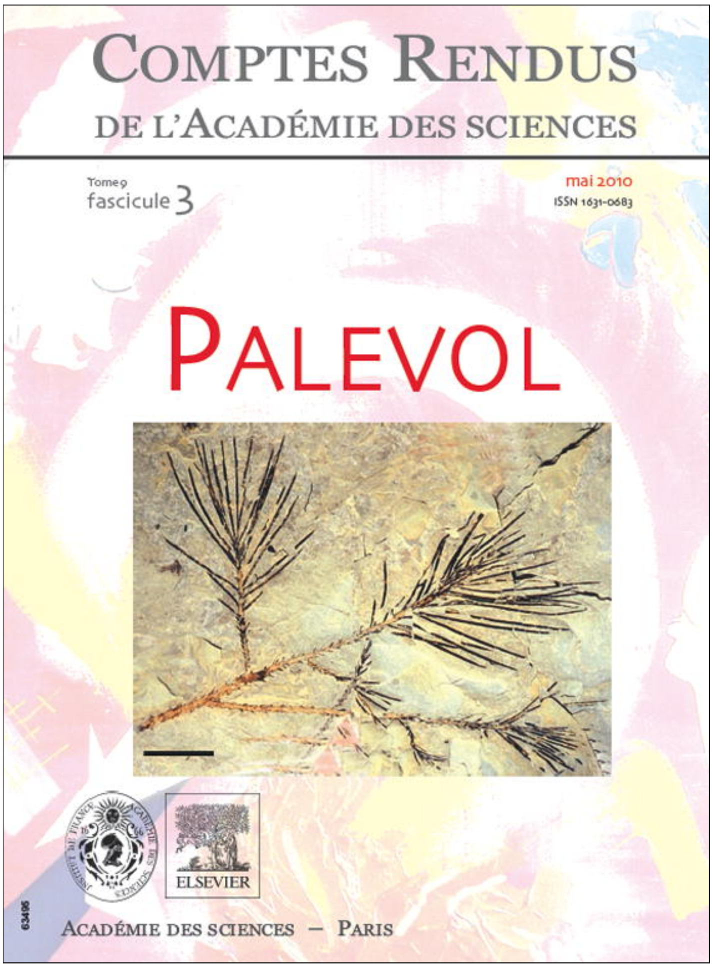
Comptes Rendus
de l'Académie des sciences
Tome 9
fascicule 3
mai 2010
ISSN 1631-0683
Palevol
Elsevier
Académie des sciences — Paris
63495

C. R. Palevol 9 (2010) 83–93

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

Systematic palaeontology (Vertebrate palaeontology)

The dentition of *Amygdalodon patagonicus* (Dinosauria: Sauropoda) and the dental evolution in basal sauropods

La denture d'Amygdalodon patagonicus (Dinosauria : Sauropoda) et l'évolution dentaire des sauropodes basaux

José Luis Carballido , Diego Pol*

CONICET, Museo Paleontológico Egidio Feruglio, Av. Fontana 140, U9100GYO, Trelew, Chubut Province, Argentina

ARTICLE INFO

Article history:
Received 2 April 2009
Accepted after revision 9 November 2009
Available online 1 April 2010

Presented by Philippe Taquet

Keywords:
Teeth
Amygdalodon
Sauropoda
Wear facets
Denticles

Mots clés :
Dents
Amygdalodon
Sauropoda
Facettes d'usure
Denticules

ABSTRACT

Amygdalodon patagonicus is the oldest record of Sauropoda from South America and is known from several teeth and fragmentary postcranial remains. Here we describe in detail its dental morphology, characterized by the presence of broad spatulated teeth (with low SI values) and the absence of denticles in their crowns. The enamel bears a particular wrinkling pattern composed only of apicobasally-aligned pits, which are frequently joined to each other by a continuous sulcus. Some worn teeth have large wear-facets that extend over only one of the crown's edges. This unique combination of characters provides a proper diagnosis for *Amygdalodon*. Despite the fragmentary available material, *Amygdalodon* is here interpreted as a non-eusauropod sauropod based on the results of a phylogenetic analysis. The presence of derived dental characters in *Amygdalodon*, such as the presence of tooth-tooth occlusion, shows several features previously thought to diagnose Eusauropoda or Gravisauria appeared earlier during the early evolution of sauropods.

RÉSUMÉ

Amygdalodon patagonicus est le plus vieux sauropode connu en Amérique du Sud et est représenté par plusieurs dents et des restes postcrâniens fragmentaires. Nous décrivons ici, en détail, sa morphologie dentaire qui se caractérise par la présence de larges dents spatulées (avec de faibles valeurs de SI) et l'absence de denticules sur les couronnes. Le plissement de l'émail a un patron particulier, composé seulement de petites dépressions alignées apicobasalement et fréquemment réunies par des sillons continus. Quelques dents possèdent une large facette d'usure qui s'étend uniquement sur un des bords de la couronne. Cette combinaison unique de caractères est diagnostique d'*Amygdalodon*. En dépit du matériel fragmentaire disponible et d'après les résultats d'une analyse phylogénétique, *Amygdalodon* est considéré ici comme un sauropode non gravisaurien. La présence de caractères dentaires dérivés chez *Amygdalodon*, comme l'existence d'une occlusion dent à dent, montre que plusieurs caractères considérés précédemment comme des apomorphies de Eusauropoda ou Gravisauria, apparaissent en réalité plus tôt dans l'histoire évolutive des sauropodes.

---

* Corresponding author.
E-mail address: dpol@mef.org.ar (D. Pol).

1631-0683/$ – see front matter © 2010 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.crpv.2010.01.003

1. Introduction

Amygdalodon patagonicus (Cabrera, 1947) represents the earliest sauropodomorph taxon from South America that has been referred to Eusauropoda (Rauhut, 2003; Wilson, 2002). The type material was collected in the Cerro Carnerero Formation (Central Patagonia). Although the exact age of this unit is uncertain, this formation has been referred to the Toarcian-Aalenian (Rauhut, 2003). *Amygdalodon* was originally described by Cabrera (1947) based on materials collected in 1948 by Dr. T. Suero, providing only a general description of the postcranial elements, four almost complete teeth, and one tooth crown. Casamiquela (1963) redescribed the original material and referred to *A. patagonicus* additional elements found at the same locality several years after the original finding. In this work, Casamiquela only briefly mentioned the teeth, noting similarities with other sauropods known at that time (e.g., *Cetiosaurus, 'Brontosaurus'*; [Cabrera, 1947]). More recently, Rauhut (2003) described all the postcranial material and considered *Amygdalodon* as one of the most basal member of Eusauropoda, although only one of the teeth of the referred material was included in his study. The purpose of this article is to describe in detail the dental anatomy of *Amygdalodon* based on the study of the tooth crowns of the referred material, and discuss its bearing on the diagnosis and phylogenetic affinities of this taxon, as well as its implications for the early evolution of sauropod dentition.

2. Systematic palaeontology

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878
Amygdalodon patagonicus Cabrera, 1947

Lectotype: MLP 46-VIII-21-1/2 (posterior dorsal vertebra).

Referred material: MLP 46-VIII-21-1/1 and MLP 46-VIII-21-1/3 through 11 (vertebral and rib remains), MLP 46-VIII-21-1/12, MLP 46-VIII-21-1/13, MLP 46-VIII-21-1/15, MLP 46-VIII-21-1/12 17 and MLP 46-VIII-21-1/12 18 (tooth crowns), MLP 46-VIII-21-1/12 14 and MLP 46-VIII-21-1/12 16 (roots), MLP 46-VIII-21-1/19 (right pubis), MLP 36-XI-10-3/1 (posterior dorsal vertebrae with attached dorsal rib).

One of the tooth crowns [MLP 46-VIII-21-1/18] has not been found in the MLP collections, so this study is based on the other four teeth. Although no repeated elements are present among all the material referred to *Amygdalodon*, Rauhut (2003) noted that size differences between the original vertebrae described by Cabrera (1947) and the subsequently collected vertebra described by Casamiquela (1963) may be indicative of the presence of two different specimens. Nonetheless, Rauhut considered both elements belonged to the same taxon and referred all the available material to *A. patagonicus* (Rauhut, 2003). Although there are no detailed information on the association of the collected material, the only differences noted by Rauhut (2003) were found between the originally collected material (which includes all the known teeth) and a vertebra subsequently collected and described by Casamiquela (1963). Given that among the original material described by Cabrera there are no repeated elements, no significant size differences, and that all the elements have a similar phylogenetic signal (i.e., showing a combination of characters known only in basal sauropods), we agree with Rauhut (2003) in referring at the moment these materials to a single taxon, *A. patagonicus.*

Horizon and locality: Cañadón Puelman, southwest from Cerro Carnerero, Sierra del Cerro Negro, Chubut Province, Argentina. Cerro Carnerero Formation (Late Toarcian to Early Aalenian (Rauhut, 2003)).

Emended diagnosis: *Amygdalodon* is a sauropod diagnosed by the following unique combination of characters (autapomorpy marked with an asterisk): lateral walls of the neural canal and centropostzygapophyseal laminae flared laterally posteriorly; neural canal strongly flexed anteroposteriorly within the dorsal neural arches; spoon-shaped teeth with low SI values (1.34–1.49); enamel wrinkled forming a pattern of pits and narrow apicobasal sulci*; total absence of denticles in both mesial and distal margins; wear facets extending mostly along one margins of the crowns (modified from Rauhut (2003)).

3. Description

Two of the preserved elements are interpreted as upper teeth and one as a lower element of the left toothrow, based on the asymmetrical profile of the mesial and distal margins and the location and orientation of the wear facets. The two upper teeth (MLP 46-VIII-21-1/12 and MLP 46-VIII-21-1/15) are only incipiently worn and preserve most of their original crown morphology, whereas the lower tooth is more extensively worn (MLP 46-VIII-21-1/13). The fourth crown (MLP 46-VIII-21-1/17) is severely damaged and we cannot infer its position.

3.1. General features

As originally described by Cabrera (1947), the tooth crowns of *Amygdalodon* are spatulate, being mesiodistally broad, buccolingually compressed, and their apex is slightly curved lingually (Fig. 1). The mesial and distal margins are asymmetrical (Rauhut, 2003), the mesial margin being more convex and the distal margin more straight (and with a small bulge at the base of the crown in some teeth). This asymmetric profile of the tooth crowns seems to be present in most (if not all) sauropod taxa with broad spatulated tooth crowns (*e.g., Tazoudasaurus* [Allain and Aquesbi, 2008], *Shunosaurus* [Chatterjee and Zheng, 2002], *Camarasaurus* [Madsen et al., 1995], *Astrodon* [Carpenter and Tidwell, 2005]). The crowns are relatively low in comparison to their maximum mesiodistal width, having an SI index (Upchurch, 1998) that varies between 1.34 and 1.50. These values are usually higher in Eusauropoda (as well as in more basal saurpodomorphs), so that *Amygdalodon* teeth are comparatively lower and broader than in most sauropodomorph taxa. The breadth of *Amygdalodon* crowns is also remarkable in comparison with eusauropods when the root width is taken into account, as the maximal crown mesiodistal width is 130–150% of the maximum root

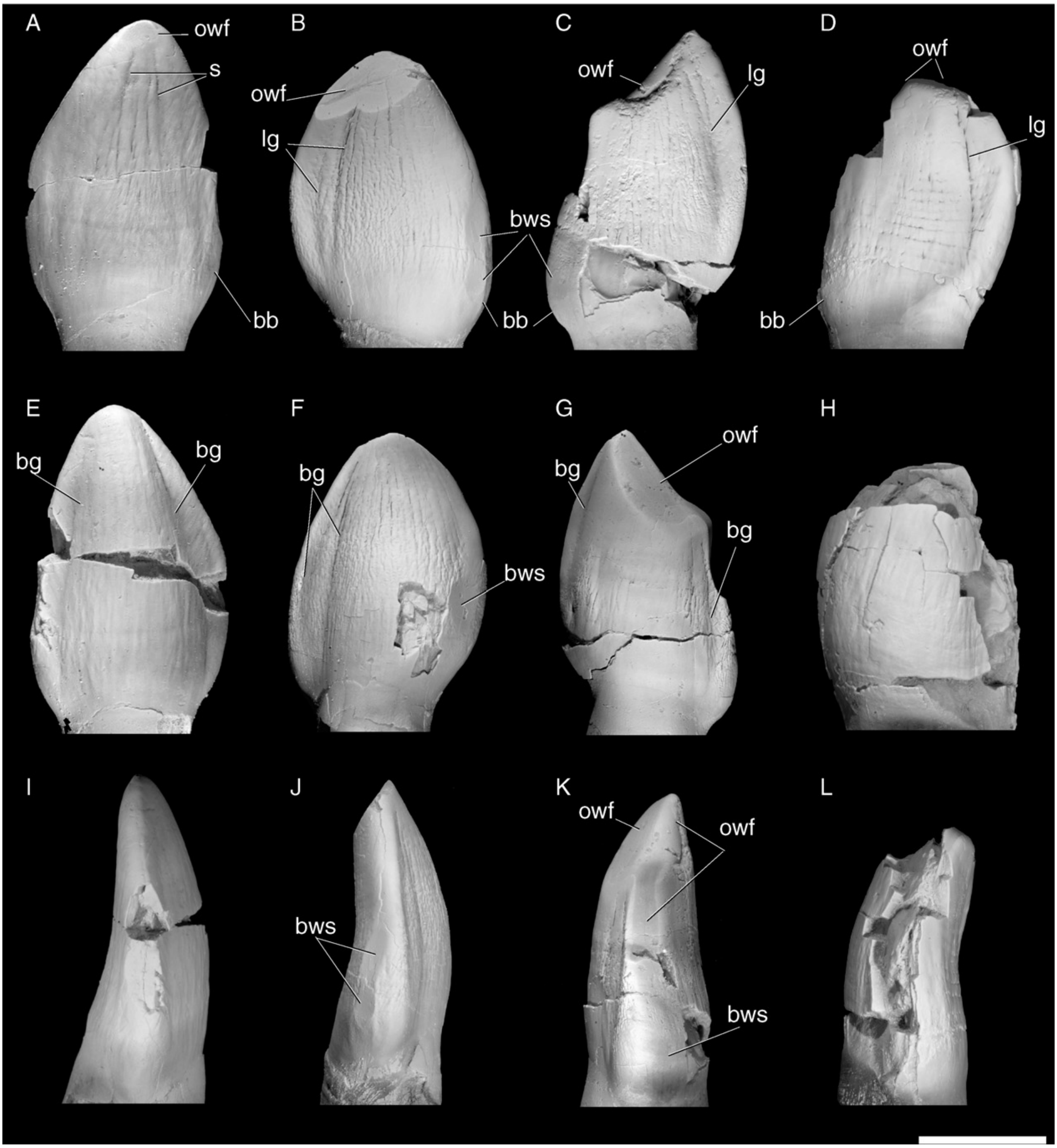

Fig. 1. Teeth of *Amygdalodon patagonicus* (MLP 46-XIII-21-1) in lingual (A–D), buccal (E–H), and mesial (I–L) views. MLP 46-XIII-21-1/15 (A, E, I), MLP 46-XIII-21-1/12 (B, F, J), MLP 46-XIII-21-1/13 (C, G, K), MLP 46-XIII-21-1/17 (D, H, L). Abbreviations: bb: basal distal bulge; bg: buccal groove; bws: basal wear surface; lg: lingual groove; owf: occlusal wear facet; s: sulcus. Scale bar equal 1 cm.

Fig. 1. Dents d'*Amygdalodon patagonicus* (MLP 46-XIII-21-1) en vue linguale (A–D), buccale (E–H), et mésiale (I–L). MLP 46-XIII-21-1/15 (A, E, I), MLP 46-XIII-21-1/12 (B, F, J), MLP 46-XIII-21-1/13 (C, G, K), MLP 46-XIII-21-1/17 (D, H, L). Abréviations : bb : renflement distal basal ; bg : cannelure buccale ; bws : surface d'usure basale ; lg : cannelure linguale ; owf : facette d'usure occlusale ; s : sulcus. Barre d'échelle 1 cm.

mesiodistal width (resembling the condition of the basal gravisaurian *Tazoudasaurus*). The crown therefore abruptly expands mesiodistally above with crown-root limit (Fig. 1). All teeth have a D-shaped cross-section with their buccal surface is mesiodistally convex and their lingual surface relatively flat (except for MLP 46-VIII-21-1/13, see Fig. 1 and below). Based on these features the teeth of *Amygdalodon* clearly fall within the broad-crowned (BC) category as defined by Barrett and Upchurch (2005).

There are two remarkable features of *Amygdalodon* dentition in comparison with those of most eusauropods with spatulate dentition. The first one is the absence of denticles on the distal and mesial margins (Fig. 1). This feature, noted by previous authors (Cabrera, 1947; Rauhut, 2003) seems

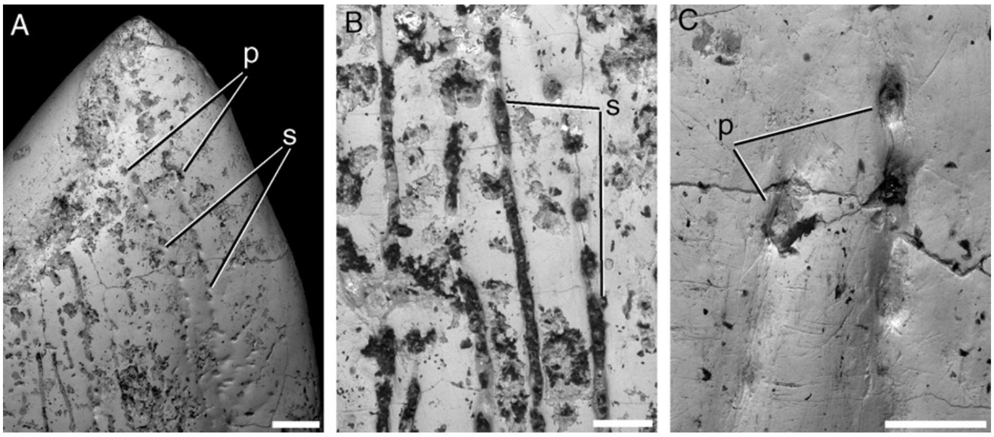

Fig. 2. SEM image of *Amygdalodon patagonicus* (MLP 46-XIII-21-1). A) Lingual surface of MLP 46-XIII-21-1/13, B) detail of lingual surface of MLP 46-XIII-21-1/13, C) detail of pits present on lingual surface of MLP 46-XIII-21-1/15. Abbreviations: p: pit; s: sulcus. Scale bars equal 1 mm. (A) and 0.5 mm (B and C).

Fig. 2. Image au MEB d'*Amygdalodon patagonicus* (MLP 46-XIII-21-1). A) Surface linguale de MLP 46-XIII-21-1/13, B) détail de la surface linguale de MLP 46-XIII-21-1/13, C) détail de petites dépressions sur la surface linguale de MLP 46-XIII-21-1/15. Abréviations : p : petites dépressions ; s : sillon. Barre d'échelle 1 mm (A) et 0,5 mm (B et C).

to be rare among non-neosauropods and is only shared with the teeth of *Shunosaurus* (Chatterjee and Zheng, 2002) and with those referred to *Kotasaurus* (Yadagiri, 2001). The second feature is the presence of a particular wrinkling pattern on the enamel outer surface. Although there is some variation in the wrinkling pattern among the preserved teeth (see below), the lingual and buccal enamel surface of all *Amygdalodon* teeth share the presence of apicobasally aligned pits, which are subovoid, deep, and relatively small (their major diameter ranges between 100 and 200 μm; Fig. 2). Each set of apicobasally-aligned pits are usually joined to each other by a continuous narrow sulcus (Fig. 2). Besides the presence of these pits and sulci, the buccal and lingual enamel surface of *Amygdalodon* teeth is mostly smooth. This pattern contrasts with the generalized condition of eusauropods and related forms (Allain and Aquesbi, 2008; Wilson and Sereno, 1998) that have a wrinkled enamel surface with much more numerous and well developed anastomized grooves and ridges. Thus, to our knowledge, the particular pattern of *Amygdalodon* (with well delimited pits joined by apicobasal sulci) seems to be different from all gravisaurians. Non-gravisaurian sauropodomorphs also differ from the condition of *Amygdalodon*, having either a smooth enamel surface (Wilson and Sereno, 1998) or a pattern of fine irregular wrinkles (Yates, 2004).

As noted by previous authors (Cabrera, 1947; Rauhut, 2003), the crowns of *Amygdalodon* have deep major grooves that extend along the mesial and distal margins on the buccal and lingual surfaces (Fig. 1). There is variation in the development of these grooves (see below) but all crowns have, at least, a well-developed distal buccal groove. The enamel of *Amygdalodon* becomes progressively thinner and gradually disappears at the crown-root limit, in contrast with the condition of several basal eusauropods in which the enamel ends abruptly at the crown-root limit (e.g., *Patagosaurus* MACN-CH 2008, BMNH 3377 [Barrett, 2006]).

The three most complete crowns of *Amygdalodon* have wear facets that only extend over one of the crown's edges. In the upper teeth the wear facets extends from the apex along the mesial edge (mostly on their lingual surface; Fig. 1A–B), whereas in the lower teeth the wear facets extends from the apex along the distal edge (mostly on their buccal surface; Fig. 1G). The most damaged tooth crown (MLP 46-VIII-21-1/17; Fig. 1D), however, has a horizontal wear facet at its apical region, suggesting that *Amygdalodon* may display the V-shaped wear facet (*sensu* Wilson and Sereno (1998)) in extensively worn teeth. Thus, the presence of wear facets on only one margin may simply reflect an early stage of tooth wear in the other three teeth (or a different position in the toothrow). Irrespective of the underlying cause for this difference, the wear facets in *Amygdalodon* are unusually asymmetrical in comparison with those of eusauropods with broad spoon-shaped crowns.

3.2. Upper teeth

Two of the preserved elements (MLP 46-VIII-21-1/12 and MLP 46-VIII-21-1/15) are interpreted as upper teeth because both have wear facets that extends over the lingual surface, as commonly found in maxillary teeth of eusauropods (e.g., *Shunosaurus* [Chatterjee and Zheng, 2002]). One of the teeth (MLP 46-VIII-21-1/12) is more extensively worn (exposing a broad surface of dentine) than the other, but both share the location, shape, and orientation of the wear facet. This facet is ovoid shaped, having its major axis directed from the crown's apex to the mesial edge (Fig. 3). The flat surface of the wear facets of these teeth bears numerous striae but no pits (Fig. 3B).

These two teeth, however, differ in several aspects that suggest they may belong to different sections of the toothrow. The crown of MLP 46-VIII-21-1/15 is apicobasally higher and more symmetrical (i.e., lacking the basal bulge on the distal margin) than that of MLP 46-VIII-21-1/12 (or any other teeth). This suggests the former may be more anteriorly located than the latter, as in most eusauropods the tooth size decreases continuously along the toothrow (e.g., *Shunosaurus* [Chatterjee and Zheng, 2002], *Omeisaurus* [Feng et al., 2001], *Mamenchisaurus*

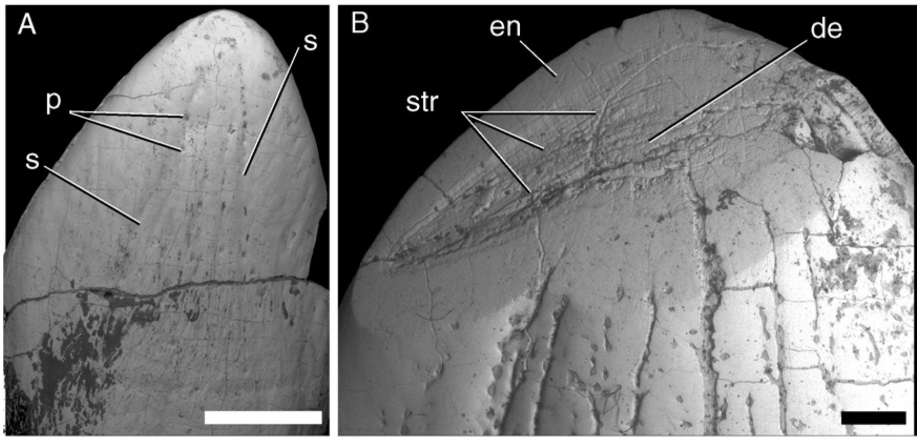

Fig. 3. SEM image of *Amygdalodon patagonicus* (MLP 46-XIII-21-1). Wear facet on lingual surface of (A) MLP 46-XIII-21-1/15 and (B) MLP 46-XIII-21-1/12. Abbreviations: de: dentine; en: enamel; p: pit; str: striae; s: sulcus. Scale bars equal 0.5 cm (A) and 1 mm. (B).

Fig. 3. Image au MEB d'*Amygdalodon patagonicus* (MLP 46-XIII-21-1). Facettes d'usure sur la surface linguale de (A) MLP 46-XIII-21-1/15 et (B) MLP 46-XIII-21-1/12. Abréviations : de : dentine ; en : émail ; p : petites dépressions ; str : striations ; s : sillon. Barre d'échelle 0,5 cm (A) et 1 mm (B).

[Russell and Zheng, 1993]); a trend that is also present in non-eusauropod sauropodomorphs (e.g., *Melanorosaurus* [Yates, 2007], *Mussaurus* [Pol and Powell, 2007a], *Massospondylus* [Sues et al., 2004]).

The crown of MLP 46-VIII-21-1/15 also differs from the other crowns of *Amygdalodon* in several characters. This crown shows two well-developed grooves: the distal buccal groove present in all preserved *Amygdalodon* crowns plus a mesial buccal groove (Fig. 1E). In addition to these two grooves, the enamel buccal surface is relatively smooth. The lingual surface of MLP 46-VIII-21-1/15 lacks well-developed grooves but bears two major sulci (Fig. 3A) and several minor sulci between them. As in the other crowns these sulci join apicobasally-aligned pits.

The crown of MLP 46-VIII-21-1/12 has a single (distal) buccal groove (Fig. 1F) and a unique but well-developed (mesial) lingual groove (Fig. 1B). The morphology of these grooves differs from the ones previously described for MLP 46-VIII-21-1/15 due to the presence of a minor groove that runs parallel to the main (deeper) groove, enclosing a slightly convex area between them (Fig. 4). Both buccal and lingual surfaces have the wrinkling pattern of pits and sulci, although a different wrinkled pattern is observed close the basal region of the distal and mesial edges (Fig. 4). The sulci in these basal areas of the crown are not apicobasally directed and form an anastomized network without well-delimited pits (see below in MLP 46-VIII-21-1/13), resembling in these restricted areas the enamel wrinkling pattern of eusauropods. In addition to the apical wear facet, there are two small areas at the base of this crown in which the enamel is worn. These surfaces are flat and lack striation (Fig. 4C). The basal lingual worn surface is located near the distal edge, whereas the basal labial worn surface is close to the mesial edge. The flat morphology and the position of these surfaces suggest they were produced by tooth-tooth contact between adjacent crowns, rather than by abrasion. Similar basal worn surfaces are present at least in some eusauropod taxa (e.g., cf. *Patagosaurus* MACN-CH 2008, MPEF-PV 3060, MPEF-PV 3055; Camarasaurus [Wilson and Sereno, 1998: Fig. 10]) in which the tooth crowns are disposed in an en-echelon tooth arrangement. Although not all taxa with an en-echelon tooth arrangement have these worn surfaces, we interpret their presence in *Amygdalodon* as an indication that the mesial margin of one crown was (buccally) overlapped by the distal margin of the preceding tooth, creating an en-echelon tooth arrangement for *Amygdalodon*, a character that has been considered as synapomorphic of Eusauropoda (Wilson, 2002) or Gravisauria (Allain and Aquesbi, 2008).

3.3. *Lower tooth*

The tooth MLP 46-VIII-21-1/13 is interpreted as a dentary element because the location of the wear facet is opposite to those of the upper teeth. First, the wear facet extends mostly over the buccal surface, as noted by Rauhut (Rauhut, 2003). Second, the facet extends from the tooth apex toward the base of the crown along its distal margin (Fig. 1G). This tooth is the most extensively worn and has a broad surface of dentine exposed. The worn surface of this tooth is actually divided in two different areas of the distal margin, divided by an abrupt step. The apical area of the wear facet faces apicodistally whereas the basal area of the wear facet is vertically oriented and faces distally (Fig. 5 A–B). The apical area is flat and much broader than the basal one and extends mostly on the buccal surface of the crown forming an angle of approximately 60 degrees with the transversal plane (Fig. 5). In this region the apical wear facet also extends onto the lingual surface of the crown, forming a small and slightly convex surface that contrasts with the flat and extensive surface that extends on the buccal side of the apical region of the crown. These differences suggest the reduced lingual surface was produced by abrasion whereas the extensive and flat worn surface on the buccal side was produced by tooth-tooth occlusion. The basal area of the wear facet is much narrower (buccolingually) than the apical area. The worn surface is flat and faces distally, resembling the condition of the wear facets

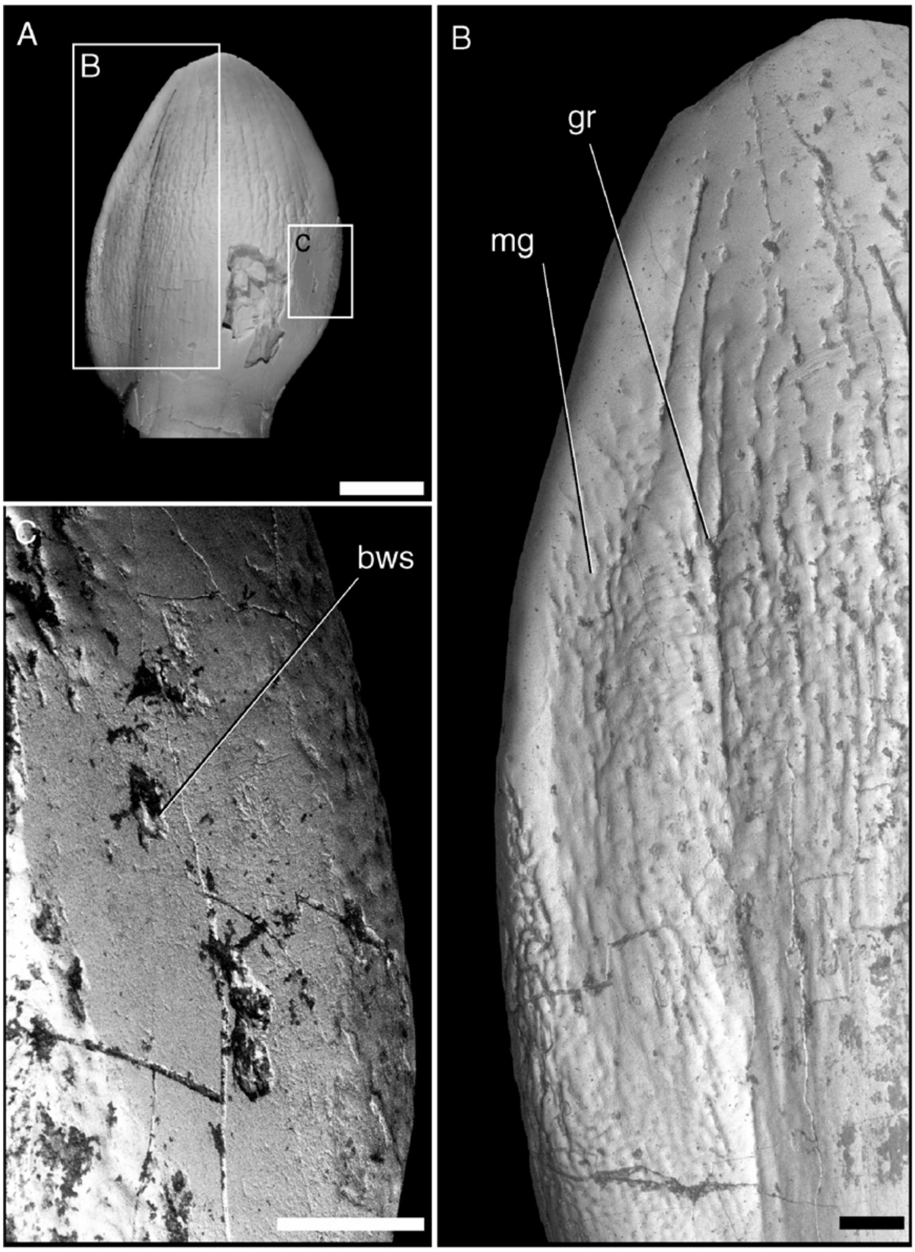

Fig. 4. SEM image of *Amygdalodon patagonicus* (MLP 46-XIII-21-1/12). A) Overview of buccal surface, B) close-up of distal groove, C) basal worn surface. Abbreviations: bws: basal worn surface; gr: groove; mg: minor groove. Scale bars equals 0.5 mm. (A); and 1 mm. (B and C).

Fig. 4. Image au MEB d'*Amygdalodon patagonicus* (MLP 46-XIII-21-1/12). A) Vue de la surface buccale, B) vue rapprochée de la cannelure distale, C) surface d'usure basale. Abréviations : gr : cannelure ; mg : cannelure mineure ; bws : surface d'usure basale. Barre d'échelle 0,5 mm. (A) et 1 mm. (B et C).

described for *Camarasaurus* (Calvo, 1994). Numerous striae and pits are observed on the apical and basal region of the wear facet.

Two deep and well-developed grooves are present on the buccal surface of this tooth (as in MLP 46-VIII-21-1/15), although much of the distal groove has been worn (Fig. 5). Below the basal end of the mesial buccal groove the crown has a large rounded depression, which may be a pathological feature of this particular tooth (Fig. 5B). The lingual surface bears a deep groove on its mesial side, which is deeper near the base of the crown and becomes progressively shallower and broader toward the apex. At the apicobasal midpoint of the crown, this groove bifurcates in two sulci that join closely spaced and well-delimited pits (Fig. 1C, 2A). This wrinkling pattern of pits and sulci is particularly well developed on the lingual surface of this crown (Fig. 1C), whereas the buccal surface is smoother, probably due to abrasive wear (except on its basal most region; Fig. 5B). As was noted for MLP 46-VIII-21-1/12, the mesial surface bears an anastomized wrinkling pattern near the base of the crown (Fig. 5C). This pattern is also present in the distal edge of this tooth, although much of this region has been worn. This anastomized wrinkling pattern resembles the condition of most basal eusauropod teeth (e.g., *Chebsaurus* [Mahammed et al., 2005], *Patagosaurus* [MACN-CH 2008], '*Cetiosaurus*' [Barrett, 2006]; see Discussion).

An unusual characteristic of this crown is that the lingual surface is slightly convex mesiodistally, a feature

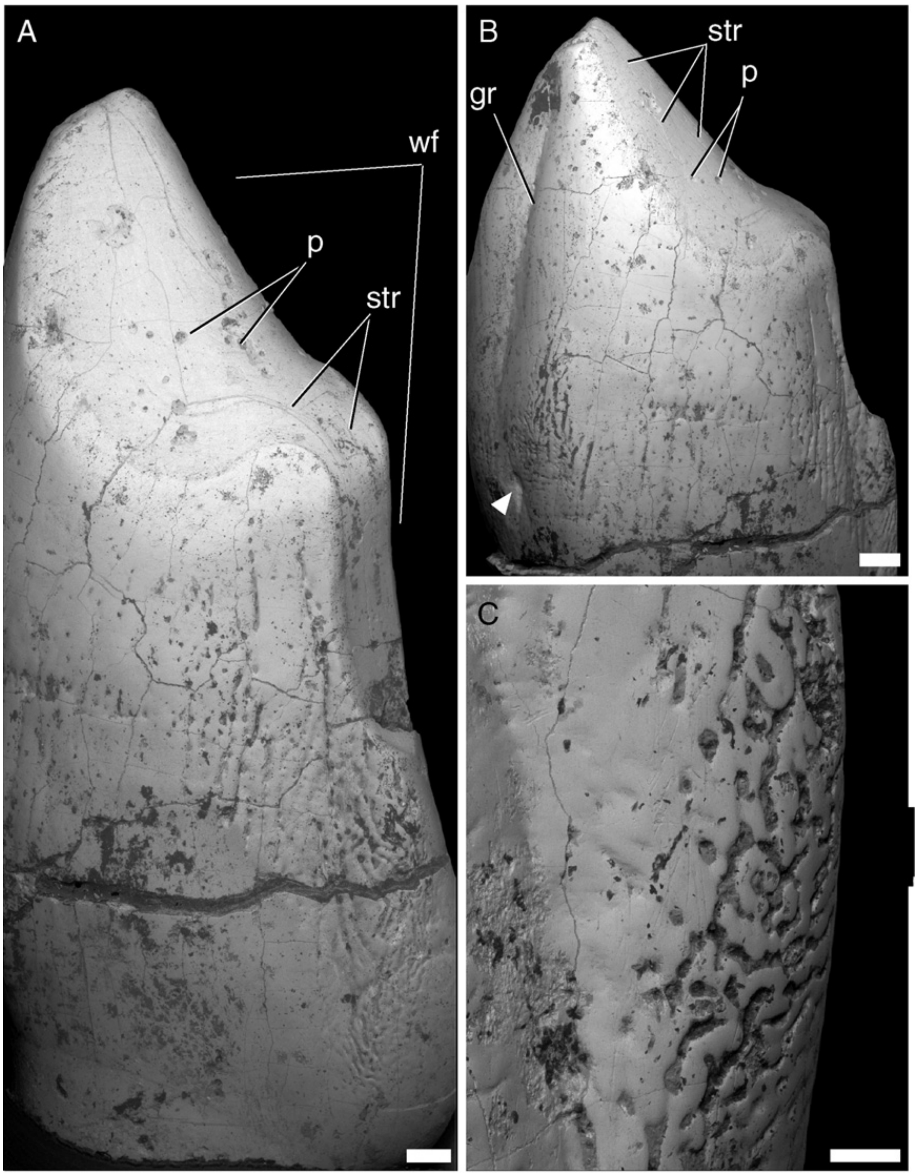

Fig. 5. SEM image of *Amygdalodon patagonicus* (MLP 46-XIII-21-1/13). Overview of (A) distobuccal and (B) buccal surfaces. C) Close-up of wrinkling pattern of mesial edge. The white arrow shows the position of the depression. Abbreviations: gr: groove; p: wear pits; str: wear striae; wf: wear facet. Scale bars equals 1 mm. (A and B); and 0.5 mm. (C).

Fig. 5. Image au MEB d'*Amygdalodon patagonicus* (MLP 46-XIII-21-1/13). Vue générale des surfaces (A) distobuccale et (B) buccale. C) Rapprochement du patron de rugosités du bord mésial. La flèche blanche montre la position de la dépression. Abréviations gr : cannelure ; p : petites dépressions d'usure ; str : striations d'usure ; wf : facettes d'usure. Barre d'échelle 1 mm. (A et B) et 0,5 mm. (C).

noted by Rauhut (2003) to resemble the crown morphology of *Cardiodon* (Upchurch and Martin, 2003). This morphology contrasts with the generalized spoon shaped crowns of most basal eusauropods that have a concave lingual surface. The spoon-shaped morphology (with a concave lingual surface) of the other teeth described above shows this feature may actually vary along the toothrow in *A. patagonicus*.

4. Discussion

4.1. Phylogenetic relationships

Up to date no published cladistic analysis of Sauropodomorpha has included *A. patagonicus*, although this taxon has been regarded as a member of Eusauropoda by Wilson (2002), Rauhut (2003), and Upchurch et al. (2004). Wilson (2002) considered this taxon as part of the clade formed by *Patagosaurus* and more derived eusauropods based on the presence of cervical ribs positioned ventrolateral to the centrum (inferred from the position of the parapophysis). Rauhut (2003) noted, however, that this feature might have been artificially produced by preservational causes. Rauhut (2003) also argued for the eusauropod affinities of *Amygdalodon* based on the presence of features then considered as eusauropod synapomorphies (e.g., high neural arch in the dorsal vertebra, cervical vertebra opisthocoelous and with centrodiapophyseal laminae), but he suggested a basal position within this clade given the absence of some derived characters present in most eusauropods (e.g., dorsal neural arches with deep depressions on cranial

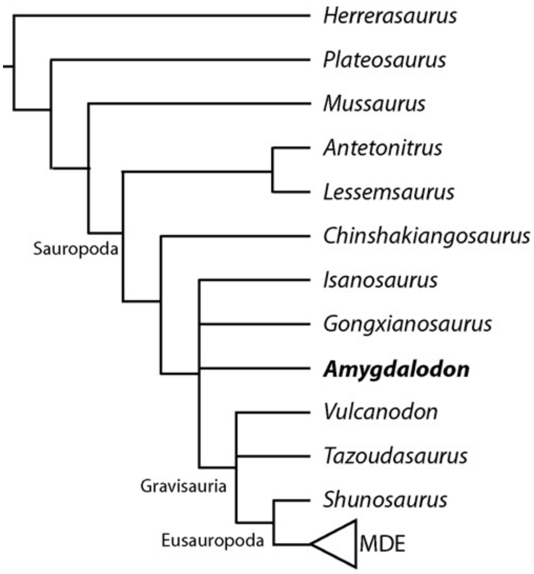

Fig. 6. Summary of strict consensus obtained in the parsimony analysis. Our usage of the taxonomic names is based on the following definitions: Sauropoda (Sereno, 2005), Gravisauria (Allain and Aquesbi, 2008), Eusauropoda (Sereno, 2005). Abbreviations: MDE (more derived eusauropods).

Fig. 6. Arbre de consensus strict simplifié, obtenu à l'issue de l'analyse par parcimonie. Notre emploi des noms taxonomiques est basé sur les définitions suivantes : Sauropoda (Sereno, 2005), Gravisauria (Allain et Aquesbi, 2008), Eusauropoda (Sereno, 2005). Abréviations : MDE (eusauropodes plus dérivés).

surface and internal cavities above neural canal, cervical vertebra with low neural arch, lacking depression above parapophysis, and lacking pleurocoels).

The morphology of the *Amygdalodon* tooth (MLP 46-VIII-21-1/13) studied by Rauhut (2003) also prompted this author to refer this taxon to Eusauropoda, based on its spatulate morphology and the presence of wrinkled enamel, buccal grooves, and V-shaped wear facets. In order to discuss the significance of the dental anatomy of *Amygdalodon* described here, we have tested its position through a cladistic analysis based on the data matrix of Wilson (2002), increasing the taxon and character sampling for non-eusauropod sauropodomorphs based on recent contributions (Allain and Aquesbi, 2008; Upchurch, 1998; Upchurch et al., 2004; Upchurch et al., 2007b; Yates and Kitching, 2003) (Appendix A). The phylogenetic analysis was conducted using equally weighted parsimony analysis through a heuristic search in TNT (Goloboff, 2008a; Goloboff et al., 2008b) which retrieved 23 most parsimonious trees of 473 steps (CI = 0.58; RI = 0.79); the abbreviated strict consensus of which is shown in Fig. 6 (Appendix A). This analysis depicts *Amygdalodon* as a non-eusauropod sauropod (Fig. 6), forming a polytomy with *Gongxianosaurus*, *Isanosaurus*, and the clade formed by Vulcanodontidae and Eusauropoda (Gravisauria *sensu* Allain and Aquesbi [2008]) The present analysis, however, depicts *Amygdalodon* as more derived than *Chinshakiangosaurus* or the *Lessemsaurus* + *Antetonitrus* clade (Fig. 6; Appendix A). *Amygdalodon,* as well as other basal sauropods such as *Chinshakiangosaurus* and *Isanosaurus,* are currently known from fragmentary material (with more than 90% of missing data). Their incompleteness creates some degree of uncertainty regarding their phylogenetic placement and consequently the basal nodes of Sauropoda and Eusauropoda have low support values (e.g., with only one extra step these three fragmentary forms can be placed in alternative positions within the basalmost nodes of Gravisauria and Eusauropoda). Nevertheless, given the available information the more parsimonious hypotheses provide a phylogenetic placement for these taxa as eusauropod outgroups, which bears implications for the early evolution of some dental features of Sauropoda that are commented in the following section.

4.2. *Evolution of dental characters in Basal Sauropods*

Within this phylogenetic context, the total absence of mesial and distal denticles in *Amygdalodon* is shared with some other basal sauropods (*e.g., Gongxianosaurus* [He et al., 1998], *Shunosaurus* [Chatterjee and Zheng, 2002]), but differs from the serrated condition of other non-neosauropod sauropods (e.g., *Tazoudasaurus* [Allain and Aquesbi, 2008], *Patagosaurus* MPEF-PV 1670). The optimisation of this character in the present phylogenetic analysis shows homoplastic transformations implying either the loss of denticles in *Amygdalodon* and more derived sauropods (with reversals to the serrated condition in *Tazoudasaurus* and some basal eusauropods such as *Patagosaurus*) or the independent loss of denticles in *Amygdalodon*, *Gongxianosaurus*, *Shunosaurus*, and Neosauropoda. Irrespective of these alternative scenarios, the available evidence suggests that this feature was a labile character during the early phases of sauropod evolution and lacks a clear phylogenetic signal, as recently noted by other authors (Barrett and Upchurch, 2005; Buffetaut, 2005; Upchurch et al., 2007a).

The peculiar tooth morphology of *Amygdalodon* and the phylogenetic position retrieved for this taxon within Sauropoda has implications for the early evolution of several dental characters in basal sauropods. The most remarkable of these characters is the presence of tooth-tooth occlusion and extensive wear facets. *Amygdalodon* is one of the oldest sauropod taxa in which extensive wear facets are known (together with *Tazoudasaurus* [Allain and Aquesbi, 2008]). This feature has previously been interpreted either as synapomorphic of Eusauropoda (Upchurch et al., 2004; Upchurch et al., 2007a; Wilson, 2002) or as an ambiguous synapomorphy of a more inclusive clade (Allain and Aquesbi, 2008): Gravisauria (Vulcanodontidae + Eusauropoda). The basal position retrieved for *Amygdalodon* in our analysis and the presence of these extensive wear facets imply these features (potentially indicating an increase in oral processing of plants (Barrett and Upchurch, 2005; Upchurch and Barret, 2000)) appeared earlier than previously thought in the evolutionary history of Sauropoda, diagnosing a more inclusive clade composed (at least) by *Amygdalodon* and more derived sauropods. Interestingly, the wear facets of *Amygdalodon* are highly asymmetrical and extend almost exclusively on the mesial edge of the upper teeth and on the distal edge of the lower tooth. This differs from the characteristic wear facets of basal eusauropods (and *Tazoudasaurus* [Allain and Aquesbi, 2008]) that have a more symmetrical V-shaped facet produced by interlocking tooth-tooth occlusion, which extend from the apex along both the mesial and distal margins (Calvo, 1994; Chatterjee and Zheng, 2002; Wilson and Sereno, 1998). The presence of asymmetrical wear facets in *Amygdalodon* may imply an early stage in the evolution of sauropod jaw mechanics, before the onset of the extensive interlocking tooth-tooth occlusion of eusauropods.

This change in the optimisation of the presence of extensive wear facets in sauropods is paralleled by the case of other dental characters (e.g., crown cross-section, enamel wrinkling, labial grooves, en-echelon arrangement) originally regarded as eusauropod synapomorphies (Upchurch et al., 2004; Upchurch et al., 2007a; Wilson, 2002), but recently reinterpreted as synapomorphies of more inclusive clades of Sauropodomorpha (Allain and Aquesbi, 2008; Upchurch et al., 2007b; Yates, 2004; Yates, 2007). Their presence in *Amygdalodon* confirms in this study the same optimisation pattern, although their distribution deserve some comments.

Tooth crown shape. All the teeth of *Amygdalodon* are greatly expanded mesiodistally with respect to the root and three of the four teeth of *Amygdalodon* have a concave lingual surface (i.e., creating a D-shaped cross-section of the crown). The former character represents the strongly spatulate condition of sauropod teeth (Upchurch, 1998; Yates and Kitching, 2003) and is currently optimised as appearing in *Amygdalodon* and more derived sauropods. The crowns of more basal sauropodomorphs (including *Chinshakiangosaurus* [Upchurch et al., 2007b]), instead, are lanceolate and not greatly expanded relative to the root. On the other hand, the strongly convex buccal surface and slightly concave lingual surface of *Amygdalodon* creates a D-shaped cross-sectional shape of the crown, a character shared with *Gongxianosaurus* (He et al., 1998), *Tazoudasaurus* (Allain and Aquesbi, 2008), and eusauropods (Wilson, 2002). As noted by Upchurch et al. (2007b), this feature was previously considered synapomorphic of Eusauropoda but may have appeared gradually starting with an incipient concavity in *Chinshakiangosaurus* (at the base of Sauropoda) and reaching the full D-shaped cross-section in *Amygdalodon* and more derived sauropods. It must be noted that, as described above (and as was noted [Rauhut, 2003]), one of the teeth of *Amygdalodon* has a slightly convex lingual surface. This implies that, at least in basal sauropods, this character can vary along the toothrow and therefore its use for taxonomic purposes should be taken with caution when is applied to fragmentary material.

Buccal grooves. The presence of buccal grooves along the mesial and distal edges was previously regarded as a synapomorphy of Eusauropoda, and was recorded in *Shunosaurus* and more derived eusauropods (Upchurch, 1998; Upchurch et al., 2004). Recent studies on the basal sauropod *Chinshakiangosaurus* showed that this taxon has only a distal groove, suggesting that this feature appeared earlier than the mesial groove (Upchurch et al., 2007b). The presence of both grooves in the more derived *Amygdalodon* expands the known distribution of the mesial groove and lends support to the step-wise appearance of these two grooves along the early evolutionary history of Sauropoda (before Eusauropoda). It is interesting to note that the absence of a mesial groove in at least one tooth of *Amygdalodon* may imply that this feature did not simultaneously appear along the entire toothrow.

Enamel wrinkling. As noted by Rauhut (2003) *Amygdalodon* shares with eusauropods the presence of wrinkled enamel outer surface, a character first considered as synapomorphic of Eusauropoda by Wilson and Sereno (1998). This derived condition is also present in other non-eusauropod sauropods such as *Tazoudasaurus*, *Gongxianosaurus*, and *Chinshakiangosaurus* (Allain and Aquesbi, 2008; Upchurch et al., 2007a; Upchurch et al., 2007b) and therefore diagnose a more inclusive group than Eusauropoda. Therefore, the evolutionary history of this character is probably more complex than currently depicted. For instance, a faintly developed wrinkling pattern has been noted for some teeth of sauropod outgroups (e.g., *Mussaurus, Anchisaurus, Melanorosaurus* [Pol and Powell, 2007a; Yates, 2004; Yates, 2007]). The wrinkling of these taxa is certainly not as developed as in *Amygdalodon* and eusauropods but differs from the plesiomorphic smooth surface present in the most basal sauropodomorphs or 'prosauropods' (e.g., *Thecodontosaurus*, *Plateosaurus*, *Massospondylus*). Within this context, the character may have gradually appeared during the evolution of Sauropodormorpha and the autapomorphic pattern of pits and sulci of *Amygdalodon* may represent an incipient condition in comparison with the more notoriously developed anastomized pattern observed in eusauropods. Although the wrinkling pattern described above for *Amygdalodon* might have been affected by wear and/or preservational causes, we consider this pattern reflects an autapomorphic feature for this taxon because: a) the abrasion on teeth with different degrees of wear does not alter significatively the wrinkling pattern in other basal sauropods (e.g., *Patagosaurus* MPEF-PV 3006, MPEF-PV 3060, MACN-CH 2008); b) if the pattern of pits and sulci were related to preservational causes, it remains to be explained why such process affected only the lingual and buccal surfaces but not the mesial and distal edges of the same teeth (e.g., MLP 46-VIII-21-1/12 and MLP 46-VIII-21-1/13) that have an anastomized wrinkling pattern.

En-echelon tooth arrangement. Another character previously regarded as synapomorphic of Eusauropoda (Wilson, 2002) or the more inclusive clade Gravisauria (Allain and Aquesbi, 2008) is the presence of an en-echelon arrangement of the tooth crowns. The basal wear facets present in some teeth are interpreted here as the product of this type of arrangement in *Amygdalodon*. Such interpretation, coupled with the similar disposition of tooth crowns in the more basal sauropodomorph *Mussaurus patagonicus* (Pol and Powell, 2007a), shows that this character has a markedly broader distribution and appeared before the origin of Sauropoda. In fact, Yates (2007) scored this condition as present in most sauropodomorphs. As in the previous character, the degree of overlapping between adjacent crowns may have increased along the evolution of Sauropodomorpha, with sauropods showing a more extensive overlap and intimate contact between adjacent crowns.

4.3. The origins of specialization to herbivory

The large morphological gap that existed until recently between the dental anatomy of eusauropods and more basal sauropodomorphs have led previous authors to infer that the origins of Eusauropoda was signed by a marked specialization toward herbivory (Upchurch and Barret, 2000; Wilson, 2005). These authors, however, recognized that the absence of knowledge on dental anatomy of basal sauropods precluded establishing if some of these features may have appeared earlier in the evolution of the group (potentially enlarging the morphological gap between eusauropods and other forms due to the lack of adequate fossil record). The remains described here of *Amygdalodon* interpreted within the context of the present phylogenetic analysis, coupled with other recent studies on basal sauropods (e.g., *Tazoudasaurus* [Allain and Aquesbi, 2008], *Chinshakiangosaurus* [Upchurch et al., 2007b]), confirm that this is in fact the case for many of the derived dental characters previously regarded as eusauropod synapomorphies. As discussed above, these features must now be interpreted as diagnostic of more inclusive groups, indicating gradual appearance of these derived dental features at different nodes below Eusauropoda and underscoring the importance of feeding adaptations in the early evolution of Sauropoda. Interestingly, within the context of the phylogenetic analysis presented here, most of the dental characters discussed above do not involve multiple instances of homoplasy, as predicted by Upchurch et al. (2007b) due to the putative plasticity of teeth in response to changes in diet and feeding habits. The major exception, however, is the optimisation of multiple transformations in the presence/absence of tooth serrations among non-neosauropod sauropods.

It must be noted that, despite this new evidence, our understanding on the early sauropod dental evolution is still fragmentary due to the incomplete nature of most of basal sauropods, including *A. patagonicus*. The incompleteness of these remains creates a considerable degree of uncertainty on the phylogenetic interrelationships of these taxa, as shown by the low values of nodal support (see above). This precludes the establishment of a solid evolutionary scenario for the dentition of basal sauropods. Furthermore, the lack of teeth in the basal sauropods *Lessemsaurus* (Pol and Powell, 2007b) and *Antetonitrus* (Fig. 6) creates ambiguous optimisations for dental characters and therefore many of them may indeed diagnose even more inclusive clades. Many of the characters discussed above, however, are absent in *Mussaurus* (and *Melanorosaurus* [Yates, 2007]) and therefore are likely to have evolved at the base of Sauropoda (or at a slightly less inclusive node).

5. Conclusions

The present study provides a more complete characterization of the tooth remains of *A. patagonicus* that allows diagnosing its dentition by a unique combination of characters (including the presence of autapomorphies). These features, together with those pointed out by Rauhut (2003), provide a solid diagnosis of this taxon considered by some authors as a potential nomen dubium (Upchurch et al., 2004). Although it has been regarded as a eusauropod, *Amygdalodon* is depicted outside Eusauropoda and therefore represents a basal sauropod from the Early-Middle Jurassic of Patagonia.

The described features of *Amygdalodon* teeth provides new information on the origins of herbivorous specializations in basal sauropods, including the presence of extensive wear facets produced by tooth-tooth occlusion. This information adds further evidence to that of recent studies (Allain and Aquesbi, 2008; Upchurch et al., 2007b) showing several characters previously thought to be exclusive of Eusauropoda had actually appeared earlier during the evolution of Sauropoda.

Acknowledgements

We would like to specially thank Aluar Aluminio Argentino SAIC for access to the SEM lab as well as the valuable help of Mr. Jaime Groizard. Z. Gasparini, E. Tonni, and M. Reguero (MLP) are thanked for allowing specimen access, loans. J. Whitlock is thanked for discussions on this subject and A. Maillet and A. Lecuona for the French translation. We also thank two anonymous reviewers for their comments that markedly improved this manuscript. This work was supported by the grant PICT 1756 from ANPCyT.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.crpv.2010.01.003.

References

Allain, R., Aquesbi, N., 2008. Anatomy and phylogenetic relationships of *Tazoudasaurus naimi* (Dinosauria, Sauropoda) from the late Early Jurassic of Morocco. Geodiversitas 30, 345–424.

Barrett, P.M., 2006. A sauropod dinosaur tooth from the Middle Jurassic of Skye, Scotland. Transactions of the Royal Society of Edinburgh: Earth Sciences 97, 25–29.

Barrett, P.M., Upchurch, P., 2005. Sauropodomorph diversity through time. In: Curry Rogers, K.A., Wilson, J.A. (Eds.), The Sauropods Evolution and Paleobiology. University of California Press, Berkeley, pp. 125–156.

Buffetaut, E., 2005. A new sauropod dinosaur with prosauropod-like teeth from the Middle Jurassic of Madagascar. Bull. Soc. Geol. France 176 (483), 9.

Cabrera, A., 1947. Un saurópodo nuevo del Jurásico de Patagonia, Notas del Museo de La Plata. Paleontología 12, 1–17.

Calvo J. O., 1994. Feeding mechanisms in some sauropod dinosaurs. Unpublished MSc Thesis, University of Illinois at Chicago, 142 p.

Carpenter, K., Tidwell, V., 2005. Reassessment of the Early Cretaceous Sauropod *Astrodon johnsoni* Leidy 1865 (Titanosauriformes). In: Tidwell, V., Carpenter, K. (Eds.), Thunderlizards: the sauropodomorph dinosaurs. Indiana University Press, Bloomington, pp. 78–114.

Casamiquela, R.M., 1963. Consideraciones acerca de *Amygdalodon* Cabrera (Sauropoda. Cetiosauridae) del Jurásico Medio de la Patagonia 3, 79–95.

Chatterjee, S., Zheng, Z., 2002. Cranial anatomy of *Shunosaurus*, a basal sauropod dinosaur from the Middle Jurassic of China. Zoolog. J. Linnean Soc. 136, 145–169.

Feng, T, Xingsheng, J., Ximin, K., Guojun, Z., 2001. *Omeisaurus maoianus:* A complete Sauropoda from Jingyan, Sichuan, Research works of the Natural Museum of Zhejiang. Chin. Ocean Press, 128 p.

Goloboff P. A., Farris S., Nixon K., 2008a. TNT (Tree analysis using New Technology), Published by the authors, Tucumán, Argentina.

Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008b. TNT, a free program for phylogenetic analysis. Cladistics 24, 774–786.

He, X.L., Wang, C.S., Liu, S.Z., Zhou, F.Y., Liu, T.Q., Cai, K.J., Dai, B., 1998. A new species of sauropod from the Early Jurassic of Gongxian County, Sichuan. Acta Geologica Sichuan 18, 1–6.

Madsen, J.M., McIntosh, J.S., Berman, D.S., 1995. The skull and atlas-axis complex of the Upper Jurassic sauropod *Camarasaurus* Cope (Reptilia: Saurischia). Bull. Carnegie Museum 31, 1–115.

Mahammed, F., Läng, E., Mami, L., Mekahli, L., Benhamou, M., Bouterfa, B., Kcemi, A., Chérief, S.A., Chaouat, H., Taquet, P., 2005. The 'Giant of Ksour', a Middle Jurassic sauropod dinosaur from Algeria, C. R. Palevol. 4, 707–714.

Pol, D., Powell, J., 2007a. Skull anatomy of *Mussaurus patagonicus* (Dinosauria: Sauropodomorpha) from the Late Triassic of Patagonia. Hist. Biol. 19, 125–144.

Pol, D., Powell, J., 2007b. New Information on *Lessemsaurus sauropoides* (Dinosauria: Sauropodomorpha) from the Upper Triassic of Argentina. Spec. Pap. Paleontol. 77, 223–243.

Rauhut, O.W., 2003. Revision of *Amygdalodon patagonicus* Cabrera, 1947 (Dinosauria Sauropoda). Mitt. Mus. Nat. Kd. Berl. 6, 173–181.

Russell, D.A., Zheng, Z., 1993. A large mamenchisaurid from the Junggar basin, Xianjiang, People's Republic of China. Can. J. Earth Sci. 30, 1095–2082.

Sereno, P. C., 2005. Stem Archosauria-TaxonSearch, URL http://www.taxonsearch.org/Archive/stem-archosauria-1.0.php [version 1.0, 2005 November 7].

Sues, H.D., Reisz, R.R., Hinic, S., Raath, M.A., 2004. On the skull of *Massospondylus carinatus* Owen, 1854 (Dinosauria:Sauropodomorpha) from the Elliot and Clarens formations (Lower Jurassic) of South Africa. Am. Carnegie Museum 73, 239–258.

Upchurch, P., 1998. The phylogenetic relationships of sauropod dinosaurs. Zoolog. J. Linnean Soc. 124, 43–103.

Upchurch, P., Barret, P.M., 2000. The evolution of sauropod feeding mechanisms. In: Sues, H.D. (Ed.), The Evolution of Herbivory in Terrestrial Vertebrates Perspectives from the Fossil Record. Cambridge University Press, Cambridge, pp. 79–122.

Upchurch, P., Martin, J., 2003. The anatomy and taxonomy of *Cetiosaurus* (Saurischia, Sauropoda) from the Middle Jurassic of England. J. Vertebr. Paleontol. 23, 208–231.

Upchurch, P., Barret, P.M., Dodson, P., Sauropoda, 2004. In: Weishampel, D.B., Dodson, P., Osmolska, H. (Eds.), The Dinosauria, Second edition. University of California Press, Berkeley, pp. 259–322.

Upchurch, P., Barrett, P.M., Galton, P.M., 2007a. A phylogenetic analysis of basal sauropodomorph relationships: implications for the origin of sauropod dinosaurs. Spec. Pap. Palaeontol. 77, 57–90.

Upchurch, P., Barret, P.M., Xijin, Z., Xung, X., 2007b. A re-evaluation of *Chinshakiangosaurus chunghoensis* Ye *vide* Dong 1992 (Dinosauria, Sauropodomorpha): implications for cranial evolution in basal sauropod dinosaurs. Geol. Mag. 144, 247–262.

Wilson, J.A., 2002. Dinosaur phylogeny: critique and cladistic analysis. Zoolog. J. Linnean Soc. 136, 215–277.

Wilson, J.A., 2005. Overview of Sauropod Phylogeny and Evolution. In: Curry Rogers, K.A., Wilson, J.A. (Eds.), The Sauropods Evolution and Paleobiology. University of California Press, Berkeley, pp. 15–49.

Wilson, J.A., Sereno, P., 1998. Early evolution and higher level phylogeny of sauropod dinosaurs. J. Vertebr. Paleontol. 18, 1–68.

Yadagiri, P., 2001. The osteology of *Kotasaurus yamanpalliensis*, a sauropod dinosaur from the Early Jurassic Kota Formation of India. J. Vertebr. Paleontol. 21, 242–252.

Yates, A.M, 2004. *Anchisaurus polyzelus* Hitchcock: the smallest known sauropod dinosaur and the evolution of gigantism amongst sauropodomorph dinosaurs. Postilla 230, 1–58.

Yates, A.M., 2007. The first complete skull of the Triassic dinosaur *Melanorosaurus* Haugthon (Sauropodomorpha: Anchisauria). Spec. Pap. Paleontol. 77, 9–55.

Yates, A.M., Kitching, J.W., 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. Proc. R. Soc. Lond. B 270, 1753–1758.