



Unrelated ornithopods with similar tooth morphology in the vicinity of Salas de los Infantes (Burgos Province, Spain): an intriguing case-study

P. E. Dieudonné^{1,2}  · F. Torcida-Fernández Baldor³  · P. Huerta-Hurtado^{3,4} 

Received: 2 March 2020 / Accepted: 18 September 2020 / Published online: 12 October 2020
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Abstract

The Lower Cretaceous of the Salas de los Infantes locality (Burgos Province, Spain) is extremely rich in monospecific ornithopod sites, each comprising a variety of cranial and postcranial remains. Among these, Vegagete and El Peñascal-1 lie in very close vicinity within the Upper Barremian–Lower Aptian Castrillo de la Reina Formation. In addition to other skeletal elements, these sites yield surprisingly similar teeth, which was viewed as an argument to regard the ornithopods from both sites as akin to each other. However, claiming phylogenetic affinity based on the sole tooth similarity is not satisfactory, as tooth similarity might also result from convergent evolution. This article tackles the question of the apparent similarity in tooth morphology between the ornithopods of both sites. Is it a result of convergent evolution or was it acquired from a close common ancestor? What are the ecological implications of their tooth morphologies and dental wear in terms of dietary niche partitioning? We discuss on the taxonomic relatedness of the ornithopods of both sites based on a detailed comparison of their teeth. We test for the morphometric differences and similarities between the tooth crowns of both assemblages through successive Student *t* tests and one Multivariate Analysis of Variance (MANOVA). Our conclusion is that although they bear similar teeth, the Vegagete and El Peñascal-1 ornithopods belong to different ornithopod lineages. The Student *t* tests show that the mesiodistal sharpness index is significantly higher in the Vegagete ornithopod. This is consistent with the formerly inferred kinship of this taxon with the family Rhabdodontidae, and probably indicates that the ancestors of this lineage became adapted to eating tough plant material since the Early Cretaceous.

Keywords Ornithopoda · Tooth morphometry · Mesiodistal sharpness index · Wear angulation · Dietary mode · Rhabdodontidae

✉ P. E. Dieudonné
dpolmil@gmail.com

F. Torcida-Fernández Baldor
fideltorcida@hotmail.com

P. Huerta-Hurtado
phuerta@usal.es

¹ Instituto de Investigación en Paleobiología y Geología (IIPG), CONICET, General Roca, 8332 Río Negro, Argentina

² Universidad Nacional de Río Negro-IIPG, General Roca, Río Negro, Argentina

³ Museo de Dinosaurios de Salas de Los Infantes and Colectivo Arqueológico-Paleontológico Salense (CAS), Plaza Jesús Aparicio 9, Salas de los Infantes, 09600 Burgos, Spain

⁴ Departamento de Geología, Escuela Politécnica Superior de Ávila, Universidad de Salamanca, Salamanca, Spain

Resumen

El Cretácico Inferior de la localidad de Salas de los Infantes (Provincia de Burgos, España) es extremadamente rico en yacimientos mono-específicos de ornitópodos que contienen una variedad de restos craneales y postcraneales. Entre ellos, los yacimientos de Vegagete y El Peñasal-1 están ubicados muy próximos entre sí dentro de la Formación Castrillo de la Reina, con una edad Barremiense Superior - Aptiense Inferior. Además, tienen la peculiaridad de haber proporcionado dientes sorprendentemente semejantes. Esto llevó a considerar los ornitópodos de ambos yacimientos como cercanamente emparentados. Sin embargo, esta afirmación no es satisfactoria ya que una similitud entre dientes podría resultar de una convergencia evolutiva. Este trabajo cuestiona la aparente similitud entre los dientes procedentes de los ornitópodos de Vegagete y El Peñasal-1. Se discute sobre las implicaciones de su morfología dental y de su desgaste dental en cuanto a adaptaciones masticatorias, nicho alimentario y relaciones filogenéticas. Analizamos la afinidad taxonómica de los ornitópodos procedentes de El Peñasal y Vegagete basándonos en una comparación detallada de sus dientes. Realizamos una comparación morfométrica de sus coronas dentales a través de unos tests *t* de Student y de un análisis multivariado (MANOVA), y discutimos sobre los resultados obtenidos. Nuestra conclusión apunta a que los ornitópodos de Vegagete y El Peñasal-1 no están emparentados. Los tests *t* de Student concluyen que los dientes del ornitópodo de Vegagete tienen un índice de esbeltez mesiodistal mayor, lo cual refuerza su afinidad con la familia Rhabdodontidae. Permite proponer que el linaje que comprende a los rhabdodontidos y a sus ancestros inmediatos habría seguido una tendencia evolutiva temprana, desarrollando dientes para alimentarse sobre plantas más duras desde el Cretácico Inferior.

Keywords Ornithopoda · Morfometría dental · Índice de esbeltez mesiodistal · Ángulo de desgaste · Modo de alimentación · Rhabdodontidae

1 Introduction

The Salas de los Infantes locality (Burgos Province, Spain) has yielded a high number of ornithopod assemblages, most of which are still poorly studied or lack any proper diagnosis (see Table 1). Notable among these are the ornithopod-bearing sites of El Peñasal-1 and Vegagete which lie in close vicinity within the Castrillo de la Reina Formation (Torcida Fernández-Baldor et al. 2005; Dieudonné et al. 2016). Torcida Fernández-Baldor et al. (2005) described the ornithopod teeth from El Peñasal-1 and observed their similarities with those of both “hypsilophodontids” (a waste-basket family that now solely contains *Hypsilophodon foxii*; see Boyd, 2015) and “rhabdomorphs” (a polyphyletic clade that was informally used to group together *Tenontosaurus*, *Muttaborrasaurus* and rhabdodontids; see Ruiz-Omeñaca 2001). No further analysis was provided up to now on what regards the systematics of the El Peñasal-1 ornithopod. The Vegagete ornithopod was first described as belonging to *Hypsilophodon* cf. *foxii* partly because of its teeth being similar to those of *Hypsilophodon foxii* (Fuentes Vidarte and Meijide Calvo, 2001). It was then referred to Ornithopoda indet. (Izquierdo et al. 2005a), and finally diagnosed as an early rhabdodontid within a broader Rhabdodontomorpha, comprising *Muttaborrasaurus langdoni*, *Rhabdodon priscus*, their common ancestor and all of their descendents (Dieudonné et al. 2016). However and sticking to the original definition of the clade that was given by Weishampel et al. (2003), the Vegagete ornithopod should in fact be seen as the closest known ornithopod outgroup of Rhabdodontidae within Rhabdodontomorpha (Dieudonné et al. 2020). Dieudonné et al. (2016)

noticed a strong morphological similarity between the teeth of the Vegagete and El Peñasal-1 sites, possibly indicating some phylogenetic affinity between the two taxa represented. However, these dental criteria could be of doubtful significance, as Fuentes Vidarte and Meijide Calvo (2001, p. 344) erroneously diagnosed the Vegagete ornithopod as belonging to *H. cf. foxii* on account of those same criteria.

Teeth are acting like “tools” for fracturing food (Strait, 1997), and their morphology might be regarded as the result of long-term adaptations to feed on a certain type of diet within a given environment (Fortelius et al. 2014; Davis and Pineda-Munoz 2016; Ungar and Hlusko 2016). On the other hand, dental wear is formed during mastication and results from attrition (i.e. the friction between upper and lower teeth), and abrasion (i.e. tooth-to-food contact, see Fortelius and Solounias 2000; Kaiser et al. 2013). The visible part of dental wear could be studied through a variety of parameters, (see a review in Ackermans 2020), and is an important element for inferring feeding habits in mammals (e.g. Fortelius and Solounias 2000; Saarinen et al. 2015; Ackermans 2020). The primary aim of this work is to disentangle the phylogenetic and ecological signals that underpin the apparent tooth similarity between the Vegagete and El Peñasal-1 ornithopods. The question of whether the teeth of both ornithopod assemblages are attributable to closely related species or not will be tackled through a detailed comparison of their dental characters, morphology, and wear facets development. Some of those comparative criteria will also be used in an integrative approach to analyse the masticatory habits of both ornithopods taxa.

Table 1 Early Cretaceous ornithopod material from the Salas de los Infantes locality (Burgos Province, Spain) that was previously mentioned, hosted at the Museo de Dinosaurios of Salas de los Infantes

| Fossil sites | Taxonomic attributions | Previous citations of the material |
|---|------------------------------|---|
| ACG: Valle del Arroyo Cisterna, La Gallega | Cf. <i>Valdosaurus</i> sp. | Ruiz-Omeñaca (2001) (fig. 13C) |
| ASMC: Arroyo San Miguel, Cabezón de la Sierra | Cf. <i>Hypsilophodon</i> sp. | Ruiz-Omeñaca (2001) (fig. 11A) |
| C-I: La Solana, Cabezón de la Sierra | <i>Hypsilophodon</i> sp. | Ruiz-Omeñaca (2001) (fig. 7D, E, 11B, C); Izquierdo et al. (2005b) |
| CPS: Carretera de Los Peñucos / La Ballesta | Hypsilophodontidae indet | Torcida Fernández-Baldor (1996); Ruiz-Omeñaca (2001) |
| VG: Vegagete, Camino de Salas a Villanueva | Rhabdodontidae indet | Fuentes Vidarte and Mejjide Calvo (2001); Izquierdo et al. (2005a); Dieudonné et al. (2016) |
| LPH: Los Peñucos, Hacinas | (?) Hypsilophodontidae indet | Ruiz-Omeñaca (2001) (fig. 11D-K) |
| OT-II: El Oterillo II | Iguanodontoidea indet | Contreras-Izquierdo et al. (2008) |
| PLS: El Peñascal | Ornithopoda indet | Torcida Fernández-Baldor et al. (2005) |
| RGH: Río Gete, Hacinas | Cf. <i>Hypsilophodon</i> sp. | Torcida Fernández-Baldor et al. (2003) |
| TBM: La Tejera | Iguanodontoidea indet | Torcida Fernández-Baldor (2006); Contreras Izquierdo et al. (2010) |
| LRZ: Las Rozas (formerly « El Horcajo ») | Cf. <i>Valdosaurus</i> sp. | Ruiz-Omeñaca (2001) |
| TV: Tenadas de Viajete | Ornithopoda indet | Unstudied (Torcida Fernández-Baldor (1996), (2006) |

2 Geological setting

The sites of Vegagete and El Peñascal (Fig. 1) are situated to about 1.5 km east of Villanueva de Carazo and 4 km southwest of Salas de los Infantes (Burgos Province, Spain). From a geological point of view, they are situated within the southeastern part of the Cameros-Demanda Massif. During the time frame extending from the Late Jurassic to the Early Cretaceous, the Burgos Province consisted in an extensional basin—the Cameros basin—and formed part of the Iberian rift system. The Salas de los Infantes area is located within the western part of the Cameros basin. It mainly hosts non-marine deposits (Salas and Casas 1993; Salas et al. 2001) with important dinosaur and other reptile sites and tracksites, all of which have been documented since the last decades (Pereda Suberbiola et al. 2003a, 2003b, 2011; Izquierdo et al. 2005a, b; Torcida Fernández-Baldor et al. 2006, 2011, 2017; Contreras-Izquierdo et al. 2008, 2010; Ruiz-Omeñaca et al. 2008; Huerta et al. 2012; Pérez-García et al. 2012; Houssaye et al. 2013). All the fossils that have been collected since that time are on display at the Museo de Dinosaurios de Salas de los Infantes. Vegagete and El Peñascal are respectively 650 m and 1200 m away from Viajete, another site that was already studied by Houssaye et al. (2013). All three are located in the southern limb of the Contreras-Hacinas anticline, within the Castrillo de la Reina Fm., and in a similar stratigraphic position within the same sedimentological context. This lithostratigraphic unit was assigned a Late Barremian–Early Aptian age (Martín-Closas and Alonso Millán 1998) based on a biostratigraphic correlation with the palynomorphs from the Abejar Fm. (Clemente and Alonso 1990). The Castrillo de la Reina Fm. is mainly composed of red mudstones alternating with

white to reddish sandstone beds up to 1 m. thick and with lenticular to tabular morphology. The mudstones have been interpreted as floodplain deposits (Platt 1986), while the sandstones occur as ribbon-shaped fluvial channel fills. The ornithopod remains from El Peñascal still have to be studied in details. They were specifically collected within levels of sandstone interpreted as crevasse splay deposits with flows not effective enough to separate the sand from the clay fraction. The remains considered in this paper were collected over an extension no greater than 6 square metres and in a single horizon within these sandstones: the horizon “1”. The name “El-Peñascal-1” refers to this specific horizon within the site of El Peñascal.

Note that all of the teeth found in El Peñascal appeared within El Peñascal-1, together with numerous cranial and postcranial ornithopod remains associated to these teeth (Torcida Fernández-Baldor et al. 2005). There is a small but singular size variation in the teeth from El Peñascal-1, but all of those teeth are similar to each other in all respects. This suggests that two differently sized individuals from the same ornithopod taxon were buried during a single event at this precise location. The remains of the El Peñascal-1 ornithopod are associated with a few isolated crocodylian osteoderms, one theropod tooth and a hollow bone that possibly belongs to a pterosaur. The ornithopod assemblage from Vegagete was surface-collected within a 1 square metre sedimentary pocket of red-clays. This assemblage also represents a monospecific herd composed by differently aged individuals, and these were buried together during a single catastrophic event (Fuentes Vidarte and Mejjide-Calvo 2001; Dieudonné et al. 2016).

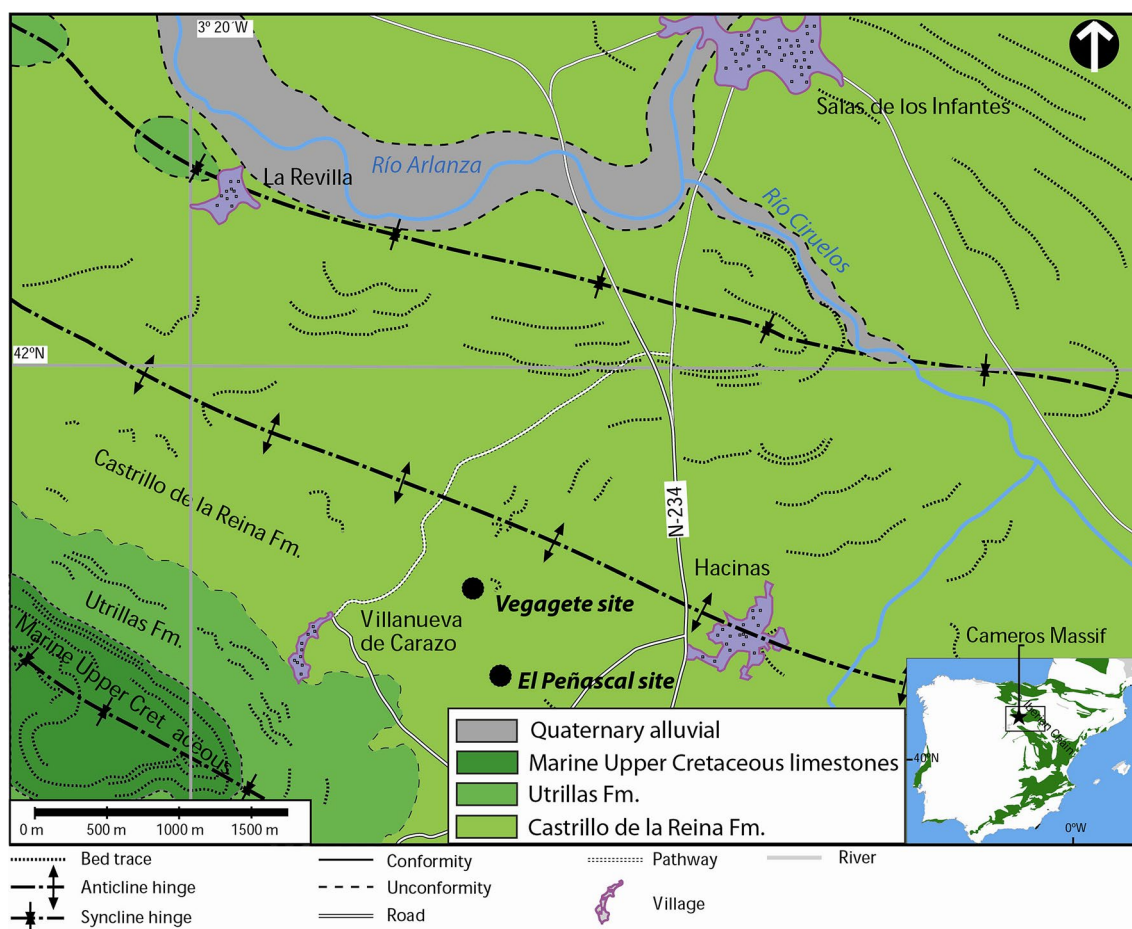


Fig. 1 Geological map of the Salas de los Infantes area in the South-Western part of the Cameros Basin, showing the locations of the Vegagete and El Peñascal sites

3 Materials and methods

All of the material described is curated at the Museo de Dinosaurios de Salas de los Infantes, legally integrated into the Museum system of the Castilla y León Autonomous Community (Order CYT/1210/2007, from June 15, 2007). The very first materials from the Vegagete site were collected by the Colectivo Arqueológico y Paleontológico de Salas and donated to the town hall of Salas de los Infantes for curation at the Dinosaur Museum. A prospecting campaign promoted by the Heritage General direction of the Castilla y León Autonomous Community (number of document 05/020-BU, Section: Research and development JDVR/MCP) was then launched to inventory the different paleontological deposits from the Salas de los Infantes area. This campaign allowed the collection of the remaining bones from the Vegagete site. Excavation campaigns that took place in 2004 and 2007 with the authorization of the Heritage General direction of the Castilla y León Autonomous Community (number of document Expte.

491/07-BU) allowed the collection of the skeletal remains from El Peñascal.

3.1 Institutional abbreviations

MDS Museo de Dinosaurios (Salas de los Infantes, Burgos, Spain).

PLS—Yacimiento de El Peñascal (Comunidad de Salas de los Infantes, Villanueva de Carazo, Hacinas, La Revilla y Barbadillo del Mercado; Burgos, Spain).

VG—Yacimiento de Vegagete (Comunidad de Salas de los Infantes, Villanueva de Carazo, Hacinas, La Revilla y Barbadillo del Mercado; Burgos, Spain).

The teeth of El Peñascal-1 were initially identified with the abbreviations PS-PLS (Torcida Fernández-Baldor et al. 2005), but are currently assigned the abbreviation MDS-PLS at the Museo de Dinosaurios de Salas de los Infantes.

We compare the wear angulations between the teeth from El Peñascal-1 and Vegagete. For doing so, we use a method of measure equivalent to that earlier proposed by

Weishampel (1984), by referring to the angle that is formed by (1) the dip of the wear surface and (2) the direction of the main occluding power stroke which correspond to a theoretical “vertical axis” (Fig. 2a, b). The main difficulty is that we only possess isolated teeth, so our theoretical vertical axis has to be defined without observing them in situ within their respective maxillae or mandibles. Roots are sometimes straight, and sometimes curving apicobasally within the tooth row (e.g. in MDS-VG, 16/17/152, Dieudonné et al. 2016, fig. 2C3). We suppose that tooth roots are parallel to the direction of the main occluding power stroke near their apicalmost region, i.e. at a point near the base of the crown. We therefore regarded our “vertical axis” as the orientation of the apical part of the maxillary and dentary tooth roots, basally to the raise of the cingulum. Such an axis should be equivalent whether we look at maxillary or dentary teeth, whence its potential interest from a taxonomic and an ecological perspective. Those wear angulations were obtained from a virtual screen protractor on photographs of teeth taken in distal views. Note that the angle that is formed by the cutting edge between the wear facet and the opposing enamelled surface is a completely different measure, and varies whether we consider the maxillary or the dentary teeth in both the El Peñascal-1 and Vegagete sites (Fig. 2a, b). This angle is more difficult to interpret and was therefore not considered.

Our morphometric analysis was performed with R (R. Core Team 2016) based on three morphological variables measured on 25 completely preserved teeth from Vegagete (6 maxillary and 8 dentary teeth) and El Peñascal-1 (4

maxillary and 7 dentary). These variables were measured on their tooth crowns and correspond to the crown height (CH), mesiodistal length (MDL) and labiolingual width (LLW, see Fig. 2 for details). In order to remove the size-effect, we transformed these variables as ratios of: (1) crown height to mesiodistal length (mesiodistal slenderness index: “MDSI”); (2) crown height to labiolingual width (labiolingual slenderness index: “LLSI”); and (3) mesiodistal length to labiolingual width (mesiodistal sharpness index: “MDSHI”). All of these variables are listed in Table 2. We wanted to test for the morphometric difference between the Vegagete and the El Peñascal-1 sites for the transformed variables MDSI, LLSI and MDSHI. The “boxplot.stats” function of R allowed detecting MDS-VG, 43 as an outlier for the variable MDSHI, with an unexpectedly high value for this variable within the Vegagete sample. MDS-VG, 43 is actually expanded mesiodistally, and further presents a drastically reduced labiolingual width at its crown base (Table 2). As briefly discussed below, the latter might have to see with its advanced stage of wear. MDS-VG, 43 was thus a posteriori removed from the analysis. The variables MDSI, LLSI and MDSHI were found as normally distributed and with a homogeneous variance ($p > 0.05$, see Table 3). We performed several two-tailed t tests for testing the pairwise difference of each variable’s mean between each site. In addition to the above-mentioned pairwise tests, we performed a Multivariate Analysis of Variance (MANOVA) to test for the tooth morphological similarity of the two ornithopod assemblages by considering all three dependent variables at the same time. Performing a MANOVA requires multivariate

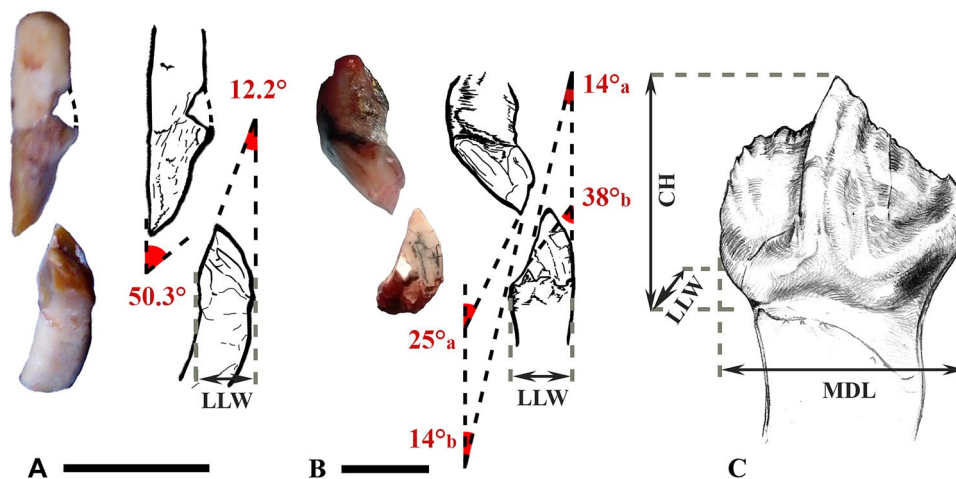


Fig. 2 Comparison of the dental occlusions in the Vegagete (a) and the El Peñascal-1 ornithopods (b), with an explanation of raw variables measurements (a–c). **A**, distal view of a maxillary tooth (MDS-VG, 35, reversed to left) and dentary tooth (MDS-VG, 33) from the Vegagete ornithopod; and **b** distal view of a maxillary tooth (MDS-PLS, 18) and a dentary tooth (MDS-PLS, 167, reversed to left) from the El Peñascal-1 ornithopod, all two with a duplicated sketch of their

photographs showing their wear angulation and a measure of labiolingual crown width. **c** Sketch of a dentary tooth from the Vegagete ornithopod (MDS-VG, 34) in lingual view, showing the measure of crown height, mesiodistal crown width, labiolingual crown widths. *CH* crown height, *LLW* labiolingual width, *MDL* mesiodistal length. Scale is 5 mm; **c** is without scale

Table 2 Descriptive table of the teeth coming from Vegagete and El Peñasal-1. Raw and transformed quantitative variables used in the present morphometric analysis are given (the former in millimetres, the latter without units)

| Specimen | Site | T | CN | MDWC | LLWC | CH | MDSI | LLSI | MDSHI | WA |
|-------------|------------|-----|----|------|------|------|------|------|-------|----------------------------------|
| MDS-VG, 9 | Vegagete | mx | 6 | 3.2 | 1.5 | 2.9 | 0.91 | 1.93 | 2.13 | 36 _{a-b} |
| MDS-VG, 32 | Vegagete | mx | 5 | 2.9 | 1.3 | 2.2 | 0.76 | 1.69 | 2.23 | 47 _{a-b} |
| MDS-VG, 35 | Vegagete | mx | 7 | 3.3 | 1.5 | 3.6 | 1.09 | 2.40 | 2.20 | 50.3 _{a-b} |
| MDS-VG, 37 | Vegagete | mx | 6 | 2.8 | 1.5 | 3.2 | 1.14 | 2.13 | 1.87 | 27.2 _{a-b} |
| MDS-VG, 41 | Vegagete | mx | 5 | 3 | 1.5 | 3.5 | 1.17 | 2.33 | 2.00 | 21.6 _{a-b} |
| MDS-VG, 43 | Vegagete | mx | 5 | 3.4 | 1.4 | 2.5 | 0.74 | 1.79 | 2.43 | 64 _{a-b} |
| MDS-VG, 3 | Vegagete | pmx | 0 | ? | ? | ? | ? | ? | ? | ? |
| MDS-VG, 36 | Vegagete | d | 4 | 3.6 | 1.8 | 2.8 | 0.78 | 1.56 | 2.00 | 18.6 _{a-b} |
| MDS-VG, 38 | Vegagete | d | 5 | 3.6 | 1.9 | 3.2 | 0.89 | 1.68 | 1.89 | 20.3 _{a-b} |
| MDS-VG, 39 | Vegagete | d | 4 | 2.9 | 1.7 | 3.8 | 1.31 | 2.24 | 1.71 | 20.5 _{a-b} |
| MDS-VG, 42 | Vegagete | d | 4 | 2.7 | 1.8 | 3.7 | 1.37 | 2.06 | 1.5 | ? |
| MDS-VG, 7 | Vegagete | d | 2 | 2.7 | 2 | 2.25 | 0.83 | 1.12 | 1.35 | ? |
| MDS-VG, 27 | Vegagete | d | 3 | 2.9 | 1.6 | 2.8 | 0.97 | 1.75 | 1.81 | 15.3 _{a-b} |
| MDS-VG, 33 | Vegagete | d | 4 | 3.4 | 1.9 | 3.2 | 0.94 | 1.68 | 1.79 | 12.2 _{a-b} |
| MDS-VG, 34 | Vegagete | d | 5 | 3.1 | 1.7 | 2.9 | 0.94 | 1.71 | 1.82 | 18 _{a-b} |
| MDS-PLS, 18 | El Peñasal | mx | 7 | 5.3 | 3.5 | 7 | 1.32 | 2 | 1.51 | 25 _a -14 _b |
| MDS-PLS, 25 | El Peñasal | mx | 6 | 3.5 | 2.1 | 4 | 1.14 | 1.9 | 1.67 | 35 _a -15 _b |
| MDS-PLS, 26 | El Peñasal | mx | 6 | 4.4 | 3 | 5.8 | 1.32 | 1.93 | 1.47 | 31.8 _a |
| MDS-PLS, 27 | El Peñasal | mx | 6 | 5 | 3 | 5 | 1 | 1.67 | 1.67 | ? |
| MDS-PLS,164 | El Peñasal | pmx | 1 | 3 | 2.1 | 3.6 | ? | ? | ? | ? |
| MDS-PLS, 21 | El Peñasal | pmx | 1 | 3.9 | 2.2 | 7.3 | ? | ? | ? | ? |
| MDS-PLS, 19 | El Peñasal | d | 3 | 5.9 | 4.1 | 7.7 | 1.31 | 1.88 | 1.44 | ? |
| MDS-PLS, 29 | El Peñasal | d | 3 | 5.3 | 3.3 | 5.2 | 0.98 | 1.58 | 1.61 | 2.7 _a -? |
| MDS-PLS, 30 | El Peñasal | d | 4 | 4.6 | 2.4 | 5.1 | 1.11 | 2.12 | 1.92 | 11 _a -30 _b |
| MDS-PLS, 35 | El Peñasal | d | 4 | 5.6 | 2.9 | 5.7 | 1.02 | 1.97 | 1.93 | 3 _a -40 _b |
| MDS-PLS, 36 | El Peñasal | d | 5 | 5.15 | 3.2 | 5.3 | 1.03 | 1.66 | 1.61 | 6 _a -? |
| MDS-PLS,167 | El Peñasal | d | 5 | 5.8 | 3.8 | 6.6 | 1.14 | 1.74 | 1.53 | 14 _a -38 _b |
| MDS-PLS,168 | El Peñasal | d | 1 | 4.45 | 2.55 | 3.8 | 0.85 | 1.49 | 1.75 | 12 _a |

Approximative values of mesowear angulations (in degrees) are also given. These were measured directly on tooth crowns photographed in distal views. Note that in the El Peñasal-1 assemblage, tooth wear is concavo-convex, so two measures are given: one for the apex of the crown (a), and another for the base of the crown (b). In the Vegagete assemblage, tooth wear is relatively straight, so wear angulation was approximately the same for the apex and the base of each crown (a-b)

d dentary, *m* maxillary teeth, *CN* number of primary and secondary ridges, *T* crown type, *MDWC* Mesiodistal crown width, *LLWC* labiolingual crown width, *CH* crown height, *Crests* number of primary and secondary ridges, *MDSI* mesiodistal slenderness index, *LLSI* labiolingual slenderness index, *MDSHI* mesiodistal sharpness index, *WA* wear angulation, *a* apex of the crown, *b* base of the crown

Table 3 Tooth shape variables and their respective mean, standard deviation (SD) and p values of the Shapiro-Wilks's normality test (H0=normal distribution), given separately for the Vegagete (V), El Peñasal (EP), and for both (V + EP) localities

| Variable\statistics | Mean (mm.) | SD (mm.) | Shapiro Wilks (p) | Levene (p) |
|-------------------------|------------|----------|-------------------|------------|
| MDSI _(V) | 1.0077 | 0.194 | 0.366 | NA |
| LLSI _(V) | 1.868 | 0.358 | 0.527 | NA |
| MDSHI _(V) | 1.869 | 0.166 | 0.672 | NA |
| MDSI _(EP) | 1.111 | 0.155 | 0.315 | NA |
| LLSI _(EP) | 1.813 | 0.197 | 0.798 | NA |
| MDSHI _(EP) | 1.646 | 0.166 | 0.275 | NA |
| MDSI _(V+EP) | 1.055 | 0.181 | 0.294 | 0.584 |
| LLSI _(V+EP) | 1.843 | 0.291 | 0.6981 | 0.153 |
| MDSHI _(V+EP) | 1.767 | 0.243 | 0.759 | 0.274 |

The p value of the Levene's test is given for both the Vegagete and El Peñasal samples as it tests for the homogeneous distribution of their variances (H0=homoscedastic distribution)

normal distribution of the whole data (R package “mvn”, Korkmaz et al. 2014). However, it was only achieved for one multivariate normality test out of four: the Royston’s test is positive with $p=0.67$, while the Mardia’s skewness test, Henze-Zirkler’s test and Doornik-Hansen’s test are negative with $p<0.05$. We therefore performed a nonparametric MANOVA with the R package “nrmv” (Ellis et al. 2017).

4 Description

Both sites yield maxillary and dentary teeth that are remarkably similar at first sight, with a similar ornamentation on their enamelled surface and a grossly similar morphology from a labiolingual view. However, the teeth from El Peñascal-1 (Fig. 3) are all somewhat larger than those from Vegagete (Fig. 4) and their premaxillary teeth are radically different.

4.1 Premaxillary teeth

In El Peñascal-1, premaxillary crowns look like labiolingually compressed isosceles-triangles (Fig. 3a1, a3). Their lingual surfaces are slightly bulbous at their bases and rather flat for the remaining part of the crown (Fig. 3a2). Their labial surfaces feature a wide central and smoothly convex apicobasal swelling (Fig. 3a3). The smaller

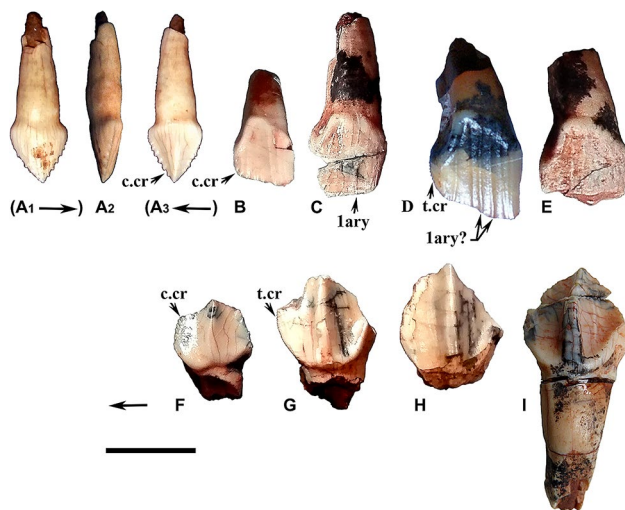


Fig. 3 Dentition of the El Peñascal-1 ornithopod. A left premaxillary tooth (MDS-PLS, 164) is visualized in lingual (a1), mesial (a2), labial views (a3). Maxillary teeth (b–e) are visualized in left labial view (b MDS-PLS, 25; c MDS-PLS, 26 reversed to left; d MDS-PLS, 18; e MDS-PLS, 27). Dentary teeth (f–i) are visualized in right lingual view (f MDS-PLS, 168; g MDS-PLS, 35; h MDS-PLS, 167; i MDS-PLS, 19 reversed to right). *lary* primary ridge, *c.cr* coarse crenulation, *t.cr* thin crenulation. Large arrows indicate the anterior direction: all the teeth have their mesial side to the left, except for MDS-PLS, 164 (a1, a2). Scale is 5 mm

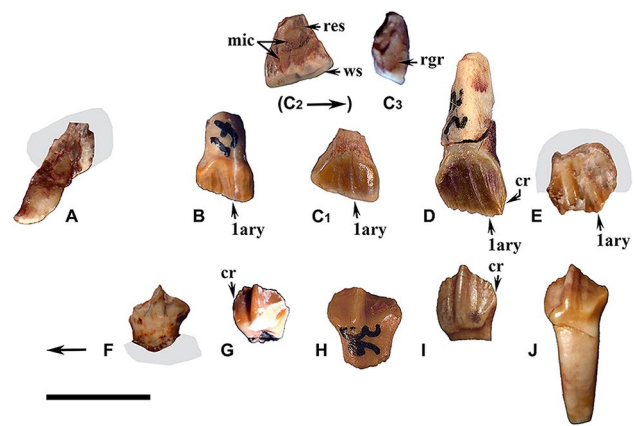


Fig. 4 Dentition of the Vegagete ornithopod. a Premaxillary tooth (MDS-VG, 3, reversed to right) visualized from right ventrolingual view. Maxillary teeth (b–e) are visualized in left labial view. b MDS-VG, 37 reversed to left; c1 MDS-VG, 43; d MDS-VG, 35 reversed to left; E, MDS-VG, 9 central, undamaged crown in situ within this posterior maxillary fragment). The left maxillary tooth MDS-VG, 43 is also visualized in lingual (c2) and mesial views (c3). Dentary teeth (f–j) are visualized in right lingual view (f MDS-VG, 27 in situ on an anterior dentary fragment; G, MDS-VG, 42 reversed to right; h MDS-VG, 36; i MDS-VG, 39 reversed to right; j MDS-VG, 34). *lary* primary ridge, *cr* crenulation, *mic* mark of incoming replacement tooth, *res* resorbed tooth root, *rgr* replacement groove, *ws* wear surface. Large arrows indicate the anterior direction: all the teeth have their mesial side to the left, except for MDS-PLS, 43 (c2, c3). Scale is 5 mm

premaxillary crown MDS-PLS, 164 maintains a straight alignment with respect to its root (Fig. 3a2), whereas the apex of the larger premaxillary crown MDS-PLS, 21 is smoothly lingually recurved (not shown). As for maxillary teeth, the mesial side of these premaxillary teeth might be recognized because of the anteriorly projecting basal protrusion of the crown (Fig. 3a3–e). Their thin, crest-like apical extremities are covered by coarse denticles all along their edges. These denticles are more heavily worn on the apicodistal side than on the apicomésial side (Fig. 3a1, a3). The denticles of the larger premaxillary tooth crown MDS-PLS, 21 are much thinner and more numerous (Torcida Fernández-Baldor et al. 2005, fig. 2A).

The premaxillary crown of the Vegagete ornithopod was analysed and photographed in medial (Fig. 4a) and medioventral views before it broke out after an unfortunate manipulation. Such a crown is unique-in-its-kind. It is small, tubular and does not swell at the root to crown transition. Rather, the whole section of the tooth shrinks at about two thirds of its height. The apical extremity is laterally convex, and its tip is medially inturned and fitted with tiny, almost undiscernible denticles (Fig. 4a). Every premaxillary teeth apparently had the same morphology as that described here, but were lost since their first description by Fuentes Vidarte and Meijide Calvo (2001).

4.2 Maxillary and dentary teeth

In both El Peñascal-1 and Vegagete, the maxillary teeth are spade-like and show a variable number of apicobasally extending secondary ridges on their labial surface. The number of secondary ridges ranges from five to seven in the maxillary teeth of both taxa, and the primary ridge is hardly discernible and the same width as them (Figs. 3b–e, 4b–e, Table 2). The cingulum swings up to a certain height mesially, and gives a mesially offset appearance of the crown from a labiolingual view. The mesial side of the crown is thicker basally than apically. The distobasal edge of the crown is thinner than the mesiobasal edge, and much less offset with respect to the outer root margin. The dentary teeth of both taxa feature a cingulum that swings up higher distally than mesially. They also feature a marked and prominent primary lingual ridge and very few, but rather straight secondary ridges (Figs. 2c, 3f–i, 4f–j). Denticles cover the distal and mesial margins of both the maxillary and dentary teeth (Figs. 3, 4). They sometimes also appear on their apical region when these are not worn. Contrary to mesial and distal denticles, apical denticles can at time develop into long secondary ridges that reach the base of the crown (Torcida-Fernández-Baldor et al. 2005, fig. 3E, 3F). In both the Vegagete and El Peñascal-1 taxa, the size of the denticles is inversely related to the size of the crown: larger crowns (Figs. 3d, g, 4d, 4i, j) feature smaller denticles, and smaller crowns feature coarser denticles (Figs. 3b, f, 4g).

This being said, some differences can be noted between the maxillary teeth and between the dentary teeth of both taxonomic assemblages. Denticles appear coarser in smaller specimens of both sites (Figs. 3f, 4g). However and considering the larger-sized teeth of both sites, the secondary ridges and denticles are thinner and much smaller in El Peñascal-1 (Figs. 3d, g, 4d, i, j). The primary ridge slightly deflects apicodistally in the apical region of the smaller maxillary tooth crown MDS-PLS, 25 (Fig. 3b), and do not deflect at all in larger maxillary tooth crowns of El Peñascal-1 (Fig. 3c–e). By contrast, the primary ridge is much apicodistally deflected from the base of the maxillary crowns apically in every maxillary teeth of the Vegagete taxon. Let us remark that the apicodistal deflection of this ridge provides the only criterion for assigning it to a primary ridge (Fig. 4b–e). In the Vegagete ornithopod, maxillary tooth crowns are covered by secondary ridges that are straight most of the times (Fig. 4c1). In a few instances however, those secondary ridges are sinuous and anastomosing on the distal region of the maxillary tooth crown (Fig. 4d). In the El Peñascal-1 ornithopod, secondary ridges are always straight and never undulate (Fig. 3b–i). As is commonly found in ornithopods, the enamel of both taxa is asymmetrically distributed and is thicker on the labial side of the maxillary teeth and on the lingual side of the dentary teeth. Although

their respective enamel thicknesses was not precisely measured, the Vegagete taxon clearly shows a thicker enamel than the El Peñascal-1 taxon (Fig. 2a, b).

4.3 Dental wear

Within the Vegagete dental assemblage, maxillary tooth wear angulation range from 20° to 64°, and dentary tooth wear angulation range from 12° to 20° (Table 2). Tooth wear occupies a relatively small area with respect to crown size and is straight in all cases. MDS-VG, 43 is the most heavily worn maxillary tooth from the Vegagete dental assemblage. This tooth features a lingual pit at the crown to root transition that is likely related with tooth resorption (Fig. 4c2). This tooth further presents markings related with the pushing of the incoming crown. Those markings appear through the crown to root transition and continue up to the apically worn surface of the crown (Fig. 4c2). MDS-VG, 43 has the most obtuse wear angulation among the Vegagete dental assemblage ($\approx 64^\circ$, Fig. 4c2, Table 2). Because of its abnormally thin crown base, we infer that MDS-VG, 43 was most certainly about to be shed at the time of the animal's death.

Within the dental assemblage of El Peñascal-1, wear angulation varies within a single tooth crown whether we consider the base or the apex of the worn surface (Fig. 2b, Table 2). Dentary teeth develop an extensively concave wear surface apicobasally in their later stage of wear. In those extensively worn dentary teeth, a labiobasal buttress is developed at the base of the labially worn surface (Fig. 2b). Conversely to dentary teeth, maxillary teeth always develop a smoothly convex wear surface (Fig. 2b). The basal wear angulation of maxillary teeth (14°–15°) and the apical wear angulation of dentary teeth (3°–14°) are acute and likely contacted against each other during the first step of dental occlusion. The apical wear angulation of maxillary teeth (25°–35°) and basal wear angulation of dentary teeth (30°–40°) form a greater angle with respect to the theoretical vertical axis, and likely contacted each other when the maxillary and dentary teeth were fully occluded with each other.

5 Morphometric results

The two-sided Student *t* tests showed a significant statistical difference between both ornithopod taxa for the parameter MDSHI ($t = 2.566$, $p = 0.0181$), but not for MDSI ($t = -1.447$, $p = 0.162$) and LLSI ($t = 0.475$, $p = 0.640$). The distribution of those variables can be better visualized in the box-plots (Fig. 3), where the boxes enclose the first and third quartiles of each variable's distribution and the median within them; minimum and maximum values are also displayed and linked to the box with the dotted-lines. Results from the MAnOVA (AnOVA-type test) showed

non-significant p-values ($T_A = 2.978$, $p = 0.064$ and $p = 0.065$ with 1000 permutations): the null hypothesis that the teeth from the El Peñascal-1 and Vegagete sites are morphologically similar and belong to a single homogeneous distribution cannot be rejected under an alpha significance level of 5%. Yet, the relative effects of each variable show that MDSHI has an important influence, and that this parameter is much higher in the Vegagete ornithopod (Table 4).

6 Discussion

6.1 Comparison of dental characters

The premaxillary teeth from El Peñascal-1 more closely resemble the premaxillary teeth of *Hypsilophodon foxii* (Galton 1974, fig. 13) than those of any other ornithopods. These are actually labiolingually compressed, lingually flat and show an isosceles-triangle outline. Premaxillary teeth of *Nanosaurus agilis* (Carpenter and Galton 2018, fig. 10A–D), *Thescelosaurus neglectus* (Boyd 2014, fig. 18A), *Convulosaurus marri* (Andrzejewski et al. 2019, fig. 5) are bulbous throughout their whole periphery and until their apices. The premaxillary teeth of *Haya griva* (Makovicky et al. 2011, fig. 1A, B, p. 631), *Jeholosaurus shangyuanensis* (Barrett and Han 2009, fig. 3A, p. 50) and *Changchunsaurus parvus* (Jin et al. 2010, fig. 3A, p. 211) are also bulbous though slenderer at their base, and lack any kind of serration. The premaxillary tooth crown of the Vegagete taxon is the only one to lack a bulbous swelling at its base within Ornithopoda (Dieudonné et al. 2016, character #133). Its premaxillary tooth crown is also very small and slender (Fig. 4a). All of these characteristics make it radically differ from the premaxillary teeth known from all other ornithopods, including those from the El Peñascal-1 taxon. Yet, the premaxillary tooth of the Vegagete taxon still shares its lingually recurved apex with other ornithopods, and the presence of denticles with ornithopods more derived than *Haya griva*, *Jeholosaurus shangyuanensis* and *Changchunsaurus parvus* (Fig. 4a). Because of the evolutionary trend toward premaxillary tooth loss in basal iguanodontians (Winkler et al. 1997; Dieudonné et al. 2016), the slenderness of the premaxillary tooth crown

of the Vegagete taxon argues in favour of a derived phylogenetic positioning of the Vegagete taxon with respect to the El Peñascal-1 ornithopod.

At first sight, the maxillary and dentary teeth of the Vegagete and El Peñascal-1 ornithopods show no major differences. In every maxillary teeth known from the El Peñascal-1 ornithopod, the crown is lingually bent with respect to the root, and depending on the degree of wear, the crown sticks out from the lingual surface of its own root in mesiodistal view (Fig. 2b). This feature appears more variable in the Vegagete ornithopod. Some maxillary teeth have their crowns aligned to their roots (Fig. 2a), some other feature a lingual bending. This character might vary within a single tooth row in the Vegagete taxon. But we are unable to affirm whether there was a similar variation within the maxillary tooth row of the El Peñascal-1 taxon or not. = The maxillary teeth of both taxa are spade-like and labially covered by five to seven subparallel secondary ridges. The width of the primary ridge is subequal to that of the secondary ridges, and is hardly discernible from them (Figs. 3, 4). These characteristics are widely distributed in clypeodont ornithopods and occur, among other examples, in *Hypsilophodon foxii* (Galton 2009, fig. 2–3), *Mochlodon vorosi* (Ösi et al. 2012, fig. 4D, F), *Tenontosaurus tilletti* (Thomas 2015, fig. 23.1), *Atlascopcosaurus loadsi*, an indeterminate ornithopod from Australia (Bell et al. 2018, fig. 6), *Galleonosaurus dorisae* (Herne et al. 2019, fig. 13.3), *Convulosaurus marri* (Andrzejewski et al. 2019, fig. 11), *Talenkauen santacrucensis* (Rozadilla et al. 2019, fig. 3A). Their dentary teeth further exhibit a very strong central ridge, as is also common for most non-dryomorphan ornithopods such as *Hypsilophodon foxii* (Galton 2009, fig. 3K, M); *Talenkauen santacrucensis* (Rozadilla et al. 2019, fig. 9B), *Kangnasaurus coetzeei* (Cooper 1985, fig. 3A, C), or rhabdodontids (e.g. Ösi et al. 2012, fig. 4a; Godefroit et al. 2009, Fig. 11A). Hence, those characters might be of poor use for differentiating among clypeodont ornithopods.

Subtle differences in the ornamentation of the enamelled surfaces of maxillary and dentary crowns were observed between the Vegagete and the El Peñascal-1 taxon, and are of potential taxonomic significance. These characters are listed as follow.

1. The denticles are thinly crenulated and more numerous in the El Peñascal-1 ornithopod than in the Vegagete ornithopod (Fig. 2). Galton (2009, p. 221, fig. 3G–O) describes the denticles on the dentary teeth of *Hypsilophodon foxii* as “numerous fine marginal denticles [...]”, so they might be comparable to those found in the larger-sized teeth from the El Peñascal-1 taxon. The denticles of *Tenontosaurus tilletti* (Thomas 2015, fig. 23.1, 23.2, 47) and dryosaurids (Carpenter and Galton 2018, fig. 28DD–FF) are relatively thin, but are

Table 4 Empirical nonparametric relative effects of treatment group (i.e. the tooth-bearing ornithopod sites of El Peñascal and Vegagete) for each tooth morphometric variable

| Site\variable | MDSI | LLSI | MDSHI |
|---------------|--------|--------|--------|
| El Peñascal | 0.6888 | 0.4161 | 0.2308 |
| Vegagete | 0.3112 | 0.5839 | 0.7692 |

The effects give the probability that one randomly selected measure for a given site is higher than all other measures of the same variable, whichever the site

also longer than those of *Hypsilophodon foxii* and the El Peñascal-1 taxon. Denticles are coarser in Late Cretaceous rhabdodontids (Chanhasit 2010, fig. 4.9C, G; Ösi et al. 2012, fig. 4A; Brusatte et al. 2017, fig. 4B), *Convulosaurus marri* (Andrzejewski et al. 2019, fig. 1A, C), *Thescelosaurus neglectus* (Boyd 2014, fig. 18B, C) and *Talenkauen santacrucensis* (Rozadilla et al. 2019, fig. 11A, B). Both *Thescelosaurus neglectus* and *Talenkauen santacrucensis* differ from every aforementioned taxa in that their denticles are confluent with very coarse secondary ridges even in their mesialmost and distal-most margins (Boyd 2014, fig. 19; Rozadilla et al. 2019, fig. 11B).

2. There is no apicodistal deflection of the primary ridge in the larger maxillary teeth of the El Peñascal-1 taxon (Fig. 3c–e). In *Tenontosaurus tilletti*, the secondary ridges are relatively straight; the primary ridge starts deflecting apicodistally from an apical region (Thomas 2015, fig. 23.1). In the Vegagete taxon however the primary ridge is systematically deflected apicodistally, starting from the base of the maxillary tooth crowns (Figs. 3b–e, 4b–e). One maxillary tooth crown of *Mochlodon vorosi* shows an apicodistally deflecting primary ridge (Ösi et al. 2012, fig. 4D), but this pattern is obscured by wear in other maxillary teeth (Ösi et al. 2012, fig. 4F). Other Late Cretaceous rhabdodontids feature straighter and apicobasally oriented primary and secondary ridges (Weishampel et al. 2003, fig. 13A, D; Godefroit et al. 2017, fig. 3C).
3. The teeth of the Vegagete taxon show overall thicker enamel than these of the El Peñascal-1 taxon (e.g. Fig. 2a, b). In *Matheronodon provincialis*, the enamel is thicker than in *Edmontosaurus* (Godefroit et al. 2017). Unfortunately, enamel thickness was never precisely measured in other, non-ankylopollexian ornithopods.

6.2 Comparison of dental wear

The maxillary and dentary teeth of ornithopods are self-sharpening by attritional and abrasive processes during mastication. This creates a common, diagonal shearing surface when both maxillary and dentary teeth are occluded (Weishampel, 1984; Williams et al. 2009). Ornithischian tooth wear angulation was first analysed by Weishampel (1984) on tooth-bearing maxillae and mandibles of “fabrosaurids”, “heterodontosaurids”, “hypsilophodontids”, iguanodontids and hadrosaurids, but has only rarely been paid attention since. Wear angulation is measured with respect to fixed plane, chosen by Weishampel (1984, p. 60) as the “horizontal plane” formed by the maxillary and dentary tooth rows in occlusion. In the present study, we mostly dispose of isolated teeth. We analyse the angle formed by the wear surface and a theoretical vertical axis, which should

in theory be perpendicular to the occlusal plane (Fig. 2a, b). This angle is therefore the difference between 90° and Weishampel’s (1984) angle. This measure is interesting as the inclination of the common wear surface formed by the occluded maxillary and dentary teeth is supposed to remain fixed at a single tooth position, and might only change with the advancement of tooth wear at a single tooth position. It is possible that wear angulation slightly changed from back to forth within a single tooth row, but such a variation was never reported or quantified in any ornithischians. The globally homodont dentition of ornithopods suggests that a large variation of the wear surface’s inclination is unlikely within a single tooth row. Therefore, wear angulation is a priori expected to be roughly similar for all teeth within a given species, and might vary only among different species.

Our data shows that wear angulation varies importantly whether we look at maxillary or dentary teeth in the Vegagete dental assemblage. Wear angulation of maxillary teeth ranges from 20°, and raises up to 64° in extremely worn maxillary tooth crowns (Table 2, see MDS-VG, 43, Fig. 4c2). By contrast, wear angulation varies roughly from 12° to 20° in dentary teeth (Table 2). Our observations suggest that dental wear increases and gets more obtuse accordingly to the advancement of wear in the maxillary teeth (see the extremely open wear angulation of MDS-VG, 43 in Table 2 and Fig. 4c3), but not in the dentary teeth. However, wear angulation is theoretically supposed to remain fixed at a given tooth position. The only explanation to such a “departure” from the baseline wear angulation in heavily worn maxillary teeth is that, as maxillary teeth are getting worn down, they are being pushed-up apicolingually by the upcoming and neighbouring maxillary tooth crowns. The tilting of their long axis could therefore induce a change in the wear surface angulation with respect to a slightly rotated tooth, but this angle would remain fixed with respect to the “real” vertical axis. The moderately worn maxillary tooth MDS-VG, 35, and the extremely worn maxillary tooth MDS-VG, 43 (Fig. 4c3) all two feature a more open wear angulation and strong replacement groove onto the mesial surface of their roots, which continue up to the base of their crowns. Replacement grooves are not observed in other maxillary teeth. The co-occurrence of replacement grooves together with a more open wear angulation suggests that both features could be related to each other in worn maxillary teeth. We might suggest that these teeth were pushed-up by incoming, adjacent maxillary tooth crowns and this induced a progressive apico-lingual tilting of their apices with respect to the “real” vertical axis. However, this might only be ruled out after observing the conjunction of these two parameters in teeth preserved in situ within their jaws. Only one complete maxillary tooth was preserved in situ within the maxillary fragment MDS-VG, 9, and this tooth does not show indices of having been tilted. In Late Cretaceous European

rhabdodontomorphs, replacement grooves are observed at the mesial and distal margins of maxillary and dentary teeth, probably for accommodating the growth of closely packed neighbouring teeth (Weishampel et al. 2003, fig. 13). In *Matheronodon provincialis*, maxillary teeth are so large that they occupy two alveoli when they are fully grown (Godefroit et al. 2017).

In the El Peñascal-1 taxon, wear angulation is smoothly convex in maxillary teeth and concave in dentary teeth. Therefore, it varies apicobasally within a single tooth. As stated above, wear angulation is supposed to be the same in two occluded teeth. Here, we have to consider the concavo-convex occlusal contact between the wear surfaces of the maxillary and dentary teeth. The apical wear of maxillary teeth (ranging from 25° to 35°) and the basal wear of the dentary teeth (from 30° to 40°) are relatively open. By contrast, the apical wear of dentary teeth (ranging from 3° to 14°) and the basal wear of maxillary teeth (around 15°) are always relatively sharp and acute. A reverse pattern of wear angulation at the base and apex of each maxillary and dentary tooth is expectable if we consider a concavo-convex occlusion. The apex of the maxillary teeth would contact the base of the dentary teeth (1), and the base of the maxillary teeth would contact the apex of the dentary teeth (2). The wear angulation that is formed during the first phase of dental occlusion should theoretically be measured at the base of the worn maxillary teeth and at the apex of worn dentary teeth (1).

In the Vegagete ornithopod, no difference in wear angulation is observed at the base or at the apex of the wear surface, and wear angulation is always straight. If we compare the wear angulation formed during the first phase of dental occlusion in the El Peñascal-1 ornithopod with the wear angulation of the Vegagete ornithopod, we see that the minimum angulation is much sharper in El Peñascal-1 than in Vegagete, and maximum wear angulation is more obtuse in the Vegagete taxon (Table 2). The wear angulation of both taxa overlaps at about 12° to 15°. The dental wear angulation of the basal ornithopods *Changchunsaurus parvus* (Chen et al. 2018, fig. 7A), *Nanosaurus agilis* (Carpenter and Galton 2018, fig. 10F) and that of the basal clypeodont ornithopod *Hypsilophodon foxii* (Galton 2009, fig. 2T) appears more acute than that of more derived iguanodonts such as rhabdodontids (Ösi et al. 2012; fig. 4G; Godefroit et al. 2017) and hadrosaurids (e.g. LeBlanc et al. 2016, fig. 1B). However, and as the measures of Weishampel (1984, Table 1) have shown, wear angulation often overlaps for some degrees between taxa. In the Vegagete ornithopod, wear angulations increases with the wear of maxillary teeth. Although this could not be proved, it is possibly an artefact resulting from the in-life tilting of the tooth. Note that the precision of our wear angulations must be subject to caution, as (1) they were obtained from photographs and (2), they

were measured on isolated teeth. As a whole, no definitive conclusions should be drawn about the apparent differences in wear angulations between the Vegagete and El Peñascal-1 taxa until precise measures (for example, by means of Ct-scans) are taken on a sufficient array of complete jaws preserving in situ teeth.

6.3 Questioning morphometric results

Two species living within the same ecosystem and featuring similar tooth morphologies might indicate stronger competition for accessing food resources (see Ricklefs and Miles 1994). Convergence in herbivorous modes is more likely to occur when considering phylogenetically contingent species (Button and Zanno 2019). A striking example is that observed in the Santonian of Hungary, where the teeth of the neoceratopsian *Ajkaceratops kozmai* and the teeth of the rhabdodontid *Mochlodon vorosi* were found to be morphologically similar to each other (Virag and Ösi 2017). In our case, the p-value given by the MANOVA is relatively close to the alpha significance level of 5% ($p = 0.065$), which is critical for accepting the null hypothesis. Given the small sample size and the closeness of the p value to the 5% alpha level, the power of the analysis might be weak, and the risk of making a Type-II error inversely elevated (Cohen 1998). Therefore, nothing should be safely concluded as to what regards the result of the MANOVA. It is worth noting that the variable MDSHI had an important “positive” effect within the MANOVA (Table 4), indicating that this variable has an influence on the results and is relatively high in the Vegagete taxon as compared to the El Peñascal-1 taxon. By contrast, MDSI and LLSI cannot safely discriminate between the dental assemblages of both sites. We might point out however that the latter two variables are calculated by accounting for the apicobasal crown height, which is biased by the advancement of tooth wear and the way that tooth wear takes place in both taxa.

It is worth noting that the teeth of Late Cretaceous rhabdodontids had evolved surprisingly large, blade like morphologies by the end of the Cretaceous (e.g. *Matheronodon provincialis*, Godefroit et al. 2017). Such extreme tooth morphologies might have emerged from a long history of environmental pressures to feed on a certain type of diet. Competition is one of the most fundamental ecological interactions between species, and an important driving force of evolution (Gause 1932; Grover 1997; Price and Kirkpatrick 2009). Two species with similar tooth morphologies and feeding on a similar food resource may coexist and compete with each other until some degree of dietary resource overlap occurs (Jaeger 1974). At this point, these species would strive to minimize interspecific competition and, by doing so, directionally evolve and specialize to get better adapted to some kind of found resource not exploited by

their closest competitor (Price and Kirkpatrick 2009). The blade like teeth of rhabdodontids might have arisen from “raw” blade-like morphology. The teeth of dryomorphs are mesiodistally short and diamond-shaped (Galton 1983, fig. 4I–R), so they are not the best ‘candidates’ for providing such a raw tooth morphology. The teeth of many other ornithopods such as *Hypsilophodon foxii* (Galton 2009, fig. 2–3) are spade-like and far more “generalized”. The El Peñascal-1 taxon shows similarities with *Hypsilophodon foxii*, notably because of the overall shape of its maxillary and dentary teeth, but also because of its retention of triangular and labiolingually compressed premaxillary teeth (Fig. 3a2, Galton 2009, fig. 2L–P). The MDSHI differs between the Vegagete and the El Peñascal-1 ornithopods, and is clearly higher in the Vegagete taxon (Figs. 2a, b, 5). The Vegagete ornithopod is the closest ancestor of the European-endemic Rhabdodontidae sensu Weishampel, Jianu, Csiki and Norman 2003 (Dieudonné et al. 2016). The thickly enamelled, blade-like teeth of this taxon are coherent with a phylogenetic rooting close to the base of the Rhabdodontidae, and suggest a distinct dietary mode for this lineage. However, caution should be brought as no thorough multivariate morphometric analysis was ever performed to tackle this question within a more exhaustive sample of Lower Cretaceous ornithopods.

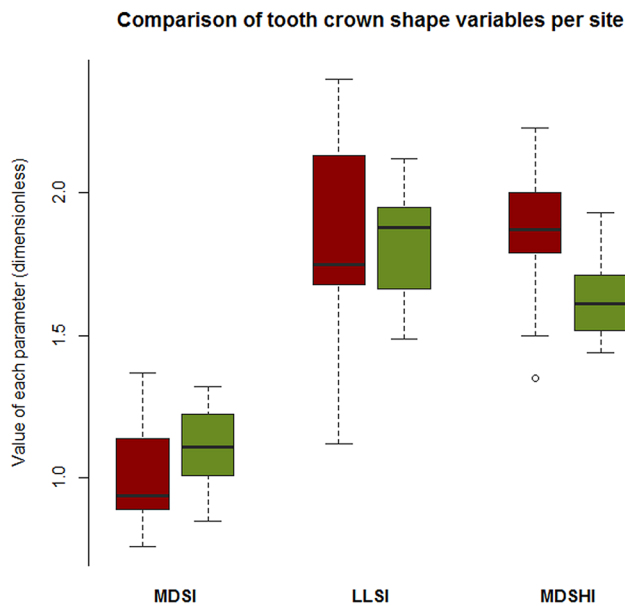


Fig. 5 Box-plots comparing the distributions of the tooth crown shape variables MDSI (Mesiodistal slenderness index), LLSI (Labiolingual slenderness index) and MDSHI (Mesiodistal sharpness index) for the Vegagete (red) and El Peñascal-1 (green) sites, with the outlier MDS-VG, 43 removed. Each box encloses the values taken between the first and third quartiles, and the horizontal black line represents the median value. Dashed-lines extend up to the maximal and minimal value of each variable

6.4 Different modes of mastication

Combining and integrating our above observations and results on the variables MDSHI, enamel thickness and wear angulation might be potentially interesting for differentiating between masticatory modes. “Long” blade-like teeth were previously argued to relate with the ability of slicing tough and high-fibred vegetation (Strait 1997; Godefroit et al. 2017). A thicker enamel cap provides additional resistance to the tooth for doing so (Strait 1997; Ungar and Hlusko 2016). Wear angulation is related to wear facet development, and therefore to the movements of the upper and lower jaws against each other (Williams et al. 2009). The wear surfaces observed in the teeth from El Peñascal-1 present some obvious differences with those observed in the teeth from Vegagete. The higher sharpness index and thicker enamel is coherent with the straighter wear surfaces observed in the teeth of the Vegagete ornithopod. The blade-like teeth of the Vegagete rhabdodontomorph would have been worn with a greater apicobasal component, so mesiodistally long teeth would have allowed for a greater resistance to the vertical shear forces applied between the upper and lower teeth. Conversely, the more acute wear angulation and development of concavo-convex wear in the teeth of the El Peñascal-1 ornithopod are coherent with their greater labiolingual thickness (Fig. 2b). In this case, the concavoconvex wear would have allowed to grind vegetation with a greater labiolingual component. The teeth of this ornithopod would have therefore coped with tooth wear by increasing their own lifetime and the total amount of tooth material to be grinded in the labiolingual direction.

7 Conclusions

Discriminating two ornithopod taxa based on their teeth can be challenging, and requires a thorough examination of dental characters. The marked differences in premaxillary tooth shapes provide undisputable evidence that the Vegagete ornithopod is more derived than the El Peñascal-1 ornithopod. Despite of sharing a number of common superficial characters, the maxillary and dentary teeth from El Peñascal-1 and Vegagete could be distinguished based on faint differences in ornamentation such as the size of the denticles or the orientation of the primary ridge on the maxillary teeth. Major differences between their cheek teeth are related to the shape and extension of their wear, their enamel thickness and their mesiodistal sharpness index. The distinct type of wear observed between both taxa—i.e. apicobasally extending and concavoconvex, or smaller and straighter—is likely related to a distinct type of chewing, while higher enamel thickness and mesiodistal sharpness indices are related to the tooth resistance to crack propagation when feeding on tough

plant materials. We suggest that tooth wear might evolve differently in the El Peñascal-1 and in the Vegagete ornithopods. Wear might take place with a greater labiolingual component in the former, and a greater apicobasal component in the latter. To end-up with, the higher mesiodistal sharpness index and thicker enamel cap of the Vegagete ornithopod teeth are coherent with the phylogenetic rooting of this taxon close to the base of the Rhabdodontidae. We suggest that the teeth of the Vegagete ornithopod presage the famous, large blade-like teeth that were found in derived Late Cretaceous rhabdodontids, marking the early steps of a long evolutionary tendency. Such a hypothesis should be tested through additional quantitative morphometric analysis including a larger array of Lower Cretaceous ornithopods teeth.

Acknowledgements We are much grateful to Caterine Arias Riesgo, conservator of the Museo de los Dinosaurios de Salas de los Infantes, for her personal investment and for her measurements of the raw variables necessary to finalize this study. We also thank Ferrán Guinovart, who prepared some of the teeth analysed in this study. We are grateful to the Museo de Dinosaurios for allowing the access and analysis of the materials included in this work, and to the Colectivo Arqueológico y Paleontológico de Salas (C.A.S.) for the information provided about the prospecting and excavation campaigns that took place in the sites of El Peñascal and Vegagete. The comments made by Attila Ősi and another anonymous reviewer greatly improved the quality of the manuscript.

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