

# Cranial ontogenetic variation in *Mapusaurus roseae* (Dinosauria: Theropoda) and the probable role of heterochrony in carcharodontosaurid evolution

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**Abstract** The carcharodontosaurid theropod *Mapusaurus roseae* (Cenomanian of Neuquén Province, Argentina) is represented by at least seven disarticulated individuals from a monospecific bonebed, all of different sizes and presumably different stages of maturity. We report a series of anatomical differences between repeated skull bones of *Mapusaurus*, which we interpret as produced by peramorphic heterochronic processes. The materials analyzed include maxillae, lacrimals, dentaries, and isolated teeth. Most of the differences were recorded in the maxilla, the most noticeable change being the reduction of the pneumaticity. We found that some of the synapomorphic

characters of derived carcharodontosaurids appear to be the result of peramorphic heterochronies, as in the strongly ornamented facial bones, and the single opening in the anteroventral corner of the antorbital fossa in the maxilla.

**Keywords** Heterochrony · Peramorphosis · *Mapusaurus* · Carcharodontosauridae

**Kurzfassung** Der carcharodontosauride Theropode *Mapusaurus roseae* (aus dem Cenoman der Provinz Neuquén, Argentinien) ist durch mindestens 7 disartikulierte Individuen verschiedener Größe und vermutlich unterschiedlicher ontogenetischer Stadien aus einem monospezifischen Bonebed repräsentiert. Wir beschreiben eine Reihe anatomischer Unterschiede zwischen mehrfach vorkommenden Schädelknochen von *Mapusaurus*, die wir als Ergebnis peramorphischer Heterochronie-Prozesse interpretieren. Die untersuchten Elemente umfassen Maxillae, Lacrimale, Dentale und isolierte Zähne. Die größten Änderungen finden sich im Maxillare, wobei besonders die Reduktion der Pneumatisierung auffällt. Wir stellen fest, dass einige der apomorphen Merkmale fortschrittlicher Carcharodontosauriden auf Heterochronie zurückzuführen sind, darunter die stark ornamentierten Schädelknochen und das Vorhandensein nur einer Öffnung im anteroventralen Teil der Fossa antorbitalis im Maxillare.

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**Schlüsselwörter** Heterochronie · Peramorphose ·  
*Mapusaurus* · Carcharodontosauridae

## Introduction

Heterochrony has been defined as evolutionary change involving variation in the time of onset or rate of

development of a character in an organism relative to its ancestor (de Beer 1930). This process is widely recognized as an important agent of evolutionary change (Zelditch and Fink 1996) or even as the most important factor (Reilly et al. 1997; Gould 2002). Six basic types of heterochronic changes have been recognized (McNamara 1986; Reilly et al. 1997; Webster and Zelditch 2005): hypomorphosis (early termination of the shape change trajectory), deceleration (decrease in the rate at which the shape change trajectory is followed), postdisplacement (late onset of the shape change trajectory), hypermorphosis (late termination of the shape change trajectory), acceleration (increase in the rate at which the shape change trajectory is followed), and pre-displacement (early onset of the shape change trajectory). Hypomorphosis, deceleration and postdisplacement produce paedomorphosis (adult descendant morphology resembles the juvenile ancestor). In turn hypermorphosis, acceleration, and pre-displacement produce peramorphosis (adult ancestor morphology present in the juvenile phase of descendant). The term isomorphosis is used when heterochrony occurs without affecting the offset shape.

Some studies have analyzed the possible role of heterochrony in dinosaur evolution (Thulborn 1985; Weishampel and Horner 1994; Long and McNamara 1995, 1997a, b; Jianu and Weishampel 1999; Salgado 1999; Sander et al. 2004; Rauhut and Fechner 2005; Guenther 2009; Bhullar et al. 2012; McNamara and Long 2012). However, in the specific case of theropods, only a few studies had explored this issue.

Rauhut and Fechner (2005) for instance discussed that the significant morphological and proportional changes observed in the ontogeny of *Allosaurus*, especially the decrease in maxillary pneumaticity, are heterochronic. These authors, based on their own results and some previous studies (Norell et al. 1994; Long and McNamara 1997a, b), postulated that heterochrony was probably a common phenomenon in the evolution of non-avian theropods. To conduct a rigorous study of ontogenetic change, numerous specimens of the same species at different stages of development are required. A good example of this is *Tyrannosaurus rex*, since the amount of collected specimens of this species has allowed highly detailed studies of ontogenetic development (Carr 1999), including calculations of growth curves and longevity (Erickson et al. 2004).

The very large body size of some dinosaurs, which occurred independently in several theropod lineages (Sereno 1997), has been associated with heterochronic changes (Long and McNamara 1997b; Salgado 1999; McNamara and Long 2012). Carcharodontosauridae constitute a particularly interesting case study on the evolution of body size. The evolutionary history of Allosauroida is characterized by a change from basally-positioned, moderate-sized allosauroids (e.g., *Allosaurus*, *Sinraptor*,

*Neovenator*) to derived, large-bodied carcharodontosaurians (e.g., *Acrocanthosaurus*, *Giganotosaurus*, *Carcharodontosaurus*) that include some of the largest known terrestrial predators (Eddy and Clarke 2011).

*Mapusaurus roseae* is one of the best-known carcharodontosaurid theropods, being represented by numerous skeletal elements belonging to at least seven individuals of different sizes (Coria and Currie 2006). These specimens were found in a monospecific accumulation. This fact, coupled with some taphonomic features observed in certain elements, has led to the hypothesis that this species exhibited some sort of social behavior (Eberth et al. 2000; Coria and Currie 2006).

Certain morphological variation in some cranial elements assigned to *Mapusaurus roseae* is here interpreted as ontogenetic variation. This paper focuses on the possible evolutionary implications of these ontogenetic changes, and investigates whether the results are applicable to other carcharodontosaurid theropods.

#### Institutional abbreviations

MCF-PVPH: Museo Municipal “Carmen Funes”, Paleontología Vertebrados Plaza Huincul, Provincia de Neuquén, República Argentina. MNN-IGU: Musée National du Niger, Iguidi collection. Níger. MPEF-PV: Museo Paleontológico Egidio Feruglio, Paleontología de Vertebrados, Provincia de Chubut, República Argentina. MUCPV-Ch: Museo de la Universidad del Comahue, Colección Chocón, Villa El Chocón, Provincia de Neuquén, República Argentina. NCSM: North Carolina State Museum of Natural Sciences, Raleigh, North Carolina, USA. SGM-Din: Ministère de l'Énergie et des Mines, dinosaur collection, Rabat, Morocco. UMNH-VP: Utah Museum of Natural History, Vertebrate Paleontology collection, Salt Lake City, Utah, USA.

#### Materials and methods

The materials of *Mapusaurus roseae* Coria and Currie (2006) analyzed in this paper are: two maxillae (MCF-PVPH 108.169, MCF-PVPH 108.115), two lacrimals (MCF-PVPH-108.5, MCF-PVPH 108.183), two dentaries (MCF-PVPH 108.2, 108.3), and several teeth (MCF-PVPH 108.131, MCF-PVPH 108.8, MCF-PVPH 108.9, MCF-PVPH 108.110, MCF-PVPH 108.169). Bone measurements are given in Supplementary Table 1.

There are other cranial and postcranial bones belonging to different specimens (see Coria and Currie 2006) that do not show substantial differences in size and morphology, or are very fragmentary, limiting morphological interpretation. As a result, these were not included in this study.

The skeletal elements known of *Mapusaurus roseae* were found disarticulated and buried in a single depositional area. Therefore, the association of several bones to a single individual is not possible. For this reason, variation for each bone is described separately, and materials of different sizes are compared. These are considered as belonging to individuals at different stages of maturity, taking into account that the maturity of an individual is diagnosed by the presence or absence of characters acquired sequentially during ontogeny (“size-independent characters” Brinkman 1988; Brochu 1996). This variation is generally related to both the age and size of the specimen. This paper starts from the premise that the largest bones exhibiting features that show progressive development (e.g., coarse subcutaneous surface) are from oldest individuals.

Main comparisons were made on the basal carcharodontosaurid *Acrocanthosaurus atokensis* (NCSM 14345), because it was established as an adult specimen by recent histological studies (DÉmic et al. 2012). *Giganotosaurus carolinii* (MUCPV-Ch 1), and *Tyrannotitan chubutensis* (MPEF-PV 1156, MPEF-PV 1157) were also used for comparisons. They were considered adults based on the degree of fusion of the vertebral neurocentral sutures, although this method is debated (Brochu 1996; Irmis 2007). In the case of *Allosaurus fragilis*, which is represented by a larger number of specimens (although primarily isolated bones), we make comparisons with characters that are invariable in that taxon.

Regarding *Carcharodontosaurus* (SGM-Din 1; MNN-IGU 2), a problem arises in that both species *C. saharicus* Depéret and Savornin (1927) and *C. iguidensis* Brusatte and Sereno (2007) are solely represented by cranial remains (Sereno et al. 1996; Brusatte and Sereno 2007). Although there are several vertebrae assigned to both species of this taxon, referral to *Carcharodontosaurus* has been questioned (Novas et al. 2005; Canale et al. 2008). For this reason, the degree of fusion of the neurocentral sutures cannot be used for the adult estimation in those taxa. Some of the cranial elements of *C. saharicus* show a partial fusion between them, such as the lacrimal-prefrontal (SGM-Din 1), which sheds doubt about the full-grown condition of these materials. For this reason, these are excluded from the first comparisons, but we made comments on them in the discussion section. The same applies to the taxon *Eocarcharia dinops* (Sereno and Brusatte 2008), which is composed by associated elements and some repeated cranial bones (frontoparietals) exhibit different degrees of fusion.

For descriptive terminology we follow the anatomical nomenclature utilized by Eddy and Clarke (2011).

## Systematic nomenclature

A phylogenetic hypothesis is essential to polarize patterns of character change in order to identify heterochronic processes (Reilly et al. 1997). In this work we use the phylogenetic scheme proposed by Novas et al. (2013), (Fig. 1). Carcharodontosauridae (Stromer 1931) is defined as the most inclusive clade containing *Carcharodontosaurus saharicus*, but not *Sinraptor dongi* or *Allosaurus fragilis* (Holtz et al. 2004).

## Description

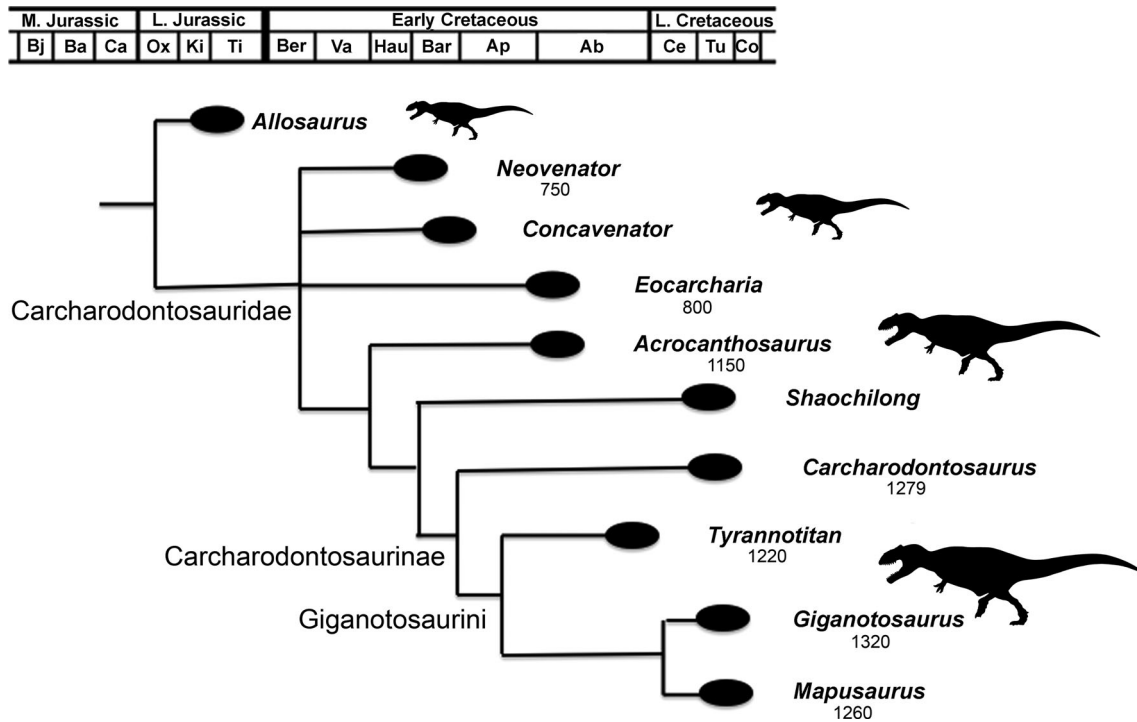
### Maxilla

Five maxillae of *Mapusaurus* are preserved. The two most complete were the basis for the description and comparisons (MCF-PVPH 108.169, MCF-PVPH 108.115). MCF-PVPH 108.169 is 19 % larger than MCF-PVPH 108.115. A third specimen, MCF-PVPH 108.11 was included for additional comparisons.

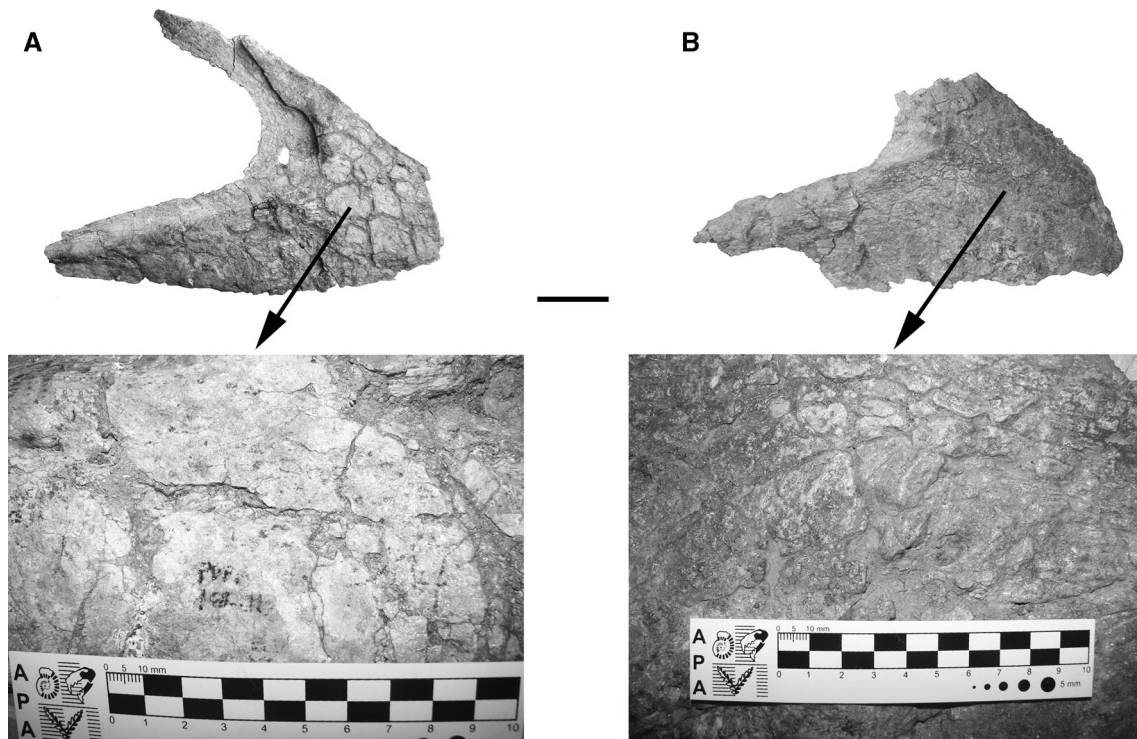
### Sculpturing

External sculpturing consisting of vertical ridges and furrows that cover the lateral surface of the maxilla was proposed as a synapomorphy present in derived allosauroids *Giganotosaurus*, *Carcharodontosaurus*, and *Mapusaurus* (Brusatte and Sereno 2008).

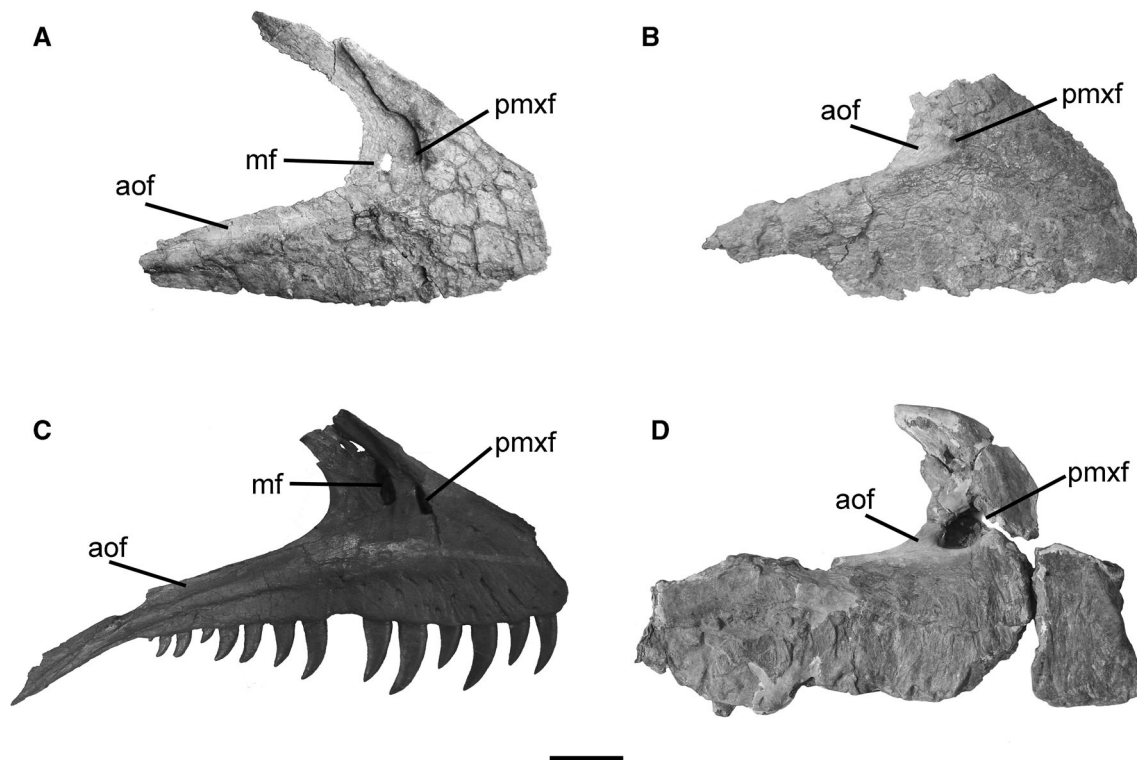
In *Mapusaurus* the small maxilla MCF-PVPH 108.115 lacks lateral ornamentation (Fig. 2a), and has only a row of foramina located dorsal to the tooth row. A similar condition can be seen in the maxillae of the basal allosauroid *Allosaurus fragilis* (UMNH-VP 9168, 9218, 9211), and in the basal carcharodontosaurid *Acrocanthosaurus atokensis* (NCSM 14345). In contrast, the larger *Mapusaurus* maxilla MCF-PVPH 108.169 exhibits conspicuous ornamentation throughout its lateral face (Fig. 2b) composed mainly of rugose bone and, to a lesser extent, grooves similar to that observed in *Giganotosaurus* (MUCPV-Ch 1). A fragmentary left maxilla of *Mapusaurus* (MCF-PVPH 108.11) is slightly bigger than other maxillae (MCF-PVPH 108.115; MCF-PVPH 108.169), and has even more marked ornamentation, with conspicuous ridges and deeper furrows. Therefore, ontogenetic change from a smooth lateral surface to a coarse lateral surface recapitulates the phylogenetic change from basal Allosauroidea and Carcharodontosauridae to derived Carcharodontosauridae.



**Fig. 1** Time calibrated phylogenetic relationships of Allosauroidea, based on the analysis of Novas et al. (2013). Numbers below names indicates estimations of maximum body length (in cm)



**Fig. 2** Maxillae of *Mapusaurus roseae* in lateral view with details of the bone surface. **a** MCF-PVPH 108.115; **b** MCF-PVPH 108.169. Scale bar 10 cm



**Fig. 3** Maxillae of *Mapusaurus roseae* (a MCF-PVPH 108.115; b MCF-PVPH 108.169), *Acrocanthosaurus atokensis* NCSM 14345 (c) and *Giganotosaurus carolinii* MUCPV-Ch 1 (d) in lateral view.

aof antorbital fossa, pmxf premaxillary fenestra, mxf maxillary fenestra. Scale bar 10 cm

#### Antorbital fossa

Another notable difference in *Mapusaurus* maxillae concerns the development of the antorbital fossa and the arrangement of its inner (medial) and outer (lateral) margins over the ventral area of the antorbital fenestra. In the small specimen (MCF-PVPH 108.115), this fossa is well developed, and its smooth surface is clearly observable in lateral view (Fig. 3a), because the inner edge of the fossa is situated dorsally to the outer edge. The same arrangement is observable in *Allosaurus fragilis* (UMNH-VP 9168, 9218, 9211) and *Acrocanthosaurus atokensis* (NCSM 14345). In the bigger maxilla of *Mapusaurus roseae* (MCF-PVPH 108.169), the outer margin of the antorbital fossa is almost at the level of the inner edge, thus, the fossa is poorly exposed in lateral view (Fig. 3b). A similar condition can be seen in *Giganotosaurus carolinii* (MUCPV-Ch 1). Therefore, ontogenetic change seen in the antorbital fossa recapitulates the phylogenetic change from basal Allosauroidae and Carcharodontosauridae to derived Carcharodontosauridae.

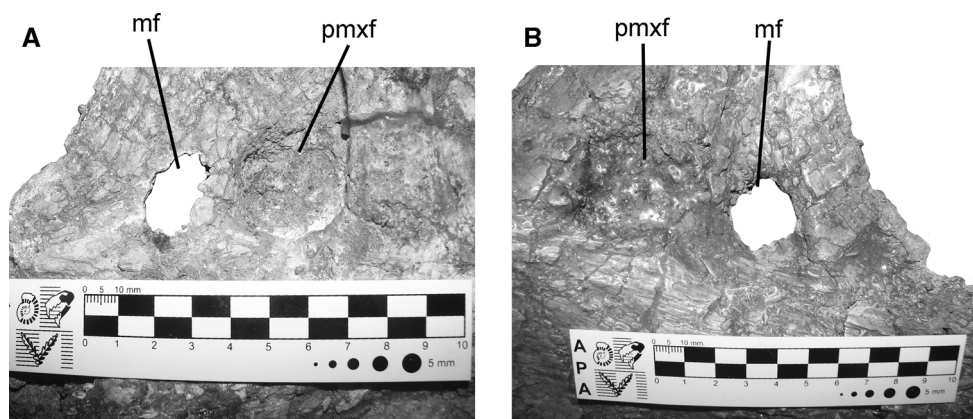
#### Openings in the antorbital fossa

The anteroventral corner of the antorbital fossa in theropods is pierced by one or more large openings. In theropods

with two openings, the anteriormost one is termed the promaxillary fenestra while the posterior one is the maxillary fenestra (Witmer 1997). Both openings are separated by the promaxillary strut (Witmer 1997). In derived carcharodontosaurids, such as *Giganotosaurus carolinii* (MUCPV-Ch 1), *Mapusaurus roseae* (MCF-PVPH 108.169), *Carcharodontosaurus saharicus* (SGM-Din 1), and *Carcharodontosaurus iguidensis* (MNN-IGU 2) a single opening is present in the anterior sector of the antorbital fossa. The probable homology of this opening has been the focus of discussion and different interpretations. Sereno et al. (1996) and Brusatte and Sereno (2007) postulated that this opening in *Carcharodontosaurus saharicus* and *Carcharodontosaurus iguidensis* is the maxillary fenestra, whereas the promaxillary fenestra is autapomorphically absent from these taxa. Similarly, Coria and Currie (2006) proposed that in *Mapusaurus* this structure could correspond to the maxillary fenestra. However, Currie and Carpenter (2000) suggested that this opening in *Giganotosaurus* and *Carcharodontosaurus* is homologous by position to the promaxillary fenestra, inferring that the maxillary fenestra is absent in these taxa.

The smaller maxilla of *Mapusaurus* (MCF-PVPH 108.115) has two openings in the anteroventral corner of the antorbital fossa (Fig. 3a). The anterior one has been tenuously interpreted as the maxillary fenestra by Coria

**Fig. 4** Detail of the openings in the maxillary antorbital fossa of *Mapusaurus roseae* MCF-PVPH 108.115. **a** Lateral view; **b** medial view. *pmxf* premaxillary fenestra, *mf* maxillary fenestra



and Currie (2006). The posterior opening, despite having been illustrated by Coria and Currie (2006, pg. 77, Fig. 2c, d), was not described because it was interpreted only as a broken surface. However, along the medial side of the maxilla, the margins of the opening are natural (Fig. 4). The edges, which have broken surfaces, are located on the lateral side of the maxilla. It is possible that an extremely thin sheet of bone would have closed the opening laterally in life. On the other hand, in the maxilla MCF-PVPH 108.169 (which is approximately 16 % bigger than MCF-PVPH 108.115) a depression is observed on the medial side that corresponds in position to the posterior opening in the maxilla MCF-PVPH 108.115, although it is much less marked.

The depression observed in the medial lamina of the maxilla MCF-PVPH 108.115 is interpreted here as the true maxillary fenestra. By its position, the opening located anteriorly, previously regarded as the maxillary fenestra, is reinterpreted here as homologous to the promaxillary fenestra. On the other hand, in the largest maxilla of *Mapusaurus*, the promaxillary fenestra is anteriorly positioned, whereas the posterior depression of the medial side is much less marked.

We interpret that the maxillary fenestra would have been lost in the course of *Mapusaurus* ontogeny, and probably also in other derived carcharodontosaurid allosauroids (*Giganotosaurus* and *Carcharodontosaurus*), apparently obliterated during ontogeny by bone tissue. Interestingly, one of the results published by Rauhut and Fechner (2005) on the ontogenetic changes in the *Allosaurus* maxilla, and those by Chure and Madsen (1996) on the ontogenetic changes in the braincase of this taxon, include a substantial reduction of the characters related to pneumaticity, which is consistent with the changes observed and interpreted in this contribution for *Mapusaurus* maxilla.

Accordingly, the ontogenetic change involving the loss of the maxillary fenestra recapitulates the phylogenetic change from basal Allosauroidae and Carcharodontosauridae to derived Carcharodontosauridae.

#### Shape of the palatal shelf

The palatal shelf consists of a rounded medial projection on the medial surface of the maxilla, located between the antorbital fenestra and the dorsal margin of interdental plates (Coria and Currie 2006). In the smallest specimen of *Mapusaurus* (MCF-PVPH 108.115) this shelf is a slightly marked low and rounded prominence (Fig. 5a), as in *Allosaurus* (UMNH-VP 9168, UMNH-VP 9218, UMNH-VP 9211) and *Acrocanthosaurus* (NCSM 14345). The shelf is a much more marked medially projected crest in the largest specimen (MCF-PVPH 108.169) (Fig. 5b) as can also be seen in *Giganotosaurus* (MUCPV-Ch 1). Consequently, the ontogenetic change in the palatal shelf from a low prominence to a strong and marked shelf recapitulates the phylogenetic change from basal Allosauroidae and Carcharodontosauridae to derived Carcharodontosauridae.

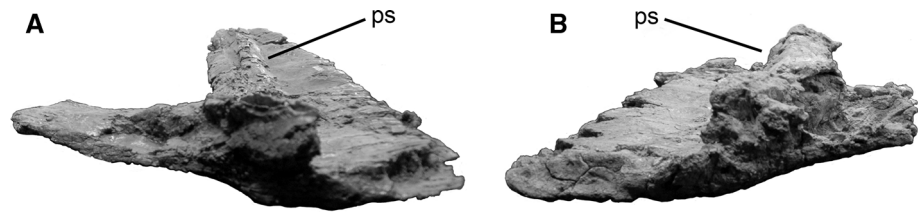
#### Lacrimal

Four lacrimals of *Mapusaurus* are preserved (MCF-PVPH 108.5, 108.100, 108.101, 108.183), two of which are almost complete (MCF-PVPH 108.5, 108.183), and they will be discussed here. The specimen MCF-PVPH 108.183 is 20 % larger than the MCF-PVPH 108.5. The fusion with the prefrontal is complete in both lacrimals.

#### Sculpturing

Both specimens (MCF-PVPH 108.5, 108.183) have ornamentation in the form of grooves, as are present generally in other allosauroids (i.e., *Allosaurus* UMNH-VP 9472, 9473; *Acrocanthosaurus* NCSM 14345). In the larger specimen, there is also a granulated ornamentation composed of small round bumps, present on both the lateral and dorsal sides (Fig. 6). In *Giganotosaurus* (MUCPV-Ch 1) a similar ornamentation can be observed. Therefore, ontogenetic change from a smooth lateral surface to a sculptured lateral surface recapitulates the phylogenetic change

**Fig. 5** Maxillae of *Mapusaurus roseae* in anteromedial view, **a** MCF-PVPH 108.115; **b** MCF-PVPH 108.169. *ps* palatal shelf



**Fig. 6** Left lacrimals of *Mapusaurus roseae* in lateral view, **a** MCF-PVPH 108.5; **b** MCF-PVPH 108.183. Scale bar 10 cm

from basal Allosauroidea and Carcharodontosauridae to highly derived Carcharodontosauridae.

#### Dentary

Four dentaries of *Mapusaurus* were recovered (MCF-PVPH 108.2, 108.3, 108.39, 108.125), varying in degree of preservation. The smallest (MCF-PVPH 108.3) and the largest (MCF-PVPH 108.2) are used here for comparison. MCF-PVPH 108.2 is 56 % larger than MCF-PVPH 108.3.

#### Ornamentation

MCF-PVPH 108.3 was interpreted as belonging to a juvenile by Coria and Currie (2006). By comparing this material with MCF-PVPH 108.2, a greater degree of ornamentation on the lateral aspect of the larger dentary is observed, as previously noted by Coria and Currie (2006). The ornamentation consists of slight grooves and granulations. The

degree of the ornamentation in the largest dentary is slightly lesser than what it is seen in both *Giganotosaurus* (MUCPV-Ch 1) and *Tyrannotitan* (MPEF-PV 1156, 1157). In contrast, MCF-PVPH 108.3 presents a lateral surface that is mostly smooth as in *Allosaurus* (UMNH-VP 9351, 6477) and *Acrocanthosaurus* (NCSM 14345). Consequently, the ontogenetic change from a smooth lateral surface to a rugose lateral surface recapitulates the phylogenetic change from basal Allosauroidea and Carcharodontosauridae to derived Carcharodontosauridae.

#### Lateral ridge

In *Mapusaurus* there is a ridge on the lateral surface of the dentary, just below the lateral sulcus that carries the neurovascular foramina (Coria and Currie 2006). This feature is faint in the smallest specimen (MCF-PVPH 108.3), and is strongly pronounced in the largest one (MCF-PVPH 108.2), especially in the central area of the dentary (Fig. 7). Moreover, the development of this ridge affects the orientation of the neurovascular foramina, which face laterally in the smallest specimen, but laterodorsally in the largest one. MCF-PVPH 108.3 shows a condition similar to that present in *Allosaurus* (UMNH-VP 9351, 6477) and *Acrocanthosaurus* (NCSM 14345), whereas in the larger dentary MCF-PVPH 108.2, the ridge is well developed, as in the derived carcharodontosaurids *Giganotosaurus* (MUCPV-Ch 1) and *Tyrannotitan* (MPEF-PV 1156, 1157). Therefore the ontogenetic change involving the development of a pronounced lateral ridge recapitulates the phylogenetic change from basal Allosauroidea and Carcharodontosauridae to derived Carcharodontosauridae.

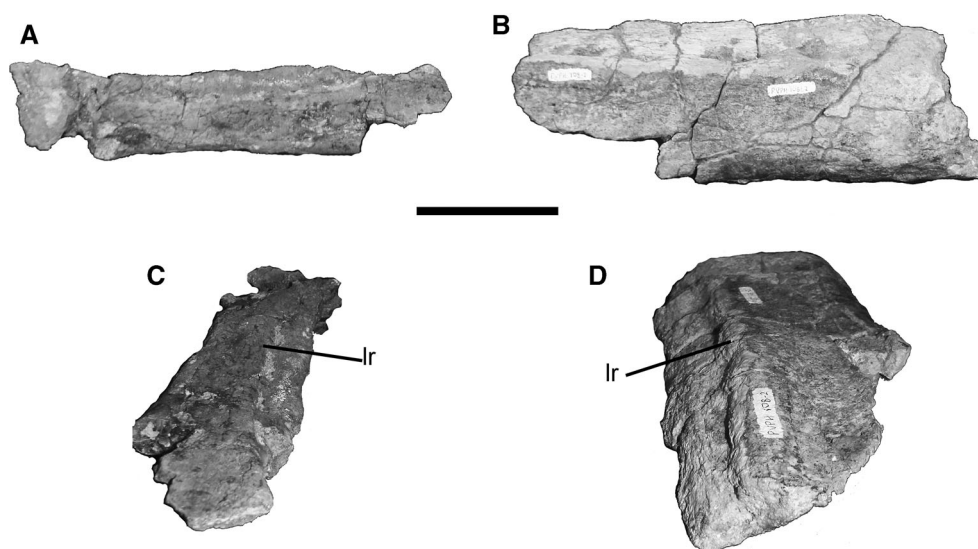
#### Teeth

Several isolated teeth have been collected. Their measurements and details are provided in Coria and Currie (2006, Table 2).

#### Denticles

In one of the smallest teeth recovered (MCF-PVPH 108.131), there are 14 denticles per 5 mm, whereas in the largest teeth (MCF-PVPH 108.8, MCF-PVPH 108.9, MCF-PVPH 108.110 MCF-PVPH 108.169) there are 8–9

**Fig. 7** Dentaries of *Mapusaurus roseae*. **a, c** Left dentary MCF-PVPH 108.3; **b, d** right dentary MCF-PPHV 108.2. **a, b** Are lateral views; **c, d** are posterolateral views. *lr* lateral ridge. Scale bar 10 cm



denticles per 5 mm. In the basal carcharodontosaurid *Acrocanthosaurus* (Currie and Carpenter 2000) there are between 13 and 15 denticles per 5 mm, while in derived forms as in *Tyrannotitan* (MPEF-PV 1156, 1157) and *Giganotosaurus* (MUCPV-Ch 1), the amount of denticles ranges from eight to ten denticles every 5 mm. Contrary to what is observed in *Mapusaurus*, in the coelurosaur *Tyrannosaurus rex*, the serration count in teeth increases through ontogeny (Long and McNamara 1997a, b). Consequently, the ontogenetic change involving decreasing in denticle quantity recapitulates phylogenetic change from basal Allosauroida and Carcharodontosauridae to derived Carcharodontosauridae.

## Discussion

The differences observed between cranial bones belonging to *Mapusaurus* individuals of different sizes are also found in basal and derived allosauroid taxa. The fact that the characters found in the smaller specimens of *Mapusaurus* (interpreted as not fully developed) are observed in basal allosauroids suggests that heterochronic-peramorphic processes have taken place in the evolution of the clade Carcharodontosauridae.

Many of the characters registered in larger specimens of *Mapusaurus* are also present in other derived carcharodontosaurids, such as *Giganotosaurus*, *Tyrannotitan* and even in *Carcharodontosaurus*, which conform a clade known as Carcharodontosaurinae (Fig. 1). For instance, there are the single opening in the antorbital fossa (here interpreted as the promaxillary fenestra), the pronounced palatal shelf, the extreme ornamentation of the facial bones, particularly the maxilla and dentary, and the marked lateral ridge in dentary. In the specific case of the lacrimal

ornamentation, the granulated pattern is observed only in *Mapusaurus* and *Giganotosaurus*, while in *Carcharodontosaurus saharicus* the lateral surface of this bone is smooth as in more basal allosauroids. On the other side, the characters recognized in the smaller specimens of *Mapusaurus* are present in *Allosaurus* and basal carcharodontosaurids, not only *Acrocanthosaurus*, but also in *Eocarcharia* and *Neovenator*. Those include the unornamented facial bones, the laterally visible antorbital fossa of maxilla and the presence of both promaxillary and maxillary fenestra.

Is interesting to point out the differences about ontogenetic dental variation found between *Mapusaurus* and *Tyrannosaurus*. As we stated in the description section, while in *Mapusaurus* the denticle density decreases through ontogeny, in *Tyrannosaurus* there occurs the opposite. It is worth mentioning that in the juvenile basal tetanuran *Sciurumimus* the tooth morphology is very different to that present in adult basal tetanurans, and similar to small-bodied coelurosaurs (strong crown curvature, absence of mesial denticles), implying that the tooth morphology of these coelurosaurs may be the result of heterochronic processes (Rauhut et al. 2012). Given the recurrence of strong differences between juvenile and adult tooth morphology in different theropod lineages, the use of certain characters like the presence/absence or quantity of denticles for taxonomic identification of isolated teeth should be used with caution.

Although we do not have conclusive evidence, some of the data analyzed can lead us to think that a peramorphic trend (“peramorphocline”: McNamara 1982) can be observed in the evolution of Carcharodontosauridae. This would be consistent with the extremely large body sizes recorded in the more derived members of the group. Plotting maximum body length of different



carcharodontosaurid species (taken from Eddy and Clarke 2011) in a recently published phylogeny (Novas et al. 2013) shows that body size increased progressively through time in successive ancestors and more than once during the evolution of the clade (Fig. 1). Gigantism is a feature widely cited for clades where peramorphic changes predominate over paedomorphosis (McNamara 2012; McNamara and Long 2012), such as in tyrannosauroid coelurosaurids (Long and McNamara 1995, 1997a, b), or diplodocine sauropods (Salgado 1999). This peramorphic gigantism usually occurs by hypermorphosis, acceleration, or a combination of both (Long and McNamara 1997b; Salgado 1999; McNamara and Long 2012). In the carcharodontosaurid *Acrocanthosaurus*, it was claimed that the predominant process was presumably acceleration of the growth rate (DÉmic et al. 2012); in the case of the coelurosaur *Tyrannosaurus rex* the acting processes would have been both acceleration (Erickson et al. 2004) and hypermorphosis (McNamara and Long 2012). Although histological studies on other carcharodontosaurids are needed, we can assume that acceleration played a primary role in the evolution of this clade, since it can be regarded as the primitive condition present in *Acrocanthosaurus*, posteriorly inherited by the later taxa. Although peramorphosis probably predominated in the evolution of Allosauroidae, at least one possible paedomorphic character is present in this group: the reduction of arms (especially the modules of forearm and hand) in proportion to body size, as seen in *Acrocanthosaurus* in comparison with *Allosaurus* (Currie and Carpenter 2000). The combination of both processes is called “dissociated heterochrony” and is also recorded in Diplodocimorpha (Salgado 1999) and Tyrannosauridae (Long and McNamara 1997b; McNamara 2012). Despite the similarities between Tyrannosauridae and Carcharodontosauridae regarding peramorphosis as the dominant process in the evolution of both groups, it is interesting to note that in the case of Tyrannosaurinae, characters related to craniofacial pneumaticity, such as the size of the maxillary fenestra, are strongly developed during later stages of ontogeny (Carr 1999), whereas in Carcharodontosauridae (and Allosauroidae in general) they are significantly reduced.

## Conclusions

Differences found in repeated in skull bones of *Mapusaurus* show evidence of peramorphic development patterns, which are inferred from a comparison with basal and derived allosauroid forms. Some synapomorphic characters of derived carcharodontosaurids appear to be the result of heterochronic processes. Synapomorphies of the clade Carcharodontosaurinae (including *Carcharodontosaurus*,

*Tyrannotitan*, *Giganotosaurus*, and *Mapusaurus*) includes the loss of maxillary fenestra, the laterally obscured ventral sector of antorbital fossa, the enhanced maxillary and dentary sculpturing, the marked palatal shelf, the pronounced lateral ridge in dentary, and the low denticle density. The strongly sculptured lacrimal is a synapomorphy of the clade formed by *Giganotosaurus* and *Mapusaurus* (Giganotosaurini). It is relevant that the ontogenetic series of *Mapusaurus* clarifies the assignment of the only opening present in the antorbital fossa in derived carcharodontosaurids as the promaxillary fenestra.

One of the most noticeable developmental changes in *Mapusaurus* is the reduction of maxillary pneumaticity. The fact that a similar process had been reported in *Allosaurus* (Rauhut and Fechner 2005; Chure and Madsen 1996) suggests that the reduction in craniofacial pneumaticity during ontogeny has been a common process in the Allosauroidae. We can conclude that the general trend in the evolution of skull morphology in Allosauroidae includes several characters that had arisen from heterochronic processes, such as the reduction of craniofacial pneumaticity and an increase in bone sculpturing.

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