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Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth

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Table of contents

Abstract

Theropod dinosaurs form a highly diversified clade, and their teeth are some of the most common components of the Mesozoic dinosaur fossil record. This is the case in the Lourinhã Formation (Late Jurassic, Kimmeridgian-Tithonian) of Portugal, where theropod teeth are particularly abundant and diverse. Four isolated theropod teeth are here described and identified based on morphometric and anatomical data. They are included in a cladistic analysis performed on a data matrix of 141 dentition-based characters coded in 60 taxa, as well as a supermatrix combining our dataset with six recent datamatrices based on the whole theropod skeleton. The consensus tree resulting from the dentition-based data matrix reveals that theropod teeth provide reliable data for identification at approximately family level. Therefore, phylogenetic methods will help identifying theropod teeth with more confidence in the future. Although dental characters do not reliably indicate relationships among higher clades of theropods, they demonstrate interesting patterns of homoplasy suggesting dietary convergence in (1) alvarezsauroids, therizinosaurs and troodontids; (2) coelophysoids and spinosaurids; (3) compsognathids and dromaeosaurids; and (4) ceratosaurids, allosauroids and megalosaurids.

Based on morphometric and cladistic analyses, the biggest tooth from Lourinhã is referred to a mesial crown of the megalosaurid *Torvosaurus tanneri*, due to the elliptical cross section of the crown base, the large size and elongation of the crown, medially positioned mesial and distal carinae, and the coarse denticles. The smallest tooth is identified as *Richardoestesia*, and as a close relative of *R. gilmorei* based on the weak constriction between crown and root, the "eight-shaped" outline of the base crown and, on the distal carina, the average of ten symmetrically rounded denticles per mm, as well as a subequal number of denticles basally and at mid-crown. Finally, the two medium-sized teeth belong to the same taxon and exhibit pronounced interdenticular sulci between distal denticles, hooked distal denticles for one of them, an irregular enamel texture, and a straight distal margin, a combination of features only observed in abelisaurids. They provide the first record of Abelisauridae in the Jurassic of Laurasia and one of the oldest records of this clade in the world, suggesting a possible radiation of Abelisauridae in Europe well before the Upper Cretaceous.

Key words: Abelisauridae, Megalosauridae, *Torvosaurus*, *Richardoestesia*, teeth, cladistic, Theropoda, Portugal, Late Jurassic

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APPENDIX

Character list

The full set of 141 dentition-based characters is listed here. 74 characters are derived from the literature and the original and sometimes previous usages of the character are indicated by citations (with the corresponding character number) in parentheses. 67 characters (47.5%) were revealed by our personal observation of the dentition of more than hundred theropod taxa. Among the 81 multistate characters, 71 were left unordered such as the elongation and thickness of the tooth, the extension of the carinae along the crown, and the development of interdenticular sulci, due to the variability of these features along the tooth row. Therefore, only characters with obvious evolutionary continuity were ordered and concern the overlap of the first and second premaxillary alveoli (char. 4), the constriction of the premaxillary tooth rows (char. 15), the posterior extension of the tooth row relative to the orbit (char. 24), and the size of the crown (char. 36 and 65) and denticles (char. 53 and 86), i.e. there must be a theropod bearing moderately large teeth/denticles between two closely related taxa with one having very small crowns (CH < 10 mm)/denticles (> 250 denticles on the carinae), and another possessing very large teeth (CH > 60 mm)/denticles (< 15 denticles on the carinae).

Characters related to the number of teeth borne by the premaxilla (char. 2), the maxilla (char. 17) and the dentary (char. 25) were also ordered. According to Miyashita *et al.* (2010), characters based on tooth count do not accurately reflect true phylogenetic signal as tooth count varies ontogenetically, intraspecifically and even between the left and right jaws of a same individual. Nevertheless, the number of premaxillary teeth is for instance remarkably stable among theropods (Miyashita *et al.* 2010; pers. obs.), and a large number of closely related theropod taxa share the same number of teeth borne by the maxilla (e.g., non-carcharodontosaurid allosauroids) and dentary (e.g., megalosaurids). Likewise, the ontogenetical variation of the number of maxillary and dentary teeth, and suggested by Carr (1999) for tyrannosaurids, was questioned by Currie (2003) and refuted by Tsuihiji *et al.* (2011). Furthermore, the tooth counts typically varies of one or two teeth between the left and right jaws of a same individual (Currie 2003). Although the tooth count variation seems to exceed two teeth for the maxilla or the dentary in some taxa (e.g., *Ceratosaurus nasicornis*, *Tyrannosaurus rex*; Carrano and Sampson 2008; Brusatte *et al.* 2012), the character states of our datamatrix regarding the maxillary and dentary tooth count corresponds, in most cases, to a range of two teeth or more, and we therefore assume that there must be a theropod with an intermediate tooth count between a more primitive one with two teeth less and a more derived with two teeth more. Given the results of the cladistic analysis, this assumption is coherent with the evolution of maxillary and dentary tooth count for most theropod clades, except perhaps for baryonychine and spinosaurine Spinosauridae that may have followed two different path in the evolution of their dentition.

Some characters concern the curvature of the labial and lingual sides of the crown, and the presence of ornamentations on their surface. The labial and lingual sides of a theropod tooth can be identified thanks to the position and orientation of the mesial and distal carinae. The mesial carina, when curving towards the base of the crown, always twists towards the lingual side, whereas the distal carina, when deflected from the centre of the distal margin, is displaced labially in the large majority of theropods. Furthermore, there is typically a centrally positioned depression on the lingual side of the root which can extends on the basal part of the crown in many taxa. If this depression appears on both labial and distal sides of the crown, the lingual depression is usually deeper than the labial one (pers. obs.).

Two characters are related to the outline of the crown base in cross-section. This feature is particularly important in mesialmost teeth which have a typical cross-section outline in many theropod clades. The following figure illustrates the different outlines and the associated terms used in this paper. Because theropod teeth morphology varies through ontogeny (Araújo *et al.* 2013), some dentition-based characters are only coded in mature (i.e., sub-adult and adult) individuals. They concern the crown size (CH), the average number of denticles (per 5 mm) on the mesial and distal carinae, and the size of