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A sauropodomorph tooth increases the diversity of dental morphotypes in the Cañadón Asfalto Formation (Early – Middle Jurassic) of Patagonia

Une dent de sauropodomorphe augmente la diversité des morphotypes dentaires dans la formation Cañadón Asfalto (Jurassique inférieur – moyen) de Patagonie

Marcos G. Becerra[a,b,*], Kevin L. Gomez[a,b], Diego Pol[a,b]

[a] *CONICET*
[b] *Museo Paleontológico Egidio Feruglio, Av. Fontana 140, U9100GYO Trelew, Chubut, Argentina*

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ABSTRACT

This communication aims to describe an isolated sauropodomorph tooth (MPEF-PV 10860) from the Cañadón Asfalto Formation and test its phylogenetic relationships with other sauropodomophs. The novelty of this specimen implies a combination of features present in non-sauropod sauropodomorphs (coarse denticles at 45° with respect to the margin, absent marginal grooves and lingual concavity) and others previously referred to as synapomorphic of Sauropoda and subgroups of this lineage (D-shaped cross section, enamel-wrinkling). A comparison with formerly defined sauropod tooth morphotypes from Cañadón Asfalto highlights major differences in enamel-wrinkling, having a simpler and more homogeneous pattern. The crown proportions, compared with other sauropodomorph teeth, retrieve MPEF-PV 10860 within the morphospace of sauropods in two different age-ratio scatterplots, and the phylogenetic analysis depicts this specimen in multiple positions within Sauropodiforms but outside Eusauropoda, indicating the presence of both eusauropods and non-eusauropods in the Cañadón Asfalto Formation, and of a putative new species.

Mots clés :
Sauropodomorpha
Sauropodiformes
Formation Cañadón Asfalto
Jurassique inférieur tardif
Chubut
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Argentine

RÉSUMÉ

Cette communication vise à décrire une dent isolée de sauropodomorphe (MPEF-PV 10860) de la formation Cañadón Asfalto, et à tester ses relations phylogénétiques avec d'autres sauropodomorphes. La nouveauté de ce spécimen se trouve dans une combinaison de caractéristiques présentes dans les sauropodomorphes non sauropodes (denticules grossiers à 45° par rapport au bord, absence de rainures marginales et concavité linguale) et dans d'autres, précédemment considérés comme des synapomorphies de Sauropoda et d'autres sous-groupes de cette lignée (section transversale en forme de D, rides de l'émail). Une comparaison avec les morphotypes dentaires précédemment définis chez les sauropodes

* Corresponding author. Museo Paleontológico Egidio Feruglio, Av. Fontana 140, U9100GYO Trelew, Chubut, Argentina.
E-mail address: mbecerra@mef.org.ar (M.G. Becerra).

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de Cañadón Asfalto met en évidence des différences majeures dans les rides de l'émail, qui ont un patron plus simple et homogène. Les proportions de la couronne, par rapport à d'autres dents de sauropodomorphes, retrouvent MPEF-PV 10860 dans le morpho-espace des sauropodes dans deux diagrammes de dispersion différents proportion – âge, et l'analyse phylogénétique indique ce spécimen dans plusieurs positions au sein des sauropodiformes mais en dehors des Eusauropoda, ce qui indique la présence d'eusauropodes et de noneusauropodes dans la formation Cañadón Asfalto, et probablement d'une nouvelle espèce.

1. Introduction

Sauropods achieved a worldwide distribution by the late Early Jurassic and early Middle Jurassic (i.e. Toarcian – Bajocian). This period, however, is characterized by the scarcity of dinosaurian faunas in comparison with either earlier or later dinosaurian assemblages in the Jurassic (Barrett et al., 2009; Mannion et al., 2011; Smith and Mcgowan, 2007; Taylor, 2006; Weishampel et al., 2004). In most regions, sauropods known from this time are usually limited to one taxon per formation (e.g., *Vulcanodon*, *Tazoudasaurus*, *Ohmdenosaurus*, *Gongxianosaurus*, *Zizhongosaurus*, *Chinshakiangosaurus* [Upchurch et al., 2004; Upchurch et al., 2007a]). The late Early Jurassic – early Middle Jurassic deposits of the Cañadón Asfalto Formation deviates from this pattern, and up to now there are two named sauropod taxa, *Volkheimeria* and *Patagosaurus*, as well as a report of another sauropod taxon (Pol et al., 2009). A possible fourth sauropod taxon from this unit is represented by the specimen MACN-CH 934, originally referred to *Patagosaurus* by Bonaparte (1986) but recently interpreted as a different unnamed species in need to revision (Rauhut, 2003). A recent study of sauropod teeth from this unit infers at least three different tooth morphotypes based on their pattern of enamel-wrinkling, likely belonging to three different species and identified further evidences to distinguish MACN-CH 934 from *Patagosaurus* specimens (Holwerda et al., 2015).

In this communication, we report a new sauropodomorph tooth representing a distinct fourth tooth morphotype from the Cañadón Asfalto Formation. This record may represent a new species with a unique combination of plesiomorphic and apomorphic dental features or could represent the first tooth remains of *Volkheimeria*, the only sauropod taxon from this unit for which there are no cranial or dental remains.

2. Materials and methods

The sauropodomorph specimen here described (MPEF-PV 10860) is housed at the MPEF collection. Pictures were taken using a camera with digital display Nikon SMZ 1000, assisted by a binocular microscope equipped with optic fiber point light. Images from the Scanning Electron Microscope (SEM) were taken in the industrial plant ALUAR Aluminio Argentino SAIC (Puerto Madryn, Chubut province), using a Jeol JSM-6460 with a secondary and backscattered electron detector (15 kV and 20 Pa). Tooth orientation follows Smith and Dodson (2003). Several clades are mentioned in the text, and its definition corresponds to the following authors: Sauropodomorpha (Sereno, 2007), Sauropodiforms (Sereno, 2007), Anchisauria (Galton and Upchurch, 2004), Gravisauria (Allain and Aquesbi, 2008), Sauropoda (Yates, 2007b), Eusauropoda (Upchurch et al., 2004) and Neosauropoda (Bonaparte, 1986). In order to test the phylogenetic affinities of MPEF-PV 10860, the specimen was included in a modified version of the data matrix of Carballido et al. (2015), adding new characters and taxa (see Supplementary Data). The phylogenetic analysis was carried out through a heuristic tree search with TNT 1.1 (Goloboff et al., 2008a; Goloboff et al., 2008b) starting from 1000 Wagner trees followed by branch swapping (TBR). The specimen MPEF-PV 10860 was included in the dataset compiled by Chure et al. (2010) to test its position in the crown shape morphospace as measured by the Slenderness Index (Chure et al., 2010; Upchurch, 1998). Additionally, the broadening of the crown versus the root was analyzed following the same protocol. This is a highly variable feature that was traditionally used as a character in phylogenetic analyses given its variation along Sauropodomorpha (Upchurch, 1995; Upchurch et al., 2004; Wilson, 2002; Wilson and Sereno, 1998). We measured the relation of the crown width against the root width, henceforth referred as Widening Index (WI), in several species of Sauropodomorpha. This ratio was plotted against the time in order to evaluate its change during the Mesozoic in a similar approach to the SI values in Sauropodomorpha (table at Supplementary Data). Plotts of SI and WI were performed using the PAST software version 2.10 (PAlaeontological STastics [Hammer et al., 2001]).

2.1. Institutional abbreviations

MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires Province, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Chubut Province, Argentina; MPM, Museo Regional Provincial Padre M. J. Molina, Rio Gallegos, Argentina; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

3. Systematic palaeontology

Dinosauria Owen, 1842
Sauropodomorpha Huene, 1932
Sauropodiforms Sereno, 2007gen. et sp. indet.

Material. MPEF-PV 10860, isolated tooth with complete crown and most of the root preserved.

Occurrence. The fossil material was collected at the Queso Rallado locality (Cañadón Asfalto Formation), located at 5.5 km to the northwest of the Cerro Cóndor scholar village, in Chubut Province, Argentina (e.g., Pol et al., 2011b; Rougier et al., 2007a). The associated fauna includes the mammals *Asfaltomylos*, *Henosferus*, *Argentoconodon*, and *Condorodon* (Gaetano and Rougier, 2012; Rauhut et al., 2002; Rougier et al., 2007a; Rougier et al., 2007b); the turtle *Condorchelys* (Sterli, 2008); the sphenodont *Sphenocondor* (Apesteguia et al., 2012); the heterodontosaurid ornithischian *Manidens* (Pol et al., 2011b); and isolated remains of anurans, crocodiles, and pterosaurs. A 10 cm-thick tuff bed located between the two lower basalt flows at the lower section of the Cañadón Asfalto Formation was recently dated in ca 178 Ma using radioisotopic methods on U – Pb from zircons (Cúneo et al., 2013). The Queso Rallado locality stratigraphically rests above the dated sediments, and although there is no accurate age for this locality, based on correlations the Queso Rallado sediments were regarded as close to the base of the formation (lower – middle Toarcian age; see Cúneo et al., 2013). Other localities from the Cañadón Asfalto Formation have yielded diverse sauropod remains and a recent study (Holwerda et al., 2015) identified different morphotypes of enamel-wrinkling among sauropod teeth from this unit. A detailed comparison with these morphotypes is provided after the description.

4. Description and comparisons

The overall morphology of the crown of specimen MPEF-PV 10860 is labiolingually compressed, mesiodistally expanded above the root, and with a basal constriction, characterizing a spatulate shape as in most Sauropodomorpha (e.g., Galton and Upchurch, 2004; Gauthier, 1986; Sander, 1997; Upchurch et al., 2004). The crown is taller than wide but rather broad, its SI value (*sensu* Upchurch, 1998) is 1.31, close to *Mussaurus* (1.68; MPM-PV 1813/4) and *Leonerasaurus* (1.47; MPEF-PV 1663, fourth dentary tooth), but lower than *Yunnanosaurus* (1.95; Chure et al., 2010) and *Melanorosaurus* (2.13; Yates, 2007a). SI values lower than 3 are also present in the basal sauropods as *Barapasaurus* (1.6; Bandyopadhyay et al., 2010), *Pulanesaura* (1.97; measured from McPhee et al., 2015: fig. 2), *Archaeodontosaurus* (1.4; Chure et al., 2010), *Amygdalodon* (1.34–1.49; Carballido and Pol, 2010), *Tazoudasaurus* (approximately 1.4–1.6; measured from Allain and Aquesbi, 2008: fig. 7). Among tooth material known from the Cañadón Asfalto Formation, SI values lower than 3 are also measured in the spatulate-shaped crowns of *Patagosaurus* and other isolated sauropod crowns (1.1–1.9 and 2.6; Holwerda et al., 2015). The crown is wider than its root (Fig. 1A and B), a widespread character amongst basal sauropods (e.g., Upchurch et al., 2004) and more pronounced than in non-sauropod sauropodomorphs as *Mussaurus* (Pol and Powell, 2007), *Plateosaurus* (Prieto-Márquez and Norell, 2011), and *Yunannosaurus* (Barrett et al., 2007).

One of the carinae has fewer denticles and originates more apically, which allows identifying this margin as the mesial side of the tooth (Galton and Upchurch, 2004). In addition, one of the crown faces is slightly concave whereas the other is markedly convex in apicobasal direction, identified as lingual and labial faces respectively (Fig. 1C and D). The labial face of the crown is completely convex mesiodistally, but its lingual face is slightly sigmoidal (Fig. 1F) with a convex area close to the distal margin (due to presence of a low apicobasal eminence) and slightly concave close to the mesial margin (especially above the apical half). These features have been used to characterize a spoon-like crown and a D-shaped cross-section (Fig. 1E and F). This shape in cross-section differs from the condition of basal sauropodomorphs such as *Plateosaurus* (Prieto-Márquez and Norell, 2011), *Thecodontosaurus* (Benton et al., 2000) and at least in the middle-posterior teeth of *Mussaurus* and *Anchisaurus* (MPM-PV 1813/4 and YPM 1883, respectively). Conversely, this feature is described in *Leonerasaurus* (Pol et al., 2011a), *Melanorosaurus* (Yates, 2007a), *Amygdalodon* (Carballido and Pol, 2010), *Pulanesaura* (McPhee et al., 2015), and most sauropods (Wilson, 2002), including *Patagosaurus* and all other isolated eusauropod teeth from Cañadón Asfalto Formation (Holwerda et al., 2015; Rauhut, 2003). The D-shaped cross-section is similarly developed in *Chinshakiangosaurus*, which combines a convex labial face in a mesiodistal direction with a lingual face bearing a slightly developed mesial concavity and a convexity along the distal region (Upchurch et al., 2007a). Thus, a marked concavity at the lingual face is clearly absent in MPEF-PV 10860 if compared with eusauropods, but shallow concavities appear as slightly developed in different non-eusauropod sauropodomorphs and may represent an early evolutionary stage of the conspicuous lingual concavities of eusauropods (Carballido and Pol, 2010; Upchurch, 1998; Upchurch et al., 2004; Upchurch et al., 2007a). Details on the development of these concavities however are difficult to analyze, as its variation along the tooth row in many of the non-eusauropod sauropods is still unknown. The crown lacks distinct narrow grooves parallel to the crown margins on both the labial and lingual surfaces (e.g., Upchurch, 1998), and despite the fact that a median low eminence is identified on the lingual surface of MPEF-PV 10860, a conspicuous crest is absent on this face. The presence of grooves has been noted as an apomorphic feature for broad-crowned eusauropods and other broad-crowned sauropods (Barrett and Upchurch, 2005; Barrett and Upchurch, 2007; Carballido and Pol, 2010; Upchurch and Barrett, 2000; Upchurch et al., 2004, Upchurch et al., 2007a), however their presence is variable in most eusauropod teeth from Cañadón Asfalto (Holwerda et al., 2015). Most of these teeth possess at least one well-developed groove (either on their labial or lingual face and either close to the distal and mesial margin), but the four types of grooves are rarely simultaneously present (e.g., MACN-CH 2008.2) and one isolated tooth (MACN-CH 2009) lacks all grooves. The latter, however, can be distinguished from MPEF-PV 10860 by considering its conspicuous lingual concavity, a V-shaped wear facet, and its distinct enamel-wrinkling (morphotype I, see below).

The crown margins bear seven (distal) and six (mesial) coarse denticles (with 1.69 and 1.82 denticles per mm in mesial and distal margins, respectively), a com-

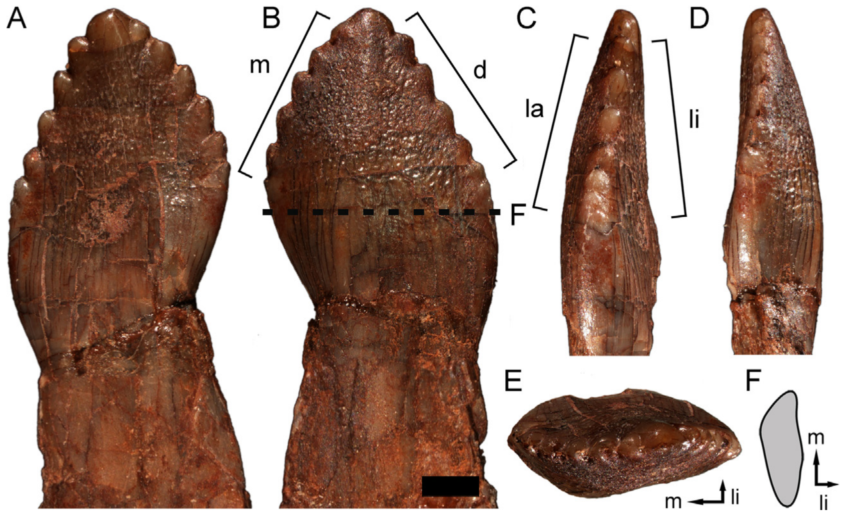

Fig. 1. Indeterminate Sauropodiform species (MPEF-PV 10860), isolated tooth in lingual (A), labial (B), distal (C), mesial (D) and apical (E) views, with a detail of the cross-section shape (F). d: distal margin; la: labial face; li: lingual face; m: mesial margin. Segmented line in (B) marks the cross-section (F). Scale equal to 1 mm of (A–E) and 2 mm for (F).

Fig. 1. Espèce indéterminée de sauropodiforme (MPEF-PV 10860), dent isolée en vues linguale (A), labiale (B), distale (C), mésiale (D) et apicale (E), avec un détail de la forme de la coupe transversale (F). d : marge distale ; la : surface labiale ; li : surface linguale ; m : marge mésiale. La ligne en pointillés dans (B) marque la section transversale (F). Échelle égale à 1 mm pour (A–E) et 2 mm pour (F).

mon feature among basal sauropodomorphs (Barrett and Upchurch, 2007; Galton and Upchurch, 2004). The denticulated margins start at the mesiodistally widest section of the crown and occupy the apical two thirds of the crown, differing from the plesiomorphic condition of basal sauropodomorphs in which the denticles occupy most of the crown margin (e.g., *Plateosaurus*). The presence of denticles is also recorded in eusauropods (e.g., *Omeisaurus*, *Shunosaurus*, *Barapasaurus*), including specimens referred to *Patagosaurus* and other isolated teeth from the Cañadón Asfalto Formation, but they usually have a lower number denticles (between 2 and 4 denticles, with the exception of one tooth [MPEF-PV 3341] with 8 denticles at the mesial margin) which are proportionately smaller (if compared to the crown size) and restricted to the apical third of the crown (Rauhut, 2003), differing from MPEF-PV 10860 (below the apical half). The denticles of MPEF-PV 10860 are subconical rather than labiolingually compressed, increase in size towards the apex and are upwardly directed forming an angle of 45° respect to the margin of the tooth, the last being a feature shared with basal species of Sauropodomorpha (e.g., Galton and Upchurch, 2004; Upchurch et al., 2004; Upchurch et al., 2007a; Upchurch et al., 2007b). The orientation of denticles in eusauropods might vary depending on the species, however as in *Patagosaurus*, its size is proportionately smaller than in MPEF-PV 10860 and are only present above the apical half (Bandyopadhyay et al., 2010; He et al., 1988; Zheng, 1996). Whereas in *Patagosaurus* denticles are regarded as apically oriented (Rauhut, 2003), other species show a more variable orientation along the carinae (*Shunosaurus*, *Omeisaurus* [He et al., 1988: fig. 16; Zheng, 1996: p. 40), or its orientation is poorly preserved in the available material (*Barapasaurus* [Bandyopadhyay et al., 2010: fig. 4]). The serrated mesial margin is slightly convex in lateral view and the distal margin is slightly concave, creating an asymmetrical profile of the crown in labial or lingual view (Figs. 1 and 2). In apical view, the denticulated mesial and distal margins form an S-shaped outline.

Both surfaces of the crown have their enamel wrinkled, covering the apical half and extending basal to the denticles close to the distal margin on both faces (Figs. 1A-B, 2A-B). This wrinkling consists of enamel globular protuberances that are separated by broad anastomosed grooves varying in depth and randomly oriented along most of the surface of the crown, but with a slightly dominant apicobasal orientation along the mesial part of the lingual face (Fig. 2). The wrinkling progressively disappears toward the base of the crown and the base of the denticles (Fig. 2). The development of the enamel-wrinkling differs from the smooth enamel surface of non-anchisaurian sauropodomorphs, such as *Thecodontosaurus*, *Yunannosaurus*, and *Plateosaurus* (Barrett et al., 2007; Carballido and Pol, 2010; Galton and Upchurch, 2004), and is far more conspicuous than the faintly wrinkling of *Leonerasaurus* (Pol et al., 2011a), *Mussaurus* (Pol and Powell, 2007), *Anchisaurus* (Yates, 2004; Yates, 2010), and *Melanorosaurus* (Yates, 2007a). In addition, MPEF-PV 10860 enamel-wrinkling pattern also lacks of the evident apicobasal orientation of grooves and crests present in *Anchisaurus* and *Melanorosaurus*.

Regardless of the crown morphology, the enamel-wrinkling pattern of rounded enamel protuberances with shallow anastomosed grooves randomly oriented of MPEF-PV 10860 resembles the finely wrinkled enamel of *Archaeodontosaurus* (Buffetaut, 2005: fig. 2), *Pulanesaura* (McPhee et al., 2015: Fig. 3), and *Tazoudasaurus* (Allain and Aquesbi, 2008: fig. 2). However, there are some differences in the enamel-wrinkling of these species and that of MPEF-PV 10860: *Tazoudasaurus* bears coarse ridges on the lingual surface of the crown (Allain and Aquesbi, 2008) that are absent in MPEF-PV 10860; and enamel-wrinkling occupies

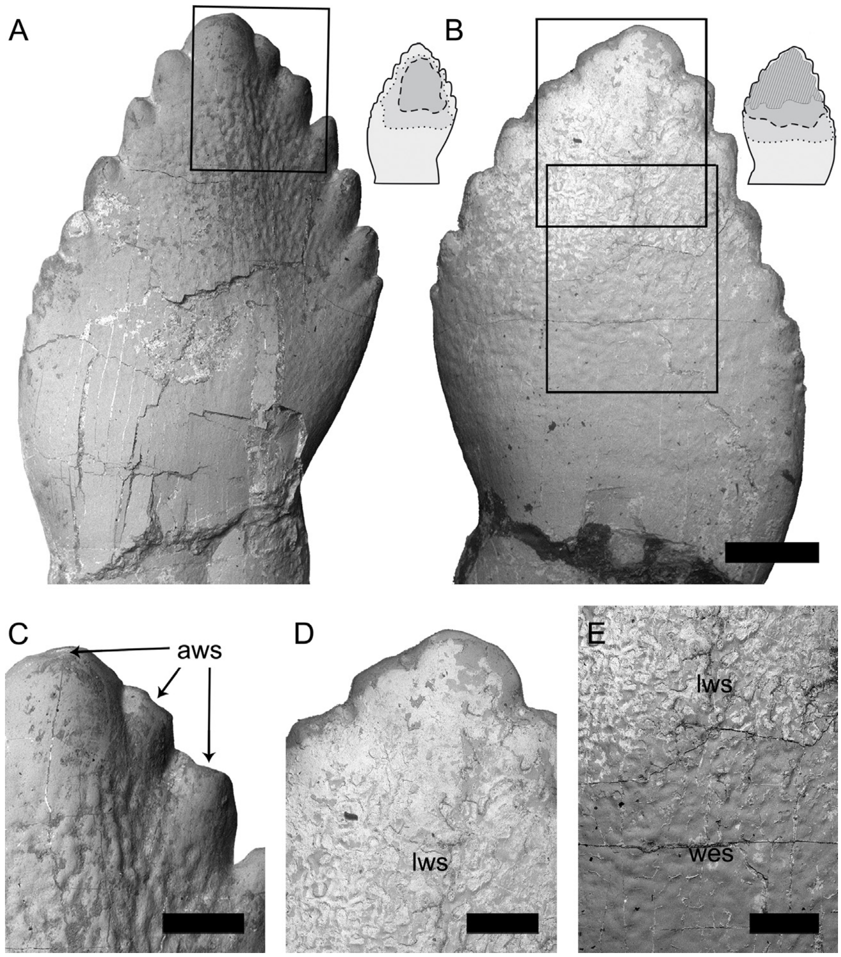

Fig. 2. Indeterminate Sauropodiform species (MPEF-PV 10860), details of the enamel-wrinkling and wear distribution using SEM images. Complete crown with line drawings showing the wrinkling distribution (A, B), and details (C–E), in lingual (A, C) and labial views (B, D, E). In the line drawings, darker gray (segmented line) corresponds to coarser enamel-wrinkling area, medium gray (dot line) indicates smoother wrinkled enamel, light gray indicate areas without enamel-wrinkling, and the oblique lines indicate worn areas. (C) Detail of the apical wear facets and the wrinkled enamel surface; (D) enamel superficially worn; (E) transition between worn and unworn enamel. aws: apical wear surfaces; lws: worn labial surface; wes: wrinkled enamel surface. Scale bars equal to 1 mm in (A, B) and 0.5 mm in (C–E).

Fig. 2. Espèces de Sauropodiformes indéterminées (MPEF-PV 10860), détails du plissement de l'émail et distribution de l'usure à l'aide d'images SEM. Couronne complète avec dessins au trait montrant la distribution des rides (A, B), et les détails (C–E), en vues linguale (A, C) et labiale (B, D, E). Dans les dessins au trait, le gris plus foncé (ligne segmentée) correspond à la surface plus grossière de l'émail ridé, le gris moyen (ligne de points) indique l'émail ridé plus lisse, le gris clair indique des zones d'émail sans rides et les lignes obliques indiquent des zones usées. (C) Détails des facettes d'usure apicales et surface de l'émail ridée ; (D) surface usée de l'émail ; (E) transition entre émail usé et non usé. aws : surfaces d'usure apicales ; lws : surface labiale usée ; wes : surface d'émail ridée. Échelle égale à 1 mm (A, B) et 0,5 mm (C–E).

the entire crown surface in *Tazoudasaurus* and *Archaeodontosaurus*, but it extends only slightly below the apical half in MPEF-PV 10860 and *Pulanesaura* (Allain and Aquesbi, 2008; Buffetaut, 2005; McPhee et al., 2015). Enamel protuberances of MPEF-PV 10860 are also smaller in size and less conspicuous than in *Chinshakiangosaurus* (Upchurch et al., 2007a), *Amygdalodon* (Carballido and Pol, 2010), and the condition commonly found within Eusauropoda (Wilson, 2005; Upchurch, 1998). In addition, MPEF-PV 10860 also differs from *Chinshakiangosaurus* in lacking of a reticulate pattern of wrinkling, and from *Amygdalodon* in having shallower and proportionally wider grooves in comparison with the enamel protuberances. *Amygdalodon* also possess enamel crests and grooves apicobasally disposed and interrupted by pits on the entire surface of the crown, autapomorphic features of this species (Carballido and Pol, 2010: figs. 4 and 5) that are clearly absent in MPEF-PV 10860. The enamel-wrinkling of MPEF-PV 10860 also differs from that of eusauropods, including the three morphotypes described for the Cañadón Asfalto Formation (see below).

The presence of small worn surfaces indicates the crown had already erupted. There are small worn areas at the crown apex and on the fifth and sixth denticles of the mesial margin (Fig. 2C). Furthermore, the apical half of the labial surface of the crown is uniformly worn but lacks a distinct wear facet, and the enamel-wrinkling is less notorious in this area (Fig. 2B, D and E). This incipiently developed

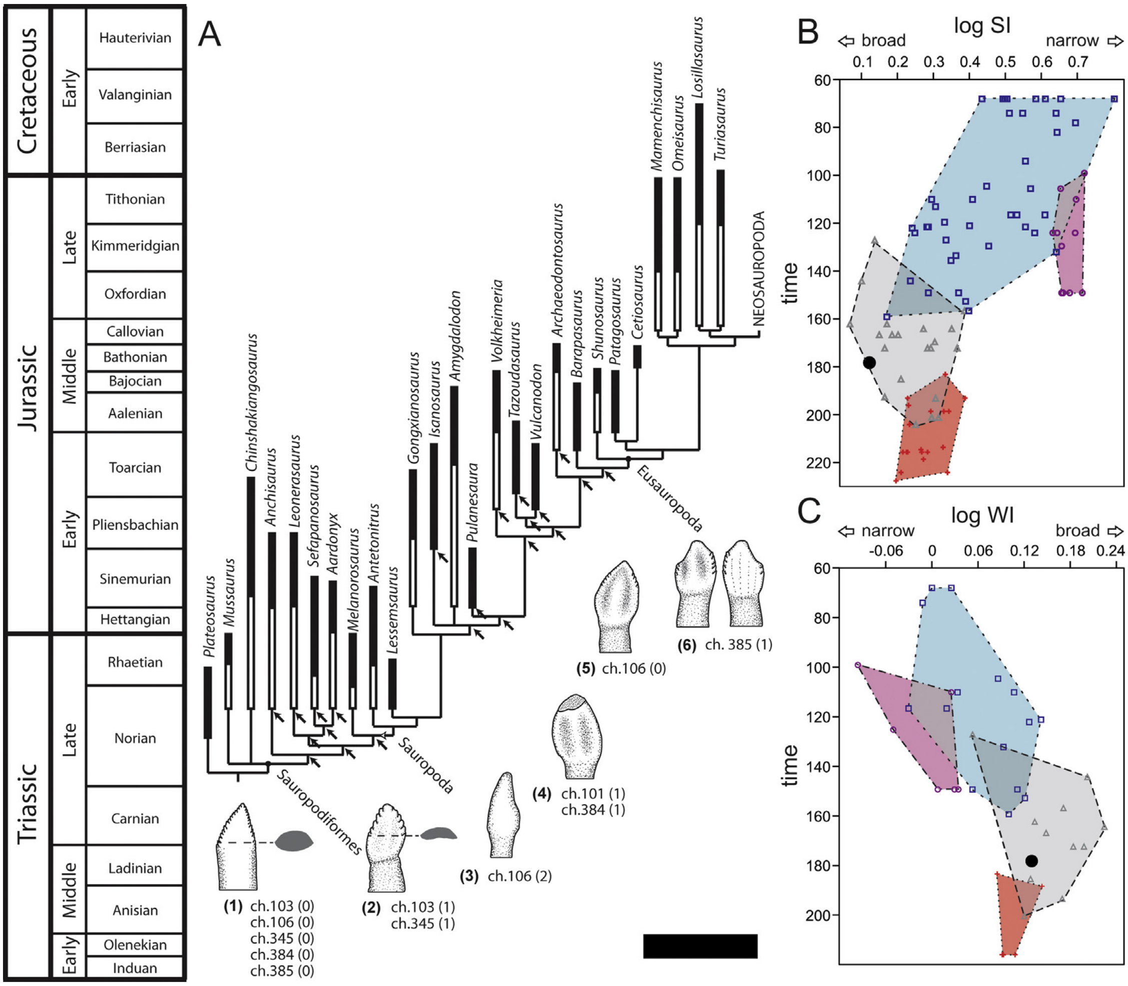

Fig. 3. Time-calibrated phylogeny (A) and sauropodomorph tooth shape (B) and broadening (C) variation in time. In (A), the phylogeny shows the resulting interrelationships and ghost lineages among basal Sauropodomorpha in a reduced strict consensus tree (pruning a posteriori the unstable taxonomic unit MPEF-PV 10860). Chronostratigraphic scale based in an updated version of Cohen et al. (2013). The clade Neosauropoda has been collapsed into a single taxonomic unit for clarity, with its origin considered as near Callovian (Zaher et al., 2011). Tooth and cross-section line drawings represent the appearing of morphologic key specializations in dentition among basal Sauropodiforms and widely distributed in Eusauropoda (from left to right in lingual and labial views). 1: *Plateosaurus*; 2: MPEF-PV 10860; 3: *Melanorosaurus*; 4: *Amygdalodon*; 5: *Tazoudasaurus*; 6: *Patagosaurus*. In (B) and (C) and following Chure et al. (2010), the values of SI and WI were transformed to the logarithm and plotted against the time interval comprising the Mesozoic (expressed in Ma). ch: character. Black arrows indicate nodes where the excluded specimen MPEF-PV 10860 was recovered (inside Sauropodiformes but outside Eusauropoda); empty white boxes indicate ghost lineages; filled black boxes indicate most accurate temporal interval for the locality or formation where the corresponding taxon was recovered. Symbols: black dot, specimen MPEF-PV 10860; circles, diplodocoids; squares, macronarians; summing crosses, non-sauropod sauropodomorphs ("prosauropods"); triangles, basal sauropods. Scale bar in (A) equals to 10 Ma, line drawings not on scale.

Fig. 3. Phylogénie étalonnée dans le temps (A), forme (B) et variation de largeur (C) des dents de sauropodomorphe dans le temps. En (A), la phylogénie montre les interrelations résultantes et les lignées fantômes chez les Sauropodomorpha de base dans un arbre de consensus strict réduit (excluant a posteriori l'unité taxonomique instable MPEF-PV 10860). L'échelle chronostratigraphique est basée sur une version mise à jour de Cohen et al. (2013). Le clade Neosauropoda a été tassé dans une seule unité taxonomique pour plus de clarté, son origine étant considérée comme proche du Callovien (Zaher et al., 2011). Les dessins au trait de dents et sections transversales représentent l'apparition de spécialisations morphologiques clés dans la dentition chez les sauropodiformes de base et largement distribuées dans Eusauropoda (de gauche à droite en vues linguale et labiale). 1 : *Plateosaurus* ; 2 : MPEF-PV 10860 ; 3 : *Melanorosaurus* ; 4 : *Amygdalodon* ; 5 : *Tazoudasaurus* ; 6 : *Patagosaurus*. En (B) et (C) et en suivant Chure et al. (2010), les valeurs de SI et WI ont été transformées en logarithme et tracées en regard de l'intervalle de temps comprenant le Mésozoïque (exprimé en Ma). ch : caractère. Les flèches noires indiquent les nœuds où MPEF-PV 10860 a été récupéré (à l'intérieur des sauropodiformes, mais à l'extérieur d'Eusauropoda) ; les cases blanches indiquent les lignées fantômes ; les cases noires indiquent l'intervalle temporel le plus précis pour la localité ou la formation où le taxon correspondant a été récupéré. Symbole : point noir, spécimen MPEF-PV 10860 ; cercles, diplodocoïdes ; carrés, macronariens ; signe plus, sauropodomorphes non sauropodes (« prosauropodes ») ; triangles, sauropodes basaux. L'échelle en (A) est égale à 10 Ma ; les dessins ne sont pas à l'échelle.

wear of MPEF-PV 10860 is likely due to abrasion (tooth-to-food interaction), and there is no evidence of a facet produced by tooth-to-tooth occlusion. The type of wear is similar to that of weathered crowns described for *Massospondylus*, *Plateosaurus*, and *Yunnanosaurus* (e.g., Galton and Upchurch, 2004). This contrasts with the extensively developed V-shaped wear facets of *Patagosaurus* and other isolated teeth for the Cañadón Asfalto Formation, a feature also present in most gravisaurians (Carballido and Pol, 2010; Holwerda et al., 2015; Wilson and Sereno, 1998). These differences, however, must be taken with caution, as it is still largely unknown how the development of wear facets varies along the tooth row in many taxa, including basal forms of Sauropoda.

4.1. Enamel-wrinkling, comparisons with other sauropods from Cañadón Asfalto

Holwerda et al. (2015) defined three different morphotypes for the sauropod teeth recovered in the Cañadón Asfalto Formation, primarily defined by the pattern of enamel-wrinkling rather than by the crown shape variation (which is more variable along the tooth row in broad-crowned eusauropods). The enamel-wrinkling of MPEF-PV 10860 is less conspicuous than in the three morphotypes described by Holwerda et al. (2015) and differs in details of its distribution and pattern. Morphotype I (referred to *Patagosaurus*) possesses crests and grooves apicobasally oriented at the crown base, whereas the crown apex have sulci, islets, and pits with grooves and crests oriented nearly mesiodistally towards the carina. MPEF-PV 10860 differs from morphotype I in lacking enamel-wrinkling at the crown base and the low protuberances with anastomosed grooves that are more randomly oriented in the middle and apical region of the crown (except for the mesial lingual portion were grooves take a slightly dominant apicobasal direction). Morphotype II (specimen MACN-CH 934) shares with MPEF-PV 10860 its wrinkling distribution above the middle-apical regions of the crown. The pebbly enamel texture of MACN-CH 934 differs from that of MPEF-PV 10860, as the latter has enamel protrusions that are less prominent, more closely spaced to each other, and more irregularly shaped (rather than the hemispherical bubble-like shape of morphotype II). MPEF-PV 10860 also lacks enamel-wrinkling or grooves at its carinae (subtle and shallow, but still present in morphotype II), although this could be affected by wear. Finally, the enamel-wrinkling of morphotype III differs from that of MPEF-PV 10860 in several features already mentioned for morphotypes I (wrinkling absent at the crown base and at the carinae, absence of pits) and II (protrusions not hemispherical and well spaced from each other). Additionally, MPEF-PV 10860 also lacks the prominent basal bulge of enamel separating the crown from the root and a reticulate pattern of crests and grooves on the central region of the crown. Summarizing, enamel-wrinkling of MPEF-PV 10860 differs from all other tooth morphotypes from Cañadón Asfalto in three important aspects: (1) enamel-wrinkling of MPEF-PV 10860 is restricted only to the apical half, excluding the crown base; (2) its pattern does not vary significantly along different regions of the crown; and (3) is incipient and rather poorly developed in comparison with the prominent and complex enamel-wrinkling of the previously described morphotypes. Finally, a major difference with all previously known sauropodomorph teeth from the Cañadón Asfalto Formation is the size of the crown. Whereas the crown of MPEF-PV 10860 measures 5.7 mm in apicobasal height, the teeth previously known from this unit ranges between 15.9 and 37.6 mm.

5. Results and discussion

5.1. Systematic affinities

The heuristic search procedure retrieved 850 most parsimonious trees (MPTs) of 1319 steps, found in 134 replicates. The trees were submitted to a final round of TBR that retrieved a total of 5950 trees. The specimen MPEF-PV 10860 is recovered in multiple alternative positions among the MPTs, ranging from a basal (non-sauropod) sauropodiform to being the sister group of *Barapasaurus* + Eusauropoda (Fig. 3A). The uncertainty in the position of MPEF-PV 10860 derives from the scarcity of the material, but this tooth bears two sauropodiform synapomorphies that support its inclusion in this clade: D-shaped cross-section (ch.103) and a relatively broad crown in relation to the root (ch. 345). A D-shaped cross-section has been previously thought to be exclusive of sauropods (e.g., Carballido and Pol, 2010), but its presence in non-sauropod sauropodomorphs (i.e. *Leonerasaurus*, *Melanorosaurus*) indicates that this feature appeared earlier in the evolution of the group (Fig. 3A). MPEF-PV 10860 is unequivocally positioned outside Eusauropoda in the analysis given it lacks the eusauropodan longitudinal labial grooves extending apicobasally on the crown (ch. 385).

The overall changes in tooth shape within Sauropodomorpha can be comparatively addressed through the variation of SI and WI during the Mesozoic (Fig. 3B and C). The inclusion of MPEF-PV 10860 in the SI dataset of Chure et al. (2010) depicts it closer to basal sauropods with broad crowns than to more basal forms of Sauropodomorpha. This similarity is reflected in the above-mentioned synapomorphy (ch. 345) supporting the non-eusauropodan sauropodiform position of MPEF-PV 10860. When considering the WI, however, MPEF-PV 10860 is also depicted close to basal sauropods, but in this ratio it also resembles the values of basal species of Sauropodomorpha (e.g., *Leonerasaurus*, *Plateosaurus*) and macronarians (e.g., *Brachiosaurus*, *Euelophus*). As in the case of SI, there is an increase in width (relative to the root) during the Middle – Late Jurassic and a subsequent trend to narrower crowns during the Cretaceous (Barrett and Upchurch, 2005; Barrett and Upchurch, 2007; Chure et al., 2010; Upchurch and Barrett, 2000).

Summarizing, MPEF-PV 10860 gathers features typically described in non-sauropod sauropodomorphs (e.g., Barrett and Upchurch, 2007; Otero et al., 2015), features formerly referred to Sauropoda but recently identified in basal sauropodiforms (e.g., Allain and Aquesbi, 2008; McPhee et al., 2015; Pol et al., 2011a; Yates, 2007a,b), and features typical of basal sauropods (e.g., SI values). The fragmentary nature of MPEF-PV 10860 involves an inherent uncertainty on its phylogenetic position that precludes an unambiguous explanation of its combination of plesiomorphic and apomorphic features. Plesiomorphies are interpreted as reversals in trees that depict this specimen as a derived sauropod, and conversely, derived features are interpreted as convergences with sauropods when it is positioned as a basal sauropodiform. Even when MPEF-PV 10860 is excluded, the available characters describing dental features have many ambiguities in the sequence of evolutionary changes towards the eusauropodan condition (Fig. 3A). Furthermore, as noted above, many traditionally used dental characters vary serially along the tooth row, and the pattern of phylogenetic change from basal sauropodomorphs to eusauropods requires further study. Some characters that previously characterized Eusauropoda (e.g., D-shaped section, enamel-wrinkling) are already shown to have a more widespread distribution among sauropodiforms (e.g., Carballido and Pol, 2010), paralleling the case of the reinterpretation of many cranial and postcranial characters traditionally regarded as eusauropod or sauropod synapomorphies (e.g., Bonnan and Yates, 2007; McPhee et al., 2014; Otero et al., 2015; Pol and Powell, 2007; Pol et al., 2011a; Yates et al., 2010).

5.2. Sauropodomorph diversity in the Cañadón Asfalto Formation

The material here presented increases the diversity of tooth morphotypes of sauropodomorphs recorded in the Cañadón Asfalto Formation. The general morphology of MPEF-PV 10860 and the wear pattern clearly differ from that of the spatulate crowns of eusauropods from the same formation, features that imply a different feeding habit and mechanics. These features include the absence of a V-shaped wear pattern, labial grooves, a conspicuously concave lingual face with a distinct apicobasal ridge, and denticles only restricted to the apical third when present (Bonaparte, 1986; Holwerda et al., 2015; Pol et al., 2009; Rauhut, 2003). In addition, the enamel-wrinkling pattern of MPEF-PV 10860 seems to be simpler than the three enamel-wrinkling morphotypes defined by Holwerda et al. (2015). Given that enamel wrinkling is less variable along the tooth row in many sauropod species (see Holwerda et al., 2015), the fourth tooth morphotype represented by MPEF-PV 10860 may represent either a yet unreported non-eusauropod taxon or dental material of *Volkheimeria chubutensis*, a taxon that lacks preserved cranial remains (Bonaparte, 1979). The only way to test these two alternative hypotheses will be the finding of associated dental and postcranial material to compare with the type of *Volkheimeria*.

6. Conclusions

The specimen MPEF-PV 10860 from the Cañadón Asfalto Formation (late Early Jurassic – early Middle Jurassic) increases the current knowledge on sauropodomorph dental diversity in this unit. The noted differences in tooth morphology, type of tooth wear, and tooth size indicate that MPEF-PV 10860 represents either a new species or the first dental record of *Volkheimeria chubutensis*, previously known from postcranial materials. Differences with all other eusauropod teeth from Cañadón Asfalto Formation may also be indicative of different feeding strategies and niche partitioning among sauropodomorphs from this unit. More complete and associated remains are clearly needed to achieve a more complete understanding of the paleoecological significance of the diverse association of megaherbivores from the Cañadón Asfalto Formation. Despite these uncertainties, the coexistence of multiple sauropodomorph lineages in the late Early to early Middle Jurassic places the Cañadón Asfalto Formation in an unparalleled position for understanding the dynamics of continental ecosystems in this key period of dinosaur evolution.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.crpv.2017.08.005.

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