



DENTITION AND HISTOLOGY IN TITANOSAURIAN DINOSAUR EMBRYOS FROM UPPER CRETACEOUS OF PATAGONIA, ARGENTINA

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Abstract: Exceptionally preserved sauropod embryos from the Late Cretaceous Anacleto Formation in Auca Mahuevo (Neuquén Province, Argentina) have provided fundamental information on titanosaurian ontogeny. This paper describes the dental composition, disposition and microstructure of the specimens. Embryonic teeth show size disparity, with lengths that vary from 1 to 3 mm and diameters ranging from 0.15 to 0.26 mm, with the most frequent length values between 2.5 and 3 mm. Apparently, a typical ‘pencil-like’ tooth morphology and a dental formula of Pm 4, M 7–8/D10? remained constant during titanosaurian ontogeny, whereas the arrangement of teeth in the skull shows notable ontogenetic changes. Absence of wear facets on teeth suggests

a lack of prenatal chewing movements. The enamel proportion is significantly higher in embryos than in mature titanosaurs, which suggests that this relationship varies during ontogeny. Embryonic bony tissue is composed of highly vascularized, cellular woven bone. The absence of osteonal tissue, the high degree of vascularization, the presence of numerous osteocytes and poor development of periosteal bone reveals that the Auca Mahuevo titanosaurs would have had a high early growth rate and that they were buried at a relatively advanced embryonic stage.

Key words: embryos, titanosaurian, histology, wear facet, dentition, ontogeny.

THE 1997 discovery of thousands of megallolithid-type eggs, many preserving *in ovo* remains of titanosaur sauropods from the Late Cretaceous Auca Mahuevo locality (Neuquén Province, Patagonia, Argentina), has provided unprecedented information on the prehatching ontogeny (Chiappe *et al.* 2001), osteology (Salgado *et al.* 2005; García 2007a), nesting architecture (Chiappe *et al.* 2004) and reproductive behaviour (Chiappe *et al.* 2005; Jackson *et al.* 2008; Sander *et al.* 2008) of these dinosaurs.

Chiappe *et al.* (1998) assigned the Auca Mahuevo embryos to Neosauropoda (defined as *Diplodocus*, *Saltasaurus* their common ancestor, and all its descendants, thereby incorporating Diplodocoidea and Macronaria: Wilson and Sereno 1998). Subsequently, Chiappe *et al.* (2001) and Salgado *et al.* (2005) assigned these embryos to Titanosauria. Traditionally, sauropod teeth have been classified into two morphotypes: spatulate or ‘spoon-shaped’ teeth, with broad wear facets typical of *Camarasaurus*, brachiosaurids and related forms; and the long, slender ‘pencil-like’ teeth with smaller wear facets, which are found in diplodocids and derived titanosaurs (Coombs 1975; Dodson 1990; McIntosh 1990).

Chiappe *et al.* (1998) and Salgado *et al.* (2005) described some aspects of the dentition of the sauropod

embryos from Auca Mahuevo. Here, we provide the first detailed morphological description of these teeth, their composition and their disposition in relation to other skull elements and analyse potential ontogenetic changes in the dentition. The study of dinosaurian embryonic dentitions is important because it allows inference of some aspects of prenatal behaviour and ontogenetic change in these reptiles.

Sauropod dinosaurs have been the focus of diverse palaeohistological studies, which have offered significant information on several aspects of their life history, including growth rate, longevity and age at sexual maturity (Rimblot-Baly *et al.* 1995; Curry 1999; Sander 2000; Sander and Tückmantel 2003; Sander *et al.* 2006; Klein and Sander 2008; Lehman and Woodward 2008). Previous work on sauropod bone histology has allowed the reconstruction of growth curves for some taxa (Erickson *et al.* 2001; Lehman and Woodward 2008) and has recognized distinctions between different ontogenetic stages (Sander 2000; Klein and Sander 2008). However, our knowledge of sauropod bone microstructure during early ontogenetic stages is very limited. Klein and Sander (2008) identified seven (A to G) ontogenetic bone tissue types in sauropod long bones, which combined to give thirteen histologic

ontogenetic stages. Although type A (embryonic) was not included in their sample, Klein and Sander (2008) argued that sauropod embryonic bone was likely to resemble *Maiasaura* embryonic bone (Horner *et al.* 2000). In this regard, the embryos from Auca Mahuevo offer a unique opportunity to document the bone histology of early growth stages in sauropod dinosaurs. The main objectives of this study are to characterize the bony histology of Auca Mahuevo embryos and to interpret what this tells us about the early growth dynamics.

Institutional abbreviations. MAUPv, Vertebrate palaeontology collection of the Museo Argentino Urquiza, Neuquen, Argentina; MCF-PVPH, Vertebrate palaeontology collection of the Museo Municipal 'Carmen Funes', Plaza Huinul, Neuquén, Argentina; MCSPV, Vertebrate palaeontology collection of the Museo Cinco Saltos, Río Negro, Argentina; MPCA, Museo Provincial 'Carlos Ameghino', Cipolletti, Argentina; UNPSJB-PV, Vertebrate palaeontology collection of the Universidad Nacional de la Patagonia San Juan Bosco, Chubut, Argentina.

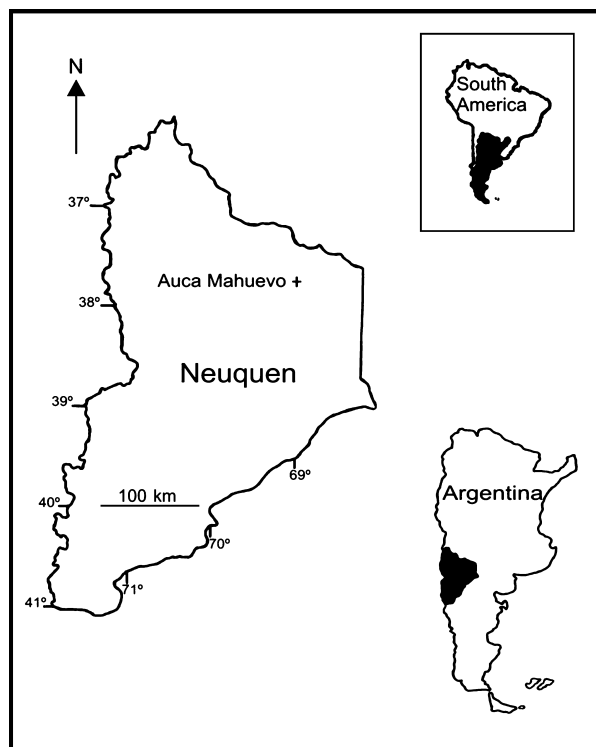
LOCALITY, MATERIAL AND METHODS

Locality

The material examined was collected from Auca Mahuevo, Neuquén Province, Argentina (Text-fig. 1; Chiappe *et al.* 1998, 2001). The fossil-bearing beds are located within the Anacleto Formation. Magnetostratigraphy (Dingus *et al.* 2000) and biostratigraphical data (Heredia and Salgado 1999) suggest that the embryos from Auca Mahuevo are early–middle Campanian in age, approximately 79.5–83.5 Ma old (Dingus *et al.* 2000).

Material examined

MCF-PVPH-263: two teeth in a left maxilla. MCF-PVPH-272: one tooth in the fourth alveolus of a left premaxilla and seven teeth in a left maxilla. MCF-PVPH-659: a fully developed tooth in the first alveolus (medial) and one in the third alveolus, both in a left premaxilla. MCF-PVPH-663: five teeth, and probably a sixth tooth in a right dentary. MCF-PVPH-664: four teeth in a right maxilla, and other isolated teeth. MCF-PVPH-693: one tooth in the first or second? alveolus of a left premaxilla. MCF-PVPH-694: one tooth in the third alveolus and other isolated teeth, near the fourth alveolus in a left premaxilla. MCF-PVPH-704: one tooth fully developed in the first alveolus in a right premaxilla, one tooth in the first and second alveolus, probably a third tooth also belonging to the second alveolus and one in the third alveolus of a left premaxilla, one tooth in a right dentary. MCF-PVPH-112-2; MCF-PVPH-250: isolated teeth. MCF-PVPH-147; MCF-PVPH-690; MCF-PVPH-300; MCF-PVPH-113; MCF-PVPH-734: isolated teeth. MCF-PVPH-766; MCF-PVPH-767; MCF-PVPH-768; MCF-PVPH-769; MCF-PVPH-770; MCF-



TEXT-FIG. 1. Map showing the geographical location of Auca Mahuevo, where the titanosaur embryos were collected.

PVPH-711: isolated teeth (studied in SEM). MCF-PVPH-772: isolated unidentified bone. MCF-PVPH-799; MCF-PVPH-800; MCF-PVPH-801; MCF-PVPH-802; MCF-PVPH-803; MCF-PVPH-804; MCF-PVPH-805; MCF-PVPH-806; MCF-PVPH-807; MCF-PVPH-802; MCF-PVPH-816: thin sections. MCF-PVPH-774: adult titanosaur tooth. MCSPV-90: adult titanosaur tooth. MCSPV-91: adult titanosaur tooth. MPCA-18; 30; 75; 112; 131; 148b; 157; 180; 195; 715; 723-725; 729; 732; 735; 736; 744; 747; 748; 750; 755; 756: adult titanosaur teeth.

Methods

Histological specimens were assessed with a Leica MZ6 binocular microscope and photographed with a Sony DSC-P32 and a Nikon Coolpix 4500 digital camera. Microscopic details were observed using a Phillips 515 Scanning Electronic Microscope (at the Facultad de Ingeniería de la Universidad Nacional del Comahue), after coating the samples with gold with an Erwin sputter coater.

Skull and appendicular bones were sampled (Table 1). As a result of the fragmentary nature of the histological specimens, it was not possible to accurately identify the element from which the section was taken. Thin sections of the embryonic bones were prepared according to the method outlined by Chinsamy and Raath (1992) and

TABLE 1. Material and porosity of thin sections used for this histological study.

Collection number	Bone	Plane of section	Porosity
MCF-PVPH-100	Maxilla	Longitudinal section	63%
MCF-PVPH-806		Longitudinal section	51%
MCF-PVPH-799	Indeterminate long bone shaft	Cross section	63%
MCF-PVPH-808	Indeterminate long bone shaft	Cross section	47%
MCF-PVPH-800	Indeterminate skull bone	*	34%
MCF-PVPH-802	Indeterminate skull bone	*	43%
MCF-PVPH-803	Indeterminate skull bone	*	**
MCF-PVPH-804	Indeterminate skull bone	*	35%
MCF-PVPH-805	Indeterminate skull bone	*	**
MCF-PVPH-807	Indeterminate skull bone	*	37%

*The plane of section is unknown.

**Porosity percentage could not be calculated in much altered sections.

were made at the Departamento de Geología, Universidad Nacional de San Luis (Argentina). These thin sections were examined with an Olympus BX40 optic binocular microscope and an Olympus SZH10 binocular microscope and photographed with a Sony SSC-DC50 video camera (at the Laboratorio de Facultad Bariloche CRUB, Argentina). A common measurement employed in histological studies is the amount of bone vascularity (Chinsamy 1993; Horner *et al.* 2001). To quantify the amount of vascularity, we measured the percentage of porosity (space occupied by vascular channels) from thin sections. Porosity percentages and the enamel–dentine ratio were determined using Image J software (Rasband 2003).

DESCRIPTION

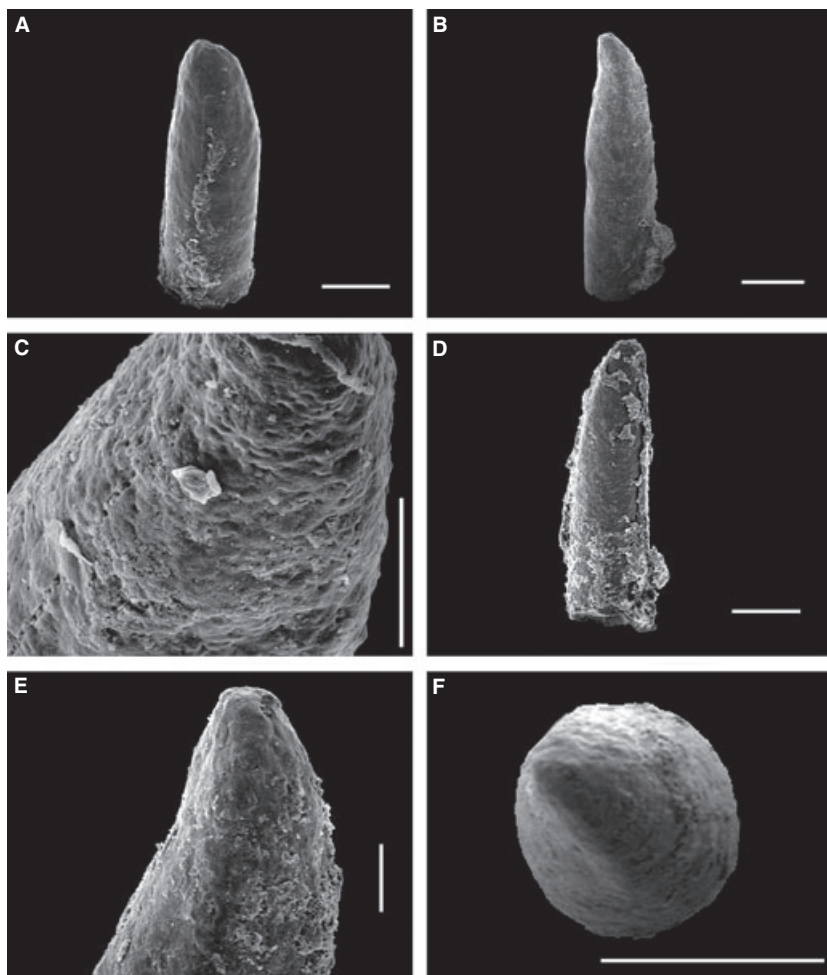
Dentition

In many cases, the teeth are positioned within their respective alveoli, while in other instances, they are scattered among various skull elements. All preserved teeth show a cylindrical morphology, with parallel margins from base to apex, where the crown tapers (e.g. MCF-PVPH-766; MCF-PVPH-767; MCF-PVPH-770; MCF-PVPH-112-2; MCF-PVPH-250: Text-figs 2, 3A, B). The tooth crowns are cylindrical, a condition that is also present in *Bonitasaura* (Apesteguía 2004), *Rapetosaurus* (Curry Rogers and Forster 2001, 2004), *Nemegtosaurus* (Wilson 2005) and other indeterminate titanosaur remains from Río Negro Province (Coria and Chiappe 2001). This morphology is unlike that of *Malawisaurus* teeth, which have the broadest portion closer to the tip (Gomani 2005). All embryonic teeth show a slight concavity or curvature to one side in their most apical portion (Text-fig. 2B–E). This slight asymmetry may not correspond to the asymmetry in adults: therefore, it is not possible to determine the position of isolated teeth

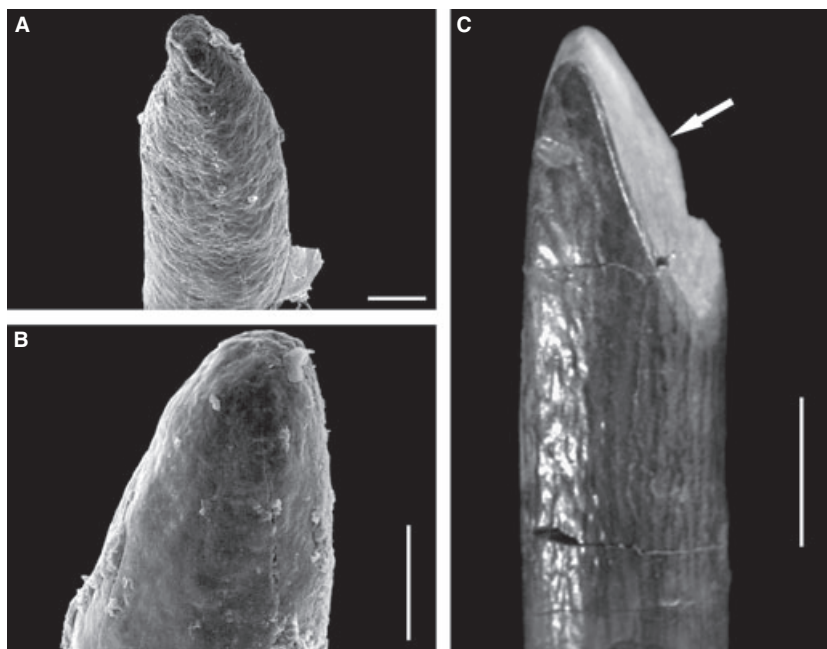
within the jaw. In contrast to adult titanosaurs, such as *Antarctosaurus wichmannianus*, *Rapetosaurus*, *Malawisaurus* and *Nemegtosaurus* (von Huene 1929; Calvo 1994; Sciotto and Martínez 1994; Curry Rogers and Forster 2004; Gomani 2005; Wilson 2005), the embryonic teeth lack lingual curvature. The straight margins of the embryonic crown tooth, as in other adult neosauropods, lack denticles or ‘primary ridges’ (Chiappe *et al.* 1998: Text-figs 2, 3). The absence of denticles is considered a synapomorphy of Neosauropoda (Wilson and Sereno 1998, character 78).

We did not observe the wear facets noted by Chiappe *et al.* (1998). Such facets are typically present in the functional teeth of adult titanosaurs (Text-fig. 3C). However, the embryonic crown apex is similar to that of the replacement teeth of adult titanosaurs. Superficially, the enamel of the tooth is smooth and dark brown in colour, and ivory white dentine can be seen within the broken teeth. The cross-section at the middle of the crown is subcircular (Text-fig. 4), as in *Nemegtosaurus*, but differing slightly from that seen in other titanosaurians (von Huene 1929; Coria and Chiappe 2001). Wilson (2002) proposed that tooth crowns with cylindrical cross-sections are synapomorphic for Nemegtosauridae (*Nemegtosaurus* + *Rapetosaurus*). More recently, Wilson (2005) noted that *Nemegtosaurus mongoliensis* was characterized by upper tooth crowns with ‘D’-shaped cross-sections and lower tooth crowns with more elliptical cross-sections (Wilson 2005). Thus, titanosaurian embryonic teeth do not agree exactly with the description given by Wilson and Sereno (1998, character 32) and Wilson (2002, character 70) for non-diplodocoid sauropods, which show a ‘D’-shaped cross-section.

The enamel/dentine ratio (total enamel area/total tooth area) is 0.34 in the embryonic titanosaurian teeth. Enamel thickness is constant around the whole circumference, unlike the condition in the diplodocoid *Nigersaurus*

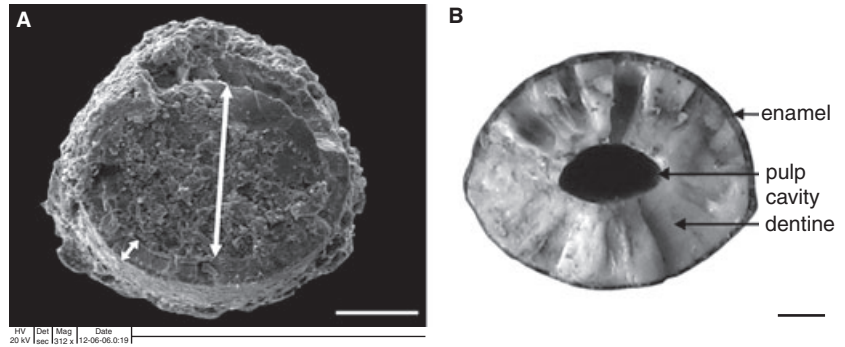


TEXT-FIG. 2. Teeth of the titanosaur embryos from Auca Mahuevo showing their morphology. The irregularities on the surface of the teeth are sediments. A, B, D, MCF-PVPH-770, MCF-PVPH-766, MCF-PVPH-768, different views showing its general morphology. C, E, MCF-PVPH-767, MCF-PVPH-766, enlarged view of apex of the crown. F, MCF-PVPH-767, apical view. Scale bars represent 0.1 mm in A, B, D, F and 0.05 mm in C, E.



TEXT-FIG. 3. Titanosaur embryonic and adult teeth compared. A, MCF-PVPH-767 and B, MCF-PVPH-770 crown apex showing lack of wear facets. C, MCF-PVPH-774, adult tooth from Auca Mahuevo site, showing typical titanosaurs wear facet (arrow). Scale bars represent 0.1 mm in A–B, and 5 mm in C.

TEXT-FIG. 4. Transverse sections of titanosaur embryonic and adult teeth. These teeth show different enamel–dentine ratios. A, MCF-PVPH-769, embryonic tooth showing dentine (long arrow) and enamel (short arrow). B, MCSPV-90 adult tooth. Scale bar represents 1 mm.

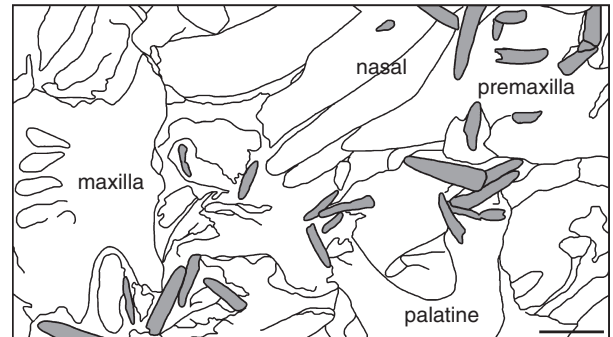
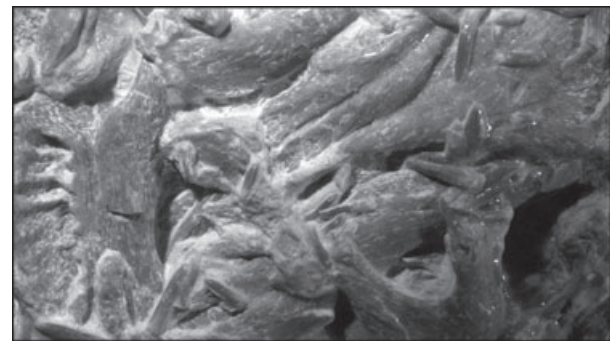


whose teeth apomorphically possess thicker enamel on their labial sides (Serenó *et al.* 1999, 2007; Wilson 2002; Sereno and Wilson 2005). The enamel/dentine ratio of adult titanosaurs is significantly lower than in the embryos: 0.34 in the embryos vs 0.14 (MCSPV-91) and 0.09 (MCSPV-90) in adults (Text-fig. 4).

The sizes of the embryonic teeth are highly variable, an observation that can be explained by their different positions in the jaws (premaxilla, maxilla or dentary, Salgado *et al.* 2005). Some small isolated teeth likely correspond to unerupted replacement teeth. Tooth length varies between 1–3 mm and is most frequently between 2.5–3 mm. Tooth diameter ranges from 0.26 to 0.29 mm in the longest teeth and from 0.14 to 0.16 mm in the shortest ones (Text-fig. 5).

The total number of functional teeth was determined based on alveolar counts. The embryonic premaxilla has four alveoli (MCF-PVPH-694 and MCF-PVPH-659), as in all adult sauropods for which appropriate material is known (García 2007b). The dentigerous portion of each maxilla (MCF-PVPH-250, MCF-PVPH-679, MCF-PVPH-653) has eight alveoli, which gradually decrease in size caudally. The caudalmost alveolus is located caudal to the preantorbital fenestra and reaches the level of the rostral third of the antorbital fenestra (García 2007a). This character has not been observed in adult titanosaur sauropods, with the exception of *Rapetosaurus*, which has a rostrally enlarged antorbital fenestra, and the caudalmost alveolus extends caudally beyond the preantorbital fenestra and the rostral margin of the antorbital fenestra (Curry Rogers and Forster 2004, text-figs 1–4). In all adult titanosaurs, the most caudal alveolus is rostral to the anterior margin of the antorbital fenestra or even rostral to the preantorbital fenestra (García and Salgado 2006; García 2007a, text-fig. 1).

Dentary and maxillary tooth counts are highly variable in sauropods (Table 2), ranging from *Shunosaurus* with 20 maxillary teeth (the plesiomorphic condition for sauropods: Chatterjee and Zheng 2002) to 7–8 in several Patagonian titanosaurs (Sciutto and Martínez 1994; Coria and Salgado 1999; RAG and IAC, pers. obs. 2007).



TEXT-FIG. 5. MCF-PVPH-250, disarticulated skull of specimen showing dispersed teeth of several sizes lying on the bones. Scale bar represents 2 mm.

Despite this variability, sauropod evolution records a reduction in the number of maxillary and dentary teeth (Upchurch *et al.* 2004), except in *Nigersaurus*, which shows at least 20 maxillary teeth (Serenó *et al.* 1999, 2007). Seven to eight maxillary teeth are commonly present in a number of different Patagonian titanosaurs, such as MAUPv-AC-01 (Coria and Salgado 1999), MAUPv-N-425/25 (RAG and IAC pers. obs. 2007) and UNPSJB-PV 583 (Sciutto and Martínez 1994). However, their relative positions differ in embryos and adults. In adult titanosaurs (as in adult Diplodocoidea Upchurch, 1995), including *Nemegtosaurus*, MAUPv-AC-01, MAUPv-N-425/25, *Antarctosaurus* and *Bonitasaura*, the teeth are restricted to the rostral segment of the alveolar margin of the maxilla and dentary. In *Antarctosaurus*

TABLE 2. Summary of the sauropodomorph dental formulae.

Taxon	Pm	M	D	Total	Age	References
<i>Plateosaurus</i>	5–6	24–31	22–28	102–130	Norian	Galton, 1984, 1985
<i>Shunosaurus lii</i>	4–5	20	25–26	99–101	Bajocian	Chatterjee and Zheng, 2002
	4–5	17–19	18–21	78–89		Zhang, 1988
<i>Mamenchisaurus youngi</i>	4	18	22–24	88–92	Kimmeridgian–Thinonian	Pi <i>et al.</i> , 1996
<i>Mamenchisaurus jingyanensis</i>	4	14–16	17–19	70–78	Late Jurassic	Zhang <i>et al.</i> , 1998
<i>Omeisaurus tianfuensis</i>	4	11	13–15	56–60	Middle to Late? Jurassic	He <i>et al.</i> , 1988
<i>Diplodocus longus</i>	4	9	10	46	Kimmeridgian–Thinonian	Hatcher, 1901; Holland, 1906
<i>Camarasaurus</i>	4	8–9	13	50–52	Kimmeridgian–Thinonian	Gilmore, 1925
<i>Camarasaurus</i>	4	9–10	13	52–54		Madsen <i>et al.</i> , 1995
<i>Nigersaurus taqueti</i>	4	24	34	124	Aptian–Albian	Sereno <i>et al.</i> , 1999, 2007
<i>Malawisaurus dixeyi</i>	4	?	15	–	Early Cretaceous	Gomani, 2005
<i>Nemegtosaurus mongoliensis</i>	4	8	13	50	Middle Maastrichtian	Nowinski, 1971; Wilson, 2005
<i>Rapetosaurus krausei</i>	?	8–?	11	–	Maastrichtian	Curry Rogers and Forster, 2001, 2004
Titanosauriform	4	11	13	56	Cenomanian?	Martínez, 1998
Titanosaurid	?	8	?	–	Late Cretaceous	Sciutto and Martínez 1994
Titanosaurid	4	7–8	11	44–46	Santonian?	Coria and Salgado, 1999
Titanosaurid	4	8	?	–	Campanian	Pers. obs. 2007
Titanosaurid embryos	4	8	10?	44?	Campanian	This study

Pm, premaxilla teeth; M, maxilla teeth; D, dentary teeth; Total, premaxillary, maxillary and lower jaws.

and *Bonitasaura*, the maxillary tooth positions are inferred from observations on dentary tooth distributions. In titanosaurian embryos, 7–8 teeth are distributed along the entire length of the maxilla.

The dentary teeth are poorly represented. The specimen MCF-PVPH-663 shows five or six teeth. However, it is probable (estimated from the available space) that it had at least four more teeth, two in the symphyseal portion and two caudal to the preserved teeth. Thus, the dentary would have had 9–10 teeth. This number is lower than in other titanosaurs, such as *Bonitasaura*, with 10–13 teeth (Apesteguía 2004) and *Antarctosaurus*, with 15 teeth (Powell 2003). Therefore, the complete dentition of the embryonic sauropods would have consisted of at least of 44 functional teeth, based upon the alveolar evidence.

In MCF-PVPH-250, which consists in a nearly complete, disarticulated skull, it is possible to count 43 dispersed teeth; MCF-PVPH-112-2, another disarticulated and incomplete skull, has 25 associated teeth.

Histology

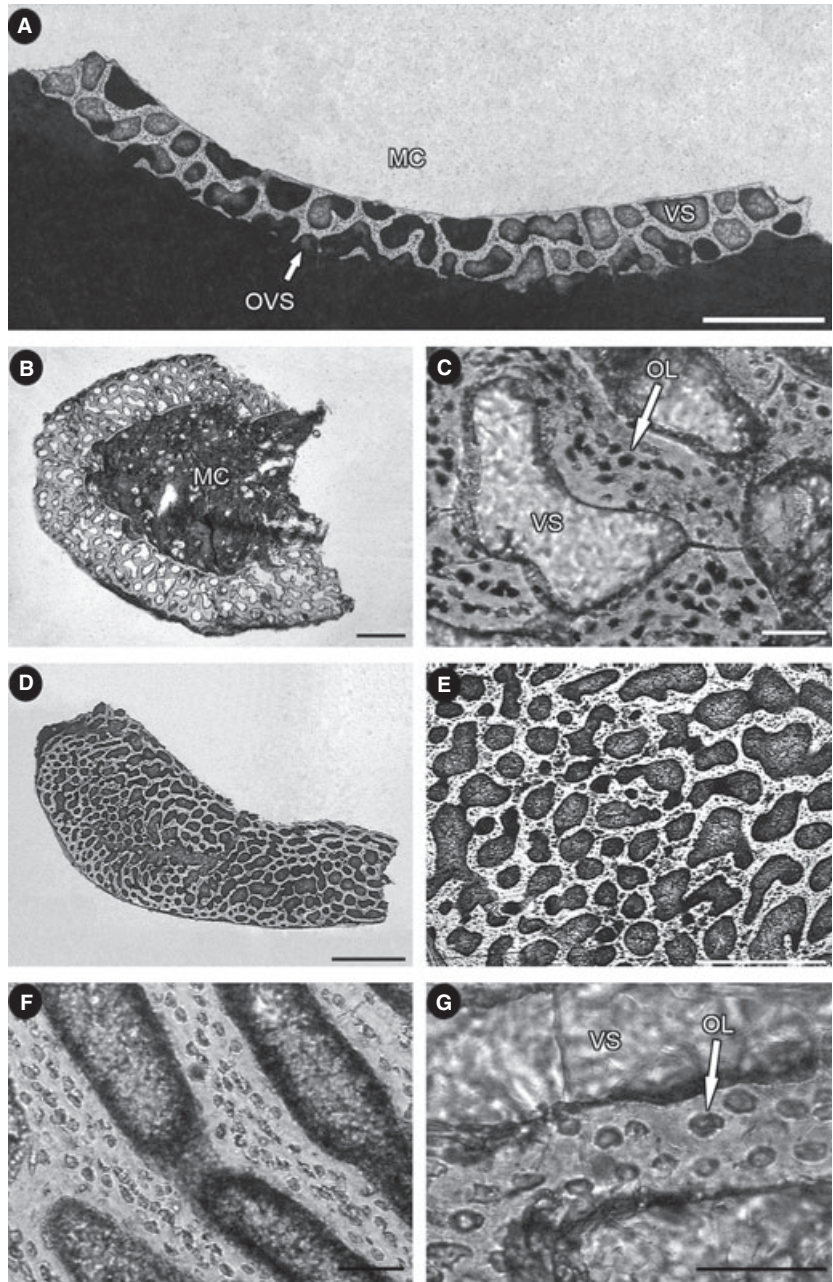
Long bones. Shafts of two (MCF-PVPH-799, MCF-PVPH-808) indeterminate long bones were analysed (Text-fig. 6A, B). In cross-section, these bones show a well-developed medullary cavity, which lacks internal trabeculae and endosteal lamellar bone. The cortex is formed by primary (not remodelled), highly cellular woven bone with numerous vascular spaces. The vascular spaces are wide and irregular in shape, and they

form a rather cancellous tissue. There is no evidence of centripetal deposition of osteonal bone within the vascular spaces. Osteocyte lacunae are large, globular structures that are randomly distributed in the woven bone matrix (Text-fig. 6C). Although all bones are well preserved, canaliculi were not observed. There is no evidence of calcified cartilage within the marrow cavity. The periosteal margins are uneven with vascular spaces open to the surface, resulting in the typical ‘grooved’ appearance of the bone surface in these sauropod embryos (see Chiappe *et al.* 2005, text-figure 10.9).

There are some differences between the two cross-sections. Although the shaft section of MCF-PVPH-799 (Text-fig. 6A) is incomplete, periosteal bone seems to be less developed and occupies a smaller proportion of the transverse area (in MCF-PVPH-808, the cortical bone occupies approximately 35% of the total area). Also, this section has wider vascular spaces, some of them occupying almost the entire thickness of periosteal bone, giving the bone a high degree of porosity (63 per cent).

Skull bone. As in the long bones, the bony tissue consists of highly vascularized woven bone (MCF-PVPH-800, MCF-PVPH-802, MCF-PVPH-803–805, MCF-PVPH-807; Text-fig. 6D–G). The porosity percentage is high, but variable (between 34 and 63 per cent). The shapes and orientations of vascular canals differ between the bones. Some have lengthened canals, arranged concentrically (Text-fig. 6F, G). In others, such as a maxillary sample (Text-fig. 6D), the canals are irregularly shaped. Deposition of primary osteonal bone is entirely absent.

TEXT-FIG. 6. Histological sections of embryonic titanosaur bones. A, MCF-PVPH-799 and B, MCF-PVPH-808, diaphyseal sections of indeterminate long bones. C, MCF-PVPH-808, enlarged view of periosteal bone. D, MCF-PVPH-806, longitudinal section of maxilla. E, MCF-PVPH-806, enlarged view of maxilla section. F, MCF-PVPH-809, enlarged view of indeterminate skull bone. G, MCF-PVPH-804, detail of osteocyte lacunae in an indeterminate skull bone. Scale bars represent 0.5 mm in A, B, E, 1 mm in D, and 0.05 mm in C, F, G. mc, marrow cavity; ol, osteocyte lacunae; ovs, open vascular space; vs, vascular space.



Osteocyte lacunae are abundant, globular and irregularly arranged (Text-fig. 6F, G). There is no evidence of a medullary cavity in any bone.

DISCUSSION

Dentition

Wear facets. The development of 'V'-shaped wear facets has been suggested as a synapomorphy of Eusauropoda (sauropods more closely related to *Saltasaurus* than to

Vulcanodon: Wilson and Sereno 1998, character 36) and attributed to 'interdigiting occlusion'. Calvo (1994) recognized that the teeth of diplodocoids and titanosaurids could be distinguished from each other on the basis of the angles of their wear facets with respect to the orientation of the labiolingual tooth axis; diplodocoids show a wear facet with an inclined plane from 10° to 40°, while the angle is usually more than 70° in titanosaurians. This is due to different feeding mechanisms. Our observations on the embryonic teeth indicate the absence of wear facets, at least until a stage close to birth. The absence of wear facets in the prenatal stage implies that the facets were generated

by tooth-to-tooth contact during biting following hatching. This differs from the condition in the hadrosaurid *Hypacrosaurus stebingeri* whose embryos possessed substantial occlusal tooth wear (Horner and Currie 1994).

Recent observations (García in prep.) have expanded our understanding of the ontogenetic development of the Auca Mahuevo embryos. Assuming that the pattern of ossification of the Auca Mahuevo embryos was similar to that in extant birds (Starck 1993), it is possible to infer, through osteohistological evidence, that the titanosaur embryos died between stages 36 and 37 of the 42 ontogenetic stages identified by Hamburger and Hamilton (see Starck 1993). Although bird and sauropod ossification patterns may not be identical, the Auca Mahuevo embryos would have died at a relatively advanced developmental stage, although sometime before near hatching.

Tooth replacement. Most species of adult dinosaurs had more than one replacement tooth in addition to the functional tooth in each alveolus (Erickson 1997), and this is considered to be the plesiomorphic condition for Dinosauria (Edmund 1960). Tooth replacement in sauropods has been studied by White (1958: *Camarasaurus*), Powell (1979: titanosaurs), Coria and Chiappe (2001: indeterminate titanosaur), Sereno *et al.* (1999, 2007: *Nigersaurus*), Chatterjee and Zheng (2002, 2005: *Shunosaurus* and *Camarasaurus*) and Wilson (2005: *Nemegtosaurus*). Among dinosaur embryos, replacement teeth have been mentioned only for *Hypacrosaurus stebingeri* (Horner and Currie 1994), a therizinosaurid (Manning *et al.* 2000) and an 'infant' of *Maiasaura peeblesorum* (Erickson 1996). In the Auca Mahuevo embryos, the alveoli, particularly in the premaxilla, are strikingly deep and wide in respect to the size of the teeth they housed. The teeth found deep within some alveoli may have been displaced from a more erupted position (see also García 2007b, text-figure 2); however, this exaggerated depth suggests the capacity to house more than one tooth per alveolus. One premaxilla (MCF-PVPH-704) shows two teeth inside the second (medial) alveolus.

Mature sauropods exhibit continuous dental replacement. For example, *Diplodocus* possesses one functional tooth and five replacement teeth in each maxillary alveolus (Hatcher 1901). *Nigersaurus* possesses one functional maxillary tooth and seven replacement teeth, as well as one functional tooth and five replacement teeth in the premaxilla (Sereno and Wilson 2005; Sereno *et al.* 2007). Finally, a titanosaurid premaxilla from the Upper Cretaceous of Patagonia shows intraalveolar packages containing four teeth, one functional and three replacement (Coria and Chiappe 2001). Embryonic samples MCF-PVPH-659 and MCF-PVPH-704 suggest that titanosaurids would have had one or two replacement teeth early in their development, at least in the premaxilla.

Enamel/dentine ratio. In accordance with our observations, the enamel/dentine ratio is a character that changes during ontogeny (with the ratio decreasing through ontogeny). This measure may, therefore, be potentially useful in identifying the ontogenetic status of a dinosaur on the basis of isolated teeth. Nevertheless, the enamel/dentine ratio may be variable within a jaw, although this cannot be assessed on the basis of current data. Other adult titanosaur teeth from the Anacleto Formation, housed in the collection of the 'Carlos Ameghino' Museum (Río Negro, Argentina), also exhibit low enamel/dentine ratios.

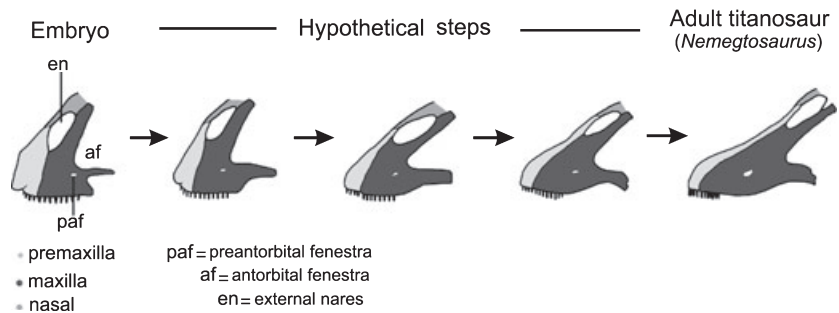
Dental formula and ontogenetic change. During their evolution, sauropods show a clear reduction in their dental formula (see Table 2), as well as a parallelism among diplodocoids and titanosaurs regarding the shape and number of teeth (Upchurch *et al.* 2004).

The dental formula (Pm 4, M 7–8/D10?) of the Auca Mahuevo embryos does not differ from that of adult titanosaurs. The ontogenetic stability in the dental formula contrasts with that of other dinosaurs, where tooth numbers usually increase through ontogeny (Varricchio 1997; Rauhut and Fechner 2005). However, although the number of teeth remains constant in titanosaurs, their distribution differs between embryos and adults. The maxillary teeth of the embryos are retracted (caudally) when compared to their positions in the adult (see above). This singular difference is interpreted as an important ontogenetic change in the maxilla during its development. The caudal portion of the maxilla appears to have undergone a rostral elongation, maintaining the tooth row in the rostral portion (Text-fig. 7).

Histology

Interelement histovariability. Minor variations in the shape and distribution of vascular canals in the skull bones are probably because of local differences in growth rate or the orientations of the thin sections. Similarly, the varying development of periosteal bone, the medullary cavity and bone porosity observed in the limb bone thin sections can be related to either the differential growth rates of different bones or (most plausibly) the varied positions of the sections (a thin bone layer and a very large marrow cavity can be seen at the extremity of several long bones). Nevertheless, embryonic bone microstructure is generally uniform. This is perhaps unsurprising as the most important histological variations among bones appear late in ontogeny (e.g. bone remodelling) and result from numerous environmental and genetic factors (A. d'Ricqlès, pers. comm. 2008).

TEXT-FIG. 7. Hypothetical ontogenetic trajectory of the frontal portion of a generalized titanosaur skull. Note allometric changes and relationship among different bones and ontogenetic relocation of the teeth.



Embryonic tissue. The presence of woven bone in limb and skull bones of titanosaurian embryos is typical of vertebrate embryos (Currey 2002; Hall 2005). Nevertheless, the limb bones do exhibit some differences from other taxa. Thin sections of limb bone shafts in crocodiles and turtles possess more compact embryonic tissue, with a low degree of vascularization and fewer osteocytes (Horner *et al.* 2001). In dinosaurs (ornithopods, non-avian theropods and birds), embryonic bone is characterized as cancellous, highly cellular and woven, with little or no osteocyte organization (Horner *et al.* 2001; Ricqlès *et al.* 2001) – this pattern is also seen in the titanosaur embryos. This resemblance is probably related to the high growth rates of dinosaurs, which were probably intermediate between those of reptiles and birds (Chinsamy and Dodson 1995; Chinsamy-Turan 2005; Lehman and Woodward 2008). Following Klein and Sander (2008), we suggest that the histology of the Auca Mahuevo embryos could be used to characterize their hypothetical bone tissue ‘type A’ (histological ontogenetic stage 1); this would represent highly vascularized woven bone, with wide, irregularly shaped vascular spaces that are irregularly distributed and lack layers of osteonal bone.

Embryonic stage. Long bone tissue of Auca Mahuevo embryonic titanosaurs is characterized by poor development of cortical bone compared with the marrow cavity (cortical bone occupies approximately 35 per cent of the total cross-sectional area in MCF-PVPH-808) and vascular canals without primary osteons and a high porosity (47 and 63%). In the dinosaur embryos described by Horner *et al.* (2001, pl. 3, fig. a–d and f), the periosteal bone is more extensive (occupying 78–95% of the traverse section) and has lower porosity (20 and 36%). These differences and the incomplete proximal and distal ossification of the limb bones in the Auca Mahuevo material reinforce the hypothesis that these titanosaur embryos were at an advanced developmental stage but not close to hatching (Chinsamy-Turan 2005).

Growth rate. The type of bone tissue and its degree of vascularity can offer valuable information concerning individual growth rates. It is well established that woven

bone is deposited more quickly than other bone types such as lamellar or paralleled-fibred bone (Currey 2002; Hall 2005). Also, the high degree of vascularization (inferred from porosity) has been proposed to reflect a high nutrient supply, which allows a very high growth rate (Horner *et al.* 2001). The strong vascularization and the high amount of osteocyte lacunae in the woven bone of the Auca Mahuevo specimens indicates that these embryos would have had a very highly growth rate in their early development. Nevertheless, it is not currently possible to quantitatively determine the rate of periosteal bone deposition. Recent studies (Castanet *et al.* 2000; Starck and Chinsamy 2002; Margerie *et al.* 2004) have demonstrated that, although depositional rate is related to bone type (as predicted by the ‘Amprino’s rule’), this rate may vary in different skeletal elements in response to diverse external and internal factors. Further work focused on extant archosaur embryos will allow more accurate growth rate estimations.

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