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DIETARY INSIGHTS OF THE PHYTOPHAGOUS DINOSAURS FROM THE LATE CRETACEOUS IBERO-ARMORICAN ISLAND

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ABSTRACT

This study presents the preliminary results of an active investigation on the diets and ecological dynamics of the main groups of megaherbivorous dinosaurs (Lambeosaurinae, Titanosauria) of the Upper Cretaceous of what was the island of Ibero-Armorica (SW of Europe). The chewing mechanics and dietary preferences of different dinosaurs from the Spanish and French Pyrenees have been interpreted by characterizing a sample of teeth and comparing their microwear. The results of this analysis show that lambeosaurines from the Basturs Poble and L'Espinau sites share similar dietary preferences and processing methods, being generalists and feeding at low altitudes on relatively tender vegetation. Conversely, the French lambeosaurine Canardia garonnensis would selectively feed on harder vegetation. The titanosaur of Els Nerets would be a generalist that would feed on tender vegetation at a medium-high height. These results indicate a potential partition of the ecological niche and the co-existence between both groups during the Lower Maastrichtian.

Keywords: Microwear, Titanosauria, Lambeosaurinae, Maastrichtian, Europe.

1. INTRODUCTION

Megaherbivores (animals with a bodyweight > 1000 kg) are one of the chief agents influencing community structure and dynamics of present terrestrial ecosystems (Hawkes & Sullivan, 2001). Unlike smaller taxa, extant megaherbivore diversity is mainly controlled by food resource availability, rather than other processes such as predation (Fritz *et al.*, 2002). As such, the study of dietary preferences of extinct megaherbivores is pivotal for un-

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derstanding changes in palaeodiversity, as well as the ecological constraints operating in the palaeoecosystems (Mallon & Anderson, 2014).

During the Maastrichtian, Ibero-Armorica represented the largest island of the European Archipelago, encompassing the area of present-day Iberia (Portugal and Spain) and southern France. Ecosystems of this region were dominated by multi-ton titanosaurian and ornithopod dinosaurs, as demonstrated by their increasingly diverse fossil record. Some palaeoecological studies have demonstrated a fluctuation in the the diversity and abundance of both groups, with a transition of titanosaurian-dominated to lambeosaurine-dominated ecosystems throughout the Maastrichtian (Vila *et al*., 2016). Microwear analysis is widely used for the study of dietary preferences of extinct taxa. This technique quantifies the shape and number of microscopic marks that food produces on the surface of the teeth, especially on the occlusal wear facets (Ösi *et al*., 2022). The morphology, size, orientation, and frequency of microwear features are determined by the dynamics of jaw movements and the physical properties of the ingested food. As a result, it represents a reliable tool for the characterisation of niche partitioning and biome occupation in extinct taxa (Ösi *et al*., 2022). The present study aims to provide the first insights on this subject, showcasing results of an ongoing research on the dietary preferences of the Maastrichtian megaherbivorous dinosaur faunas of the Ibero-Armorican Island during the Late Cretaceous. This work will focus on the differences in tooth microwear of sympatric and phylogenetically closely related taxa of both groups in order to discern palaeodietary adaptations that elucidate their niche occupation, as well as its palaeobiological implications.

2. MATERIALS AND METHODS

2.1. Materials

The elements herein analyzed include: two titanosaur teeth (MCD (Museu de la Conca Dellà)-9885.20, MCD-9885.44) from a single individual found at the early Maastrichtian site of Els Nerets (Vázquez *et al*., 2023), one lambeosaurine tooth (MCD-5014) from the early Maastrichtian Basturs Poble site (Gaete, 2021), and two lambeosaurine teeth from the late Maastrichtian localities of L'Espinau (field number ESP-813; Vila *et al*., 2016)

2.2. Microwear analysis

Owing to the thinness of enamel in dinosaur teeth (≈100µm), we analyzed orthodentine microwear, unless otherwise stated, as it has been demonstrated to preserve an equivalent dietary signal to that of enamel (Green, 2009), albeit slightly coarser. The microwear patterns were microphotographed using a scanning electron microscope (SEM) 3-SEM QUANTA-200 at the facilities of the Centres Científics i Tecnològics de la Universitat de Barcelona. Secondary electron images were acquired at variable pressure with a beam current of 12 Kv and 500X magnification. The resulting

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images were processed with IMAGEJ/FIJI v2.14 to obtain the microwear parameters. Microwear features are categorized after Ungar (1996) as either "pits" (length/width ratio <4) or "scratches" (length/width ratio >4). Additionally, both types of features were subcategorised: scratches as "fine" (width <3µm) or "coarse" (width >3µm) and pits as "small" (diameter <8µm) or "large" (diameter >8µm).

3. RESULTS

Sample	MCD-9885.20	MCD-9885.44	ESP-813 (apical)	ESP-813 (central)	MA3.16 (apical)	MA3.16 (central)	MCD-5014
	Els Nerets	Els Nerets	L'Espinau	L'Espinau	Tricouté-3	Tricouté-4	Basturs Poble
nS	40	93	86	79	23	20	37
Size_S	Fine	Fine	Fine	Fine	Coarse	Coarse	Coarse
Mean_S	Fine		Fine		Coarse		Coarse
nP	6	1	27	56	13	12	24
Size_P	Small	Small	Small	Small	Small	Large	Small
Mean_P	Small		Small		Large		Small
P/S	0.15	0.01	0.31	0.71	0.57	0.60	0.65
SW	1.21	2.40	2.76	2.34	3.30	4.02	3.42
Mean_W	1.81		2.55		3.66		3.42
PD	3.00	8.00	6.05	4.25	5.60	12.19	6.33
Mean_D	5.50		5.15		8.90		6.33
%P	13.04	1.06	23.89	41.48	36.11	37.50	39.34
%S	86.96	98.94	76.11	58.52	63.89	62.50	60.66

Table 1. Microwear parameters of the studied teeth. nS/nP: number of scratches/pits; Size_S/P: size of scratches/pits; Mean_S/P: mean size of the scratches/pits of a specimen; P/S: ratio of pits/scratches; SW: mean scratch width; PD: mean pit diameter; Mean_W/D: mean scratch width/pit diameter of a specimen; %P/S: percentage of pits/scratches. Dimensions are in µm.

The parameters used to study the microwear patterns are shown in Table 1. All the studied specimens showed some degree of dental microwear on their wear facets.

3.1. Lambeosaurinae

In ESP-813 and MA3.16, we analysed the microwear of the apical and central labiolingual areas in order to assess the variation of microwear patterns among tooth regions. In both areas, ESP-813 microwear features consist of fine scratches and small pits. These features are arranged in frequent cross-scratching following a bimodal general distribution, with a primary

oblique (140º-150º) and a mesiodistal (0º-5º) main orientation. Additionally, the proportion of pits against scratches varies greatly among the two regions (up to 23.89% in the apical vs. up to 41.48% in the central).

In both areas analysed in MA3.16, microwear is represented by coarse scratches with a high proportion of large pits (36% in the apical and 38% in the central regions). Although damage to the wear facet hampers its identification, cross-scratching is rarely present. Features in both areas follow a monomial distribution with a mesiodistal (350º-20º) orientation. Microwear features in MCD-5014 consist of fine scratches with common cross-scratching and a high proportion of small pits (up to 39.34%). The general arrangement of these features is that of a bimodal distribution, with a primary apicobasal (80-110º) and a more steeply inclined (30-40º) orientation.

3.2. Titanosauria

Microwear features in MCD-9885.20 and MCD-9885.44 are very similar. This consists of fine scratches and a low proportion of small pits. These marks are oriented in a bimodal distribution in both teeth. One predominant orientation follows a somewhat tilted apicobasal axis (140-161º) whereas the second is oriented mesiodistally (80-90º). On both teeth, cross-scratching is common. Since the dentine that makes for most of the surface on the wear facets in both teeth was completely ablated, the enamel rim surrounding each occlusal wear facet was used for microwear analysis instead.

4. CONCLUSIONS

In the studied sample, titanosaurian teeth share a high proportion of scratches and very few pits (<13%) and a similar bimodal distribution. The later indicates some proal-palinal motion (jaw motion parallel to the tooth-throw during occlusion), which conflicts with previous assumptions of a purely orthal jaw movement (Fiorillo, 1998). On the contrary, pit proportion in the lambeosaurine sample is very consistent (≈ 40%), indicating either similar feeding heights or similar dietary preferences. However, coarser features in MA3.16 indicate a preference for harder food items, implying that the similar pitting proportion shown in the lambeosaurine dataset may relate to similar feeding heights. Additionally, the monomial distribution of the microwear features in MA3.16 greatly contrasts with the bimodal distribution found in the Spanish taxa, and in fact, most hadrosaurids (Mallon & Anderson, 2014). This may potentially indicate a greater proal-palinal component during food processing, or rather greater processing times in this lambeosaurine, both cases agreeing with a preference for hard foodstuff.

Altogether, the results of this work potentially indicate that niche partitioning was in effect among these dinosaur groups, with generalist titanosaurs feeding on soft, mid-to-canopy level vegetation and a generalist, ground-level diet for lambeosaurine taxa based on harder food. Furthermore, microwear also hints at differences in food hardness and oral biome-

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chanics between Iberian and Occitanic lambeosaurines. Further research will focus on expanding the sample size, and both the taxonomical and geographical diversity of the studied dataset in order to further validate these results. This in turn will allow further characterization of the microwear and mechanical patterns herein presented, and allow for significant quantitative comparisons with mainland taxa.

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