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Preliminary assessment of hadrosaur dental microwear from the Cerro del Pueblo Formation (Upper Cretaceous: Campanian) of Coahuila, northeastern Mexico

Héctor E. Rivera-Sylva[a,*], Christina I. Barrón-Ortíz[b], Rafael Vivas González[c], Rosalba Lizbeth Nava Rodríguez[d], José Rubén Guzmán-Gutiérrez[a], Fernando Cabral Valdez[a], Claudio de León Dávila[e]

[a] Museo del Desierto, Carlos Abedrop Dávila 3745, 25022, Saltillo, Coahuila, México.
[b] Royal Alberta Museum, 9810 – 103a Avenue, T5J 0G2, Edmonton, AB, Canadá.
[c] Villa Nápoles 6506, Colonia Mirador de las Mitras, 64348, Monterrey, Nuevo León, México.
[d] Universidad Autónoma de San Luis Potosí, Dr. Manuel Nava 8, Zona Universitaria Poniente, 78290, San Luis Potosí, San Luis Potosí, México.
[e] Benemérita Escuela Normal de Coahuila, Calz. de los Maestros 858 pte., Zona Centro, 25000, Saltillo, Coahuila, México.

[*] hrivera@museodeldesierto.org

Abstract

Here we report new hadrosaur remains recovered from the Cerro del Pueblo Formation (Upper Cretaceous: Campanian) at La Parrita locality, northeastern Mexico. Although the material is fragmentary, the identification of dental microwear in three out of the four teeth collected is notable. This sample allows for a preliminary assessment of hadrosaur dental microwear from this geographic region and time frame. The variables studied were the orientation and average count of scratches, average count of pits, and average microwear feature width in an area of 400 X 400 µm at 35X magnification. The results show a predominance of dorsodistally-ventromesially inclined scratches in all three teeth indicating that the mandible primarily moved in an orthopalinal direction during the power stroke. The pattern of scratch orientation we recorded is comparable to that reported for different hadrosaur species from Alberta, Canada, and Wyoming, U.S.A.; suggesting similar jaw mechanics in the hadrosaurs from Coahuila. In contrast, there are significant differences in the average number of pits and microwear feature width between the Alberta and the Coahuila hadrosaurs samples, with the latter presenting more pits and finer microwear features. Given the similar jaw mechanics between the Alberta and Coahuila hadrosaurs, suggested by our analysis, the difference in average number of pits and microwear feature width is probably due to differences in diet and/or the type and amount of grit ingested during feeding. The greater number of pits in the hadrosaurs from Coahuila might indicate that these individuals ingested a greater proportion of hard food items than the Alberta hadrosaurs.

Keywords: Palaeogeography, Palaeoecosystem, Hadrosauridae, microwear, Coahuila, Mexico.

Resumen

Aquí reportamos nuevos restos de hadrosaurio recuperados de la Formación Cerro del Pueblo (Cretácico Superior: Campaniano) provenientes de la localidad de La Parrita, noreste de México. A pesar de que el material es fragmentario, la identificación de microdesgaste dental en tres de los cuatro dientes recolectados es notable. Esta muestra permite una evaluación preliminar del microdesgaste dental en hadrosaurios de esta región geográfica y durante este marco de tiempo. Las variables estudiadas fueron la orientación y el número promedio de rayones, el número promedio de fosas y el ancho promedio de los rasgos de microdesgaste en un área de 400 X 400 µm con un aumento de 35X. Los resultados muestran que la mayoria de los rayones estan inclinados dorsodistal-ventromesialmente en los tres dientes, lo que indica que la mandíbula se movió principalmente en dirección ortopalinal durante el golpe masticatorio. El patrón de orientación de los rayones que registramos es comparable al reportado para diferentes especies *de hadrosaurios de Alberta, Canadá y Wyoming, EE. UU.; Lo que sugiere una mecánica del movimiento mandibular similar en los hadrosaurios de Coahuila. En contraste, existen diferencias significativas en el número promedio de fosas y en el ancho de los rasgos de microdesgaste entre las muestras de hadrosaurios de Alberta y Coahuila, y esta última presenta más fosas y rasgos de microdesgaste más finos. Dada la similutud en el movimiento mandibular entre los hadrosaurios de Alberta y Coahuila, sugerida por nuestro análisis, la diferencia en el número promedio de fosas y el ancho promedio de los rasgos de microdesgaste probablemente se deba a las diferencias en la dieta y/o el tipo y la cantidad de sedumento ingerido durante la alimentación. El mayor número de fosas en los hadrosaurios de Coahuila podría indicar que estos individuos ingirieron una mayor proporción de alimentos duros que los hadrosaurios de Alberta.*

Palabras clave: Paleogeografía, Paleoecosistema, Hadrosauridae, microdesgaste, Coahuila, México.

1. Introduction

Fossils of hadrosaurs have been found in many localities around the world and the largest concentration of sites is located in North America. Hadrosaur remains are particularly abundant in localities from western North America, ranging from southern Canada to northeastern Mexico (Ryan and Russell, 2001; Ramírez-Velasco *et al.*, 2015). Despite their abundance in the fossil record, there are still important gaps in the understanding of hadrosaur biogeography and paleobiology. Here we report new hadrosaur remains recovered from the Cerro del Pueblo Formation at La Parrita locality, which is located in the municipality of General Cepeda, southeast Coahuila, Mexico. The fossil locality is situated 53 km northwest of Saltillo (Figure 1). Although the material is fragmentary, the identification of dental microwear in three out of the four teeth collected is notable. This prompted us to examine additional hadrosaur teeth from the Cerro del Pueblo Formation housed at the Museo del Desierto. However, no additional specimens with well-preserved dental microwear were identified. Thus, this report presents the results of the dental microwear analysis of these teeth. Even though the sample size is far from ideal, it does serve to provide a preliminary assessment of the feeding ecology and jaw mechanics of the hadrosaurs from the Cerro del Pueblo Formation. The results are discussed in the context of what is known about the paleoenvironments of Laramidia during the late Campanian.

Several authors have observed that throughout western North America, the biotic associations of terrestrial and marine vertebrates as well as invertebrates vary in composition (Russell, 1967; Russell and Chamney, 1967; Armstrong, 1978; Horner, 1988; Fiorillo, 1989; Nicholls and Russell, 1990; Hunt and Lucas, 1992; Rowe *et al.*, 1992; Hotlz, 1993; Lehman, 1985, 1989, 1993, 1997; Eberth, 1997). Lehman (1997) pointed out that the dinosaur faunas and other terrestrial vertebrates corresponding to the Late Campanian were not homogenous but differed latitudinally from Canada to Mexico, which is reflected particularly in the sorts of hadrosaurs (including hadrosaurines and lambeosaurines) identified at the moment. Due to this situation, Lehman (1997) identified provinciality and defined the existence of two different faunal assemblages:

Northern Fauna: from Alberta and Saskatchewan in Canada, as well as Montana, Wyoming, Utah, and northern and central Colorado in the United States, and Southern Fauna: from southern Colorado, New Mexico and western Texas in the United States to northeastern Mexico.

During the Late Cretaceous (Late Campanian), each of these faunas was comprised of a series of very characteristic hadrosaurs corresponding to one or the other subfamily. For example, in the case of the Northern Fauna it has been denominated by Lehman (1997) as the "*Corythosaurus* Fauna" due to the presence of a greater predominance of lambeosaurines than hadrosaurines, whereas in the southern fauna, which has been called the "*Kritosaurus* Fauna", the situation is inverted. In addition to this pattern, there was a significant difference in the diversity of hadrosaur taxa represented in the two faunas. Lehman (1997) speculated about the possible factors that could influence the provinciality between faunas and argued that geographic barriers did not exist that had prevented the dispersal of organisms across Laramidia. In his work, he considered temperature, precipitation, the circulation of the ocean currents, and the distribution of the flora as the factors that determined provinciality in Laramidia.

The palynological records indicate that during the Late Cretaceous, North America was divided by an epicontinental sea in two floral provinces (Batten, 1984; Herngreen and Chlonova, 1981; Srivastava, 1994). The province of Aquilapollenites was found from western North America to eastern Asia and was characterized by a closed canopy forest with relatively cool temperatures and high humidity. The province of Normapolles was located from eastern North America to Western Europe and its vegetation corresponded to an open canopy forest with warm temperatures and moderate droughts (Graham, 1987). It is important to note that different localities in the southwestern region of North America show mixed deposits of pollen, for example in New Mexico and Texas (Anderson, 1960; Newman, 1965; Tschudy, 1980; Manfrino, 1984). Some deposits contain palynomorphs corresponding to the province of Normapolles, particularly within the Aguja Formation

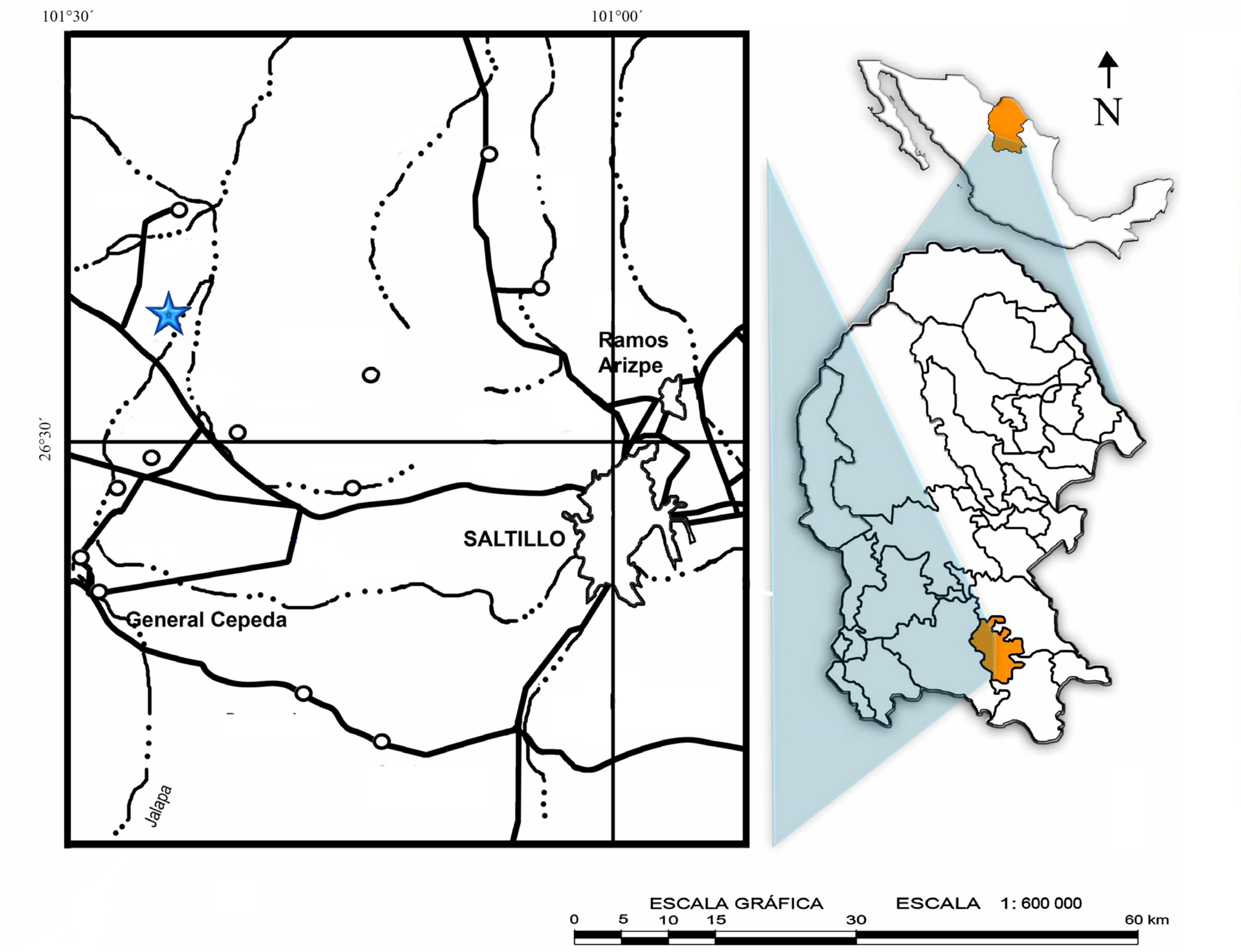

Figure 1. Geogrpahic location of La Parrita locality (star), Coahuila, Mexico.

(Baghai, 1994) and in the northeastern region of Mexico (Medus and Almeida-Lenero, 1982). By comparing the palynological records and the hadrosaur assemblages from North America, Lehman (1997) observed that the limits between the hadrosaur faunas were similar to the limits of floral transition (forest of closed canopy – forest of open canopy) and climatic transition (mesothermal temperature – megathermal temperature). The combination of the oceanic circulation and the latitudinal zonation of temperature and precipitation, produced a series of warm and semi-dry conditions south of paleolatitude 45°N and cool and humid conditions north of this paleolatitude, which could have induced faunistic as well as floral provinciality.

It is important to emphasize that in spite of the diverse fossil remains of hadrosaurs that have been collected from northeastern Mexico, this region was not considered as an important region and, therefore, was not included as part of the southern fauna ("*Kritosaurus* Fauna") of the great plains of North America (Lehman, 1997). Nevertheless, the most recent studies in Coahuila indicate the presence of rich hadrosaur faunas with a greater proportion of hadrosaurines than lambeosaurines, which is consistent with the data obtained for the Fruitlan Formation (New Mexico, USA), as well as the Aguja and San Carlos Formations (Texas, USA).

2. Geology

In Saltillo, the Cerro del Pueblo (CdP) Formation has a thickness of 162 m, but to the west the formation grows thicker up to 449 m in Rincon Colorado (35 km west of Saltillo) and 540 m in Porvenir de Jalpa (70 km west of Saltillo). In several localities in the area, a stratigraphic interval of intercalated grey-green and red layers has been detected which, because of its composition, has been assigned to the Cerro Huerta (CH) Formation. The CdP Formation is at the base of the Difunta Group (Late Cretaceous – Paleocene), and is dated between 71 and 72.5 million years in age (Obradovich, 1993; Eberth *et al.,* 2004; Vogt *et al.,* 2015). Its layers on the south part of the Parras Basin near Saltillo and to the west are made of intercalated marine, brackish water and fresh water sediments, which were deposited to the east and north of the Sierra Madre Oriental. The CdP Formation records deposits of coastal plain environments, influenced by changes in the sea level and storms. Multicolored rocks from the Difunta Group are composed by volcanic rocks and fluvial deposits, deltaic environments and of platform. The red, green and purple rocks are from normal deltaic, and the darker colors are present in all facies (Eberth *et al.,* 2004). The fossils recorded for the CdP Formation include several invertebrates: *Ethmocardium*, *Inoceramus vanuxemi*, *Turritella vertibroides*, *Eutreohoceras*, *Sphenodiscus*, among others. On the other hand, among the vertebrates, the following families have been reported: Alligatoridae, Kinosternidae, Trionychidae, Tyrannosauridae, Ornithomimidae, Ankylosauridae, Ceratopsidae, and Hadrosauridae, (Eberth *et al.*, 2004; Rivera-Sylva and Espinosa-Chávez, 2006; Carbot-Chanona, 2014; Rivera-Sylva and Carpenter, 2014a, b).

The locality of La Parrita is part of the Cerro del Pueblo Formation, and recorded shore line environments and low marine conditions which were influenced by sea-level fluctuations and storm events (Eberth *et al.,* 2004; Vogt *et al.,* 2015) and its facies illustrate low channels, wetlands with high concentration of vegetation, lakes, swamps, lagoons and deltaic systems (McBride, 1974; Hill, 1988; Vogt *et al.,* 2015). La Parrita is composed by alternation layers of sandstone, siltstone and shale (Figure 2) and for a detailed description of the geology see Rivera-Sylva *et al.* (2019). This sequence of alternating sediments suggests that La Parrita suffered a series of events related to marine regressions and transgressions during its deposition, which is consistent with other localities associated to the Cerro del Pueblo Formation that reflect those events (Eberth *et al.,* 2004).

3. Materials and methods

We examined the hadrosaur teeth (Figure 3) from La Parrita locality, Coahuila, Mexico, for dental microwear using high-resolution clear epoxy casts and a Nikon SMZ1500 stereomicroscope. Sixty-seven additional teeth from the Cerro del Pueblo Formation housed at the Museo del Desierto were also examined for dental microwear using the same methodology. We were unable to use the partial dentaries and maxillaries at the Paleontology Collection of the Museo del Desierto, because the tooth batteries were damaged. We acknowledge that the use of isolated teeth introduces an additional assumption in the study of hadrosaur dental microwear, namely that isolated teeth can provide microwear data which is characteristic of the complete tooth row. Some studies lend support to this assumption (*e.g.*, Williams *et al.*, 2009; Fiorillo, 2011), but others suggest that this may not always be the case (Mallon and Anderson, 2014). Additional research on well preserved specimens is needed to further evaluate the trends presented in these studies, but this is beyond the scope of this study.

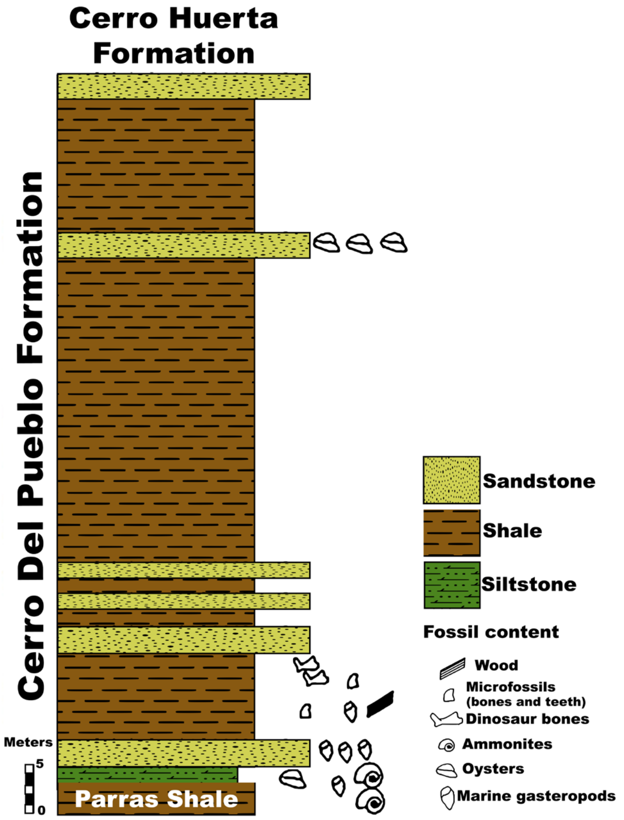

Figure 2. Stratigraphic column of La Parrita, Cerro del Pueblo Formation, Coahuila, Mexico.

Isolated hadrosaur teeth cannot be identified to species and as a result we treated each tooth separately, given the possibility that they could represent different species. At least two hadrosaur species inhabited the region, the hadrosaurine *Latirhinus huitstlani* and the lambeosaurine *Velafrons coahuilensis* (Gates *et al.*, 2007; Prieto-Márquez and Serrano-Brañas, 2011). Teeth that have been taphonomically altered (e.g. postmortem abrasion and weathering) were identified following the criteria outlined by Teaford (1988) and were discarded from the study; these consisted of 68 specimens. After a thorough assessment of the sample, only three teeth that were collected from La Parrita locality showed sufficiently well preserved dental microwear (CPC 1857, CPC 1858 [Figure 4A], and CPC 1859). Most of the specimens we studied were surface collected and although they present distinct wear facets, when examined under the microscope they show signs of postmortem abrasion and weathering which obscure or obliterate dental microwear features (Figure 4B). Other researchers have noted the difficulty in finding dinosaur teeth that show well preserved microwear features despite the presence of wear facets (*e.g.*, Mallon and Anderson, 2014). As a result, many of the studies that have examined dental microwear in hadrosaurs have been conducted on relatively small sample sizes (*e.g.* Williams *et al.*, 2009;

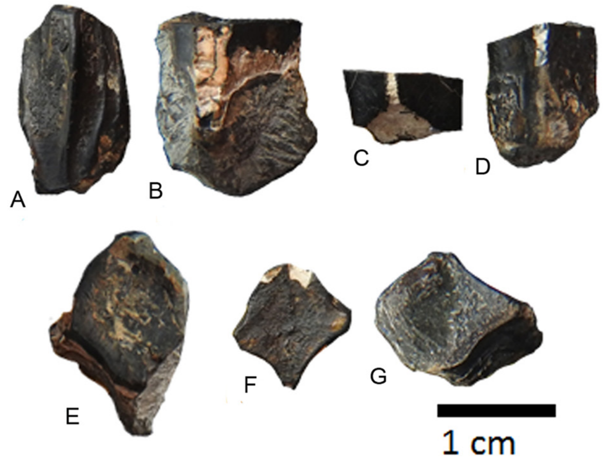

Figure 3. Hadrosaur teeth from La Parrita. lingual views of A) CPC 2612; B) CPC 1859; C) CPC 1857, and D) CPC 1858; dorsal view of teeth E) CPC 1859; F) CPC 1857; and G) CPC 1858.

Fiorillo, 2011; Mallon and Anderson, 2014). A possible explanation for this observation is that dentine, which is known to be softer than tooth enamel (Green, 2009), might be more susceptible to taphonomic alterations. Unlike in mammals where dental microwear analysis is typically performed on the occlusal enamel (Teaford, 2007), dental microwear analysis in hadrosaurs and other megaherbivorous dinosaurs is more commonly performed on the dentine, because the enamel is very thin (~100 µm) (Mallon and Anderson, 2014). Despite these differences, dentine has been shown to preserve a comparable dietary signal to tooth enamel (Green, 2009).

We used high dynamic range imaging following the methodology of Fraser *et al.* (2009), to obtain high contrast photographs of the occlusal surface of the teeth for microwear analysis. This was accomplished using a Nikon D200 digital camera coupled to a Nikon SMZ1500 stereomicroscope at 35X magnification. For each photographed specimen, the orientation and number of scratches as well as the number of pits were counted in an area of dentine 400 X 400 µm on the occlusal surface of the tooth as described by Mallon and Anderson (2014). When possible two sets of counts were obtained at different locations of the occlusal surface and average counts of scratches and pits were calculated. In addition, we measured the width of each microwear feature. We conducted Rao's test in order to test the null hypothesis of random orientation of scratches for each of the specimens studied. We compared scratch orientation in the Coahuila hadrosaurs to the values reported in previous studies, including the study by Williams *et al.* (2009) for *Edmontosaurus* Lambe, 1917 from the Lance Formation (Upper Cretaceous, Late Maastrichtian) of Wyoming, U.S.A., as well as the study by Mallon and Anderson (2014) for *Lambeosaurus* Parks, 1923, *Corythosaurus* Brown, 1914, and *Prosaurolophus* Brown, 1914 from the Dinosaur Park Formation (Late Campanian) of Alberta, Canada. In addition, we conducted a PCA analysis on the correlation matrix using the average number of scratches, pits, and feature width for the specimens we studied and the data reported by Mallon and Anderson (2014). The data reported by Fiorillo (2011) could not be included in the analysis, because this author used a different methodology from that employed in our study and the study by Mallon and Anderson (2014). All statistical analyses were conducted using the software PAST 3.1 (Hammer *et al.*, 2001). The significance level for all tests was set to a *p*-value of 0.05.

4. Systematic palaeontology

Hadrosauridae Cope, 1869
Gen. et sp. indet.

Material: Four teeth (CPC 1857-1859, CPC 2612) (Figure 3). These elements are housed and registered in the Museo del Desierto, Saltillo, Coahuila, Mexico. CPC = Colección Paleontológica de Coahuila.

Horizon and Locality: Cerro del Pueblo Formation, La Parrita locality, 53 km northwest of Saltillo; municipality of General Cepeda, Coahuila, Mexico.

Age: Late Cretaceous (Upper Campanian).

Description: *Teeth* (CPC 1857; CPC 1858; CPC 1859; CPC 2612) – The four teeth have worn crowns. All of them bear prominent middle ridges on the enamel. CPC-2612 has a lingual rhomboidal shape. The largest tooth (CPC 2612) is 18 mm high, the smallest (CPC 1857) 5 mm. The specimens were identified as hadrosaur teeth based on their morphology and characteristics: enamel on a single side, and in the middle of this enamelled face, there is a strong median carina (Horner *et al.*, 2004).

5. Results of dental microwear analysis

The hadrosaur teeth from the Cerro del Pueblo Formation, Coahuila, Mexico, possess a greater average number of scratches than average number of pits, with an average feature width that ranges between 6.36 µm and 7.37 µm (Table 1). The microwear scratches are not oriented at random (Table 2). All of the specimens in this study show a predominance of dorsodistally-ventromesially inclined scratches (Figure 5), and possess a high average number of pits and small microwear feature widths relative to the hadrosaurs from the Dinosaur Park Formation of Alberta studied by Mallon and Anderson (2014) (Figure 6). A PCA of the microwear variables for the specimens from Coahuila and the hadrosaurs from Alberta reveals that the Coahuila specimens occupy a separate region of the microwear multivariate space (Figure 7). According to the factor loadings (Table 3), these specimens differ from the Dinosaur Park Formation hadrosaurs because they possess a greater number of pits and finer microwear features.

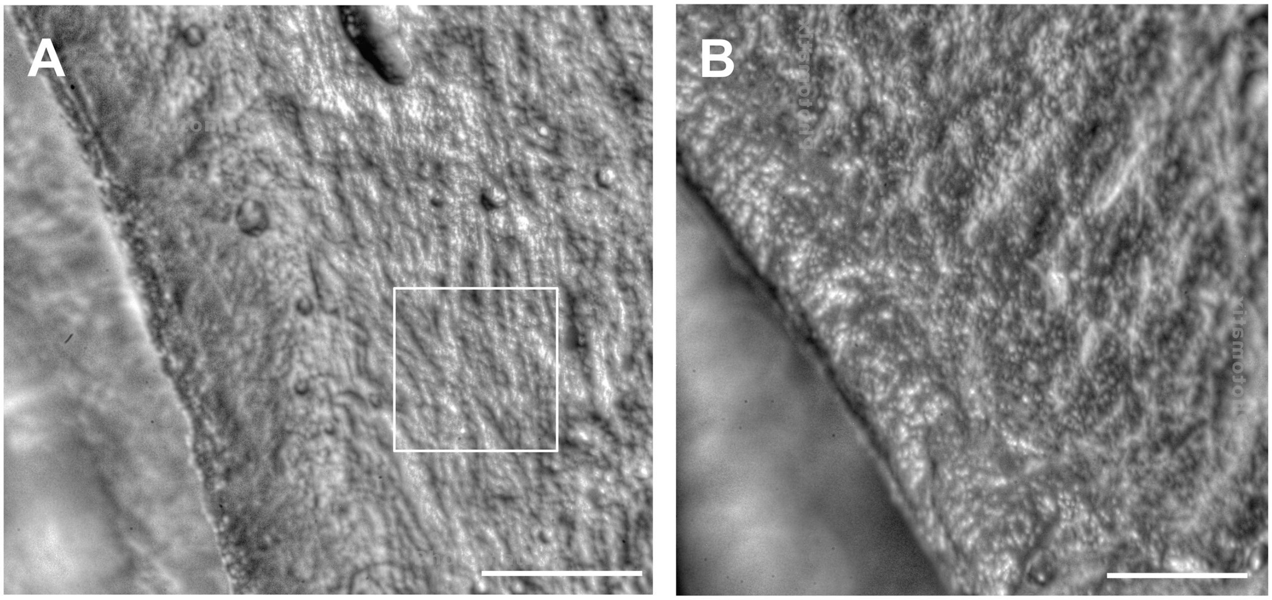

Figure 4. Occlusal surface of two hadrosaur teeth from the Cerro del Pueblo Formation, Coahuila, Mexico. A) Portion of the occlusal surface of CPC-1858 showing one of the 400 X 400 µm counting areas indicated by the white square. B) Portion of the occlusal surface of CPC-2070 showing the total lack of dental microwear features as a result of postmortem abrasion and weathering. In both images the carina is oriented vertically and the scale bar corresponds to 400 µm.

Table 1. Summary statistics of microwear variables of the hadrosaur teeth from the Cerro del Pueblo Formation, Coahuila, Mexico. s = average number of scratches; p = average number of pits; w = average microwear feature width (µm).

Specimen	s	p	w
CPC 1857	36	11	7.37
CPC 1858	42	9.83	6.36
CPC 1859	40.7	9	6.47

Table 2. Results of Rao's *U* test for scratch orientation of the hadrosaur teeth from the Cerro del Pueblo Formation, Coahuila, Mexico. n = sample size.

Specimen	n	Rao's U	p-value
CPC 1857	36	187.6	< 0.001
CPC 1858	84	211.5	< 0.001
CPC 1859	41	237.2	< 0.001

Table 3. Eigenvalues, percentage variance, and factor loadings for the principal components resulting from PCA of the microwear variables in Table 1 and those reported by Mallon and Anderson (2014) for the hadrosaur dinosaurs from Dinosaur Park Formation, Alberta, Canada. S = average number of scratches; P = average number of pits; W = average microwear feature width.

	PC1	PC2	PC3
Eigenvalue	1.975	0.7816	0.2435
% variance	65.83	26.05	8.12
Factor loadings			
S	0.4526	0.8642	0.2198
P	0.6048	-0.4786	0.6366
W	-0.6553	0.1552	0.7392

6. Discussion

Hadrosaur occurrences throughout North America are common in deposits from coastal plains, deltas and rarely, in marine shales. Serrano-Brañas (2006) suggested a preference by hadrosaurs for coastal habitats bordering the sea. In western North America, the assemblages of terrestrial and marine vertebrates, and also of invertebrates, differ in composition latitudinally, resulting in peculiar endemism during the Late Cretaceous (Russell and Chamney, 1967; Horner, 1988; Fiorillo, 1989; Holtz, 1993; Lehman, 1997, 2001; Zanno *et al.*, 2005). Our preliminary evaluation of hadrosaur dental microwear from the Cerro del Pueblo Formation is consistent with this pattern of latitudinal provinciality in western North America.

The predominance of dorsodistally-ventromesially inclined scratches observed in the hadrosaur teeth from the Cerro del Pueblo Formation of Coahuila, Mexico, indicates that the mandible in these individuals primarily moved in an orthopalinal direction during the power stroke. This pattern of scratch orientation is comparable to that reported by Mallon and Anderson (2014) for *Lambeosaurus*, *Corythosaurus*, and *Prosaurolophus* from the Dinosaur Park Formation of Alberta, Canada; suggesting similar jaw mechanics in the hadrosaurs from Coahuila. Similar results were obtained by Williams *et al.* (2009) for *Edmontosaurus* from the Lance Formation of Wyoming, indicating an orthopalinal motion of the jaw during the power stroke for this hadrosaur. The fact that both hadrosaurine (*Edmontosaurus* and *Prosaurolophus*) and lambeosaurine

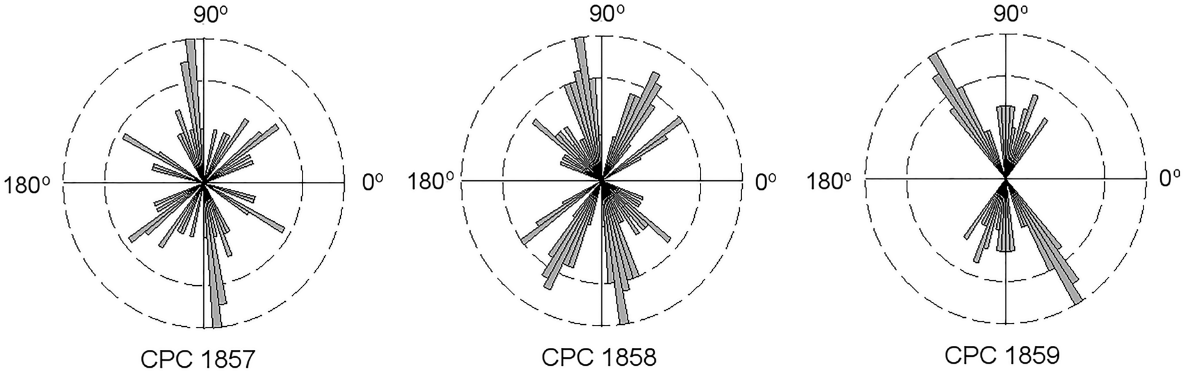

Figure 5. Rose diagrams showing the orientation of microwear scratches in the hadrosaur teeth from the Cerro del Pueblo Formation, Coahuila, Mexico. 0° = mesial; 90° = apical.

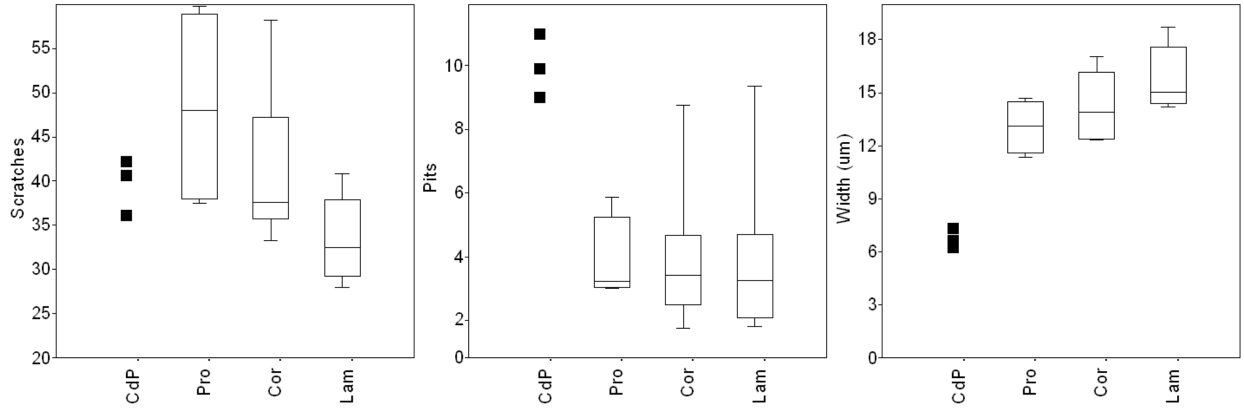

Figure 6. Mean scratches, pits, and microwear feature width of the hadrosaur specimens from the Cerro del Pueblo Formation, Coahuila, Mexico (this study), and the Dinosaur Park Formation, Alberta, Canada (Mallon and Anderson, 2014). CdP = Cerro del Pueblo hadrosaurs; Pro = *Prosaurolophus*; Cor = *Corythosaurus*; Lam = *Lambeosaurus*.

(*Lambeosaurus* and *Corythosaurus*) hadrosaurs show similar jaw mechanics suggests that this trait may have originated prior to the origin of these subfamilies.

The interpretation of dental microwear in relation to dietary habits of herbivorous dinosaurs remains difficult. This is largely because there is little direct evidence of the type of plants consumed by herbivorous dinosaurs (*e.g.* Currie *et al.*, 1995; Chin, 2007; Tewwt *et al.*, 2008), a limitation that hampers an assessment of the association between specific dietary habits and specific dental microwear patterns. Nonetheless, the study of dental microwear in extant vertebrates, particularly mammals, can assist in the interpretation of dinosaur dental microwear and its relationship to dietary habits at a broad level. The analysis of dental microwear in extant mammals reveals that comparable microwear patterns can be produced in animals with very disparate dietary habits. For example, a higher proportion of pits is generally found in fruit-dominated browsing ungulates (Solounias and Semprebon, 2002), frugivorous and hard-object feeding primates (Semprebon *et al.*, 2004; Merceron *et al.*, 2005), insectivorous and some frugivorous murid rodents (Gomes Rodriguez *et al.*, 2009), and bone-crushing carnovores (Van Valkenburgh *et al.*, 1990; Bastl *et al.*, 2012). These observations highlight that dental microwear primarily records the physical properties of the food items eaten (Ungar, 2010). A relatively high number of pits is generally associated with the consumption of hard food items, whereas a relatively high number of scratches and low number of pit is generally associtated with the consumption of tough food items (*e.g.* Van Valkenburgh *et al.*, 1990; Solounias and Semprebon, 2002; Semprebon *et al.*, 2004; Merceron *et al.*, 2004, 2005; Gomes Rodrigues *et al.*, 2009; Bastl *et al.*, 2012). Moreover, grit and soil adhering to food items has been proposed to also contribute to the formation of dental microwear, particularly in animals feeding close to the ground or in open and arid habitats (*e.g.* Ungar *et al.*, 1995; Sanson *et al.*, 2007; Lucas *et al.*, 2013). Exogenous grit ingested during feeding has been proposed to contribute to the formation of scratches in extant ungulate mammals that feed relatively close to the ground and in open, arid habitats (Sanson *et al.*, 2007). Thus, three factors can potentially interact to produce dental microwear

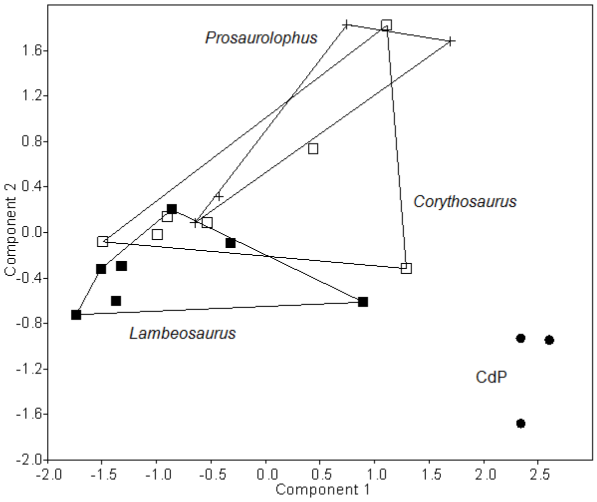

Figure 7. Plot of the first two principal components resulting from PCA of the microwear data (scratches, pits, and microwear feature width) of the hadrosaurs from the Dinosaur Park Formation, Alberta, Canada (Mallon and Anderson, 2014) and the Cerro del Pueblo Formation (CdP), Coahuila, Mexico (this study).

in herbivorous animals: 1) the type of vegetation eaten (i.e. tough or hard), 2) feeding height, and 3) whether the animal inhabited an open or closed habitat. It seems reasonable to assume that similar factors could interact to produce dental microwear in hadrosaur dinosaurs.

In the context of the foregoing discussion, different hypotheses can be devised regarding the feeding behaviour of hadrosaur dinosaurs from Alberta and Coahuila. Examination of the average number of scratches shows a trend in which *Lambeosaurus* possesses the lowest number of scratches, followed by the Coahuila hadrosaur specimens, *Corythosaurus*, and *Prosaurolophus* (Figure 6). These results suggest that *Lambeosaurus* had the less tough and less abrasive diet, *Prosaurolophus* the tougher and most abrasive diet, with *Corythosaurus* and the specimens from Coahuila occupying an intermediate position. Assuming that the degree of food toughness is the primary factor responsible for the formation of microwear scratches, then the results would indicate that *Lambeosaurus* primarily fed on soft leaves and twigs, whereas *Prosaurolophus* had a diet of tougher and coarser plants, and *Corythosaurus* and the Coahuila specimens fed on plants with intermediate toughness. Alternatively, if exogenous grit is identified as the main agent responsible for the formation of scratches, it follows that *Lambeosaurus* may have fed high above the ground or in closed habitats, whereas *Prosaurolophus* fed close to the ground or in open habitats, and *Corythosaurus* and the Coahuila hadrosaur specimens had an intermediate feeding height or preferred transitory habitats. Mallon and Anderson (2014) also suggested feeding height and habitat type (closed versus open) as possible explanations to account for the differences in dental microwear between *Prosaurolophus* and *Lambeosaurus*. The interpretation that these dinosaurs inhabited different habitats would be consistent with the study presented by Carrano *et al.* (1999), which suggested that lambeosaurines typically inhabited closed habitats, while hadrosaurines preferred open habitats.

Analysis of additional microwear variables, particularly the mean feature width, provides further insights into the feeding ecology of these dinosaurs and modifies some of the hypotheses presented above. In extant herbivore mammals, such as ungulates (Solounias and Semprebon, 2002) and murid rodents (Gomes Rodrigues *et al.*, 2009), animals feeding on hard food items tend to have wide microwear features (i.e. wide scratches and large pits). In the case of the hadrosaurs, the specimens from Coahuila show the smallest mean feature width, followed by *Prosaurolophus*, *Corythosaurus*, and *Lambeosaurus* (Figure 6). A combination of a high number of scratches but fine microwear features may indicate that *Prosaurolophus* was a herbivore feeding on generally soft food items that inhabited open habitats, where grit could adhere to the vegetation eaten. The relatively large mean feature width, but a low number of scratches in *Lambeosaurus* is suggestive of a herbivore feeding on soft food items as well as a smaller proportion of hard food items in a more closed habitat. *Corythosaurus* is regarded as a generalist, which probably fed on plants with varying degrees of toughness and hard food items. The greater number of pits and relatively low number of scratches in the hadrosaurs from Coahuila suggest that these dinosaurs ingested a greater quantity of hard food items, than the Alberta hadrosaurs. The small mean feature width observed in the specimens studied further indicates that these hard food items were small in size. These dietary hypotheses can be tested with further analyses of dental microwear in addition to better paleonvironmental reconstructions of the areas where these dinosaurs lived.

The flora reported from the Upper Campanian Cerro del Pueblo Formation mostly comprises abundant Zingiberales (ginger weed, *e.g. Tricostatocarpon silvapinidae* and *Striatornata sanantoniensis*), Alismantales (alismatids), Malvales (mallows, *e.g. Wheeleroxylon*), Laurales (laurels, *e.g. Olmosoxylon*), possible Sapindales (balsam trees), Caryopyllales (cloves, *e.g. Coahuilacarpon*) and Arecales (palms) (Estrada-Ruíz and Cevallos-Ferríz, 2007; Calvillo-Canadell and Cevallos-Ferríz, 2007; Cevallos-Ferríz *et al.*, 2008). In the northern province of Laramidia there is a record of Sapindales (*e.g. Porosia*), Cornales (Coniferales, *e.g. Geinitzia*) with many affinities to the floras known from coeval Asia (Koppelhus, 2005; Estrada-Ruiz *et al.*, 2010; Halamski, 2013). This floral provinciality must evidently have had an impact on herbivores, as they encountered diverging food sources in the north and south of Laramidia. The clustering of the hadrosaur specimens from Coahuila in a separate region of the microwear multivariate space from that occupied by the hadrosaurs from Alberta is consistent with this interpretation; however, additional studies with a larger sample size are needed to evaluate these results.

7. Conclusions

The analysis of dental microwear provided a preliminary assessment of the jaw mechanics and feeding ecology of the hadrosaurs from the Cerro del Pueblo Formation of northeastern Mexico. The predominance of dorsodistally-ventromesially inclined scratches indicates that the mandible primarily moved in an orthopalinal direction during the power stroke. This is comparable to what has been reported for *Edmontosaurus* from the Late Maastrichtian of Wyoming, U.S.A. (Williams *et al.*, 2009) as well as *Prosaurolophus*, *Corythosaurus*, and *Lambeosaurus* from the Late Campanian of Alberta, Canada (Mallon and Anderson, 2014).

In contrast, there are differences in the average number of pits and microwear feature width between the Alberta and the Coahuila hadrosaurs, with the latter presenting more pits and finer microwear features. Given the similar jaw mechanics between the Alberta and Coahuila hadrosaurs suggested by our study, the difference in average number of pits and microwear feature width are probably due to differences in the physical properties of the vegetation consumed and/or the type and amount of grit ingested. The greater number of pits and relatively low number of scratches in the hadrosaurs from Coahuila suggest that these dinosaurs ingested a greater quantity of hard food items, than the Alberta hadrosaurs. The small mean feature width observed in the specimens further indicates that these hard food items were small in size.

The floral diversity during the Late Cretaceous of the Cerro del Pueblo Formation suggests a hitherto unknown Upper Cretaceous ecological barrier that separated northeastern Mexico, located along the southern shoreline of Laramidia, from North Laramidia. The differences in dental microwear between the Coahuila hadrosaurs and the Alberta hadrosaurs are consistent with this interpretation. This barrier prevented terrestrial faunal interchange. In addition, a second ecological barrier must have existed within Coahuila separating the northern area (Aguja Formation) from the Parras Basin (Cerro del Pueblo Formation) to the south. This barrier was likely formed by specific plants that may have radiated within a small area. This interpretation is suggested by Rivera-Sylva *et al.* (2017) because of the separation of roughly coeval taxa of chasmosaurine ceratopsians (*Agujaceratops mavericus* in the north of Coahuila, *Coahuilaceratops magnacuerna* in the south). The existence of this ecological barrier is also suggested by the distribution of *Deinosuchus* (Rivera-Sylva *et al.*, 2011). This giant crocodilian is widely distributed in the southern U.S.A. and extends south into northern Coahuila, where it occurs in the Aguja Formation at La Salada. However, the taxon is characteristically absent in the Parras Basin (Cerro del Pueblo Formation) of southern Coahuila (Rivera-Sylva *et al.*, 2011).

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Table S1. Direction (0 – 360 degrees) of microwear scratches relative to the mesiodistal plane of the tooth in hadrosaur teeth from the Cerro del Pueblo Formation (late Campanian), Coahuila, Mexico. In CPC 1857 and CPC 1859 scratches were counted in a 400 X 400 µm area on the occlusal surface of the tooth. In CPC 1858 scratches were counted in two 400 X 400 µm areas on different locations of the occlusal surface of the tooth.

CPC 1857	CPC 1858	CPC 1859
82.266	77.347	51.34
82.476	77.735	52.253
84.428	86.634	53.843
84.753	86.028	54.926
82.011	79.796	55.67
83.758	75.466	56.004
88.238	74.578	56.31
79.261	81.573	56.976
83.66	83.157	57.031
83.928	79.461	57.995
83.911	80.407	59.3
83.884	85.815	59.589
77.196	80.727	59.676
137.834	76.504	59.744
156.705	70.71	59.744
149.216	45	59.826
125.34	55.257	60.141
137.231	49.236	61.991
100.84	34.695	63.435
142.496	39.806	64.359
112.443	125.311	64.398
115.641	120.579	65.376
141.17	124.216	71.565
125.166	104.931	85.135
142.907	110.556	86.055
63.435	117.474	87.274
30.735	111.038	87.397
30.579	122.735	90
29.859	116.095	92.01
15.945	120.141	94.865
71.274	109.25	95.826
66.615	119.745	97.524
69.146	115.866	104.876
79.461	77.242	106.074
33.275	24.624	108.122
20.807	118.179	108.178
	147.875	109.44
	141.71	113.07
	140.44	117.121
	141.633	123.977
	82.057	124.756
	80.074	
	83.047	
	81.085	
	81.404	
	71.565	
	72.734	
	70.224	
	78.996	
	81.634	
	76.43	
	84.382	
	64.799	
	42.138	
	56.023	
	66.801	
	74.476	
	126.193	
	114.944	
	112.306	
	115.201	
	119.932	
	146.535	
	144.246	
	145.84	
	124.216	
	120.141	
	113.356	
	140.826	
	116.565	
	120.256	
	141.953	
	112.479	
	115.821	
	110.556	
	29.745	
	45.674	
	50.194	
	51.34	
	41.424	
	41.424	
	70.201	
	72.408	
	70.821	