ASIAN SAUROPODS IN THE LOWER BARREMIAN (LOWER CRETACEOUS) OF SPAIN?*

José Ignacio CANUDO[1], José Ignacio RUIZ-OMEÑACA[1,2] José Luis BARCO [1,2] y Rafael ROYO TORRES [1,3]

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Abstract

We describe here three sauropod teeth from the Lower Cretaceous (lower Barremian) of La Cantalera (Josa, Teruel, Spain). The teeth are spoon-shaped with a lingual cingulum-like structure. The general morphology is closer to Camarasauridae, but the presence of cingular structure indicates a different group, more derived that this family. The problematic genus *Euhelopus* from the Upper Jurassic or Lower Cretaceous of China and some isolated teeth from the Lower Cretaceous of China, Russia and Mongolia are the only sauropods with similar teeth. We suggest the presence of a sauropod group in Asian and European Lower Cretaceous. This group is included in the family Euhelopodidae and the Titanosauriformes clade. This European - Asian Lower Cretaceous geographic connection has been previously observed with mammals and ornithopod dinosaurs.

Key words: Dinosauria. Sauropoda. Titanosauriformes. Lower Cretaceous. Lower Barremian. Spain.

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[1]Museo Paleontológico y Área de Paleontología. Facultad de Ciencias. Universidad de Zaragoza. 50009 Zaragoza. España. jicanudo@posta.unizar.es/ jigruiz@posta.unizar.es
[2]Paleoymás. Nuestra Señora del Salz, 4, local, 50017 Zaragoza. España. jlbarco@posta.unizar.es
[3]Fundación Conjunto Paleontológico de Teruel. Edificio Dinópolis, 44002 Teruel. España. Dinopolis@navegalia.com

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Introduction

During the Lower Cretaceous one can recognize two large paleobiogeographic continental units based on their tetrapod content: Gondwana in the southern hemisphere, with significant elements in common between Africa and South America (Calvo and Salgado, 1996); and Laurasia in the northern hemisphere consisting of Asia, Europe and North America (Le Loeuff, 1997; Norman, 1998). The taxa in common between Asia and Europe pertain to diverse groups of tetrapods, from large dinosaurs like *Iguanodon bernissartensis* (Ornithopoda) present in Europe and Mongolia (Norman, 1998), to small mammals, like *Gobiconodon* "the traveler" (Sigogneau-Russell, 1991), an amphilestid ("Triconodontidae") present in the upper Barremian of Spain (Cuenca-Bescós and Canudo, 1999) and Mongolia (Kielan-Jaworoska and Dashezeveg, 1998). In this work we describe new remains from a group of sauropod dinosaurs of uncertain systematic affinity, whose isolated remains have been found in the Lower Cretaceous of Asia and Europe. The remains consist of isolated teeth found in lower Barremian strata from La Cantalera (Teruel, Spain).

The isolated teeth of sauropods have often been employed systematically to the family level, and in practice are not used for generic or specific determination. Nevertheless, there have been many genera described solely on the basis of isolated teeth; these are usually considered "*nomina dubia*" (see McIntosh, 1990). There is an apparent difficulty to link isolated teeth with skeletal remains owing to the scarcity of complete exemplars. This lack of information impedes, but does not preclude, the use of sauropod teeth to make generic determinations. Traditionally, the teeth of sauropods have been separated into two morphological groups: "spoon-shaped", as in *Camarasaurus* Cope and "pencil-shaped", as in *Diplodocus* Marsh (McIntosh, 1990). However, this simplification does not encompass the morphological complexity present in the teeth, so Calvo (1994) differentiated four distinct morphologies, each an adaptation to a different feeding strategy. The objective of the present work is to study teeth found at the locality of La Cantalera, discuss in general the morphology of "spoon-shaped" teeth of some Lower Cretaceous sauropods, and their possible paleobiogeographic implications.

Geologic Framework

The locality of La Cantalera is found in the central part of the Iberian geological system, near the locality of Josa (Teruel, Spain) (figure 1). It can be accessed from the local highway linking the towns of Cortes de Aragón and Josa. Before arriving at this locality it is necessary to take a road toward the La Cantalera river that ends at the locality. Geologically, the area is in the sedimentary Oliete Basin, which is composed of Lower Cretaceous (lower Barremian to Albian) sediments north of the province of Teruel. The rocks at the locality consist of gray clays of the Cabezo Gordo Member of the Margas Formation and Blesa limestones (sensu Canerot et al., 1982). The presence of the charophyte *Atopochara trivolvis triquetra* Grambast at La Cantalera (Ruiz-Omeñaca et al., 1997) indicates a lower Barremian age for the locality (Martín-Closas,

2000). La Cantalera is exceptionally rich in disarticulated vertebrate remains (table 1), in particular shed ornithopod teeth. This abundance, along with study of coprolites and the sedimentology of La Cantalera, yields a paleoenvironmental interpretation of a shallow lake with abundant charophytes that served as a feeding site for ornithopods (Ruiz-Omeñaca et al., 1997).

Sauropod teeth are a minor component of the finds at La Cantalera. More than 250 dinosaur teeth have been recognized, from which only two teeth and the fragment of a third are from sauropods.

Systematic Paleontology

Class DINOSAURIA Owen, 1842
Order SAURISCHIA Seeley, 1888
Infraorder SAUROPODA Marsh, 1878
TITANOSAURIFORMES Salgado, Coria and Calvo, 1997
Family EUHELOPODIDAE Romer, 1956
Euhelopodidae indet.

Material. The studied material can be found in the Museo Paleontológico de la Universidad de Zaragoza (MPZ) with specimen numbers MPZ 97/464, MPZ 97/465 and MPZ 01/206. Measurements can be found in table 2. MPZ 97/464 is a tooth with a complete crown (figure 2), except for a fragment of enamel on its labial face near its apex. The tooth is fractured along the neck that separates the root from the crown, preserving only part of the root. MPZ 97/465 is a fragment of the lingual part of the crown. MPZ 01/206 is a complete tooth.

Description. MPZ 97/464 is a left functional maxillary tooth. It is generally spoon-shaped, as exemplified by the ratio of the maximum breadth and labiolingual width measured at the base of the crown (0.91). In lingual view (figure 2.B) the crown has two different parts: the apex and the base of the crown are separated by a belt of cusps. The entire crown has enamel, which is differentiated at the apex; the labial side has a greater development than the lingual. The enamel of the apex is smooth and the base of the crown is ornamented. On the lingual face the ornamentation is better developed in the central part of the tooth, where there are small tubercles aligned mesiodistally with an anastomosing pattern. On the mesial and distal borders there is a similar ornamentation, but smaller in size and with the orientation less evident. On the labial face the ornamentation is distributed in a similar manner (figure 2.D).

The labial face is convex (figure 2.D), and near the mesial and distal borders there are two longitudinal sulci that extend parallel to both borders. They are better developed towards the base of the crown than at the apex, where they end much reduced in size. The lingual face is more complex (figure 2.B). The apex is concave with a typical spoon-shaped morphology. In the central part extends a gentle crest that ends at the extreme of the apex, and which delimits two

longitudinal grooves (mesial and distal). The crest is curved, extending parallel to the rest of the crown. The base of the crown is convex, although less than on the labial side. Consequently, the section of the base of the crown is elliptical with the development of a sharper contour at the mesial and distal extremes, forming gentle curves (figures 2.F and 3.F). On the base of the crown, the central crest unites to the other two pointed crests, which are developed on the mesial and distal edges of the tooth. Thus, these three crests form a trident morphology, which forms an incipient cingulum (figures 2.B and 3.B). The extremes of the mesial and distal crests end along a belt of cusps, better developed distally (figures 2.B and 3.B).

The mesial and distal edges of the crown are sharp and have wear facets in which the enamel has disappeared, exposing dentine. These wear facets form a 'V'. The distal facet is better developed and progressively decreases in size until disappearing at the widest part of the crown (figures 2.A and 3.A) The distal part of the facet is slightly wider at its basal part. The distal part of the cingular cusp has an elliptical wear facet that is elongated mesiodistally. Both wear facets are angled towards the lingual side, varying in angle with respect to the apical/adapical axis. The largest angle measured is at the apex, where it reaches 50 degrees. The dentine and enamel of the apex have a uniform wear. The separation of enamel from the dentine on the mesial wear facet is abrupt at the labial side, which could be interpreted as microwear. These are even more apparent on the distal wear facet, where the dentine preserves an additional incision that extends parallel to the mesiodistal length of the wear facet (figure 2.B). The tooth MPZ 97/464 has two attritional surfaces. One is found in a disto-lingual position, immediately in contact with the wear facet (figures 2.B and 2.C). The other is found in a mesio-labial position, also in contact with the wear facet (figure 2.A).

MPZ 97/465 is a lingual fragment of crown of a tooth that was larger than MPZ 97/464 (table 2), considering the preserved section. It has an attritional surface where the dentine outcrops (figure 4). Comparison with MPZ 97/464 indicates that this surface coincides with a cingular cusp that is totally worn. MPZ 97/464 has an ornamentation of anastomosing tubercles similar to MPZ 97/464, but is better developed (figure 4). These tubercles have a slight mesiodistal orientation. In the area where this ornamentation ends lies the beginning of some smooth crests that we interpret as being arranged in an apical-adapical direction.

MPZ 01/206 is a left maxillary tooth or right mandibular tooth. It is generally spoon-shaped, with a marked crest at its apical extreme in lingual view (figure 5.B). The crown and the root are separated by a neck only visible in labial view (figure 5.D). The enamel is fine and is not ornamented. This tooth is more asymmetric than MPZ 97/464; in its mesial edge, the widest part of the crown corresponds to the part medial to the apex; but at the distal border the widest part is near the neck of the tooth (figures 5.B, D). Another significant difference is that MPZ 01/206 is more compressed labiolingually, with much sharper borders (figures 5.A, C). The thin enamel is difficult to differentiate from the dentine, giving the tooth a uniform appearance. The root is not

totally formed (figure 5.F). MPZ 01/206 has an almost imperceptible and small attritional surface disto-lingually (figure 5.B), and lacks wear facets.

Discussion

The taxonomic assignment of the teeth of the sauropod of La Cantalera is based on tooth MPZ 97/464. We consider the fragment 97/465, with similar ornamentation, cingular cusps and wear surfaces pertains to the same taxon. MPZ 01/206 is similar in general morphology to MPZ 97/465, but with less marked development of the morphological characters, so we interpret it as a replacement tooth from the same taxon (Ruiz-Omeñaca, in press). The orientation of the isolated teeth of sauropods is usually complicated, but using the general morphology and the wear facets the tooth can be oriented in some cases, as with MPZ 97/464. The "spoon-shaped" teeth that curve distally on both the lingual and labial faces are easy to identify (figure 2). The tooth is asymmetric with respect to an anteroposterior plane, so we consider it to be a lateral tooth (maxillary or mandibular), in labial view it appears as if the apex is angled slightly towards the side (figure 2) that we consider distal. In this manner MPZ 97/464 could be a left maxillary or right mandibular tooth. To determine this more precisely, we will use the wear facets. The facets in MPZ 97/464 can be explained by tooth to tooth contact (Calvo, 1994) In Camarasauromorpha maxillary teeth touch the labial side of the mandibular teeth, so the wear facet of the upper teeth is angled toward the lingual side. In contrast, mandibular teeth have wear facets angled labially (see Calvo, 1994). Since in MPZ 97/464 the wear facet is angled lingually, we have interpreted it as a left maxillary tooth.

The presence and position of the attritional wear surfaces implies that the teeth of the La Cantalera sauropod were imbricated. Using the skull of *Camarasaurus lentus* (Marsh) as a model, as figured in Wilson and Sereno (1998), we attempted to situate the attritional surfaces. As such, the premaxillary teeth of *Camarasaurus* contact one another on their mesial and distal borders, but the maxillary and mandibular teeth are imbricated. This contact locates the attritional surfaces in a mesio-labial and disto-lingual location in the maxillary and mandibular teeth (figure 2). The attritional surfaces indicate that the teeth were in contact, and mark the extent of occlusion. The 'V-shaped' wear facets of MPZ 97/464 indicate that it had an interdigitated occlusion (Wilson and Sereno, 1998), which is in line with the model of "sauropod with complete occlusion" proposed by Calvo (1994) for sauropods like *Camarasaurus lentus*. The La Cantalera sauropod differs from Camarasaurus in the better development of wear facets, which suggests better developed occlusion.

MPZ 97/464 indicates that the La Cantalera sauropod used two movements during mastication. The first is marked by the occlusion of the teeth in a vertical motion of closing and opening the mouth, which can be observed in the wear facets located on the superior part of the tooth and which extend parallel to the mesial and distal borders. The second can be deduced due to the differentiation of enamel at the apex, which is best developed on the labial side. This

differentiation is explained by the movement of the mandible mediolaterally. This pattern seems like that proposed by Calvo (1994) for the mastication of *Camarasaurus*, and is typical of sauropods with a certain feeding style. Besides, MPZ 97/464 has an incision (figure 2.B), possibly the result of contact with hard food, which indicates a certain amount of oral processing before ingestion.

As mentioned above, MPZ 97/464 is considered a shed functional maxillary tooth, which has a clear break across the crown and the root (figure 2.D). This tooth does not present any hint of resorption as are typical of the abundant teeth of La Cantalera (Ruiz-Omeñaca et al., 1997). It has well developed wear facets, but had not reached state 6 of White (1958), which would have occurred before the shedding of the tooth.

Imbricated, spoon-shaped mandibular and maxillary teeth,with with a half-moon shaped cross section or at least a 'D-shape' distally, wrinkled enamel, and V-shaped wear facets are characters present in eusauropods (Wilson and Sereno, 1998). The La Cantalera sauropod differs from derived eusauropod groups such as diplodocoids, brachiosaurids and titanosaurs, which have developed subcylindrical or cone-shaped crowns, lacking tooth imbrication and able to form elliptical wear facets (McIntosh, 1990; Calvo, 1994; Wilson and Sereno, 1998). The general shape, ornamentation, and the presence of a cingulum in the La Cantalera sauropod relates them to teeth identified as Camarasauridae indet. Form A, of the lower Barremian of Galve (Sanz et al., 1987). In a preliminary report we considered the La Cantalera sauropod as Camarasauridae indet. (Ruiz-Omeñaca et al., 1997). The inclusion within this family seems adequate, as they compare well with the teeth of Camarasaurus from the Upper Jurassic of the United States in their general spoon shape (see figures in Ostrom and McIntosh, 1966) and the presence of two longitudinal grooves on the mesial and distal ends (Russell and Zheng, 1993). Still, is it correct to consider all of the Lower Cretaceous sauropods with "spoon-shaped" teeth to be camarasaurids?

Spoon-shaped sauropod teeth in the Cretaceous

Aside from the classic division of teeth into "spoon-shaped" and "pencil-shaped", there have been broad systematic proposals, feeding mechanisms and related diets (see discussion in Calvo, 1994). "Spoon-shaped teeth" of the uppermost Jurassic and Cretaceous have been generally attributed to the family Camarasauridae, and as we have seen above, this has been the criterion used to study isolated teeth in the Barremian of the Iberian Cordillera (Sanz et al., 1987; Ruiz-Omeñaca et al., 1997).

The tooth character "spoon-shaped" is found in distinct sauropod families. Besides the camarasaurids, it is common in primitive sauropods, like *Mamenchisaurus sinocanadorum* Russell and Zheng from the Upper Jurassic of China, and is also present in sauropods of the Lower Cretaceous, such as *Jobaria tiguidensis* Sereno et al. from the Neocomian of Niger. The genus *Jobaria* is a primitive eusauropod well differentiated from more derived sauropods such as

camarasaurids. Its teeth are significantly primitive in possessing marginal denticles and a crown that is distinctly expanded from the root (Wilson and Sereno, 1998; Sereno et al., 1999), characters that distinguish them from the teeth of camarasaurids. More relevant to our discussion is *Euhelopus zdanskyi* (Wiman) from the Jurassic to Lower Cretaceous of China (for discussion of the age consult Dong, 1995 and Lucas and Estep, 1998). This genus has been considered a camarasaurid for having spatulate or "spoon-shaped" teeth, among other characters (Mateer and McIntosh, 1983), notwithstanding modern systematic revisions that have separated it from this family (Wilson and Sereno, 1998; Upchurch, 1998). Therefore, there clearly would have been sauropods with "spoon-shaped" teeth in the Lower Cretaceous that are not camarasaurids, but are there camarasaurids in the Lower Cretaceous?

As we mentioned for *Euhelopus*, in modern revisions there has been a disappearance of Lower Cretaceous genera attributed to Camarasauridae (Wilson and Sereno, 1998; Upchurch, 1998), with only *Aragosaurus ischiaticus* Sanz et al. from the upper Hauterivian of Teruel remaining (Calvo, 1994; Upchurch, 1998). Because the presence of a lateral bulge on the proximal extreme of the femur excludes *Aragosaurus* from this family (Canudo et al., 2001), there are not, in this moment, valid taxa attributed to Camarasauridae in the Lower Cretaceous. Nonetheless, there are possible "camarasaurids" in the Lower Cretaceous, for example a tooth that could pertain to a camarasaurid that is the holotype of "*Oplosaurus armatus*" Gervais from the Wessex Formation (Barremian) of the United Kingdon (Naish and Martill, 2001). Although tentatively it has been linked to brachiosaurids (McIntosh, 1990), it differs from them in lacking a "compressed-cone" morphology (Calvo, 1994). Its spoon shape is similar to that of *Camarasaurus*, from which it only differs in having less developed enamel wrinkling. In sum, in the Lower Cretaceous there are other sauropods with "spoon-shaped" teeth besides camarasaurids, which suggests a revision of the assignment of the La Cantalera sauropod to this family.

Asian dinosaurs in the Barremian of Spain?

The question that we pose is: can we differentiate "spoon-shaped" teeth of the La Cantalera sauropod from those of Camarasauridae of the Upper Jurassic? The teeth of the genus *Camarasaurus* are characterized by having a spatulate ("spoon-shaped") crown and wrinkled enamel formed by longitudinal striations (White, 1958). The teeth of the La Cantalera sauropod seem like those of *Camarasaurus*, but they have two significant differences: the ornamentation is less well developed, and it has a cingulum on its lingual edge. The first fits perfectly within common variability, including ontogenetic variation. However, the cingular cusps are an evolutionary novelty that in these sauropods could be significant in differentiating a group closely related to, but distinct from, camarasaurids. Teeth of sauropods with cingular cusps aside from those from La Cantalera and those from Galve (Sanz et al., 1987) have been described from the Lower Cretaceous of Asia. The teeth of the genus *Euhelopus* are characterized by the

presence of cingular cusps (Wiman, 1929; Martin-Rolland, 1999; Starkov, 1999), also the teeth of *Asiatosaurus mongoliensis* Osborn (Aptian-Albian of Mongolia) have ornamentation, a cingulum structure, and wear facets (Osborn, 1924) similar to those of the La Cantalera sauropod. The systematic position of *Euhelopus* and other related sauropods is problematic. The genus *Euhelopus* has been used in recent phylogenetic proposals with contradictory results. According to Wilson and Sereno (1998) it is the sister taxon of Titanosauria, whereas for other investigators it is a member of exclusively Asian sauropods well represented in the Jurassic. This second hypothesis is reflected in Upchurch (1998) who places *Euhelopus* with primitive sauropods like *Mamenchisaurus* Young, totally separated from Titanosauria. If the analysis is only restricted to teeth, it would seem difficult to situate *Euhelopus* in one of these groups. Sauropods like *Mamenchisaurus* have primitive teeth that have marginal denticles and a wider crown labiolingually (Russell and Zheng, 1993) than in *Euhelopus*. Titanosaurs have cylindrical teeth, although more primitive species like *Malawisaurus dixeyi* Haughton have a lightly spatulate tooth (Jacobs et al., 1993). Using only teeth makes it difficult to distinguish the two phylogenetic interpretations and it seems that *Euhelopus* does not fit well with either of the two hypotheses.

Osborn (1924) described *Asiatosaurus* based on two isolated teeth (holotype and paratype) and, as with other sauropods defined on isolated teeth, McIntosh (1990) considered *Asiatosaurus* a "*nomen dubium*." However, Calvo (1996) affirmed the validity of this taxon and noted that it should be included in Titanosauriformes; as Calvo (1994) included it in sauropods with "compressed-cone-chisel" shaped teeth like in *Brachiosaurus*. However, *Asiatosaurus* has wear facets (see figures in Osborn, 1924), which implies an interdigitating occlusion similar that found in spoon-shaped teeth. In addition, the presence of cingular cusps relates these teeth to those of the La Cantalera sauropod as well as those of *Euhelopus*. Isolated teeth similar to those of *Asiatosaurus* and *Euhelopus*, some defined as *Chiayusaurus,* a synonym of *Asiatosaurus* following Calvo (1996), also seem to be present in the Cretaceous of China and Russia (McIntosh, 1990; Starkov, 1999), which suggests that this group of sauropods was already widely distributed in Asia by the lowest Cretaceous.

Following Salgado et al. (1997), the camarasaurids are included in the clade Camarasauromorpha, which also contains another clade, Titanosauriformes, with *Brachiosaurus* as the most basal taxon. Among the evolutionary novelties proposed by Salgado et al. (1997), there are none related to teeth. At present there are no described titanosauriform genera with "spoon-shaped" teeth, and the most primitive known Titanosauriformes have "cone-shaped" teeth as in *Brachiosaurus* and *Aragosaurus* (Calvo, 1994; Sanz et al., 1987; Canudo et al., 2001). However, it cannot be discounted that other titanosauriformes could have had "spoon-shaped" teeth. One argument to consider that some titanosauriforms could have had teeth of this shape is found in the primitive titanosaur *Malawisaurus* from the Lower Cretaceous of Malawi. This sauropod has elongate teeth as in titanosaurids, put the apex maintains a "spoon-shape" (Jacobs

et al., 1993). This shape could indicate an intermediate state between "spoon-shaped" and the cylindrical teeth of derived titanosaurs of the Upper Cretaceous.

Wilson (1999:93) considered the presence of well developed lingual cingular cusps to be an autapomorphy of *Euhelopus* ("well developed crown buttresses on lingual crown surface"). We assign the teeth of the La Cantalera sauropod to Euhelopodidae indet., and consider the presence of cingular cusps as an autapomorphy of Euhelopodidae, a family composed of Euhelopus, *Asiatosaurus* (= *Chiayusaurus*) and the La Cantalera sauropod. Very recently a new euhelopodid from the Lower Cretaceous of Korea has been described, *Pukyongosaurus* (Dong et al., 2001). This indicates that euhelopodids were already widely distributed by the Early Cretaceous.

Other sauropods that have been considered euhelopodids (see Upchurch, 1995, Martin-Rolland, 1999) have more primitive teeth than the Euhelopodidae mentioned above. In those taxa, the teeth are more mesiodistally expanded, without cingular cusps, and sometimes have denticles. These sauropods do not pertain to Euhelopodidae from this point of view. The synonomy of Euhelopodinae Romer with Mamenchisaurinae Young and Chao or with Shunosaurinae McIntosh seems uncertain, since Euhelopodidae is a family of Titanosauriformes, whereas Mamenchisaurinae (*Mamenchisaurus* Young, *Omeisaurus* Young, *Zigongosaurus* Hou, Chao and Chu), Shunosaurinae (*Datousaurus* Dong and Tang, *Shunosaurus* Dong, Zhou and Zhang) and other Jurassic Chinese sauropods (*Bellusaurus* Dong, *Klamelisaurus* Zhao, *Tienshanosaurus* Young, *Zizhongosaurus* Dong, Zhou and Zhang) would remain outside of Titanosauriformes (Salgado et al., 1997; Wilson and Sereno, 1998).

Conclusions

The presence of a cingular structure links the teeth of the La Cantalera sauropod (lower Barremian of Spain) with some sauropods from the Jurassic-Cretaceous boundary to Lower Cretaceous of Asia. Their systematic position is problematic. While waiting to recover postcranial material, we can assign the teeth of the La Cantalera sauropod to the family Euhelopodidae, which is included in the clade Titanosauriformes. The hypothesis of this work that comes from this observation is that in the Early Cretaceous there was a group of sauropods distributed in Europe and Asia that has a dental morphology similar to but more derived than those of the camarasaurids of the Late Jurassic. Euhelopodidae might contain *Asiatosaurus* (= *Chiayusaurus*), *Euhelopus*, and the La Cantalera sauropod.

Acknowledgments, Bibliography, Figures, Tables and Captions

See original text.