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Histology of teeth and tooth attachment in titanosaurs (Dinosauria; Sauropoda)

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ABSTRACT

Dental histology of periodontal tissues (cementum, periodontal ligament and alveolar bone) has been studied in mammals, crocodylians and some basal tetrapods, but these structures have never been studied in titanosaur sauropods. The goal of this work was to study the structures of dental insertion in Titanosaurs. Like many physiological processes, histological analysis of titanosaur teeth shows hard tissue formation, characterized by a circadian rhythm. From thin sections it was possible to observe microstructures such as incremental lines of von Ebner, dentinal tubules and cross striations, all key to the understanding of developmental tooth dynamics. The structural and histological analyses carried out here on teeth of Late Cretaceous titanosaurs reveals the presence of acellular and cellular cementum, periodontal ligament, and alveolar bone, all structures necessary for a truly thecodont dentition. This is the first time documented for a dinosaur via histological tissue, and is an important finding that will help elucidate aspects of dinosaurian dentition, tooth replacement rate, feeding strategy, metabolism, and general biology.

1. Introduction

Titanosaurs are a derived group of sauropod dinosaurs, first recognized in the late nineteenth century (Depéret, 1896; Lydekker, 1877, 1893). During the last century, this clade has been studied by many researchers around the world, recognizing more than 50 genera that have been recorded from all continental landmasses (Curry Rogers, 2005; García & Salgado, 2013; Hunt, Lockley, Lucas, & Meyer, 1994; Wilson & Upchurch, 2003;). With notable exceptions (e.g. Curry Roger and Forster 2002; Wilson 2005), the advancement of knowledge of titanosaur biology and systematics was mostly thanks to abundant postcranial material, with limited cranial remains available for study (Filippi, García, & Garrido, 2011; García, Paulina Carabajal, & Salgado, 2008; García et al. 2015; Paulina Carabajal, Coria, & Chiappe, 2008; Paulina Carabajal, 2012; Zaher et al. 2011). Therefore, the knowledge of titanosaur dental histology, dentition, dental replacement, and tooth replacement rate is limited (Díez Díaz, Pereda Suberbiola, & Sanz, 2012; García, 2013; García & Cerda, 2010a, 2010b; Nowinski, 1971). Like all vertebrate teeth, titanosaur teeth consist of a crown and a root. However, compared to mammals, the teeth of titanosaurs and most reptiles (except some crocodylomorphs; e.g.O'Connor et al. 2010) are simple in terms of external morphology, and are generally less diagnostic.

As with all sauropods dinosaurs, titanosaurs were a group of obligate herbivorous dinosaurs (Calvo, 1994; D'Emic et al. 2013; Sereno & Wilson, 2005; Upchurch & Barrett, 2000), with particular dentitions (morphologies, dental compositions, tooth replacement rate) that probably reflect specialized adaptations to their modes of feeding (Díez Díaz et al. 2012; García, 2013; García & Cerda, 2010a; Nowinski, 1971). Although, their tooth implantation has always been regarded as thecodont (i.e. an attachment type whereby teeth are placed within a socket by a complex of tissues including cementum, periodontal ligament, and alveolar bone; Gaengler, 2000), this claim has only been superficially justified at the histological level. Whereas the histological features of a true the

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codontal implantation have been well studied in mammals and crocodylians, these features (e.g. periodontal ligament) have rarely been documented in dinosaurs. To date, the only description of these histological structures consists of a preliminary report published by García and Cerda (2010a). In this contribution, we describe different dental structures, including those related to tooth implantation.

2. Materials and methods

All titanosaur specimens (isolated teeth) (Table 1) came from the Upper Cretaceous (Campanian – Maastrichtian) Anacleto and Allen formations from the localities of Salitral Moreno, Cinco Saltos and Lago Pellegerini (Fig. 1), accessioned at the Museum Provincial Carlos Ameghino, Río Negro, Argentina (MPCA-Ph 1–20, 39, 41). Thin-sections were created from these specimens. Additionally, we revised thin sections of the titanosaur dentary published by García and Cerda (2010) (MUCPh 251-5, MUCPh 251-6, MUCPh 251-7, MUCPh 251-8 longitudinal sections and MUCPh 251–3, MUCPh 251–4 transversal sections) accessioned at the Museum Cinco Saltos, Río Negro Province, Argentina. The examined teeth are assigned to derived titanosaur sauropods on the basis of several anatomical characters, including: cylindrical shape with parallel margins, thin and slightly curved morphology, absence of denticles, enamel surface smooth to slightly rough, and presence of a proportionally small root. Also, titanosaurs are the only sauropods found in the Allen and Anacleto Formations, Upper Cretaceous of Patagonia (Apesteguía, 2004; Filippi et al. 2011; García, 2013; García & Cerda, 2010a; García & Salgado, 2013; Huene, 1929; Martinelli & Forasiepi, 2004; Mannion & Otero, 2012; Salgado, Apesteguia, & Heredia, 2005). Given the variation observed among the examined specimens (e.g. regarding the degree of enamel ornamentation), it is possible that more than one taxon is included in the sample. Thin sections of the teeth were prepared according to the method outlined by Chinsamy and Raath (1992). All teeth were cut in longitudinal (in those cases, the section was cut in a labiolingual direction) and transverse (cross) sections, with the latter implemented at crown and root level (Fig. 2a). All thin sections of the teeth were viewed using polarized binocular microscopy (LABKLASS) at a magnification of x 40-100-400, and photographed using a Sony SSC-DC50 video camera. Some specimens (MPCA-Pv21, 161, 166) were examined directly using scanning electron microscope (SEM) Philips 515. For SEM examination, the samples were coated with a gold–palladium alloy in Edwards Sputter Coater S150B. The terminology used for the external description of the teeth comes from Nowinski (1971) and Upchurch and Barrett (2000), and the microscopic description follows that of Erickson (1996a,b).

3. Results

The teeth are ‘chisel’-like, with parallel margins. Their overall shape is cylindrical, and they are slightly curved lingually. They exhibit a “D” shape in cross section at crown level. The crown is three times longer than the root, and its external surface is slightly wrinkled. The teeth lack any denticles, and have wear facets of variable development (Fig. 2a). The tooth replacement rate is high and shows a functional tooth, along with up to two or three replacement teeth in each alveolus (Apesteguía, 2004; Coria & Chiappe, 2001; García & Cerda, 2010a; Huene, 1929).

3.1. Enamel

The enamel, an ectodermal originated tissue, is the hardest of the vertebrate tissues, which allows its crystallographic preservation, even in fossil forms (Hwang, 2010). During growth of the tooth, the enamel is secreted by ameloblasts (enamel forming-cells) which migrate outward towards what becomes the surface of the crown (Carlson, 1990; Hwang, 2005). The enamel grows from the enamel–dentine junction in the opposite direction to the dentine (Fig. 2b, c). Similar to the dentine, enamel in its mature state is acellular (Maxwell et al. 2010), and shows incremental lines. These lines (called incremental lines or cross striations) are actually observed as successively deposited growth layers of equal thickness (Fig. 3a, b). Incremental lines record variation in the ameloblastic activity during amelogenesis (Carlson, 1990). The spacing intervals of the incremental lines is approximately 4–5.2 μm (MPCA-Ph 4), 5.2–6.5 μm (MPCA-Ph20), 5 μm (MPCA-Ph18) wide, and the incremental lines possibly reflect daily rhythms of ameloblastic activity under circadian control (Kierdorf, Breuer, Richards, & Kierdorf, 2014; Zheng et al. 2013). In longitudinal section, an oblique line to enamel–dentine junction is observed towards the outer surface of the tooth. Those lines are here interpreted as Tomes' processes, lines that leave the ameloblasts during amelogenesis (Fig. 3a). The spacing interval of lines is 5 μm, which would be equal to the size of the prisms. Tooth crowns show considerable variation of enamel presence and thickness among different teeth and within the same tooth (e.g. 147 μm–343 μm thickness in MPCA-Ph 10).

3.2. Dentine

The teeth develop from two germ cell layers (Carlson, 1990; Ten Cate, 1995, 1997). The enamel, as mentioned above, is ectodermic in origin, and the dentine is of mesoderm origin. These two tissues grow from the enamel–dentine junction in opposite directions (Fig. 2b, c). This enamel–dentine junction is clearly observed in many examples studied here (MPCA-Ph 4, 15, 17, 19, 20; MUCPh 251-5), and dentinal tubule concentrations are greater at the

Table 1
Measurements of labiolingual and mesodistal width, length of Crown, number of wear facets and angle of wear facets. All the measures are in millimeters.

	Labiolingual width	Mesodistal width	Length of crown	Number of wear facets	Angle of wear facets
MPCA-PV21	2.5 mm	3 mm	9 mm	1	32°
MPCA-PV72	4 mm	5.5 mm	26.5 mm	4	11° 45°*
MPCA-PV96	5 mm	7 mm	30 mm	2	12°
MPCA-PV129	3 mm	4 mm	20 mm	2	3° 27°*
MPCA-PV161	5.5 mm	7 mm	–	1?	13°
MPCA-PV166	5.5 mm	6.5 mm	–	–	–
MPCA-PV168	3 mm	4 mm	13 mm	2	7° 20°*
MPCA-PV217	3.5 mm	5 mm	20 mm	1	9°
MPCA-PV715	4.5 mm	6 mm	22 mm	3	14° 25°*
MPCA-PV730	5 mm	5.5 mm	34 mm	2	3° 27°*

Note: ° Angle of the wear facet in relation with the crown main axis; * Angle of lingual facet in relation with the crown main axis.