Titanosaurian tooth morphotypes as supporting evidence of Late Cretaceous landbridges between North Africa and Southern Europe (#25985)

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Titanosaurian tooth morphotypes as supporting evidence of Late Cretaceous landbridges between North Africa and Southern Europe

Femke M Holwerda Corresp., [1, 2, 3] , **Roel Montie** [1, 2, 3] , **Verónica Díez Díaz** [4] , **Jelle WF Reumer** [1]

[1] Faculty of Geosciences, Utrecht University, Utrecht, Netherlands
[2] Vertebrate Palaeontology, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Bavaria, Germany
[3] Department of Earth and Environmental Sciences and GeoBioCenter, Ludwig-Maximilians-Universität München, Munich, Bavaria, Germany
[4] Leibniz-Institut für Evolutions-und Biodiversitätsforschung, Museum für Naturkunde, Berlin, Germany

Corresponding Author: Femke M Holwerda
Email address: f.holwerda@lrz.uni-muenchen.de

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Femke Holwerda*[1, 2,3], Roel Montie[1,2,3] Verónica Díez Díaz[4], and Jelle Reumer[1]

[1] Faculty of Geosciences, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands
[2]Staatliche Naturwissenschaftliche Sammlungen Bayerns (SNSB), Bayerische Staatssammlung für Paläontologie und Geologie, Richard Wagnerstrasse 10, 80333 Munich, Germany;
[3] Department of Earth and Environmental Sciences and GeoBioCenter, Ludwig Maximilians Universität, 80333 München, Germany
[4] Museum für Naturkunde, Leibniz-Institut für Evolutions-und Biodiversitätsforschung, Invalidenstraße 43, 10115 Berlin, Germany

*Corresponding autor: Femke Holwerda, f.holwerda@lrz.uni-muenchen.de

Abstract

The early Late Cretaceous (Cenomanian, 100.5Ma – 93.9Ma) Kem Kem beds of Morocco and equivalent beds in Algeria have produced a rich fossil assemblage, yielding, among others, many isolated teeth which can be used in species diversity studies. As this area is rare in herbivore body fossils, these isolated teeth provide a different approach to analyzing past faunal assemblages. Eight isolated sauropod teeth from these North African sites are studied here, to assess whether the teeth can be ascribed to a specific clade, and if different tooth morphotypes can be found in the samples. Two general morphotypes are found, based on enamel wrinkling and general tooth morphology, as well as by comparison with other late Cretaceous sauropods from North Africa and Southern Europe. All morphotypes are titanosaurian in origin; even though rebbachisaurids have been reported in earlier studies, these were not convincingly found amongst the tooth sample. Moreover, striking similarities are found between the North African tooth morphotypes, and tooth morphotypes from titanosaurs from the Late Cretaceous (Campanian-Maastrichtian, 83.6Ma – 66.0Ma) of the Iberoarmorican Island. This result suggests the presence of landbridge connections in the Cretaceous between North Africa and Southern Europe, as has been proposed by previous authors.

Key Words: Titanosauria, Late Cretaceous, Africa, Europe, teeth, diversity.

INTRODUCTION

The Cenomanian of North Africa is well-known for its rich fauna, ~~and~~ many taxa having been described in particular from the ~~Cenomanian (100.5 – 93.9 Ma)~~ Kem Kem beds of Morocco, and the equivalent continental intercalaire of Algeria. ~~The~~ Moroccan Kem Kem beds include sharks, lungfish, coelacanths, bony fish, amphibians, squamates, turtles, crocodylomorphs, pterosaurs, sauropods, and an abundance of theropods (Wellnhofer & Buffetaut, 1999; Cavin et al., 2010; ~~Richter, Mudroch & Buckley, 2013;~~ Läng et al., 2013; Mannion & Barrett, 2013). Despite this ~~large~~ diversity, the majority of the fossil material is ~~represented by~~ carnivorous dinosaurs (e.g. *Spinosaurus*, *Carcharodontosaurus*, abelisaurids). Läng et al. (2013) ~~contributed~~ this to the deltaic palaeoenvironment being unsuitable for the ~~setting~~ of stable terrestrial vegetation. Because of this, the herbivorous fauna has not received much attention thus far. Studies of sauropod material from this region have noted rebbachisaurids (de Lapparent and Gorce, 1960~~,~~ Mannion & Barrett 2013) and ~~several~~ titanosauriform ~~remains~~ (De Broin et al, 1971; Mannion & Barrett, 2013~~, (Ibrahim et al., 2016)(~~Ibrahim et al., 2016). Lapparent and Gorce (1960) also mentioned brachiosaurid ~~finds, however~~ this claim was considered invalid due to poor preservation and description (Mannion and Barrett, 2013~~; Mannion, 2009~~).

While sauropod body fossils are scarce, teeth are preserved in relative abundance. Teeth are commonly preserved in the fossil record due to their hardness, resilience against weathering, and high replacement rates (see e.g. Calvo, 1994; Erickson, 1996; Garcia & Cerda, 2010). Studying isolated teeth has previously been applied to assess theropod species diversity in North Africa (Richter, Mudroch & Buckley, 2013). Sauropod teeth can be used for this as well, as morphological classifications based on shape, size and wear facets (Calvo, 1994; Salgado & Calvo, 1997; Chure et al., 2010; Carballido et al., 2017), and enamel wrinkling patterns (e.g. Carballido & Pol, 2010; Díaz, Suberbiola & Sanz, 2012; Díaz, Tortosa & Le Loeuff, 2013; Holwerda, Pol & Rauhut, 2015) have succesfully classified tooth assemblages into morphotypes or even to a taxonomic level.

Mannion & Barrett (2013) suggested that the ~~N~~orth African titanosauriforms may not be closely related to ~~S~~outh African forms, as the lineages were cut off from each other by the trans Saharan seaway. Moreover, close relations between North African sauropods and Italian (Zarcone et al., 2010; Dal Sasso et al., 2016), Iberian (Sallam et al., 2018; Díez Díaz et al., submitted) and more specifically, close relations between Egyptian and European sauropods (Sallam et al., 2018) and

Tunesian and European sauropods (Fanti et al., 2015) have suggested the existence of landbridges between ~~N~~orth Africa and ~~S~~outhern Europe. Several routes have been suggested, such as the Apulian route ~~at~~ the Early Cretaceous (Canudo et al., 2009)**.** Landbridges would have been made possible by relative sea level fluctuations, creating sand banks and islets, making migration possible between the ~~N~~orth African and ~~S~~outhern European islands and peninsulas (Zarcone et al., 2010).

Here, we present a morphological analysis of a sauropod tooth assemblage from the Cenomanian of Morocco and Algeria. Teeth are categorized into two morphotypes, which are then compared to contemporaneous sauropod tooth morphotypes from Africa and ~~S~~outhern Europe.

Institutional abbreviations:

BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany

MB.R: Museum für Naturkunde, Berlin

MHN-AIX-PV: Natural History Museum Aix en Provence, France

MCCM-HUE: Museo de las Ciencias de Castilla-la Mancha, Spain

FAM: Fox-Amphoux-Métissons, France

GEOLOGICAL SETTING

Four of the teeth studied ~~here~~ are from the Kem Kem beds of Morocco, and four were found in the Late Cretaceous Continental Intercalaire of Algeria. The Kem Kem area is located on the ~~S~~outh-~~E~~astern side of Morocco (Figure 1). Here, the Kem Kem beds lie exposed over 250 km north and south of the town of Erfoud (Cavin & Forey, 2004~~; Wellnhofer & Buffetaut 1999~~*)*. The Kem Kem beds are usually considered to be made up of two formations (see Figure 1): ~~T~~he fossil-rich lower Ifezouane Formation and the upper Aoufous Formation, rich in ichnofossils (Belvedere et al., 2013~~; Cavin 2010~~), also mentioned as the lower sandy unit and the upper marly unit respectively (Mannion & Barrett, 2013; Ibrahim et al., 2014). The sandy Ifezouane Formation is interpreted as a braided fluvial system, a continental environment ~~formed in~~ high energy ~~systems~~ (~~Belvedere et al. 2013; Cavin et al., 2010;~~ Wellnhofer & Buffetaut 1999). The Aoufous ~~Fm.~~ is thought to represent a coastal lagoon, as characterized by supratidal to foreshore deposits (Belvedere et al., 2013~~, Cavin et al., 2010~~). As vertebrate fossil assemblages are retrieved mostly from the lower Ifezouane Formation, our Morrocan Kem Kem tooth assemblage most likely will have its provenance from here (*Cavin et al. 2010*). The Continental Intercalaire of Algeria is less studied tan the Kem Kem, and the age ranges from Barremian to Aptian-Albian, however, most authors set the age of the beds close to the Moroccan border, where our Algerian specimens allegedly are from (Taouz, Algeria), to ranging from the Cenomanian to Turonian, with the Cenomanian layers being most fossil rich (Benyoucef et al., 2015; Meister et al., 2017), see Figure 1. Unfortunately, many of the fossils retrieved from the Kem Kem area and equivalent beds from Algeria have no clear origin and can therefore not be assigned to any particular formation within the Kem Kem area (Forey and Cavin, 2007, Rodrigues et al. 2011(Forey & Cavin, 2007).

MATERIALS AND METHODS

In this study, eight isolated sauropod teeth from the Cenomanian Kem Kem beds are analysed using detailed measurements, photography and Scanning Electron Microscope (SEM) images for the enamel wrinkling patterns, and the microwear analysis. The four teeth from the Kem Kem beds of Morocco are BSPG 1993 IX 331A, BSPG 1993 IX 331B, BSPG 1993 IX 331C, and BSPG 1993 IX 313A. The four Algerian (Taouz) specimens are BSPG 1993 IX 2A, BSPG 1993 IX 2B, BSPG 1993 IX 2C, and BSPG 1993 IX 2D. Measurements were taken with a caliper. For the imaging, the teeth were photographed with a Nikon D500 camera with a Nikon dx af-s nikkor 18-55mm lens. SEM pictures were taken of the samples at the Zoologisches Institut in Munich to obtain a detailed view of the wear facets and enamel wrinkling patterns. The specimens were gently cleaned if necessary, then mounted on SEM-stubs and examined using a LEO 1430VP SEM (Electron Microscopy Ltd., Cambridge, United Kingdom). In this study, the proposed dental orientations of Smith and Dodson (2003) are followed. The Slenderness Index (SI, *sensu* Upchurch, 1998) was measured for each tooth by dividing the apicobasal length by the mesiodistal width. The Compression Index (CI, *sensu* Díez Díaz et al., 2013) was measured for each tooth by dividing the labiolingual width by the mesiodistal width. The angles of the wear facets were measured with respect to the labiolingual axes of the teeth.

DESCRIPTION

Teeth from Morocco

BSPG 1993 IX 331A (Figure 2.A)

The crown is more or less cylindrical, tapering towards the apex, mesiodistally as well as labiolingually. The labial side is strongly convex, the lingual side is straight to concave. The convexity increases towards the apex as the distal 1/3rd bends more strongly towards the lingual side. The tooth has an almost circular cross-section at the base of the crown, becoming slightly more flattened in the labiolingual direction apically.

Two distinct wear facets are present on the lingual and the apical side of the tooth. The first is a slightly V-shaped wear facet with an angle of almost 90 degrees with respect to the labiolingual axis, containing abundant microscratches with an apicobasal orientation (see Figure 2.A). The apical wear facet shows wear on both lingual and labial sides, although a slight labial inclination seems to be present. A polished surface is found on the labial side of the crown, containing thin scratches with an almost apicobasal orientation (angling distally). Either damage or wear is present on the mesial and distal edges on the carinae, exposing the dentine.

The enamel wrinkling pattern on the labial side is more pronounced than on the lingual side of the tooth (see Figure 3A-B). On the labial as well as the lingual side, the pattern is more pronounced in the middle of the tooth, and fades out slightly toward the apex and the base. The labial enamel wrinkling pattern consists of frequently anastomosing, parallel, wavy grooves and crests of varying width with a general apicobasal orientation. Grooves and crests are discontinuous; crests are often interrupted by pits and islets. The crests are rounded to triangular in shape. The distribution of crests and grooves is roughly equal. Compared to the other teeth, the ridges appear high, and grooves quite deep. On the lingual side, more pits are present, and the grooves and crests appear slightly less rounded in shape, but retain their apicobasal orientation. The grooves appear more shallow on the lingual side.

BSPG 1993 IX 331B (Figure 2.B)

The entire tooth curves towards the lingual side, with the labial side slightly more convex on the upper half, resulting in a labiolingually tapering apex. The tooth crown is convex toward the distal side, tapering to a mesiodistally narrow apex. The tooth is generally distally inclined, however, the apex curves slightly towards the mesial side. It has an oval cross-section at the base, becoming slightly more "lemon-like" (*sensu* Díez Díaz, Tortosa & Le Loeuff, 2013) apically due to the presence of pronounced carinae on the mesial and distal edges. The carina on the distal side is slightly more pronounced and continues further basally than the one on the mesial side. The apex contains a polished surface on the mesial side of about 0.5 cm long, ~~stretching~~ towards the base. The enamel wrinkling pattern consists of very sharp, angular, narrow and discontinuous grooves with seemingly no preferred orientation (see Figure 3C-D). Some pits and sulci are present. The wrinkling on the lingual side is slightly more pronounced than the labial side, and also appears slightly more rounded.

This specimen differs morphologically from the other teeth in this study. Most of these characteristics (curved shape, low SI ratio) are probably attributed to a distal (posterior) placement of the tooth in the jaw, as also seen in the teeth of *Giraffatitan* (MB.R.2181.21).

*BSPG 1993 IX 331C (Figure 2.*C*)*

This tooth differs from the first two Kem Kem teeth, in that it is rather straight both labially and lingually. It has a labiolingual apical tapering caused by the presence of labial and lingual wear facets, and also a slight apical mesiodistal tapering. A very slight curvature toward the lingual side is present. The base of the tooth is oval in cross-section, this appears to remain constant throughout the tooth, except for the apex.

Four possible wear facets are present on the tooth, ~~one~~ on the labial, lingual, mesial, and distal surfaces, respectively. The lingual wear facet is angled at around 60 degrees with respect to the labiolingual axis. The labial wear facet is angled at almost 90 degrees with respect to the labiolingual axis. Both the mesial and the distal wear facet are more pronounced on the lingual side, just below the lingual wear facet. They appear almost parallel to the tooth's main axis.

The enamel of BSPG 1993 IX 331C is ornamented with thick mesiodistally oriented grooves and deep ridges. They slope towards the base from the mesial and distal edges and meet in the centre. Some grooves seem to be connected, sometimes forming a rhomboid like morphology. The enamel wrinkling pattern is either not visible due to damage, or the apparent damage is the enamel wrinkling.

The four wear facets of BSPG 1993 IX 331C are not seen in similar shapes in any of the other teeth. The deep grooves on the labial and lingual sides of the tooth do not resemble any taphonomic patterns as described by King et al. (1999), however this does not rule out taphonomic processes completely. The peculiar pattern could still be natural, and would then be a very distinctive enamel wrinkling pattern. However, the markings could also be damage from excavation or preparation of the tooth.

<u>*BSPG 1993 IX 313A*</u> *(Figure 2.D)*

The upper half of the crown is inclined towards the lingual side, with the labial side showing significantly more convex curvature than the lingual concave side. The apex tapers mesiodistally, and the mesial side of the tooth shows a slight incline towards the distal end, creating a slightly convex mesial apical end. The tooth has an oval cross-section at the base, becoming more “lemon-like” (*sensu* Díez Díaz, Tortosa & Le Loeuff, 2013) toward the apex due to the presence of carinae on the mesial and distal edges. The carina on the distal edge continues further towards the base than the carina on the mesial edge.

The crown ~~contains~~ one wear facet on the lingual side, angled at around 75 degrees with respect to the labiolingual axis of the tooth.

The enamel appears smooth except for thin apicobasally oriented (angular, not rounded) lines or fractures running continuously towards the apex (see Figure 3E-F).

Teeth from Algeria

<u>*BSPG 1993 IX 2A*</u> *(Figure 2.E)*

The tooth appears fairly straight. The mesial and distal sides, as well as the labial and lingual sides taper towards the apex. The mesial side, however, shows a slight convexity and curves towards the distal side, which is straight apically. A very slight mesiodistal expansion ~~appears to be~~ present ~~at~~ the middle of the crown, before tapering toward the apex. Carinae are present on the mesial and distal edges of the upper third of the crown. The distal carina reaches slightly further basally. The cross-section at the base is oval, becoming lemon-like at the apex due to the carinae. A slight difference in enamel thickness appears to be present, with the labial side bearing ~~the~~ thicker enamel.

A wear facet is present on the lingual side, angled at around 50 degrees with respect to the labiolingual axis. The apical part of the labial side appears slightly polished.

The enamel wrinkling pattern on both the labial and lingual sides consists of apicobasally oriented grooves and ridges, which are less broad and more sinuous on the labial side (see Figure 3G-H).

<u>BSPG 1993 IX 2B</u> (see Figure 2.F)

The tooth is curved lingually, with the labial side convex, and the lingual side concave. This curvature seems slightly more exaggerated at the apex. A very slight mesiodistal tapering can be seen at the apical part of the crown, however the tooth appears very square when observed from the labial and lingual side. Labiolingual tapering seems to appear due to the presence of a labial and lingual wear facet intersecting at the apex. The lingual side of the tooth is relatively flat in the mesiodistal direction when compared to the labial side, giving the middle of the tooth a slight D-shaped cross-section. Carinae are present on the mesial and distal edges, although the distal carina is more pronounced and continues further basally. The tooth has an oval cross-section at the base, becoming D-shaped toward the centre, and more lemon-like apically due to the presence of carinae. Two distinct wear facets are present on BSPG 1993 IX 2B, ~~one~~ on the labial and ~~one on the~~ lingual side. The labial wear facet is larger (almost 1.5 cm in apicobasal length), and angles toward the mesial side. The labial wear facet is angled at around 72 degrees with respect to the labiolingual axis of the crown. The lingual wear facet is smaller. It cuts the labiolingual axis at almost 90 degrees, and shows some very faint apicobasally oriented microscratches. The enamel wrinkling pattern consists mainly of apicobasally oriented, sinuous grooves and ridges (see Figure 3I-J).

The enamel wrinkling pattern of BSPG 1993 IX 2B appears quite similar to BSPG 1993 IX 331A and the labial side of BSPG 1993 IX 2A. The enamel of BSPG 1993 IX 331A appears to be slightly more pronounced and severely wrinkled than the enamel of BSPG 1993 IX 2B, a difference perhaps caused by more wear on the latter.

A noteworthy difference between the enamel wrinkling patterns of this tooth and all other teeth from this research is that the enamel wrinkling is more pronounced on, what seems to be, the lingual side instead of the labial side.

<u>BSPG 1993 IX 2C</u> (Figure 2.G)

The tooth is badly preserved and largely covered with reddish sediment, the enamel appears brown. The crown is fairly straight and tapers apically (mesiodistally as well as labiolingually). The curvature on the mesial apical side is more pronounced. Towards the apex, the crown expands slightly labiolingually, while from the middle of the tooth, it tapers to the apex. This expansion mainly seems to occur on the convex (probably labial) side. At least one carina is present on the (probably) mesial edge. The distal edge also seems to show remains of a carina but that can-not currently be accurately determined. The cross-section at the base is slightly oval, becoming almost circular at the middle of the crown, and then becoming more lemon-like apically due to the presence of carina(e). A possible wear facet can be seen on the labial side, cutting the labiolingual axis of the crown at a low angle (35 degrees). Because of the damaged state of this tooth, no SEM pictures were taken.

BSPG 1993 IX 2D (Figure 2.H)

The crown shows very strong apical tapering mesiodistally, as well as labiolingually, resulting in a sharp tip. One side shows slightly more curvature, as such this is named the labial side. The upper third of the crown shows stronger mesiodistal tapering on one side, therefore determined to be the mesial side. Very distinct carinae are present on the mesial and distal edges of the crown. The mesial carina seems to be slightly more distinct due to the curvature of the mesial apical part, but the distal carina continues further basally (halfway down mesially, three quarters down distally). The tooth has an oval cross-section at the base, becoming strongly lemon-shaped apically due to the distinct carinae.

Wear facets are not present. The enamel is smooth except for some pits (see Figure 3K-L).

DISCUSSION

Systematic discussion and comparisons

The tooth sample from North Africa shares the presence of mesial and distal margins extending parallel to each other along almost the entire length of the crown with titanosauriform and diplodocoid sauropods – with the exception of BSPG 1993 IX 331B and BSPG 1993 IX 2D –, and the absence of a mesio-distal expansion at the base of the crown (Calvo, 1994; Upchurch, 1995a; Salgado & Calvo, 1997; Upchurch, 1998a; Wilson & Sereno, 1998; Upchurch & Barrett, 2000; Barrett et al., 2002; Wilson, 2002; Upchurch, Barrett & Dodson, 2004). These teeth also share with diplodocoids and titanosaurs the loss of some plesiomorphic features of Sauropoda, which are retained in basal titanosauriforms (e.g. *Giraffatitan*), such as the presence of a lingual concavity with a median ridge, and labial grooves (Upchurch, 1998; Barrett et al., 2002).

The general crown outline is similar in all the teeth of the sample: parallel-sided crowns slightly labiolingual compression, and mesial and distal ridges. The labiolingual compression and the ridges are more conspicuous in the Algerian teeth. BSPG 1993 IX 331B and BSPG 1993 IX 2D present a different crown morphology. The mesial and distal edges of these teeth begin to taper distally slightly above the middle of their crowns. However, this difference in the crown morphology between these teeth and the rest of the sample could be due to different positions in the tooth row, as occurs in most eusauropods and other sauropodomorphs (e.g. Carballido and Pol, 2010; (Holwerda, Pol & Rauhut, 2015; Carballido et al., 2017). In addition, two enamel types can be found in the sample too: rugose (BSPG 1993 IX 331A, 331B, 331C, 2B and 2C) and smooth (BSPG 1993 IX 313A, 2A, and 2D) enamel. However, these differences in the enamel ornamentation could be due to the wear of the tooth and the diet of the individual animal.

Thanks to the morphological descriptions and similarities, two tentative morphotypes could be distinguished, based on the development of the mesial and distal ridges, but that also coincide (more or less) with the geographical distribution: the “Kem Kem morphotype” and the “Algerian morphotype”.

The “Kem Kem morphotype” ~~comprises of~~ BSPG 1993 IX 331A, BSPG 1993 IX 331B, BSPG 331C. BSPG 1993 IX 331A and BSPG 1993 IX 331B are not very similar in shape, something that ~~in this case can~~ be explained by ~~a~~ differing ~~placement~~ of the teeth in the tooth row, BSPG 1993 IX 331A ~~being~~ a more anterior tooth than BSPG 1993 IX 331B. Due to this placement, their SI ratios differ greatly (4.39 vs 2.61). However, various other morphological traits are shared. Both teeth display mesiodistal and labiolingual tapering toward the apex. Also, similar carinae are present on the mesial and distal ridge on both teeth. The enamel on both teeth is ornamented with mainly apicobasally oriented, highly sinuous grooves and ridges, with pits and islets frequently visible. Finally, the enamel wrinkling of both teeth is very pronounced. Small differences in enamel wrinkling patterns can be explained by the differing stages of wear between these teeth.

BSPG 1993 IX 331A seems morphologically similar (crown length and shape) to a titanosaurian tooth from Argentina described by Garcia (2013, Fig. 1). Both teeth contain longitudinal scratches on their wear facets, although these are oriented more apicobasally in BSPG 1993 IX 331A. The crown-root transition is also similar between both teeth, and both have high CI and SI ratios (0.73 vs 0.85 and 3.73 vs 4.36 for the tooth described by Garcia (2013) and BSPG 1993 IX 331A respectively). However, the enamel wrinkling patterns between these two teeth show great differences; the enamel of BSPG 1993 IX 331A shows highly sinuous patterns not visible on the tooth described by Garcia. The age difference is also significant, with the Kem Kem fossil dating back to the Cenomanian, and the tooth described by Garcia (2013) to the middle Campanian–lower Maastrichtian. The teeth of *Rapetosaurus* from Madagascar also share a similar morphology with BSPG 1993 IX 331A, however, *Rapetosaurus* is restricted to the Late Cretaceous (Maastrichtian~~,~~ Rogers & Forster, 2004). The teeth of the Cenomanian-Campanian Chinese *Huabeisaurus* show some similarities in size and shape, ~~however~~ not in enamel wrinkling (D’Emic et al., 2013). Finally, the tooth resembles the cylindrical morphotype with circular cross-section of the southeastern French Fox-Amphoux-Métissons morphotype (FAM 03.06, 03.11, and 04.17, (Díaz et al., 2012~~,~~ Fig. 9). The SI ratios are high in both morphotypes (between 4 and 5, excepting BSPG 1993 IX 331B). The teeth also display a similar labial convexity, which becomes stronger towards the apex in both morphotypes. The enamel wrinkling differs between the morphotypes, however, as the Kem Kem teeth show ~~a~~ much more pronounced enamel wrinkling.

However, BSPG 1993 IX 331C differs slighty from the other teeth in the Kem Kem sample, in shape and enamel wrinkling pattern. The high angle lingual wear facet of BSPG 1993 IX 331C, along with the mesial and distal wear facet (possibly caused by inclined growth of the tooth in the alveolus), high SI ratio (3.7), high CI ratio (0.75) and general chisel-shape (sensu Calvo, 1994), all fit well within the classification criteria for Titanosauria. This tooth can not be classified more precisely than Neosauropoda indet., however a titanosaurian origin is likely.

The “Algerian morphotype” comprises of BSPG 1993 IX 313A, BSPG 1993 IX 2A BSPG 1993 IX 2B and BSPG 1993 IX 2C and BSPG 1993 IX 2D. Even though BSPG 1993 IX 313A is from the Moroccan sample, the morphology matches more that of the Algerian type. BSPG 1993 IX 313A is largely similar to the *Atsinganosaurus* teeth described by Díez Díaz, Tortosa & Le Loeuff, 2013, Fig. 3, MHN-AIX-PV.1999.22), by showing a labiolingual compression (CI: 0.76) and a lemon-shaped cross-section due to the presence of apical carinae. It also contains one apical wear facet with a high inclination angle relative to the labiolingual tooth axis (75 degrees). The enamel appears smooth on both morphotypes, but contains apicobasally oriented longitudinal lines (grooves or fractures**).** The only main differences between BSPG 1993 IX 313A and the teeth from *Atsinganosaurus* are the size of the tooth (2.75 cm vs around 1 cm respectively) and the SI ratio (3.35 vs 4 respectively). Almost all other characteristics are similar. BSPG 1993 IX 2A and BSPG 1993 IX 2C present a very similar morphology, with low-angled wear facets (~50 degrees relative to the labiolingual tooth axis) at their apices, and carinae at the mesial and distal edges. The teeth have similarly high SI and CI indices (see Table 1). Either the mesial or distal edge is curved slightly more than the opposite edge. Their cross-sections change from basally circular to more lemon-like apically due to the carinae, which is similar to that of *Atsinganosaurus* (Garcia et al., 2010; Díez Díaz, Tortosa & Le Loeuff, 2013). Furthermore, the morphology of the tooth BSPG 1993 IX 2C, just as BSPG 1993 IX 2A, shows similarities with the teeth of *Karongasaurus* as pictured by Gomani (2005), and perhaps the teeth of *Maxakalisaurus* (Kellner, 2006). The lingual wear facet of BSPG 1993 IX 2A is of relatively low angle (50 degrees) for Titanosauria, but does not appear to be a low-angle labial wear facet as seen in Diplodocoidea. Finally, the two teeth (but especially 2A) resemble the morphotype B of Lo Hueco, Spain (MCCM-HUE 2687, Díaz, Ortega & Sanz, 2014, Fig. 5). Both morphotypes are cylindrical, have a high SI (>4,3, Diaz, Ortega & Sanz, 2014), a strong apical distal or medial inclination of the tooth, (giving the tooth a far from straight outline) with a high-angled wear facet. Moreover, the enamel wrinkling of BSPG 1993 IX 2A matches that of the Lo Hueco morphotype, in that both morphotypes show course, but not rugose, discontinuous wrinkling, with smooth longitudinal ridges, although 2A shows more pronounced enamel wrinkling than Lo Hueco morphotype B. BSPG 1993 IX 2C is very smooth, and shows a slightly different shape than 2A and Lo Hueco morphotype B, therefore, this tooth could still pertain to a different type of sauropod.

The shape, squared apex and presence of BSPG 1993 IX 2B with two wear facets (labial and lingual) seem to resemble the teeth of *Nigersaurus* as described by Sereno & Wilson (2005) (p.166, figure 5.7), however the position of the wear facets does not match, nor does the curvature or the size. The tooth does seem to contain some asymmetrical enamel thickness as seen in rebbachisaurids like *Nigersaurus*, however this was merely estimated from the SEM pictures and is unconfirmed. Due to the small sample size histological sampling was not possible for this study. The labial wear facet is said to be characteristic for diplodocids and dicraeosaurids, however these clades no longer existed in the early Late Cretaceous, except in South America (Gallina et al., 2014). The tooth, however, also is similar to a titanosaur tooth mentioned by Garcia and Cerda (2010, MPCA-Pv-55, fig. 5). Moreover, the flat lingual side of the tooth gives it a D-shaped cross-section, something Mannion (2011) states is something only seen in upper teeth of titanosaurs.

Therefore, BSPG 1993 IX 2B is probably titanosaurian in origin, based on general tooth shape (apical curvature, and lingual flatness) and a high angle lingual wear facet, under the condition that the labial wear facet is either an extremely polished surface, or a wear facet formed in the manner proposed by Garcia and Cerda (2010). BSPG 1993 IX 2B is most likely an upper tooth, classified within Titanosauria.

Finally, the lemon-shaped cross-section, as with BSPG 1993 IX 313A, is indicative of *Atsinganosaurus* MHN-AIX-PV.1999.22, (Díez Díaz, Tortosa & Le Loeuff, 2013).

BSPG 1993 IX 2D shows some morphological resemblance to the Spanish *Demandasaurus* tooth photographed by (Torcida Fernández-Baldor et al., 2011), which also shows a very sharp tip and very distinct carinae. However BSPG 1993 IX 2D does not show the longitudinal crests of enamel on the labial and lingual face described for *Demandasaurus*. The enamel seems undifferentiated in thickness, although this is unconfirmed, and as such would not fit the description of *Demandasaurus*. The enamel of the Argentinian *Limaysaurus* is described as undifferentiated and smooth, and the description of the unworn teeth of the *Limaysaurus* holotype by Calvo & Salgado (1995) appears quite similar to BSPG 1993 IX 2D. The holotype teeth were initially ascribed to *Rebbachisaurus tessonei*, but were later revised and ascribed to *Limaysaurus* (Salgado et al., 2004). It is also possible that the enamel of the tooth was not always smooth, but simply smoothened by taphonomic processes. However as has been pointed out before by Chiappe et al. (2001), the dental identification as proposed by Calvo (1994) is mainly based on position of wear facets, which this tooth lacks. The unworn teeth described by (Coria & Chiappe, 2014) morphologically resemble BSPG 1993 IX 2D as well. As with BSPG 1992 IX 313A, and 2B, 2D shows a lemon-shaped cross-section, indicative of Atsinganosaurus MHN-AIX-PV.1999.22 (Díez Díaz, Tortosa & Le Loeuff, 2013).

Finally, and although the CI is similar in both morphotypes, the SI is slightly higher in the "Algerian morphotype" than in the "Kem Kem morphotype". Both morphotypes present teeth with both rugose and smooth enamel ornamentation.

To summarize, when compared with the biogeographically nearest tooth assemblages, namely titanosaurian teeth found in the Iberoarmorican Island (see Garcia et al., 2010; Díaz et al., 2012; Díaz, Suberbiola & Sanz, 2012; Díez Díaz et al., 2013; Díez Díaz, Tortosa & Le Loeuff, 2013; Díaz, Ortega & Sanz, 2014), we can assess several similarities for each morphotype:

- The "Kem Kem morphotype" teeth shows some similarities with the cylindrical morphotype teeth found in Fox-Amphoux-Métisson (southeastern France, Díez Díaz et al., 2012b, see Figure 4). However, the enamel seems to be more rugose in the Kem Kem sample, and the ridges slightly more developed.
- The "Algerian morphotype" teeth seem to be more similar to the teeth of *Atsinganosaurus* (Garcia et al., 2010, see Figure 4) and the morphotype B from Lo Hueco

(Díaz, Ortega & Sanz, (2014), see Figure 4). These sample has more developed mesial and distal ridges, that create a lemon-shaped cross-section of the crown, as in the Spanish and French specimens.

Titanosaurian diversity and palaeobiogeographical implications

The tooth sample from the (mainly) Cenomanian Kem Kem beds of Morocco and the Continental Intercalaire of Algeria show a predominantly titanosaurian assemblage, with only one tooth (BSPG 1993 IX 2B) showing possible rebbacchisaurid affinities. This is supported by the assessment of the mid-Cretaceous African sauropod fossil record by Mannion and Barrett (2013), who found that *Rebbachisaurus* and some tentatively placed indeterminate titanosauriforms and rebbachisaurids were present in the Kem Kem beds of Morocco. Also Ibrahim et al., (2016) found evidence of titanosaurian sauropods in the Kem Kem beds of Morocco. This titanosaurian predominance is also seen in the later stages of the Cretaceous of Egypt (Lamanna et al., 2017; Sallam et al., 2018), as well as Spain and France (see e.g. Le Loeuff, 1995, 2005; Sanz et al., 1999; Garcia et al., 2010; Díaz et al., 2016; Vila, Sellés & Brusatte, 2016). Moreover, the morphological similarities between the "Kem Kem morphotype" with the cylindrical morphotype from Fox-Amphoux-Métisson in southeastern France (Díaz et al., 2012), and the "Algerian morphotype" with the French taxon *Atsinganosaurus* and the morphotype B from Lo Hueco (Spain) (Díaz, Ortega & Sanz, 2014) show a close affinity between Cenomanian and Campanian/Maastrichtian North African and Campanian Maastrichtian Southern European titanosaurs. In previous studies, landbridges have been proven to exist between North Africa and Italy, forming the ''Apulian route'' (Figure 4, and Canudo et al., 2009).

Moreover, Gheerbrant & Rage (2006) and Canudo et al. (2009) spoke of a possible sporadic land bridge between Laurasia and Gondwana at the end of the Barremian (125 Ma). (Torcida Fernández-Baldor et al., 2011) and (Canudo et al., 2009) claimed that this so called "Apulian Route" (see Figure 4) allowed for the divergence of *Demandasaurus* and *Nigersaurus*. Perhaps this also allowed titanosaurs to interchange between Laurasia and Gondwana.

The discovery of titanosaurian teeth with similar morphologies in the Cenomianian of Algeria (“Algerian morphotype”) and the late Campanian-early Maastrichtian of Spain (morphotype B) and southeastern France (*Atsinganosaurus*) could indicate that this taxon had a Gondwanan origin. However, this hypothesis needs to be taken with caution until postcranial remains are found and described in Algeria and Lo Hueco. This is also the case of the “Kem Kem morphotype” and the cyilindrical morphotype of Fox-Amphoux-Métisson, southeastern France. Besides this, these findings do indicate a palaeobiogeographical relationship between the Northafrican and Iberoarmorican titanosaurian faunas from the Late Cretaceous, as previously stated (Fanti et al., 2015; Dal Sasso et al., 2016; Sallam et al., 2018).

The presence of a possible rebbachisaurid (BSPG 1993 IX 2B) would be unusual, given the titanosaurian predominance, however, rebbachisaurids are reported from Morocco (Mannion & Barrett, 2013), as well as the Late Cretaceous of Tunesia (Fanti et al., 2013, 2015).

CONCLUSIONS

Though some of the isolated teeth were not classifiable into higher order clades, and rebbachisaurid presence cannot be confirmed with this research, it has shown that titanosaurs were abundantly present in North Africa during the Cenomanian. Two distinct morphotypes, The Kem Kem morphotype and the Algerian morphotype, are found. The ‘’Kem Kem morphotype’’ is characterised by more pronounced enamel wrinkling, and shows titanosaurian affinities, mainly with a cylindrical tooth morphotype from Southeastern France. The ‘’Algerian morphotype’’ is distinguished by a higher SI and more pronounced medial and distal ridges, and is most similar to *Atsinganosaurus* from France, and tooth morphotype B from Lo Hueco, Spain. Therefore, at least three diffe titanosaurian tooth types are found in this sample.

This shows a mobility of titanosaurs between North Africa and Southern Europe in the late Cretaceous, which is in accordance with previous findings on Cretaceous landbridges between Africa and Europe by means of the Apulian route. This study confirms and emphasizes the necessity to study more material from the Kem Kem and equivalent beds in order to get a more complete picture of the paleoecology of the Late Cretaceous of North Africa, and its possible palaeoecological interrelationships with Europe.

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FIGURE AND TABLE LEGENDS

Figure 1: Geological setting of Kem Kem beds, Morocco, and continental intercalaire, Algeria. Lo Hueco, Spain, and Fox-Amphoux-Métissons are also portrayed. A: stratigraphical column of Kem Kem beds (after Ibrahim et al., 2014). B: stratigraphical column of continental intercalaire, Algeria, (after Forey and Cavin, 2010).

Figure 2. Images of BSPG 1993 IX 331A (A), BSPG 1993 IX 331B (B), BSPG 1993 IX 331C (C), BSPG 1993 IX 313A (D), BSPG 1993 IX 2A (E), BSPG 1993 IX 2B (F), BSPG 1993 IX 2C (G), and BSPG 1993 IX 2D (H) in basal view (1), apical view (2), labial view (3), lingual view (4), distal view (5, and mesial view (6). The scale bar equals 1 cm.

Figure 3. SEM pictures of BSPG 1993 IX 331A in labial (A) and lingual (B) view, BSPG 1993 IX 331B in labial (C) and lingual (D) view, BSPG 1993 IX 313A in labial (E) and lingual (F) view, BSPG 1993 IX 2A in labial (G) and lingual (H) view, BSPG 1993 IX 2B in labial (I) and lingual (J) view, and BSPG 1993 IX 2D in labial (K) and lingual (L) view. The scale bar equals 500µm.

Figure 4. Palaeobiogeographical reconstruction of Northwest Africa and Southern Europe during the Cenomanian (black line) and Campanian-Maastrichtian (grey line) with the matching morphotypes from the Kem Kem beds (A), the Continental Intercalaire (B), Fox-Amphoux-Métissons cylindrical morphotype (C), *Atsinganosaurus* (D), and morphotype B from Lo Hueco (E), after (Diez, Ortega & Sanz 2014; Diez, Tortosa, & Le Loeuff 2013).

TABLE LEGENDS

Table 1. Measurements of each tooth in cm.

Figure 1 (on next page)

Geological setting of Kem Kem beds, Morocco, and continental intercalaire, Algeria. Lo Hueco, Spain, and Fox-Amphoux-Métissons are also portrayed.

A: stratigraphical column of Kem Kem beds (after Ibrahim et al., 2014). B: stratigraphical column of continental intercalaire, Algeria, (after Forey and Cavin, 2010).

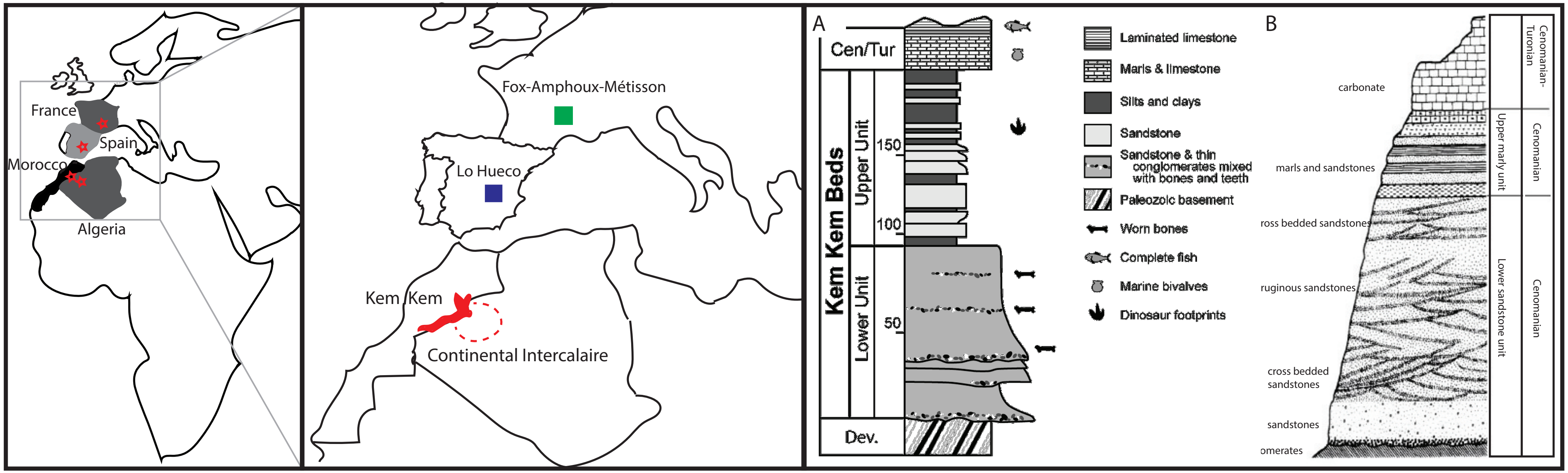
France
Spain
Morocco
Algeria
Fox-Amphoux-Métisson
Lo Hueco
Kem Kem
Continental Intercalaire
A
Cen/Tur
Kem Kem Beds
Upper Unit
Lower Unit
Dev.
150
100
50
Laminated limestone
Marls & limestone
Silts and clays
Sandstone
Sandstone & thin conglomerates mixed with bones and teeth
Paleozoic basement
Worn bones
Complete fish
Marine bivalves
Dinosaur footprints
B
carbonate
marls and sandstones
ross bedded sandstones
ruginous sandstones
cross bedded sandstones
sandstones
omerates
Upper marly unit
Lower sandstone unit
Cenomanian-Turonian
Cenomanian
Cenomanian

Figure 2(on next page)

Images of BSPG 1993 IX 331A (A), BSPG 1993 IX 331B (B), BSPG 1993 IX 331C (C), BSPG 1993 IX 313A (D), BSPG 1993 IX 2A (E), BSPG 1993 IX 2B (F), BSPG 1993 IX 2C (G), and BSPG 1993 IX 2D (H).

In basal view (1), apical view (2), labial view (3), lingual view (4), distal view (5, and mesial view (6). The scale bar equals 1 cm.


A
1
2
3
4
5
6
B
1
2
3
4
5
6
C
1
2
3
4
5
6
D
1
2
3
4
5
6
E
1
2
3
4
5
6
F
1
2
3
4
5
6
G
1
2
3
4
5
6
H
1
2
3
4
5
6

Figure 3(on next page)

SEM pictures of enamel wrinkling.

SEM pictures of enamel wrinkling. BSPG 1993 IX 331A in labial (A) and lingual (B) view, BSPG 1993 IX 331B in labial (C) and lingual (D) view, BSPG 1993 IX 313A in labial (E) and lingual (F) view, BSPG 1993 IX 2A in labial (G) and lingual (H) view, BSPG 1993 IX 2B in labial (I) and lingual (J) view, and BSPG 1993 IX 2D in labial (K) and lingual (L) view. The scale bar equals 500µm.

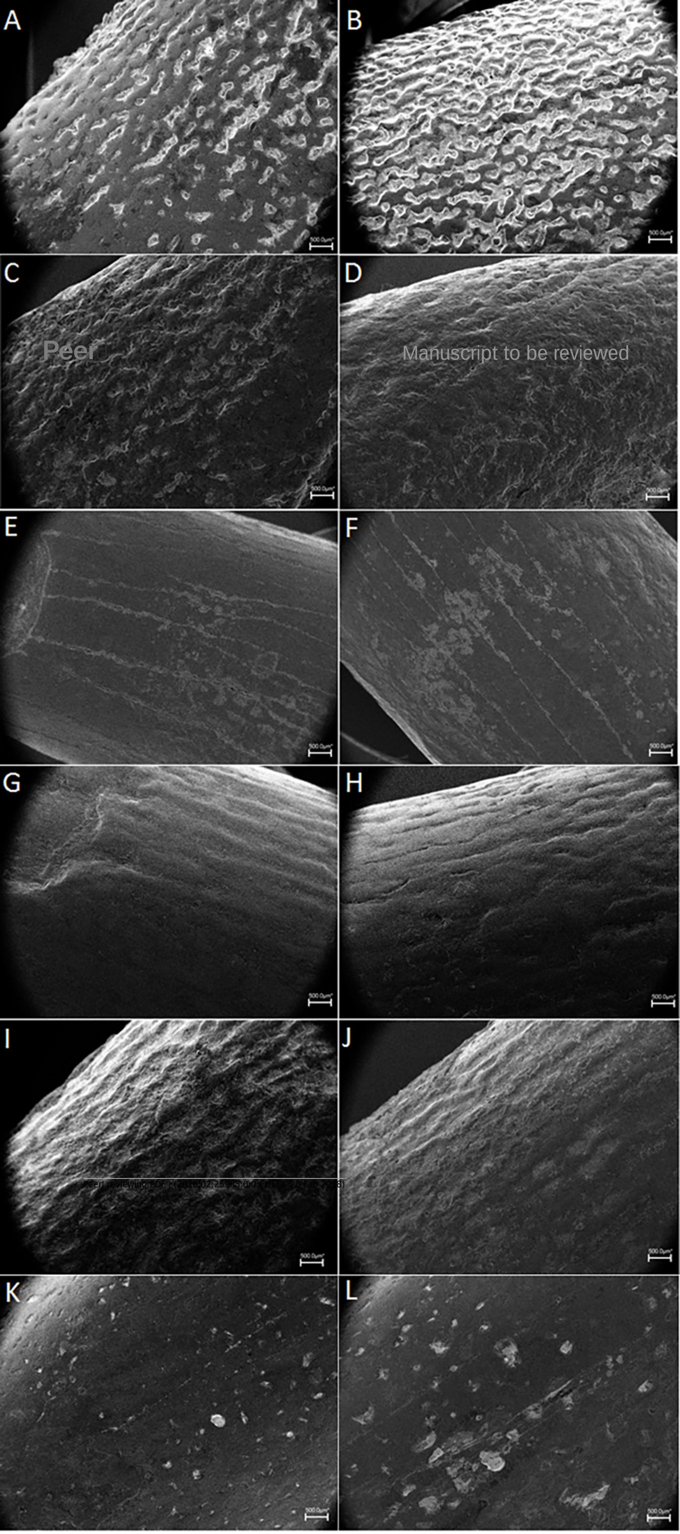
A
B
C
D
E
F
G
H
I
J
K
L

Figure 4 (on next page)

Palaeobiogeographical reconstruction of Northwest Africa and Southern Europe during the Cenomanian (black line) and Campanian-Maastrichtian (grey line).

Matching tooth morphotypes from the Kem Kem beds (A), the Continental Intercalaire (B), Fox-Amphoux-Métissons cylindrical morphotype (C), *Atsinganosaurus* (D), and morphotype B from Lo Hueco (E), after (Diez, Ortega & Sanz 2014; Diez, Tortosa, & Le Loeuff 2013).

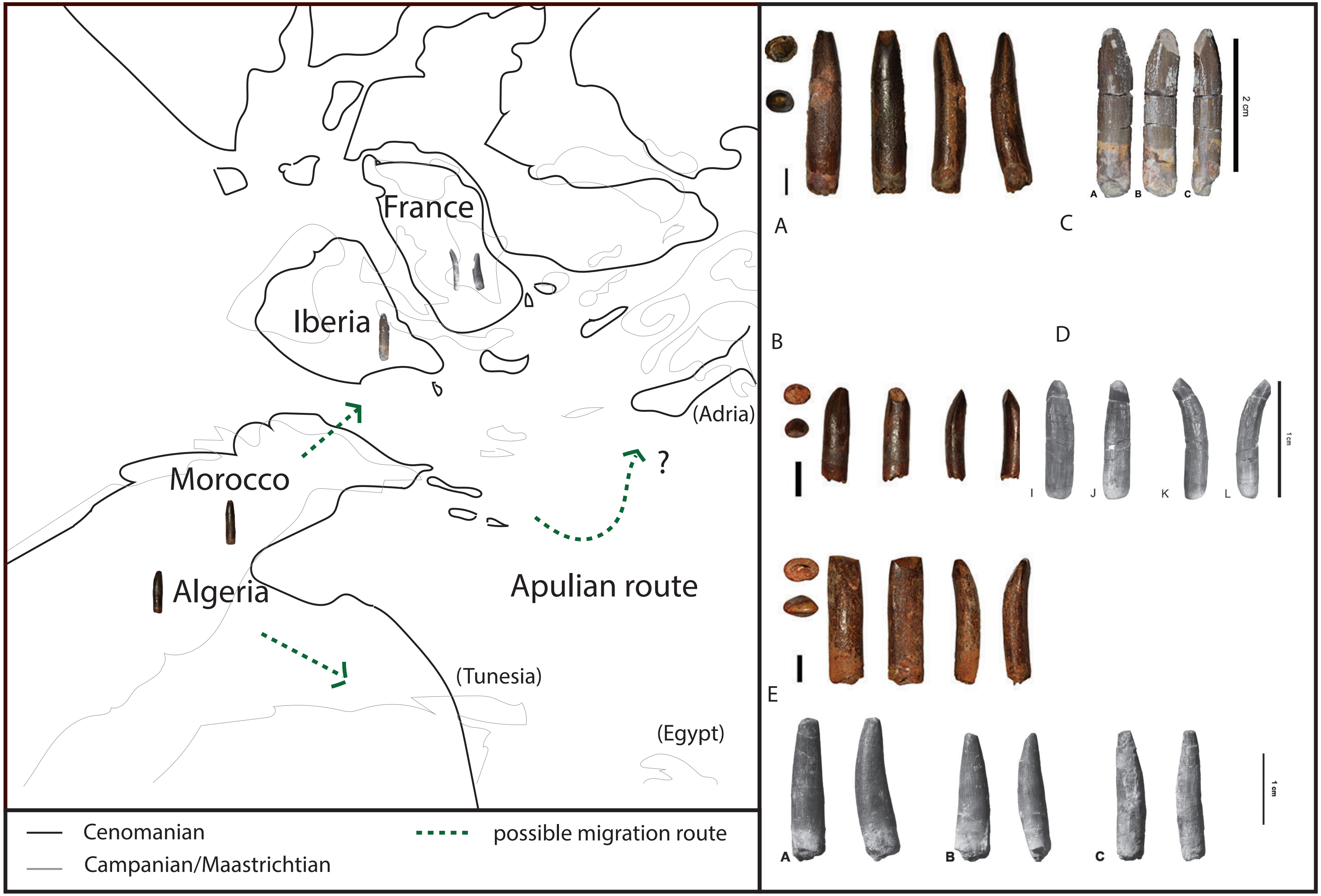
France
Iberia
Morocco
Algeria
Apulian route
(Adria)
?
(Tunesia)
(Egypt)
Cenomanian
Campanian/Maastrichtian
possible migration route
A
B
C
D
E
A
B
C
I
J
K
L
A
B
C

Table 1(on next page)

Measurements of each tooth in cm.

	Apicobasal length	Enamel coverage	Mesiodistal base	Mesiodistal middle	Mesiodistal apex	Labiolingual Base	Labiolingual middle	Labiolingual apex	SI	CI
BSPG 1993 IX 331A	6	5,3	1,2	1,23	0,62	1	1,05	0,4	4,4	0,9
BSPG 1993 IX 331B	4,8	2,4	1,08	1,11	0,45	0,85	0,85	0,3	2,6	0,8
BSPG 1993 IX 331C	3,7	3,7	1	0,9	0,55	0,75	0,75	0,2	3,7	0,8
BSPG 1993 IX 313A	2,75	2,75	0,82	0,82	0,45	0,6	0,62	0,1	3,4	0,8
BSPG 1993 IX 2A	5,1	5	1,05	1,15	0,55	0,85	0,9	0,2	4,4	0,8
BSPG 1993 IX 2B	4,75	4,75	1,3	1,3	1,15	0,9	0,92	0,3	3,7	0,7
BSPG 1993 IX 2C	4,7	-	1	1,15	0,5	0,8	1	0,2	4,1	0,9
BSPG 1993 IX 2D	3,8	3,8	0,95	1,05	0,15	0,65	0,75	0,15	3,6	0,7