

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

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ABSTRACT

The Late Pleistocene (late Wisconsinan glacial stage) deposits of the archeological-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.

RESUMEN

Los sedimentos del Pleistoceno Tardío (etapa glacial del Wisconsiniano tardío) del sitio arqueológico-paleontológico de Cedral, centro-norte de México, han producido abundantes restos fósiles de tres especies de équidos, los cuales han sido identificados como *Equus*

mexicanus, *E. conversidens* y *E. sp.* Estos caballos al parecer fueron simpátricos, no solamente en esta localidad, sino también en diferentes sitios de México y el suroeste de Estados Unidos, lo que plantea la posibilidad de que presentaban una partición de los recursos alimenticios disponibles para coexistir. En el presente estudio, se investigaron los hábitos alimenticios de los caballos de Cedral a través del análisis del desgaste dental. Se emplearon los métodos de mesodesgaste y microdesgaste de baja magnificación para inferir la paleodieta de cada especie de caballo. El análisis de mesodesgaste muestra diferencias significativas en la forma de las cúspides de los molares entre *E. mexicanus* y las otras dos especies, ya que *E. mexicanus* presenta un mayor porcentaje de cúspides redondeadas y menores porcentajes de cúspides aguzadas y romas. Estas diferencias son consistentes con los resultados reportados en un estudio reciente de isótopos estables. Por otra parte, el análisis de microdesgaste dental indica diferencias significativas en el patrón de microdesgaste de los tres équidos. Los resultados del análisis de microdesgaste sugieren que cada especie tendía a ingerir materiales con diferentes propiedades físicas, lo cual apoya la hipótesis de que presentaban una partición de recursos alimenticios. Integrando los resultados derivados del estudio de mesodesgaste y microdesgaste con aquéllos reportados en un estudio de isótopos estables, se sugiere que *E. conversidens* y *E. sp.* presentaban una dieta predominantemente pasedora y posiblemente se alimentaban a diferentes alturas del suelo y/o en diferentes microhábitats. *Equus mexicanus* parece también haber incorporado en su dieta una gran proporción de pastos, pero con un hábito alimenticio más generalista que los otros dos équidos.

Palabras clave: paleodieta; mesodesgaste; microdesgaste; *Equus*; Cedral; México.

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

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 $21,960 \pm 540$ and $31,850 \pm 1,600$ ^{14}C 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*), mastodon (*Mammot 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 paleodiets 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. Ticul Álvarez Solórzano', 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 high 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

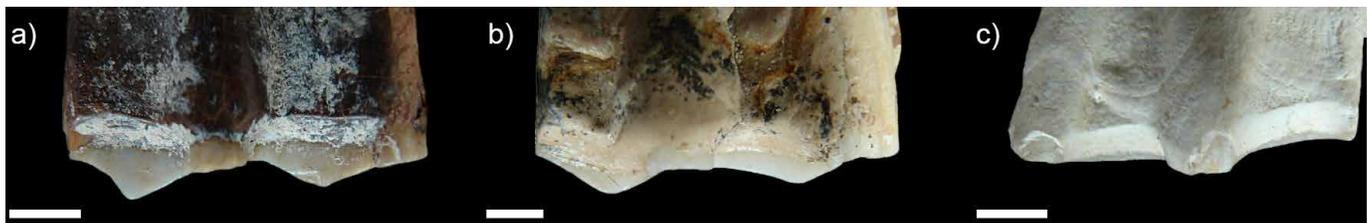


Figure 2. Buccal view of the apices of three equid upper cheek teeth from Cedral. a) M2 of *Equus conversidens* (DP-2308) showing high relief as well as round (anterior) and sharp (posterior) cusps; mesowear score: 0. b) M1 of *E. mexicanus* (DP-3838) displaying low relief and round cusps; mesowear score: 2. c) M2 of *E. conversidens* (DP-4532) with low relief and blunt cusps; mesowear score: 3. Scale bar = 5 mm.

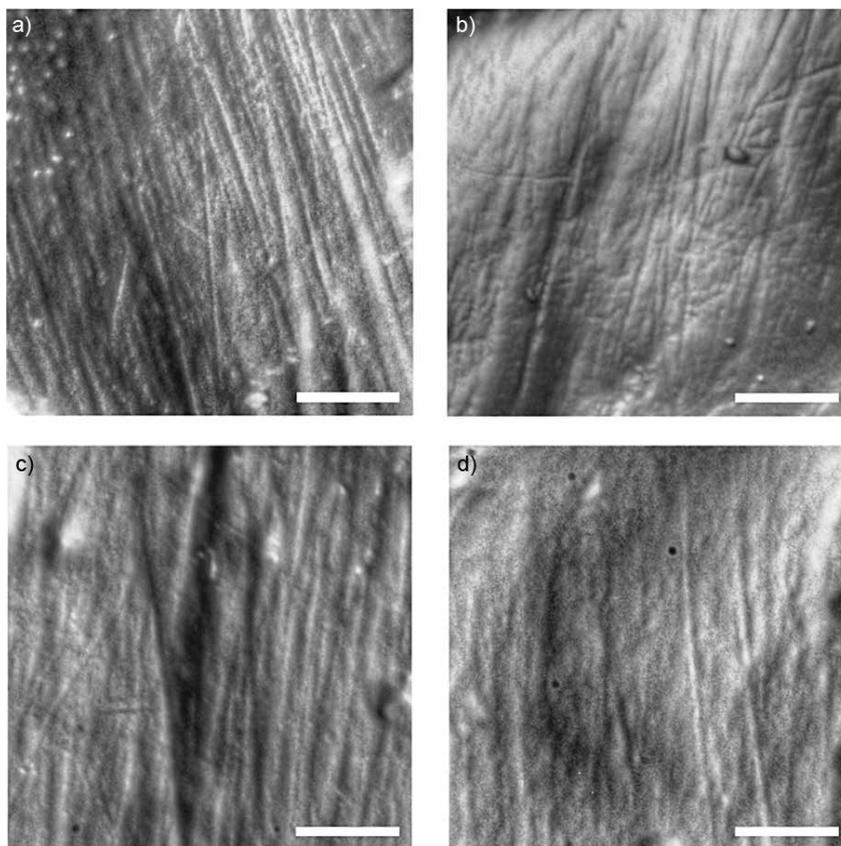


Figure 3. Photographs of microwear in equid molars from Cedral. Each photograph correspond to a 0.4 x 0.4 mm counting area.. a) M2 of *Equus* sp. (DP-2316) showing mostly fine and sub-parallel scratches. b) M2 of *E. conversidens* (DP-2308) presenting fine and coarse scratches oriented at various angles. c) M2 of *E. mexicanus* (DP-2537) with an exceptionally wide scratch at the center of the image. d) m2 of *E. mexicanus* (DP-2567) displaying relatively few scratches and a high concentration of pits. Scale bar = 0.1 mm.

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 0.4×0.4 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 et al., 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 Shapiro-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 1. Summary of mesowear data for the Cedral equids.

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

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

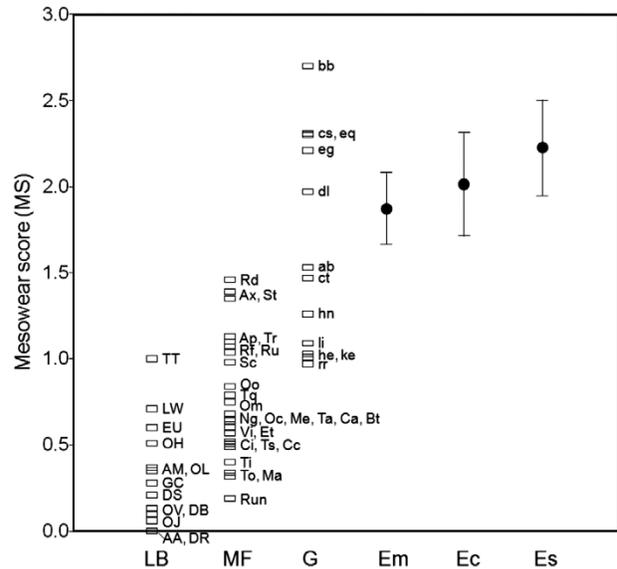


Figure 4. Mesowear scores for the Cedral fossil horses and extant ungulate species, transformed from Fortelius and Solounias (2000), excluding the minute abraded brachydonts. Each data point is the average for a species sample. Error bars indicate 95 % confidence intervals. Abbreviations: LB = leaf browsers, MF = mixed feeders, G = grazers, Em = *Equus mexicanus*, Ec = *E. conversidens*, Es = *E. sp.* Leaf browsers: *Alces alces* (AA), *Antilocapra americana* (AM), *Capreolus capreolus* (OL), *Dicerorhinus sumatrensis* (DS), *Diceros bicornis* (DB), *Giraffa camelopardalis* (GC), *Litocranius walleri* (LW), *Odocoileus hemionus* (OH), *Odocoileus virginianus* (OV), *Okapia johnstoni* (OJ), *Rhinoceros sondaicus* (RU), *Tragelaphus strepsiceros* (TT), *Tragelaphus euryceros* (EU). Mixed feeders: *Aepyceros melampus* (Me), *Antidorcas marsupialis* (Ma), *Axis axis* (Aa), *Axis porcinus* (Ap), *Boselaphus tragocamelus* (Tr), *Budorcas taxicolor* (Bt), *Capra ibex* (Ci), *Capricornis sumatraensis* (Ca), *Cervus canadensis* (Cc), *Eudorcas thomsonii* (Et), *Nanger granti* (Ng), *Ourebia ourebi* (Oo), *Ovibos moschatus* (Om), *Ovis canadensis* (Oc), *Redunca fulvorufula* (Rf), *Rhinoceros unicornis* (Run), *Rucervus duvaucelii* (Rd), *Rusa unicolor* (Ru), *Saiga tatarica* (St), *Syncerus caffer* (Sc), *Taurotragus oryx* (To), *Tetracerus quadricornis* (Tq), *Tragelaphus angasii* (Ta), *Tragelaphus imberbis* (Ti), *Tragelaphus scriptus* (Ts), *Vicugna vicugna* (Vi). Grazers: *Alcelaphus buselaphus* (ab), *Bison bison* (bb), *Ceratotherium simum* (cs), *Connochaetes taurinus* (ct), *Damaliscus lunatus* (dl), *Equus grevyi* (eg), *Equus quagga* (eq), *Hippotragus equinus* (he), *Hippotragus niger* (hn), *Kobus ellipsiprymnus* (ke), *Redunca redunca* (rr), *Sigmoceros lichtensteinii* (li).

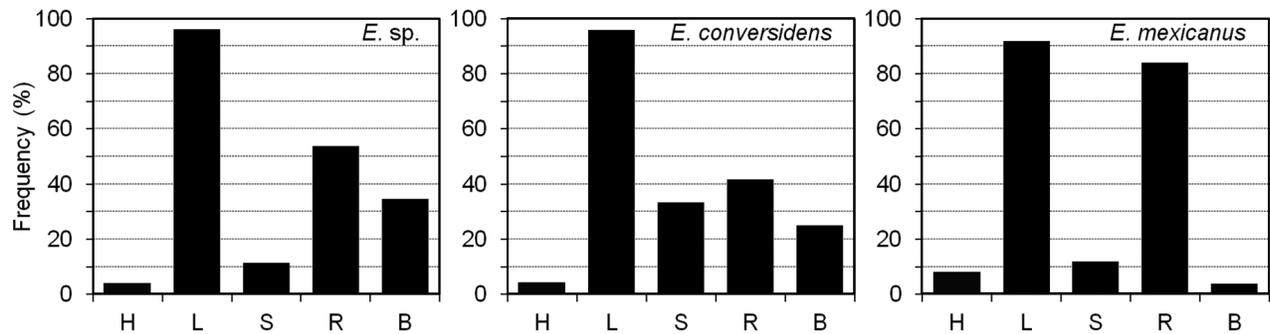


Figure 5. Histograms showing the distribution of the mesowear variables for each equid species. Abbreviations: H = high occlusal relief, L = low occlusal relief, S = sharp cusps, R = round cusps, B = blunt cusps.

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

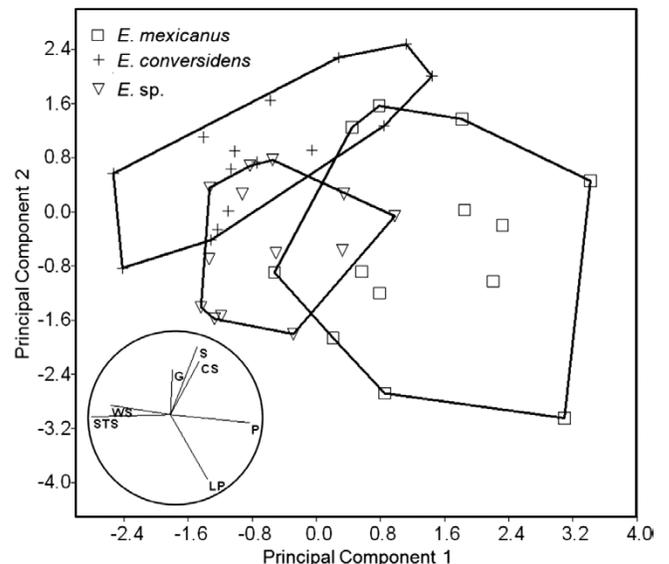


Figure 6. Plot of the first two principal components resulting from PCA of the microwear data (Table 2A of the Appendix) for the Cedral equid species. The vectors shown in the inset (circle) depict the relative contribution of each microwear variable to the components. Abbreviations: S = average number of scratches, P = average number of pits, CS = average score of cross scratches, LP = average score of large pits, G = average score of gouges, WS = average number of wide scratches, STS = average scratch texture score.

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.

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	1.98	1.68	1.07	0.90	0.56
% variance	28.23	24.06	15.30	12.87	8.05
% cum. variance	28.23	52.29	67.59	80.46	88.51
<i>Factor loadings</i>					
S	0.19	0.58	-0.12	-0.16	0.74
P	0.58	-0.07	0.41	0.07	0.15
CS	0.20	0.45	0.42	-0.46	-0.51
LP	0.27	-0.55	0.41	0.03	0.27
G	0.01	0.38	0.23	0.86	-0.13
WS	-0.44	0.08	0.60	-0.11	0.19
STS	-0.57	-0.02	0.26	-0.02	0.19

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, WS = average number of wide scratches, STS = average scratch texture score.

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 $\delta^{13}\text{C}$ values, -2.1‰ for *E. conversidens*

and -2.7‰ for *E. sp.*, fall close to the average value ($\sim 0.5\text{‰}$) of extant C_4 grazers (Koch *et al.*, 1998; Hoppe and Koch, 2006); although their range, particularly in *E. sp.*, extends into the $\text{C}_3\text{-C}_4$ 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 $\text{C}_3\text{-C}_4$ mixed feeder, with a mean $\delta^{13}\text{C}$ value of -4.9‰ (Pérez-Crespo *et al.*, 2009). This may indicate that it fed on a combination of C_4 grasses and C_3 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 C_3 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 C_3 grazers tend to have occlusal enamel surfaces covered by numerous, fine scratches, suggesting that this attribute could be used to differentiate C_3 from C_4 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 3. Summary of microwear data for the Cedral equids.

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

n = number of specimens, S = average number of scratches \pm standard deviation, P = average number of pits \pm 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.

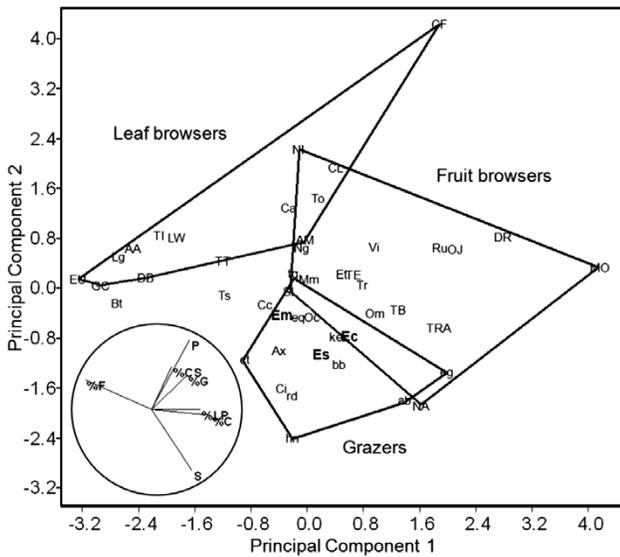


Figure 7. Plot of the first two principal components resulting from PCA of the microwear data in Table 3 for the fossil horses and the extant ungulate dataset published by Solounias and Semprebon (2002). Each data point is the average for a species sample. The vectors shown in the inset (circle) depict the relative contribution of each microwear variable to the components. Abbreviations: S = average number of scratches, P = average number of pits, % 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. Fossil horses: *Equus mexicanus* (Em), *E. conversidens* (Ec), *E. sp.* (Es). Fruit dominated browsers: *Cephalophus dorsalis* (DR), *Cephalophus natalensis* (NA), *Cephalophus niger* (NI), *Cephalophus silvicultor* (SL), *Moschus moschiferus* (MO), *Okapia johnstoni* (OJ), *Tragulus* spp. (TRA), *Tapirus bairdii* (TB), *Tapirus terrestris* (TE). Leaf browsers: *Alces alces* (AA), *Antilocapra americana* (AM), *Camelus dromedarius* (CL), *Camelus ferus* (CF), *Diceros bicornis* (DB), *Giraffa camelopardalis* (GC), *Litocranius walleri* (LW), *Tragelaphus eurycerus* (EU), *Tragelaphus imberbis* (TI), *Tragelaphus strepsiceros* (TT). Seasonal-regional mixed feeders: *Axis axis* (Ax), *Boselaphus tragocamelus* (Tr), *Budorcas taxicolor* (Bt), *Capricornis sumatraensis* (Ca), *Eudorcas thomsonii* (Et), *Lama glama* (Lg), *Muntiacus muntjak* (Mm), *Nanger granti* (Ng), *Ovis canadensis* (Oc), *Taurotragus oryx* (To), *Tragelaphus scriptus* (Ts), *Vicugna vicugna* (Vi). Meal-by-meal mixed feeders: *Capra ibex* (Ci), *Cervus canadensis* (Cc), *Ovibos moschatus* (Om), *Rusa unicolor* (Ru). Grazers: *Alcelaphus buselaphus* (ab), *Bison bison* (bb), *Connochaetes taurinus* (ct), *Equus grevyi* (eg), *Equus quagga* (eq), *Hippotragus niger* (hn), *Kobus ellipsiprymnus* (ke), *Rucervus duvaucelii* (rd), *Tetracerus quadricornis* (tq).

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

Table 4. Eigenvalues and factor loadings for the first five principal components resulting from PCA of the microwear data in Table 3 and the extant ungulate dataset published by Solounias and Semprebon (2002).

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	2.43	1.38	1.13	0.93	0.52
% variance	34.77	19.76	16.17	13.35	7.44
% cum. variance	34.77	54.53	70.70	84.05	91.49
<i>Factor loadings</i>					
S	0.33	-0.54	0.31	0.28	0.35
P	0.31	0.63	-0.25	0.03	-0.00
% CS	0.16	0.38	0.66	-0.34	0.47
% LP	0.40	0.00	-0.58	0.07	0.58
% G	0.29	0.30	0.27	0.73	-0.27
% F	-0.54	0.26	-0.02	0.06	0.28
% C	0.48	-0.05	0.02	-0.51	-0.41

S = average number of scratches, P = average number of pits, % 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.

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.

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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.

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