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Research paper

Basal titanosauriform (Dinosauria, Sauropoda) teeth from the Lower Cretaceous Yixian Formation of Liaoning Province, China

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Abstract

The Yixian Formation of Liaoning Province, People's Republic of China has yielded a diverse fauna of non-avian dinosaurs, but is dominated by small-bodied taxa. Here, we describe a series of isolated teeth from the Lujiatun Beds of the formation that are referable to a basal titanosauriform sauropod. Some of the teeth possess a distinctive circular boss on the lingual surface, which suggests that they are referable to cf. *Euhelopus* sp. This identification provides some additional support for biostratigraphical correlations between the Jehol Group and the Mengyin Formation of Shandong Province that suggest an Early Cretaceous age for the latter unit. Moreover, the titanosauriform affinities of the teeth provide further evidence for the dominance of this sauropod clade in eastern Asia during the Cretaceous.
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Keywords: Yixian Formation; Sauropoda; Lower Cretaceous; Titanosauriformes

1. Introduction

The Jehol Group consists of the Jiufotang, Yixian and Dabeigou (?) Formations and crops out in Liaoning Province and adjacent areas of northeastern China (Chen et al., 1980; Chen, 1988; Wang and Zhou, 2003). Although biostratigraphical correlations initially indicated a Late Jurassic age for these units, recently obtained radiometric dates and reinterpretation of the biostratigraphical evidence indicate that the group was deposited during the late Early Cretaceous (Swisher et al., 1999, 2002; Barrett, 2000; Smith et al., 2001; Wang et al., 2001; He et al., 2004, 2006a,b). The past decade has witnessed an explosion of interest in the Jehol Group, due largely to the discovery of non-avian dinosaur specimens that provide unequivocal evidence for the presence of feathers and 'protofeathers' (e.g. Chen et al., 1998). As a result of this increased collection and research activity, the Jehol Group has yielded a rich and diverse assemblage of plant, invertebrate and vertebrate taxa that has been dubbed the Jehol Biota (e.g. Chang et al., 2003; Zhou et al., 2003). The most productive vertebrate-bearing horizons within the Jehol Group pertain to the Yixian Formation (Zhou, 2006).

Non-avian dinosaurs were important components of all Jehol Group ecosystems, often representing the dominant terrestrial vertebrate taxa in terms of abundance and species richness (reviewed in Xu and Norell, 2006). To date, 24 species have been named from the Jehol

Abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; PMU, Palaeontological Museum, University of Uppsala, Uppsala

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Biota, representing most major clades of coelurosaurian theropods (compsognathids, a tyrannosauroid, oviraptorosaurians, a therizinosauroid, an ornithomimosaurian, dromaeosaurids, troodontids and several taxa of uncertain phylogenetic position) and various ornithischians (including an ankylosaur, an ornithopod, a basal ornithischian and a diversity of basal ceratopsians). Some taxa, such as the basal ceratopsian *Psittacosaurus*, are represented by hundreds, or even thousands, of individuals (Xu and Norell, 2006). However, sauropod dinosaurs are poorly represented in the fauna: the occurrence of indeterminate sauropod material has been noted in faunal lists for the Yixian (e.g. Wang et al., 1998, 1999, 2000a,b) and Jiufotang (Xu and Norell, 2006) Formations, but none of this material has been formally described. Xu and Norell (2006) noted that this material consists largely of isolated teeth and fragmentary postcranial elements and postulated that at least some of this material may be referable to Titanosauria: however, they did not figure or discuss any of these specimens. Here, we provide the first description of sauropod dinosaur material from the Yixian Formation, on the basis of a series of isolated teeth. Several of these teeth exhibit character states that allow them to be referred to the Titanosauriformes: the palaeobiogeographical and taphonomic implications of these specimens are also discussed, below.

2. Geological setting

The sauropod teeth were discovered at the Lujiatun locality, which is situated to the southwest of Shangyuan, Beipiao, Liaoning Province (N41°36′25.4″; E120°54′40.8″). All of the teeth were recovered as isolated elements and were not discovered in association with each other. The specimens pertain to the Lujiatun Beds (formerly known as Member 1 of the Daohugou Beds of the Yixian Formation), which reach a thickness of up to 40 m and form the lowermost part of the Yixian Formation in this region (Wang et al., 2000a,b; Wang and Zhou, 2003). This horizon consists of unstructured tuffaceous conglomerates, sandstones and silty mudstones that were deposited in an alluvial environment (Wang and Zhou, 2003). Radiometric dates obtained from $^{40}Ar/^{39}Ar$ step heating analyses on bulk K-feldspars from the main fossil-bearing tuffaceous layer within the Lujiatun Beds provide a weighted mean age of 123.2 ± 1.0 Ma (He et al., 2006a,b), indicating deposition during the lower part of the Aptian stage of the Early Cretaceous (Gradstein et al., 2004). Vertebrate material from the Lujiatun Beds lacks the spectacular soft-tissue preservation that characterises specimens from other horizons within the Yixian Formation (e.g. the Jianshangou and Dawangzhangzi beds). However, skeletal material from the Lujiatun deposits is usually articulated and three-dimensionally preserved, in comparison with the two-dimensional preservation of specimens from other members of the Yixian Formation (Zhou, 2006).

3. Description of teeth

Remains of 10 partial sauropod tooth crowns (IVPP V15010.1–10) have been recovered from Lujiatun to date. In most cases only the apicalmost part of the crown is present. Three of the teeth (IVPP V15010.8–10) are badly shattered, yield little information and are not considered further herein. It is not possible to determine whether the teeth pertain to the premaxilla, maxilla or dentary.

The most complete tooth (IVPP V15010.1) is apicobasally elongate, with a slenderness index (SI: Upchurch, 1998) of at least 3.11 (Fig. 1A and F). The crown is mesiodistally narrow with the mesial and distal margins of the tooth extending parallel to each other before converging apically. Wrinkled enamel covers most of the labial and lingual surfaces, but the enamel close to the crown apex is smooth and unwrinkled. Although the tooth lacks recurvature, the apex is slightly lingually inclined. The lingual surface of the crown is mesiodistally concave, while the labial surface is strongly convex, resulting in a D-shaped transverse cross-section. This cross-section is asymmetrical in apical view, with the apex of the 'D' situated closer to one crown margin (mesial?) than the other. As a result, the mesial (?) part of the labial surface is angled away more steeply from the mesiodistal axis of the tooth crown (at a tangent of approximately 75°) than the distal (?) part (with a tangent of 45°). Labial grooves, lingual ridges and denticles are absent. Large, high-angled mesial and distal wear facets are present on the lingual surface of the crown, which converge apically and are continuous around the tip of the tooth. The base of the crown has a sub-circular cross-section. Three other teeth in the sample (IVPP V15010.2 and V15010.6–7) are almost identical to IVPP V15010.1, but are more poorly preserved. There is some indication of faint labial grooves in IVPP V15010.2 and of a lingual ridge, but all of these features are very subtle and could be artefacts caused by crushing (Fig. 1B and G). Roots are absent from all of these teeth.

IVPP V15010.3 has a much stouter crown, with an SI of approximately 1.90 (Fig. 1C and H). However, the tooth is very heavily worn and this value may considerably underestimate the original crown height. In most

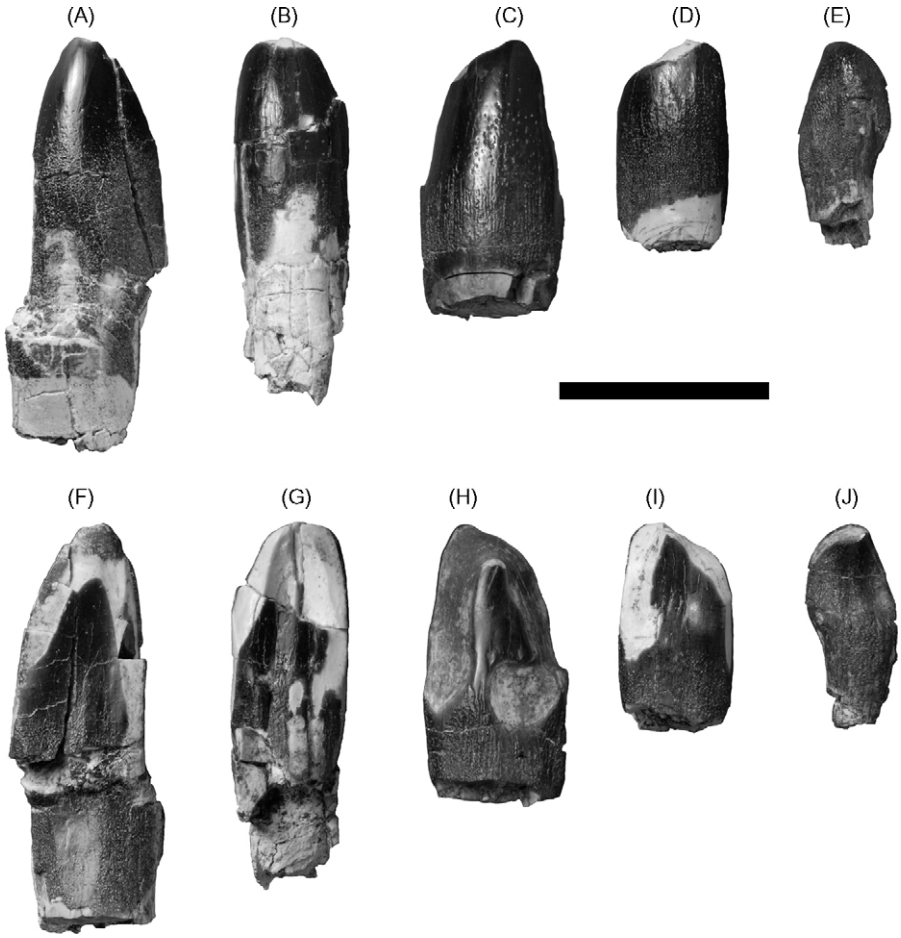

Fig. 1. Isolated teeth of cf. *Euhelopus* sp. from the Lujiatun Beds of the Yixian Formation (Aptian) of Lujiatun, Liaoning Province in labial (A–E) and lingual (F–J) views. (A and F) IVPP V15010.1, (B and G) V15010.2, (C and H) V15010.3 and (D and I) V15010.4. Note the rounded boss situated just below the distal (?) wear facet in lingual view (E and J) V15010.5. Scale bar = 30 mm.

other respects this tooth is similar to IVPP V15010.1–2 and V15010.6–7. However, IVPP V15010.3 differs from the former in the following ways: mesial and distal labial grooves are present in IVPP V15010.3, though they are weakly developed; the D-shaped cross-section of IVPP V15010.3 is more symmetrical than in the aforementioned teeth; and the wear facets are more extensive, leading to the development of a 'shoulder' (cf. Upchurch and Barrett, 2000) on the distal (?) crown margin. However, the differences in wear may simply be indicative of a longer functional life for the tooth crown. A very small portion of root is preserved: it has a sub-circular cross-section and demonstrates that the crown was not mesiodistally expanded relative to the root. IVPP V15010.4 (Fig. 1D and I) is similar to V15010.3, but the former possesses a raised sub-circular swelling or boss that is situated on the unworn part of the lingual crown surface close to the distal (?) margin (Fig. 1I). A similar boss is present in an analogous position on IVPP V15010.7.

The final tooth, IVPP V15010.5, represents a partial crown that has been broken basally (Fig. 1E and J). It has a minimum SI of 2.27. It differs from the other teeth in several respects. A lingual ridge is present in IVPP V15010.5, which extends apicobasally along the lingual concavity. Moreover, wear is present, but is only developed along the mesial crown margin. Most importantly, the apical part of the crown is mesiodistally expanded with respect to the more basal section and the crown apex is curved slightly distally, giving it an asymmetrical outline in labial view.

4. Identification and comparisons

Several features present on all of the teeth from Lujiatun support their referral to Sauropoda, includ-

ing: wrinkled tooth enamel; the possession of a lingual concavity; a D-shaped crown cross-section; and the appearance of mesial and/or distal grooves on the labial crown surface (Upchurch, 1998; Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2004). Similarly, all of the Lujiatun teeth exhibit well-developed mesial and distal wear facets: these are indicative of dental occlusion and are consistent with referral to the less inclusive sauropod clade Eusauropoda. The lack of mesiodistal expansion of the base of the tooth crowns relative to the roots is a feature that appeared convergently in several eusauropod lineages, including *Shunosaurus*, *Mamenchisaurus*, Titanosauriformes and Diplodocoidea (Upchurch, 1998; Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2004), narrowing referral of the Lujiatun teeth to one of these clades.

Diplodocoids and titanosaurians have very slender, peg-like teeth with SI values >4.0 and reduced lingual concavities (Upchurch, 1998), indicating that none of the Lujiatun teeth can be referred to either of these clades. However, the SI values obtained from IVPP V15010.1 and 2 (minimum SI > 3.0 in both cases) are consistent with referral to a basal titanosauriform (Barrett et al., 2002), a *Shunosaurus*-like taxon (Chatterjee and Zheng, 2002) or a *Mamenchisaurus*-like form (Ouyang and Ye, 2002). The presence of high-angled mesial and distal wear facets is congruent with any of these interpretations (Upchurch and Barrett, 2000). However, *Shunosaurus* and *Mamenchisaurus* specimens are limited to Middle and Late Jurassic deposits, respectively (Zhang, 1988; Ouyang and Ye, 2002), whereas basal titanosauriforms have a global distribution in the Lower Cretaceous (Upchurch et al., 2004; Weishampel et al., 2004). As a result, it is most parsimonious to conclude that IVPP V15010.1 and 2 pertain to a basal titanosauriform (i.e. a non-titanosaurian titanosauriform) on the basis of combined anatomical and stratigraphical data. Strong similarities between IVPP V15010.1–2 and IVPP V15010.6–7 suggest that all of these specimens are referable to the same taxon.

Damage obscures some features of the other Lujiatun teeth (such as accurate determination of a minimum SI) and differences exist in the extent of tooth wear, the presence/absence of a lingual ridge and the mesiodistal expansion of the apical part of the crown. However, some variation in all of these features is present within associated dentitions of the basal titanosauriforms *Brachiosaurus* (Janensch, 1935–1936) and *Euhelopus* (Wiman, 1929). For example, differences in tooth wear can be explained by position within the tooth row and the functional age of the tooth. In other respects, the Lujiatun teeth are extremely similar: all possess well-developed mesial and/or distal wear facets, a lingual concavity, narrow tooth crowns relative the root and faint mesial and distal labial grooves. Consequently, and in the absence of features indicating referral to other clades, we refer all of the remaining Lujiatun teeth (IVPP V15010.3–5) to the same taxon.

A variety of sauropod taxa have been named on the basis of isolated teeth from the Early Cretaceous of eastern Asia, including '*Asiatosaurus mongoliensis*'. '*Asiatosaurus kwangshiensis*' and '*Chiayusaurus lacustris*'. However, these species are currently regarded as *nomina dubia* and as indeterminate eusauropods: their teeth can be distinguished from those of basal titanosauriforms due to their low SI values (Barrett et al., 2002). Moreover, these specimens lack a lingual boss (Osborn, 1924; Bohlin, 1953; Hou et al., 1975). The teeth from Lujiatun cannot, therefore, be referred to any of the aforementioned taxa. Other isolated teeth from China, Japan, Thailand and South Korea do represent basal titanosauriforms, however (reviewed in Barrett et al., 2002). These include '*Chiayusaurus asianensis*' (Lee et al., 1997), 'aff. *Mongolosaurus*' and 'aff. *Chiayusaurus*' (Bohlin, 1953), and generically indeterminate teeth from Japan (Barrett et al., 2002) and Thailand (Buffetaut and Suteethorn, 2004: listed as 'euhelopodid'). All of the latter share a large number of titanosauriform symplesiomorphies with IVPP V15010.1–7 (e.g. crowns with SI > 3.0), but lack specific autapomorphies or unique character combinations (e.g. the presence of a lingual boss) that would allow the Lujiatun teeth to be referred to any of these taxa. Finally, teeth of *Mongolosaurus haplodon*, a possible nemegtosaurid titanosaur (Wilson, 2005), also share titanosauriform symplesiomorphies with IVPP V15010.1–7: however, *Mongolosaurus* teeth can be distinguished from the Lujiatun teeth on the basis of several features. The mesial and distal crown margins of *Mongolosaurus* are developed into narrow carinae (Gilmore, 1933), whereas those of IVPP V15010.1–7 are labiolingually broader and more rounded. In addition, *Mongolosaurus* teeth exhibit sub-cylindrical cross-sections, in contrast to the 'D'-shaped cross-section of IVPP V15010.1–7. Finally, *Mongolosaurus* teeth lack the lingual concavity present in the teeth from Lujiatun (Gilmore, 1933).

Raised sub-circular bosses are present on the lingual surfaces of numerous teeth from the type specimens of *Euhelopus zdanskyi* (PMU M2983; Wiman, 1929). There is some variability in this feature, however, and bosses are not present on all of the teeth attributed to this taxon (PMU M2983; Wiman, 1929): this variation may be positional or ontogenetic, but the absence of complete tooth rows prevents testing of these hypotheses.

Where present, the consistent positioning and the smooth surfaces of the bosses suggest that they are not pathological features. These bosses are morphologically distinct from the prominent ridges that surround the lingual concavity in numerous sauropod taxa (e.g. *Camarasaurus*, *Shunosaurus*, *Omeisaurus* and *Mamenchisaurus*: PMB, personal observation; Tang et al., 2001; Ouyang and Ye, 2002). Similar bosses are absent from almost all other sauropod teeth, including those of *Mamenchisaurus*, *Omeisaurus* and *Shunosaurus* (PMB, personal observation; Tang et al., 2001; Ouyang and Ye, 2002), but are present on isolated titanosauriform teeth from the Lower Cretaceous of Spain (Canudo et al., 2002). A close phylogenetic and palaeobiogeographical relationship between *Euhelopus* and the Spanish taxon was inferred on the basis of this close resemblance (Canudo et al., 2002). Identical bosses, in terms of size, shape and positioning on the tooth crown, are present on two of the teeth from Lujiatun (IVPP V15010.4 and 7). As the teeth from Lujiatun share this feature with *Euhelopus* (and the unnamed *Euhelopus*-like Spanish material), and as all other features of IVPP V15010.1–7 are consistent with those present in the former taxon, we refer the Lujiatun teeth to cf. *Euhelopus*.

5. Discussion and conclusions

Although fragmentary, the sauropod material from the Lujiatun Beds yields some significant taxonomic, palaeobiogeographical and biostratigraphical data. For example, the type horizon for *Euhelopus* is the Mengyin Formation of Shandong Province (Wiman, 1929; Weishampel et al., 2004). This unit is usually regarded as Upper Jurassic (Tithonian) in age on the basis of biostratigraphical correlations (Chen, 1982; Chen et al., 1982). However, this age assessment is based on the presence of the *Eosestheria–Ephemeropsis–Lycoptera* assemblage, a fauna that has also been reported from other lithostratigraphical units in northeastern China, notably the Jehol Group of Liaoning. All of the units sharing this fauna were regarded as Late Jurassic (e.g. Chen, 1982, 1988; Chen et al., 1980, 1982), but radiometric dates obtained from the Jehol Group have demonstrated that the *Eosestheria–Ephemeropsis–Lycoptera* assemblage is of late Early Cretaceous age (Swisher et al., 1999; He et al., 2006a,b). Consequently, it is likely that the Mengyin Formation should also be regarded as an Early Cretaceous (?Aptian) unit: the shared presence of cf. *Euhelopus* in the Mengyin and Yixian Formations provides another datum supporting the biostratigraphical correlations between these deposits.

Previously, the phylogenetic interrelationships of *Euhelopus* have been controversial, with some authors regarding this taxon as a non-neosauropod (Upchurch, 1998; Upchurch et al., 2004): however, there is now a consensus that this form represents a basal titanosauriform (Wilson and Sereno, 1998; Wilson, 2002; Curry Rogers, 2005; Upchurch, personal communication, 2007). This indicates that all adequately known Cretaceous Asian sauropods were titanosauriforms (Barrett et al., 2002; Wilson, 2005). Titanosauriforms first appear in the Middle Jurassic of Europe and Madagascar, are present in Europe, Africa and North America in the Late Jurassic, and achieve a global distribution by the Lower Cretaceous (Upchurch et al., 2004; Weishampel et al., 2004). They were absent from the Jurassic of East Asia and their arrival in this area during the Lower Cretaceous represents part of the marked faunal changes that were occurring in the region at this time (e.g. Manabe et al., 2000; Barrett et al., 2002). The presence of *Euhelopus*-like teeth in the Lower Cretaceous of Europe provides additional support for faunal exchange between Europe and East Asia (Canudo et al., 2002; Cuenca-Bescós and Canudo, 2003).

Finally, although dinosaur material is relatively abundant in the Yixian Formation, remains of large dinosaurs are exceptionally rare (Zhou, 2006). The cf. *Euhelopus* teeth from Lujiatun and specimens of the iguanodontian ornithopod *Jinzhousaurus* (Wang and Xu, 2001) represent the only large taxa in the fauna (i.e. with body lengths >3 m). It is unknown whether this situation results from genuine scarcity or from taphonomic biases that prevented preservation of large animals. For example, it may be that larger animals were less susceptible to the mass mortality events that occurred during deposition of the Jehol Group or were less likely to be preserved in these lacustrine and volcaniclastic sedimentary settings. Alternatively, the local environment may not have been suitable to sustain large populations of these taxa and the rare finds of cf. *Euhelopus* and *Jinzhousaurus* may simply represent a small resident population or animals that were only present in the fauna on an infrequent (seasonal?) basis. Additional work on Jehol palaeoecology and palaeoenvironments is needed in order to distinguish between these hypotheses.

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