cyber-shot DSC-H9 digital camera. Prior to data collection, the order of the photographs was randomized to ensure observer blindness. Subsequently, the computer software ImageJ 1.47 (Rasband, 2013) was used to measure the depth of the valley between the paracone and metacone cusps as well as the anteroposterior length of each tooth, in order to determine cusp relief. These measurements were taken three separate times and an average was calculated with the objective of reducing measurement error. The teeth were scored as possessing low cusps if the cusp height index, determined by dividing the valley depth by the anteroposterior length, was lower than 0.1 (Fortelius and Solounias, 2000). Cusp shape was scored by direct observation of the specimens. The frequency of the mesowear variables was recorded for each equid species. In addition, we calculated the mesowear score (e.g., Rivals and Semprebon, 2006; Rivals et al., 2007), which combines cusp relief and shape into a single value that ranges from 0 (high relief and sharp cusps) to 3 (low relief and blunt cusps).

A Kruskal-Wallis test and randomization tests of independence (Monte Carlo simulations using 100,000 replicates) were used to test, respectively, for significant differences between equid species in mesowear score and frequency distributions of the mesowear variables. In addition, a discriminant function analysis (DFA) was conducted using the dataset of extant ungulates published by Fortelius and Solounias (2000), with the exclusion of the minute abraded brachydonts and species with a sample size lower than ten specimens. The variables percent high, percent sharp, and percent blunt cusps were employed in the DFA analysis. These variables were normalized using the arcsine transformation prior to performing the analysis. We followed the conservative dietary classification in Fortelius and Solounias (2000). The DFA was performed assuming equal prior classification probabilities for all groups. The classification functions derived from the DFA were subsequently used to classify the Cedral horses into one of the extant ungulate dietary categories: browsers, mixed feeders, and grazers.

**Low magnification microwear**

Several methodologies exist for the study of dental microwear of which low magnification microwear (e.g., Solounias and Semprebon, 2002; Semprebon et al., 2004; Merceron et al., 2004, 2005; Nelson et al., 2005; Gomes Rodrigues et al., 2009) and microwear texture analysis (e.g., Ungar et al., 2003, 2010; Scott et al., 2005, 2006; Merceron et al., 2010) are currently the most widely applied. In this study, we examined dental microwear at a low magnification (35 X) using high-resolution clear epoxy casts. Microwear features were counted on photographs (Figure 3) prepared following the methodology in Fraser et al. (2009), using a Nikon D200 digital camera and a Nikon SMZ1500 stereomicroscope; the digital resolution of the images obtained is 0.6 pixels/μm. Cleaning, molding, and casting of the teeth studied were done.
Dietary resource partitioning in the horses from Cedral according to Solounias and Semprebon (2002). As for the mesowear method, only teeth in middle stages of wear were used. In addition, to minimize measurement error, the order of the photographs was randomized prior to data collection to ensure observer blindness (Mihlbachler et al., 2012), and microwear variables were quantified three separate times per specimen with the resulting average values used in further calculations.

We studied microwear features on the lingual enamel band of the paracone of M2 teeth as well as the enamel band of the protoconid of lower second molars (m2), according to Semprebon et al. (2004). However, in some cases we had to analyze other (adjacent) enamel bands, because the desired enamel band was damaged, and we also included three specimens that were tentatively identified as second molars (Table 2A of the Appendix). The microwear variables scored per tooth specimen included the average number of scratches and pits of two counting areas on the enamel band, each 0.4x0.4 mm. Pits are microwear features that are circular to sub-circular in outline, whereas scratches are elongated features typically with a length to width ratio of at least 4:1. The presence of the following variables was also scored: more than four cross scratches (Scratches oriented at an oblique angle with respect to the majority of scratches), more than four large pits (at least twice the diameter of small pits), gouges (large, irregular microwear scars), fine scratches (scratches that appear the narrowest), coarse scratches (scratches that appear wider), and mixed scratches (a combination of both fine and coarse scratches) (Solounias and Semprebon, 2002). For each species we then calculated the percentage of individuals presenting these variables. Because the percentage of fine, coarse, and mixed scratches adds up to 100 percent, only the first two variables were used in the analysis. All of the percentages were normalized for statistical analyses using the arcsine transformation.

We used the data collected following the methodology outlined above for comparison with the extant ungulate dataset gathered by Solounias and Semprebon (2002) using a principal component analysis (PCA) on the correlation matrix. We also conducted a DFA on the Solounias and Semprebon (2002) dataset, assuming equal prior classification probabilities for all groups, and used the classification functions generated to classify the Cedral equids into one of their dietary categories: browsers, fruit browsers, grazers, meal-by-meal mixed feeders, and seasonal mixed feeders. It should be noted that comparison of our microwear data with the Solounias and Semprebon (2002) dataset is considered tentative, as some recent studies have found high inter-observer error in the scoring of microwear features using low magnification procedures (e.g., Mihlbachler et al., 2012).

In order to test for significant differences between the three equid species, we modified the scoring procedure described above and included additional variables, with the objective of obtaining a finer characterization of dental microwear. In addition to the average number of scratches and pits, the number of exceptionally wide scratches (at least twice the width of coarse scratches) on the visible enamel band of the photograph was counted. The variables more than four cross
scratches and more than four large pits were quantified for each counting area, providing a score of 1 if the features are present or 0 if they are absent, and calculating the average of the two counting areas to obtain an average score for these variables. The presence or absence of gouges on the enamel band visible in the photograph was scored as 1 and 0, respectively. Finally, we also scored scratch texture (e.g., Rivals and Athanassiou, 2007; Rivals and Athanassiou, 2008). For each counting area, we gave a score of 0 if it consisted of fine scratches, 1 if it consisted of fine and coarse scratches, and 2 if it consisted of coarse scratches; the average score of the two counting areas was then calculated for each specimen.

A PCA employing the correlation matrix was used for visualization of each equid specimen in microwear multivariate space. In order to test for significant differences between species, we conducted a non-parametric multivariate analysis of variance test (NP-MANOVA), in which significance is estimated by permutation, using 100,000 replicates and the Mahalanobis distance measure. Bonferroni corrected pairwise comparisons were used to identify which species are significantly different from each other. We also examined the distribution of individual scratch counts for each species to assess if there is seasonality in the diet; seasonal mixed feeding taxa tend to display a bimodal distribution of scratches (Solounias and Semprebon, 2002). A Shaprio-Wilk test of normality was employed to test whether the distributions of individual scratch counts depart significantly from a normal distribution.

**RESULTS**

**Mesowear**

The results of the mesowear analysis are summarized in Table 1. *Equus mexicanus* shows the lowest mesowear score of the three equids, whereas *E. sp.* has the highest mesowear score, with *E. conversidens* occupying an intermediate position (Figure 4; Table 1); however, these differences are not statistically significant (Kruskall-Wallis test, \( H = 3.516, p = 0.1066 \)). Likewise, the distribution of the variables relating to cusp relief are not significantly different (Monte Carlo simulations, \( p > 0.05 \)), with all three equids showing a high frequency of low cusps (Figure 5). In contrast, there is a significant difference between *E. mexicanus* and the two other species in the distribution of the variables concerning cusp shape (Monte Carlo simulations, \( p < 0.05 \)), with the former showing a higher percentage of rounded cusps and lower percentages of sharp and blunt cusps (Fig 5).

The DFA conducted on a subset of the extant ungulate dataset of Fortelius and Solounias (2000) correctly classifies 75.6 % of the species by diet; 77.8 % for browsers, 76.0 % for mixed feeders, and 72.7 % for grazers. The discriminant functions generated classify the three fossil equids within the grazers (posterior probabilities greater than 0.95), such as the white rhinoceros (*Ceratotherium simum*) and the plains zebra (*Equus quagga*).


<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>MS</th>
<th>% H</th>
<th>% L</th>
<th>% S</th>
<th>% R</th>
<th>% B</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Equus sp.</em></td>
<td>26</td>
<td>2.23</td>
<td>3.85</td>
<td>96.15</td>
<td>11.54</td>
<td>53.85</td>
<td>34.62</td>
</tr>
<tr>
<td><em>Equus conversidens</em></td>
<td>24</td>
<td>2.02</td>
<td>4.17</td>
<td>95.83</td>
<td>33.33</td>
<td>41.67</td>
<td>25.00</td>
</tr>
<tr>
<td><em>Equus mexicanus</em></td>
<td>25</td>
<td>1.88</td>
<td>8.00</td>
<td>92.00</td>
<td>12.00</td>
<td>84.00</td>
<td>4.00</td>
</tr>
</tbody>
</table>

n = number of specimens, MS = mesowear score, % H = percentage of specimens with high occlusal relief, % L = percentage of specimens with low occlusal relief, % S = percentage of specimens with sharp cusps, % R = percentage of specimens with round cusps, % B = percentage of specimens with blunt cusps.

**Microwear**

Analysis of the low magnification microwear indicates significant differences between the three horse species. Examination of the first two components of a PCA analysis (Figure 6; Table 2) calculated using the modified microwear variables (Table 2A of the Appendix), shows that each species tends to occupy a different region of the microwear multivariate space. Based on the PCA factor loadings (Table 2), *Equus mexicanus* separates from the other equids along the first principal component by possessing a greater number of pits, a lower scratch texture score, and a lower number of wide scratches. *E. conversidens* separates from *E. sp.* along the second principal component by presenting a greater number of scratches, a higher incidence of cross scratches and gouges, and a lower incidence of large pits. Moreover, the NP-MANOVA test reveals that there are significant differences in the multivariate means of the three horse species (\( F = 2.707, p < 0.001 \)). Bonferroni corrected pairwise comparisons demonstrate significant differences between *E. mexicanus* and the other species (\( p < 0.02 \), as well as a marginally significant difference between *E. conversidens* and *E. sp.* (\( F = 2.204, p = 0.0419 \)).

The distribution of individual scratch counts (not shown) for each species.
species does not follow a bimodal distribution. Furthermore, application of the Shapiro-Wilk test indicates that none of the distributions depart significantly from normality ($p > 0.05$), suggesting a lack of seasonality in the diet of the specimens studied. However, these results do not demonstrate that the Cedral equids did not have seasonally variable diets as it is not known, at present, whether animal remains at Cedral tended to accumulate on a particular season. If accumulation of animal remains tended to be seasonally concentrated, for instance during the dry season, then microwear would be reflecting the dry season diet, but not the diet during the rainy season.

Comparison of the standard microwear variables for the fossil horses (Table 3) with the extant ungulate dataset of Solounias and Semprebon (2002) through a PCA analysis (Figure 7; Table 4), shows that the fossil equids plot along extant grazers, but also in close proximity with meal-by-meal mixed feeders (e.g., Cervus canadensis), as these dietary groups largely overlap in the plot. The DFA correctly classifies 75% of extant species by diet; 90.0% for browsers, 100% for fruit browsers, 77.8% for grazers, 75.0% for meal-by-meal mixed feeders, and 41.8% for seasonal mixed feeders. The discriminant functions generated classify $E$. sp. and $E$. conversidens among the grazers, with posterior probabilities of 0.69 and 0.54, respectively. In contrast, $E$. mexicanus is classified with the meal-by-meal mixed feeders (posterior probability of 0.66).

**DISCUSSION**

The analyses of dental microwear and, to a lesser extent, mesowear support the hypothesis of dietary resource partitioning in the horses from Cedral. Microwear is significantly different in all three species, whereas mesowear (specifically cusp shape) is only significantly different in $E$. mexicanus.

The discrepancy in the results between mesowear and microwear is not surprising and has been reported in other extinct ungulate species (e.g., Fortelius and Solounias, 2000; Rivals and Semprebon, 2006; Merceron et al., 2007; Rivals et al., 2008; Rivals et al., 2010). Mesowear and microwear provide insights into dietary preferences at different scales. Mesowear reflects the overall abrasive nature of the diet over a relatively long period of an individual’s lifetime, whereas microwear represents distinct microscopic features produced within weeks or days prior to death, by the food and/or exogenous grit ingested (Teaford and Oyen, 1989; Fortelius and Solounias, 2000; Solounias and Semprebon, 2002). Taking this distinction into account, the results for the analysis of mesowear indicate that the three equid species had an overall highly abrasive diet comparable to that seen in extant grazers; however, $E$. mexicanus appears to have had a somewhat less abrasive diet than the other equids. A similar highly abrasive diet was recently reported for samples of $E$. mexicanus and $E$. conversidens from Tlaxcala (Bonilla-Toscano et al., 2013), as well as for samples of $E$. conversidens from Hidalgo (Bravo-Cuevas et al., 2011) and Chiapas, Mexico (Carbot-Chanona and Gómez-Pérez, 2013). This may not have been the case, however, for a sample of $E$. conversidens from Michoacán, Mexico, where a mixed feeding diet has been reported on the basis of the study of dental microwear (Marín Leyva et al., 2013).

On a finer scale, the results of the microwear analysis for the Cedral specimens indicate that individual equids of each species tended to feed on different foodstuffs and/or ingested different types of grit, with varying physical properties, which produced distinctive microwear patterns. Although these results support the hypothesis of dietary resource partitioning, the analysis of dental microwear provides little insight into the mechanism by which this division of resources might have taken place. Extant ungulates partition dietary resources in a variety of ways, such as feeding on different plant species, feeding on...
different plant parts of the same species, feeding at different heights and/or in distinct microhabitats (e.g., Bell, 1971; Jarman and Sinclair, 1979; McNaughton and Georgiadis, 1986; du Toit, 1990; Spencer 1995; Stewart et al., 2002). Which of these alternatives for partitioning food resources was employed by the Cedral equids cannot be presently determined from the microwear data alone. This is partly because, despite extensive research, there is still no consensus about the primary agent responsible for the formation of microwear features. Phytoliths, lignin and cellulose, as well as exogenous grit have each been proposed as the primary factor producing microwear features (Walker et al., 1978; Ungar et al., 1995; Sanson et al., 2007; Merceron et al., 2007; Lucas et al., 2013; Schulz et al., 2013; Tütken et al., 2013). Determining whether microwear primarily records the type of vegetation eaten by a herbivore or whether it mainly records the amount and type of grit ingested, may allow for the formulation of more specific dietary hypotheses. Nevertheless, drawing from ecomorphological studies, it seems likely that the Cedral equids segregated according to microhabitat use and/or feeding height, as evidenced by differences in limb proportions as well as differences in body size (Marín Leyva, 2011).

The isotopic study conducted by Pérez-Crespo et al. (2009) also found evidence of dietary resource partitioning, albeit only between *E. mexicanus* and the other equid species of the Cedral locality. The isotope data for *E. conversidens* and *E. sp.* are not statistically different; however, the sample size for both equids is reduced. Integrating our results with those reported by Pérez-Crespo et al. (2009), it appears that *E. conversidens* and *E. sp.* were predominantly grazers. These equids have mesowear and microwear patterns indicative of a grazing diet. Additionally, their mean δ¹³C values, -2.1 ‰ for *E. conversidens* and -2.7 ‰ for *E. sp.*, fall close to the average value (~0.5 ‰) of extant C₃ grazers (Koch et al., 1998; Hoppe and Koch, 2006); although their range, particularly in *E. sp.*, extends into the C₃-C₄ region. The statistically significant differences in the microwear patterns of these two species suggest that, despite showing a predominantly grazing diet, these equids partitioned available food resources. Similar instances of dietary resource partitioning among sympatric grazing ungulates have been reported for some extant species, such as between wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus quagga*) (e.g., McNaughton and Georgiadis, 1986; Voeten and Prins, 1999) and between three species of alcelaphine antelopes (Murray and Brown, 1993).

*Equus mexicanus* also appears to have grazed substantially, but with a greater degree of dietary flexibility, and there are alternative scenarios for the reconstruction of the dietary preferences of this equid. The isotope analysis demonstrates that *E. mexicanus* was an isotopically C₃-C₄ mixed feeder, with a mean δ¹³C value of -4.9 ‰ (Pérez-Crespo et al., 2009). This may indicate that it fed on a combination of C₃ grasses and C₄ forbs growing close to the ground, accounting for its more generalist microwear pattern and its abrasive mesowear signal. Alternatively, this equid might have periodically incorporated in its diet woody browse and forbs, possibly during dry periods, as it has been reported in some extant equid species (Grubb, 1981; St-Louis and Côté, 2009).

Serial isotope analyses and, perhaps, determining the season of death through the study of dental cementum (e.g., Burke and Castanet, 1995) of a sample of the teeth from which microwear was obtained, could elucidate this matter. In addition, feeding on a portion of C₄ grasses for this and the other equids is a possibility that cannot be ruled out, according to the results presented here and those from the analysis of stable isotopes. Many teeth of *E. mexicanus* and a few specimens of the other equids show high numbers of fine scratches. Different authors have noted that many C₄ grazers tend to have occlusal enamel surfaces covered by numerous, fine scratches, suggesting that this attribute could be used to differentiate C₃ from C₄ grazing (Solounias and Semprebon, 2002; Merceron et al., 2004; Rivals et al., 2007). However, as indicated by Merceron et al. (2004), more studies, especially experimental studies with controlled diets, are needed to confirm this.

Instances of dietary resource partitioning among sympatric equid taxa have been previously reported through the analysis of dental wear, ecomorphological, and/or geochemical data (e.g., MacFadden and Shockey, 1997; MacFadden et al., 1999; Barrón Ortiz and Guzmán Gutiérrez, 2009). As presented in this study, the Cedral equids also follow this pattern. Nonetheless, there are reports where the data do not clearly support dietary resource partitioning among sympatric equid species (e.g., Sánchez et al., 2006; MacFadden, 2008; Bonilla-Toscano et al., 2013). In any case, continued study of the feeding ecology of equids as well as other herbivores will open the way to better understand the feeding structure of herbivore communities, and elucidate shifts as well as restructuring brought about by large scale changes in vegetation over time. Of particular relevance to these studies is the integration

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>S</th>
<th>P</th>
<th>% CS</th>
<th>% LP</th>
<th>% G</th>
<th>% F</th>
<th>% C</th>
<th>% M</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Equus sp.</em></td>
<td>13</td>
<td>25.51 ± 3.2</td>
<td>13.36 ± 2.2</td>
<td>46.15</td>
<td>11.54</td>
<td>49.02</td>
<td>7.69</td>
<td>12.82</td>
<td>79.49</td>
</tr>
<tr>
<td><em>Equus conversidens</em></td>
<td>15</td>
<td>27.68 ± 4.3</td>
<td>13.57 ± 1.6</td>
<td>70.00</td>
<td>0.00</td>
<td>85.71</td>
<td>4.44</td>
<td>16.67</td>
<td>78.89</td>
</tr>
<tr>
<td><em>Equus mexicanus</em></td>
<td>13</td>
<td>26.06 ± 3.3</td>
<td>15.64 ± 2.4</td>
<td>61.54</td>
<td>28.21</td>
<td>61.90</td>
<td>42.31</td>
<td>0.00</td>
<td>57.69</td>
</tr>
</tbody>
</table>

n = number of specimens, S = average number of scratches ± standard deviation, P = average number of pits ± standard deviation, % CS = percentage of specimens with cross scratches, % LP = percentage of specimens with large pits, % G = percentage of specimens with gouges, % F = percentage of specimens with fine scratches, % C = percentage of specimens with coarse scratches, % M = percentage of specimens with mixed scratches.

Table 2. Eigenvalues and factor loadings for the first five principal components resulting from PCA of the microwear data in Table 2A of the Appendix.

<table>
<thead>
<tr>
<th>Component</th>
<th>Eigenvalue</th>
<th>% variance</th>
<th>% cum. variance</th>
<th>Factor loadings</th>
</tr>
</thead>
<tbody>
<tr>
<td>PC1</td>
<td>1.98</td>
<td>1.68</td>
<td>1.07</td>
<td>0.90 0.56</td>
</tr>
<tr>
<td>PC2</td>
<td>28.23</td>
<td>24.06</td>
<td>15.30</td>
<td>12.87 8.05</td>
</tr>
<tr>
<td>PC3</td>
<td>28.23</td>
<td>52.29</td>
<td>67.59</td>
<td>80.46 88.51</td>
</tr>
</tbody>
</table>

Factor loadings:

- S = average number of scratches, P = average number of pits, CS = average score of cross scratches, LP = average score of large pits, G = average score of gouges, S = average number of scratches, P = average number of pits, CS = average score of cross scratches, LP = average score of large pits, G = average score of gouges, % F = percentage of specimens with fine scratches, % C = percentage of specimens with coarse scratches, % M = percentage of specimens with mixed scratches.

- STS = average scratch texture score.
of different dietary proxies, which, despite some of the shortcomings discussed above, ultimately allows for a finer reconstruction of feeding ecology than using each proxy in isolation.

CONCLUSIONS

Considering the results here presented and those of a previous analysis of stable isotopes (Pérez-Crespo et al., 2009), we conclude that E. conversidens and E. sp. from Cedral had a primarily grazing diet. The results also suggest that E. mexicanus grazed considerably, but it may have had a more generalized dietary behavior. Moreover, the study of dental wear, particularly microwear, provides evidence of dietary resource partitioning, as there are statistically significant differences in the microwear patterns of the three equid species. Feeding at different heights and/or in distinct microhabitats may have been the manner by which the Cedral equids partitioned available food resources. The present study highlights that finer reconstructions of feeding ecology may be obtained by integrating a variety of dietary and ecomorphological proxies.

ACKNOWLEDGEMENTS

We would like to thank the Consejo de Arqueología, INAH, for granting permission to study the equid material from Cedral. Thanks are also extended to the INAH staff for their hospitality when visiting the collection. We also extend our gratitude to Elizabeth Romo Rábago for her assistance in data collection and molding of the teeth studied. Danielle Fraser and Victor Adrián Pérez Crespo provided useful suggestions and comments during the development of the project. Funding for this study was provided by a graduate scholarship to CRBO from the Consejo Nacional de Ciencia y Tecnología de México (CONACYT scholarship No. 310423) and a graduate scholarship from the University of Calgary, as well as a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to JMT. Finally, we thank the reviewers, Victor M. Bravo Cuevas and Florent Rivals, for their comments which helped improve an earlier version of this manuscript.

APPENDIX. SUPPLEMENTARY MATERIAL

Tables 1A and 2A can be found at the journal website <http://rmcg.unam.mx/>, in the table of contents of this issue.

REFERENCES

Dietary resource partitioning in the horses from Cedral


Van Andel, R., 1983, Turns: pattern and process in the faunal record: Journal of Vertebrate Paleontology, 3(2), 229-244.


Manuscript accepted: April 30, 2014

Manuscript received: January 26, 2014

Corrected manuscript received: April 1, 2014

Manuscript received: January 26, 2014