1  **Dietary adaptability of Late Pleistocene *Equus* from West Central Mexico**

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**Abstract**

Most of the Pleistocene species of *Equus* from Mexico have been considered to be grazers and highly specialized on the basis of their craniodental features, and therefore analogous to their modern relatives from an ecological point of view. Here we rely on dental wear analyses of three different species of Rancholabrean *Equus* that exhibit differences in limb proportions and body mass and occurred in two different habitats in order to test whether species exhibited more heterogeneous dietary capabilities compared to modern horses. Overall, and although our analyses show grazer lifestyles, there is a significant degree of dietary variability among taxa according to the site, apparently as a response to differences in climate and environmental conditions, with intermediate feeding preferences on the basis of the last items consumed during the last days prior to death in some cases. Accordingly, fossil *Equus* might have been more sensitive to different environments and diverse in terms of dietary preferences, thus incorporating a higher proportion of browse vegetation if necessary, than their modern relatives. These results highlight the dietary plasticity of certain fossil species, and evidence the caution that should be paid when reconstructing the ecology of fossil species using their modern relatives as analogues.

**Keywords:** Equids, Dental mesowear/microwear, Palaeoecology, environment change, Rancholabrean.

**1. Introduction**

The horses of the genus *Equus* are the end members of a family with a wide geographic distribution and high diversity of genera and species (MacFadden, 2005). Several species of *Equus* inhabited large parts of North America during the late Pleistocene (Winans, 1989) and became extinct around 10,000 years ago in the New World (MacFadden, 2005).

48    Overall, extant *Equus* have a variable body mass, which reflects adaptation to different

49    climates and habitats (from semi-desert habitats to high mountain ecosystems) (Alberdi *et*

50    *al*., 1995; Rubenstein, 2011), and they have high-crowned (or hypsodont) dentitions

51    (Damuth and Janis, 2011), and primarily grazer diets (Schulz and Kaiser, 2012), although

52    leaves of trees and shrubs constitute a significant part of the diet of some populations

53    (Janzen, 1981, Berger, 1986, Mohr, 1971).

54    Pleistocene *Equus* have been mainly considered to be grazer species based on their

55    craniodental features and their dental wear signatures (Bravo-Cuevas *et al*., 2011;

56    Mihlbachler *et al*., 2011), and they are therefore commonly used as indicators of open and

57    arid ecosystems (MacFadden, 2005). However, several works based on dental mesowear

58    (Kaiser and Franz-Odendaal, 2004) and stable isotope signatures (Pérez -Crespo *et al*.,

59    2009) have asserted that some horse *Equus* from the Pleistocene exhibited mixed feeder

60    (both browsing and grazing) diets.

61    *Equus* were widely distributed in Mexico during the Rancholabrean, and occupied

62    various morphotectonic provinces and different environments (Ferrusquía-Villafranca *et*

63    *al*., 2010). This lead us to think that the species of horses of late Pleistocene of Mexico

64    should have a degree of dietary variance like some extant horses, that would reflecting the

65    environmental conditions of the sites where they used to feed, and therefore prove that the

66    equids do not have to be correlated with some a specific diet or habitat.

67    Interestingly, in West Central Mexico there are two fossil localities exhibiting an

68    impressive variability of *Equus* species (*Equus cedralensis* Alberdi *et al*. (2014) with small

69    size and slender limbs, *E. conversidens* Owen (1869) with medium size and robust limbs

70    and *E. mexicanus* Hibbard (1955) large size and robust limbs) that are similar in age

(Rancholabrean) and location, but highly different from a palaeoenvironmental point of view. In this respect, one of the fossil localities implies the existence of a palaeo-lake and is characterized by an heterogeneous geomorphology and different ecological niches, while the other concerns a fluvial system and a more homogeneous geomorphology and habitats (Marín-Leyva, 2011). Accordingly, we consider this scenario as an excellent example for evaluating the variability of the genus from a palaeoecological perspective. Hereby it is tested whether *Equus* body mass and dietary capabilities are always homogeneous or significantly differ according to environmental conditions.

## 2. Material and Methods

### 2.1. Geographical location, fossil sites information and data collection

The material here studied belongs to the Late Pleistocene sites of La Cinta-Portalitos (LC-PT) (Cuitzeo Basin) and La Piedad-Santa Ana (LP-SA) (Lerma River Basin), both located in West Central Mexico, and only separated by around 100 kilometers (Figure 1). Vertebrates from these sites are dated as Rancholabrean NALMA (c.a. 160 Ka to 9.5 Ka, Bell *et al*., 2004). The faunal assemblage is varied and extensive, with numerous vertebrate taxa (also including amphibians and reptiles) of which 14 are large mammals. The perissodactyls are the most numerous and important components of the terrestrial ecosystems, followed by proboscideans, artiodactyls, and rodents.

Fossils from LC-PT (Fig. 1a) belong to fluvial-lacustrine facies. The associated large fauna includes the proboscidean *Mammuthus columbi*, the bovid *Bison* sp., the camelids

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*Camelops hesternus* and *Hemiauchenia* sp*.,* the cervid *Odocoileus virginianus*, and the tayasuid *Platygonus* sp. Other fauna includes the rodents *Microtus* sp*., Neotoma* sp*., Sygmodon* sp. and *Spermophilus* sp., the reptiles *Elaphe guttata* and the amphibians *Lithobates pipiens* and *Ambystoma* sp. (García-Zepeda, 2006; Pérez and Godínez, 2007; Marín-Leyva, 2008, 2011; Plata-Ramírez, 2012; Díaz-Sibaja, 2013; Gutiérrez-Bedolla, 2014). The material from LP-SA (Fig. 1b) belongs to fluvial deposits, originated from the interposition of fine- and medium-sized sediments. There is also the presence of the proboscidea *Mammuthus columbi*, the bovid *Bison sp.,* the camelids *Camelops hesternus* and *Hemiauchenia* sp., and the cervids *Odocoileus virginianus* and *Cervus elaphus canadensis* (Plata-Ramírez, 2012; Díaz-Sibaja, 2013; Gutiérrez-Bedolla, 2014). A similar faunal composition is thus evident in both sites, a fact that contrasts with the different (lake and fluvial, respectively) environments that they represent. Several palaeoenvironmental studies (including analyses of palynoflora and diatoms) have been carried out in LC-PT (Israde-Alcántara *et al*., 2002, 2010; Caballero *et al*., 2010), but no palaeoenvironmental reconstructions exist of LP-SA.

Our study was applied to the dentition (for mesowear and microwear analyses, and hypsodonty evaluation) and the skeleton (for body mass inferences) of three species of the horse *Equus* (*Equus cedralensis* Alberdi *et al*., 2014, *E. conversidens* Owen, 1869 and *E. mexicanus* Hibbard, 1955). Thus, a total of 96 dental (13 upper fourth premolars [P4], 16 upper first molars [M1], 28 upper second molars [M2], 31 upper third molars [M3], and 8 lower third molars [m3]), and 21 limb remains (4 third metacarpals [MCIII] and 17 first phalanxes of the central digit [1FIII]) were selected for analysis (Table 1). The material analyzed is housed at the Facultad de Biología of the Universidad Michoacana de San

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118    Investigación (La Piedad Cabadas, Michoacán, México).

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120    *2.2. Body mass estimation*

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122    Because body size is somewhat related to with ecological aspects, such as food

123    resources, type of habitat, and density, dispersion and demography of populations (Brown,

124    1995), we estimated the body mass of the three species of horses from both sites (except for

125    *E. mexicanus* from LC-PT, since there are not sufficient remains for infer its mass)

126    following Alberdi *et al*. (1995) and using the distal minimal depth of the lateral condyle of

127    the third metacarpal (MCIII) and the proximal depth of the first phalanx of the central digit

128    (1FIII) (Eisenmann *et al*., 1988).

129

130    *2.3. Proxies for dietary characterization*

131

132    There are several methods for inferring a species diet, and thus reconstructing the

133    environmental and climatic conditions of the ecosystems where past ungulates occurred.

134    Here we use the degree of hypsodonty of a species, since it is somewhat related with the

135    foods and/or with the abrasiveness of the exogenous particles consumed (Janis, 1988;

136    Damuth and Janis, 2011). As non-morphological methods, dental meso- and microwear

137    analyses provide more direct information on the properties of the foods consumed

138    independently from adaptation (Fortelius and Solounias 2000; Solounias and Semprebon

139    2002, Solounias *et al*., 2000). These latter methodologies are also focused on teeth, which

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140 tend to dominate fossil assemblages and provide short- (hours, days) and long-term (weeks,

141 months) dietary signals of the species, and have previously been applied to fossil horses

142 (Kaiser *et al*., 2000; Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003; Kaiser and

143 Franz-Odendaal, 2004, Rivals and Athanassiou, 2008; Bravo-Cuevas *et al*., 2011;

144 Mihlbachler *et al*., 2011; Schulz and Kaiser, 2012). Other non-morphological methods

145 commonly used for palaeodietary assessment are those that use the stable isotope

146 geochemistry, such as stable carbon isotope ratios that are related to the photosynthetic

147 pathways $C_3$, $C_4$ and CAM of the plants, usually obtained in fossil tooth enamel (Koch *et*

148 *al*., 1998; MacFadden *et al*., 1999). Here we are concerned in the use in tandem of tooth

149 micro- and mesowear (see further explanation of the methods below) in order to provide

150 insights into both the short- (hours, days) and long-term (weeks, months) diets of fossil

151 horses form West Central Mexico.

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153 *2.3.1. Hypsodonty index*

154     Also, and in order to provide data on the diet and abrasiveness of the items ingested, we

155 measured crown height in fossil equids according to the index proposed by Janis (1988).

156 The hypsodonty Index (HI) for the lower third (unworn) molars was determined as m3

157 height divided by m3 width. As a result, the term brachydont is restricted to ungulates with

158 an index of less than 1.5; the term mesodont is here applied to ungulates with an index

159 ranging between 1.5 and 3; the term hypsodont is applied to those species with an index

160 greater than 3 (and highly hypsodont to species with indices of a greater value than 4.75).

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162 *2.3.2. Dental Mesowear*

163    Mesowear is a method developed by Fortelius and Solounias (2000) to provide insights

164    on the abrasiveness of the items eaten (both foods and exogenous particles as dust and grit)

165    and characterize dietary traits of species (Fortelius and Solounias, 2000; DeMiguel *et al.*,

166    2008, 2011, 2012; Kaiser, 2003; Kaiser *et al.*, 2003; Rivals and Semprebon, 2006; Rivals *et*

167    *al.*, 2007; Semprebon and Rivals, 2007, 2010), and is based on the physical properties of

168    food as reflected in the relative amounts of wear that they cause on the teeth (Fortelius and

169    Solounias, 2000). In selecting specimens, preference was given to M2 if available. If not,

170    M1 and M3 (and P4 if necessary) dental positions were selected according to Kaiser and

171    Solounias (2003). Teeth of medium height were used to avoid change to the mesowear

172    signature caused by ontogenetic-age (Rivals *et al.*, 2007). We evaluated the mesowear

173    traditional variables, occlusal relief (classified as either high or low) and cusp shape (scored

174    as sharp, rounded, and blunt according to their degree of facet development). Then,

175    following Kaiser *et al.* (2009), traditional variables were converted to a single mesowear

176    score (MS) as follows: A combination of high relief and sharp cusps was assigned a score

177    of 0; a combination of high relief and rounded cusps was assigned a score of 1; a

178    combination of low relief and sharp cusps was assigned a score of 2; a combination of low

179    relief and rounded cusps was assigned a score of 3; and a combination of low relief and

180    blunt cusps was assigned a score of 4. Essentially, low abrasion mesowear signatures are

181    related to browser species whereas that high abrasion patterns are typical of a grazer diet.

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183    *2.3.3. Dental Microwear*

184    Microwear is the result of the abrasion of a tooth´s surface by food items and exogenous

185    abrasives consumed. The method applied in this study was performed following the

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procedure developed by Solounias and Moelleken (1992), which has been widely used for dietary research. Microscopic features (scratches and pits) were examined at 500x magnification using an Environmental Scanning Electron Microscope (ESEM). In order to increase sample size, we abandoned the original microwear method, limited to the second upper (M2) and lower (m2) molars, and micrographs of the occlusal enamel surfaces of the investigated teeth were taken in the paracone enamel band on the mesial area of the prefossette of all available P4, M1, M2 and M3, following Rivals *et al*. (*in press*), in a 0.20 mm$^2$ delimited area. We extended sample size to all these specimens because of taphonomic alterations in the enamel bands of most of the available M2 that prevented for suitable analyses of the microscopic marks. Microwear features were directly categorized on the basis of the ratio length/width (pits: ratio= 4, scratches: 4<ratio<100), and analyzed with Microwear 4.02 software (Ungar, 2002) by a single author (AHM-L) in order to avoid inter-observer error. The number of scratches and pits were transformed into a density score in order to simplify the comparison with other taxa (Rivals and Deniaux, 2003). Overall, a high density of scratches usually reflects abrasive diets (such as those of extant grazers), while a high density of pits reveals low abrasive diets (such as those of extant browsers).

*2.4. Comparative samples*

Data reported in Janis (1988) was used for the HI of the extant species. The mesowear pattern of fossil species was investigated through comparisons with a database compiled by Fortelius and Solounias (2000) for 54 living species with well-known diets. Alternative "conservative" (14 browsers, 28 mixed feeders, and 12 grazers) and "radical" (18 browsers,

209    17 mixed feeders, and 19 grazers) dietary classifications were used to accommodate cases

210    where dietary information is controversial or unclear (see DeMiguel *et al*. (2011) for further

211    explanation). With regard to microwear, the comparative extant database of Solounias *et al*.

212    (2000) was followed for reference. This dataset includes 30 extant species with well-known

213    diets: 7 leaf browsers; 3 fruit browsers; 7 grazers 9 seasonal; and 4 non-seasonal (or meal

214    by meal) mixed feeders. The results of this study were compared with those derived from

215    other authors for other Pleistocene fossil horses: *Equus capensis* from Elandsfontein (South

216    Africa, 0.4-0.7 Ma) (Kaiser and Franz-Odendaal, 2004), *Equus mosbachensis* from the

217    Arago Cave (France, 0.45 Ma) (Kaiser and Franz-Odendaal, 2004), and *Equus*

218    *conversidens* from five different sites from Hidalgo (México, 0.16-0.01 Ma) (Bravo-Cuevas

219    *et al*., 2011).

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221    *2.5. Statistical procedures*

222

223    Chi-square tests were applied to estimate differences in body mass between fossil taxa.

224    For mesowear analysis, bivariate diagrams were made using the mesowear scores and the

225    HI of 54 and 49 extant species for comparison with fossil horses. For the microwear

226    analysis, a bivariate diagram was made using the density score of scratches and pits of 30

227    extant species to compare with extinct species of *Equus*. For meso- and microwear

228    analyses, hierarchical cluster analyses were performed using the Ward´s method and the

229    Euclidean distance and the variables %high occlusal relief, %round cusps and % blunt

230    cusps for mesowear and scratch and pit density for microwear. Discriminant analyses was

231    carried out using the same variables, leaving as outgroups this study´s populations. For the

232  mesowear analysis the conservative and radical classification was used as a group category.

233  For microwear we used the categories: browser (leaf browsing, fruit browsing); grazer;

234  seasonal mixed feeders and non-seasonal mixed feeders.

235

236  **3. Results**

237

238  Body mass, hypsodonty index, and meso- and microwear results of fossil species are

239  given in Table 1 (and supplementary data).

240  *3.1. Body mass estimation*

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242  *Equus cedralensis* has an estimated body mass of 126 kg (LP-SA) and 145.5 kg (LC-PT)

243  using the MCIII and 1FIII respectively; *E. conversidens* of 229.5 kg (LP-SA) and 307.9 kg

244  (LC-PT) using the MCIII and 1FIII respectively; and *E. mexicanus* of 476.7 kg (LP-SA)

245  using the 1FIII.

246  According to the statistical tests, there is no significant differences in body mass

247  between the populations of *E. cedralensis* ($X^2$, p=0.7324) from LC-PT and LP-SA, and the

248  populations of *E. conversidens* ($X^2$, p=0.3798) from both sites. In contrast, there are

249  significant differences in body mass between *Equus cedralensis*, *E. conversidens* and *E.*

250  *mexicanus* ($X^2$, p=0.0006). This indicates that the population of each species displayed the

251  same body mass in each fossil site and different body mass between species was found.

252  Comparison to the body mass of extant horses shows, we found that *E. cedralensis* was a

253  different size to that of any extant horse, whereas that *E. conversidens* exhibits a similar

254  size to those of *E. zebra* (260 kg), *E. africanus* (220 kg), *E. hemionus* (250 kg), *E. kiang*

255  (300 kg) and *E. przewalskii* (350 kg) (Alberdi *et al*., 1995). Finally, *E. mexicanus* has a

256  similar body mass to both *E. grevyi* (400 kg) and *E. quagga* (400 kg) (Alberdi *et al*., 1995).

257

258  *3.2 Hypsodonty index*

259

260  The mean hypsodonty value (HI) obtained is 5.15 for *Equus cedralensis*, 5.99 for *E.*

261  *conversidens* and 5.06 for *E. mexicanus* from LC-PT, and 5.68 for *E. mexicanus* from LP-

262  SA (Table 1), which indicate highly hypsodont teeth for all the species. It must be noted

263  that there were no available m3s to calculate the HI for *E. cedralensis* and *E. conversidens*

264  from LP-SA.

265

266  *3.3. Dental mesowear*

267

268  In terms of mesowear signature, all the taxa analyzed show different patterns of abrasion

269  in their teeth. Overall, all the *Equus* species exhibit wear patterns dominated by low relief

270  and rounded cusps. Despite this general trend, a more heterogeneous mesowear for the

271  species from LC-PT, is observed which points towards a somewhat high dietary flexibility

272  exhibited by the species in this site.

273  The population of *Equus cedralensis* from LC-PT (43.2%L, 62.2%r, 13.5%b and

274  1.72MS) has a lower value of low relief and predominant rounded cusps, and a lower

275  mesowear score than its relative from LP-SA (78.9%L, 78.9%r, 5.3%b and 2.47MS) (Table

276  1). As such, the former shows similarities in mesowear with like the extant mixed feeder

277  *Saiga tatarica* and the grazers *Alcelaphus buselaphus* and *Connochaetes taurinus*, whereas

278    the latter points towards a higher proportion of abrasives in the diet, thus suggesting

279    similarity with the grazer *Damaliscus lunatus*. *Equus conversidens* (71.4%L, 67.9%r,

280    10.7%b, and 2.32MS) from LC-PT displays mesowear with a predominance of both low

281    relief and rounded cusps (Table 1), suggesting similarity to *D. lunatus*. In contrast the

282    population from LP-SA (100%L, 65%r, 20%b and 3.04MS) exhibits higher values of low

283    relief and blunt cusps, and a higher mesowear score, thus resembling the extant grazer

284    *Ceratotherium simum.* As such, *Equus conversidens* from LC-PT also exhibits lower levels

285    of abrasion than its relative from LP-SA. Finally, *Equus mexicanus* from LC-PT (92.3%L,

286    38.5%r, 38.5%b and 3.01MS) has a very high value of low relief, blunt cusps, and

287    mesowear score (Table 1), similar to the grazers *E. quagga* and *E. grevyi*. In contrast, its

288    relative from LP-SA (86.7%L, 66.7%r, 13.3%b, and 2.71MS) is characterized by a

289    predominance of low relief and rounded cusps, and has mesowear more similar to that of *D.*

290    *lunatus*. In this occasion, *Equus mexicanus* seems to have exhibited a more abrasive diet in

291    LC-PT than in LP-SA.

292    When the mesowear score is analyzed in combination with the type of diet exhibited

293    today by different ungulates (Fig. 2a), *E. cedralensis* from LC-PT overlaps with both extant

294    grazers (*Alcelaphus buselaphus*, *Connochaetes taurinus*) and intermediate species more

295    inclined to grazing (*Rucervus duvaucelii*, *Saiga tatarica* and *Axis axis*), whereas the

296    remaining extinct *Equus* clearly fall into the grazer domain. The figure also depicts that

297    species from LC-PT cover a wider range of relative abrasiveness than those from LP-SA.

298    The bivariate diagram of hypsodonty index and mesowear score (Fig. 2b) reveals diet-

299    related patterns in fossil and extant ungulates. More specifically, and among extant horses,

300    *E. burchelli* and *E. grevyi* have a mesowear score of 3 and 2.93 and HI of 5.83 and 5.8,

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301  respectively, indicating high levels of abrasion in diet and extremely hypsodont teeth.

302  Among fossil horses, *E. cedralensis* from LC-PT displays a mesowear score of 1.72 and

303  highly hypsodont teeth, with an HI of 5.15, hereby being similar in these attributes to the

304  mixed feeder *Saiga tatarica* and the grazers *Alcelaphus buselaphus* and *Connochaetes*

305  *taurinus*, and indicating therefore a somewhat less abrasive diet than *E. burchelli* and *E.*

306  *grevyi*. The populations of *E. conversidens* from LC-PT and *E. mexicanus* from both LC-

307  PT and LP-SA show mesowear scores ranging from 2.32 to 2.71, and highly to extremely

308  hypsodont teeth, with HI from 5.06 to 5.99, thus overlapping with the extant grazers

309  *Damaliscus lunatus, Ceratotherium simum* and the zebras *E. grevyi* and *E. quagga*, and

310  indicating highly abrasive diets.

311  *3.4. Dental Microwear*

312

313  Overall, the *Equus* species from LC-PT displays a microwear comprising of high

314  scratching and intermediate pitting, similar to extant non-seasonal mixed feeders, while

315  horses from LP-SA show a moderately high scratching and low pitting incidences, thereby

316  more overlapping with extant grazers. All these facts indicate a more variable and less

317  abrasive diet in LC-PT and a more homogeneous and abrasive diet en LP-SA.

318  More specifically, the population of *E. cedralensis* from LC-PT shows enamel surfaces

319  comprised of high scratching (1977 scratches/mm$^2$) and intermediate pitting (350

320  pits/mm$^2$), similar to those of the extant non-seasonal mixed feeders *Rusa unicolar* and

321  *Capra ibex*. In contrast, *E. cedralensis* from LP-SA has less intensively striated enamel

322  surfaces (1452 scratches/mm$^2$) and intermediate pit incidences (336 pits/mm$^2$), similar to

323  the signatures exhibited by the grazer *Bison bison*. *E. conversidens* from LC-PT also shows

324 high striation (1906 scratches/mm$^2$) and intermediate pitting (422 pits/mm$^2$), thus

325 resembling the extant non-seasonal mixed feeders *Cervus elaphus canadensis* and *Capra*

326 *ibex*. Teeth of *E. conversidens* from LP-SA are characterized by a moderately high

327 scratching (1439 scratches/mm$^2$) and low pit incidences (210 pits/ mm$^2$), similar to the

328 grazer *Hippotragus niger*. Finally, teeth of *E. mexicanus* from LC-PT indicate a high

329 scratching (1808 scratches/mm$^2$) and an intermediate pitting signature (350 pits/mm$^2$); a

330 microwear pattern similar to that of the non-seasonal mixed feeder *Capra ibex*.

331 Examination of *E. mexicanus* from LP-SA shows moderately high scratching (1420

332 scratches/mm$^2$) and low pitting (265 pits/mm$^2$), more similar to the grazer *Bison Bison*.

333 Figure 2c shows a bivariate plot of the densities score (scratches vs. pit densities) for

334 extant ungulates and extinct horses. It shows that the averages of scratches and pits are

335 greater (specially the former) in *Equus* from LC-PT. This fact situates the equids from LC-

336 PT in the non-seasonal mixed feeder domain, and the populations from LP-SA within the

337 grazer domain.

338

339 *3.5. Statistical Analyses*

340

341 The cluster analysis based on dental mesowear signatures (Fig. 3a) yields two main

342 clusters separating browsers and mixed feeders (B+M) from grazers (G). Within this former

343 group, two clear tendencies are observed; one consisting of low levels of abrasion and

344 associated with browsing diets (subcluster B), the other consisting of intermediate levels of

345 abrasives and mixed diets (subcluster M). Extinct *Equus*, with the exception of *E. capensis*

346 from South Africa, are grouped with gazer species in cluster G. *E. cedralensis* from LC-PT

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347    is grouped in subcluster G1, together with two extant mixed feeders (*Saiga tatarica*,

348    *Rucervus duvaucelii*) and two grazers (*Alcelaphus buselaphus* and *Connochaetes taurinus*).

349    *E. mexicanus* from LC-PT is included in subcluster G3, together with extant *B. bison*, and

350    the African zebras (*E. grevyi* and *E. quagga*), and fossil *E. conversidens* from (five deposits

351    from Hidalgo State), which are characterized by very high levels of abrasion and pure

352    grazing diets. The remaining fossil *Equus* clump together with other grazers (e.g, *D.*

353    *lunatus*, *C*. *simum*, *A*. *buselaphus*) in subcluster G2, thus displaying somewhat lower levels

354    of abrasives in their diets.

355       The cluster analysis based on the microwear signatures (Fig. 3b) yields two main cluster

356    separating browsers and seasonal mixed feeders (B) from grazers and non-seasonal mixed

357    feeders (G). In this former group, two clear tendencies are observed, one consisting in low

358    scratches associated with browsing diets (B1), the other consisting of intermediate levels of

359    scratches associated with seasonal mixed feeder diets (B2 and B3). All the extinct *Equus*

360    are grouped in the cluster G, which is divided into two subclusters; one with high levels of

361    scratches and low levels of pits, thereby associated with grazer diets (G1), and the second

362    subcluster showing higher levels of striations and intermediate to high levels of pits,

363    thereby related to non-seasonal mixed feeder habits (G2). All the species from LP-SA are

364    grouped in G1 with extant grazers, whereas populations from LC-PT appear clustered in G2

365    with non-seasonal mixed feeders.

366       The discriminant analyses of mesowear provided a satisfactory dietary discrimination,

367    with 71.93% of extant taxa correctly classified according to the conservative classification

368    (Wilks's lambda, Value 0.2923464 p>0.0001), and 75.44% to the radical (Wilks's lambda,

369    Value 0.3279821 p>0.0001). The analyses classified all the fossil *Equus* as grazers (Table

370    2, Fig. 4a and 4b).

371    There was also a very high discrimination for the microwear analysis, with a correct

372    classification rate of 93.33% (Wilks's lambda, Value 0.0805682 p>0.0001). Results show a

373    wider spectrum of dietary assignments amongst fossils according to the last items ingested,

374    with Equus from LC-PT being classified as non-seasonal mixed feeders, and *Equus* from

375    LP-SA being considered as grazers (Table 2, Figure 4c).

376

377    **4. Discussion**

378

379    Results obtained for the fossil species of *Equus* here analyzed show different limb

380    proportions (Marín-Leyva, 2011) and significant body mass differences, as observed today

381    in the sympatric horses *E. grevyi- E. africanus* and *E. grevyi -E. guagga* in West Africa,

382    and *E. zebra-E. guagga* in Southwest Africa. Accordingly, different ecological preferences

383    (Forsten, 1998; Alberdi *et al*., 1995) and/or microhabitats could be also deduced for *E.*

384    *cedralensis, E. conversidens* and *E. mexicanus* in West Central Mexico.

385    Further, data and argument from two independent methodologies of dietary assessment

386    and morphological traits (hypsodonty analyses) conclude that fossil *Equus* here analyzed

387    were mainly grazers. This additionally can be deduced from the mesowear signature and

388    their highly hypsodont cheek teeth. However, there is a significant degree of variation

389    shown in the dental wear features across the *Equus* sample. Species were not dependent on

390    a limited type of vegetation and, consequently, were able to exploit different food

391    resources. In this regard, and if compared with the highly specialized ecology of extant

17

392    *Equus*, fossil horses were somewhat diverse in terms of foods ingested and had a significant

393    eclectic behavior according to the site in where they inhabitated, which is confirmed by the

394    microwear signature, a more sensitive measure of fluctuations in feeding related to

395    seasonality.

396    Hypsodonty values indicate highly hypsodont dentitions for all the fossil taxa analyzed

397    (Table 1), showing similarity to extant grazers *Alcelaphus buselaphus*, *Damaliscus lunatus*,

398    *Equus quagga* and *Equus grevyi*, among others.

399    The mesowear analysis indicates that the fossil horses here analyzed had highly abrasion

400    dominated diets, similar to those exhibited today by most extant grazers. However, we

401    found a certain degree of variability in the mesowear signature of the species, with taxa

402    from LC-PT having more heterogeneous patterns than those from LP-SA. As such, the

403    locality of LC-PT could have accommodated both grazers (*E. conversidens* and *E.*

404    *mexicanus*) and either more variable grazers or grass-dominated mixed feeders (*E.*

405    *cedralensis*). In LP-SA, all the species show a more homogeneous mesowear, and highly

406    specialized (grazing) diets with a stronger emphasis on abrasive items.

407    These differences are even more pronounced when the dental microwear is observed,  as

408    more eclectic feeding patterns were exhibited by *Equus* species from LC-PT, with taxa

409    displaying diets more similar to those of extant non-seasonal mixed feeders. In contrast,

410    *Equus* species from LP-SA apparently relied more strongly on grasses and abrasives shortly

411    prior to death.

412    Differences in signatures between mesowear and microwear have been reported

413    previously for other extinct ungulates (e.g. Rivals and Semprebon, 2006; Merceron *et al.*,

414    2007; Rivals *et al.*, 2008, Rivals *et al.*, 2010; Barrón-Ortiz *et al.*, 2014), since these two

methods reflect dietary preferences at different scales; mesowear shows the overall abrasive nature of the diet over a relatively long period of time (months to years), whereas microwear provides information on the food consumed shortly prior to an individual´s death, a phenomenon referred to as the "Last Supper Effect" (Grine, 1986). We assume therefore that the variation in wear signatures (both among species belonging to the same locality and also between localities) could be attributed to the display of different diets (i.e., dietary plasticity) and levels of non organic abrasives (grit and dust). This point towards a certain flexibility and adaptive ability in fossil *Equus* from West Central Mexico, probably higher than that exhibited today by species of the genus. Such a heterogeneous behavior is attributable to 1) a more effective partitioning of the vegetal resources for avoiding competition, and 2) differences in the environmental conditions (and seasonal fluctuations) of the localities here investigated, since they represent two very distinct ecosystems. These same facts have been observed for other numerous genera of herbivorous mammals, when the extinct taxa exhibited more diverse palaeodiets and palaeoecology than their extant relatives. Such mammals include, amongs others, Pleistocene populations of *Bison* from North America (Rivals and Semprebon, 2011), Miocene giraffids (Solounias *et al*., 2000), and Camelidae and Antilocapridae (Semprebon and Rivals, 2007, 2010).

Since diets of fossil artiodactyls and perissodactyls tend to reflect habitats (DeMiguel *et al*., 2010, 2011), the wear signals and assignments here obtained can be used as proxies for the palaeoenvironmental reconstruction of the sites. Despite this link between diet (and dental wear patterns) and habitat is generally accepted and widely used in palaeoecological studies, they are not always directly related, and some inconsistencies exist in this respect. For example, and because grass and browse material can be available in open and closed

438    habitats in some ecosystems, it is possible to obtain a dental wear signal related with

439    grazing in some closed-habitats, and a pattern associated with browsing in open

440    environments. In order to solve this, a very successful way to establish closed vs. open

441    habitats is to perform stable isotope studies in the teeth of the ungulate community (Pérez–

442    Crespo *et al*., 2009; 2014) and/or studies of the palaeovegetation of each fossil locality.

443    Because a study of the stable isotopes of fossil *Equus* teeth of both fossil localities is in

444    progress by the authors, we have reinforced our results obtained from dental wear analyses

445    with additional data from pollen assemblages of the fossil localities from previous

446    published works (Israde-Alcántara *et al*., 2010).

447        Overall, two possible different types of feeding styles in LC-PT are represented (grazer

448    and non-seasonal mixed feeder), which are indicative of a mixture of components,

449    including abrasive grass and herbs, and non organic particles, and more soft browse

450    elements such as shrub and trees. This allows the reconstruction LC-PT as a mixed (both

451    closed and open area) ecosystem, with a strong component of environmental heterogeneity.

452    This finding is in concordance with its varied faunal association and a wide range of

453    feeding styles obtained, as reflected by the record of forest dwelling browsers such as

454    *Odocoileus* (Koch *et al*., 1998), grazer taxa adapted to more open areas such as *Bison*

455    (Koch *et al*., 2004), and ecologically intermediate taxa such as *Mammuthus columbi*,

456    *Camelops* and *Hemiauchenia* (Koch *et al*., 1998; Feranec and MacFadden, 2000; Feranec,

457    2007; Higgins and MacFadden, 2009; Semprebon and Rivals, 2010, Pérez-Crespo *et al*.,

458    2012, Gutiérrez-Bedolla, 2014). Further, the presence of amphibians registered by Pérez

459    and Godínez (2007) suggests an area with permanent water. The results shown here from

460    wear patterns are also consistent with vegetation data, as pollen studies (Israde-Alcántara *et*

*al*., 2010) from the site show a great variation in the floral composition with the presence of grasses, herbs and shrubs (Poaceae, *Cheno-Am*, *Ambrosia*, Asteraceae, *Cirsium* and *Thalictrum*) and some elements of gallery vegetation. According to all these, a highly heterogeneous habitat is deduced for LC-PT, with a mixture of forest in the areas of higher altitude, grassland or savanna in the open areas and wetlands near the lake.

In contrast, the grazing diets (and little dietary heterogeneity) of *Equus* from LP-SA reflect a drier and more seasonal ecosystem, with more open scenarios and a higher diversity of grasses and abrasives. This is corroborated by an abundance of *Bison* (Koch *et al*., 2004). Certainly, the presence of other taxa in this fossil site such as *Odocoileus*, and *Cervus elaphus canadensis*, *Mammuthus columbi*, *Camelops* and *Hemiauchenia* (Koch *et al*., 1998; Feranec and MacFadden, 2000; Feranec, 2007; Semprebon and Rivals, 2010; Mattioli, 2011; Pérez-Crespo *et al*., 2012; Gutiérrez-Bedolla, 2014) informs of the presence of woody vegetation such as shrubs and trees. This is compatible with the dietary homogeneity that we found in this site, since *Equus* species from LP-SA would have been probably restricted to the more open landscapes.


**5. Conclusions**


Most of the sympatric species of fossil *Equus* from West Central Mexico have shown significant differences in limb proportions and body mass, which apparently could reflect adaptations to different ecological niches during the late Pleistocene (Rancholabrean), and a more heterogeneous ecology (and higher adaptive ability) if compared to extant species of the genus, which are known to be strict grazers of open environments.

484  Mesowear and hypsodonty analyses concluded that fossil assemblages of horses were

485  mainly grazers. However, there is a certain degree of variability in mesowear patterns

486  among taxa, with species from LC-PT exhibiting a higher dietary plasticity (and more

487  heterogeneous diets) than those from LP-SA. Our results indicate therefore that late

488  Pleistocene *Equus* apparently relied on more diverse food resources than their modern

489  relatives and, importantly, responded to differences in climate and habitat. This is indeed

490  confirmed by microwear signatures, which are more sensitive to seasonal fluctuations in

491  feeding. Thus, it is suggested the presence of more eclectic feeders in the LC-PT, and more

492  strict or pure grazer in LP-SA. Therefore, differences in wear signatures (both among

493  species belonging to the same locality and also between localities) could be attributed to

494  different diets (i.e., dietary plasticity) and/or levels of non-organic abrasives (grit and dust).

495  As diets of fossil ungulates tend to reflect habitats, the two possible different types of

496  feeding styles in LC-PT (grazer and non-seasonal mixed feeder) are indicative of mixed

497  habitats, with abundant presence of abrasive grass and herbs and non organic particles, and

498  a certain amount of soft browse elements (such as shrub and trees). In contrast, the grazing

499  diets of *Equus* from LP-SA reflect a drier and more seasonal ecosystem, with more open

500  scenarios and a higher diversity of grasses. Previous palaeomastological evidence,

501  however, also suggests the presence of woody vegetation, such as shrubs and trees.

502  Overall, our results highlight the dietary flexibility of some fossil species, and evidence

503  that caution should be paid when reconstructing their palaeoecology using their modern

504  relatives as analogues, as some other works have pointed out before (Semprebon and

505  Rivals, 2007, 2010; Rivals and Semprebon, 2011).

506

517

518     **Supplementary data**

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520     Supplementary data associated with this article can be found as electronic supplementary

521     material at doi:

522

523     **References**

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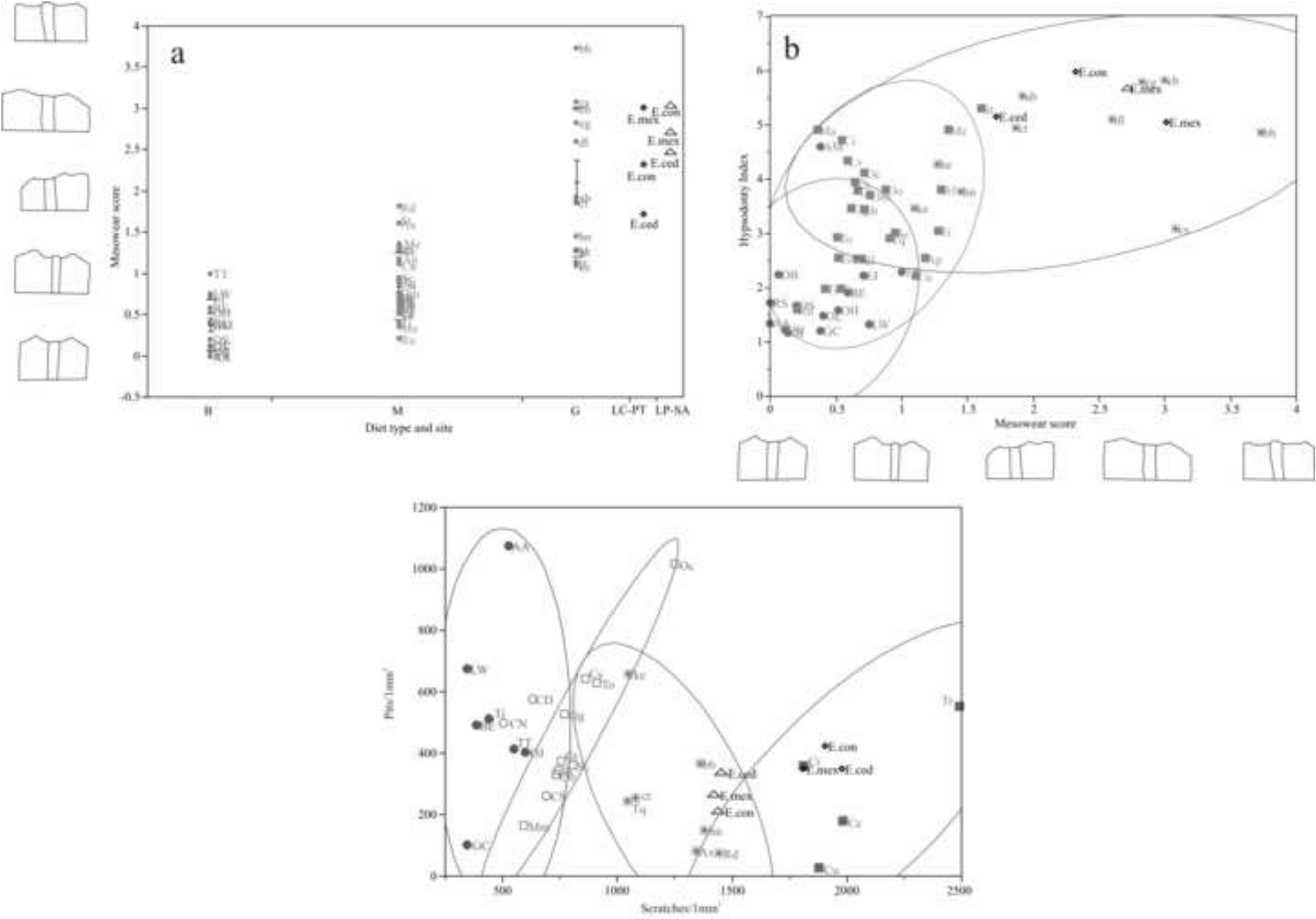717   University Press, USA, pp. 263-297.

**Figure 1.** Geographical location of La Cinta-Portalitos (a) and La Piedad-Santa Ana (b).

**Figure 1.** Geographical location of La Cinta-Portalitos (a) and La Piedad-Santa Ana (b).

**Figure 2.** Diagram of mesowear score vs. diet (a). Bivariate diagram showing hypsodonty index and mesowear score (b). Bivariate diagram showing scratch and pit densities (c). Symbols: full circles, leaf browsers (a and b); empty circles, fruit browser (c); full squares, mixed feeders (a and b) and non-seasonal mixed feeder (c); empty squares, seasonal mixed feeders (c); asterisks, grazers; diamonds, LC-PT; triangles, LP-SA. The ellipses being defined as the 95% confidence intervals. Abbreviations: *Alces alces*: AA; *Ammodorcas clarkei*: EI; *Antilocapra americana*: AM; *Tragelaphus euryceros*: BE; *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*: RS; *Tragelaphus strepsiceros*: TT; *Cephalophus dorsalis*: CD; *Cephalophus niger*: CN; *Cephalophus silvicultor*: CS; *Aepyceros melampus*: Me; *Antidorcas marsupialis*: Ma; *Axis axis*: Ax; *Axis porcinus*: Ap; *Boselaphus tragocamelus*: Tr; *Budorcas taxicolor*: Bt; *Camelus dromedarius*: Cl; *Capra ibex*: Ci; *Capricornis sumatraensis*: Cs; *Cervus elaphus canadensis*: Cc; *Rucervus duvaucelii*: Rd; *Rusa unicolor*: Cu; *Nanger granti*: Gg; *Eudorcas thomsonii*: Gt; *Lama glama*: Lg; *Vicugna vicugna*: Lv; *Ourebia ourebi*: Oo; *Ovibos moschatus*: Om; *Ovis canadensis*: Oc; *Redunca fulvorufula*: Rf; *Rhinoceros unicornis*: Ru; *Saiga tartarica*: St; *Syncerus caffer*: Sc; *Taurotragus oryx*: To; *Tetracerus quadricornis*: Tq; *Tragelaphus angasii*: Ta; *Tragelaphus imberbis*: Ti; *Tragelaphus scriptus*: Ts; *Muntiacus muntjak*: Mm; *Alcelaphus buselaphus*: ab; *Alcelaphus lichtensteini*: al; *Bison bison*: bb; *Ceratotherium simum*: cs; *Connochaetes taurinus*: ct; *Damaliscus lunatus*: dl; *Equus quagga*: eb; *Equus grevyi*: eg; *Hippotragus equinus*: he; *Hippotragus niger*: hn; *Kobus ellipsiprymnus*: ke; *Redunca redunca*: rr.

**Figure 3.** Hierarchical cluster diagrams. Mesowear dendogram based on percentage of high occlusal relief, round cusps and blunt cusps (a). Microwear dendogram based on scratch and pit densities (b).

**Figure 3 Revised Marín-Leyva et al**
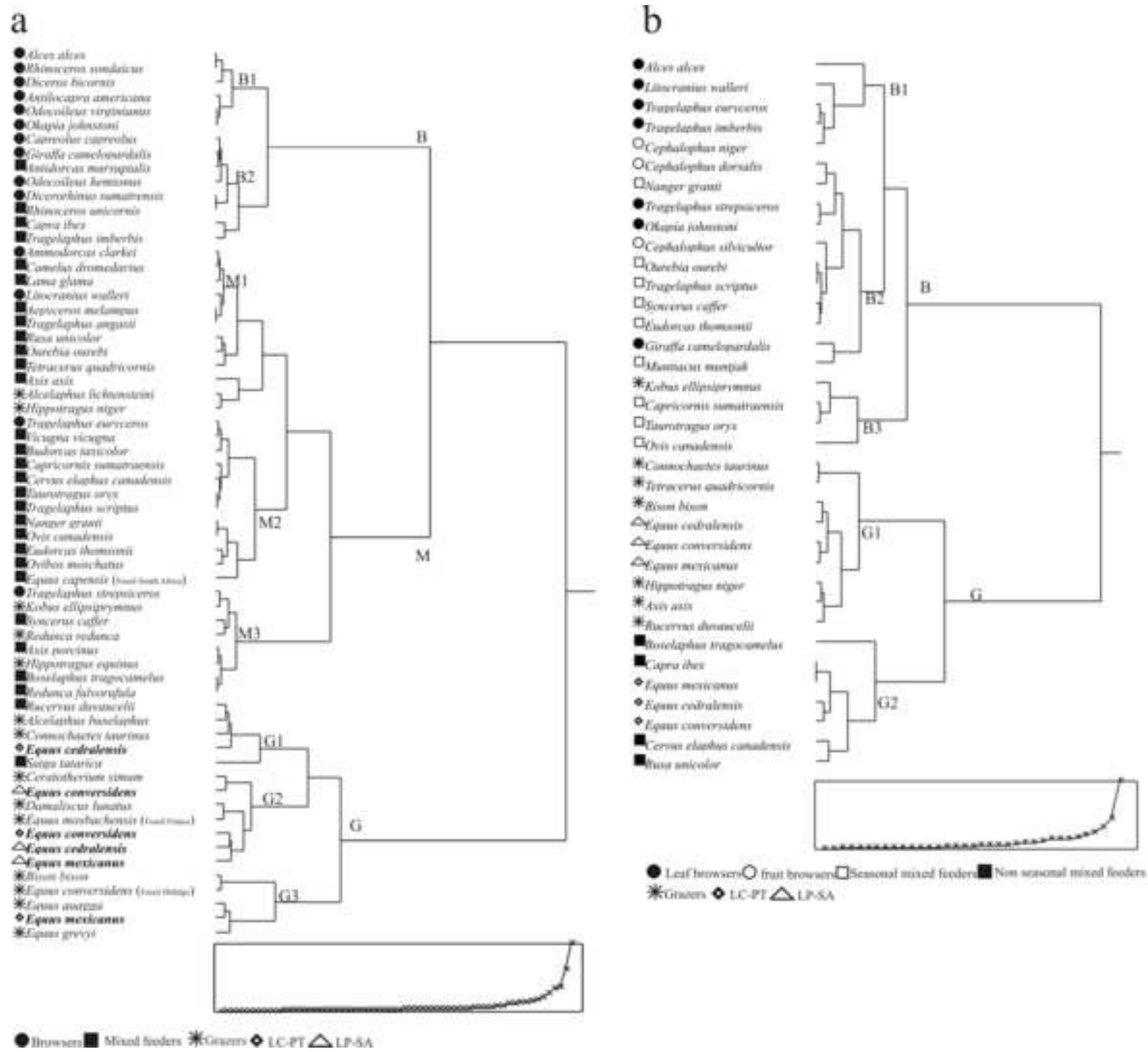
**Figure 4.** Discriminant analyses diagrams. Distribution of fossil population based on mesowear signatures using conservative (a) and radical (b) classifications, and microwear signatures (c). Key for dietary assignments: (B) browsers, (M) mixed feeders, (S-M) seasonal mixed feeders, (NS-M) non-seasonal mixed feeders, (G) grazers. Symbols and abbreviations as in Figure 2. The ellipses being defined as the 100% confidence intervals.

**Table 1.** Summary of body mass estimation, hypsodonty index and mesowear and microwear patterns. Abbreviations: m3, third lower molar; HI, hypsodonty index; N, number of individuals; %H, %L, percentage of individuals with high and low occlusal relief; %s, %r, %b, percentage of individuals with sharp, rounded and blunt cusps; MS, mesowear score; S, scratches/mm$^2$; P, pits/mm$^2$; (SD), standard deviation.[1]Inferences of body size based on the third metacarpal (MCIII) and [2]the first phalanx of the central digit (1FIII).

Table 1.

| Species | Locality | Body mass | | HI | | Mesowear | | | | | | | Microwear | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | N | kg | N | m3 | N | %H | %L | %s | %r | %b | MS | N | S(SD) | P(SD) |
| *E. cedralensis* | LC-PT | 7[2] | 145.5[2] | 2 | 5.15 | 20 | 56.8 | 43.2 | 24.3 | 62.2 | 13.5 | 1.72 | 10 | 1977.5(221.258) | 350(92.779) |
| *E. conversidens* | LC-PT | 2[2] | 344.7[2] | 3 | 5.99 | 31 | 28.6 | 71.4 | 21.4 | 67.9 | 10.7 | 2.32 | 11 | 1906.81(294.76) | 422.72(86.21) |
| *E. mexicanus* | LC-PT | _ | | 2 | 5.06 | 7 | 7.7 | 92.3 | 23.1 | 38.5 | 38.5 | 3.01 | 6 | 1808.33(383.29) | 350(83.66) |
| *E. cedralensis* | LP-SA | 3[1] | 126.0[1] | | | 11 | 21.1 | 78.9 | 15.8 | 78.9 | 5.3 | 2.47 | 9 | 1452.77(425.81) | 336.11(158.66) |
| *E. conversidens* | LP-SA | 1[1]/7[2] | 229.5[1]/297.3[2] | | | 11 | 0.0 | 100 | 15 | 65.0 | 20.0 | 3.04 | 7 | 1439.29(579.84) | 210(125.71) |
| *E. mexicanus* | LP-SA | 1[2] | 476.7[2] | 1 | 5.68 | 8 | 13.3 | 86.7 | 20 | 66.7 | 13.3 | 2.71 | 5 | 1420(505.01) | 265(152.68) |

**Table 2.** Summary of discriminate analyses. Mesowear using conservative (A) and radical (B) classifications, and microwear (C). Key for dietary assignments: browsers (B), mixed feeders (M); seasonal (S-M) and non-seasonal mixed feeders (NS-M); grazers (G).

Table 2.

| Original group Species/ localities | Mesowear | | | | | | Microwear | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Extant classification rate | A (71.93%) | | | B (75.44%) | | | C (93.33%) | | | |
| Classification | Conservative predicted group | | | Radical predicted group | | | Predicted group | | | |
| | B | M | G | B | M | G | B | S-M | NS-M | G |
| *E. cedralensis*/ LC-PT | | | X | | | X | | | X | |
| *E. conversidens*/ LC-PT | | | X | | | X | | | X | |
| *E. mexicanus*/ LC-PT | | | X | | | X | | | X | |
| *E. cedralensis*/ LP-SA | | | X | | | X | | | | X |
| *E. conversidens*/ LP-SA | | | X | | | X | | | | X |
| *E. mexicanus*/ LP-SA | | | X | | | X | | | | X |
| Total of fossil populations (N(%)) | | 6(100%) | | | 6(100%) | | | | 3(50%) | 3(50%) |