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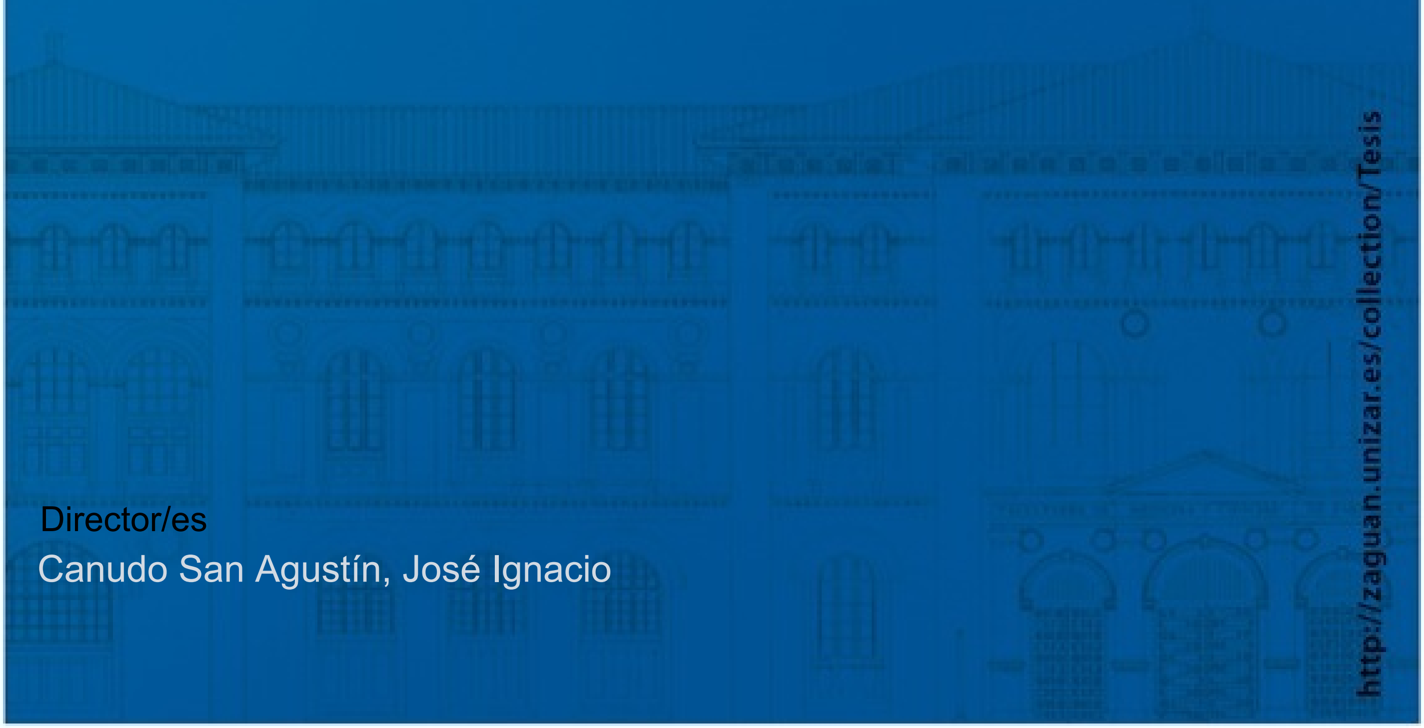
Antonio Alonso German

Nuevas contribucionaes a la paleodiversidad de dinosaurios terópodos del Jurásico y Cretácico de España a partir de dientes aislados



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NUEVAS CONTRIBUCIONAES A LA PALEODIVERSIDAD DE DINOSAURIOS TERÓPODOS DEL JURÁSICO Y CRETÁCICO DE ESPAÑA A PARTIR DE DIENTES AISLADOS

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Grupo
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Memoria presentada por Don **Antonio Alonso Germán** para optar al título de Doctor en Ciencias, por la Universidad de Zaragoza, bajo la dirección del doctor José Ignacio Canudo Sanagustín (Catedrático del Departamento de Ciencias de la Tierra de la Universidad de Zaragoza)

A mi familia y amigos.

Esta Tesis por compendio de publicaciones se compone de los siguientes trabajos:

Alonso, A., Canudo, J.I. 2016. On the spinosaurid theropod teeth from the early Barremian (Early Cretaceous) Blesa Formation (Spain). *Historical Biology* 28(6), 823-834.
Historical Biology. Factor de Impacto (JCR) en 2016: 1.556. Área temática: Paleontology.

Alonso, A., Gasca, J.M., Navarro-Lorbés, P., Núñez-Lahuerta, C., Galán, J., Parrilla-Bel, J., Rubio, C., Canudo, J.I. 2016. La asociación faunística de Barranco del Hocino 1, un nuevo yacimiento de vertebrados del Barremiense (Cretácico Inferior) de Teruel. *Cuadernos del Museo Geominero* 20, 303-307.

Alonso, A., Canudo, J.I., Torcida Fernández-Baldor, F., Huerta, P. 2017. Isolated theropod teeth associated with sauropod remains from El Oterillo II (Early Cretaceous) site of Salas de los Infantes (Burgos, Spain). *Journal of Iberian Geology* 43(2), 193-215.
Journal of Iberian Geology. Factor de Impacto (JCR) en 2017: 1.302. Área temática: Geology.

Alonso, A., Gasca, J.M., Navarro-Lorbés, P., Rubio, C., Canudo, J.I. 2018. A new contribution to our knowledge of the large bodied theropods from the Barremian of the Iberian Peninsula: the "Barranco del Hocino" site (Spain). *Journal of Iberian Geology* 44(1), 7-23.
Journal of Iberian Geology. Factor de Impacto (JCR) en 2017/2018: 1.302. Área temática: Geology.

ÍNDICE

ESTRUCTURAL FORMAL Y UNIDAD TEMÁTICA

Esta tesis se ha realizado por compendio de publicaciones siguiendo la normativa de la Universidad de Zaragoza. Las aportaciones científicas presentadas en el volumen de la tesis doctoral representan una unidad temática en torno a los dientes aislados de dinosaurios terópodos del Jurásico Superior y Cretácico Inferior de España. Los artículos que forman parte de esta tesis suponen aportaciones novedosas al conocimiento de los dinosaurios terópodos de la península ibérica y son relevantes para los objetivos planteados en la tesis doctoral. Además de los artículos que forman el compendio de publicaciones, se incluye un artículo en preparación. Los artículos originales publicados se han incluido en los anexos.

El volumen se compone de un resumen, ocho capítulos y cinco anexos. El capítulo 1 es una introducción general a la tesis. El capítulo 2 explica los materiales y métodos utilizados mientras que el capítulo 3 trata del contexto geográfico y geológico de donde procede el material estudiado. Los capítulos 4 a 7 son manuscritos de trabajos científicos, donde el 5, 6 y 7 han sido publicados en revistas internacionales incluidas en el Journal Citation Reports. El capítulo 4 es un manuscrito inédito en preparación que será enviado próximamente. El capítulo 8 corresponde a las conclusiones de la tesis. El Anexo 1 corresponde al análisis cladístico del trabajo inédito del Jurásico Superior de Asturias (Capítulo 4). Los Anexos 2 al 5 corresponden a los artículos publicados en las revistas *Historical Biology* (Anexo 2), *Cuadernos del Museo Geominero* (Anexo 3) y *Journal of Iberian Geology* (Anexos 4 y 5). Estos últimos, además, incluyen el desarrollo de los análisis filogenéticos realizados en ambos trabajos. Por último, los datos de los análisis estadísticos realizados en las publicaciones se incluyen en archivos .xlsx en el CD adjunto.

Los capítulos del 4 al 7 están escritos en inglés, dado que son manuscritos de artículos bien inéditos (Capítulo 4) o bien ya publicados (Capítulos 5, 6 y 7). La tesis opta a mención internacional, de forma que el resumen y las conclusiones están escritas en inglés y en castellano.

Capítulo 1: Introducción

Escrita en castellano. En este capítulo se realiza una introducción a la temática tratada en la tesis, explicando brevemente el origen, las relaciones, las características y los principales grupos de dinosaurios terópodos. Asimismo se han realizado unos antecedentes para los restos de terópodos del Jurásico Superior y Cretácico Inferior de Europa occidental y la península ibérica, junto a una introducción específica de los dientes de dinosaurios terópodos. Finalmente se plantean los objetivos de la tesis doctoral.

Capítulo 2: Material y métodos

Capítulo escrito en castellano. Aquí se incluye una relación del material estudiado, los museos donde se encuentra depositado y una breve explicación de la metodologia de estudio y actividades relacionadas llevadas a cabo por el doctorando como la prospección y excavación de yacimientos paleontológicos.

Capítulo 3: Contexto geográfico y geológico

Escrito en castellano. En este apartado se realiza una introducción a los aspectos geográficos y las características geológicas de las áreas de las que proceden los dientes aislados de terópodos, identificando las formaciones geológicas, los medios de depósito y el contexto general de las cuencas donde se depositaron.

Capítulo 4: Revisión de la paleobiodiversidad de grandes terópodos del Jurásico Superior de Asturias (N España) a partir de dientes aislados.

Escrito en inglés. Se trata de un manuscrito inédito donde se realiza un estudio de los dientes aislados de dinosaurio terópodo de las Formaciones Vega, Tereñes y Lastres del Kimmeridgiense de la cuenca de Gijón-Villaviciosa y su comparación con faunas contemporáneas de Europa occidental y la península ibérica. A partir de este estudio se ha identificado la diversidad de terópodos en el área empleando análisis estadístico y filogenético (Anexo 1).

Capítulo 5: Sobre los dientes de terópodos espinosaurios del yacimiento La Cantalera 1 (Barremiense inferior, Cretácico Inferior)

Escrito en inglés. Este capítulo corresponde al manuscrito del artículo publicado en 2016 en la revista científica *Historical Biology,* incluído en el Anexo 2. En él se realiza un estudio de los morfotipos de espinosáuridos presentes en el yacimiento y se realiza un análisis multivariante de componentes principales (ACP). Se plantea la posible presencia de terópodos espinosaurinos en el yacimiento, además de los de tipo barioniquino, y se realiza una comparación con otros yacimientos del Cretácico Inferior de España.

Capítulo 6: Una nueva contribución al conocimiento de los grandes terópodos del Barremiense de la península ibérica: el yacimiento de Barranco del Hocino (España)

Escrito en inglés. Este capítulo corresponde a los manuscritos publicados en 2016 y 2018 en las revistas *Cuadernos del Museo Geominero* y *Journal of Iberian Geology*, incluidos en los anexos 3 y 4. En estos artículos se realiza una evaluación de la paleobiodiversidad de vertebrados continentales de un nuevo yacimiento de la secuencia superior de la Formación Blesa, particularmente de los dinosaurios terópodos en base a los dientes aislados hallados. Se distinguen varios morfotipos de tetanuros incluyendo un morfotipo de espinosáurido y un posible carcarodontosaurio, empleando análisis estadísticos y filogenéticos.

Capítulo 7: Dientes aislados de terópodos asociados con restos de un saurópodo del yacimiento El Oterillo II de Salas de los Infantes (Burgos, España)

Escrito en inglés. Este capítulo corresponde al manuscrito publicado en 2017 en la revista científica *Journal of Iberian Geology* incluido en el Anexo 5. En este trabajo se identifica la asociación de terópodos presente en el yacimiento, identificándose una asociación de tetanuros basales y derivados. Además se discute el posible aprovechamiento de la carcasa del titanosauriforme *Europatitan eastwoodi* por parte de los terópodos, mediante rasgos de la acumulación y la presencia de marcas de dientes en algunos de los huesos del saurópodo, comparándose con casos similares.

Capítulo 8: Conclusiones

Escrito en castellano y en inglés. En este capítulo se presentan las principales conclusiones obtenidas en el desarrollo de la tesis.

FORMAL STRUCTURE AND THEMATIC UNIT

This PhD dissertation is presented as a compendium of scientific papers. The contributions included in this dissertation represent a thematic unit around the isolated theropod teeth from the Late Jurassic and Early Cretaceous of Spain. The scientific papers included in this volume represent new contributions to the knowledge of theropod dinosaurs of the Iberian Peninsula; they are relevant to the objectives of the PhD. In addition to the published papers, a new manuscript is included. The original papers have been included in the Appendices.

The PhD dissertation consists of an abstract, eight chapters and five appendices. Chapter 1 is a general introduction to the dissertation. Chapter 2 explains the materials and methods used during the study and the Chapter 3 is about the geographical and geological setting of the areas where the studied material comes from. Chapters 4 to 7 are the manuscripts of scientific publications; the Chapters 5, 6 and 7 are already published in international scientific journals included in the Journal Citation Reports. Chapter 4 is an inedit manuscript that will be submitted soon. Chapter 8 presents the general conclusions of the dissertation. Appendix 1 includes the cladistic analysis of the inedit manuscript on the theropod palaeobiodiversity from the Late Jurassic of Asturias (Chapter 4). The Appendices 2 to 5 include the original papers published in scientific journals. Appendices 4 and 5 also include the philogenetic analyses performed in those works. In addition, the statistic datasets used in these manuscripts are included in the attached CD.

Chapters 4 to 7 are written in english. This PhD dissertation opts to an international mention so the abstract and conclusions are written in English as well as in Spanish.

Chapter 1: Introduction

Chapter written in Spanish. This chapter introduces the general topic of the dissertation, explainig the origin, relations, main traits and relevant clades of Theropoda. Besides, there is an overview on the historical background of the theropod record from the Late Jurassic and Early Cretaceous of western Europe and the Iberian Peninsula, and specific remarks concerning theropod teeth. In addition, the main goals of the PhD dissertation are presented.

Chapter 2: Material and methods

Chapter written in Spanish. It references the studied material, the institutions where it is housed and a brief explanation on the methods and activities performed during the PhD, including prospection and digging campaings.

Chapter 3: Geographical and geological setting

Chapter written in Spanish. This chapter explains the main geographical and geological aspects of the areas where the isolated teeth come from; also the geological formations, depositional environment and general context are described.

Chapter 4: A revision of the large-bodied theropod (Dinosauria: Saurischia) palaeobiodiversity from the Late Jurassic of Asturias (N Spain) on the basis of isolated teeth.

Chapter written in English. This is an inedit manuscript where the isolated theropod teeth from the Vega, Tereñes and Lastres Formations (Kimmeridgian in age) are studied. In addition there is a comparison between this material and contemporary faunas of western Europe and the Iberian Peninsula. The palaeobiodiversity of theropods is identified; philogenetic (Appendix 1) and statistic analyses were performed.

Chapter 5: On the spinosaurid theropod teeth from the early Barremian (Early Cretaceous) La Cantalera 1 site

Chapter written in English. This chapter corresponds to the paper included in Appendix 2, published in 2016 in *Historical Biology.* An study on the spinosaurid morphotypes is performed using a principal components analysis (PCA). The possible presence of spinosaurine theropods is proposed. Also this chapter compares the mprphotypes with teeth from the Early Cretaceous Spanish sites.

Chapter 6: A new contribution to our knowledge of the large-bodied theropods from the Barremian of the Iberian Peninsula: the "Barranco del Hocino" site (Spain)

Chapter written in English. It includes the manuscripts published in 2016 and 2018 in *Cuadernos del Museo Geominero* and *Journal of Iberian Geology* respectively (Appendices 3 and 4). This chapter evaluates the terrestrial vertebrate palaeobiodiversity of a new site from the upper Blesa Fm. sequence wtih an special focus on the isolated theropod teeth. Several morphotypes are described, including spinosaurids and a basal tetanuran probably related to Carcharodontosauria. Philogenetic and statistic analyses are performed.

Chapter 7: Isolated theropod teeth associated with sauropod remains from El Oterillo II (Early Cretaceous) site of Salas de los Infantes (Burgos, Spain)

Chapter written in English. This chapters corresponds to the 2017 paper published in the *Journal of Iberian Geology* (Appendix 5). This work identifies the theropod association present in the Oterillo II site. A combination of basal and derived tetanurans is recognized. In addition, the possible feeding on the carcass of the sauropod *Europatitan eastwoodi* is discussed on the basis of the accumulation and the presence of tooth marks on some bones.

Chapter 8: Conclusions

Chapter written in English and Spanish. This chapter presents the main conclusions obtained during this PhD.

RESUMEN

Los dinosaurios son un grupo de vertebrados fósiles que ejercen una gran fascinación. Los hallazgos paleontológicos suscitan un gran interés entre el gran público, con numerosas apariciones en prensa, medios de divulgación, documentales o incluso la ciencia-ficción. El interés científico de estos vertebrados es enorme, al haber dominado los ecosistemas terrestres durante más de 200 millones de años.

Los dinosaurios terópodos incluyen a todos los dinosaurios carnívoros estrictos. Su estudio es fundamental para el conocimiento de las complejas relaciones de los organismos terrestres mesozoicos y para reconstruir una parte fundamental en la historia evolutiva de los dinosaurios que aún perduran, las aves. En esta tesis se estudian los dientes aislados de dinosaurios terópodos de yacimientos del Jurásico Superior y el Cretácico Inferior de España.

Los restos del Jurásico Superior, del Kimmeridgiense, provienen de la llamada "costa de los dinosaurios" en la comunidad de Asturias, de yacimientos localizados en las formaciones Vega, Lastres y Tereñes. Los dientes aislados del Cretácico Inferior provienen de la Cordillera Ibérica, de yacimientos localizados en la provincia de Teruel (Aragón): La Cantalera 1, situado en el entorno de Josa, y Barranco del Hocino 1, un yacimiento descubierto recientemente en el término municipal de Estercuel. También se ha estudiado la asociación de un yacimiento de la provincia de Burgos, El Oterillo II, en el entorno de Salas de los Infantes.

Esta tesis se presenta como compendio de artículos publicados en revistas internacionales e incluye un manuscrito inédito preparado para publicación. El Capítulo 1 es una introducción a los dinosaurios terópodos donde se repasan los antecedentes del estudio de dinosaurios terópodos y de dientes aislados. En los Capítulos 2 y 3 se presentan la metodología y contexto geográfico y geológico de las áreas estudiadas. El Capítulo 4 es un manuscrito inédito sobre la paleobiodiversidad de terópodos del Jurásico Superior de Asturias donde se reconocen megalosáuridos, un posible abelisáurido y averostra indeterminados. El Capítulo 5 se presenta un estudio de los dinosaurios espinosáuridos del yacimiento de La Cantalera 1. En el Capítulo 6 se presenta la diversidad de vertebrados mesozoicos y en particular de terópodos del nuevo yacimiento de Barranco del Hocino 1, que incluye un morfotipo de espinosáurido y otros tetanuros basales. En el Capítulo 7 se presentan los resultados obtenidos en el estudio de la asociación de terópodos, que incluye espinosáuridos, posibles carcarodontosaurios, dromaeosaurios y un singular coelurosario de El Oterillo II y su relación con los restos de un saurópodo.

Finalmente, el capítulo 8 presenta las conclusiones de la Tesis Doctoral.

ABSTRACT

Dinosaurs are one of the most popular groups in Paleontology. Paleontological discoveries have a deep impact among the media, the press or even sci-fiction. The scientific interest of this group is big due to their prominent role on the terrestrial ecosystems for more than 200 million years.

Theropod dinosaurs include all the strictly carnivorous dinosaurs. The study of theropods has a big importance in order to understand the complex relationships between terrestrial Mesozoic organisms and it is also key to reconstruct the evolutionary history of the extant dinosaurs, the birds. In this PhD dissertation isolated theropod teeth from the Late Jurassic and Early Cretaceous of Spain are studied.

Late Jurassic theropod teeth come from the "dinosaur coast" in Asturias region (N Spain), from sites located in the Vega, Tereñes and LastresFormations. Isolated theropod teeth from the Early Cretaceous come from the Iberian Range. Two sites are located in Aragón (Teruel province): La Cantalera 1, located within the municipality of Josa, and Barranco del Hocino 1, a new fossiliferous locality near the town of Estercuel. In addition, another locality from the Iberian Range has been studied: El Oterillo II site, near Salas de los Infantes (Burgos province).

This PhD dissertation is presented as a compendium of scientific papers published in international journals and also includes an inedit manuscript that will be submitted soon. The first Chapter is a general introduction on Theropoda and theropod teeth. Chapters 2 and 3 explain the general methodology and the geographical and geological setting. The Chapter 4 is an inedit work on the theropod palaeobiodiversity from the Late Jurassic of Asturias. Chapter 5 is a published paper on the spinosaurids from La Cantalera 1. Chapter 6 studies the vertebrate assemblage of Barranco del Hocino 1, with the focus on theropods. Chapter 7 studies the relationship between a broad set of theropods and a sauropod carcass from El Oterillo II site.

The last chapter presents the general conclusions of the PhD dissertation.

INTRODUCCIÓN

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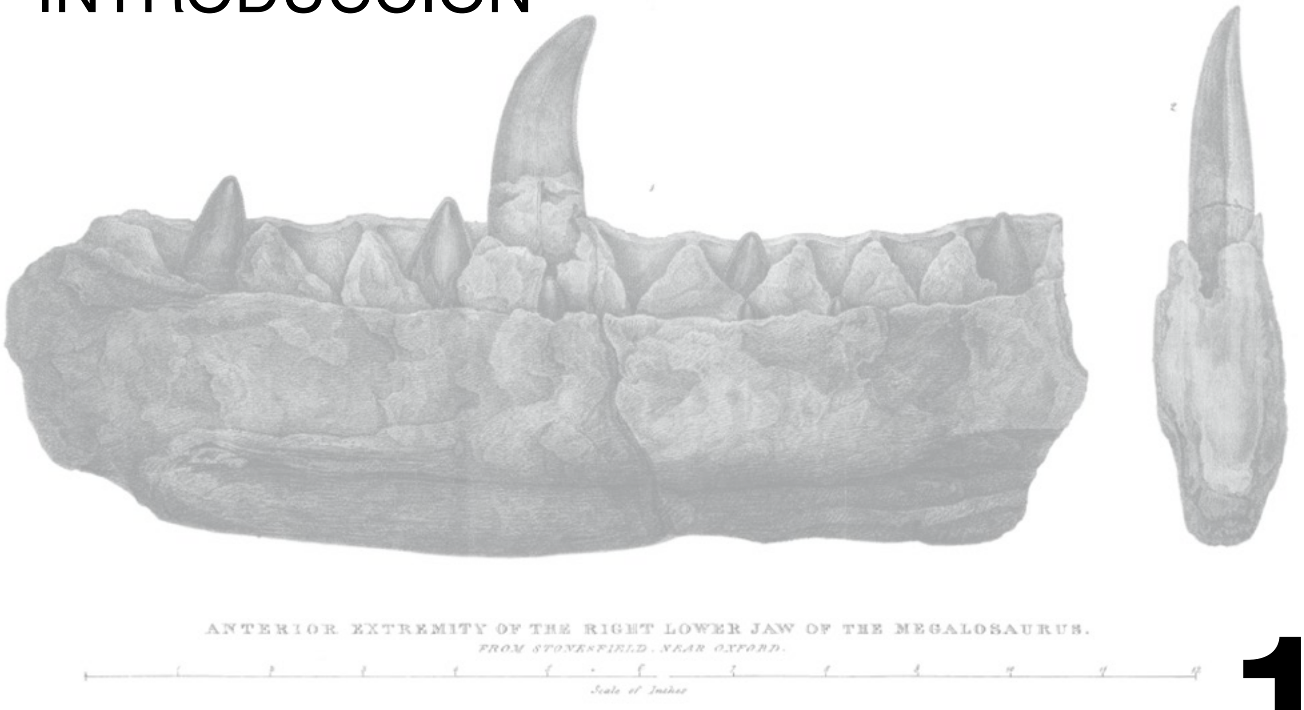


ANTERIOR EXTREMITY OF THE RIGHT LOWER JAW OF THE MEGALOSAURUS.
FROM STONESFIELD, NEAR OXFORD.

1. INTRODUCCIÓN

Los dinosaurios son un grupo de vertebrados fósiles que ejercen una gran fascinación. Los hallazgos paleontológicos suscitan un gran interés entre el gran público, con numerosas apariciones en prensa, medios de divulgación, documentales o incluso la ciencia-ficción. El interés científico de estos vertebrados es enorme, al haber dominado los ecosistemas terrestres durante más de 200 millones de años.

Los dinosaurios terópodos incluyen a todos los dinosaurios carnívoros estrictos. Su estudio es fundamental para el conocimiento de las complejas relaciones de los organismos terrestres mesozoicos y para reconstruir una parte fundamental en la historia evolutiva de los dinosaurios que aún perduran, las aves.

Los restos de dinosaurios terópodos son escasos dado su menor número en los ecosistemas respecto a los dinosaurios herbívoros y las condiciones de fosilización que dificultan la preservación de sus restos, al ser más gráciles que otros grupos de dinosaurios (Canudo, 2007). En estas condiciones, es habitual que los dientes aislados de dinosaurios terópodos sean la única evidencia existente en las formaciones mesozoicas, debido al mayor potencial de fosilización que posee el esmalte, la parte biomineralizada más dura de un vertebrado. Suelen ser los restos de dinosaurios más abundantes en las formaciones geológicas del Mesozoico; una abundancia también propiciada con el reemplazo constante de dientes en los terópodos, que permitía que un único ejemplar pudiera producir cientos de dientes susceptibles de fosilizar (Torices, 2007).

Desde finales del siglo XX (Currie *et al.,* 1990) el estudio de dientes aislados de dinosaurios terópodos se ha convertido en una línea de investigación de gran interés debido a la aparición de nuevas metodologías que han permitido realizar nuevas aportaciones en cuestiones de sistemática, funcionalidad, afinidad paleobiogeográfica y cuantificación de la paleobiodiversidad.

La península ibérica posee un registro de dientes aislados de dinosaurios terópodos de gran interés. En general se trata de material fragmentario con un significativo interés científico que en muchos casos no ha sido estudiado o puede ser reestudiado a la luz de los últimos avances metodológicos que complementa la información aportada por otros restos esqueléticos. Este conjunto de evidencias permite comprende la paleobiodiversidad, distribución y características de este clado con mayor precisión.

2. SOBRE LOS DINOSAURIOS

El Diccionario de la lengua española, en su 23ª edición, define dinosaurio como "*reptil fósil de gran tamaño, con cabeza pequeña, cuello largo, cola robusta y larga, y, en general, extremidades posteriores más largas que las anteriores*". Es una definición imprecisa y que hace únicamente referencia a los dinosaurios saurópodos. Los dinosaurios son un grupo de tetrápodos amniotas diápsidos que aparece durante el Triásico y que perdura en la actualidad en las aves, el grupo de vertebrados tetrápodos más diverso, con casi 10.000 especies (Monroe y Sibley, 1993).

Los primeros vertebrados, desde su aparición en el Cámbrico hace aproximadamente 525 millones de años, inician su historia evolutiva como animales acuáticos. No será hasta el Devónico superior cuando se produce uno de los hitos evolutivos más importantes para este grupo: la aparición, primero, de formas transicionales y en torno a unos 10 millones de años después, durante el Frasniense superior y Fameniense, de verdaderos tetrápodos (*sensu* Anderson en Laurin y Anderson, 2004), con extremidades y dedos como *Acanthostega* e *Ichthyostega* (Clack, 2012). De esta forma se inicia la ocupación de medios continentales por parte de los vertebrados.

Uno de los retos de los primeros anfibios a la hora de ocupar nichos terrestres fue la necesidad de retornar a un entorno acuático para la reproducción. Esta dificultad es superada con la aparición del huevo amniota durante el Carbonífero, estructura que protege el embrión, permitiendo su desarrollo, respiración y nutrición. Es también en el Carbonífero cuando aparecen los primeros reptiles a partir de anfibios reptiliomorfos (Clack, 2012).

La clase Reptilia (Laurenti, 1768) en su definición histórica constituye un grupo parafilético al no incluir a todos sus descendientes; actualmente se incluye bien dentro o como equivalente a Sauropsida (Goodrich, 1916; Watson, 1957; Gauthier, 1994). El uso de Sauropsida *sensu* Gauthier (1994) como grupo monofilético ha sido considerado inadecuado debido a incertidumbres sobre la posición filogenética de las tortugas, por lo que Modesto y Anderson (2004) definen Reptilia como el clado más inclusivo que contiene a *Lacerta agilis* y *Crocodilus niloticus* pero no a *Homo sapiens*.

Los dinosaurios pertenecen al linaje de los diápsidos (Osborn, 1903a), caracterizados por la presencia de dos fenestras temporales a ambos lados del cráneo. Dentro de Diapsida, los dinosaurios se encuentran dentro del clado Archosauria (Cope, 1869), linaje que incluye a los crocodilomorfos, pterosaurios y dinosaurios (**Figura 1**). Durante el Triásico aparece el antepasado común al clado Ornithodira (Gauthier, 1986) que engloba a los pterosaurios y a los dinosauriomorfos, entre los que se encuentran los lagerpetónidos, silesáuridos o los

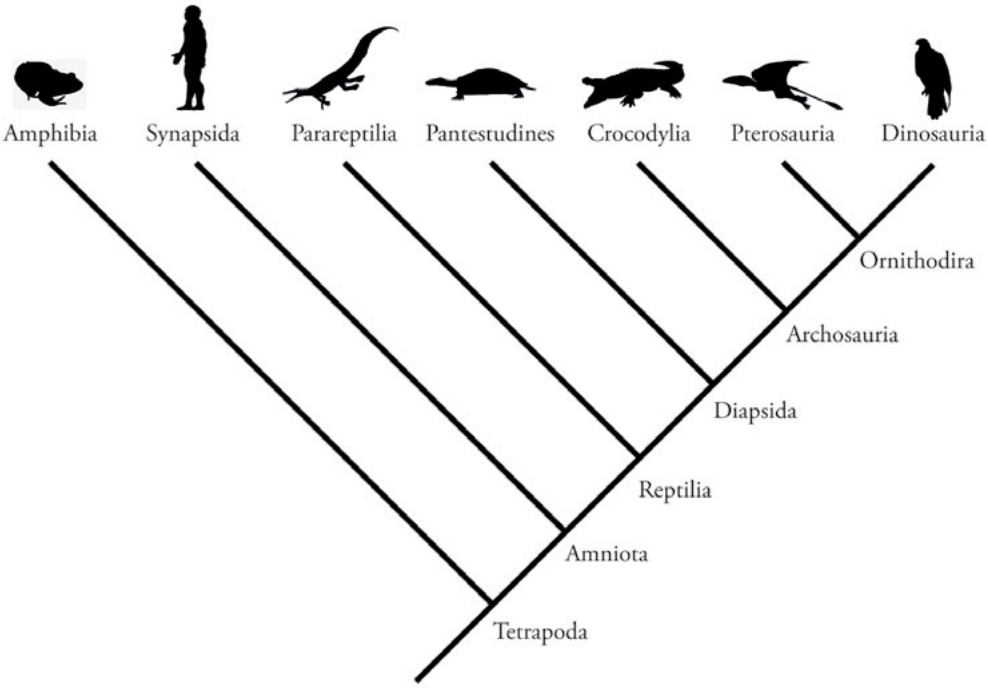


Fig. 1: Cladoglama simplificado con la relación de Dinosauria con otros tetrápodos. Siluetas de PhyloPic (http://www.phylopic.org). Crédito a Nobu Tamura, A. Vèrriere, Scott Hartman, Mark Witton y Anthony Caravaggi.

dinosaurios.

El término Dinosauria ("lagarto terrible") fue definido por Sir Richard Owen en 1842, e incluía originalmente a *Megalosaurus*, *Hylaeosaurus* e *Iguanodon* pero no a otros taxones como *Streptospondylus*, considerado un cocodrilo en aquel momento (Hendrickx *et al.*, 2015a). En la actualidad, Dinosauria se define, habitualmente, como el clado que contiene al ancestro común más reciente de *Triceratops horridus* (Marsh, 1889) y *Passer domesticus* (Linnaeus, 1758) y a todos sus descendientes (Sereno, 2005; Butler *et al.*, 2008).

Los caracteres diagnósticos más consistentes del clado Dinosauria son (Brusatte *et al.*, 2010b):

- Cresta dectopectoral alargada.
- Acetábulo perforado.
- Musculatura temporal que se extiende anteriormente hacia la parte superior del cráneo.
- Presencia de epipófisis en las vértebras cervicales.
- Una faceta articular de la fíbula que ocupa menos del 30% de la anchura transversal del astrágalo.
- Cuarto trocánter asimétrico.
- Proceso posterior del yugal bifurcado para articular con el cuadradoyugal.

Algunos caracteres considerados tradicionalmente diagnósticos pero que también están presentes en otros dinosauriomorfos incluyen:

- Presencia de fosa brevis.
- Presencia de al menos tres vértebras sacras.

Tradicionalmente, los dinosaurios se han diferenciado según la estructura de la cadera (Seeley, 1888), distinguiéndose dos órdenes: Saurischia ("cadera de reptil") y Ornithischia ("cadera de ave"). En la configuración de la cadera de los saurisquios el pubis apunta hacia la parte anterior, mientras que en los ornitisquios el pubis se orienta hacia la parte posterior, paralelamente al isquion.

Dentro del orden Saurischia se han incluido los clados Theropoda y Sauropodomorpha, mientras que el orden Ornithischia incluye a Fabrosauridae, Ornithopoda, Thyreophora y Marginocephalia (**Figura 2a**).

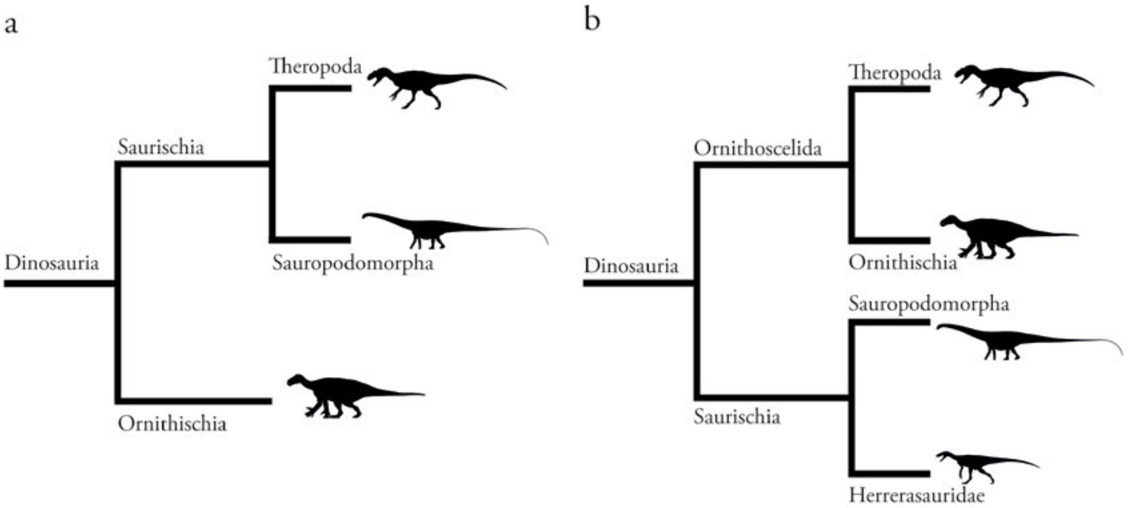


Fig. 2: Clasificación simplificada de Theropoda. **a)** Clasificación tradicional; **b)** hipótesis de Baron *et al.*, (2017a) simplificada. Siluetas de PhyloPic (http://www.phylopic.org. Crédito Scott Harman.

Sin embargo, esta hipótesis ha sido disputada recientemente con el trabajo de Baron *et al.* (2017a) donde se propone una nueva clasificación de Dinosauria. En esta nueva hipótesis filogenética se recupera el término Ornithoscelida, originalmente propuesto por Huxley (1870), que aquí incluye a los clados Ornithischia y Theropoda (**Figura 2b**), y definido como el clado menos inclusivo que contiene a *Passer domesticus* y *Triceratops horridus* (Marsh, 1889). La propuesta de Baron *et al.* (2017a) también redefine el clado Saurischia incluyendo a los herrerasáuridos y sauropodomorfos, o el clado menos inclusivo que contiene a *Diplodocus carnegii* (Hatcher, 1901) pero no a *Triceratops horridus*. Esta hipótesis también ha sido denominada Pachypodosauria-Ornithoscelida, según Holtz (2017).

Esta propuesta supuso una pequeña revolución, con posturas en contra y a favor. Así Langer *et al.* (2017) recodifican los caracteres que consideran erróneos y añaden taxones, recuperando un árbol filogenético con la división tradicional de Saurischia + Ornithischia. Baron *et al.* (2017b) recodifican la matriz y vuelven a recupera de nuevo a Theropoda y Ornithischia como grupo hermano de Sauropodomorpha, con el cambio de Herrerasauridae como grupo hermano de Dinosauria. Otros análisis han apoyado al clado Ornithoscelida (Müller y Dias-da-Silva, 2017; Parry *et al.,* 2017, 2018). Se trata por tanto de una cuestión abierta, dado lo inestable de la matriz de los dinosaurios en su primera radiación. La solución pasa por el descubrimiento de nuevos y más completos ejemplares que ayuden a clarificar las complejas relaciones filogenéticas de los primeros dinosaurios y sus formas hermanas.

Las evidencias de fósiles de dinosaurios más antiguas conocidas provienen de depósitos de Sudamérica, de las Formaciones Ischigualasto en Argentina y Santa María en Brasil (Langer *et al.,* 2018), en el Triásico Superior, aunque se ha apuntado que pudieron aparecer en el Triásico Medio (Nesbitt *et al.,* 2010). Tradicionalmente su origen ha sido situado en Gondwana (por ej., Nesbitt *et al.,* 2009, 2010; Brusatte *et al.,* 2010b) aunque algunos autores han propuesto recientemente un posible origen laurasiático (Baron *et al.,* 2017a).

Los primeros dinosaurios eran animales relativamente pequeños y bípedos (Langer, 2003; Brusatte *et al.*, 2010b) como *Herrerasaurus* (Reig, 1963), *Eoraptor* (Sereno *et al.*, 1993), *Saturnalia* (Langer *et al.*, 1999) o *Eodromaeus* (Martinez *et al.*, 2011). Durante el Triásico Superior y Jurásico Inferior aparecen los principales clados de Dinosauria, consiguiendo una distribución global (Brusatte *et al.*, 2010b; Hendrickx *et al.*, 2015a).

La posición filogenética de algunos grupos basales de dinosaurios es incierta. Los herrerasáuridos han sido recuperados en análisis filogenéticos como saurisquios basales (Novas *et al.*, 2010), terópodos basales (Sues *et al.*, 2011), grupo hermano de Sauropodomorpha (Baron *et al.*, 2017a), grupo hermano de Dinosauria (Baron *et al.*, 2017b) o como grupo hermano de Sauropodomorpha y Ornithoscelida (Cau, 2018).

2.1 ¿Qué es un terópodo?

El término Theropoda ("pie de bestia") fue acuñado por el paleontólogo norteamericano Othniel Charles Marsh en 1881 para incluir a los dinosaurios triásicos y a los carnívoros del Jurásico y el Cretácico. Los terópodos constituyen un grupo de dinosaurios bípedos que incluye a las aves y a los dinosaurios carnívoros estrictos (Hendrickx *et al.,* 2015a) aunque algunos grupos desarrollan estrategias de alimentación herbívoras (Kirkland *et al.,* 2005; Zanno y

Makovicky, 2011) u omnívoras (Holtz *et al.,* 1998; Lee *et al.,* 2014; Larson *et al.,* 2016) . En este grupo se encuentran algunos de los dinosaurios más pequeños, como *Microraptor* (Xu, *et al.,* 2000) junto con alguno de los mayores depredadores terrestres, como *Tyrannosaurus* (Osborn, 1906b) o *Spinosaurus* (Stromer, 1915). Actualmente Theropoda está definido como el clado más inclusivo que contiene a *Passer domesticus* (Linnaeus, 1758) pero no a S*altasaurus loricatus* (Bonaparte y Powell, 1980; Sereno, 2005).

Los dinosaurios terópodos se pueden caracterizar por la presencia de ectopterigoides con una fosa ventral; el solapamiento entre el dentario y los huesos postdentarios se reduce, produciendo una articulación intramandibular; las epipófisis cervicales son elongadas; poseen huesos pneumatizados; las zigapófisis anteriores de las vértebras caudales distales son alargadas; las manos experimentan una transformación, con la reducción del dedo V y la aparición de facetas articulares intermetacarpales entre los metacarpos I y III; y la presencia de depresiones extensoras profundas en los metacarpos I y III (Holtz y Osmólska, 2004).

2.2 Clasificación de los terópodos

El terópodo más antiguo conocido, *Eodromaeus murphi* (Martinez *et al.,* 2011) proveniente de los depósitos del Carniense de la Formación Ischigualasto en Argentina. Los primeros terópodos son animales bípedos, de cráneo alargado y pequeño tamaño que retienen la dentición zifodonta, presente en arcosaurios más primitivos (Holtz, 2012; Hendrickx *et al.*, 2015a). A continuación se presenta un repaso de los principales clados de terópodos (**Figura 3**).

Durante el Triásico Superior surge el clado Neotheropoda (Bakker, 1986) apareciendo clados de terópodos más derivados como Coelophysoidea (Nopsca, 1928) de pequeño y mediano tamaño que sobreviven el tránsito del Triásico al Jurásico, o Dilophosauridae (Hendrickx *et al.*, 2015a), terópodos de tamaño medio a grande del Jurásico Inferior.

Averostra (Paul, 2002) es el clado que engloba a los dos grupos principales de dinosaurios terópodos: Ceratosauria (Marsh, 1884) y Tetanurae (Gauthier, 1986).

El clado Ceratosauria aparece en el Jurásico Inferior e incluye a terópodos de pequeño a gran tamaño, principalmente carnívoros. Este grupo incluye a los ceratosáuridos, con los géneros *Ceratosaurus* (Marsh, 1884), uno de los dinosaurios icónicos de la Formación Morrison de Norteamérica, con una estructura similar a un cuerno en los huesos nasales y osteodermos; y *Genyodectes* (Rauhut, 2004). Hay evidencias de ceratosáuridos en Europa (Mateus *et al.*, 2006), Norteamérica (Madsen y Welles, 2000), Sudamérica (Rauhut, 2004; Soto y Perea, 2008) y África (Rauhut, 2011). Los ceratosáuridos poseen dentición zifodonta,

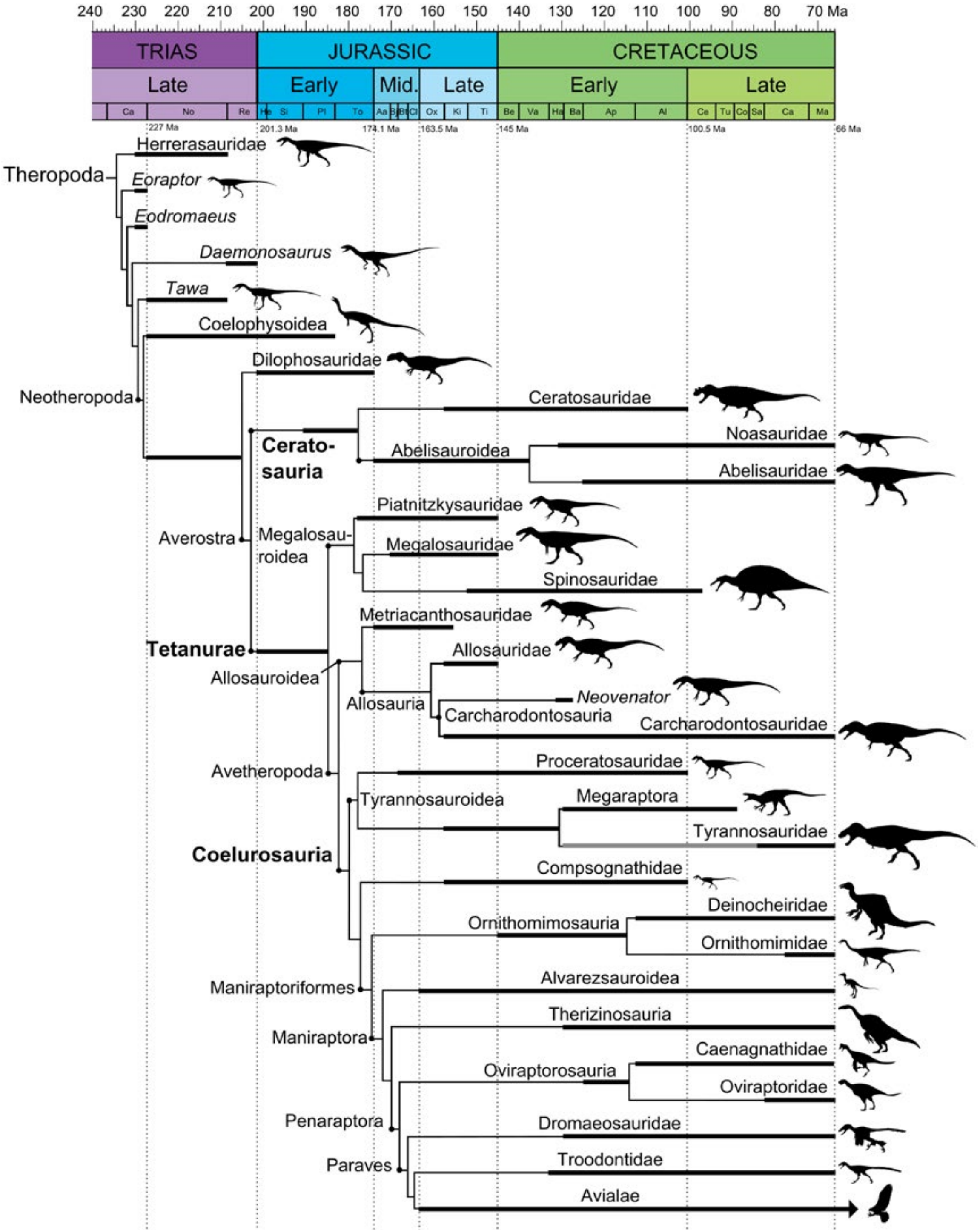


Fig. 3: Distribución estratigráfica y filogenia de los clados de dinosaurios terópodos. Extraído de Hendrickx *et al.,* 2015a.

muy comprimida en los dientes laterales y dientes mesiales más engrosados, que en el caso de *Ceratosaurus* están ornamentados con estrías en la cara lingual (Madsen y Welles, 2000; Rauhut, 2011; Mateus *et al.,* 2006).

Ceratosauria también incluye a Abelisauroidea, dividido en las familias Abelisauridae y Noasauridae, formas que aparecen en el Jurásico y tienen gran desarrollo en el Cretácico de Gondwana (Delcourt, 2018). Los abelisáuridos se caracterizan por ser terópodos de tamaño medio a grande, con un cráneo corto, robusto, ornamentado y con protuberancias óseas (Carrano y Sampson, 2008; Canale *et al.*, 2009; Pol y Rauhut, 2012), con manos y extremidades reducidas (Ruiz *et al.*, 2011) y dientes zifodontos robustos, poco curvados y elongados, con las carenas cubriendo ambos márgenes (Hendrickx y Mateus, 2014b; Smith, 2007). Los noasáuridos, por su parte, son un grupo de terópodos pequeños y gráciles como *Masiakasaurus* (Sampson *et al.*, 2001). Estudios recientes han sugerido que también incluyen a los dinosaurios relacionados con *Elaphrosaurus* (Canale *et al.*, 2009; Rauhut y Carrano, 2016). La dentición de los noasáuridos es de pequeño tamaño, con dientes mesiales folidontos y dientes laterales zifodontos con carenas que alcanzan el cérvix y dentículos distales mayores que los mesiales (Sampson *et al.,* 2001; Hendrickx *et al.,* 2015b).

El clado Tetanurae se define como el clado más inclusivo que contiene a *Passer domesticus* pero no a *Ceratosaurus nasicornis* (Allain *et al.*, 2012) (**Figura 4a**). Es un clado con gran diversidad de tamaños y estrategias de alimentación, y que incluye a las aves y al primer dinosaurio que recibió un nombre válido, *Megalosaurus* (Buckland, 1824; Mantell, 1827). Los primeros tetanuros aparecen en el Jurásico Inferior y durante el Jurásico Medio alcanzan una distribución global (Carrano *et al.*, 2012).

Una radiación importante de los tetanuros es la que da lugar al clado Megalosauroidea (Fitzinger, 1843), que contiene a Piatnitzkysauridae (Carrano *et al.*, 2012), Megalosauridae (Fitzinger, 1843) y Spinosauridae (Stromer, 1915). El descubrimiento de un megalosauroideo muy completo del Jurásico Superior de Alemania (Rauhut *et al.*, 2012) que muestra protoplumas ha probado la presencia de estas estructuras en tetanuros basales.

Los piatnitzkysáuridos son un grupo de terópodos de tamaño medio de América (Madsen, 1976a; Bonaparte, 1986; Rauhut, 2005), con dientes zifodontos con dentículos distales mayores que los mesiales, no muy comprimidos labiolingualmente (Hendrickx *et al.,* 2015b). Por su parte, los megalosáuridos son un grupo de terópodos del Jurásico Medio y Superior de tamaño medio a muy grande (Hendrickx *et al.*, 2015a) que probablemente se extinguieron en el tránsito Jurásico-Cretácico (Carrano *et al.*, 2012). Incluye a alguno de los dinosaurios terópodos más grandes que se conocen, como *Torvosaurus* (Galton y Jensen, 1979). Los dientes de megalosáuidos son zifodontos, presentan una carena mesial que no alcanza el cérvix, carena distal a lo largo de todo el margen; ambas carenas están centradas en la corona, los dentículos tienen un tamaño similar y pueden alcanzar grandes tamaños (Hendrickx *et al.,* 2015b).

Los espinosáuridos constituyen uno de los grupos más particulares dentro de los terópodos, con un cráneo alargado y distintivo (**Figura 4b**), dientes cónicos con estrías longitudinales y dentículos pequeños (Charig y Milner, 1997; Sereno *et al.*, 1998; Canudo *et al.*, 2008a; Buffetaut, 2012). Estos caracteres son interpretados como evidencia de una tendencia piscívora, apoyada por el alargamiento del cráneo, el contenido estomacal, la composición isotópica de los huesos y los datos biomecánicos (Charig y Milner, 1997; Rayfield *et al.*, 2007; Amiot *et al.*, 2010), aunque hay evidencias de alimentación en pterosaurios u otros dinosaurios (Charig y Milner, 1997; Buffetaut *et al.,* 2004; Allain *et al.*, 2012). Estudios recientes han apuntado a una serie de posibles adaptaciones del taxón *Spinosaurus* congruentes con un estilo de vida semiacuático (Ibrahim *et al.*, 2014; Arden *et al.*, 2019), aunque otros autores (Henderson, 2018) señalan más bien una posible adaptación a medios de vida costeros o señalan con esta novedosa reconstrucción de *Spinosaurus* de 2014 (Evers *et al.*, 2015).

Los espinosáuridos son abundantes durante el Cretácico Inferior, apareciendo en el norte de África, Europa, Asia y Sudamérica (Kellner *et al.*, 2011; Allain *et al.*, 2012; Fanti *et al.*, 2014; Alonso y Canudo, 2016; Sales y Schultz, 2017) desapareciendo en el Cretácico Superior (Hone *et al.*, 2010). Se ha observado una correlación positiva en la presencia de espinosáuridos en paleoambientes cercanos a la costa (Sales *et al.*, 2016; Gasca *et al.*, 2018) vista en otros megalosauroideos (Rauhut *et al.*, 2016).

Avetheropoda es el clado menos inclusivo que incluye a *Allosaurus fragilis* y a *Passer domesticus* (Allain *et al.*, 2012), contiene a Allosauroidea y a Coelurosauria. Los alosauroideos constituyen un grupo importante de dinosaurios terópodos que abarca a metriacantosáuridos, alosáuridos, neovenatóridos y carcarodontosáuridos.

Metriacanthosauridae, descrito por Paul, (1988) es similar a Sinraptoridae (Currie y Zhao, 1993) e incluye a terópodos del Jurásico de Asia y Europa (Von Huene, 1923; Dong *et al.*, 1978; Dong, 1984; Wu *et al.*, 2009) y a un género del Cretácico Inferior de Tailandia (Buffetaut *et al.*, 1996) con dientes zifodontos poco curvados y borde distal prácticamente recto (Hendrickx *et al.,* 2015b).

Allosauridae (Marsh, 1878) es un grupo de terópodos del Jurásico Superior de Norteamérica (Madsen, 1976b) y Portugal (Mateus *et al.*, 2006) caracterizado por la estructura del lacrimal. Son zifodontos con dientes mesiales en sección de D y laterales con la carena distal desplazada a labial (Madsen, 1976b; Hendrickx *et al.,* 2015b). Son dinosaurios carnívoros de tamaño grande y unos de los depredadores importantes de sus ecosistemas. Incluye al conocido *Allosaurus* (Marsh, 1877).

Neovenatoridae (Benson *et al.*, 2010) es un clado que incluye terópodos carnívoros gráciles y de gran tamaño, con dentición zifodonta (**Figura 4c**), como *Neovenator* (Hutt *et al.*, 1996; Brusatte *et al.*, 2008).

Dentro de los alosauroideos destaca el clado Carcharodontosauridae (Stromer, 1931). Es un grupo de carnívoros cuyas primeras evidencias aparecen el Jurásico (Rauhut, 2011;

Malafaia *et al.*, 2018a) experimentando una gran diversificación y llegando a ser parte de los depredadores más importantes durante el Cretácico Inferior y "medio" en Europa (Ortega *et al.*, 2010), Asia (Brusatte *et al.,* 2009), África (Rauhut, 1995; Brusatte y Sereno, 2007) y América (Currie y Carpenter, 2000; Novas *et al.*, 2005; Coria y Currie, 2006). Poseen dientes

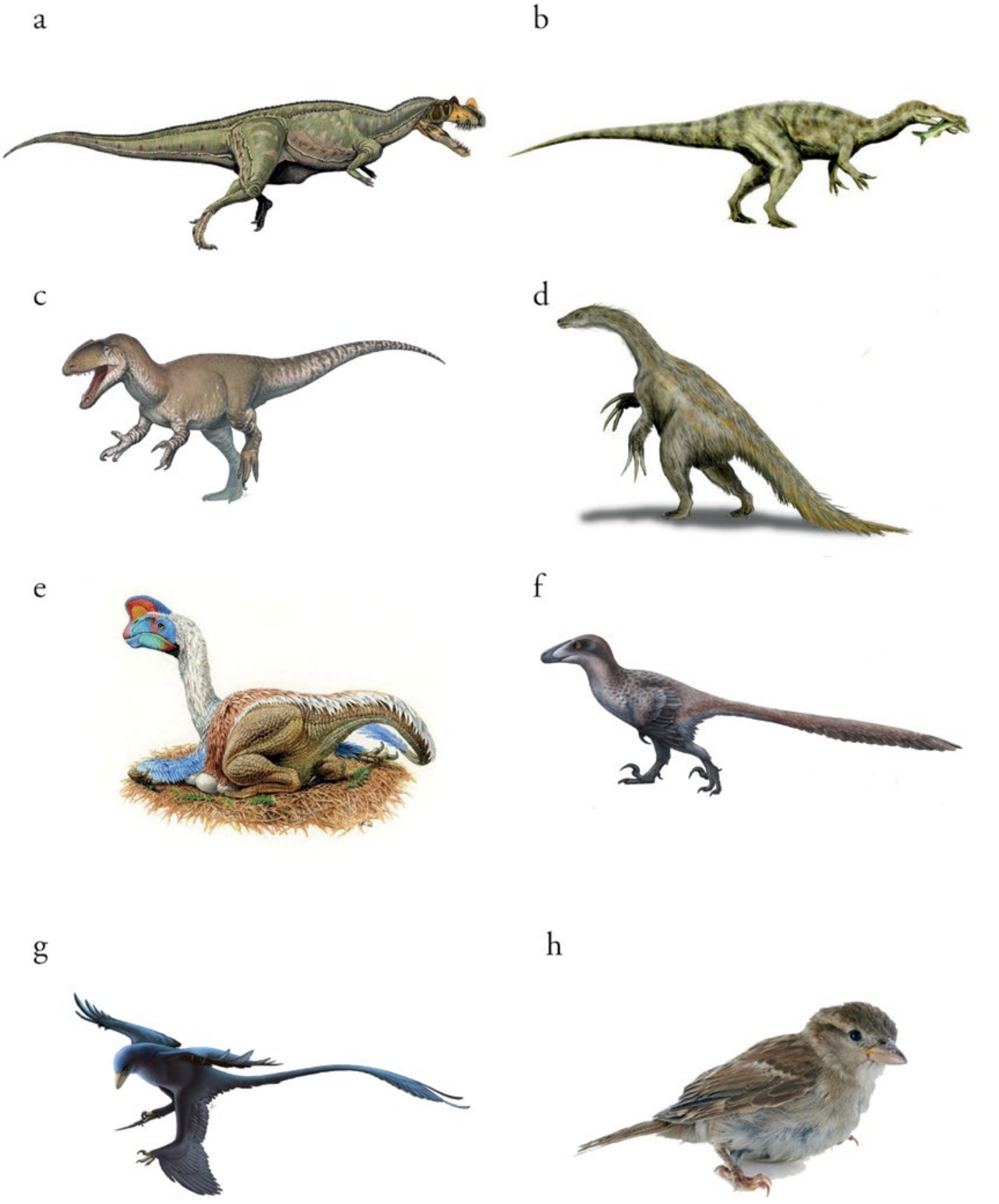


Fig. 4: Diversidad morfológica del clado Theropoda. **a)** *Ceratosaurus nasicornis* (dibujo de Dmitry Bogdanov); **b)** *Baryonyx walkeri* (ilustración de Nobu Tamura); **c)** *Neovenator salerii* (Fred Wierum); **d)** *Nothronychus mkinleyi* (Arthur Weasley); **e)** *Oviraptor philoceratops* (Julius Cstonyi); **f)** *Deinonychus antirrhopus* (Emily Willoughby); **g)** *Microraptor gui* (Fred Wierum); h) *Passer domesticus* (www.pngall.com).

zifodontos comprimidos que pueden alcanzar gran tamaño, con la carena mesial generalmente extendiéndose hasta el cérvix (Hendrickx *et al.,* 2015b).

Coelurosauria (Von Huene, 1914a) es el clado más inclusivo que contienen a *Passer domesticus* pero no a *Allosaurus fragilis*, *Sinraptor dongi* o *Carcharodontosaurus saharicus* (Sereno, 2005). Es un clado con una amplia diversidad de terópodos derivados que contiene a las aves y a formas carnívoras, herbívoras y omnívoras.

Uno de los grupos más populares de los coelurosaurios son los tiranosauroideos, clado que incluye a la familia Proceratosauridae (Rauhut *et al.*, 2010), Tyrannosauridae (Osborn, 1906a) y, según algunos autores, a Megaraptora (Benson *et al.*, 2010).

Megaraptora es un clado de terópodos de tamaño medio del Cretácico de Sudamérica, Asia y Australia, que sobrevive hasta el Cretácico Superior (Azuma y Currie, 2000; Currie y Azuma, 2006; Novas *et al.*, 2008; Porfiri *et al.*, 2014, 2018; White *et al.*, 2015; Coria y Currie, 2016), caracterizados por un cráneo alargado y extremidades largas y robustas (Hendrickx *et al.,* 2015a). Existe incertidumbre en la posición de Megaraptora dentro de Neovenatoridae o como grupo hermano de Tyrannosauroidea (Novas *et al.*, 2013; Zanno y Makovicky, 2013; Canale *et al.*, 2014a; Porfiri *et al.*, 2014; Bell *et al.*, 2016; Coria y Currie, 2016; Rolando *et al.,* 2019). Poseen dientes zifodontos recurvados con una carena distal serrada y una mesial reducida (White *et al.,* 2015).

Los proceratosáuridos son un clado de terópodos de pequeño tamaño de Europa y Asia cuyo rango abarca del Jurásico Medio (Rauhut *et al.*, 2010) al Cretácico Inferior (Ji *et al.*, 2009), caracterizados por una cresta sagital en los huesos nasales (Averianov *et al.,* 2010).

En Tyrannosauroidea también se incluyen una serie de géneros de pequeño y mediano tamaño del Jurásico Superior y Cretácico de Norteamérica, Europa y Asia como *Aviatyrannis*, *Juratyrant, Eotyrannus* o *Dilong* (Hutt, 2001; Rauhut, 2003; Xu *et al.*, 2004; Brusatte y Benson, 2013).

La familia más icónica es sin duda Tyrannosauridae (Brusatte *et al.,* 2010a), conocida por especies como *Tyrannosaurus rex* (Osborn, 1906b) y otros grandes depredadores del Cretácico Superior de Norteamérica como *Albertosaurus* (Osborn, 1905) o *Daspletosaurus* (Russell, 1970). Los tiranosáuridos son animales de gran tamaño y robustez, con grandes cráneos y mandíbulas potentes y extremidades reducidas, dos dedos funcionales en las manos (Holtz, 2004; Hendrickx *et al.*, 2015a) y dientes con coronas engrosadas (Smith, 2005). También aparecen representantes en Asia, como *Tarbosaurus* (Maleev, 1955) o *Alioramus* (Kurzanov, 1976), un tiranosáurido de Cretácico Superior de Mongolia grácil y de rostro alargado (Brusatte *et al.*, 2012).

Se han estudiado numerosos aspectos de la paleobiología de los tiranosaurios, como la locomoción (Sellers *et al.*, 2017), la alimentación (Erickson y Olson, 1996; Jacobsen, 1998; Gignac y Erickson, 2017), los sistemas sensoriales, la audición y la visión (Stevens, 2006; Witmer y Ridgely, 2009; Carr *et al.*, 2017), la dentición (Samman *et al.,* 2005; Smith, 2005; Buckley *et al.,* 2010) o los aspectos paleobiogeográficos (Loewen *et al.*, 2013).

Coelurosauria también engloba a clados de terópodos derivados como Compsognathidae (Cope, 1871), terópodos gráciles de pequeño tamaño (Holtz *et al.,* 2004) del Jurásico Superior y Cretácico Inferior de Europa (Bidar *et al.*, 1972; Göhlich y Chiappe, 2006), América (Naish *et al.,* 2004) y Asia (Hwang *et al.,* 2004). Los dientes son de pequeño tamaño, zifodontos y con dentículos muy pequeños en la carena distal (Hendrickx *et al.,* 2015b).

Ornithomimosauria (Barsbold, 1976) es un grupo de terópodos omnívoros y herbívoros (Zanno y Makovicky, 2011; Lee *et al.*, 2014) de tamaño pequeño a grande del Cretácico, con cráneos ligeros, extremidades alargadas, cuyos representantes basales conservan una dentición reducida que desaparece en taxones más derivados (Makovicky *et al.,* 2004). Se han hallado restos en Europa (Pérez-Moreno *et al.*, 1994) Asia, (Kobayashi y Lü, 2003; Liyong, Jun y Godefroit, 2012), África (De Klerk *et al.*, 2000; Choiniere *et al.,* 2012) y Norteamérica (Russell, 1972).

El grupo hermano de Ornithomimosauria es Maniraptora (Gauthier, 1986), definido como el clado más inclusivo que contiene a *Passer domesticus* pero no a *Ornithomimus velox* (Marsh, 1890; Maryańska *et al.*, 2002). Estos terópodos se caracterizan por un proceso lateral del cuadrado muy desarrollado, un esternón con placas esternales osificadas y un carpal semilunar (Holtz, 2012; Hendrickx *et al.*, 2015).

Los maniraptores más basales incluyen a los alvarezsauroideos, terizinosaurios y oviraptores. Alvarezsauroidea (Choiniere *et al.*, 2010) incluye a terópodos de pequeño tamaño, gráciles, con el cráneo alargado y dentición zifodonta y folidonta, de pequeño tamaño y con constricción basal (Choiniere *et al.*, 2010; Hendrickx, 2015). Therizinosauria (Russell, 1997) (=Segnosauria, Barsbold y Perle, 1980), por su parte, pueden alcanzar grandes tamaños, y se caracterizan por una cabeza pequeña y cuerpo y brazos robustos rematados por largas garras (**Figura 4d**), con dientes folidontos pequeños, con constricción basal y dentículos en los taxones más primitivos (Kirkland *et al.,* 2005; Hendrickx, 2015), apareciendo en el Cretácico de Norteamérica y Asia (Clark *et al.,* 2004; Kirkland *et al.,* 2005). Oviraptorosauria (Barsbold, 1976) son otro grupo derivado de maniraptores de tamaño variable, caracterizado por cráneos cortos, extremidades anteriores con dedos alargados y colas cortas (**Figura 4e**), que retienen dientes folidontos sin dentículos (Hendrickx, 2015) que se pierden en los derivados; teniendo una alimentación parcialmente herbívora (Maryańska *et al.,* 2002; Lü *et al.,* 2013; Hendrickx *et al.,* 2015a)

El resto de maniraptores se engloban dentro del clado Paraves (Sereno, 1997), definido como el clado más inclusivo que contiene a *Passer domesticus* pero no a *Oviraptor philoceratops* (Osborn, 1924; Holtz y Osmólska, 2004) e incluye a dos grupos de terópodos no avianos y a las aves.

Dromaeosauridae (Matthew y Brown, 1922; Colbert y Russell, 1969) constituye un grupo de dinosaurios carnívoros de tamaño pequeño a grande de gran extensión geográfica que probablemente aparecen en el Jurásico junto a otros miembros de Paraves (Hendrickx *et al.,* 2015a) y que se distribuyen en todos los continentes durante el Cretácico Superior. Este clado incluye a dinosaurios muy conocidos, como *Dromaeosaurus* (Matthew y Brown, 1922), *Velociraptor* (Osborn, 1924) o *Deinonychus* (Ostrom, 1969) (**Figura 4f**). A partir del estudio de este último comienza un cambio en la manera de ver los dinosaurios, de animales lentos grandes y torpes a animales activos y ágiles, generando la *dinosaur renaissance* (Bakker, 1975). Se trata de dinosaurios bípedos, con tres dedos en las extremidades anteriores rematadas por garras afiladas y tres dedos en las extremidades posteriores con dedo II alargado y retráctil (Norell y Makovicky, 2004), aunque el taxón *Balaur bondoc* también tiene el dedo I elongado en el pie (Csiki *et al.,* 2010). Algunos taxones de dromeosáuridos han revelado una serie de adaptaciones interpretadas como propias de una vida semiacuática, parecida a la de algunas aves actuales (Cau *et al.,* 2017). Otros grupos, como los microraptores, han revelado una serie de caracteres interpretados como adaptaciones al planeo (Xu *et al.,* 2003)(**Figura 4g**). Los dientes son zifodontos pudiendo aparecer taxones sin carena mesial o con la carena mesial desplazada a lingual, dentículos de diferente tamaño en las carenas mesial o distal y la presencia de concavidades en las superficie labial o lingual (Currie *et al.,* 1990; Hendrickx *et al.,* 2015b).

Troodontidae (Gilmore, 1924) es un clado de terópodos derivados no avianos de pequeño tamaño, ligeros, del Cretácico de Asia y Norteamérica (Makovicky y Norell, 2004). Es un grupo de dinosaurios probablemente herbívoros en sus formas basales (Hendrickx *et al.,* 2015a), adquiriendo una dieta carnívora u omnívora en taxones más derivados, aunque limitada por la morfología dental (Zanno y Makovicky, 2011; Torices *et al.,* 2018). Los dientes, de pequeño tamaño, pueden ser zifodontos o folidontos, con dentículos poco numerosos y de gran tamaño (Currie *et al.,* 1990; Hendrickx, 2015; Torices *et al.,* 2018).

Avialae (Gauthier, 1986) es el clado más inclusivo que contiene a *Passer domesticus* pero no a *Dromaeosaurus albertensis* o *Troodon formosus* (Leidy, 1856; Godefroit *et al.*, 2013). Tradicionalmente, la distinción entre terópodos no avianos y aves se ha situado alrededor de *Archaeopteryx* (Meyer, 1861; Cau, 2018) y su posición presenta cierta incertidumbre, recuperado bien como Avialae basal (Agnolín y Novas, 2013), como Avialae más derivado (Godefroit *et al.,* 2013) o como deinonicosaurio (Xu *et al.*, 2011). En cambio, trabajos recientes enfatizan en la adquisición del plan corporal aviano como un proceso que se extiende durante 160 millones de años en sucesivas etapas no reducibles a la aparición de un único taxón o a única adaptación (Cau, 2018).

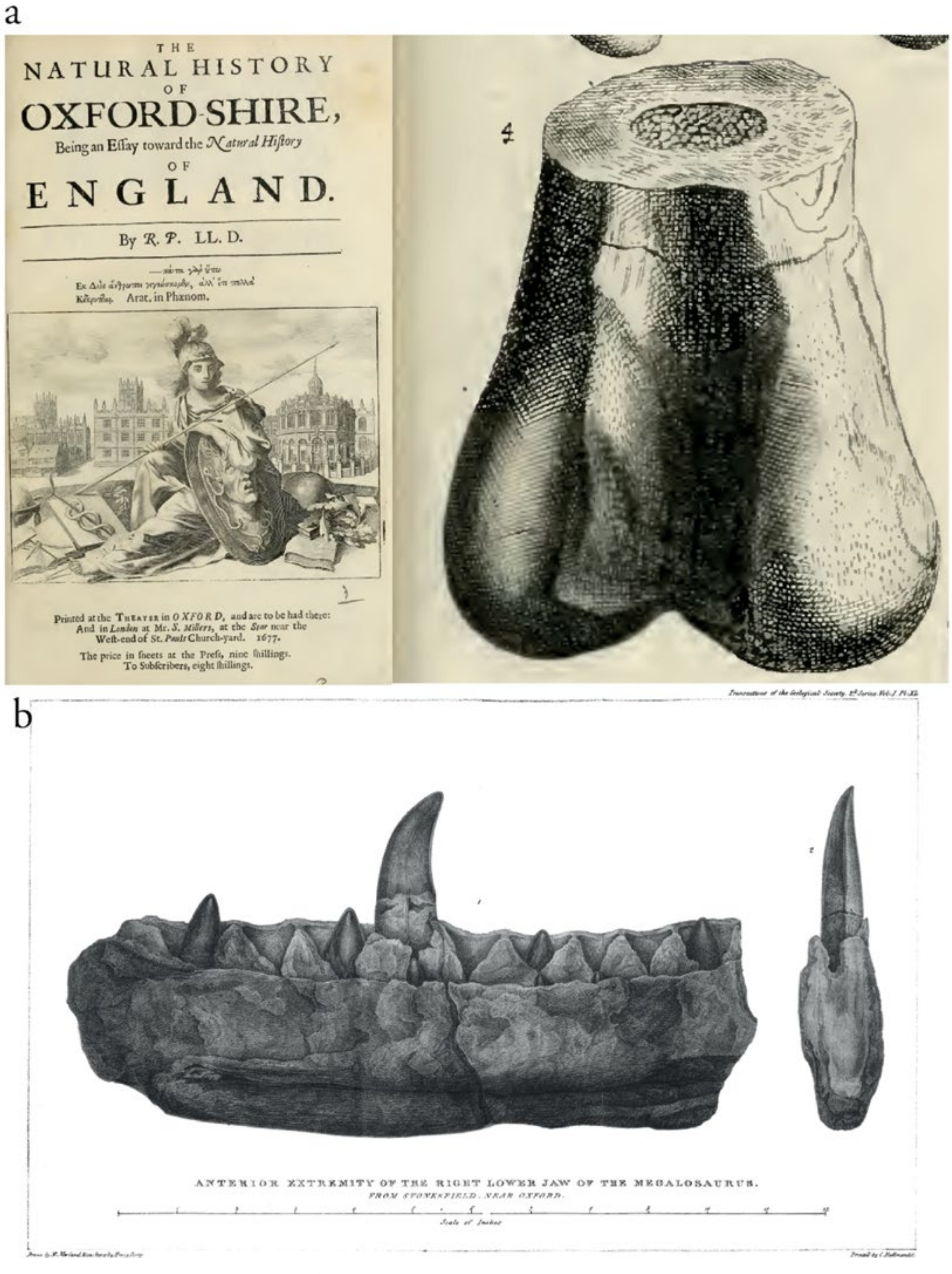
Algunos grupos de aves fueron los únicos dinosaurios que sobrevivieron a la extinción de finales del Cretácico (**Figura 4h**). Recientemente se ha propuesto la hipótesis de la pérdida de la dentición y la aparición del pico como un posible factor, al permitir un cambio en la dieta orientado al consumo de semillas (Brusatte, 2016; Larson *et al.,* 2016). Para la aparición del pico también se ha propuesto la hipótesis de que la formación de dientes limita la velocidad de desarrollo embrionario, permitiendo la pérdida de dientes un desarrollo más rápido y un tiempo de incubación menor (Yang y Sander, 2018). Las aves son un grupo de gran éxito con una distribución global (Monroe y Sibley, 1993).

3. ANTECEDENTES DE HALLAZGOS EN EL JURÁSICO SUPERIOR Y EL CRETÁCICO INFERIOR DE EUROPA

Es en Europa durante el siglo XIX donde se identifican los primeros fósiles de dinosaurios terópodos. Anteriormente diversos restos fósiles habían sido encontrados por humanos de diferentes culturas, atribuidos a criaturas míticas o legendarias. El primer registro de un resto de terópodo publicado corresponde a un fémur incompleto detallado por Rober Plot (1677), atribuido en primer lugar a un gigante. El fémur fue ilustrado por el naturalista Richard Brookes (1763), que denominó a la figura *Scrotum Humanum* (**Figura 5a**), el primer nombre binomial dado a un resto de dinosaurio. Es también en el siglo XVII cuando el naturalista Edward Lhuy figura dientes aislados de terópodo que identifica como dientes de pez (Hendrickx *et al.,* 2015a).

Habría que esperar hasta el siglo XIX para reconocer y describir al primer dinosaurio terópodo, *Megalosaurus*, por William Buckland (1824) (**Figura 5b**). Un poco más tarde Gideon Mantell (1827) fue el primero en realizar un diagnóstico de los restos y nombrar la especie *Megalosaurus bucklandii*. Poco tiempo después se describen dos nuevas especies en Francia, *Streptospondylus altdorfensis* (Meyer, 1832) y *Poekilopleuron bucklandii* (Eudes-Deslongchamps, 1836) todas ellas del Jurásico Medio. Destacan las aportaciones paleontológicas de los naturalistas Gideon Mantell, Georges Cuvier y Richard Owen al conocimiento de los dinosaurios, entre otros grupos. Estos científicos describieron los dientes de *Suchosaurus*, que atribuyeron a crocodilomorfos y que ahora se consideran cercanos al espinosaurio *Baryonyx* (Mateus *et al.*, 2011).

A mediados del siglo XIX se describen nuevas especies de terópodo como *Nuthetes destructor*, del Cretácico Inferior de Inglaterra (Owen, 1854), *Compsognathus longpipes*



THE
NATURAL HISTORY
OF
OXFORD-SHIRE,
Being an Eſſay toward the *Natural Hiſtory*
OF
ENGLAND.

By *R. P.* LL. D.

Arat. in Phænom.

Printed at the Theater in *OXFORD*, and are to be had there:
And in *London* at Mr. *S. Millers*, at the *Star* near the
Weſt-end of St. *Pauls* Church-yard. 1677.

The price in ſheets at the Preſs, nine ſhillings.
To Subſcribers, eight ſhillings.

ANTERIOR EXTREMITY OF THE RIGHT LOWER JAW OF THE MEGALOSAURUS.
FROM STONESFIELD, NEAR OXFORD.

Fig. 5: Primeros registros de Theropoda. **a)** *Historia Natural* de Robert Plot (1677) e ilustración de la parte distal de un fémur izquierdo de terópodo; **b)** Dentario derecho de *Megalosaurus*, illustrado por William Buckland (1824).

(Wagner, 1861) o *Archaeopteryx litographica* (Meyer, 1861) del Jurásico Superior de Solnhofen, Alemania. Es en esta época cuando comienzan a realizarse descubrimientos de dinosaurios en otros lugares del mundo, como Norteamérica.

Hacia finales del siglo se realizan nuevas contribuciones, reconociéndose taxones como *Aristosuchus* (Owen, 1876; Seeley, 1887). Pero es durante el siglo XX cuando más se ha ampliado el conocimiento sobre dinosaurios terópodos europeos, describiéndose numerosas especies del Jurásico Superior y el Cretácico Inferior y publicándose trabajos que han contribuido a ampliar el conocimiento de este grupo (por ej., Von Huene, 1932; Hutt *et al.,* 1996; Charig y Milner, 1997; Dal Sasso y Signore, 1998; Hutt, 2001; Milner, 2002; Sweetman, 2004; Göhlich y Chiappe, 2006; Peyer, 2006; Brusatte *et al.,* 2008; Lindgren *et al.,* 2008; Benson *et al.,* 2009; Naish y Sweetman, 2011; Rauhut *et al.*, 2012; Brusatte y Benson, 2013; Csiki-Sava *et al.,* 2016; Gerke y Wings, 2016; Foth y Rauhut, 2017; Louchart y Pouech, 2017; Austen y Batten, 2018).

3.1 Terópodos en el Jurásico Superior-Cretácico Inferior de la península ibérica

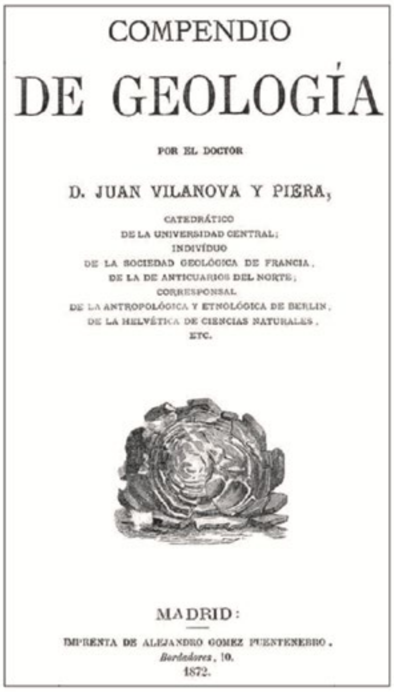
Como en el resto de Europa, los primeros hallazgos de dinosaurios terópodos en la península se remontan al siglo XIX. El fósil más antiguo conocido en España es un diente de terópodo del Jurásico Superior de Asturias, descrito en 1858 como un diente de tiburón por el geólogo Justo Egozcue (Pereda-Suberbiola y Ruiz-Omeñaca, 2005). Pocos años después, en 1863, el ingeniero de minas Carlos Ribeiro descubre dos dientes de terópodo en la localidad portuguesa de Porto das Barcas (Antunes y Mateus, 2003).

En 1872 el naturalista Juan Vilanova Piera cita unos restos fósiles procedentes de las localidades de Utrillas y Morella, que atribuyen en aquel momento a *Iguanodon* (**Figura 6**). Los restos de Utrillas serán asignados más tarde, en 1927, como pertenecientes a un dinosaurio terópodo por José Royo Gómez. (Pereda-Suberbiola y Ruiz-Omeñaca, 2005).

A partir de 1940 la investigación de dinosaurios en la península experimenta una reactivación con la presencia de paleontólogos como Georges Zbyszewski, Albert Félix de Lapparent, Emiliano Aguirre, Walter Kühne y Bernard Krebs. No será hasta los años 70-80 cuando los estudios ibéricos de dinosaurios comiencen a aflorar, como muestran trabajos como el de Santafé *et al.,* (1982) (Cuenca-Bescós *et al.,* 1999; Ortega *et al.,* 2006). Este proceso se hace patente al llegar al primer dinosaurio descrito en España, el saurópodo *Aragosaurus ischiaticus* (Sanz *et al.*, 1987).

Desde los años 90 hasta la actualidad existen numerosos grupos de investigación sobre dinosaurios en la península. En los últimos 20 años el estudio de los dinosaurios en Aragón ha estado encabezada por los investigadores de la Universidad de Zaragoza del Grupo Aragosaurus, dirigido por los profesores Gloria Cuenca-Bescós y José Ignacio Canudo.

Los lugares más ricos en restos de dinosaurios del Jurásico Superior y el Cretácico Inferior de la península ibérica se localizan en la cuenca lusitánica de Portugal, en la "costa de



COMPENDIO

DE GEOLOGÍA

POR EL DOCTOR

D. JUAN VILANOVA Y PIERA,

CATEDRÁTICO
DE LA UNIVERSIDAD CENTRAL;
INDIVÍDUO
DE LA SOCIEDAD GEOLÓGICA DE FRANCIA,
DE LA DE ANTICUARIOS DEL NORTE;
CORRESPONSAL
DE LA ANTROPOLÓGICA Y ETNOLÓGICA DE BERLIN,
DE LA HELVÉTICA DE CIENCIAS NATURALES,
ETC.

MADRID:

IMPRENTA DE ALEJANDRO GOMEZ FUENTENEBRO,
Bordadores, 10.
1872.

Fig. 6: Primera cita de un resto de dinosaurio en España por D. Juan Vilanova y Piera. Extraído de Pereda-Suberbiola y Ruiz-Omeñaca, 2005.

los dinosaurios" de Asturias y en la Cordillera Ibérica.

En los depósitos del Jurásico Superior, en las Formaciones Lourinhã y Alcobaça se han identificado diversos taxones de dinosaurios terópodos, como *Lourinhanosaurus antunesi* (Mateus, 1998), *Avyatirannis jurassica* (Rauhut, 2003), *Ceratosaurus* sp. y *Allosaurus europaeus* (Mateus *et al.,* 2006) y *Torvosaurus gurneyi* (Hendrickx y Mateus, 2014a), un alosauroideo indeterminado en la Formación Praia da Amoreira-Porto Novo (Malafaia *et al.,* 2017a) y un carcharodontosaurio indeterminado de la Formación Freixal (Malafaia *et al.*, 2018a). Se han identificado otros grupos mediante el estudio de dientes aislados de dinosaurios terópodos, tales como abelisáuridos, tetanuros basales, coelurosaurios, maniraptores y cf. *Archaeopteryx* sp. (Rauhut y Kriwet, 1994; Weigert, 1995; Zinke, 1998; Rauhut, 2000; Hendrickx y Mateus, 2014b; Malafaia *et al.,* 2017b).

En la Formación Papo Seco del Cretácico Inferior de Cabo Espichel se han identificado dientes y un dentario izquierdo y otros restos postcraneales asignados a *Baryonyx* o afines (Mateus *et al.*, 2011; Figueiredo *et al.,* 2015).

Las Formaciones Vega, Lastres y Tereñes del Jurásico Superior de Asturias han aportado evidencias sobre los dinosaurios del Kimmeridgiense de España (García-Ramos *et al.,* 2006). Los restos de terópodo consisten principalmente en dientes aislados (Martínez *et al.,* 2000; Ruiz-Omeñaca *et al.,* 2008; Ruiz-Omeñaca *et al.*, 2012a) y una vértebra caudal anterior de gran tamaño de un megalosáurido (Rauhut *et al.,* 2018b) junto con icnitas.

Entre los fósiles recuperados en España destacan los de la Cordillera Ibérica. En la Formación Villar del Arzobispo se han hallado fósiles de terópodos tetanuros, principalmente restos aislados (por ej., (Canudo *et al.,* 1997b, 2005a, 2006; Barco y Ruiz-Omeñaca, 2001; Canudo y Ruiz-Omeñaca, 2003; Sánchez-Hernández *et al.,* 2007; Royo-Torres *et al.,* 2009; Suñer y Martín, 2009; Gascó *et al.,* 2012; Cobos *et al.,* 2014).

En el Cretácico Inferior de Cuenca se han descrito nuevas especies como ornitomimosaurio *Pelecanimimus polyodon* (Pérez-Moreno *et al.,* 1994), *Concavenator corcovatus*, uno de los carcarodontosáuridos más completos del registro fósil (Ortega *et al.,* 2010), y las aves *Iberomesornis romerali* (Sanz y Bonaparte, 1992), *Concornis lacustris* (Sanz y Buscalioni, 1992) y *Eoalulavis hoyasi* (Sanz *et al.,* 1996), todos del yacimiento de Las Hoyas, del Barremiense superior. También se han referido dientes aislados en otros yacimientos de la provincia como Uña (Rauhut, 2002)

En la Cuenca de Cameros se han citado dientes aislados de terópodos espinosáuridos y coelurosaurios (Torcida *et al.,* 1997; Pereda-Suberbiola *et al.,* 1999; Torcida Fernández-Baldor *et al.*, 2003; Torcida Fernández-Baldor, 2006; Alonso *et al.,* 2017) y restos poscraneales atribuidos a *Baryonyx* (Fuentes Vidarte *et al.,* 1999) provenientes de los yacimientos del entorno de Salas de los Infantes (Burgos). En la provincia de la Rioja se ha citado un maxilar de *Baryonyx* (Viera y Torres, 1995), y recientemente se ha llevado a cabo el primer estudio sobre dientes aislados de esta región (Navarro-Lorbés y Torices, 2018).

El único taxón de terópodo erigido en Aragón es *Camarillasaurus cirugedae* (Sánchez-Hernández y Benton, 2012) de la subcuenca de Galve en la Cuenca del Maestrazgo (Teruel). Se han citado otros restos pertenecientes a terópodos en esta cuenca como un fémur de un carcharodontosaurio del Barremiense de la Formación Mirambel (Gasca *et al.,* 2014), una falange ungueal de un megalosauroide de la Formación El Castellar (Gasca *et al.,* 2018), restos postcraneales de espinosáuridos en la Formación Morella (Gómez-Fernández *et al.,* 2007; Malafaia *et al.,* 2018b), y numerosos restos de dientes aislados de espinosáuridos y otros tetanuros basales, junto con maniraptores (por ej., Ruiz-Omeñaca *et al.,* 1995, 1997; Canudo *et al.,* 1997a; Cuenca-Bescós *et al.,* 1999; Ruiz-Omeñaca y Canudo, 2003; Canudo y Ruiz-Omeñaca, 2003; Infante *et al.,* 2005; Ruiz-Omeñaca *et al.,* 2005; Canudo *et al.,* 2008a, 2010, Gasca *et al.,* 2008, 2009, 2011; Pereda-suberbiola *et al.*, 2010; Alonso y Canudo, 2016; Alonso *et al.,* 2018).

Durante los últimos años se ha recolectado material de nuevos yacimientos (Alonso *et al.,* 2016) de la secuencia superior de la Formación Blesa, una formación con un contenido destacado de vertebrados continentales en su parte inferior, como atestigua el yacimiento de La

Cantalera 1 (Canudo *et al.,* 2010a). Las nuevas investigaciones aportan resultados prometedores sobre el potencial fosilífero de esta formación, para entender la paleobiodiversidad de terópodos del Barremiense de la península.

4. SOBRE LOS DIENTES DE DINOSAURIOS TERÓPODOS

Los dinosaurios terópodos fueron un grupo diverso y frecuente tal como apuntan las evidencias paleoicnológicas y la abundancia de dientes aislados en las formaciones mesozoicas. No obstante, los restos óseos son más escasos. Es posible que esté relacionado con la fragilidad de los huesos de los terópodos comparada con otros grupos de dinosaurios (Canudo, 2007), junto a que los predadores existen en menor número que los consumidores primarios en los ecosistemas terrestres.

Por esta razón, el estudio de dientes aislados de terópodos tiene gran interés al ser el resto que aparece con mayor frecuencia en el registro fósil debido a la elevada resistencia de los tejidos dentales (Martin, 1999), permitiendo la identificación de los grupos de terópodos incluso a nivel de familia.

El estudio de dientes aislados comienza en el siglo XIX al observarse su abundancia en los depósitos mesozoicos. Como consecuencia de estos estudios se definen numerosos taxones que tras la revisión llevada a cabo por Von Huene, (1914b) pasan a ser considerados *nomina dubia* (Torices, 2007). Pasan casi 90 años hasta que Currie *et al.,* (1990) vuelvan a demostrar la utilidad sistemática de estos fósiles. Desde ese momento el estudio de dientes de terópodos ha sido una línea viva de investigación en dinosaurios, publicándose numerosos trabajos año a año. Numerosos investigadores han estudiado la paleobiodiversidad, aspectos morfológicos o paleobiológicos. La identificación de los taxones ha mejorado con la determinación de nuevos caracteres dentales, mediciones, con el uso de técnicas de análisis multivariante y aportaciones recientes como el análisis cladístico, que permite incorporar rasgos no recogidos en estudios morfométricos. (por ej., Farlow *et al.,* 1991; Fiorillo, 1991; Fiorillo y Currie, 1994; Rauhut y Werner, 1995; Buscalioni *et al.*, 1997; Park *et al.* 2000; Sankey *et al.* 2002; Hasegawa *et al.* 2003; Samman *et al.* 2005; Smith, 2005; Smith *et al.* 2005; Brusatte *et al.*, 2007; Longrich, 2008; Casal *et al.*, 2009; Buckley *et al.*, 2010; Gascó *et al.*, 2012; Lindoso *et al.*, 2012; Furtado *et al.,* 2013; Larson y Currie, 2013; Torices *et al.*, 2013, 2018; Serrano-Brañas *et al.*, 2014; Williamson y Brusatte, 2014; Hendrickx *et al.,* 2015a, 2015b; Alonso y Canudo, 2016; Gerke y Wings, 2016; Serrano-Martínez *et al.*, 2016; Candeiro *et al.*, 2017).

En la península ibérica destacan los estudios en dientes de terópodos realizados en las tesis doctorales de Torices, (2007), centrada en los terópodos del Cretácico Superior de la Cuenca Surpirenaica, y Hendrickx, (2015) caracterizando los rasgos de los diferentes clados de

Theropoda.

Los dientes de terópodo se dividen en corona y raíz. La corona es la parte que sobresale de la encía hacia el exterior; está compuesta de una capa de esmalte duro en la parte exterior y una capa interior compuesta de dentina excavada por la cavidad pulpar. La raíz, compuesta únicamente de dentina, está insertada en un alveolo (Hillson, 2005).

La composición de estas capas de esmalte y dentina es apatito y materia orgánica como en el resto de vertebrados. El esmalte es prácticamente inorgánico (96%) en su totalidad, con apenas un 1% de materia orgánica siendo agua el resto. No está formado por células; su composición se aproxima al hidroxiapatito. Los cristales de apatito son mayores que los presentes en la dentina o en los huesos y se apiñan con gran densidad (Hillson, 2005). La dentina se compone de un 20% de materia orgánica, principalmente colágeno, 10% de agua y 70% cristales de hidroxiapatito. A diferencia del esmalte es un tejido vivo, con presencia de odontoblastos que ocupan los túbulos de dentina (Hendrickx, 2015). La variación de túbulos de dentina también está relacionada con la alimentación, se ha observado que los dinosaurios herbívoros tienen mayor densidad que los carnívoros, probablemente debido a la abrasión de la dieta (Brink *et al.*, 2016).

A diferencia de los mamíferos, los terópodos son polifiodontos (Whitlock y Richman, 2013), reemplazando dientes a lo largo de toda la vida del organismo. Estudios como Erickson, (1996) han estimado una duración funcional de 777 días para un diente de *Tyrannosaurus* adulto, y en torno a 300 para *Troodon* adulto y *Albertosaurus* juvenil.

La mayoría de terópodos poseen dentición zifodonta (D'Amore, 2009), caracterizada por presentar dientes comprimidos labiolingualmente, curvados hacia posterior y con carenas en los márgenes mesial y distal cubiertos de finas serraciones formadas por dentículos, rasgos que facilitan una dieta hipercarnívora (Brink *et al.,* 2015). La zifodoncia es la condición primitiva de los terópodos. No obstante, a lo largo de la historia evolutiva del clado surgen diferentes morfologías de dientes (Hendrickx *et al.,* 2015c), desarrollando coronas folidontas como las de los therizinosaurios (Kirkland *et al.,* 2005), coronas engrosadas como en *Tyrannosaurus* (Smith *et al.,* 2005), o cónicas como en los espinosáuridos (Sereno *et al.,* 1998).

La variación en la dentición en el clado Theropoda puede dividirse en (Canudo *et al.,* 1999):

Variación posicional: La mayoría de terópodos poseen pseudoheterodoncia ya que la morfología de la corona va cambiando gradualmente dentro de la mandíbula resultando en diferencias entre los dientes mesiales y laterales (Torices, 2007; Hendrickx, 2015). Por ejemplo en el caso de *Ceratosaurus* los dientes anteriores tienen sección subcircular y la cara lingual ornamentada con estrías longitudinales en dirección apicobasal, mientras que los dientes laterales están fuertemente comprimidos y carecen de ornamentación (Madsen y Welles, 2000; Rauhut, 2011), algo similar a lo que se observa en *Dromaeosaurus* (Currie *et al.,* 1990). En *Tyrannosaurus* existen grandes diferencias entre los dientes premaxilares, maxilares y del dentario (Smith, 2005; Reichel, 2010). En general los dientes mesiales suelen tener secciones más engrosadas que los laterales (**Figura 7a**), probablemente por sufrir mayores tensiones en la depredación y alimentación (Hendrickx, 2015).

Variación ontogénica: La variación ontogenética es difícil de calcular debido a la falta de registro de especímenes de un taxón en diferentes estados de crecimiento. En algunos taxones se han observado casos extremos de variación como *Limusaurus*, cuyos juveniles poseen dientes que son sustituidos por una ranfoteca en adultos (Wang *et al.,* 2017). En el caso de *Torvosaurus* se ha observado que los embriones poseen dientes sin dentículos (Araujo *et al.,* 2013), a diferencia de los especímenes adultos (Hendrickx y Mateus, 2014a) (**Figura 7 b, c, d**). Diferencias ontogenéticas también se han observado en tiranosáuridos (Samman *et al.,* 2005; Tsuihiji *et al.,* 2011; Williamson y Brusatte, 2014). Estas diferencias en las proporciones del diente han de ser tenidas en cuenta, sobre todo a la hora de realizar análisis morfométricos.

Variación intraespecífica: Se denomina a la observada entre individuos de la misma edad y especie. Puede deberse a dimorfismo sexual, diferencias geográficas o variabilidad genética, aunque para realizar un estudio adecuado se necesita un número suficiente de dientes de poblaciones conocidas. Se han realizado diversos estudios a este respecto (por ej., Torices, 2007; Buckley *et al.,* 2010).

Variación interespecífica: Variación existente entre especies y taxones, debido a la morfología de la corona, presencia o ausencia de carenas, dentículos, diferencias en sección, densidad de dentículos, tamaño u ornamentación, que permite identificar los dientes aislados y asignarlos a distintos clados de Theropoda (**Figura 7e, f**).

Variación quimérica: Variación debida a traumas o problemas en el desarrollo que generan morfologías anómalas en el diente (**Figura 7g**). Se ha señalado la presencia de carenas divididas (Erickson, 1995) o la presencia de dentículos bilobulados (Hendrickx, 2015)

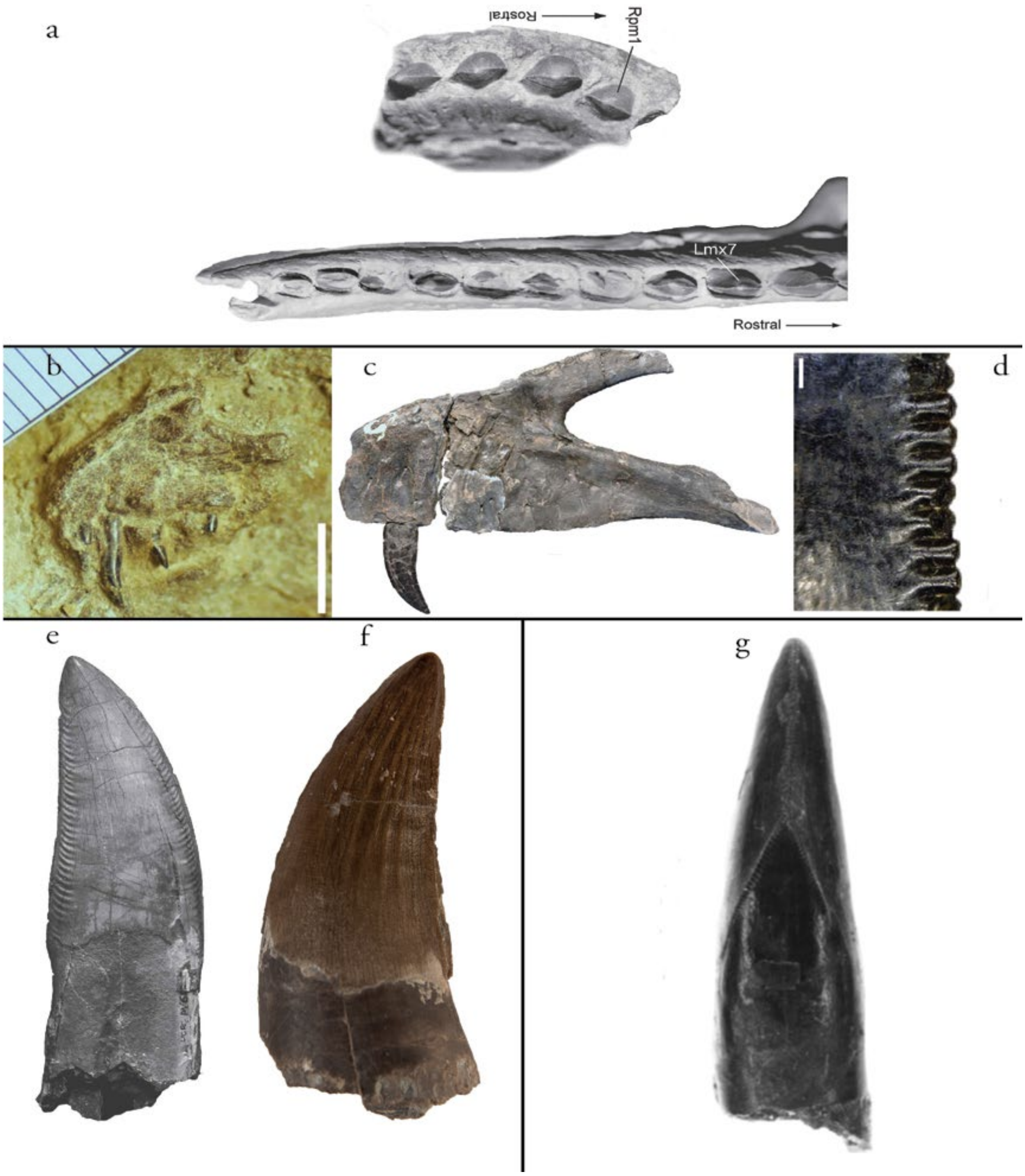


Fig. 7: Variación en dientes de terópodo. a) Variación posicional, arriba premaxilar derecho de *Majungasaurus*, abajo maxilar izquierdo. Obsérvese la variación en el contorno del diente y la posición de las carenas. Extraído de Smith, (2007). b) Maxilar derecho de *Torvosaurus* (embrión). Extraído de Araújo *et al.,* 2013. c, d) Maxilar derecho y detalle dentículos distales de diente de *Torvosaurus* adulto, extraído de Hendrickx *et al.,* 2014a. e) Diente de *Carcharodontosaurus*, extraído de Brusatte *et al., (*2007). f) Diente de espinosaurio barioniquino. g) Carena mesial dividida en diente de tiranosaurio. Extraído de Erickson, (1995). Imágenes no a escala.

5. OBJETIVOS

El principal objetivo que se plantea en esta tesis doctoral es aportar nuevos datos al registro fósil de dientes aislados de dinosaurios terópodos del Jurásico Superior y Cretácico Inferior de España, con énfasis en la Cordillera Ibérica, abordando la sistemática, la paleobiodiversidad y aspectos paleobiogeográficos. En este contexto de investigación, los objetivos específicos son los siguientes:

- Prospección de las áreas susceptibles de contener dientes aislados de dinosaurios terópodos del Cretácico Inferior de la Cordillera Ibérica aragonesa.

- Caracterización geológica y paleoambiental de los yacimientos donde se han hallado dientes aislados de dinosaurios terópodos.

- Excavación de un nuevo yacimiento del Cretácico Inferior de la Cordillera Ibérica aragonesa, donde se han encontrado dientes aislados de terópodo (Barranco del Hocino 1, Estercuel, Teruel).

- Estudio de dientes aislados del Barremiense de la Formación Blesa (Teruel) y cuantificación de la paleobiodiversidad de grupos de terópodos.

- Estudio de la paleobiodiversidad de terópodos de la Formación Castrillo de la Reina, del Barremiense-Aptiense inferior de Burgos a partir de los dientes aislados.

- Estudio de las evidencias de arpovechamiento en la carcasa del saurópodo *Europatitan eastwoodi* del Barremiense-Aptiense inferior de Burgos.

- Comparación de las faunas de terópodos del Jurásico Superior de la cuenca de Gijón-Villaviciosa (Asturias) con las faunas contemporáneas de Europa occidental y la península ibérica.

MATERIAL Y MÉTODOS

2

1. MATERIAL

En esta tesis doctoral se han estudiado fósiles provenientes de distintas localidades de la península ibérica, depositados en el Museo de Ciencias Naturales de la Universidad de Zaragoza, el Museo del Jurásico de Asturias (Colunga, Asturias) y el Museo de Dinosaurios de Salas de los Infantes (Salas de los Infantes, Burgos). Estas colecciones se componen de material recuperado en prospecciones paleontológicas llevadas a cabo por diferentes grupos de investigación (incluyendo al doctorando), campañas de excavación, recuperación mediante el triado con lupa binocular del material proveniente del lavado-tamizado de sedimentos y descubrimientos casuales realizados por aficionados a la paleontología (**CD**).

2. MÉTODOS

El trabajo realizado durante la tesis doctoral puede dividirse en trabajo de campo, trabajo de laboratorio y trabajo de gabinete.

2.1 Trabajo de campo. Prospección y excavación paleontológica

Fig. 1: Panorámica de prospección en la Formación Blesa, en el término municipal de Estercuel (provincia de Teruel).

Se ha realizado trabajo de campo con el fin de localizar y ubicar yacimientos susceptibles de recuperar dientes aislados de terópodo y otros fósiles de vertebrados del Mesozoico de la cordillera ibérica (**Figura 1**). Se han realizado jornadas de campo en las localidades de Josa, Obón y Estercuel (Teruel), donde se documentaron 7 nuevos yacimientos, se recogieron restos fósiles de vertebrados en superficie y en alguno de ellos se procedió a la excavación. El trabajo de prospección se ha centrado en la Formación Blesa, en la subcuenca de Oliete (Cuenca del Maestrazgo). La prospección ha consistido en la búsqueda y recolección de acumulaciones de fósiles en superficie tanto en yacimientos ya conocidos, como La Cantalera 1 y 2, como en nuevas áreas de los términos municipales citados anteriormente.

Fig. 2: Excavación de Barranco del Hocino 1. a) Vista panorámica del yacimiento. b, c) excavación, consolidado y engasado de los fósiles. d, e) Dientes aislados de terópodo en el yacimiento.

Asimismo se han realizado, bajo la dirección del doctorando, tres campañas de excavación (2016-2018) en el yacimiento Barranco del Hocino-1 del Barremiense (Formación Blesa) (**Figura 2, a**) localizado en el término municipal de Estercuel (Teruel). Estas campañas junto a la previa de 2015 han permitido recuperar aproximadamente 500 restos fósiles de vertebrados, incluyendo dientes aislados de terópodo. Durante estas campañas se ha procedido a una excavación sistemática del yacimiento. El nuevo material fósil ha sido siglado y se le ha atribuido un punto en un sistema de coordenadas para determinar posibles orientaciones o acumulaciones preferentes, referenciadas en un cuaderno de campo.

Los restos han sido excavados con diversas herramientas como punzones metálicos o de madera, bisturís, destornilladores y escoplos (**Figura 2, b**). Los fósiles de vertebrados son muy vulnerables tras su exposición, por lo que los restos fueron consolidados con Paraloid B72 diluido al 5% en acetona o etanol. Para proteger los restos y facilitar su extracción, los fósiles fueron sometidos al proceso de engasado, en el cual son cubiertos con pequeñas tiras rectangulares de gasa humedecidas con Paraloid al 10% (**Figura 2, c**). En el caso de fósiles de mayor tamaño ha sido necesario realizar una cubierta de yeso ("momia") para su protección y transporte. Por último los fósiles fueron protegidos con un embalaje y transportados al laboratorio de vertebrados de la Universidad de Zaragoza (**Figura 3, a**) donde se procedió a su preparación.

2.2 Trabajo de laboratorio

2.2.1 *Preparación paleontológica*

El material debe ser preparado y limpiado previamente a su estudio separando la matriz que rodea a los restos fósiles. Las técnicas de preparación y limpieza de los restos son convencionales en paleontología de vertebrados. Los restos fósiles estudiados fueron preparados previamente a la tesis por miembros del equipo Aragosaurus-IUCA, el Museo de Dinosaurios de Salas de los Infantes y el Museo del Jurásico de Asturias durante las décadas de 1990-2010. Los dientes aislados del yacimiento Barranco del Hocino 1 fueron preparados por el doctorando.

2.2.2 *Preparación mecánica*

Se ha usado la preparación mecánica que consiste en la eliminación de la roca que envuelve al resto fósil mediante abrasión o percusión.

Las herramientas utilizadas durante el proceso de preparación incluyen:

- Percutores de aire comprimido.

- Chorro de arena con vitrina cerrada y extractor de arena.

- Herramientas de precisión, incluyendo bisturí, punzones o pinceles.

- Uso de lupas y lupa binocular para la preparación en detalle.

- Equipo de protección personal (EPIs).

Se han usado pegamentos reversibles del tipo imedio o Paraloid B72 poco diluido. En algunos casos se han usado pegamentos más permanentes como cianocrilatos o resinas de tipo epoxi.

En la preparación de los fósiles se han realizado las siguientes tareas:

- Consolidación del resto fósil. Fueron consolidados utilizando Paraloid B72 diluido al 5% en etanol o acetona. En esta concentración puede penetrar en el interior del resto dándole mayor consistencia, de forma que ha quedado protegido durante la manipulación. En algunos casos se ha preferido evitar la consolidación con Paraloid para evitar el enmascaramiento de texturas en el esmalte.
- Limpieza del resto fósil, que ha consistido en la retirada de la matriz rocosa que lo envuelve. Para ello se han empleado punzones, bisturí o percutor. En caso de fractura el resto se ha pegado mediante resinas o pegamentos (**Figura 3**).
- En el caso de los huesos fósiles puede ser necesaria una consolidación final y un relleno con resina epoxi en zonas fracturadas para dar mayor consistencia. En el caso de los dientes estudiados en esta tesis no ha sido necesario, pero si en otro material excavado en el yacimiento de Barranco del Hocino 1.
- Tras este procedimiento se procedió al siglado y embalado de la pieza, construyendo los soportes necesarios para su transporte sin que peligrara la integridad del fósil.

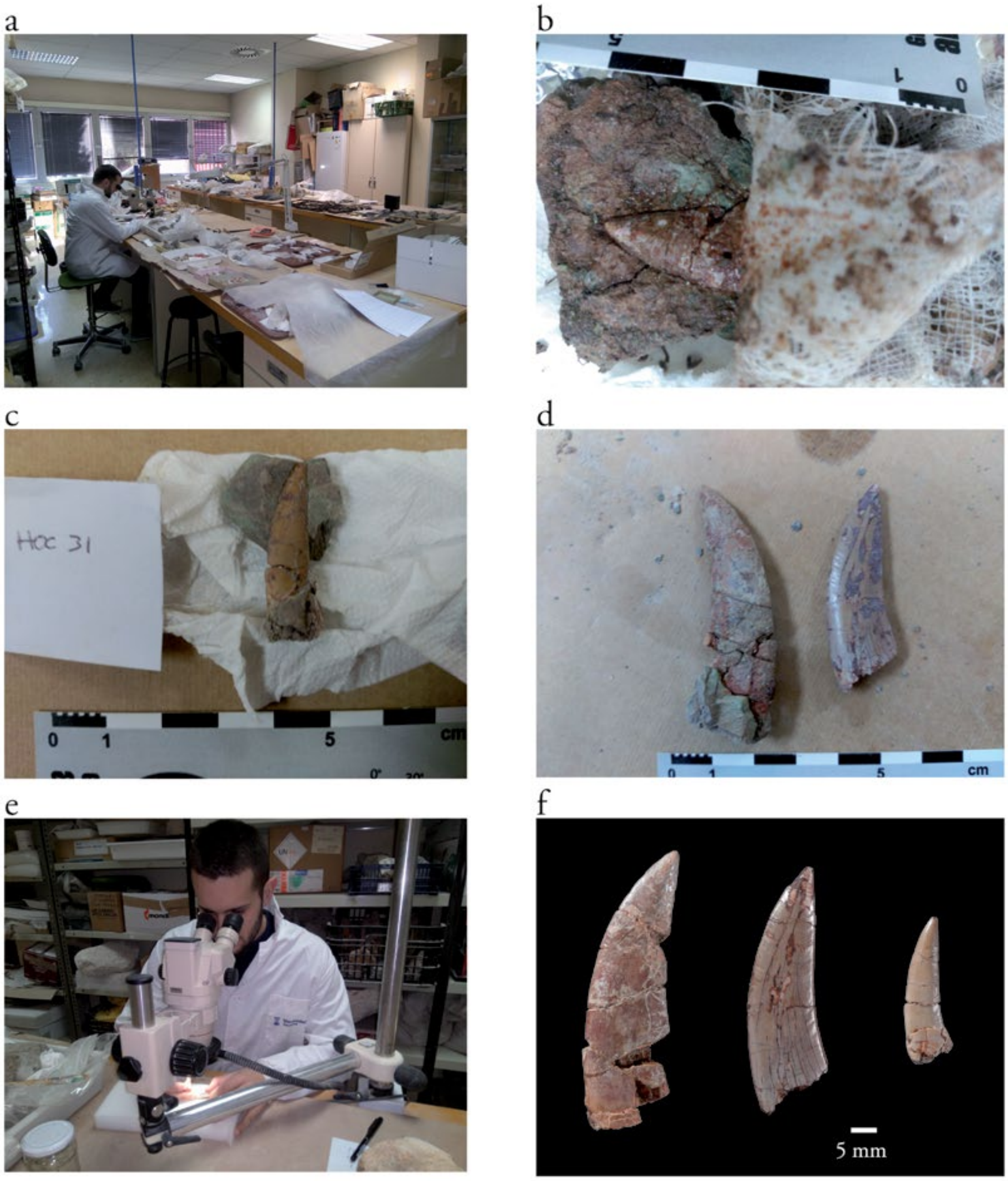


Fig. 3: Trabajo de laboratorio. a) Laboratorio de vertebrados del área de Paleontología de la Universidad de Zaragoza. b, c) Limpieza, pegado y consolidación de HOC 26 y HOC 31. d) Limpieza de la superficie de HOC 26 y HOC 17 tras la eliminación de la matriz que rodeaba los fósiles. e) Observaciones y limpieza empleando una lupa binocular. f) HOC 26, HOC 17 y HOC 31 tras la preparación.

2.3 Trabajo de gabinete

2.3.1 *Estudio del material fósil*

El trabajo de gabinete incluye la identificación de los diferentes elementos anatómicos, descripción de los restos, toma de mediciones, realización de fotografías y observaciones con lupa binocular, la determinación de los taxones, el estudio tafonómico y la revisión bibliográfica.

Las mediciones realizadas a los dientes han sido posibles mediante el uso de un calibre electrónico Mitutoyo Digimatic Series Nº 500 y el software ImageJ y Matrox Inspector para las medidas más pequeñas. También se ha utilizado un microscopio digital de bolsillo para la toma de fotografías de detalle como dentículos y superficie del esmalte. La toma de fotografías ha sido realizada con una cámara digital Sony α200 por el propio doctorando. Javier Rubio, de Paleoymás SL ha realizado las fotografías de los especímenes de Alonso y Canudo, (2016). El tratamiento de fotografías y preparación de figuras se ha realizado mediante Adobe Illustrator y Adobe Photoshop.

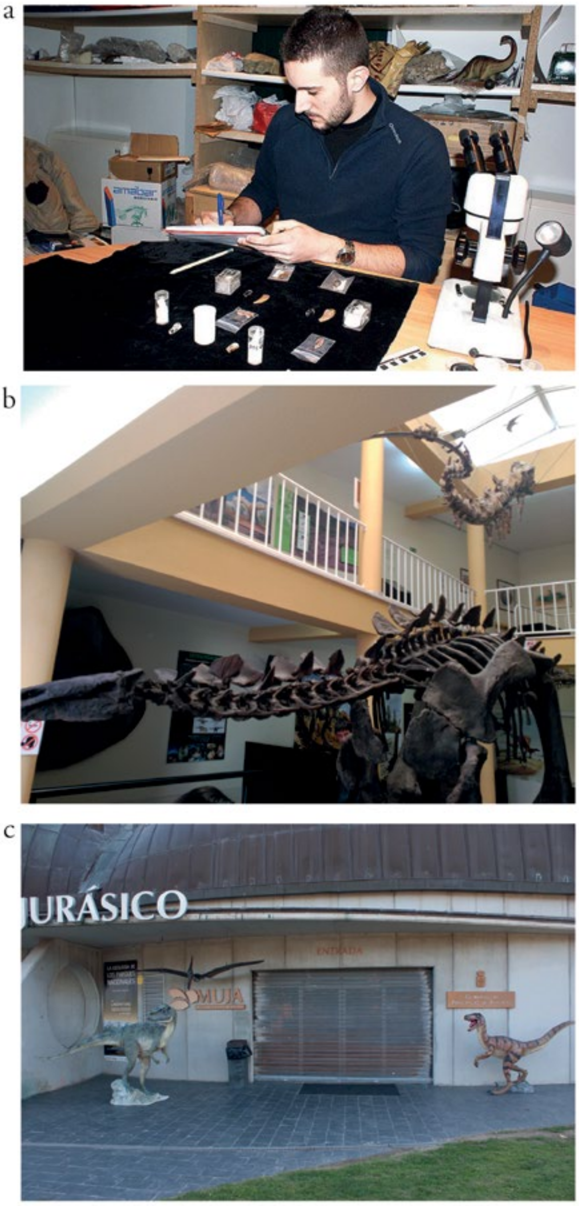


Fig. 4: a) Estudio de gabinete, medición y descripción de ejemplares en el Museo de Salas de los Infantes (Burgos). Crédito Museo de Dinosaurios. b) Museu da Lourinhã (Lourinhã, Portugal). c) Museo del Jurásico de Asturias (Colunga, Asturias).

Para la determinación de los taxones se ha realizado una revisión bibliográfica de la literatura científica relevante y se han visitado colecciones científicas del Museo del Jurásico de Asturias bajo la supervisión de la Dra. Laura Piñuela y el Dr. Juan Carlos García Ramos, el Museo de Salas de los Infantes bajo la supervisión del Dr. Fidel Torcida y el Museu da Lourinhã bajo la supervisión del Dr. Octávio Mateus (**Figura 4**).

2.3.2 *Caracteres cualitativos y cuantitativos*

Para el estudio de los dientes se han estudiado caracteres cuantitativos y cualitativos. Los caracteres cualitativos se refieren a las mediciones anatómicas tomadas en cada uno de los dientes de terópodo que permiten su estudio estadístico y su comparación con bases de datos tomadas de la literatura científica. También se han incluido caracteres cualitativos para complementar la información morfométrica, incluyendo la forma del diente (Torices *et al.,* 2015), la presencia y características de las carenas mesiales y distales (Currie *et al.,* 1990, Torices, 2007; Hendrickx, 2015), la morfología y densidad de los dentículos (Currie *et al.,* 1990; Rauhut y Werner, 1995; Smith *et al.,* 2005; Torices *et al.,* 2013; Hendrickx *et al.,* 2015c), la sección de la corona, la ornamentación (Brusatte *et al.,* 2007*;* Hendrickx, 2015) y el estado de conservación del diente.

2.3.3 *Análisis estadístico multivariante*

Se han realizado análisis estadísticos para entender la variación en las muestras de dientes aislados. Estos análisis permiten establecer una comparación entre datos morfométricos previamente recopilados por otros autores sobre dientes aislados de terópodo en la península ibérica y a nivel mundial. Los análisis estadísticos se han ejecutado con PAST (Hammer *et al.,* 2001) y SPSS 20.0 (SPSS Inc., Chicago, Illinois).

2.3.3.1 Análisis de componentes principales

Un análisis de componentes principales reduce una matriz de datos con múltiples variables en pocas dimensiones, generalmente dos, de forma que preserva la máxima varianza posible facilitando su visualización (Hammer y Harper, 2006).

Se ha realizado un análisis de componentes principales en Alonso y Canudo, (2016) sobre los datos morfométricos de Ruiz-Omeñaca *et al.,* (1997); Torcida *et al.,* (1997); Torcida Fernández-Baldor *et al.,* (2003); Infante *et al.,* (2005); Smith *et al.,* (2005); Sánchez-Hernández *et al.,* (2007); Canudo *et al.,* (2008); Gasca *et al.,* (2008) y las medidas aportadas por los autores.

2.3.3.2 Análisis discriminante

El análisis discriminante es una técnica de ordenamiento aplicada a datos previamente identificados o recopilados para encontrar las variables más discriminantes. Tiene poder predictivo y puede clasificar datos desconocidos en los grupos previamente identificados y conocidos (Hammer y Harper, 2006).

Se ha realizado análisis discriminante en Alonso *et al.,* (2017, 2018, en prep.). Se ha empleado la matriz de Hendrickx *et al.,* (2015b), incluyendo datos de White *et al.,* (2015) y Csiki-Sava *et al.,* (2016), sumando en total datos morfométricos de más de 1000 dientes de terópodo de los principales clados del grupo.

2.3.4 *Análisis filogenético*

Los análisis cladísticos han comenzado a ser utilizados recientemente por algunos autores para evaluar la posición filogenética de dientes aislados de terópodo. Los dientes estudiados en el volumen han sido analizados utilizando la supermatriz recopilada por Hendrickx y Mateus, (2014b). Se han incluido las modificaciones propuestas por Gerke y Wings, (2016). Esta supermatriz incluye 60 taxones de terópodos y 1972 caracteres, de los cuales 144 están basados en rasgos anatómicos dentales. Los análisis se han realizado con TNT (Goloboff *et al.,* 2008) y TNT 1.5 (Goloboff y Catalano, 2016) (Goloboff y Catalano, 2016), empleando *Traditional Search*, con 1000 replicaciones, manteniendo 10 árboles por replicación. El protocolo de Hendrickx y Mateus utilizado también por Gerke y Wings empleando *New Technology Search*, seleccionando *Sectorial Search*, *Ratchet* y *Drift* y *Tree fusing*, estabilizando el consenso dos veces con un factor de 75, junto a una nueva ronda de TBR produce los mismos resultados.

2.4 Nomenclatura

2.4.1 *Nomenclatura anatómica*

La nomenclatura utilizada a lo largo del volumen es la propuesta por Smith y Dodson, (2003) y Hendrickx *et al.,* (2015a). Los dientes de terópodo se componen de una corona formada por una capa de esmalte y dentina y una raíz formada por dentina. La transición entre la raíz y la corona se denomina cérvix. Los extremos de la raíz y la corona se denominan ápices de la raíz y de la corona respectivamente. La superficie del diente apuntando hacia el labio se denomina labial mientras que la parte del plano sagital medial del cráneo es la lingual. La superficie más cercana a la sínfisis mandibular se denomina mesial y la superficie más cercana a la articulación de la mandíbula es la distal. La dirección basal se refiere a dirección del ápice de la corona al cérvix, mientras que el sentido opuesto, del cérvix al ápice, se denomina apical (**Figura 5**).

Los bordes mesial y distal de la corona normalmente presentan estructuras en dirección apicobasal denominadas carenas que pueden estar cubiertas de serraciones formadas por dentículos. Los dientes pueden presentar ornamentaciones, como ondulaciones del esmalte, estrías, surcos, crestas y depresiones en la superficie de la corona. El patrón de la superficie se denomina textura del esmalte. Los dentículos se encuentran separados, este espacio se denomina espacio interdenticular. Entre los dentículos puede haber surcos en la superficie de la corona, denominados surcos interdenticulares (*blood grooves sensu* Currie *et al.,* 1990).

2.4.2 *Nomenclatura morfométrica*

La nomenclatura morfométrica utilizada en esta tesis sigue las abreviaciones y términos propuestos por Rauhut y Werner, (1995), Smith *et al.,* (2005) y Hendrickx *et al.,* (2015a), que quedan reflejadas en la siguiente tabla (**Tabla 1, Figura 5**).

2.4.3 *Abreviaciones institucionales*

MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza; MUJA, Museo del Jurásico de Asturias (Colunga, Asturias); MDS, Museo de Dinosaurios de Salas de los Infantes (Salas de los Infantes, Burgos).

Abreviatura	Significado
AL (apical length)	Extensión apicobasal del margen mesial de la corona
CBL (crown base length)	Longitud mesiodistal basal de la corona
CBW (crown base width)	Anchura labiolingual basal de la corona, perpendicular a CBL
CBR (crown base ratio)	CBW/CBL, expresa la compresión labiolingual de la corona
ce (cervix)	Cérvix, transición entre la corona y la raíz
CH (crown height)	Extensión apicobasal del margen distal de la corona desde el punto más distal del cérvix a la más elevada del ápice
CHR (crown height ratio)	CH/CBL, expresa la elongación de la corona
dca (distal carina)	Carena distal
flu (flutes)	Estriaciones longitudinales del esmalte de la corona en dirección apicobasal
DA (distoapical denticle density)	Número de dentículos por 5 mm en la zona apical de la carena distal
DB (distobasal denticle density)	Número de dentículos por 5 mm en la zona basal de la carena distal
DC (distocentral denticle density)	Número de dentículos por 5 mm en la zona central de la carena distal
DSDI (denticle size density index)	MC/DC, expresa la diferencia de tamaño entre los dentículos mesiales y distales
MA (mesioapical denticle density)	Número de dentículos por 5 mm en la zona apical de la carena mesial
MB (mesiobasal denticle density)	Número de dentículos por 5 mm en la zona basal de la carena mesial
MC (mesiocentral denticle density)	Número de dentículos por 5 mm en la zona central de la carena mesial
mca (mesial carina)	Carena mesial
mun (marginal undulations)	Ondulaciones del esmalte en los márgenes mesial o distal de la corona
tun (transverse undulations)	Ondulaciones del esmalte transversales a la corona

Tabla 1: Abreviaciones utilizadas en esta memoria.

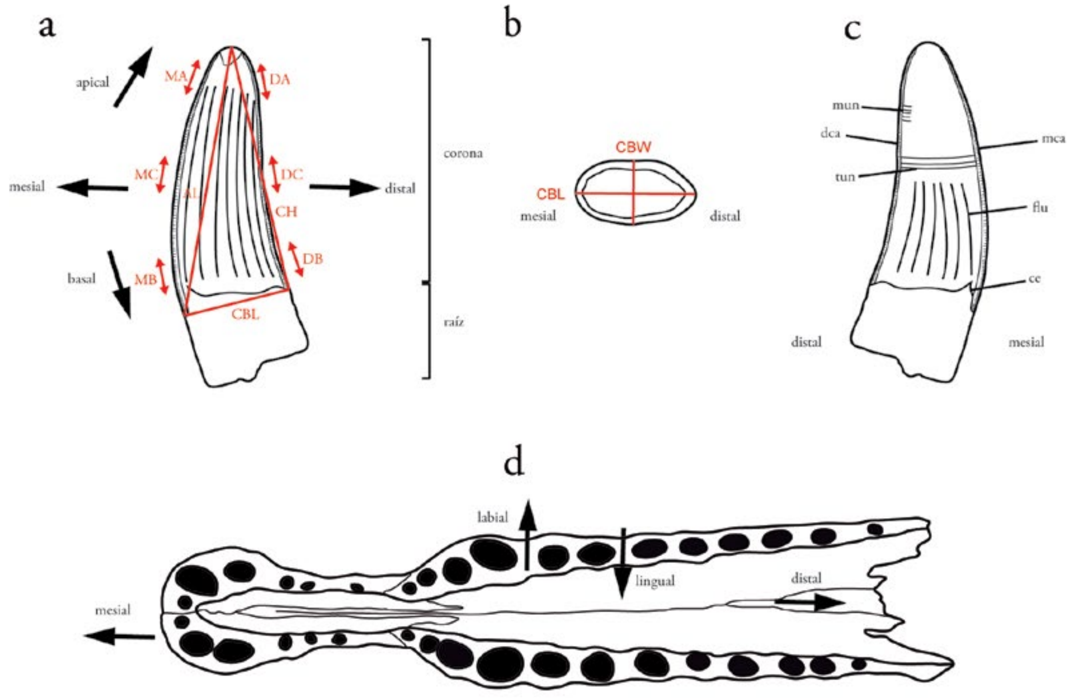
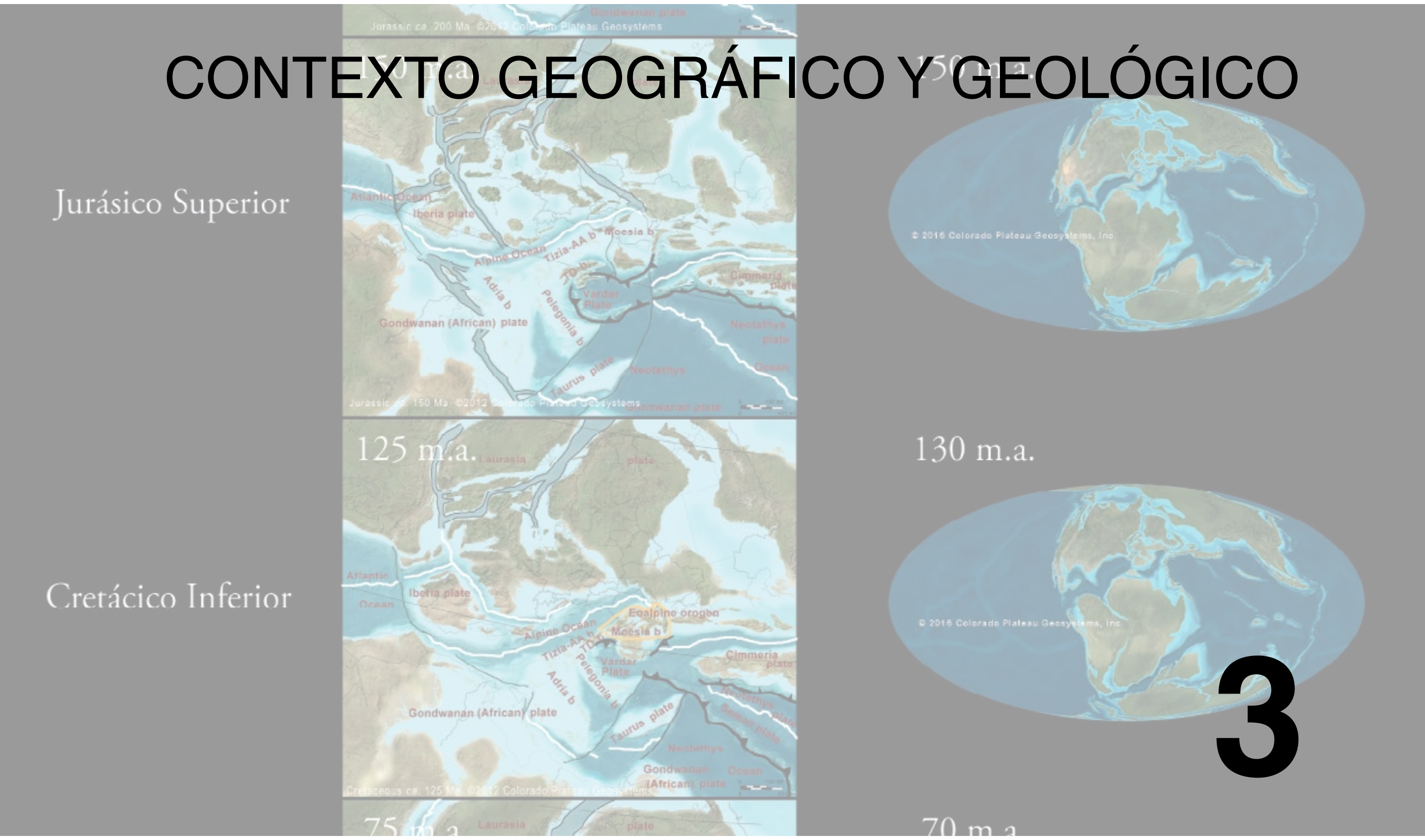


Fig. 5: Nomenclatura anatómica y morfométrica empleada en el estudio de dientes aislados de dinosaurios terópodos. a, c) vista lateral; b) vista basal en el nivel del cérvix; d) vista dorsal de la mandíbula superior de *Spinosaurus*. Modificado de Dal Sasso *et al.,* (2005).

CONTEXTO GEOGRÁFICO Y GEOLÓGICO



3

1. INTRODUCCIÓN

El material estudiado en esta tesis doctoral proviene de las comunidades autónomas de Asturias, Castilla y León y Aragón. El material de Asturias proviene de yacimientos localizados en la denominada "costa de los dinosaurios". El material de Castilla y León proviene de la provincia de Burgos, de yacimientos en el entorno de la localidad de Salas de los Infantes; los restos aragoneses provienen de la provincia de Teruel, de las comarcas de Cuencas Mineras y Andorra-Sierra de Arcos **(Figura 1)**.

Fig. 1: Ubicación de los yacimientos de los que procede el material estudiado en esta tesis. Imagen tomada de Google maps.

Los fósiles estudiados se han encontrado en la cordillera cantábrica y en la cordillera ibérica. La cordillera cantábrica comprende el tramo de la cordillera pirenaica emergido situado al oeste de la falla de Pamplona (Barnolas y Pujalte, 2004) y es el resultado de la colisión entre la placa euroasiática y la microplaca ibérica (Alonso *et al.,* 2009). La cordillera ibérica es un sistema montañoso intraplaca resultado de la inversión de la cuenca ibérica mesozoica (Salas *et al.,* 2001).

El basamento anterior al Mesozoico de Europa occidental y central estuvo afectado por un gran evento de formación de cordilleras denominado orogenia varisca que transcurrió a finales del Paleozoico, a consecuencia de la convergencia de los continentes de Laurusia y Gondwana. Los materiales del orógeno varisco afloran sobre todo en la zona occidental de la península, en el denominado macizo ibérico (Pérez-Estaún *et al.,* 2004). La orogenia varisca resultó en la consolidación del basamento de Iberia y un régimen tectónico compresivo. Estas condiciones tectónicas cambiaron con la ruptura de Pangea, donde Iberia se vio afectada por procesos tectónicos extensionales relacionados con la apertura y expansión hacia el oeste del Tetis y la

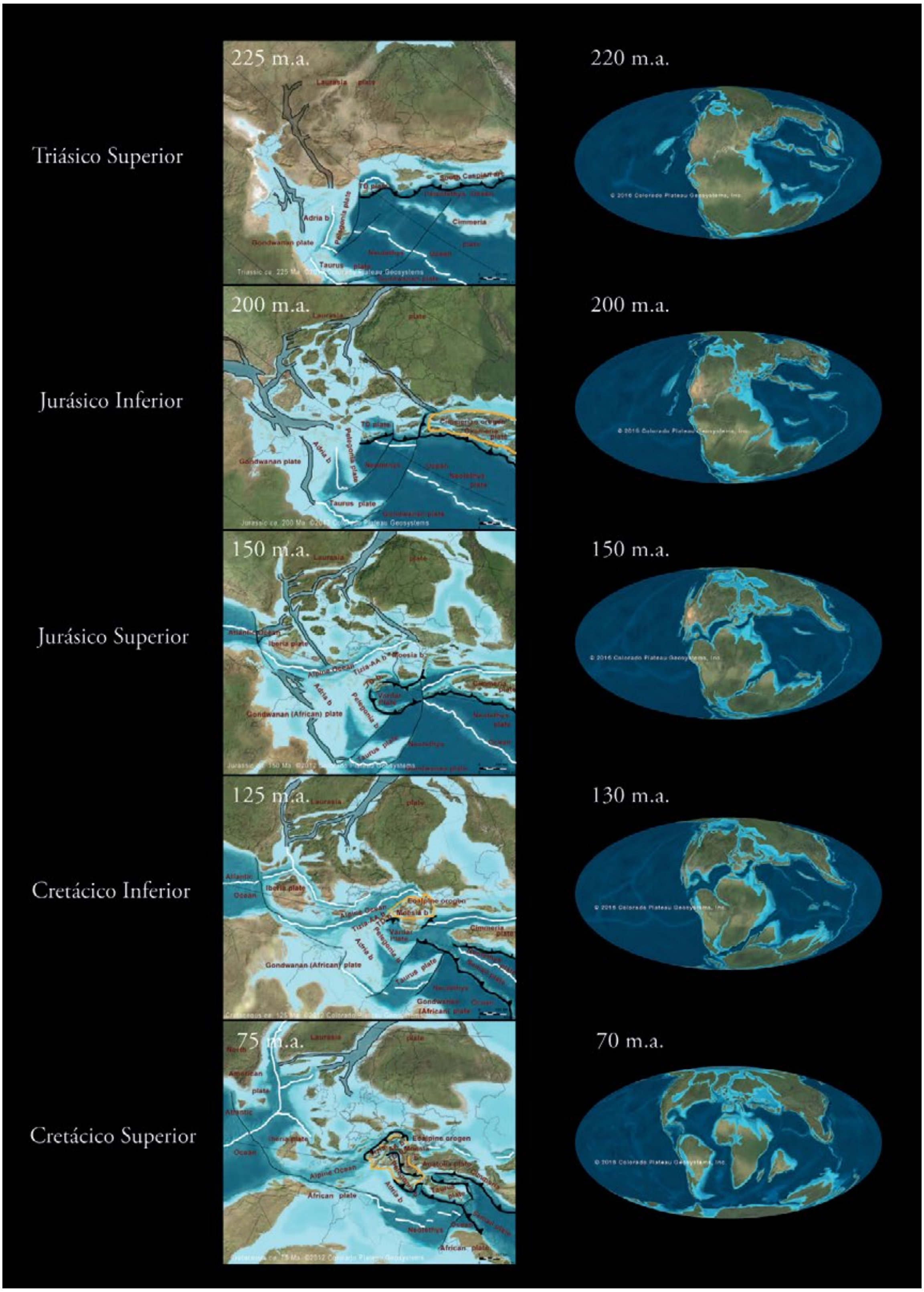


Fig. 2: Evolución paleogeográfica de Europa y a nivel global durante el Mesozoico. Crédito R. Blakey (http:// http://deeptimemaps.com/).

apertura del Atlántico norte (Salas *et al.*, 2001; López-Gómez *et al.*, 2002) (**Figura 2**).

En el sector central de la cordillera cantábrica, un primer episodio extensional dio lugar a cuencas permotriásicas que terminaron con las cuencas de plataforma del Jurásico

(Lepvrier y Martínez-García, 1990). Una segunda etapa extensional apareció en el Jurásico Superior y Cretácico Inferior relacionado con la apertura del Golfo de Vizcaya, durante la que se formaron las principales cuencas mesozoicas. Durante el Terciario, la orogenia alpina dio lugar a la inversión tectónica de las cuencas con el levantamiento de los Pirineos. (García-Ramos, 1997; Alonso *et al.,* 2009).

Durante el Triásico comenzó a formarse la cuenca ibérica, de dirección NO-SE. En el desarrollo de la cuenca se identifica una primera etapa de rifting durante el Pérmico-Triásico relacionada con la expansión del Tetis y la propagación hacia el sur de rift del Atlántico Norte, que reactiva fallas de la orogenia varisca. Tras esta primera etapa se identifica una etapa post-rift que conlleva el desarrollo de plataformas carbonatadas durante el Jurásico. En el Jurásico superior comienza una nueva etapa de *rifting* desde el Oxfordiense hasta el Albiense que coincide con la propagación hacia el norte del *rift* del Atlántico central. Durante esta etapa se fragmentan las plataformas carbonatadas y aparecen nuevas cuencas extensionales que incluyen a las cuencas de Cameros, Maestrazgo, Columbretes y Suribérica. Finalmente, durante el Cretácico Superior se da una nueva etapa post-rift que está caracterizada por el ascenso del nivel del mar y el desarrollo de extensas plataformas carbonatadas. Durante el Terciario comienza la inversión tectónica que dará lugar a la cordillera (Salas *et al.,* 2001; Sánchez-Moya y Sopeña, 2004).

2. EL JURÁSICO SUPERIOR DE ASTURIAS

En la zona central de la cordillera cantábrica afloran principalmente materiales del Precámbrico y Paleozoico de la Zona Cantábrica y Asturoccidental Leonesa del macizo ibérico. Además de estos afloramientos variscos, se encuentran depósitos posteriores que incluyen materiales permotriásicos, con una distribución amplia, y depósitos jurásicos y cretácicos (Barnolas y Pujalte, 2004).

Los materiales jurásicos afloran en una franja estrecha de casi 60 kilómetros de extensión en la zona costera de Asturias (**Figura 3**), entre el Cabo Torres en Gijón y la playa de Arra en Ribadesella (Arenas *et al.,* 2015). Geológicamente se sitúan en la Cuenca de Gijón-Villaviciosa (Ramírez del Pozo, 1969), limitada al oeste por la falla de Veriña, y al este por la falla de Ribadesella (Lepvrier y Martínez García, 1990; Alonso *et al.,* 2009). Estos depósitos se sitúan sobre unidades y estructuras precámbricas, paleozoicas y permotriásicas (Arenas *et al.,* 2015, Rauhut *et al.,* 2018b).

Durante el Jurásico se encuentra emergida parte de la placa ibérica correspondiente con el macizo ibérico. Este terreno emergido está rodeado por cuencas intracratónicas ocupadas por

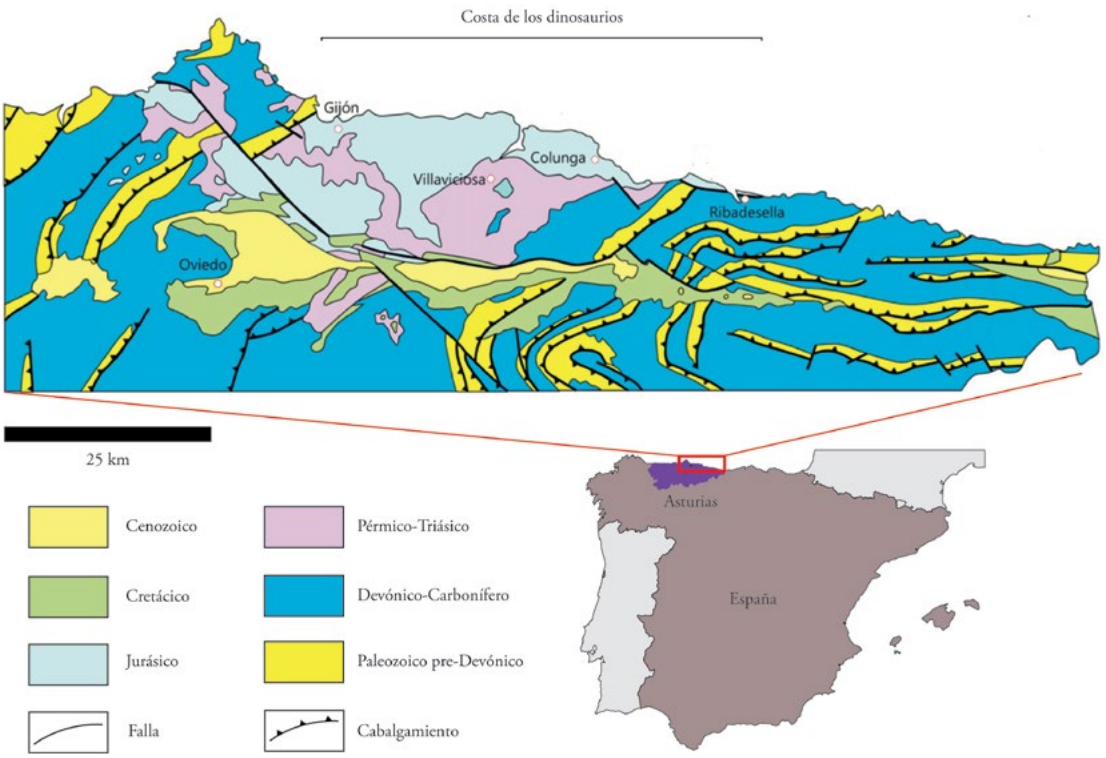


Fig. 3: Contexto geológico de la costa de los dinosaurios. Modificado de Lozano *et al.,* (2016).

mares epicontinentales, que incluyen la cuenca Asturiana, la Vasco-Cantábrica, Pirenaica e Ibérica (Aurell *et al.,* 2002).

Entre el final del Jurásico y el Cretácico Inferior tuvieron lugar procesos extensionales en el área. Durante el Jurásico Superior se produjo una etapa de *rifting* y creación de semigrabens limitados por fallas de dirección ONO-ESE a NO-SE, que estructuraron el área precediendo a la apertura del Golfo de Vizcaya y el Atlántico Central. Las primeras evidencias de actividad tectónica aparecen en el Aaleniense-Bajociense (Lepvrier y Martínez-García, 1990; Lozano *et al.*, 2016). A consecuencia de esta actividad se produjo el levantamiento de una gran área que en la actualidad es Asturias que había permanecido bajo el nivel del mar durante el Jurásico Inferior y Medio. En la región suroccidental apareció un área elevada cuya erosión produce los primeros aportes siliciclásticos continentales a la cuenca (García-Ramos, 1997; Arenas *et al.,* 2015).

Los depósitos jurásicos pueden dividirse en dos secuencias distintas (**Figura 4**) (Valenzuela *et al.,* 1986). La secuencia inferior incluye a las formaciones Gijón y Rodiles, del Triásico Superior, Jurásico Inferior y Medio. La Formación Gijón incluye materiales carbonatados y margosos que se formaron en medios litorales y de sebja. Durante el Sinemuriense se produjo un aumento del nivel del mar que sumergió el área y alcanzó profundidades de hasta 100 metros, generando los niveles calizos y margosos de la Formación Rodiles. La emersión debida a la actividad tectónica provocó la karstificación de las sucesiones carbonatadas del Triásico y Jurásico Inferior y Medio, apareciendo brechas y excavando paleovalles (Arenas *et al.,* 2015).

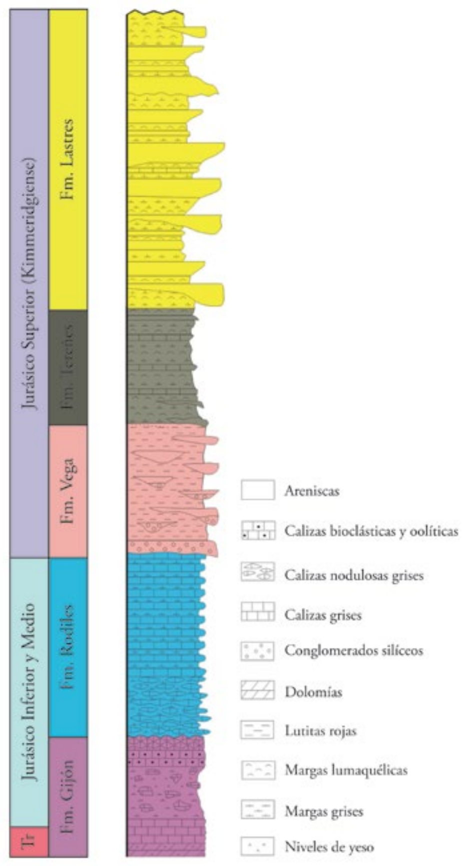


Fig. 4: Columna estratigráfica con las unidades del Jurásico de Asturias en el sector Tazones-Ribadesella (modificado de García-Ramos *et al.,* 2006).

La secuencia superior es principalmente siliciclástica, de origen fluvial, lagoon y deltaica (Valenzuela *et al.,* 1986; Rauhut *et al.,* 2018b) y comprende a las formaciones Vega, Tereñes y Lastres, del Kimmeridgiense (Jurásico Superior). La Formación Vega tiene una potencia estimada de 150 metros y está formada por capas alternas de areniscas y lutitas con intercalación de conglomerados y calizas en diferentes posiciones estratigráficas. Estas depósitos se originaron en un sistema meandriforme y llanuras de inundación con desarrollo de paleosuelos (García-Ramos *et al.,* 2010; Gutierrez y Sheldon, 2012; Arenas *et al.,* 2015). La Formación Tereñes tiene una potencia estimada de 160 metros y está formada por margas, niveles de lumaquelas y limolitas que se depositaron en un *lagoon* restringido confinado tectónicamente (Fürsich *et al.,* 2012). La Formación Lastres está formada por areniscas con intercalaciones de lutitas, niveles de lumaquelas, margas y algunos niveles calcáreos formados en un complejo deltaico con dominio fluvial (Harris *et al.,* 2006; Fürsich *et al.,* 2012; Arenas *et al.,* 2015).

3. EL CRETÁCICO INFERIOR DE LA CUENCA IBÉRICA

La segunda etapa de *rifting* de la Cuenca Ibérica comenzó a finales del Oxfordiense extendiéndose hasta el Albiense medio coincidiendo con la apertura progresiva de la cuenca oceánica del Atlántico norte (Mas *et al.,* 2004). Esta extensión generó cuatro cuencas con una alta subsidencia: Cameros, Maestrazgo, Columbretes y Suribérica (Salas *et al.,* 2001). Su evolución estuvo controlada por la actuación de fallas normales de dirección variable, con el bloque hundido generalmente hacia el S-SE (Salas y Guimerà, 1996; Aurell *et al.,* 2004).

El proceso de *rifting* se inició en la Cuenca del Maestrazgo para después propagarse al resto de cuencas. Durante este inicio en las cuencas del Maestrazgo y Cameros se produjo una elevación del nivel marino durante el Jurásico Superior. En el Maestrazgo, la secuencia *syn-rift* está caracterizado por el predominio de carbonatos marinos someros hasta el Aptiense y Albiense, con la aparición de sistemas deltaicos. La secuencia *syn-rift* de la Cuenca de Cameros está dominada por depósitos aluviales y lacustres con incursiones marinas ocasionales (Mas *et al.*, 2004).

Paleogeográficamente, el área de la Cuenca Ibérica se caracterizó al inicio de la etapa de *rifting* por la presencia del estrecho de Soria, que conecta el océano Atlántico con el Tetis, limitado por el macizo ibérico y el macizo del Ebro. A finales del Jurásico el estrecho se cerró durante el Oxfordiense, es reabierto durante el ascenso del nivel del mar del Kimmeridgiense y cerrado de nuevo en el Titoniense. A partir de este momento la subsidencia fue acusada y aparecen rellenos continentales o marinos someros. Durante el inicio del Cretácico Inferior la actividad tectónica disminuyó y las cuencas adquirieron un carácter local. A partir del Aptiense el proceso de *rifting* vuelve a activarse (Salas *et al.,* 2001; Mas *et al.,* 2004).

3.1 Cuenca del Maestrazgo. Subcuenca de Oliete

La Cuenca del Maestrazgo es una de las cuencas formadas durante la extensión de la Cuenca Ibérica. Está dividida en siete subcuencas (Oliete, Morella, La Salzedella, Galve, Penyagolosa, Las Parras, Perelló). Los fósiles estudiados provienen de la subcuenca de Oliete, la más noroccidental de la cuenca (**Figura 5, a**).

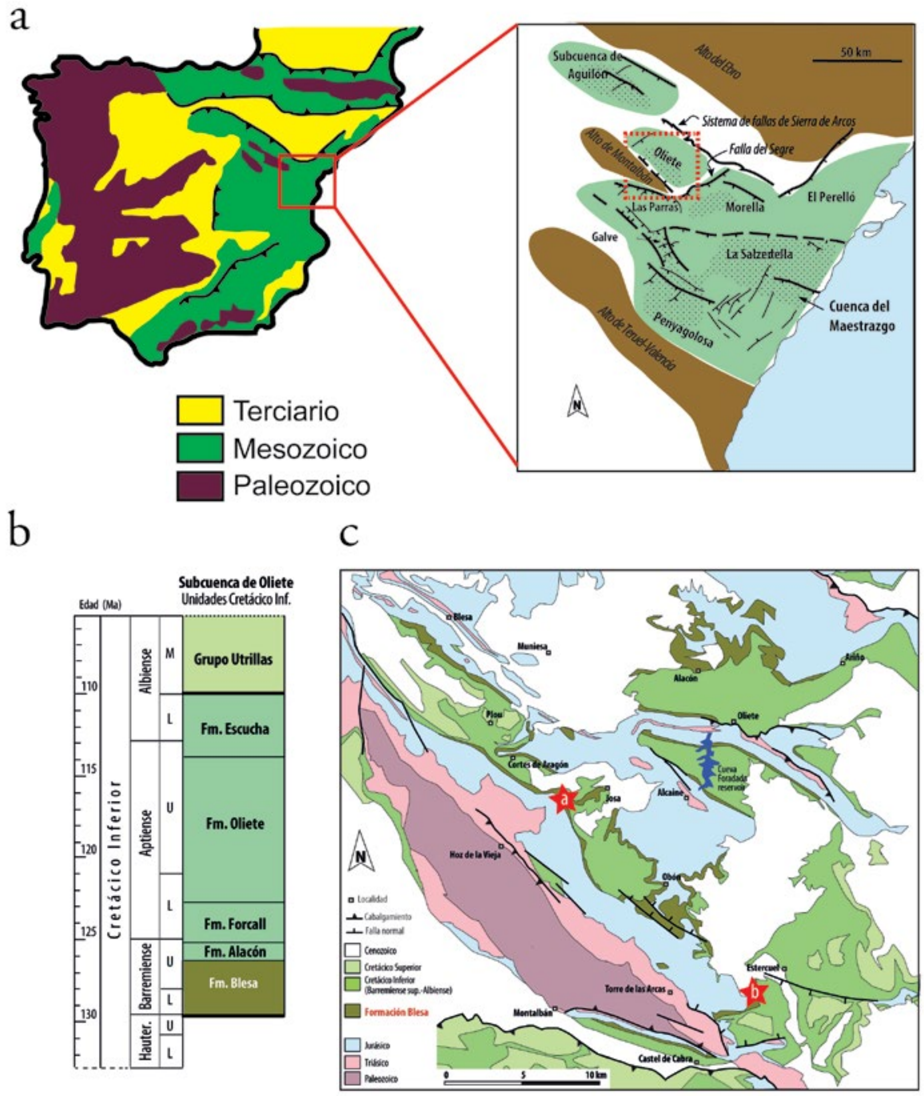


Fig. 5: a) Ubicación de la Cuenca del Maestrazgo y la subcuenca de Oliete. b) Unidades del Cretácico Inferior de la subcuenca. c) Mapa de la subcuenca de Oliete; la estrella a indica la ubicación del yacimiento de La Cantalera 1; la estrella b la posición de Barranco del Hocino 1. Modificado de Aurell *et al.,* 2018.

3.1.1 *Formación Blesa*

La parte más baja de los depósitos cretácicos de la subcuenca de Oliete comprende sedimentos en facies *Weald* (Canudo *et al.,* 2010a) como la Formación Blesa, de edad Barremiense, de donde proceden los fósiles aragoneses estudiados en esta tesis. Canerot *et al.,* (1982) diferencian cinco formaciones atribuidas al grupo Josa que abarcan del Barremiense inferior al Albiense: la Formación Margas y Calizas de Blesa, la Formación Calizas de Alacón, la Formación Margas de Forcall, la Formación Calizas de Oliete y la Formación Lignitos de Escucha (**Figura 5, b**).

La Formación Blesa tiene una potencia entre 90 y 150 metros de espesor, con las mayores potencias localizadas en el sector sureste de la subcuenca (Aurell *et al.,* 2018). Canerot *et al.,* (1982) definen y dividen a la formación en los miembros Cabezo Gordo, Morenillo y Valdejunco. Soria *et al.,* (1995) añaden el nuevo miembro Margas y Calizas con Ostreídos de Josa en la parte basal (Soria, 1997). La Formación Blesa está depositada sobre unidades jurásicas, como las calizas bioclásticas de Barahona (Pliensbachiense), las margas de la Formación Turmiel (Toarciense), la Formación Chelva (Batoniense) y la Formación Pozuel (Kimmeridgiense) (Aurell *et al.,* 2004).

Trabajos recientes (Aurell *et al.,* 2018) han permitido distinguir tres secuencias en la formación: la secuencia Blesa inferior, media y superior.

Secuencia Blesa inferior: De potencia variable, de entre 10 y 100 metros. Corresponde a los miembros Cabezo Gordo y Morenillo. Está formada por materiales depositados en ambientes continentales, con depósitos de margas y arcillas con intercalaciones de niveles de arenisca y conglomerados en su parte inferior. La parte inferior de la secuencia muestra evidencias de laterización con pisoides ferruginosos en arcillas rojas. Esta secuencia se formó, en su parte inferior, en *mudflats* y depósitos de *debris-flow*. La parte superior muestra margas y arcillas con depósitos de *wackstone* y *packstone* formados en depósitos palustres, lacustres y aluviales (Aurell *et al.,* 2018). Los restos fósiles de la secuencia inferior incluyen una amplia diversidad de vertebrados terrestres, como se evidencia en el yacimiento de La Cantalera 1 (Canudo *et al.,* 2010a).

Secuencia Blesa media: Con una potencia entre 25 y 50 metros, los depósitos de esta secuencia se formaron en una bahía restringida somera y ambientes costeros, con ocasionales depósitos lacustres y palustres (Aurell *et al.,* 2018). Estos niveles muestran mayor riqueza de fósiles de vertebrados marinos como plesiosaurios, testudines, picnodontiformes y peces osteíctios junto con algunos resto de pterosaurios y dinosaurios terópodos y saurópodos (Holgado *et al.,* in press; Medrano-Aguado *et al.,* 2018a, 2018b; Parrilla-Bel y Canudo, 2015, 2018).

Secuencia Blesa superior: de potencia variable, entre 15 y 70 metros, formada por depósitos aluviales, palustres y lacustres con influencia marina local, e incluye margas y arcillas, *wackestone-packstone* de ostrácodos y carofitas, margas y niveles de areniscas (Aurell *et al.,* 2018). Hallazgos recientes (Alonso *et al.,* 2016, 2018) han puesto de manifiesto el potencial fosilífero de esta secuencia.

3.1.1.1 Secuencia Blesa inferior. El yacimiento de La Cantalera 1

El yacimiento está situado al NE de la península ibérica, en el entorno de la localidad de Josa (**Figura 5**). Los restos fósiles aparecen en arcillas grises (**Figura 6**) caracterizadas por la presencia de carofitas, ostrácodos y gasterópodos. También aparecen cantos jurásicos con fósiles de invertebrados marinos, tales como braquiópodos y ammonites. La presencia de nódulos cementados se ha interpretado como evidencia de paleosuelos debido a cambios en el nivel freático. Estas facies son el resultado de depósitos de arcillas distales de abanicos aluviales (Aurell *et al.,* 2004; Canudo *et al.,* 2010a).

Fig. 6: Panorámica del yacimiento La Cantalera 1.

Los invertebrados reconocidos en el yacimiento incluyen gasterópodos de agua dulce (Viviparidae indet. y Basommatophora indet.). Otros microfósiles incluyen ostrácodos y carofitas. Entre los ostrácodos se ha reconocido a *Cypridea* (Ulwellia) *soriana* (Kneuper-Haack, 1966) que aparece en el Hauteriviense y Barremiense de la península ibérica. Respecto a las carofitas, se han identificado utrículos de *Hemiclavator adnatus* (Martín-Closas y Grambast-Fessard, 1986; Schudack, 1989) y *Clavatoraxis* sp. (Martín-Closas y Diéguez, 1998). La presencia de oogonios de *Atopochara trivolvis triquetra* ha permitido datar esta sección de la formación como Barremiense inferior (Riveline *et al.,* 1996; Canudo *et al.,* 2010a; ver discusión en Canudo *et al.,* 2012). La asociación de carofitas es similar bioestratigráficamente a la Formación El Castellar de la subcuenca de Galve (Canudo *et al.,* 2010a).

Las carofitas y ostrácodos de La Cantalera 1 son compatibles con entornos de agua dulce y salobre; sin embargo, los gasterópodos vivipáridos se encuentran exclusivamente en agua dulce, por lo que se puede descartar un ambiente salobre. Estos gasterópodos son frecuentes en las facies *Weald*, asociados con moluscos bivalvos como *Anodonta*, *Emiodon*, *Margaritifera*, *Teruella* y *Unio* (ver Ruiz-Omeñaca *et al.,* 1997b y referencias ahí) en entornos dulceacuícolas. No obstante, estos moluscos no aparecen en La Cantalera 1. Esto evidencia la ausencia de un cuerpo de agua temporal, dado que estos invertebrados son más sensibles a los entornos áridos que los gasterópodos vivipáridos (Ruiz-Omeñaca *et al.,* 1997b). El paleoambiente de La Cantalera-1 se ha interpretado como un medio palustre con una lámina de agua intermitente y rodeada por un relieve calcáreo Jurásico (Aurell *et al.,* 2004; Canudo *et al.*, 2010a).

El yacimiento de La Cantalera-1 presenta la una de las mayores paleobiodiversidades de vertebrados del Barremiense (Canudo *et al.,* 2010a) europeo. Entre los restos de dinosaurios se han identificado anquilosaurios emparentados con *Polacanthus*, saurópodos, ornitópodos, con hasta tres taxones de iguanodontios y terópodos; incluyendo tetanuros basales de tipo espinosáurido, carcharodontosaurios, y diversos maniraptores (Canudo *et al.,* 2010a; Alonso y Canudo, 2016; Aurell *et al.,* 2018). También se han recuperado numerosos dientes aislados de crocodilomorfos (Puértolas-Pascual *et al.,* 2015), junto con restos de peces osteíctios, anfibios, lacértidos, testudines, mamíferos y abundantes cáscaras de huevo (Badiola *et al.,* 2008; Canudo *et al.,* 2010a; Moreno-Azanza *et al.,* 2014a, b, 2015).

3.1.1.2 Secuencia Blesa superior. El yacimiento de Barranco del Hocino 1

El yacimiento de Barranco del Hocino 1 está situado en el término municipal de Estercuel, en la provincia de Teruel, en la secuencia superior de la Formación Blesa, donde los hallazgos de fósiles son más escasos que en el resto de secuencias. A comienzos de la década de los 2010, el aficionado Juan Rubio, vecino de Estercuel, informó del descubrimiento de los primeros fósiles de vertebrados en esta área. El equipo de investigación Aragosaurus ha realizado cuatro campañas de excavación hasta la fecha (2015, 2016, 2017 y 2018) donde se han recuperado aproximadamente 500 restos fósiles de vertebrados que hasta el momento revelan la paleobiodiversidad del yacimiento. La presencia de oogonios de carofitas atribuidos a *Atopochara trivolvis triquetra* en la parte baja de la Formación Blesa indica una edad de Barremiense inferior en esa parte del depósito (Riveline *et al.,* 1996; Canudo *et al.,* 2010a, 2012). El tránsito del Barremiense inferior al superior se considera presente en la parte media de la formación (Aurell *et al.,* 2018).

La capa de Barranco del Hocino 1 (**Figura 7**) está depositada sobre una sucesión estratigráfica de lutitas y margas, con desarrollo de paleosuelos alternados con calizas grises con evidencias de bioturbación. La capa fosilífera consiste en lutitas grises con moteado rojo, verde y amarillento, con presencia de bioturbación (trazas de invertebrados), nódulos de carbonato y calcretas. El contenido fósil consiste en moluscos bivalvos, gasterópodos, ostrácodos, carofitas y vertebrados. El paleoambiente de depósito ha sido interpretado como una llanura aluvial con exposición aérea, episodios palustres y desarrollo de paleosuelos. Los restos fósiles han aparecido dispersos en un área de más de 10 metros de extensión lateral.

Los restos fósiles de vertebrados de este yacimiento incluyen elementos desarticulados incompletos con un alto grado de fractura, abrasión y meteorización; algunos restos presentan marcas de dientes. La asociación está dominada por macrorrestos aislados de dinosaurios ornitópodos, junto a los que han aparecido restos de anquilosaurios, dientes de terópodo, microvertebrados (dientes de crocodilomorfos y osteíctios), fragmentos de placas de tortugas, coprolitos y cáscaras de huevo (Alonso *et al.,* 2016, 2018).

Fig. 7: Panorámica del yacimiento Barranco del Hocino 1.

3.2 Cuenca de Cameros

La Cuenca de Cameros se forma durante el periodo de extensión del Jurásico Superior y Cretácico Inferior de la Cuenca Ibérica. Se trata de un semigraben rellenado durante el Jurásico Superior y el Cretácico Inferior (Platt, 1986, 1990; Martin-Closas y Alonso Millán, 1998; Salas *et al.,* 2001; Mas *et al.,* 2004) por una sucesión de sedimentos fluviales y lacustres con casi 9000 metros de potencia en su depocentro (Clemente y Pérez-Arlucea, 1993; Salas y Casas, 1993; Salas *et al.,* 2001).

La cuenca se ha dividido tradicionalmente en las áreas este y oeste. En la zona este se encuentra el depocentro y los depósitos han sufrido metamorfismo de grado bajo, escaseando los restos fósiles óseos aunque sí aparecen icnitas (Canudo *et al.,* 2010b; Castanera *et al.,* 2014). La zona oeste, también denominada subcuenca occidental de Cameros, presenta una mayor abundancia de restos de vertebrados e icnitas (Torcida Fernández-Baldor, 2006).

La estratigrafía de la Cuenca de Cameros es compleja y se han realizado diferentes propuestas, habiéndose dividido los sedimentos en los grupos Tera, Oncala, Urbión, Enciso y Oliván (Platt, 1989; Arribas *et al.,* 2003; Clemente, 2010). Los fósiles estudiados provienen del área oeste de la cuenca, en concreto en la Formación Castrillo de la Reina, perteneciente al grupo Urbión (Torcida Fernández-Baldor *et al.,* 2017).

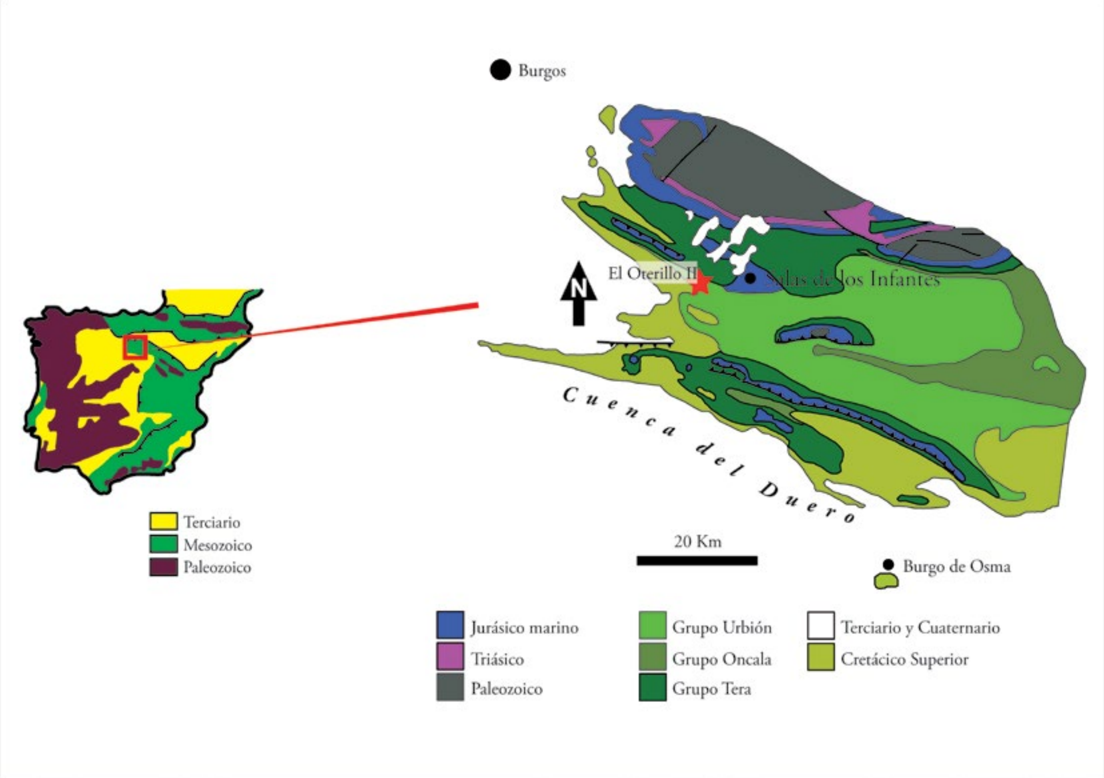


Fig. 8: Situación geográfica y geológica del yacimiento El Oterillo II.

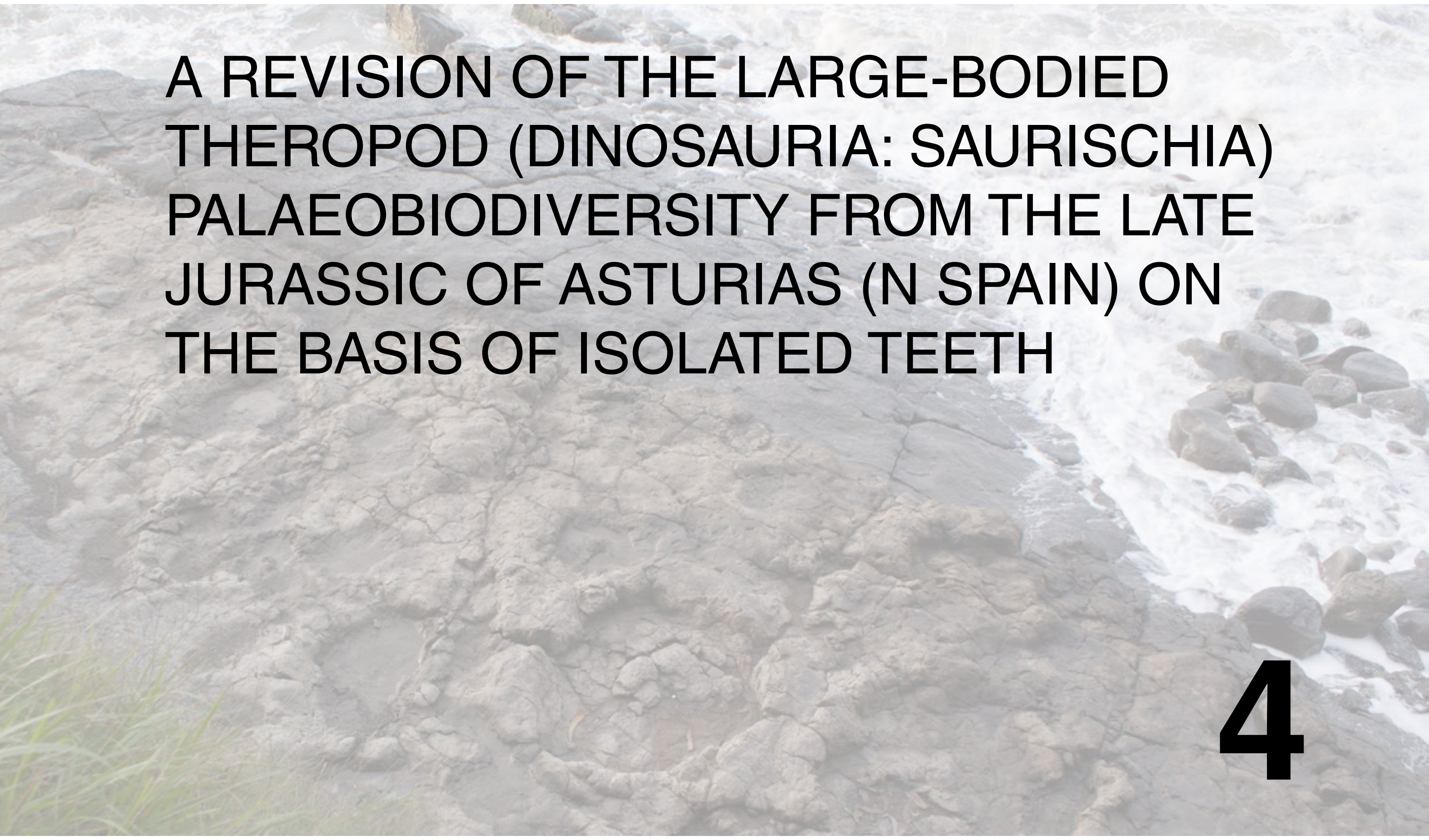
3.2.1 *Formación Castrillo de la Reina. Yacimiento El Oterillo II*

Formación compuesta por conglomerados y una alternancia de capas de arenisca de 50 a 200 cm intercaladas por niveles de lutitas rojas. La formación representa un sistema fluvial-aluvial distal originado en la zona suroeste que drenaba la cuenca hacia el noreste. De acuerdo a los estudios bioestratigráficos, la formación tiene una edad Barremiense superior-Aptiense inferior (Martin-Closas y Alonso Millán, 1998; Schudack y Schudack, 2009)

Geográficamente, el yacimiento de El Oterillo II se encuentra en la provincia de Burgos (NE España), a unos 6.5 kilómetros al noroeste de la localidad de Salas de los Infantes (**Figura 8**). Los restos de dinosaurio en el yacimiento de El Oterillo II se recuperaron en la parte superior de un canal de arenisca de unos 0.5 metros de espesor con clastos de cuarcita de entre 1 y 2.5 cm de diámetro. La capa de arenisca es de color rojizo y marrón y pasa a colores grises y azules a techo según el tamaño de grano disminuye cambiando a lutitas. Los huesos de dinosaurio están parcialmente articulados y han sido asignados a un nuevo saurópodo llamado *Europatitan eastwoodi* (Torcida Fernández-Baldor *et al.,* 2009, 2017).

En relación a los restos de *Europatitan* se recuperaron dientes aislados de terópodo (**Figura 9**) y crocodilomorfos. Las paleocorrientes indican una dirección oeste, aunque no se ha detectado una orientación preferente en los dientes aislados (Alonso *et al.,* 2017).

Fig. 9: Diente aislado de terópodo espinosáurido en el yacimiento de El Oterillo II. Crédito Museo de Dinosaurios de Salas de los Infantes.



A REVISION OF THE LARGE-BODIED THEROPOD (DINOSAURIA: SAURISCHIA) PALAEOBIODIVERSITY FROM THE LATE JURASSIC OF ASTURIAS (N SPAIN) ON THE BASIS OF ISOLATED TEETH

4

1. INTRODUCTION

Among saurischians, the study of theropods is of particular interest due to the prominent role that they occupied in the Mesozoic continental ecosystems, with some clades being the apex or main predators of those associations. Understanding theropods is necessary to know the complex relationships among Mesozoic terrestrial organisms.

The Late Jurassic fossil record yields some of the most popular theropods such as *Allosaurus* (Marsh, 1877) or *Ceratosaurus* (Marsh, 1884) and other faunas from the North American Morrison Formation (Foster and Lucas, 2006). There are evidences in other parts of the world such as South America (e.g. Rauhut and Pol, 2017), Africa (e.g. Janensch, 1920, 1925; Rauhut, 2011) and Asia (e.g. Currie and Zhao, 1993; Xu *et al.,* 2009)

Concerning Europe, there are Upper Jurassic theropod evidences in France, England, Germany, Switzerland and the Iberian Peninsula (see Rauhut *et al.,* 2018b and references therein). Remains from the Lusitanian Basin (Mateus, 2006) include *Torvosaurus* (Hendrickx and Mateus, 2014a), *Lourinhanosaurus* (Mateus, 1998) and *Allosaurus* (Mateus et al., 2006), and also carcharodontosaurids (Malafaia *et al.,* 2018a) and other evidences suggested by isolated theropod teeth (e.g. Zinke, 1998; Hendrickx and Mateus, 2014b; Malafaia *et al.,* 2017b).

In Spain, remains from the Upper Jurassic appear on the Iberian range and the “dinosaur coast” in Asturias (N Spain). Several skeletal remains and tracksites have been reported. Isolated theropod teeth from this area has been previously reported or studied (see Martínez *et al.,* 2000; Ruiz-Omeñaca *et al.,* 2009; Ruiz-Omeñaca *et al.,* 2012a). The main goal of this paper is to perform a revision of the theropod palaeobiodiversity from the Upper Jurassic Vega, Tereñes and Lastres formations (Kimmeridgian in age).

2. MATERIALS AND METHODS

The fossils were recovered during fieldwork campaigns carried out by the Museo del Jurásico de Asturias team. The material recovered is housed in this institution. Observations were made with a stereomicroscope and a Dino-Lite digital microscope. The teeth were measured with a Mitutoyo Digimatic Digital Calliper, Series No. 500. Ten theropod teeth (Supplementary appendix A) from the Vega, Tereñes and Lastres Formations were analysed during the course of this research (Table 1).

Specimen	**Fm**	**Locality**
4262		
1226	**Vega**	**Acantilados de playa de Vega (Leces, Ribadesella)**
4443	**Lastres**	**Acantilados de Aranzón (Quintueles, Villaviciosa)**
0813	**Tereñes**	**Tereñes (Ribadesella)**
1219	**Lastres**	**Puerto de Tazones (Tazones, Villaviciosa)**
1217	**Lastres**	**Arroyo de la Escalera (Quintes, Villaviciosa)**
1018	**Vega**	**Acantilados de playa de Vega (Leces, Ribadesella)**
1218	**Lastres**	**Puerto de Tazones (Tazones, Villaviciosa)**
0856	**Lastres**	**Acantilados de Aranzón (Quintueles, Villaviciosa)**
3697	**Vega**	**Acantilados de Abeu (Leces, Ribadesella)**

Table 1. Specimens and locations.

2.1 Statistical analysis

A discriminant function analysis (DFA) was carried out using PAST3 (Hammer et al., 2001) on the dataset of Hendrickx *et al.* (2015b) as explained in Chapter 2 (Materials and Methods). The dataset includes more than 1000 teeth from different theropod clades as well as the Asturias teeth (CD).

Due to their state of preservation, not all the teeth were analysed; this was in order to avoid interference. Only MUJA 0813, MUJA 0856, MUJA 1018, MUJA 1218, MUJA 1219, MUJA 4262 and MUJA 4443 were included.

The variables used are CBL, CBW, CH, AL, MC and DC. In order to better reflect a normal distribution all data were log-transformed (see rationalization in Samman *et al.,* 2005 and references therein). When a character was absent or missing it was coded with a question mark. (CD). Two different analyses were performed separating mesial and lateral teeth due to the pseudoheterodonty and differentiation between mesial and lateral dentition in theropods.

2.2 Cladistic analysis

Cladistic analysis has been used by some authors to classify isolated theropod teeth and to evaluate their phylogenetic position (Hendrickx and Mateus, 2014b; Gerke and Wings, 2016; Csiki-Sava *et al.,* 2016; Alonso *et al.,* 2018).The teeth from the Vega, Tereñes and Lastres formations were analysed as explained in Chapter 2 (Materials and Methods).

3.RESULTS

3.1 Systematic palaeontology

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
THEROPODA Marsh, 1881

3.1.1 *Theropoda indet.*

Material: One shed tooth, MUJA 0856

Horizon and location: Lastres Formation, Acantilados de Aranzón (Quintueles, Villaviciosa), Kimmeridgian, Upper Jurassic.

3.1.1.1 Description

This morphotype comprises one theropod tooth crown partially embedded in the limestone holder (**Figure 1**). Only the left side of the crown is exposed. The surface has transverse fractures on the apical part of the crown and the apex is eroded. The tooth crown is ziphodont, serrated and distally curved.

The tooth crown is small-sized, with a crown base length (CBL) 8.78 of mm, an estimated crown base width (CBW) of around 5 mm (exposed half is 2.4 mm), and a crown height of 12.09 mm. The estimated CBR is around 0.55 and the CHR value is 1.37; the crown is labiolingually compressed and weakly elongated. The exposed side of the crown has a flattened surface centrally positioned from base to mid-crown.

In lateral view, MUJA 9856 has a convex mesial margin and a concave distal margin; being the mesial margin more recurved than the distal profile. Both margins are covered by carinae bearing serrations. The tip of the crown surpasses the base mesiodistally.

In mesial view, the mesial carina of MUJA 0856 seems to be centrally positioned on the crown. The mesial carina does not seem to reach the cervix, finishing at the mid-crown. In distal view, the distal carina is serrated and runs along the entire distal margin; it seems to be centrally positioned as well.

In apical view, the first half of the tooth has a lenticular cross-section and the serrated edges make the margins both acute. In basal view, the central flattened surface on the exposed side of the crown creates a half eight-shaped cross-section at the level of the cervix.

The mesial carina shows around 25 denticles per 5 mm at the mid-crown. The mesial denticles are perpendicular to the mesial margin of the tooth. The preserved denticles are subquadrangular in shape, with parabolic and symmetrically convex external margins.

The distal carina has around 27 denticles per 5 mm at the mid-crown, and the denticle size density index (DSDI) is around 1. The denticles are perpendicular to the distal margin of the crown. The denticles have a gradual decrease in size towards the base. The distal denticles are proximodistally elongated and the external margin is parabolic or semi-circular, either symmetrically or asymmetrically convex. The space between denticles is broad and deep, and there are interdenticular sulci on the distocentral area of the crown, short, basally inclined and poorly developed.

The crown surface texture is ornamented with transverse undulations which are apically concave. The transverse undulations are numerous but they are better seen at a certain angle. The enamel texture seems to be braided (*sensu* Hendrickx *et al.,* 2015c).

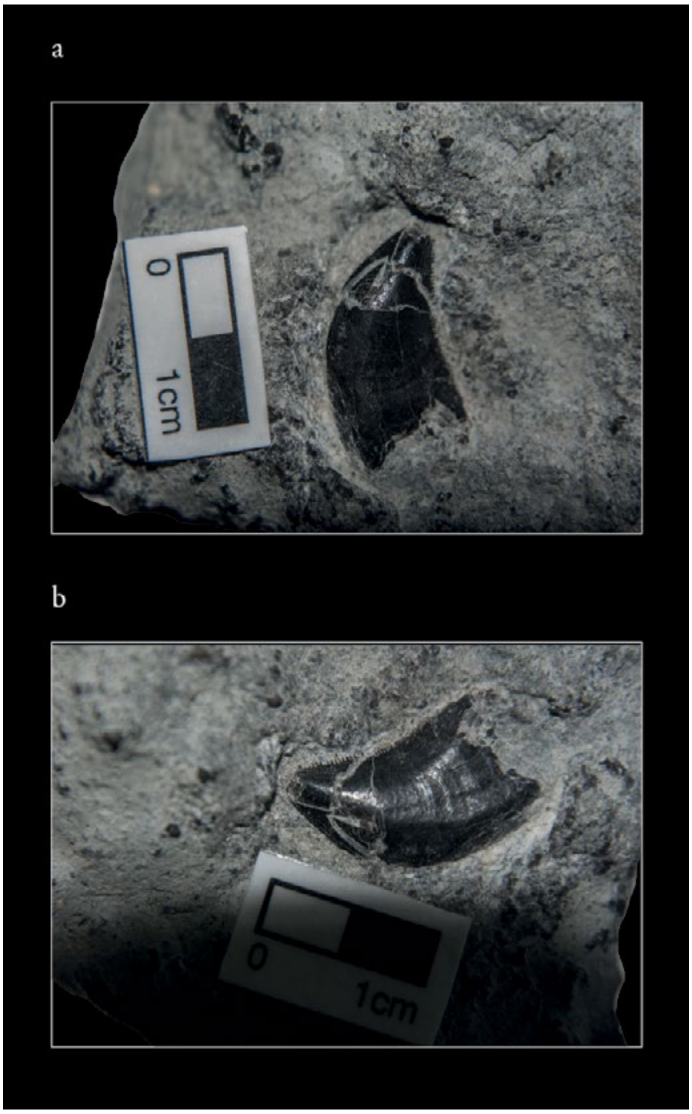


Fig. 1: Theropoda indet. a) lateral view. b) basal depression and enamel texture.

3.1.1.2 Discussion

The most relevant characters of this morphotype are the distal curvature, both carinae bearing serrations, a central depression on the exposed side of the crown, braided enamel texture, the presence of transverse undulations on the enamel surface and the presence of interdenticular sulci on the central area of the distal carina. This morphology excludes clades with no ziphodont dentition, unserrated carinae and big or minute denticles, including spinosaurids, derived tyrannosaurids, compsognathids, ornithomimosaurs, alvarezsauroids, therizinosaurs, oviraptorosaurs and troodontids (Csiki-Sava *et al.,* 2016).

The discriminant analysis considers (CD) this morphotype as a non-averostran neotheropod. The cladistics analysis (Appendix 1) recovers this morphotype with *PIatnitzkysaurus* and *Erectopus.* A reduced strict consensus using the prining option in TNT recovers this morphotype as the sister taxon of Averostra, or as the sister taxon of *Piatnitzkysaurus* (Appendix 1). *Piatnitzkysaurus* has higher DSDI, concave area adjacent to the distal carina and a mesial carina reaching the cervix (Hendrickx, 2015). Other piatnitzkysaurids such as *Condorraptor* (Rauhut, 2005) have a mesial carina that terminates in the apical half of the crown but the mesial profile is not as recurved as in MUJA 0856 and they are also larger and elongated, around 30 mm, and do not display interdenticular sulci. *Marshosaurus* (Madsen, 1976a) teeth have mesial serrations smaller than the distal ones and an eight-shaped cross-section which cannot be assured in this tooth (Hendrickx, 2015).

Small-sized and recurved theropod crowns are usually classified as dromaeosaurids. However, dromaeosaurids are not the only theropods presenting these features, like Proceratosaurus (Rauhut *et al.,* 2010), among others. In addition, a recurved profile is not only present in small taxa but in juvenile specimens as well (e.g Rauhut *et al.,* 2012). Ontogenetic teeth changes in theropods are not completely known due to the scarcity of complete ontogenetic series. In the case of *Torvosaurus*, the hatchling crowns lack the denticles (Araujo *et al.,* 2013) and differences among juvenile and adult tyrannosaurids have also been noticed (e.g. Tsuihiji *et al.*, 2011; Williamson and Brusatte, 2014). The possibility of this morphotype representing a juvenile crown cannot be ruled out.

Due to the uncertainty and preservation here we prefer to consider this morphotype as Theropoda indet.

AVEROSTRA Paul, 1988

3.1.2 *Averostra indet. 1.*

Material: One shed tooth, MUJA 0813

Horizon and location: Tereñes Formation, Tereñes (Ribadesella), Kimmeridgian, Upper Jurassic.

3.1.2.1 Description

This morphotype comprises one theropod tooth crown (**Figure 2**). The enamel surface of the crown is worn and is covered by apicobasal, transverse and diagonally oriented fractures and scratches. Some parts of the enamel are missing. The left side of the crown is the worst preserved; both mesial and distal margins were eroded and miss part of the enamel and some of the denticles. The tooth crown is ziphodont, labiolingually compressed and distally curved. The tooth crown is medium-sized, with a crown base length (CBL) of 16.59 mm, a crown base width (CBW) of 7.38 mm, and a crown height (CH) of 30.6 mm. With a CBR and a CHR of 0.44 and 1.84 respectively, the crown is strongly flattened and moderately elongated. The cross-section is ovoid. One of the sides has a concave surface adjacent to the distal carina; this concavity appears on the central and basal parts of the surface.

The tooth crown has a convex mesial margin and the distal profile is slightly concave. Both margins are covered by carinae bearing serrations along the entire crown length. In mesial view, the mesial carina of MUJA 0813 is placed on the central area of the mesial margin. The left side of the tooth crown is basoapically convex while the right side is straight. In distal view, the distal carina is straight and it is very slightly displaced to the right side. Both mesial and distal surfaces are mesiodistally convex.

In apical view, the tooth crown has a lenticular cross-section and the serrated edges make the margins sharp. In basal view, the cross-section at the level of the mid-crown and at the level of the cervix is lenticular.

The mesial carina displays around 16 denticles per 5 mm at the mid-crown but unfortunately they are not entirely preserved so the shape of the denticles cannot be determined. The distal carina has 15 denticles per 5 mm at the mid-crown, and the denticle size density index (DSDI) is around 1. The denticles are perpendicular to the distal margin of the tooth. The denticles have a gradual increase in size towards the base. The preserved denticles are horizontal subrectangular and the external margin is parabolic and the space between denticles is broad. The interdenticular sulci are present on the right side of the distal carina as well as on the left side of the mesial margin; the sulci are short and basally inclined.

The crown surface is ornamented with transverse undulations, apically concave. The enamel texture is braided (*sensu* Hendrickx *et al.,* 2015c).

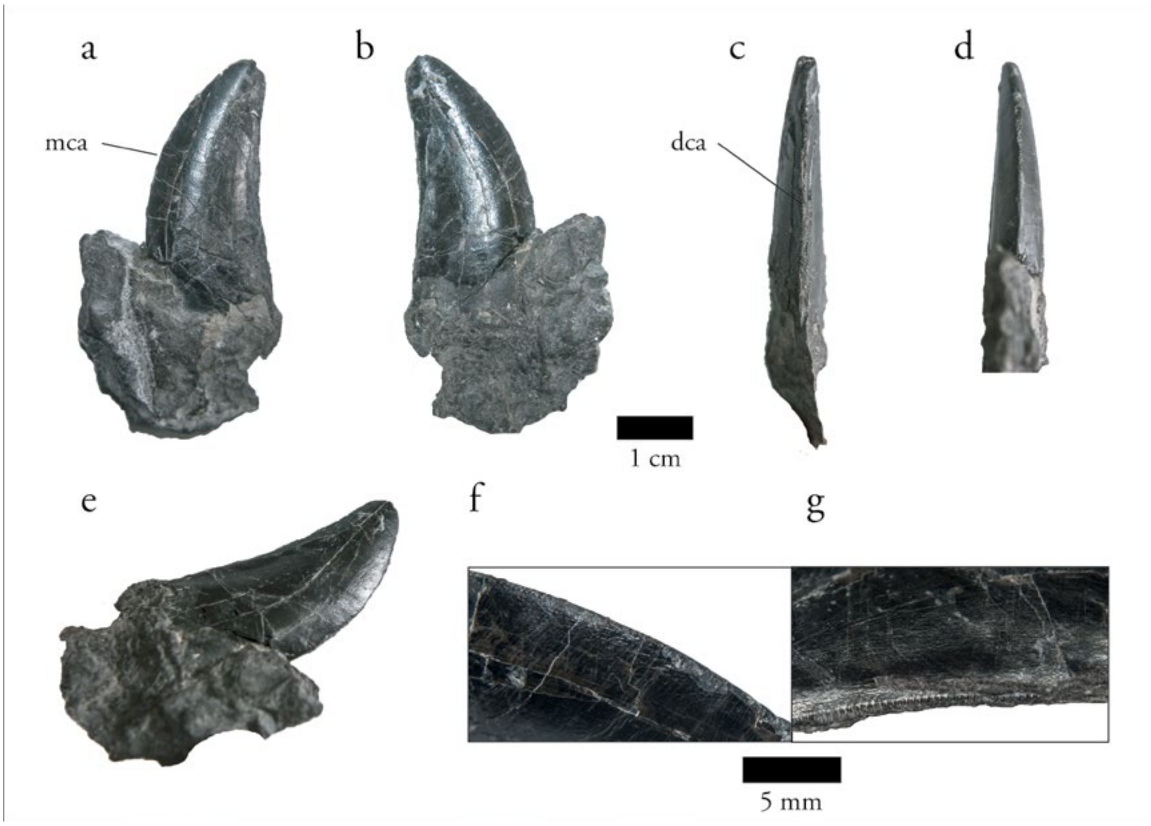


Fig. 2: Averostra indet. 1. a, b) lateral views. c) distal view. d) mesial view. e) detail on enamel texture. f) mesial carina and eroded denticles. g) depression adjacent to the distal carina and denticles. dca: distal carina; mca: mesial carina.

3.1.2.2 Discussion

This tooth was previously cited by García-Ramos and Aramburu (2010) and was previously described by Ruiz-Omeñaca *et al.* (2012).

The most relevant traits of this morphotype are serrated mesial and distal carinae that reach the cervix, a concave surface adjacent to the distal carina, a lenticular and strongly compressed cross-section and a DSDI close to 1. Those characters are seen in a broad set of theropod taxa, including ceratosaurids, allosaurids, neovenatorids, and tyrannosauroids (Hendrickx, 2015).

DFA (CD) classifies this morphotype as a megalosaurid tooth. The cladistic analysis **(**Appendix 1) recovers this morphotype in a polytomy with carcharodontosaurids, *Australovenator*, neovenatorids, *Allosaurus*, *Sinraptor*, *Piatnitzkysaurus* and *Erectopus*. A reduced strict consensus was calculated using the pruning trees option in TNT. The tooth is either recovered as the sister taxon of *Piatnitzkysaurus*, the sister taxon of *Erectopus*, as the sister taxon of *Berberosaurus* + *Genyodectes* + *Ceratosaurus*, as the sister taxon of *Australovenator* + *Fukuiraptor,* as the sister taxon of Carcharodontosauridae or within this clade.

Piatnitzkysaurids usually have smaller denticles on the mesial carina and are thicker labiolingually (Madsen, 1976a; Hendrickx *et al.,* 2015b; Canale *et al.,* 2017). Megalosaurids usually have a mesial carina that does not reach the cervix and lack a concave surface adjacent to the distal carinae (Hendrickx *et al.,* 2015b).

Erectopus is a basal allosauroid from the Albian of France (Allain, 2005) and is considered a possible metriacanthosaurid (Carrano *et al.,* 2012). The *Erectopus* teeth have similarities with this morphotype: a concave surface adjacent to the lingual carina, a mesial carina that reaches the cervix, 15 denticles per 5 mm on the mesial carina and 13 denticles per 5 mm on the distal carina.

The *Australovenator* lateral dentition is characterized (White *et al.,* 2015) by an eight-shaped cross-section, a mesial carina that presents denticles occasionally, around 9-15 mid-crown denticles per 5 mm on the distal carina and they are not strongly flattened as seen in this morphotype. On the other hand, *Fukuiraptor* has strongly labiolingually compressed teeth with serrations on both carinae and hooked distal denticles, which are not present in MUJA 0813 (Azuma and Currie, 2000; Currie and Azuma, 2006).

This tooth shares traits with ceratosaurids. The lateral teeth of ceratosaurids usually are heavily compressed (Rauhut, 2004; Malafaia *et al.,* 2017b) as seen in this tooth and the presence of a concave or flat surface adjacent to the carinae has been interpreted as a ceratosaurian synapomorphy; however this character is present in other theropod groups (Hendrickx, 2015).

The morphology of the tooth also resembles the lateral dentition of some carcharodontosaurids with a mesial carina reaching the cervix and a distal profile almost straight (Hendrickx et al., 2015b). Among carcharodontosaurians, neovenatorids have a concave surface adjacent to the carinae (Hendrickx, 2015).

The presence of both ceratosaurids and carcharodontosaurians has been documented in the Late Jurassic (Rauhut, 2011) and it is also known in the Iberian Peninsula (Mateus *et al.,* 2006; Malafaia *et al.,* 2018a).

The analyses of the morphotype leave uncertainty on its producer and the preserved traits are shared by different theropod groups, so here we prefer to be cautious and consider this morphotype as Averostra indet.

3.1.3 *Averostra indet. 2.*

Material: One shed tooth, MUJA 1218

Horizon and location: Lastres Formation, Puerto de Tazones (Tazones, Villaviciosa), Kimmeridgian, Upper Jurassic.

3.1.3.1 Description

The morphotype comprises one tooth which lacks the root (**Figure 3**). In its present state, there are several areas where the enamel is lacking, mostly the apex and the base; parts of the carinae are missing. The apical zone of the mesial margin shows an apicobasally oriented wear facet composed by two grooves. The tooth crown is ziphodont, labiolingually compressed and distally curved.

MUJA 1218 is a medium-sized theropod tooth, with a crown base length (CBL) of 10.57 mm, a crown base width (CBW) of 5.44 mm and an estimated crown height (CH) of 35-36 mm. With a CBR and a CHR of 0.51 and 1.69 respectively, the crown is labiolingually compressed and elongated.

In lateral view, the mesial margin of the crown is convex and the distal margin is concave. The apex surpasses the base mesiodistally. The apex is not acute due to its state of preservation. The tooth has a distal carina along the entire height of the crown. As stated before, the mesial margin is worn and this precludes the recognition of a possible mesial carina. In mesial view, the exposed surfaces of the crown are mesiodistally convex. In distal view, the distal carina bears denticles and it is slightly displaced labially.

In basal view, the cross-section of the crown is slightly eight-shaped at the level of the cervix, with depressions on both the labial and lingual basal surfaces. In apical view, the cross-section at the level of the mid-crown is lenticular-lanceolate.

The distal carina has around 18 denticles per 5 mm at the mid-crown. The denticles are perpendicular to the distal margin of the crown. The denticles are proximodistally subrectangular and the external margin is parabolic, either symmetrically or asymmetrically convex. The interdenticular space is broad and deep. There are interdenticular sulci on the distal carinae, short, basally inclined and poorly developed. The remaining enamel on the crown surface shows apically concave transversal undulations and the enamel texture is braided (*sensu* Hendrickx et al., 2015c).

The crown surface is worn and the enamel surface shows horizontally oriented transverse undulations, apically concave, and they curve towards the apex as they approach the carinae. The enamel texture is braided (*sensu* Hendrickx *et al.,* 2015c), easily visible with light.

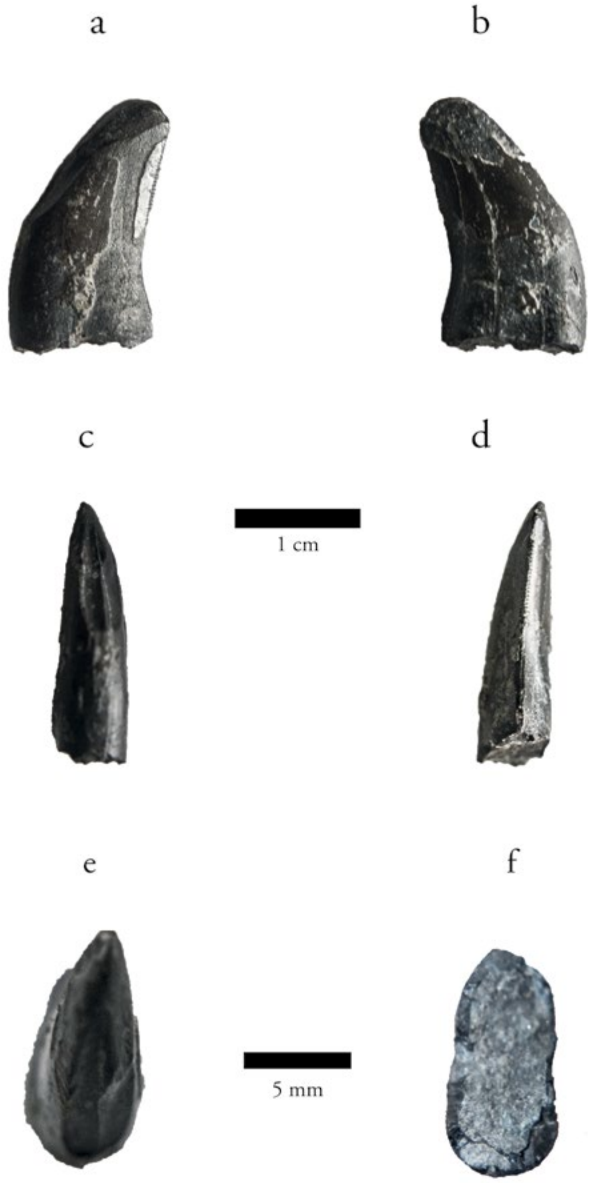


Fig. 3: Averostra indet. 2. in a) labial, b) lingual, c) mesial, d) distal, e) apical and f) basal views.

3.1.3.2 Discussion

The most striking feature of this morphotype is the eight-shaped cross-section due to the slight depressions both in the labial and lingual areas of the base. The eight-shaped cross-section has been noticed in *Berberosaurus*, metriacanthosaurids such as *Sinraptor* (Hendrickx and Mateus, 2014b), basal tyrannosauroids such as *Proceratosaurus, Alioramus* (Rauhut *et al.,* 2010; Brusatte *et al.,* 2012), megaraptorans including *Megaraptor*, *Orkoraptor* and *Australovenator* (Porfiri *et al.,* 2014; White *et al.,* 2015), dromaeosaurids such as *Pyroraptor* (Gianechini *et al.,* 2011), *Saurornitholestes*, the enigmatic *Richardoestesia* (Currie *et al.,* 1990; Sankey *et al.,* 2002), and troodontids (Hendrickx *et al.,* 2015b).

The discriminant analysis (CD) recovers this morphotype as Neovenatoridae. Neovenatorid teeth do not have the figure-eight-shaped cross-section, so this result could be a consequence of the size-dependent classification of this type of analysis. The cladistic analysis (Appendix 1) recovers this morphotype in a polytomy with *Tyrannosaurus*, *Alioramus*, *Raptorex*, *Eotyrannus*, *Proceratosaurus*, *Sinraptor, Piatnitzkysaurus* and *Erectopus*. Using the pruning option in TNT recovers this morphotype as the sister taxa of *Berberosaurus* + *Ceratosaurus* + *Genyodectes,* as the sister taxa of *Sinraptor* and as the sister taxa of *Tyrannosaurus*.

Neither *Piatnitzkysaurus* nor *Erectopu*s have an eight-shaped cross-section but it does appear on the metriacanthosaurid *Sinraptor* and some tyrannosauroids (Hendrickx, 2015). Tyrannosauroid taxa are known in the Late Jurassic, such as *Aviatyrannis* (Rauhut, 2003) from the Late Jurassic of Portugal, *Stokesosaurus* (Madsen, 1974) from North America or *Juratyrant* (Benson, 2008; Brusatte and Benson, 2013) from the United Kingdom. Other authors have reported the presence of tyrannosauroids from the Late Jurassic of Germany using isolated teeth (Gerke and Wings, 2016).

The state of preservation of this tooth does not leave much information to make a precise attribution. For this reason here we prefer to be cautious and consider MUJA 1218 as Averostra indet. 2.

3.1.4 *Averostra indet. 3.*

Material: Two shed teeth, MUJA 1018 and MUJA 4443

Horizon and location: MUJA 1018, Vega Formation, playa de Vega (Leces, Ribadesella), Kimmeridgian; MUJA 4443, Lastres Formation, Aranzón (Quintueles, Villaviciosa), Kimmeridgian, Upper Jurassic.

3.1.4.1 Description

This morphotype includes two teeth which have the base still embedded in the limestone holder (**Figure 4**). The surface of MUJA 1018 is worn due to erosion and wear. There are breaks on the base and minor fractures; and some parts of the enamel are missing as well as some denticles on both carinae; it also lacks the tip of the crown. The enamel surface of MUJA 4443 is worn and lacks parts of the enamel. It also has transverse breaks across the crown and lacks part of the basal and labial area.

The teeth are ziphodont with the typical blade-like morphology of theropods with labiolingually compressed and a distally curved crown. The mesial and distal carinae are eroded; and some parts of the enamel are missing as well as some denticles on both carinae. MUJA 1018 and 4443 are medium-sized theropod teeth. The crown base length (CBL) is 13.74mm and 14.14 mm respectively, the crown base width (CBW) is around 7 mm and the crown height (CH) is around 36 mm and 35.1 mm respectively. The crown is strongly labiolingually compressed (CBR = 0.56, 0.49) and elongated (CHR = 2.6 and 2.48), with an ovoid cross-section at its base.

In lateral view, the mesial margin of the teeth is convex and the distal margin is concave. The crowns possess mesial and distal carinae; both carinae are serrated. In MUJA 1018, the distal carina extends along the whole distal margin whereas the mesial carina extends more than two thirds of the crown height. The labial surface has a planar surface adjacent to the distal carina. In the case of MUJA 4443; the mesial carina extends from the apex to the half of the crown, from this point it is not preserved. On the other hand, the distal carina extends from the apex to the base of the crown. The planar surface adjacent to the distal carina is not seen, probably due to preservation.

In mesial view, the mesial carina bears denticles and it is placed on the mesiodistal axis of the crown. Towards the base, the carina of MUJA 1018 is slightly twisted lingually. The lingual side of MUJA 4443 is slightly basoapically sigmoid; the labial side is not well preserved enough to tell.

In distal view, the distal carina is strongly displaced labially and it is not bowed on the distal margin. The labial surface is mesiodistally flattened, whereas the lingual side is convex.

In apical view, the crowns have a lenticular cross-section with both the mesial and distal margins acute. In basal view, the cross-section of the crowns at the level of the cervix is oval-lanceolate while the cross-section at the level of the mid-crown remains lenticular in shape.

The mesial carina of MUJA 1018 has 18-19 denticles per 5 mm at the level of the mid-crown. The remaining denticles are subquadrangular in shape, perpendicular to the external margin of the crown and the external margin is parabolic; they are either symmetrically or asymmetrically convex. The space between denticles is broad.

The mesial carina of MUJA 4443 preserves 19-20 denticles per 5 mm at the mid-crown. In lateral view, the apicobasal and mesiodistal axis of the denticles is roughly the same size, giving them a subquadrangular outline. The external margin of the denticles is parabolic and they are perpendicular to the carina.

The distal carina of MUJA 1018 has around 18 denticles per 5 mm at the mid-crown. They are perpendicularly placed to the distal margin of the crown and decrease in size towards the base. The denticles are proximodistally subrectangular and the external margin is parabolic. As seen in the mesial carina, the margin is either symmetrically or asymmetrically convex. The space between denticles is broad and deep. The interdenticular sulci are located on both sides of the distal carina, short and basally inclined; they are not easily seen. The distal carina of MUJA 4443 has around 18 denticles per 5 mm at the mid-crown and none of them are preserved.

The crown surface displays marginal and transverse undulations, they are short and are better seen at certain angles. Transverse undulations are apically concave and they curve towards the apex as they approach the carinae. There are interdenticular sulci on the mesial and distal carinae. The enamel texture seems to be braided (*sensu* Hendrickx *et al.*, 2015c).
light.

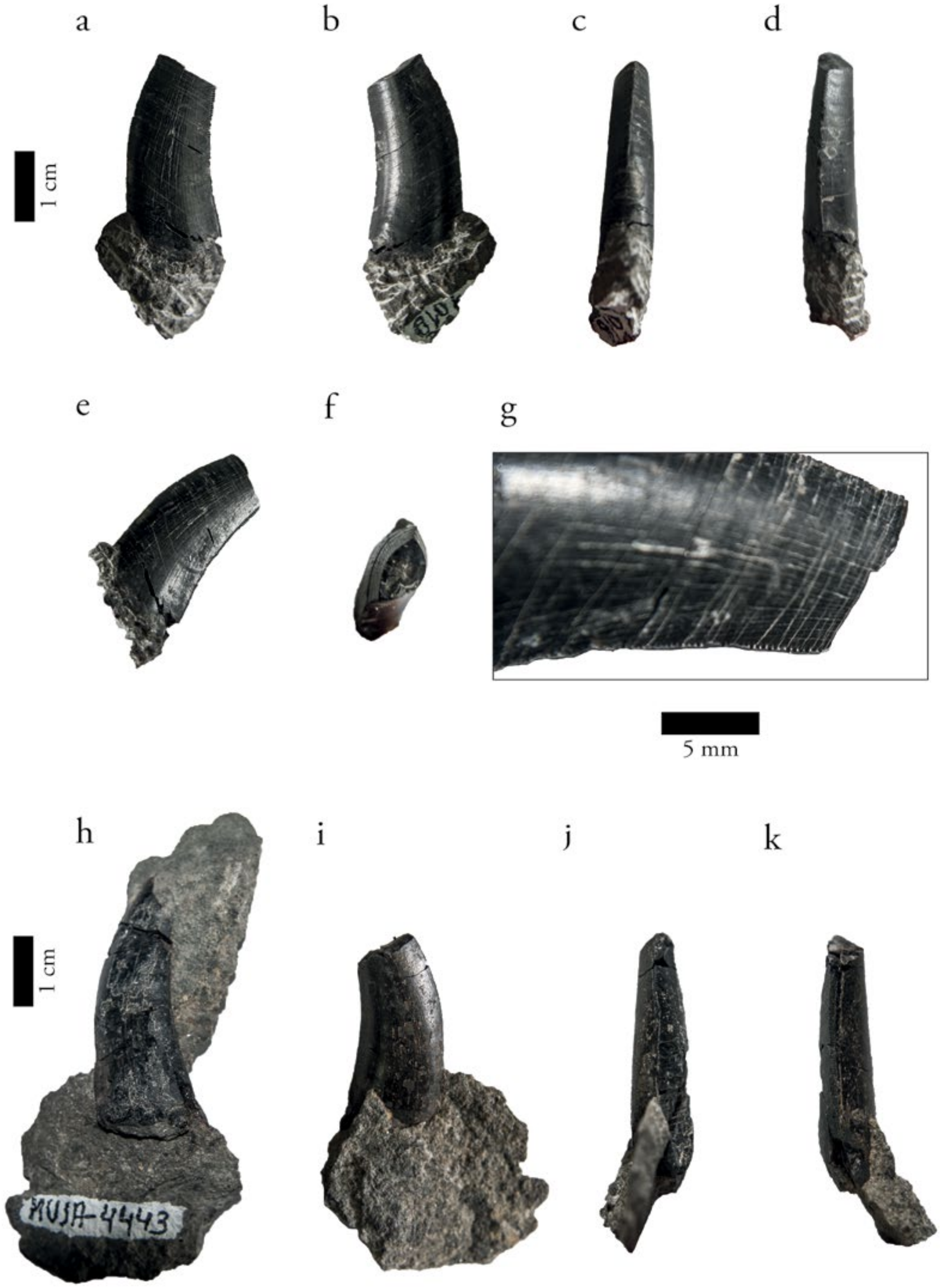


Fig. 4: Averostra indet. 3. MUJA 1018 in a) labial, b) lingual, c) mesial, and d) distal views. e) Surface adjacent to the distal carina. f) apical view. g) detail on distal carina. MUJA 4443 in h) labial, i) lingual, j) mesial and k) distal views.

3.1.4.2 Discussion

The principal traits of MUJA 1018 and 4443 are a mesial carina that does not reach the cervix, a distal carina strongly displaced labially, the presence of a planar surface adjacent to the distal carina on the labial surface, around 20 and 18 denticles per 5 mm at the mid-crown on the mesial and distal carina respectively (DSDI= 1.1), braided enamel texture, interdenticular sulci, and the presence of marginal and transverse undulations on the enamel.

With a strongly compressed cross-section at the level of the cervix, this tooth is considered a lateral tooth. The size of the crown, number of denticles and general morphology excludes basal theropods, spinosaurids, derived tyrannosauroids, and derived coelurosarians such as therizinosaurs, ornithomimosaurs, troodontids or alvarezsauroids (Brusatte *et al.*, 2010a; Turner *et al.,* 2012; Hendrickx and Mateus, 2014b; Csiki-Sava *et al.,* 2016; Alonso and Canudo, 2016).

A distal carina strongly displaced labially can be found on ceratosaurids (Hendrickx, 2015). A mesial carina that does not reach the cervix excludes the lateral dentition of *Ceratosaurus* but not *Genyodectes* (Rauhut, 2004; Hendrickx *et al.,* 2015b).

Unlike abelisaurids, which usually have low and weakly recurved teeth, MUJA 4443 is an elongated and recurved crown (Hendrickx and Mateus, 2014b; Smith, 2007). In addition, abelisaurids have an irregular enamel texture.

Piatnitzkysaurids usually have a mesial carina that does not reach the cervix, but some taxa such as *Marshosaurus* and *Piatnitzkysaurus* have a DSDI higher than 1.2, which is not shared by this tooth (Madsen, 1976a; Hendrickx, 2015).

Megalosaurid lateral teeth are labiolingually compressed, have braided enamel texture, the mesial carina does not reach the cervix, they could possess marginal and transverse undulations but they do not have a strongly labially offset distal carina and lack the flat surface adjacent to the carina (Hendrickx *et al.,* 2015b).

Regarding metriacanthosaurids, there are some differences between them and MUJA 4443. Metriacanthosaurid teeth usually have a concave surface adjacent to carinae, an eight-shaped cross-section, a weakly recurved distal margin and the mesial denticles reach the cervix (Hendrickx, 2015).

The discriminant analysis (CD) classifies MUJA 1018 as Piatnitzkysauridae and MUJA 4443 as *Erectopus*. The cladistic analysis (Appendix 1) recovers this morphotype at the base of Averostra close to *Piatnitzkysaurus* and *Erectopus*. A reduced strict consensus was calculated using the pruning trees option in TNT. The pruning of this morphotype either recovers it as the sister taxon of *Piatnitzkysaurus* + *Erectopus* or as the sister taxon of *Genyodectes* + *Ceratosaurus* + *Berberosaurus*.

The possible presence of piatnitzkysaurids has been cited in other Late Jurassic associations (Gerke and Wings, 2016; Malafaia *et al.,* 2017b) based on isolated teeth. However, as stated above, this morphotype does not have a DSDI higher than 1.2, also the distal carina of *Piatnitzkysaurus* is not labially offset. Regarding *Erectopus*, the mesial carina reaches the cervix, which is not the case on MUJA 1018 and 4443 (Allain, 2005). *Berberosaurus* has an eight-shaped cross-section, which is not found on this morphotype (Hendrickx, 2015).
Due to the ambiguity of the characters on this morphotype, these teeth are tentatively attributed to Averostra indet. on the basis of both the DFA and cladistic analyses.

It is remarkable that the teeth of this morphotype come from different formations. This could mean that the same taxon extended along the Kimmeridgian or, at least, related taxa, or maybe that different taxa produced the same morphotype. Further remains are needed in order to clarify this point.

CERATOSAURIA Marsh, 1884
ABELISAUROIDEA Bonaparte, 1991
ABELISAURIDAE Bonaparte and Novas, 1995

3.1.5 *Abelisauridae? indet.*

Material: One shed tooth, MUJA 1219

Horizon and location: Lastres Formation, Puerto de Tazones (Tazones, Villaviciosa) Kimmeridgian, Upper Jurassic.

3.1.5.1 Description

MUJA 1219 is a well-preserved theropod tooth crown. The surface of the crown is covered by diagonally oriented fractures plus minor breaks. The crown is worn and parts of the enamel are missing as well as some areas on the mesial and distal margins. The carinae are eroded and the external margin of some denticles is missing (**Figure 5**). The tooth is ziphodont; it shares the blade-like morphology of most theropod teeth.

MUJA 1219 is a medium-sized tooth crown. The crown base length (CBL) is 9.18 mm, the crown base width (CBW) is 4.16 mm and the crown height is 16.7 mm. The crown is strongly labiolingually compressed (CBR = 0.45) and slightly elongated (CHR = 1.81), and it has an elliptical cross-section.

In lateral view, the mesial profile is convex and the distal profile is straight. Both margins have carinae bearing denticles. In mesial view, the mesial carina is centrally positioned on the mesial margin and has serrations. The left side of the crown is basoapically convex and the right side seems to be basoapically sigmoid with the basal part of the crown concave and the apical convex. However this could be a result of the fractures present in this tooth.

In distal view, the distal carina is not displaced and bears denticles all along the edge. Both right and left sides are mesiodistally convex.

In apical view, the tip is distally positioned on the crown and the cross-section at the mid-crown is lenticular. In basal view, the cross-section at the level of the base is elliptical, with basal flattened surfaces on both sides, with the mesial and distal margins both acute.

The mesial carina of MUJA 1219 has around 20 denticles per 5 mm at the mid-crown. The size of the denticles increases from the apex towards the mid-crown and they display a regular variation in size. In lateral view, the apical-central denticles possess a horizontal subrectangular outline. The mesial denticles became subquadrangular towards the apex and then vertical subrectangular close to the tip and the external margin is parabolic.

The distal carina of MUJA 1219 has around 20 denticles per 5 mm at the mid-crown, and the denticle size difference index (DSDI) has a value of around 1. The denticles are smaller on the base and on the tip of the crown. They are chisel-shaped and proximodistally subrectangular; the mesiodistal axis that is greater than the apicobasal axis except in the apical and basal denticles which are subquadrangular in shape. The main axis of the denticle is apically inclined.

The external margin of both mesial and distal denticles is parabolic and either symmetrically or asymmetrically convex. The interdenticular space between denticles is broad and deeper in the distal denticles. There are sulci between the denticles, short and basally inclined along the margins of both carinae.

The crown surface is covered with scratches due to wear and erosion. The enamel has both marginal and transverse undulations; the marginal undulations are diagonally oriented. The transverse undulations are apically concave, covering the enamel surface, and are better seen at certain angles.

The original enamel texture appears to be irregular (*sensu* Hendrickx *et al.,* 2015c).

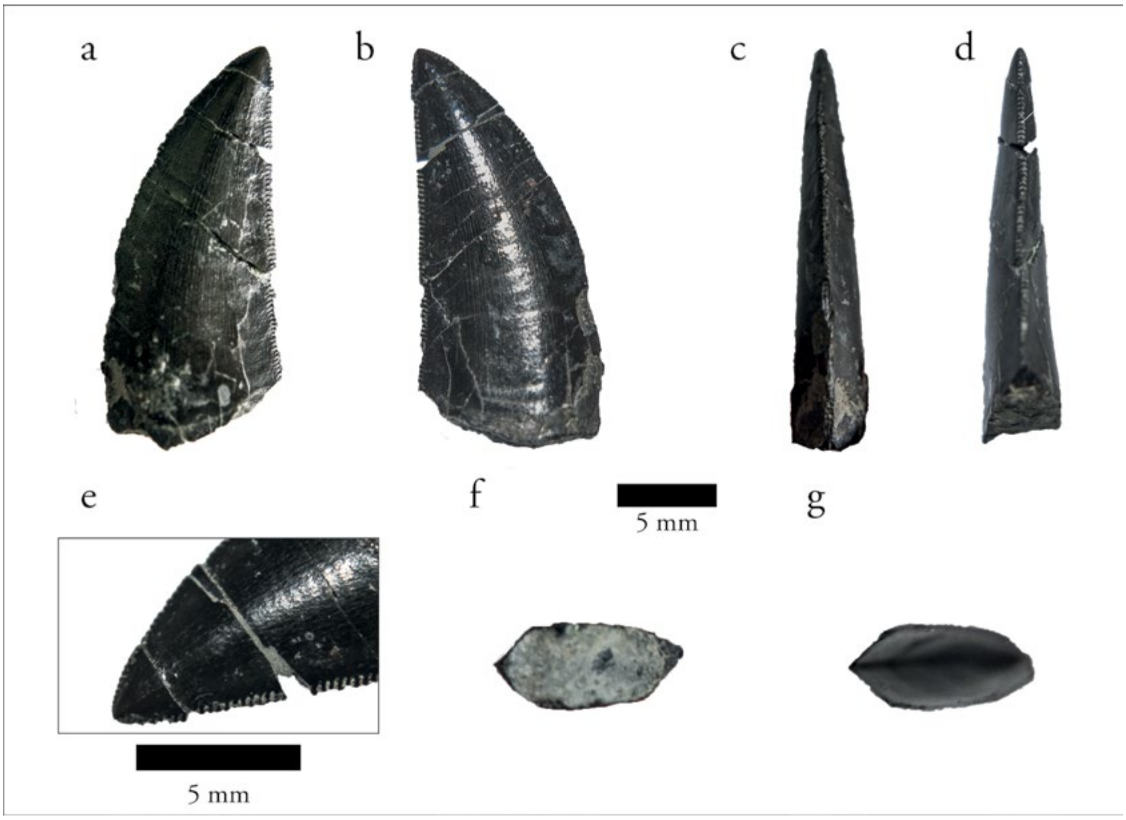


Fig. 5: Abelisauridae? indet. MUJA 1219 in a), b) laterial views, c) mesial, and d) distal views. e) mesial, apical and distal denticles. f) basal view. g) apical view.

3.1.5.2 Discussion

The most relevant traits of this morphotype are serrated mesial and distal carina that reaches the cervix, a straight distal carina, a strongly compressed cross-section, a DSDI close to 1 and the apically inclined distal denticles.

Apically inclined are present in numerous theropod taxa, including abelisaurids, allosaurids and carcharodontosaurids, tyrannosauroids, dromaeosaurids and troodontids (Carrano *et al.,* 2012; Hendrickx and Mateus, 2014b; Malafaia *et al.,* 2017b; Sweetman, 2004; Tavares *et al.,* 2014).

A straight distal carina appears on basal theropods, ceratosaurids, noasaurids, allosauroids, tyrannosauroids and some coelurosaurs (Hendrickx, 2015), but the size, age and teeth features exclude basal theropods, noasaurids and most clades of coelurosaurs (Csiki-Sava *et al.,* 2016; Lindoso *et al.,* 2012; Sampson *et al.,* 2001; Smith *et al.,* 2005). Among the clades aforementioned, an irregular enamel texture excludes carcharodontosaurids but that trait could be present in some theropod taxa such as allosaurids, tyrannosaurids and most coelurosaurs, whereas a centrally positioned distal carina excludes allosaurids such as Allosaurus and some tyrannosauroids (Hendrickx, 2015).

A DSDI lower to 1.2 excludes microraptorinae dromaeosaurids and the shape and number of denticles also is different to those of troodontids (Currie *et al.,* 1990; Hendrickx, 2015; Holtz *et al.,* 1998; Torices *et al.,* 2018).

The discriminant analysis (CD) classifies this morphotype as a non-tyrannosaurid tyrannosauroid. The cladistics analysis (Appendix 1) recovers this morphotype in a polytomy within Abelisauridae, among *Majungasaurus* and *Kryptops*. Abelisaurids are known from the Late Jurassic of Portugal (Hendrickx and Mateus, 2014b).

Given the combination of features and the results of the cladistics analysis here we tentatively consider this morphotype as Abelisauridae? indet.

TETANURAE Gauthier, 1986
MEGALOSAUROIDEA Fitzinger, 1843
MEGALOSAURIDAE Fitzinger, 1843

3.1.6 *Megalosauridae indet. 1.*

Material: One tooth, MUJA 4262

Horizon and location:

3.1.6.1 Description

MUJA 4262 is a ziphodont tooth preserving most of the crown and part of the root (**Figure 6**). In its present state, one of the sides of the tooth is embedded in the limestone holder. It preserves the basal-most part of the root, and it is more complete near the anterior margin. The enamel shows small fractures and some parts are missing; the tip and the base of the crown have damaged areas which lack fragments of the crown. A transverse break is located on the apical-central area. The enamel surface is covered with micro scratches and parts of the original enamel are worn due to abrasion.

Despite this condition, the tooth is well-preserved. The crown base length (CBL) is 26.62 mm. Since the tooth is embedded in the limestone, the exact crown base width (CBW) is difficult to determine. However, the exposed half width is 10.2 mm, so here we consider the real crown base width value around 20 mm. The crown height (CH) is 67.76 mm. The tooth morphology is ziphodont. According to the estimated CBR (>0.75) and CHR (2.54), the crown is weakly labiolingually compressed and basoapically elongated, with a broad cross-section at its base.

In lateral view, the mesial and distal profiles are convex and slightly concave, respectively. The crown is moderately recurved; being the mesial profile more recurved than the distal profile. The base length of the crown is longer than the mid-crown mesiodistally.

In mesial view, the mesial surface bears a mesial carina. The mesial carina is serrated and ends before the cervix. In addition, the mesial carina stands centrally located on the crown, facing mesially.

In distal view, the distal carina bears denticles and extends along the whole distal edge. It is centrally positioned on the crown and does not show twisting. In apical view, the tip is distally positioned on the crown and the exposed side is convex. In basal view, the cross-section of the crown is difficult to verify due to the embedding in the limestone holder but it probably is elliptical-lanceolate. The serrated margins are both acute.

The mesial carina has a low number of denticles per 5 mm (8) at the mid-crown. The denticles vary gradually in size towards the basalmost area of the crown. Denticle size decreases towards the base, thus there is a higher number of denticles basally than at the mid-crown and the apex. Denticles are better preserved at the tip and the main axis is inclined apically from the mesial margin. Apical denticles are longer mesiodistally than basoapically, being proximodistally subrectangular. Mesiocentral and mesiobasal denticles seem to be subquadrangular and vertically subrectangular, respectively. The external margin of the denticles is parabolic; they are symmetrically or asymmetrically convex. The interdenticular space is broad. There are short and basally inclined interdenticular sulci present on the mesioapical and mesiocentral areas.

The distal carina has a low number of denticles per 5 mm as well (7). The denticles are perpendicular to the distal margin of the crown and they decrease in size towards the base as previously seen on the mesial carina, displaying a gradual variation. The distoapical and distocentral denticles are proximodistally subrectangular, while the distobasal denticles become broader and shorter, giving them a subquadrangular shape. The external margin of the denticles is parabolic, symmetrically or asymmetrically convex. The space between denticles is broad and deep on the apical and central denticles and narrow on the basal denticles. There are interdenticular sulci on the distoapical area of the crown, short, basally inclined and poorly developed.

The crown surface is worn and covered with micro scratches due to erosion and wear. The enamel surface also shows horizontally oriented transverse undulations, apically concave, but they are not too numerous, they are better seen at a certain angle.

The enamel texture of the crown is braided (*sensu* Hendrickx *et al.,* 2015c) and it is clearly visible with light.

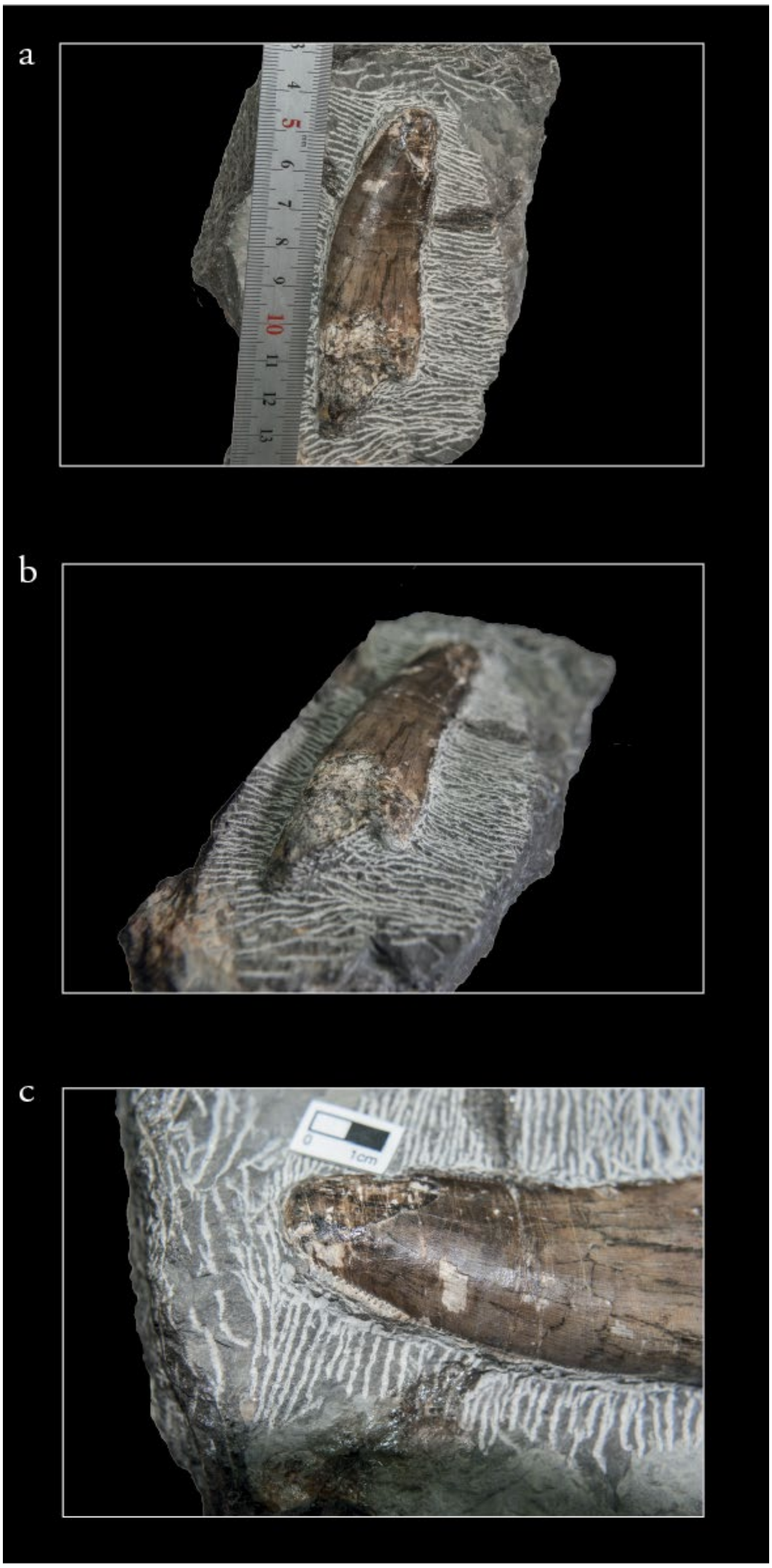


Fig. 6: Megalosauridae indet. 1. MUJA 4262 in a), lateral view. b) basal view. c) detail on the apex of the crown and enamel texture.

3.1.6.2 Discussion

One of the most conspicuous characters of this tooth crown is the low number of denticles per 5 mm both in mesial and distal carinae. A similar number of denticles per 5 mm (around 7-9) has been reported among the clade Ceratosauridae (*Ceratosaurus*); Abelisauridae (*Abelisaurus*, *Indosuchus*, *Rugops* and *Majungasaurus*), Megalosauridae (*Afrovenator*, *Duriavenator*, *Megalosaurus*, *Torvosaurus*); Allosauridae (*Allosaurus*); Carcharodontosauridae (*Carcharodontosaurus*, *Mapusaurus*, *Giganotosaurus*); Tyrannosauridae (*Gorgosaurus*, *Daspletosaurus*, *Tyrannosaurus*) and Troodontidae (*Troodon*, *Pectinodon*) (Madsen and Welles, 2000; Smith *et al.,* 2005; Smith, 2007; Longrich, 2008; Sankey, 2008; Hendrickx *et al.,* 2015b). The size of this tooth is also notable, almost 70 mm in crown height; it was produced by a large theropod. Among the aforementioned taxa, troodontids do not reach those sizes and abelisaurid teeth are usually smaller (e.g. *Majungasaurus* crown height varies between 18-36 mm; Smith *et al.,* 2005 dataset). In addition, abelisaurid crowns are low and weakly recurved (Hendrickx and Mateus, 2014b).

Due to the high estimated CBR (>0.75) MUJA 4262 is interpreted as a mesial tooth. In theropods, lateral teeth are usually more compressed than the mesial ones, probably due to the higher stress that the mesial dentition received during prey capture, biting and feeding (Hendrickx, 2015).

Teeth of a comparable size were produced by North American Late Cretaceous tyrannosaurids such as *Gorgosaurus*, *Daspletosaurus* and *Tyrannosaurus*. Those taxa have heterodont dentition with D or U-shaped premaxillary teeth and incrassate lateral crowns (Currie *et al.,* 1990; Samman *et al.,* 2005). However, it is unlikely that the Asturias tooth was produced by one of those derived tyrannosaurid taxa due to the huge temporal gap from the Late Jurassic to the Late Cretaceous. It is remarkable that earlier tyrannosauroid taxa do not have the incrassate lateral crowns (Rauhut *et al.,* 2010) and are smaller in size. In addition, MUJA 4262 does not have a U-shaped cross-section (Hendrickx *et al.,* 2015b), so the tyrannosauroid origin of this tooth has been ruled out.

Ceratosaurid, megalosaurid, allosaurid and carcharodontosaurid remains are known from the Upper Jurassic of the Iberian Peninsula, particularly in the Lusitanian Basin (Mateus *et al.,* 2006; Hendrickx and Mateus, 2014a,b; Malafaia *et al.,* 2018a). In Spain, there are Late Jurassic megalosaurid remains in Asturias and the Iberian Range (e.g. Cobos *et al.,* 2014; Rauhut *et al.,* 2018b).

Premaxillary teeth of *Ceratosaurus* and its closest relatives are easily recognizable due to the striations present on the lingual side of the crown (Madsen and Welles, 2000; Soto and Perea, 2008; Rauhut, 2011) and some crowns lack a mesial carina (Currie and Carpenter, 2000). On the other hand, *Genyodectes* lacks these striations on the lingual surface, has 12 denticles per 5 mm mesially and distally (Rauhut, 2004, 2011) and the mesial carina covers the apical half of the crown, the distal carina is displaced labially and premaxillary teeth are strongly elongated (Hendrickx *et al.,* 2015b).

MUJA 4262 does not meet the criteria to be considered a mesial *Ceratosaurus* tooth. There are no striations (at least on the exposed side), the mesial carina is serrated and it is strongly elongated (CHR= 2.54). On the other hand, it is more similar to *Genyodectes* mesial teeth: It is strongly elongated and the mesial carina does not reach the cervix, but in MUJA 4262 surpasses two thirds whereas in *Genyodectes* covers the apical half. It is difficult to tell if the distal carina is offset, but it is true than the number of denticles per 5 mm is lower than in *Genyodectes*.

The lateral teeth of ceratosaurs are strongly compressed labiolingually (Madsen and Welles, 2000; Rauhut, 2004) and usually have a flat or concave surface adjacent to the mesial or distal carinae (Malafaia *et al.,* 2017b). It also has been noticed that *Ceratosaurus* has apical denticles inclined apically from mesial margin (Hendrickx and Mateus, 2014b dataset) on the lateral teeth. In *Ceratosaurus* both carinae reach the cervix (Hendrickx *et al.,* 2015b; Malafaia *et al.,* 2017b) whereas in *Genyodectes* extends on the apical half of the crown. While it is true that MUJA 4262 have the apically inclined apico-mesial denticles, it does lack the flat or concave surface adjacent to one or both the carinae and the compressed cross-section, so the ceratosaur origin of the tooth as lateral dentition remains unlikely.

Mesial teeth of *Allosaurus* have a D-shaped cross-section due to the twisting of the mesial carina towards the lingual side (Hendrickx *et al.,* 2015b) which is not the case of MUJA 4262. The lateral dentition, on the other hand, is not as elongated and broad as MUJA 4262 (Smith et al., 2005 dataset). MUJA 4262 does not have apically inclined distal denticles (Han *et al.,* 2011; Gerke and Wings, 2016; Malafaia *et al.,* 2017b). It is difficult to tell if the distal carina is offset labially, as usual in allosaurids (Hendrickx et *al.,* 2015b).

The mesial dentition of carcharodontosaurids has a mesial carina facing mesially and a distal carina strongly displaced labially (Hendrickx *et al.,* 2015b) so the mesial and distal carinae are not aligned (Hendrickx and Mateus, 2014b). In the case of MUJA 4262 both carinae seem to be located on the same plane.

The lateral dentition of carcharodontosaurine carcharodontosaurids reaches the cervix or finish just above it. However those teeth usually have marginal undulations on the surface of the crown that MUJA 4262 lacks (Hendrickx *et al.,* 2015b).

It is remarkable that *Carcharodontosaurus*, *Giganotosaurus* and *Mapusaurus* do not reach CBR and CHR values comparable to MUJA 4262 (Smith *et al.,* 2005 dataset).

Megalosaurid teeth, on the other hand, share a set of traits with MUJA 4262. The lateral dentition is ruled out due to the labiolingual compression of the crowns. However, the mesial teeth could reach comparable CBR (from 0.63 to 0.75) and CHR values (from 2 to 2.8) (Hendrickx et al., 2015b). According to the these authors, megalosaurid mesial dentition has a centrally positioned mesial carina that does not reach the cervix and occupy between 55-65% of the crown height, a distal centrally positioned distally carina that faces posteriorly (avoiding D, U or J-shaped cross-sections), a DSDI close to 1, and tenuous transverse undulations. MUJA 4262, as described above, shares these traits.

In summary, MUJA 4262 resembles either the ceratosaur *Genyodectes* mesial teeth or the mesial dentition of megalosaurids. Both ceratosaurids and megalosaurids are known from the Late Jurassic of the Iberian Peninsula.

The discriminant analysis (CD) excluding lateral dentition classifies MUJA 4262 as a tyrannosaurid tooth; this could be related to the size-dependant classification of this type of analysis. The cladistics analysis (Appendix 1) recovers MUJA 4262 within a polytomy with *Torvosaurus*, *Megalosaurus*, *Duriavenator* and *Afrovenator*; all of them megalosaurids. For these reasons, here we consider MUJA 4262 a megalosaurid mesial tooth.

3.1.7 *Megalosauridae indet. 2.*

Material: One tooth, MUJA 1226

Horizon and location: Vega Formation, playa de Vega (Leces, Ribadesella), Kimmeridgian, Upper Jurassic.

3.1.7.1 Description

The morphotype comprises one tooth lacking the root and part of the base (**Figure** 7). The tooth is embedded in the limestone holder, displaying one side of the crown. The tooth is a ziphodont theropod crown, with a labiolingually compressed and curved morphology. The tooth crown has apicobasal breaks: There are two major breaks along the crown plus minor fractures. The mesial region is worst preserved, it is eroded, lacks some fragments and some denticles are missing.

MUJA 1226 is a big-sized theropod tooth, with a preserved crown base length (CBL) of 28.48 mm and a preserved crown height (CH) of 44.45 mm. The crown could have reached a crown height larger than 60 mm. The exact preserved crown base width (CBW) is difficult to ascertain. The width of the exposed side is 4.33 mm, so here we consider the value of CBW around 10-11 mm. In that case, the tooth crown is strongly labiolingually compressed (CBR

<0.4) and is not strongly elongated.

In lateral view, the mesial margin of the tooth crown is convex whereas the distal margin is straight; the apex does not surpass the distobasal region. The apex is acute and does not have spalled surfaces at least on the exposed side. The tooth crown has both mesial and distal carinae; both carinae extend along the whole preserved margins of the crown.

In mesial view, the mesial carina bears denticles, and it is placed on the mesiodistal axis of the crown. The mesial carina is not twisted.

In distal view, the distal carina bears serrations, and it seems to be positioned on the mesiodistal axis of the tooth. The exposed surface of the crown is mesiodistally convex. In basal view, the cross-section of the crown seems to be lenticular at the level of the mid-crown and at the level of the cervix, with the mesial and distal margins both acute due to the carinae. In apical view, the tip bears denticles.

The mesial carina has 8 denticles per 5 mm at the preserved mid-crown. The denticles display a gradual decrease in size towards the basalmost part of the crown; they are also smaller on the tip of the tooth. Mesial denticles are not completely preserved on the apex and mid-section; the basal denticles are proximodistally horizontal in shape and are perpendicular to the mesial margin of the tooth. The external margin of the denticles is parabolic and symmetrically or asymmetrically convex. The space between denticles is broad and deep. There are interdenticular sulci on the preserved areas of the mesiocentral area; they are short, basally inclined and are easily visible.

The distal carina has 8 denticles per 5 mm at the preserved mid-crown. The denticles are perpendicular to the distal margin of the tooth. The denticles decrease in size towards the base; they are also smaller on the tip. The distocentral, distobasal and most of the distoapical denticles are proximodistally subrectangular. The denticles become subquadrangular and then apicobasally subrectangular towards the tip. The external margin of the denticles, as seen on the mesial carina, is parabolic and they are either symmetrically or asymmetrically convex. The interdenticular space is broad and deep. There are interdenticular sulci all along the carina, short, basally inclined and easily visible.

The crown surface is worn and the enamel surface shows horizontally oriented transverse undulations, apically concave, and they curve towards the apex as they approach the carinae. The enamel texture is braided (*sensu* Hendrickx *et al.,* 2015c) and is easily visible with light.

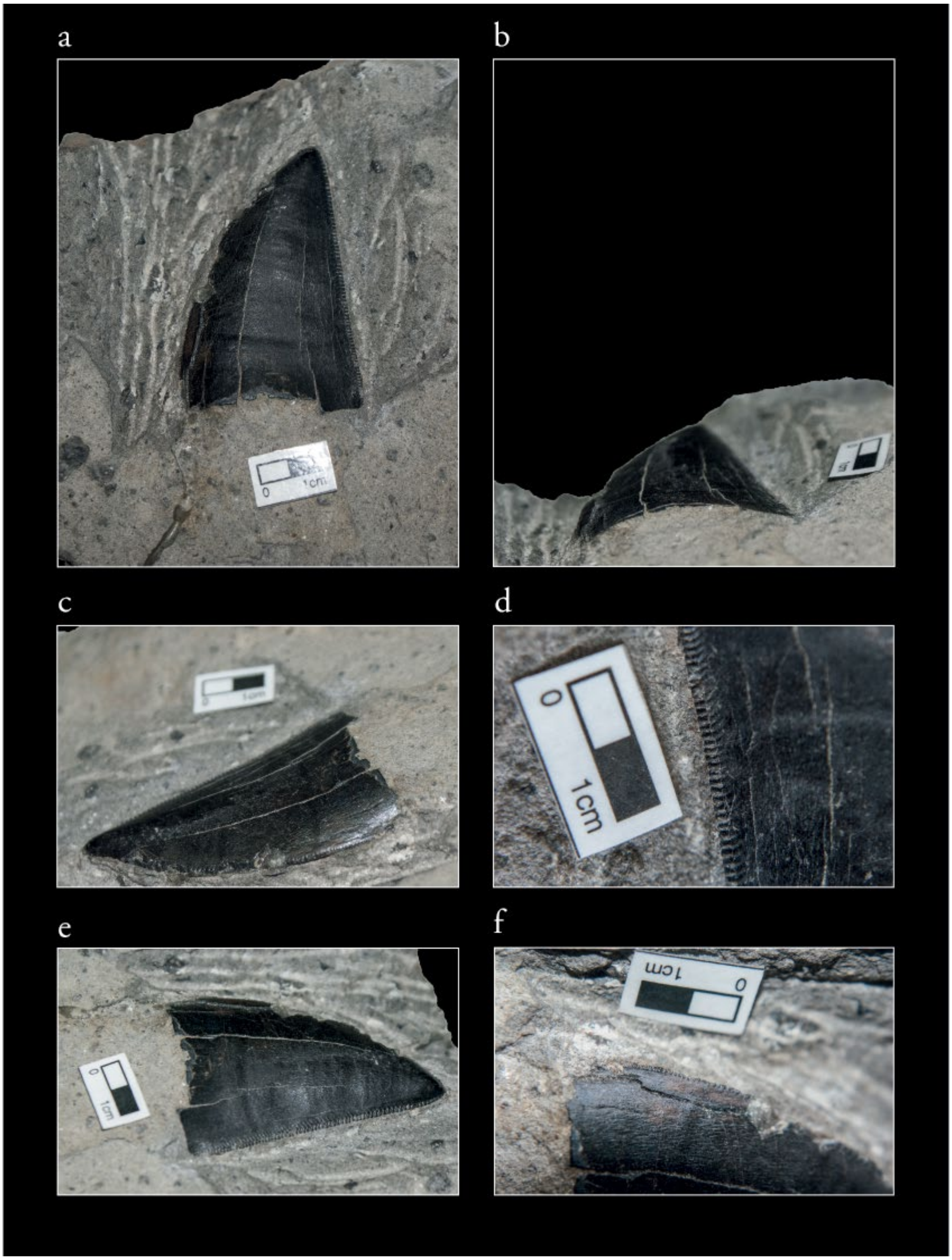


Fig. 7: Megalosauridae indet. 2. MUJA 1226. a) lateral view. b) basal view. c) mesial carina. d) distobasal denticles. e) interdenticular sulci. f) enamel texture and mesial carina.

3.1.7.2 Discussion

This tooth was previously reported by Martínez *et al.* 2000 and described by Ruiz-Omeñaca *et al.* (2009) which considered it Theropoda indet. and stated that it was similar to *Torvosaurus tanneri* teeth. MUJA 1226 is mentioned by Rauhut *et al.* (2018) and it is considered a megalosaurid tooth.

As seen in MUJA 4262, MUJA 1226 has a size and number of denticles per 5 mm that exclude most of theropod clades, leaving ceratosaurids, megalosaurids, allosaurids, and carcharodontosaurids as the probable producers. Late Cretaceous tyrannosaurids have been excluded for the same reason as MUJA 4262.

Unlike MUJA 4262, MUJA 1226 is most likely a lateral tooth due to the strong labiolingual compression of the crown. There is no evidence of concave or flat surfaces close to the mesial or distal carinae or apically oriented denticles (Rauhut, 2004; Hendrickx and Mateus, 2014b; Hendrickx *et al.,* 2015b; Malafaia *et al.,* 2017b) as seen in ceratosaurid lateral dentition.

The lateral dentition of allosaurids usually has a distal carina displaced labially, which is hard to determine in MUJA 1226, but it does not have apically inclined distal denticles (Han *et al.,* 2011; Gerke and Wings, 2016; Malafaia *et al.,* 2017b).

The traits seen in MUJA 1226 are similar to those in both megalosaurids and carcharodontosaurids. The preserved crown has a relatively straight distal margin; however, it lacks other traits with affinities to carcharodontosaurids, like marginal undulations in the enamel that are well visible in normal light (Csiki-Sava *et al.,* 2016).

There are a few skeletal remains of carcharodontosaurians from this age such as *Veterupristisaurus milneri* from the Upper Jurassic of Tendaguru (Tanzania) (Rauhut, 2011) and an indeterminate carcharodontosaurian from the Upper Jurassic of Portugal (Malafaia *et al.,* 2018a) but those remains consist of postcranial material. Rauhut, (2011) also describes a possible carcharodontosaurid tooth (*Megalosaurus* (?) *ingens* Janensch, 1920) from Tendaguru as well. The marginal enamel wrinkles on the Tendaguru tooth are well marked.

The cladistics analysis (Appendix 1) recovers MUJA 1226 in a polytomy with megalosaurids, carcharodontosaurids, the metriacanthosaurid *Sinraptor*, *Allosaurus* and *Piatnitzkysaurus*. A reduced strict consensus was calculated using the pruning trees option in TNT. The pruning of this morphotype either recovers MUJA 1226 at the base of *Torvosaurus* + *Megalosaurus* or at the base of *Mapusaurus* + *Giganotosaurus*. Both *Mapusaurus* and *Giganotosaurus* are carcharodontosaurids from the Late Cretaceous of Argentina.

In general MUJA 1226 is more similar to megalosaurid teeth than to carcharodontosaurids. Due to the incompleteness of the tooth and the embedding in the limestone holder is difficult to determine a more precise evaluation of the relevant characters. However, due to the similarity of the tooth to those of megalosaurids, and the distance both spatial and temporal to the Late Cretaceous of Argentina, here we consider that the most likely producer of this tooth was a megalosaurid theropod.

There are differences between this morphotype and Megalosauridae indet 1. (MUJA 4262). The latter is a mesial tooth whereas the former is lateral dentition. Also they could be produced by different megalosaurid taxa.

3.18 *Megalosauridae indet. 3.*

Material: Two teeth, MUJA 1217 and MUJA 3697

Horizon and location: MUJA 3697, Vega Formation, Abeu (Leces, Ribadesella), Kimmeridgian; MUJA 1217, Lastres Formation, Arroyo de la Escalera (Quintes, Villaviciosa), Kimmeridgian, Upper Jurassic.

3.1.8.1 Description

MUJA 1217 is an incomplete theropod tooth preserving part of the crown and part of the root (**Figure 8**). The tooth is not well preserved: It lacks the mesiobasal area; some parts of the enamel are missing, especially on the right side of the crown. The enamel shows small fractures and there are damaged areas on the margins. There are transverse breaks on the apical/central area. The enamel surface is covered with microscratches and the crown is worn due to wear and abrasion.

MUJA 3697 is a poorly preserved theropod tooth crown. The crown lacks the apex and the basal area; only the apico-central zone and part of the distal margin are preserved (Fig. 8). The surface has some fractures and parts of the enamel are missing due to erosion and wear. MUJA 1217 and MUJA 3697 are big-sized theropod teeth. The crown base lengths (CBL) are 30 mm and 36 mm, the crown base widths (CBW) are 11.28 mm and 16 mm and the crown heights (CH) are 57.15 mm and around 75 mm. The teeth are ziphodont, displaying the blade-like morphology typical of theropods. The crown base ratio (CBR) and the crown height ratio (CHR) are around 0.4 and 1.9. The crowns are strongly labiolingually compressed and basoapically elongated, with an ovoid cross-section at its base.

In lateral view, the teeth have a convex mesial margin and a concave distal profile. The crown is moderately recurved being the mesial profile more recurved than the distal margin; the tip surpasses the base of the distal carina.

In mesial view, the mesial margin bears a serrated mesial carina. The carina extends along the preserved mesial surface, centrally positioned on the crown, facing mesially. The complete extension of the mesial carina cannot be determined due to the state of preservation of the teeth.

In distal view, the distal carina is serrated and extends along the entire distal margin. It is centrally positioned in MUJA 1217 and slightly offset labially in MUJA 3697. The carina does not twist. In apical view, the tip of MUJA 1217 is distally positioned and the sides of the crown are convex and the cross-section is lenticular. The cross-section varies along the tooth crowns. In basal view, the cross-section of the crown is elliptical-lanceolate, with both sides of the crown convex. Both margins are acute due to the carinae.

The mesial carinae have a low number of denticles per 5 mm, around 7-8. Denticles are better preserved at the apical third of the crown and the main axis is perpendicular to the mesial margin. The tip of the denticles is eroded thus it is difficult to determine the shape and morphology. Some parts of the mesial carina seem to have short and basally inclined interdenticular sulci.

The distal carinae also have a low number of denticles per 5 mm (7-9). The denticles are perpendicular to the distal margin of the crown and they decrease in size towards the base, displaying a gradual graduation. In MUJA 1217 the distal denticles are eroded and the margins are not preserved but they probably were proximodistally subrectangular. In MUJA 3697 the preserved denticles are subquadrangular on the apico-central area and horizontal subrectangular at the base. Denticles are smaller on the base so the number of denticles increases towards the basalmost part of the crown. The main axis of the denticles is perpendicular to the distal carina. The external margin is parabolic and either symmetrically or asymmetrically convex. The space between denticles is broad and deep. There are interdenticular sulci among mesial and distal denticles. Distal denticles are more developed than the mesial ones. Both sulci are short and basally inclined.

MUJA 1217 has a worn surface, has microscratches and there are transverse undulations, just a few. They are better seen at a certain angle. On the other hand, MUJA 3697 is ornamented with marginal and transverse undulations. The marginal undulations are diagonally oriented. Transverse undulations are basally convex, they are not too numerous and are better seen at certain angles. The original enamel texture is braided (*sensu* Hendrickx *et al.,* 2015c).

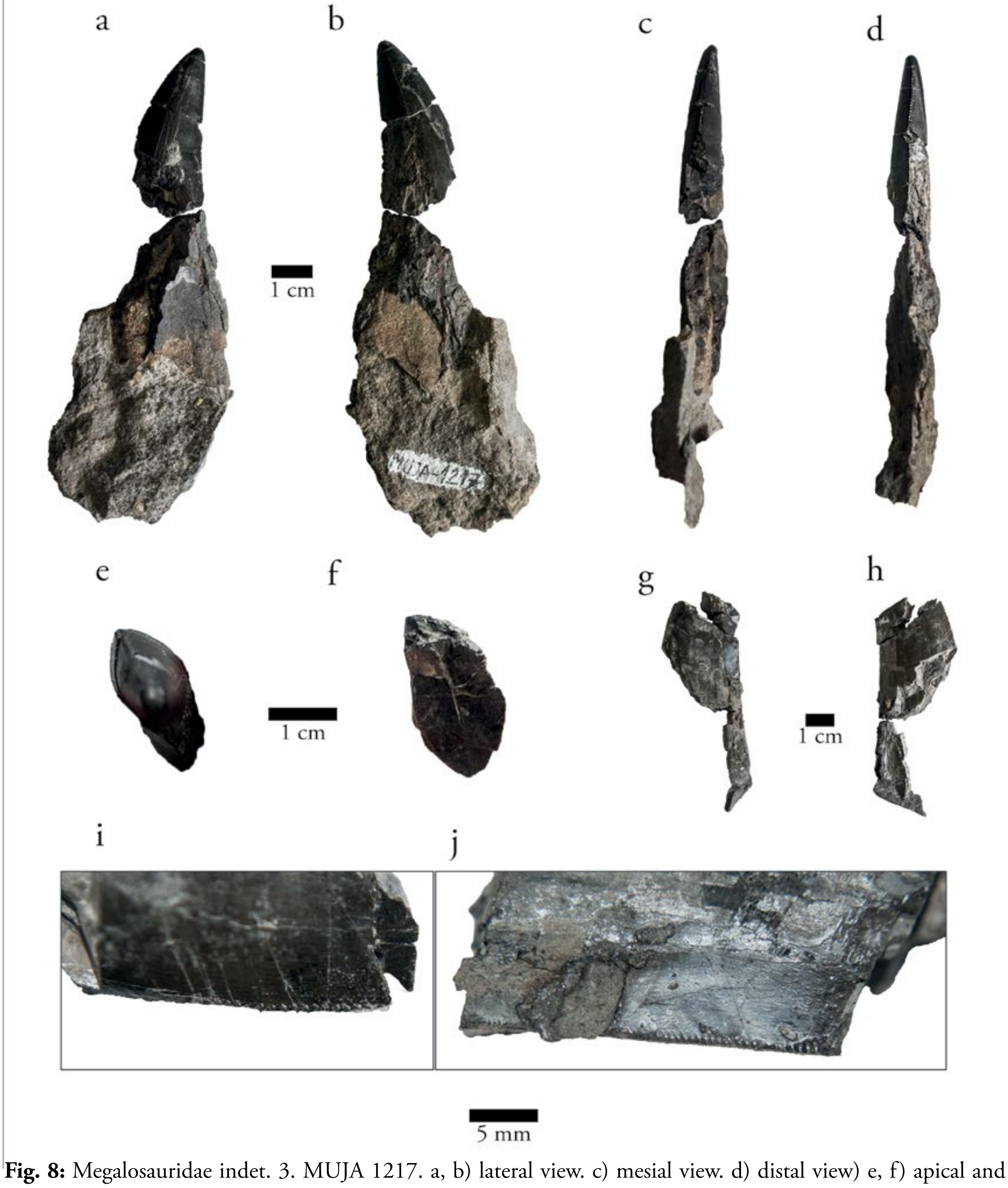


Fig. 8: Megalosauridae indet. 3. MUJA 1217. a, b) lateral view. c) mesial view. d) distal view) e, f) apical and basal views. MUJA 3697 in g, h) lateral views. i) mesial carina. j) distal carina.

3.1.8.2 Discussion

This morphotype is also characterized by large-sized teeth with a low number of denticles per 5 mm, braided enamel texture, serrated mesial and distal carinae, centrally or slightly displaced carinae, strongly labiolingually compressed crowns with transverse and marginal undulations and interdenticular sulci. This combination of traits, as stated above, excludes most of theropod clades, leaving ceratosaurids, megalosaurids, allosaurids, and carcharodontosaurids as the probable producers. Among those clades, MUJA 1217 and MUJA 3697 resemble more the megalosaurid dentition, lacking concave surfaces, displaced distal carinae, apically inclined denticles or other relevant traits, as stated in the previous morphotypes (Rauhut, 2004; Han *et al.,* 2011; Malafaia *et al.,* 2017b).

The cladistics analysis (Appendix 1) recovers this morphotype within Megalosauridae, as the sister-taxon of *Afrovenator* and *Torvosaurus* + *Megalosaurus*.

MUJA 1217 was previously described by Ruiz-Omeñaca *et al.* (2009) and considered Theropoda indet., but it was stated that the morphotype was similar to the teeth of *Torvosaurus tanneri.*

This morphotype is different from Megalosauridae indet. 1. (MUJA 4262) due to the labiolingual compression; this one is composed by lateral dentition. Here also prefer to distinguish this morphotype from Megalosauridae indet. 2. (MUJA 1226) due to the overall differences in shape. Those differences could be related to different positions along the tooth row as seen in D'Amore (2009, fig. 12) or maybe due to different taxa.

It is noteworthy that those teeth come from different formations from the Kimmeridgian. This could be related to the presence of the same taxon during the entire Kimmeridgian or related taxa in that time and place.

4.DISCUSSION

The palaeobiodiversity of theropods from the Upper Jurassic is well known in productive areas such as the Morrison Formation from the Kimmeridgian-Tithonian of North America. So far, this formation has the presence of the ceratosaurid *Ceratosaurus* (Madsen and Welles, 2000), other indeterminate ceratosaurians (Carrano and Sampson, 2008), the piatnitzkysaurid *Marshosaurus* (Madsen, 1976a), the megalosaurid *Torvosaurus* (Galton and Jensen, 1979), allosaurids such as *Allosaurus* (Madsen, 1976b; Chure, 1995), a broad set of coelurosaurs including *Ornitholestes* (Osborn, 1903b; Carpenter *et al.,* 2005) and the tyrannosauroids *Stokesosaurus*, *Coelurus* and *Tanycolagreus* (Benson, 2008; Carpenter and Miles, 2005; Madsen, 1974; Marsh, 1879).

The theropod record from the Upper Jurassic of Western Europe includes taxa such as the metriacanthosaurid *Metriacanthosaurus* from the Oxfordian of England (Von Huene, 1923; Walker, 1964), the Kimmeridgian megalosauroid *Sciuromimus* (Rauhut *et al.,* 2012, 2018b), coelurosaurians such as *Juravenator* (Göhlich and Chiappe, 2006), *Archaeopteryx* from the Kimmeridgian-Tithonian of Germany (Rauhut *et al.,* 2018a), or the tyrannosauroid *Juratyrant* (Brusatte and Benson, 2013) from the Tithonian of England. In addition, the presence of ceratosaurids, abelisauroids, megalosauroids, allosaurids, carcharodontodosaurians and tyrannosauroids has been inferred studying isolated theropod teeth from Kimmeridgian deposits of Northern Germany (Gerke and Wings, 2016).

In the Iberian Peninsula, the diversity of theropods from the Upper Jurassic is better known in deposits from the Kimmeridgian-Tithonian of Portugal (Mateus, 2006). There are evidences of ceratosaurids (Antunes and Mateus, 2003; Mateus *et al.,* 2006), *Torvosaurus* (Hendrickx and Mateus, 2014a; Malafaia *et al.,* 2017c), allosauroids such as *Allosaurus* (Mateus et al., 2006), *Lourinhanosaurus* (Mateus, 1998) and other remains (Malafaia *et al.,* 2017a), carcharodontosaurids (Malafaia et al., 2018a), the tyrannosauroid *Avyatirannis* (Rauhut, 2003), and isolated teeth attributed to abelisaurids, *Compsognathus*, Tyrannosauroidea, Dromaeosauridae, *Richardoestesia* and *Archaeopteryx* (Zinke, 1998; Hendrickx and Mateus, 2014b; Malafaia *et al.,* 2017b).

Concerning the Spanish record of theropods, there is other evidence from Asturias region, specifically from the “dinosaur coast” area. Recent studies have revealed the presence of large-bodied theropods from the Kimmeridgian including both skeletal remains of a large megalosaurine megalosaurid of the Vega Formation and the presence of footprints of at least two taxa of giant theropods in the Lastres Formation (Rauhut *et al.,* 2018b). The evidence from the Iberian Range also reveals the presence of large megalosauroids (Cobos *et al.,* 2014).

Thus the isolated theropod teeth record from the dinosaur coast is congruent with the known record of theropods from the Late Jurassic of the Iberian Peninsula. The megalosaurid morphotypes described here resemble the mesial and lateral dentition of megalosaurids such as *Torvosaurus* (Hendrickx and Mateus, 2014a; Hendrickx *et al.,* 2015b) and other isolated teeth (Malafaia *et al.,* 2017b) and is congruent with the presence of a large megalosaurine megalosaurids in the Vega Formation, representing the largest predators of the Late Jurassic European landmasses (Rauhut *et al.,* 2018b). Isolated abelisaurid teeth have been described from the Kimmeridgian-Tithonian of the Lourinhã Formation (Hendrickx and Mateus, 2014b).

The presence of four smaller theropod morphotypes (Theropoda indet, Averostra indet. 1, 2, and 3) could be related to the presence of other theropod clades such allosauroids or megalosauroids related to metriacanthosaurids or piatnitzkysaurids.

5.CONCLUSIONS

Ten isolated theropod teeth have been studied and eight different morphotypes have been identified. One morphotype has been assigned to Theropoda indet; three morphotypes have been attributed to Averostra indet, one morphotype has been tentatively attributed to Abelisauridae? indet. and three morphotypes have been assigned to Megalosauridae indet. These results represent a new contribution to the knowledge of the palaeobiodiversity and distribution of theropods from the Kimmeridgian (Late Jurassic) of the Iberian Peninsula.
The presence of very large isolated teeth related to megalosaurids is congruent with the known record of theropods of Iberia. The presence of smaller morphotypes sheds light on the possible presence of abelisaurid theropods and other taxa probably related to smaller allosauroids or megalosauroids still not identified by other skeletal remains in this area.

ON THE SPINOSAURID THEROPOD TEETH FROM THE EARLY BARREMIAN (EARLY CRETACEOUS) LA CANTALERA 1 SITE

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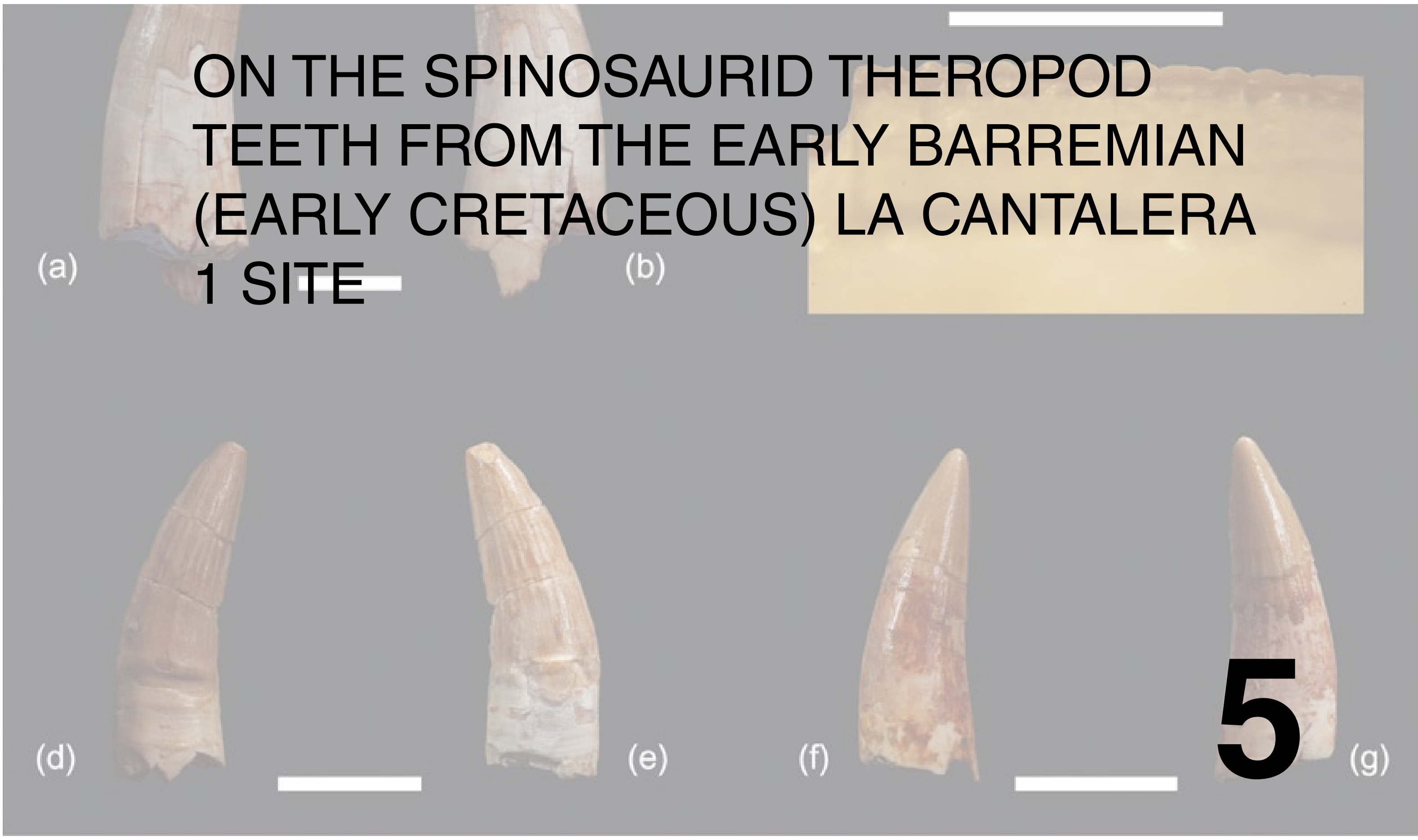


1. INTRODUCTION

Spinosaurids are one of the most striking groups among the theropods, featuring an elongated, distinctive skull and conical teeth with fluted enamel and small denticles (Charig and Milner 1997; Sereno *et al.,* 1998; Canudo *et al.,* 2008a; Buffetaut, 2012). These characters have been interpreted as evidence of a dominant piscivorous tendency in their eating strategies, a hypothesis supported by several observations relating to features such as the skull morphology, stomach contents (Charig and Milner, 1997), the oxygen isotopic composition of the bones (Amiot *et al.,* 2010) and biomechanical data (Rayfield *et al.,* 2007), though there is also evidence of spinosaurids feeding on other vertebrates such as pterosaurs (Buffetaut *et al.,* 2004) and ornithopods (Charig and Milner, 1997; Allain *et al.,* 2012). Recently, some authors (Ibrahim *et al.,* 2014; Arden et *al.,* 2019) have shown a series of adaptations in *Spinosaurus* that fit with a semiaquatic lifestyle, although there is still discussion (Evers et *al.,* 2015; Henderson, 2018).

Spinosaurids had a wide distribution both in space and time during the Late Jurassic, the Early Cretaceous and the older part of the Late Cretaceous. It has been thought that the first reported spinosaurids appeared during the Late Jurassic (Buffetaut, 2012) although new research suggests that early spinosaurids are Middle Jurassic in age (Serrano-Martínez *et al.,* 2015). They became abundant in the Early Cretaceous, disappearing during the Late Cretaceous (Hone *et al.,* 2010). Spinosaurid remains are mainly distributed in North Africa, Europe and South America although there is other evidence of them in Asia and Australia (Buffetaut & Ingavat, 1986; Hasegawa *et al.,* 2003; Barrett *et al.,* 2011; Allain *et al.,* 2012). Most remains of the spinosaurids from the Iberian Peninsula are isolated teeth (Pereda-Suberbiola *et al.,* 2012). The study of isolated theropod teeth is of particular interest because they are the most common fossilised remains. It is due to the resistance of the enamel and the constant replacement of the teeth during their lifetime (Currie *et al.,* 1990; Torices, 2007).

La Cantalera-1 (=La Cantalera) is one of the sites with the greatest vertebrate palaeobiodiversity in the early Barremian of the Iberian Peninsula. The fossil accumulation consists of teeth, postcranial remains, eggshells and coprolites; amphibians, a chelonian, a lizard, crocodylomorphs, pterosaurs, ornithopod dinosaurs, a thyreophoran, sauropods and theropods have been identified, as well as mammals (e.g. Badiola *et al.,* 2008; Canudo *et al.,* 2010a; Gasca *et al.,* 2014b; Moreno-Azanza *et al.,* 2014b; Puértolas-Pascual *et al.,* 2015). Until recently, La Cantalera-1 was the only site of the Blesa Formation with spinosaurid teeth (Ruiz-Omeñaca *et al.,* 2005). In this context, the aim of the present article is to study the isolated spinosaurid teeth from the lower Barremian founded in this site.

1.1 Institutional abbreviations

MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza, Spain; UNIZAR, Universidad de Zaragoza, Zaragoza, Spain.

1.2 Other abbreviations

AL, apical length; CBL, crown base length; CBR, crown base ratio; CBW, crown base width; CH, crown height; DA, distoapical denticle density; DAVG, average distal denticle density; DB, distobasal denticle density; DC, distocentral denticle density; DSDI, denticle size density index; FESEM, field emission scanning electron microscope; MA, mesioapical denticle density; MAVG, average mesial denticle density; MC, mesiocentral denticle density; MB, mesiobasal denticle density.

2. MATERIALS AND METHODS

The fossils were recovered from surface prospections, excavation campaigns and the screen-washing of 3 tons of sediment, using a sieve with a 0.5mm mesh. In addition, another 20 kg of sediment were screen-washed using a 0.150mm mesh in order to get a representative sample of non-vertebrate microfossils (Ruiz-Omeñaca *et al.,* 1997a; Canudo *et al.,* 2010a). The recovered teeth show a variable state of preservation, with shed and functional teeth without evidence of transport.

Part of the material had previously been studied by electron microscopy in the FESEM service of UNIZAR. Other observations were made with an Olympus SZX7 zoom stereomicroscope with a KL1500 LCD lamp. Matrox Inspector 8.0 was used as imaging software. The teeth were measured with a Mitutoyo Digimatic Digital Caliper Series No 500 and Matrox Inspector 8.0 measurement tools. The measurements performed on scanning electron microscope images obtained in previous studies were conducted with ImageJ software.

Seventeen theropod (plus two crocodylomorph) teeth from La Cantalera have been analysed during the course of this research. Other teeth from the sites of Vallipón (Castellote) (Ruiz-Omeñaca *et al.,* 1998) have been studied; data of spinosaurids from Iberia have also been included (Torcida *et al.,* 1997; Torcida Fernández-Baldor *et al.,* 2003; Infante *et al.,* 2005; Sánchez-Hernández *et al.,* 2007; Canudo *et al.,* 2008a; Gasca *et al.,* 2008).

2.1 Statistical analysis

A statistical analysis has been performed in order to understand the variation among the spinosaurid teeth from La Cantalera-1 site as explained in Chapter 2 (Materials and Methods). In addition, morphometric data from crocodylomorph teeth were also included. The main reason was to use them as a control group in the analysis due to the similarity between spinosaurid and crocodylomorph teeth.The crocodylomorph teeth included in the analysis belong to Morphotype 1 of La Cantalera site crocodylomorphs (Puértolas-Pascual *et al.,* 2014, 2015). This morphotype has usually been attributed to Goniopholididae, but it is also found in other neosuchians and heterodont crocodylomorphs.

When studying theropod teeth, it is common to log-transform the values in order to better reflect a normally distributed multivariate dataset (Smith *et al.,* 2005; Kear *et al.,* 2013; Larson and Currie, 2013; Hendrickx *et al.,* 2015b; see justification in Samman *et al.,* 2005). Here the values were not log-transformed, as the absence of mesial and distal denticles was taken into account. The absent data were coded with a zero value; the missing data were coded with a question mark.

A PCA analysis has been performed on the dataset; the variables selected are CBL, CBW, CH, MAVG and DAVG. All measurements are expressed in mm. The dataset from Smith *et al.,* (2005) has been included with the data for isolated teeth from the Iberian Chain. The aim is to check the validity of the morphotypes studied in the Systematic Palaeontology, and test whether the spinosaurids occupy the same region of the morphospace. A total of 119 teeth have been included. The measurements from Smith *et al.,* (2005) included in this analysis comprise *Baryonyx, Suchomimus* (Spinosauridae), Carcharodontosauridae, Troodontidae, Dromaeosauridae and Ceratosauridae.

3. SYSTEMATIC PALEONTOLOGY

Clade DINOSAURIA Owen, 1842
Clade SAURISCHIA Seeley, 1887
Clade THEROPODA Marsh, 1881
Clade TETANURAE Gauthier, 1986
Superfamily SPINOSAUROIDEA Stromer, 1915
Family **Spinosauridae** Stromer, 1915

Subfamily **Baryonychinae** Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson & Wilson, 1998

3.1 Baryonychinae indet

3.1.1 *Material*

Thirteen teeth: CAN1 953, CAN1 957, CAN1 958, CAN1 959, CAN1 977, CAN1 983, CAN1 984, CAN 1 999, CAN1 1001, CAN1 1616, MPZ 97/468-CAN1 974, MPZ 2001/207 and MPZ 2001/208.

3.1.2 *Description*

Baryonychinae indet. teeth show a variable state of preservation (**Fig. 1**). The mesial margin of the teeth is convex, while the distal margin is concave or straight. The cross-section varies between elliptical and subcircular. Crown height ranges from 6 to 28 mm. All teeth have mesial and distal carinae, but some teeth do not have serration on the mesial carina. Carinae are located on the mesiodistal axis of the crown and start close to the cervix. Denticles are chisel-shaped and their height and width vary between 0.1 and 0.12 mm. Denticle density per mm ranges from 6 to 12. The denticle size density index values are close to one, so there is no difference between the mesial and the distal size of the denticles. The denticles are perpendicular to the margin of the teeth. Both faces of the teeth bear enamel ornamentation which consists of 6–7 ridges (on average) orientated apicobasally; the ridges do not reach the apex.

3.1.3 *Discussion*

Unlike other theropods, spinosaurid teeth have a subcircular-elliptical cross-section. The crown is usually straight, with very slight distal curvature. Spinosaurid teeth usually have fluted enamel and small denticles, and a veined enamel texture (Ruiz-Omeñaca *et al.,* 2005; Gasca *et al.,* 2008; Hendrickx *et al.,* 2015b). Baryonychine teeth have an ornamentation based on ridges, the cross-section is not as subcircular as in spinosaurine teeth, and the distal curvature is more pronounced than in Spinosaurinae (Canudo *et al.,* 2008a).

Previous papers (Canudo and Ruiz-Omeñaca, 2003; Ruiz-Omeñaca, 2006) have differentiated between two morphotypes of baryonychine spinosaurid teeth in the Barremian. The first morphotype includes all teeth with serration on the mesial and distal carina, and the second morphotype only has serration on the distal carina.

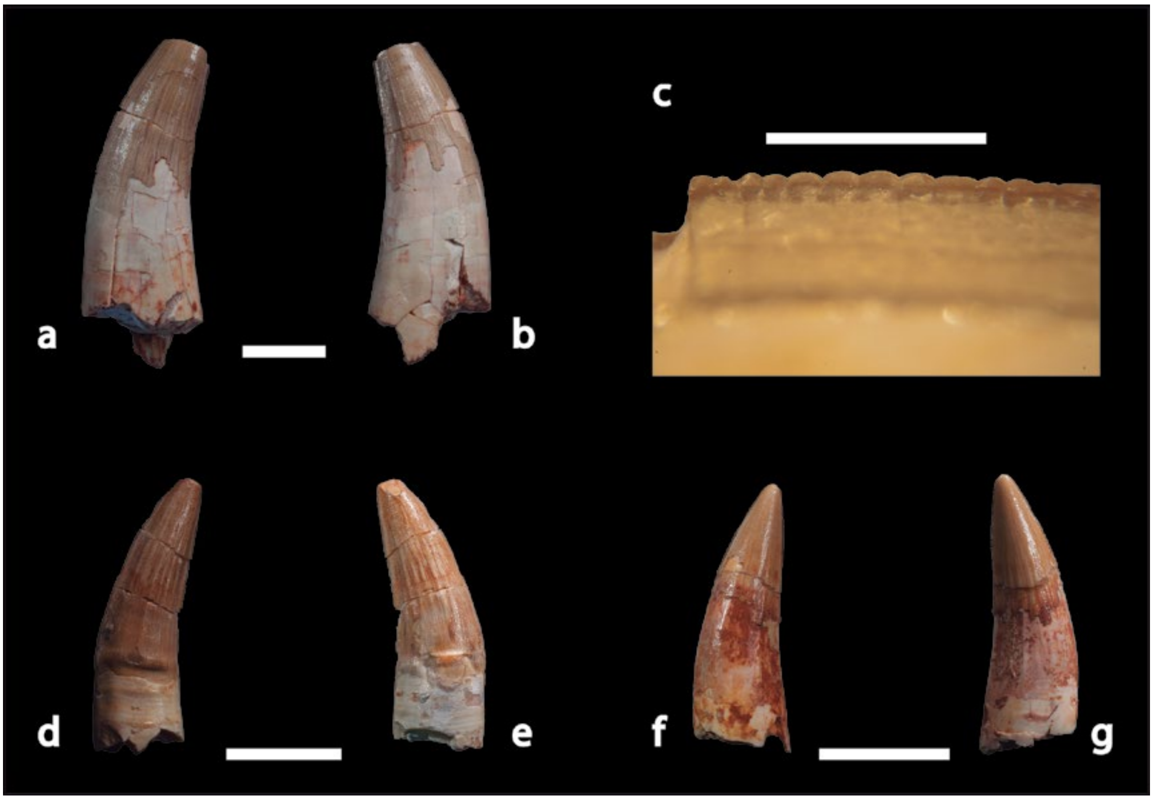


Fig. 1: Baryonychinae teeth from La Cantalera-1 site in lingual (a, d, g) and labial (b, e, f) views, with detail of mesial denticles (c). (a–c) MPZ 2001/207; (d, e) MPZ 2001/208; (f, g) CAN1 957. Scale bar: 1 cm (a, b, d, g) or 1mm (c).

Here we do not differentiate these morphotypes because sometimes the presence or absence of denticles on the mesial carina is difficult to determine due to the state of preservation of the teeth. In addition, this is the only difference between the morphotypes; they share all other features. There are no differences in size, denticle density per mm, ridges, enamel texture, etc. so we prefer to include them, for the moment, in a one morphotype in La Cantalera-1 site.

This morphotype of baryonychine teeth differs from that of other spinosaurids. *Baryonyx walkeri* teeth do not have fluted enamel on the labial surface (Charig and Milner, 1997). *Ostafrikasaurus crassiserratus* teeth have larger denticles and, in consequence, a lower denticle density per mm (Buffetaut, 2012). Asiatic forms such as *Siamosaurus suteethorni* have more ridges on the teeth surface (Buffetaut and Suteethorn, 1999; Hasegawa *et al.,* 2003).

It is interesting to draw comparisons between the teeth from La Cantalera and other data from Spain. Baryonychine teeth from the early Aptian of the Morella Formation (Canudo *et al.,* 2008a) differ from this morphotype; the teeth from La Cantalera-1 lack the enamel wrinkles of these teeth. Teeth from El Castellar Fm. (Gasca *et al.,* 2008) show more similarities with this morphotype. In addition, El Castellar Fm. is biostratigraphically similar to the Blesa Fm. spinosaurid teeth from Barremian-Aptian sites of the Wealden facies of Burgos (Torcida *et al.,* 1997; Torcida Fernández-Baldor et al., 2003) have similar features both in terms of ridges and denticle density per mm. Teeth from the late Barremian of Vallipón (Ruiz-Omeñaca *et al.,* 1998), early Barremian of Ladruñán (Infante *et al.,* 2005) and some teeth from the late Hauterivian-early Barremian of Galve (Sánchez-Hernández *et al.,* 2007) show a similar appearance to the remains from La Cantalera-1.

Subfamily **Spinosaurinae** Stromer, 1915

3.2 Spinosaurinae? indet

3.2.1 *Material*

Four teeth: CAN1 960, CAN1 968, CAN1 973 and CAN1 990.

3.2.2 *Description*

Spinosaurinae? indet. teeth show a variable state of preservation. The teeth have a convex mesial margin, while the distalmargin is concave or straight. The teeth have a subcircular cross-section. Estimated crown height values range from 16 to 22mm. The apex is pointing very slightly towards the distal margin. CHR values are high due to the elongation of the crowns. These teeth do not have carinae with the exception of CAN1 990, which has a distal carina without any serration (**Fig. 2**). The teeth have ornamentation based on apicobasal crenulation, which is faint and shallow. This ornamentation is more subtle and numerous than the ridges of the Baryonychinae indet. morphotype.

3.2.3 *Discussion*

Four teeth have been tentatively attributed to Spinosaurinae on the basis of their features that do not fit in the Baryonychinae subfamily. Spinosaurine teeth are usually less curved on the distal margin, ornamentation is less marked or absent, and the cross-section is heavily subcircular (Martill and Hutt, 1996; Canudo *et al.,* 2008a; Fanti *et al.,* 2014), though some spinosaurines such as *Irritator* (Sues *et al.,* 2002) do not share these features. This morphotype can be hard to distinguish from crocodylomorph teeth. Crocodylomorph teeth have a lingual curvature, but the teeth from Spinosaurinae? indet. lack this trait.

Fig. 2: Spinosaurinae? indet. teeth from La Cantalera-1 (a–d) and Cerrada Roya sites (e, f), in labial (a, d), lingual (b, c, f), and distal (e) views. (a, b) CAN1 990; (c, d) CAN1 968; (e, f) MPZ 2014/444. Scale bar: 1 cm.

The spinosaurine teeth from La Cantalera site differ from *Spinosaurus aegyptiacus* (Stromer, 1915). The holotype of *Spinosaurus* does not have fluted enamel (though other remains attributed to *Spinosaurus* do have some ornamentation), and the carinae are unserrated. *Irritator challengeri* (Martill *et al.,* 1996) have teeth with serrated carinae and fluted enamel. *Oxalaia quilombensis* (Kellner *et al.,* 2011) teeth have unserrated carinae and fluted enamel, and also enamel wrinkles that do not appear on the teeth from La Cantalera-1.

The ornamentation of the teeth from La Cantalera bears some similarities with Morphotype 5 reported by Fanti *et al.,* (2014) from the Albian of Tunisia. These teeth have a faint and shallow crenulation along the tooth crown, extending neither straight nor parallel along the crown. However, the teeth from La Cantalera-1 belonging to Spinosaurinae? indet. seem to have a higher number of ornamentations than Morphotype 5 from North Africa, and there is no difference in number between the lingual and labial surfaces.

Another tooth, from the site of Cerrada Roya (Camarillas Formation, Barremian) (MPZ

2014/444) in Galve, has traits similar to the teeth from La Cantalera-1: the absence of carinae, a relatively straight crown, numerous and subtle crenulation, though it is more labiolingually compressed. However, this compression could be explained in terms of heterodonty, so we consider this tooth to belong to the same morphotype as the above.

Sánchez-Hernández *et al.,* (2007) have also reported spinosaurine teeth from Galve, at the sites of Cerrada Roya and San Cristóbal. These teeth lack ornamentation with the exception of one tooth (MPG-SC 2), have both a mesial and distal unserrated carina (the ornamented tooth only has a distal carina), and the crown height ranges from 12 to 21 mm. It is possible that these teeth, though considered non-ornamented, may in fact have an ornamentation based on weak crenulation like the Cerrada Roya tooth (MPZ 2014/444) because they come from the same site. However, some differences exist. The teeth studied by Sánchez-Hernández *et al.,* (2007) have an unserrated mesial and distal carina, absent in the teeth from La Cantalera-1 (with the exception of the distal carina of CAN1 990) and the Cerrada Roya MPZ tooth. Despite these differences, here we have considered all the teeth from Galve to belong to a single morphotype that also includes the Spinosaurinae? teeth from La Cantalera-1, due to the heterodonty present in theropods. Nevertheless, further studies are required in order to clarify this point.

4. RESULTS

The principal component analysis shows the variation in the dataset in two axes or components (**Fig. 3**). The first component (X-axis) explains 95.01% of the variance. The second component (Y-axis) explains only 2.44% of the variance. The first component loadings are CH, CBL and CBW; these variables show the size of the teeth. DAVG and MAVG load the second component and explain the denticle density of the teeth (Hendrickx *et al.,* 2015b).

Quadrant 1 in the plot includes theropods with large teeth and a high denticle density. Quadrant 2 has theropods with small teeth and a high denticle density. Quadrant 3 shows theropods with small teeth with a low denticle density on the carinae, and quadrant 4 has large theropod teeth with a low denticle density.

The largest theropod teeth (belonging to *Suchomimus* and Carcharodontosauridae) are found in quadrants 1 and 4. Their positions on the Y-axis vary with the denticle density, which is higher in spinosaurids.

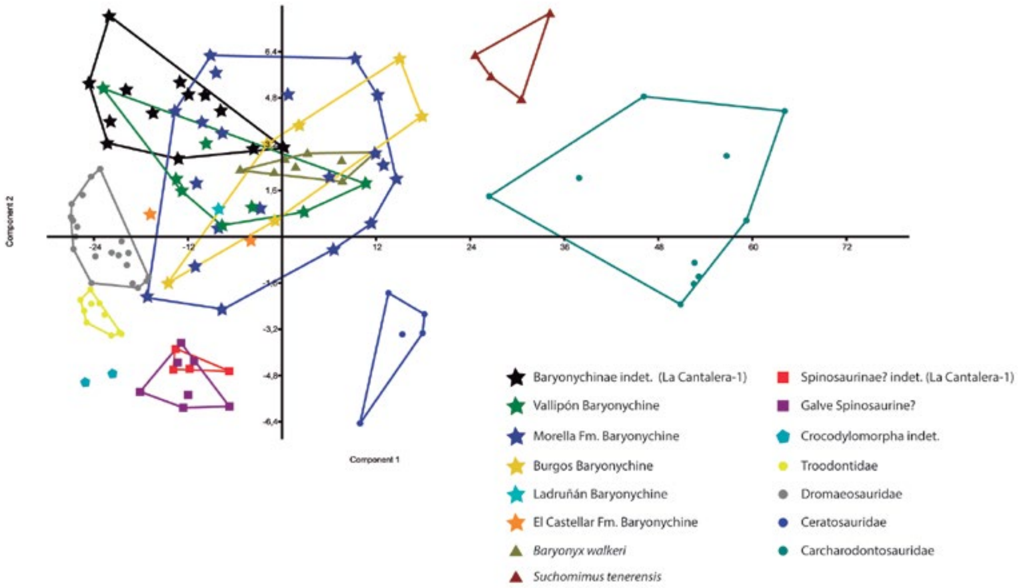


Fig. 3: Principal component analysis plot using CBL, CBW, CH, MAVG and DAVG.

Baryonychine spinosaurids are located between quadrants 1 and 2. It is notable that the values for these baryonychine teeth lie in the area around *Baryonyx* values, while the *Suchomimus* values remain separate from them. The dataset from the Iberian Chain shows greater variation than the theropods in the Smith *et al.,* (2005) dataset. The high range of variation of the Iberia dataset could be attributed to their origin in isolated teeth, unlike the data for the rest of the teeth. Data from isolated teeth may have a larger variation because they come from more different specimens. It is also notable that the state of preservation of isolated teeth has an effect when measuring and inferring data.

Ceratosauridae and Carcharodontosauridae are found in the 4th quadrant, which corresponds to medium–large sized teeth and a low denticle density.

Dromaeosaurid teeth are found between the 2nd and the 3rd quadrant. Small teeth with a low denticle density belonging to Troodontidae are located in the 3rd quadrant, close to the teeth from Spinosaurinae? indet. from Galve and La Cantalera-1 and Crocodylomorpha indet. teeth, with no denticles at all.

The baryonychine teeth from the Iberian Chain overlap. The teeth with the most similar values to the teeth from La Cantalera-1 site are from Vallipón, but these teeth are larger in size. The largest teeth from the Iberian Chain belong to the baryonychine spinosaurids of Burgos and the Morella Fm.

The teeth from La Cantalera-1 site are the smallest teeth among the baryonychine spinosaurids; only one of them is similar in size to *Baryonyx* teeth. The overall size is comparable with the data from dromaeosaurid, troodontid and other small theropod teeth.

Other baryonychine spinosaurids do not share this feature and have large teeth, comparable with *Baryonyx*. Also remarkable is the grouping of the Spinosaurinae? indet. teeth of Galve and La Cantalera- 1. Crocodylomorpha indet. teeth remain separate from those of Spinosaurinae? indet., the most similar teeth in the dataset.

5. DISCUSSION

The grouping of baryonychine spinosaurids from the Iberian Chain around the *Baryonyx* values, as seen in the PCA analysis, suggests that they are closer to this dinosaur than to other baryonychine spinosaurids such as *Suchomimus tenerensis*. This is congruent with other fossil remains from the Iberian Chain, such as the mandibular fragment reported by Viera and Torres, (1995) in La Rioja. This fragment was identified as a left maxilla belonging to *Baryonyx walkeri*. Postcranial remains attributed to baryonychine theropods have also been cited: a tibia (Gasulla e*t al.,* 2006) and cervical, dorsal and caudal vertebrae (Ortega *et al.,* 2006). However, the tooth remains from the Iberian Peninsula do not have the same appearance as *B. walkeri* teeth fromEngland; this is also seen in jaw fragments reported by Buffetaut, (2007) from the Barremian of Portugal and attributed to *Baryonyx* sp. These fragments include some teeth that develop ornamentation both on the labial and lingual sides. It is possible that this difference between *B. walkeri* and other baryonychine teeth could be explained in terms of geographical variation, but in any case herewe prefer to ascribe the teeth from La Cantalera site to Baryonychinae indet.

The possible presence of spinosaurine spinosaurids in the Early Cretaceous of Ibera is also of particular interest. The grouping of the teeth from La Cantalera-1 and Galve suggests that they belong to the same morphotype, as we proposed above. The separation between them and crocodylomorph teeth leads us to regard them as dinosaur teeth.

But are they really spinosaurine teeth? These teeth show a set of features that differ from the primitive condition in theropods. The primitive condition for theropod teeth is to be labiolingually compressed, with serrated carinae and the apex facing distally. Spinosaurinae? indet. teeth show scarce labiolingual compression, absent or unserrated carinae, and a relatively straight crown; these traits are considered present in spinosaurine spinosaurids by some authors (Martill & Hutt, 1996; Canudo *et al.,* 2008a; Fanti *et al.,* 2014). They also can lose ornamentation, which is congruent with the subtle ornamentation found on these teeth.

The derived features in these teeth lead us to rule out their attribution to other basal tetanurans which have primitive teeth. Other teeth with derived features can also be found in dinosaurs from the Early Cretaceous of the Iberian Peninsula, such as maniraptoran dinosaurs, but these have different traits in terms of shape, the presence or absence of denticles, carinae, DSDI, cross-section and size, so they can be ruled out. Other groups such as megalosaurids have mesial teeth with a rounded outline (Hendrickx and Mateus, 2014b), but the teeth from La Cantalera-1 do not share their traits. Features such as the absence of lingual curvature, differences in ornamentation and divergent PCA results suggest that they do not belong to crocodylomorphs. We consider that the most probable producer of these teeth was a spinosaurine spinosaurid.

It is particularly remarkable that the teeth from La Cantalera are smaller than other spinosaurid teeth from Iberia. A taphonomic accumulation produced by transportation is ruled out due to the absence of evidence for the transport of the teeth. Other possibilities are the presence in La Cantalera-1 of small taxa and the presence of juvenile specimens. The latter appears to be the more plausible answer due to the presence of teeth with similar features in different parts of Iberia, such as the teeth from the Vallipón and Burgos sites. Nevertheless, further studies are required in order to answer this question.

Whatever the case, the spinosaurid teeth from La Cantalera-1 are small in size, though they are not the only fossil remains from this site with this trait. Other theropod teeth with different affinities such as Carcharodontosauridae? indet. teeth are small in size. The crocodylomorph teeth also show a small size, as reported by Puértolas-Pascual *et al.,* (2014). Fossil remains from sauropods and ornithopods are also characterised by their small size in comparison with other sites in Iberia.

A possible explanation for such small-sized remains is attributable to the features of La Cantalera-1 site: a marshy environment with periodic droughts, surrounded by a Jurassic relief, resulting in a non-permanent body of water and a marshy vegetated area. This small lacustrine area has been interpreted as a feeding area for herbivore dinosaurs (Ruiz-Omeñaca et *al.,* 1997b). Moreover, the great biodiversity of vertebrates can be explained by the fact that palustrine areas tend to undergo an increase in organisms (especially during dry periods) due to the displacement of animals to flooded areas where food is found (Puértolas-Pascual *et al.,* 2014, 2015). Here we propose that the small size of La Cantalera-1 site did not allow the presence of large animals, either crocodylomorphs or dinosaurs: the fact that large animals could not be sustained in the area led to the increased biodiversity of small-sized animals (juveniles and/or small taxa).

The lack of fish in La Cantalera-1 site implies that the spinosaurid theropods that have been found did not have a piscivorous diet. They probably had to feed on herbivore dinosaurs, smaller theropods such as maniraptorans, pterosaurs and other organisms found at the site (Ruiz-Omeñaca *et al.,* 2005).

6. CONCLUSIONS

Two morphotypes of spinosaurid teeth have been recognised in the early Barremian of La Cantalera-1 site: Baryonychinae indet. and Spinosaurinae? indet.

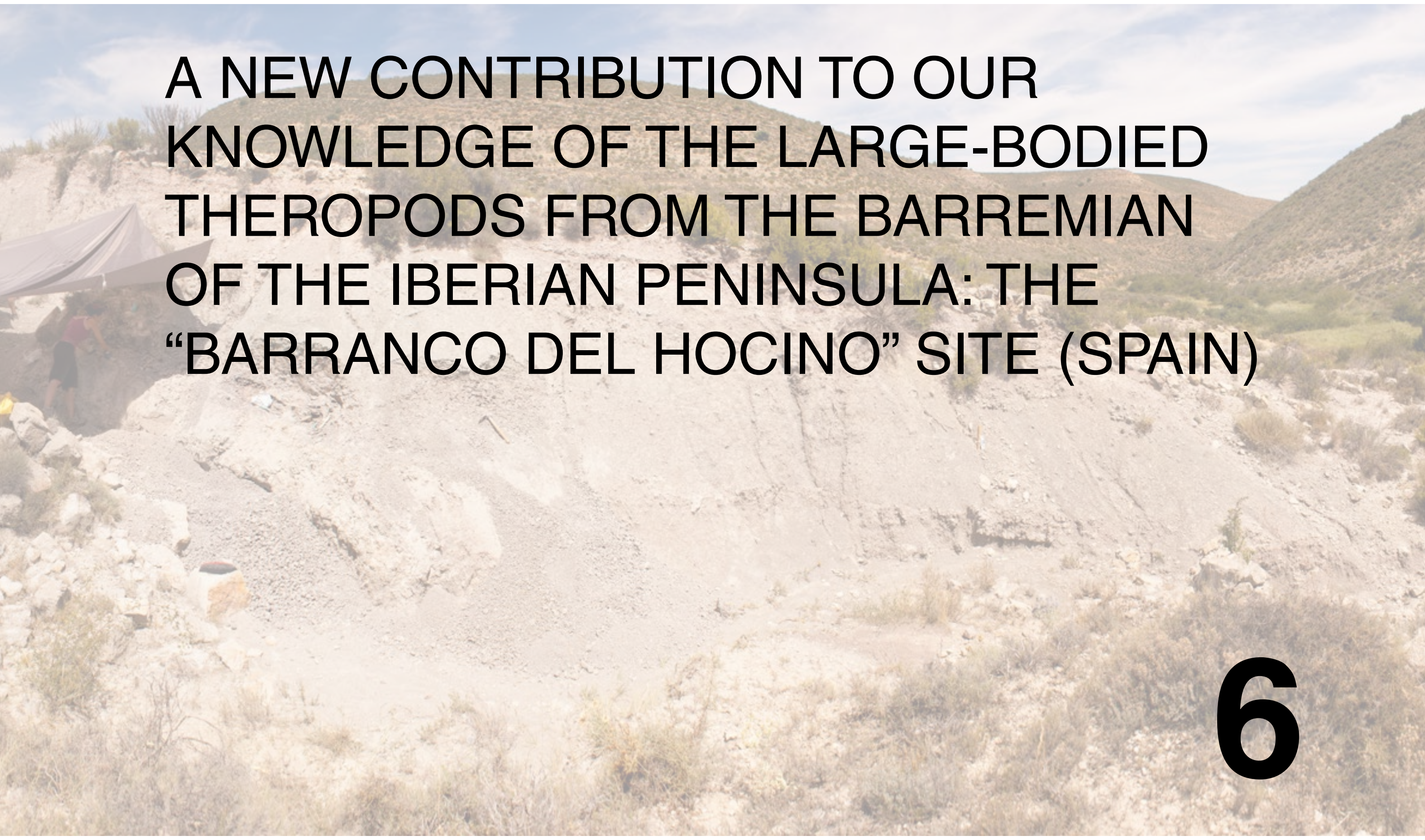
Except for their size, the Baryonychinae indet. teeth are quite similar to those from other Iberian sites. The teeth from the Morella Fm. have enamel wrinkles that Baryonychinae indet. lacks, so it is possibler that the Morella Fm. teeth belong to another baryonychine spinosaurid.

Baryonychine spinosaurids from Iberia are grouped closer to the values for *Baryonyx walkeri* than *Suchomimus tenerensi*s in the PCA analysis. We consider that all the baryonychine spinosaurids studied from the Iberian Peninsula teeth are of a type closer to *Baryonyx walkeri*. This is congruent with the presence in Iberia of skull remains attributed to *Baryonyx walkeri* (Viera and Torres, 1995; Mateus *et al.,* 2011).

Here we present new evidence that supports the idea of the presence of a spinosaurine spinosaurid in Iberia during the Early Cretaceous, as first proposed by Sánchez-Hernández e*t al.,* (2007). We have ruled out attribution to other theropods or crocodylomorphs, although we remain cautious due to the scarce fossil record known. Features of these teeth are similar to Morphotype 5 of Fanti *et al.,* (2014), which has a different location both in space and time, tentatively assigned to cf. *Spinosaurus* sp. Nevertheless, Spinosaurinae? indet. does not fit exactly with any of the described spinosaurine teeth, so we regard them as belonging to an unknown spinosaurine spinosaurid, probably closer to *Spinosaurus* than any other member of Spinosaurinae. The presence of this spinosaurine is scarce when compared with its baryonychine relatives, which are present in abundance in the sites of the Iberian Chain. Teeth remains of Spinosaurinae? indet. are also less frequent than Baryonychinae indet. within La Cantalera-1 site.

Small-sized teeth both from Spinosaurinae and Baryonychinae have been observed. This small size has also been observed in other fossil remains belonging to other dinosaurs and crocodylomorphs, leading us to propose that the characteristics that prevailed at La Cantalera-1 site allowed the concentration of small-sized organisms because the ecosystem could not sustain large vertebrates.

A NEW CONTRIBUTION TO OUR KNOWLEDGE OF THE LARGE-BODIED THEROPODS FROM THE BARREMIAN OF THE IBERIAN PENINSULA: THE “BARRANCO DEL HOCINO” SITE (SPAIN)



6

1. INTRODUCTION

The presence of dinosaur remains is well-known in the Early Cretaceous sediments of the Iberian Peninsula (e.g., Pereda-Suberbiola *et al.,* 2012). These include theropods, sauropods (basal macronarians, titanosauriforms and rebbachisaurid diplodocoids), thyreophorans and ornithopods (iguanodontoids, dryosaurids and basal euornithopods). The Cretaceous Maestrazgo Basin, located in the Iberian Range, has yielded some of the most remarkable examples of these faunas. Particularly noteworthy within this record are dinosaurs such as the sauropods *Aragosaurus* and *Tastavinsaurus* (Sanz *et al.,* 1987; Canudo *et al.,* 2008b) and the ornithopods *Gideonmantellia, Delapparentia* (which has been recently proposed as belonging to *Iguanodon* sp.) and *Morelladon* (Ruiz-Omeñaca, 2011; Ruiz-Omeñaca *et al.,* 2012b; Gasulla *et al.,* 2015; Verdú *et al.,* 2017), as well as a single theropod taxon, *Camarillasaurus* from the Barremian of Teruel (Sánchez-Hernández and Benton, 2014). However, isolated tetanuran theropod teeth and theropod eggshells are also relatively abundant (Ruiz-Omeñaca *et al.,* 1996; Infante *et al.,* 2005; Sánchez-Hernández *et al.,* 2007; Moreno-Azanza *et al.,* 2014b).

The Oliete sub-basin, situated in the northwestern part of the Maestrazgo Basin, presents a Wealden facies where just a few vertebrate fossil localities are known. The geological formations of this sub-basin have an enormous potential to add to what is known of the Barremian vertebrate faunas of the Iberian Peninsula. A good example is La Cantalera 1 (= La Cantalera) site, which has provided the most diverse assemblage of tetrapods (amphibians, squamates, mammals, crocodylomorphs and dinosaurs) from the early Barremian of the Iberian Peninsula (Badiola *et al.,* 2008; Canudo *et al.,* 2010a; Puértolas-Pascual *et al.,* 2015; Alonso and Canudo, 2016). So far, isolated vertebrate remains (ornithopod dinosaurs, plesiosaurs) have also been found in other parts of the sub-basin (fossiliferous sites from Obón and Josa, Gasca *et al.,* 2014a; Parrilla-Bel and Canudo, 2015).

Recently, the amateur palaeontologist Juan Rubio found a new Wealden outcrop in the sub-basin. No vertebrate remains were reported here until the discovery of the locality of Barranco del Hocino-1 (Alonso *et al.*, 2016). Four fieldwork campaigns (in 2015, 2016, 2017 and 2018) enabled us to recover roughly 500 bone remains, revealing the vertebrate palaeodiversity of the site. The fossil locality of Barranco del Hocino 1 is a bonebed composed of disarticulated elements with a notable degree of breakage and incompleteness. The fossil association consists of ornithopods, ankylosaurs, theropod teeth, scarce microvertebrate remains (crocodylomorph and osteichthyan teeth), turtle shell fragments, coprolites and eggshells are also present (**Fig. 1**). Isolated macroremains of ornithopods dominate the assemblage. So far, craneal and postcranial elements have been recovered (Alonso *et al.,* 2016), including shed teeth, a jugal, dorsal, sacral and caudal vertebrae, complete ribs, an ilium, large bone fragments and autopodial elements.

Among thyreophorans, fossils are represented by osteoderm fragments and two well-preserved dermal spines that resemble those of La Cantalera 1 site (Canudo *et al.,* 2010a).

The fossil remains of crocodylomorphs consist of isolated teeth probably related to Goniopholididae? and Atoposauridae. They are similar to isolated teeth from other parts of the Blesa Fm. (Puértolas-Pascual *et al.,* 2015).

The aim of the current paper is to give first insights into the theropod fauna from this site.

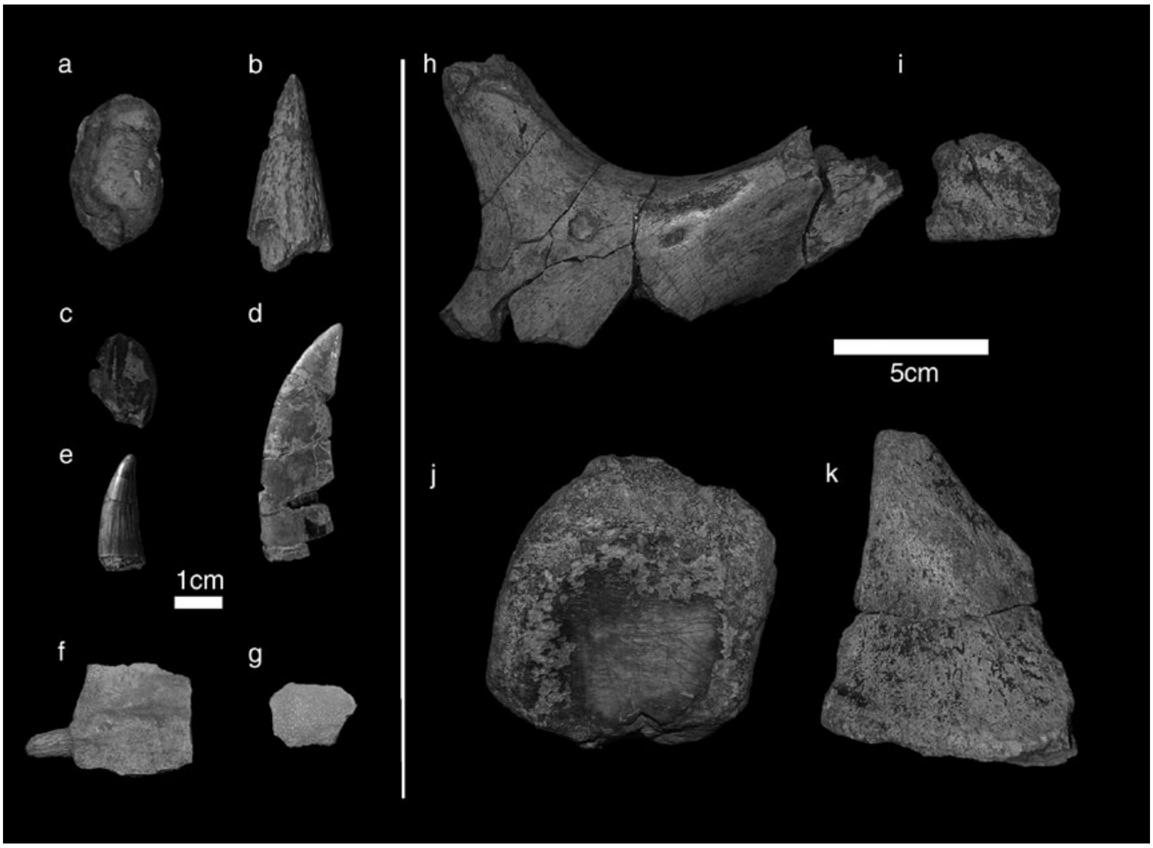


Fig. 1: Barranco del Hocino 1 remains. a) HOC 32. Coprolite. b, c) HOC 12 and HOC 6. Pollex and shed teeth from an styracosternan iguanodont. d,e) HOC 26 and HOC 17. Carcharodontosaurian and spinosaurid theropod teeth. f,g) HOC 33, HOC 34. Testudine shell fragment. h) HOC 1. Iguanodont jugal. i) HOC 21. Thyreophoran osteoderm. j) HOC 16. Iguanodont caudal vertebra. k) HOC 27. Thyreophoran dermal spine.

2. MATERIAL AND METHODS

The fossils were recovered during the fieldwork campaign of 2015 carried out by the Aragosaurus-IUCA research team (University of Zaragoza). The material recovered is provisionally housed in the Natural History Museum of the University of Zaragoza ("Museo de Ciencias Naturales de la Universidad de Zaragoza", Spain). Observations were made with a stereomicroscope. The teeth were measured with a Mitutoyo Digimatic Digital Calliper, Series No. 500. Six theropod teeth (Supplementary appendix A) from Barranco del Hocino-1 were analysed during the course of this research.

2.1 Statistical analysis

A discriminant function analysis (DFA, **Fig. 2**) was carried out using PAST3 (Hammer *et al.*, 2001) on the dataset of Hendrickx *et al.*, (2015b); data from White *et al.* (2015) and Csiki-Sava *et al.* (2016) were also included. The dataset contains 1015 teeth from different theropod clades and taxa, as well as the Barranco del Hocino-1 teeth: basal saurischians (*Eoraptor*), basal theropods (*Ischisaurus* = *Herrerasaurus*, *Eodromaeus*), non-averostran neotheropods (*Coelophysis*, *Liliensternus*, *Dilophosaurus*), Ceratosauridae (*Genyodectes, Ceratosaurus*), Noasauridae (*Noasaurus, Masiakasaurus*), Abelisauridae (*Abelisaurus, Rugops, Indosuchus, Majungasaurus, Aucasaurus, Skorpiovenator, Carnotaurus*), the possible metriacanthosaurid Erectopus, Piatnitzkysauridae (*Piatnitzkysaurus*), Megalosauridae (*Afrovenator, Duriavenator, Megalosaurus, Dubreuillosaurus, Torvosaurus*), Baryonychinae (*Baryonyx, Suchomimus*), Spinosaurinae (*Irritator, Spinosaurus*), Allosauridae (*Allosaurus*), Neovenatoridae (*Neovenator*), Carcharodontosauridae (*Acrocanthosaurus, Eocarcharia, Carcharodontosaurus, Giganotosaurus, Mapusaurus*), Megaraptora (*Australovenator, Fukuiraptor, Aerosteon*), non-tyrannosaurid Tyrannosauroidea (*Eotyrannus, Raptorex*), Tyrannosauridae (*Alioramus, Gorgosaurus, Daspletosaurus, Albertosaurus, Tyrannosaurus*), the possible dromaeosaurid Nuthetes, Dromaeosauridae (*Bambiraptor, Deinonychus, Dromaeosaurus, Velociraptor, Saurornitholestes, Atrociraptor, Zapsalis*), Troodontidae (*Troodon, Zanabazar, Pectinodon*), and *Richardoestesia*. The analysis performed was a discriminant function analysis (DFA) as explained in Chapter 2 (Materials and Methods).

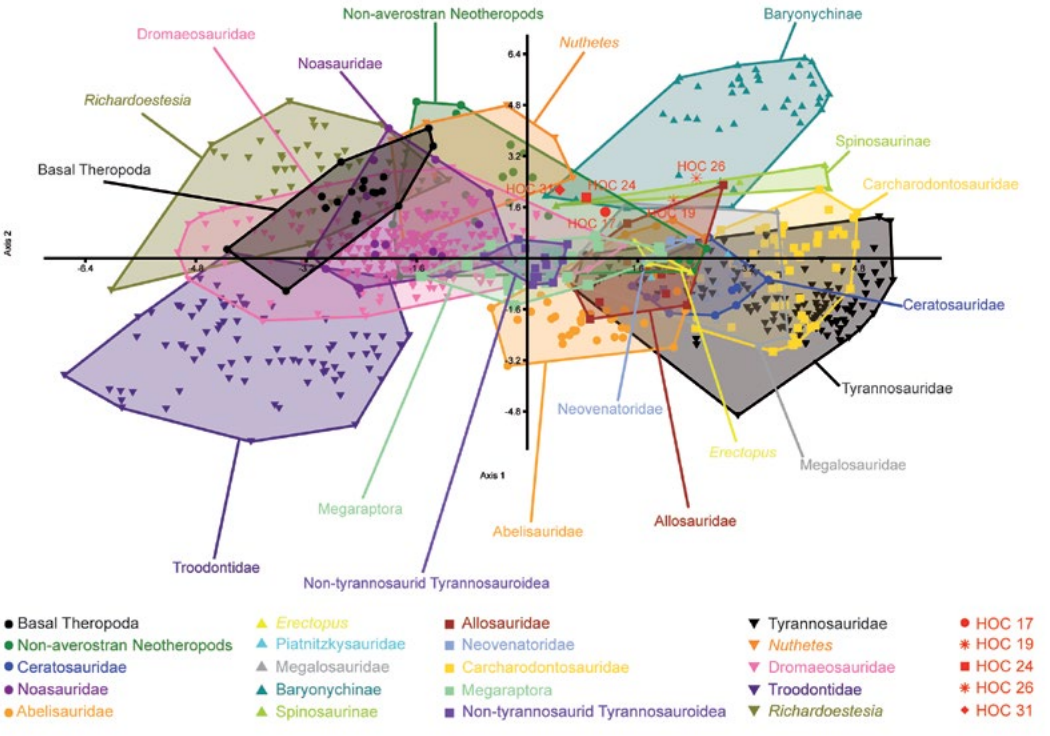


Fig. 2: Results of the DFA conducted on a dataset of 1015 teeth, including Barranco del Hocino-1 teeth. The first function explains the 56.86% of variance; the second canonical function explains the 23.72% of the variance.

The variables used are CBL, CBW, CH, AL, MC and DC. Absent data were coded as a question mark and missing values were estimated with a mean value for that measurement from across the sample. To better reflect a normal distribution, all the data were log-transformed (see Samman *et al.,* 2005). In order to avoid interference and overlapping between groups, and given the absence of mesial teeth from Barranco del Hocino 1 site, the mesial teeth were removed from the dataset.

The presence of small groups affects the accuracy of the analysis; in this case we maintained low number groups due to the relevance of some of them from comparison with Barranco del Hocino 1 morphotypes, even though this was at the expense of an improved analysis.

Also, we maintained isolated teeth that have been identified on generic level, for the same reason as above. Ideally, the dataset would consist of non-isolated teeth. Nonetheless, some taxa include isolated teeth; the relevance of those groups leads us to do not exclude the specimens.

The DFA of the 860 remaining teeth returned 70.99% correctly classified teeth (CD). The functions obtained explain the variance of the dataset. The first and the second functions explain 80.58% of the variance (CD). These canonical functions can be used to create a plot showing the graphical representation of the morphospace occupied by the teeth in a dispersion graph. The weight of each variable in the canonical functions can be found in CD.

2.2 Cladistic analysis

Cladistic analyses have been used by some authors to evaluate the phylogenetic position of isolated theropod teeth. The teeth from Barranco del Hocino-1 were analysed as detailed in Chapter 2 (Materials and Methods).

3 RESULTS

3.1 Systematic palaeontology

TETANURAE Gauthier, 1986

3.1.1 *Tetanurae indet. 1*

Material: HOC 24, one shed tooth.

3.1.1.1 Description

This morphotype includes one tooth_lacking the apex and a small part of the base (**Fig. 3**). The enamel surface is worn, show microstratches and the lingual area has some white marks on its apical and central regions that were caused by the roots of modern plants. The tooth is ziphodont, with a labiolingually compressed and a distally curved crown. The tooth crown also bears serrations but lacks a few denticles on the mesial and distal carina. A transverse break is located at the mid-crown. Another break affects the lowermost part of the lingual surface, where a small fragment was detached from the crown. In basal view the tooth crown reveals the pulp cavity. HOC 24 is a medium-sized theropod tooth, with a crown base length (CBL) of 9.43 mm, crown base width (CBW) of 5.63, and preserved crown height (CH) of 14.32 mm. The estimated value of the crown height (CH) is 20.2 mm. With a CBR and a CHR of 0.6 and 2.15 respectively, the crown is moderately labiolingually flattened and moderately elongated, with an ovoid cross-section at its base. The mesial and distal profiles are convex and concave, respectively. The mesial margin of the tooth crown is more recurved than the distal margin; the crown has carinae on both mesial and distal margins. The mesial carina extends from the apex to the basal third of the crown, finishing well above the cervix.

On the other hand, the distal carina extends along the entire distal margin. In addition, the labial surface adjacent to the distal carina is flattened.

The mesial carina bears denticles and is centrally positioned. The labial surface is slightly basoapically sigmoid with the basal part of the crown convex and the apical part concave. The lingual surface, however, seems to remain basoapically convex.

In distal view, the distal carina is displaced labially and bears denticles all along the edge. The labial and lingual surfaces are mesiodistally convex, with the lingual side more convex than the labial side.

In apical view, the tooth crown has a lenticular cross-section and both the mesial and distal carinae are acute. In basal view, the cross-section of the crown is oval and slightly lanceolate whereas the cross-section at the level of the midcrown is lenticular.

The mesial carina preserves nine denticles per 2 mm (around 22.5 denticles per 5 mm). In lateral view, the apicobasal axis of the denticles is greater than the mesiodistal axis, giving them an apicobasally subrectangular outline. The external margin of the denticles is parabolic.

The distal carina has around 20 denticles per 5 mm at the mid-crown. The denticles gradually decrease in size towards its base. Morphologically, they are chisel-shaped and the mesiodistal axis of the denticles is greater than the apicobasal length, which give them a subrectangular outline. The denticles are positioned perpendicularly to the carina and the external margin is parabolic to semicircular. In addition, the outline of the denticles is either symmetrically or asymmetrically convex. The interdenticular space between denticles is narrow and deeper in the distal denticles. The distal carina shows interdenticular sulci diagonally oriented basally towards the base of the tooth crown. They are short and are better seen at low light angle.

The crown surface is covered with microscratches on both lingual and labial sides due to wear and erosion. The surface also displays marginal undulations, which are short and are better seen at certain angles. In addition there are transverse undulations covering the complete surface of the crown; they are apically concave and they curve towards the apex as they approach the carina. The enamel texture is braided (*sensu* Hendrickx *et al.,* 2015c).

3.1.1.2 Discussion

HOC 24 is a moderately compressed crown, suggesting that it is a lateral tooth.

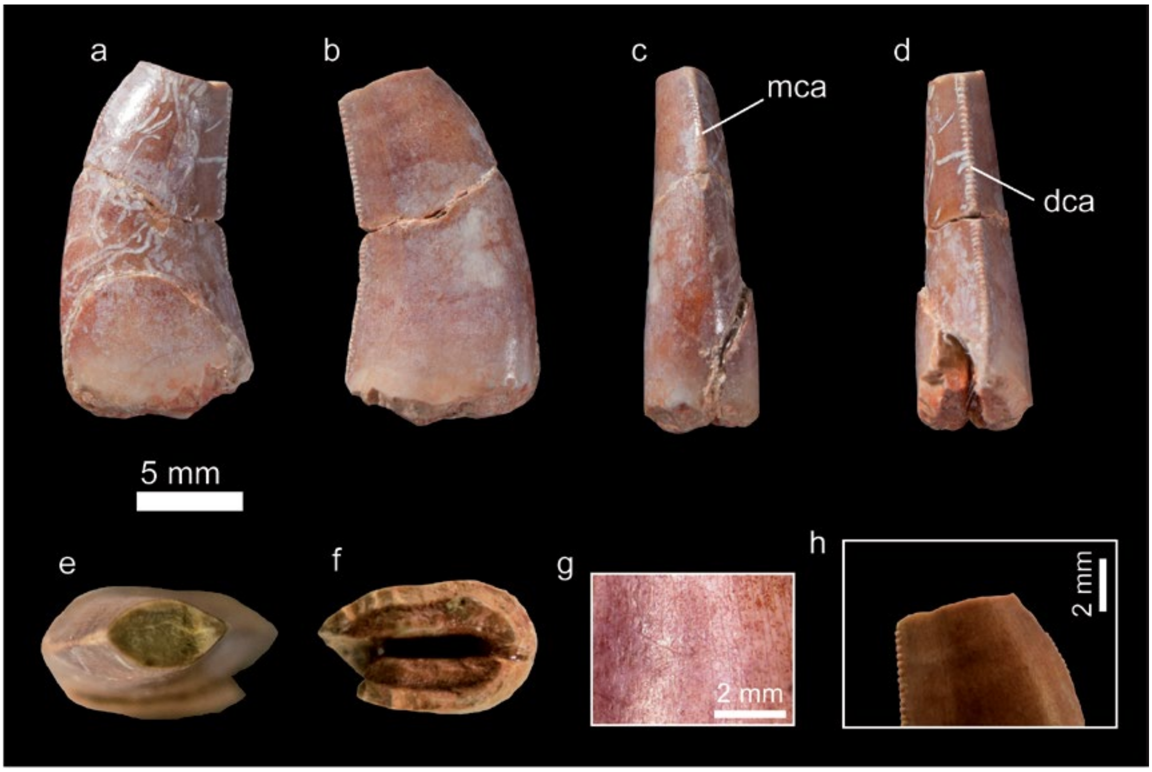


Fig. 3: Tetanurae indet. 1. HOC 24. a) Lingual, b) labial, c) mesial, d) distal, e) apical, f) basal views. g, h) Enamel surface and denticles. *dca* distal carina, *mca* mesial carina

This tooth is different from other theropod clades. Coelophysids and compsognathids have small crowns bearing minute denticles (Buckley, 2009; Hendrickx and Mateus, 2014b). The dentition of abelisaurid theropods is usually squat, weakly recurved and some of them have hooked denticles and the mesial carina reaches the cervix (Hendrickx *et al.,* 2015b) whereas non-abelisaurid ceratosaurs have a mesial carina that extends at a certain distance from the cervix. HOC 24 is also clearly different from the conidont teeth with apicobasal enamel flutes, minute denticles and deeply veined enamel texture of spinosaurids (Charig and Milner, 1997; Canudo *et al.,* 2008a; Hendrickx and Mateus, 2014b). In addition, it does not possess the thickened and incrassate crowns of derived tyrannosauroids (Brusatte *et al.,* 2010a; Csiki-Sava *et al.,* 2016) and it is significantly different from troodontids, therizinosaurs, ornithomimosaurs, alvarezsauroids, oviraptorosaurs or avialans, which have small, conical, folidont and/or unserrated crowns. When serrated, the carinae bear either particularly large, often hooked denticles, or minute serrations (Pérez-Moreno *et al.,* 1994; Norell *et al.,* 2009; Hendrickx and Mateus, 2014b; Hendrickx *et al.,* 2015b; Csiki-Sava *et al.,* 2016).

One of the most striking features of this morphotype is a mesial carina that does not reach the cervix. This trait is seen in basal theropods such as *Eoraptor*, non-spinosaurid megalosauroids and most piatnitzkysaurid mesial and lateral teeth (Hendrickx *et al.,* 2015b), neovenatorids (Hutt *et al.,* 1996), carcharodontosaurids such as *Acrocanthosaurus*, megaraptorans (White *et al.,* 2015), therizinosaurs, dromaeosaurids and microraptorans (Hendrickx, 2015). The presence of transverse and marginal undulations is common among non-neocoelurosaur averostrans (Brusatte *et al.,* 2007; Hendrickx and Mateus, 2014b).

A slightly concave or planar surface adjacent to the distal carina is seen among non-neocoelurosaur theropods. The slightly concave or planar surface is observable in *Skorpiovenator, Erectopus, Piatnitzkysaurus, Afrovenator, Sinraptor, Neovenator, Fukuiraptor* and *Australovenator*, as well as *Coelophysis, Dilophosaurus* and *Ceratosaurus* (Hendrickx, 2015).

DFA (CD) classifies HOC 24 as a member of the group Neovenatoridae. The cladistic analysis (Appendix 4) recovers HOC 24 as a tyrannosauroid. This tooth shows some differences with respect to Tetanurae indet. 2 and Tetanurae cf. Carcharodontosauria indet. (**see below**). The tooth has a thicker cross-section and the general shape of the crown is more squat. It also possesses a planar surface adjacent to the distal carina. Despite this, they share some common features, including the presence of transverse and marginal undulations, a relatively similar denticle density, a mesial carina that does not reach the cervix and a distal carina that is displaced labially. The differences between the morphotypes could be explained by ontogenetic variation, different tooth positions, or the presence of two different taxa.

Given the incompleteness of the tooth crown here we prefer to be cautious and consider this morphotype as Tetanurae indet.

3.1.2 *Tetanurae indet. 2*

Material: HOC 31, a shed tooth.

3.1.2.1 Description

The morphotype comprises one tooth lacking the root and part of the base (**Fig. 4**). The enamel surface is worn and shows microscratches. The tooth is ziphodont, with a labiolingually compressed and curved crown. The tooth crown has transverse breaks and the basalmost part is broken; this is the most damaged area. In basal view, it reveals a pulp cavity filled with sediment.

HOC 31 is a medium-sized theropod tooth, with a preserved crown base length (CBL) of 8.75 mm, a preserved crown base width (CBW) of 4.2 mm, and preserved crown height (CH) of 25.2 mm. The tooth crown is strongly labiolingually compressed (CBR around 0.4) and elongated (CHR around 2.8).

In lateral view, the mesial margin of the tooth crown is convex, while the distal margin is concave. The mesial margin is more recurved than the distal margin. The apex is acute and has spalled surfaces both on labial and lingual sides. The tooth crown has mesial and distal carinae, and the mesial carina terminates well above the cervix whereas the distal carina extends on the whole crown.

In mesial view, the mesial carina bears denticles and is located on the mesiodistal axis of the crown. The labial surface of HOC 31 is slightly sigmoid basoapically, with the basalmost part of the crown convex whereas the apical part is concave.

In distal view, the distal carina bears serrations as well and is very slightly displaced labially. The labial and lingual surfaces of the tooth crown are weakly mesiodistally convex.

In apical view, the tip is distally positioned on the crown. In basal view, the cross-section of the crown is lanceolate at the level of the cervix with the mesial surface being broader than the distal surface. The cross section at the level of the mid-crown is lenticular with the mesial and distal margins both acute.

The mesial carina has 24 denticles per 5 mm at the midcrown. The denticles display a gradual variation in size towards the basalmost part of the crown. The mesial denticles have the same basoapical and mesiodistal length which give them a subquadrangular shape. The external margin of the denticles is parabolic.

The distal carina has 20 denticles per 5 mm at the midcrown, and the denticle size density index (DSDI) is 1.2. The denticles are perpendicular to the distal margin of the tooth. The denticles decrease in size towards the base, displaying a gradual variation. The distocentral denticles are subquadrangular. There is, however, variation in shape: the distobasal denticles are proximodistally subrectangular. The main axis of the denticles is perpendicular to the mesial carina and the external margin of the denticles is parabolic to semicircular; they are either symmetrically or asymmetrically convex. The space between denticles is narrow and deeper in the distal denticles. There are interdenticular sulci; they are short, basally inclined and they are present on the distal margin.

The crown surface is worn and is covered with microscratches probably due to wear and erosion. The enamel surface displays horizontally oriented marginal undulations which bend towards the tip of the crown near the mesial and distal carinae. In addition, there are horizontally oriented transverse undulations, which are apically concave, and they curve apically as they approach the carinae. The transverse undulations completely cover the enamel surface of the tooth crown.

The original enamel texture appears to be braided (*sensu* Hendrickx *et al.,* 2015c).

3.1.2.2 Discussion

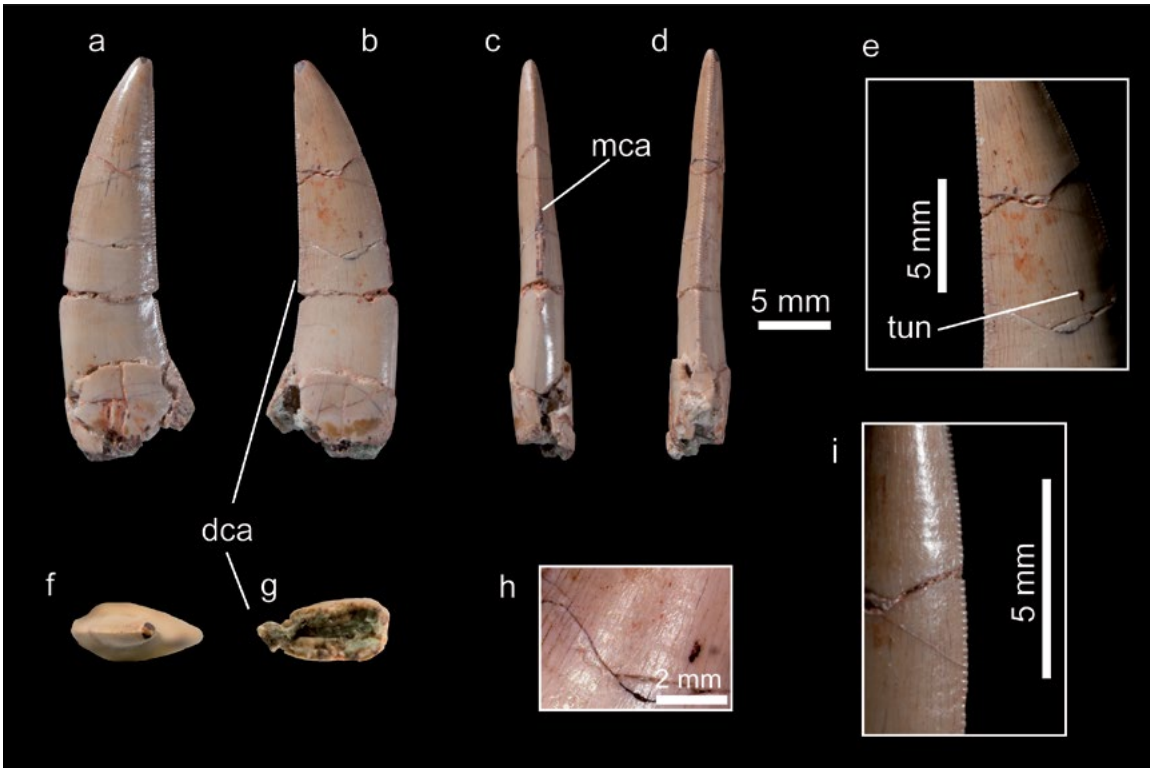


Fig. 4: Tetanurae indet. 2. HOC 31 in a) labial, b) lingual, c) mesial, d) distal view. e) detail of undulations, mesial and distal carinae. f) Apical, g) basal views. h) Enamel surface, i) mesial carina.

This tooth share traits commonly found in non-maniraptoriform tetanurans. HOC 31 is strongly labiolingually compressed, the mesial carina does not reach the cervix, the distal carina is slightly displaced labially, and it also has transverse and marginal undulations, interdenticular sulci, a braided enamel texture and a lenticular crosssection. However, the tooth crown shows some differences with respect to Tetanurae cf. Carcharodontosauria indet. (**see below**). The DSDI is 1.2 and the distocentral denticles are subquadrangular instead of proximodistally subrectangular. The labial and lingual surfaces are similarly mesiodistally convex instead of a lingual surface more mesiodistally convex in shape.

DFA analysis (CD) classifies this tooth as *Erectopus*. The cladistic analysis (Appendix 4) recovers a polytomy at the base of Averostra. A reduced strict consensus was calculated using the pruning trees option in TNT (Appendix 4), resulting in the pruning of HOC 31. It is recovered either as the sister taxon of Averostra, as the sister taxon of *Dubreuillosaurus*, as the sister taxon of *Piatnitzkysaurus* or as the sister taxon of Spinosauridae.

The difference in size between the mesial and distal denticles in this morphotype is remarkable. This character is present in the lateral dentition of noasaurids such as *Noasaurus* and *Masiakasaurus,* piatnitzkysaurids such as *Marshosaurus* and *Piatnitzkysaurus*, non-tyrannosaurid Tyrannosauroidea such as *Proceratosaurus* (Rauhut *et al.,* 2010), *Dilong, Guanlong, Eotyrannus* and *Xiongguanlong*. Dromaeosaurids such as *Velociraptor* and *Deinonychus* show this condition as well (Hendrickx, 2015).

Despite the similarity between Tetanurae cf. Carcharodontosauria indet. (**see below**) and this tooth, the high denticle size index (DSDI) and the absence of this feature in allosauroids leads us to consider this morphotype as another morphotype of Tetanurae indet. However, we do not exclude that the differences between this morphotype and Tetanurae cf. Carcharodontosauria indet. could be explained by ontogenetic variation, different tooth positions, or the presence of two different taxa. New discoveries are required to resolve this issue.

TETANURAE Gauthier, 1986
MEGALOSAUROIDEA Fitzinger, 1843
Spinosauridae Stromer, 1915
Spinosaurinae Sereno, Beck, Dutheil, Gado, Larsson,
Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson
and Wilson, 1998

3.1.3 *Spinosaurinae? indet.*

Material: HOC 17, HOC 28, two shed teeth.

3.1.3.1 Description

HOC 17 is a conical tooth from a theropod dinosaur preserving most of the crown and a small part of the root (**Fig. 5**). The enamel shows small fractures, and some parts are missing. A transverse break is located at the end of the apical third. The lingual surface has a damaged area in its basal region, which is lacking fragments of the crown. The surface is also covered with microscratches, and some parts of the original enamel texture are worn, possibly due to abrasion. HOC 28 is a poorly preserved theropod tooth fragment but here it is considered to represent the same morphotype as HOC 17 because of its general similarity and the presence of longitudinal flutes along the crown. Therefore, the description of this morphotype is based on the better-preserved tooth, HOC 17.

HOC 17 is a medium-sized tooth from a theropod dinosaur, with a crown base length (CBL) of 10.27 mm, crown base width (CBW) of 8.61 mm, and crown height (CH) of 23.25 mm. The tooth is conidont (*sensu* Hendrickx *et al.,* 2015c). With a CBR and a CHR of 0.8 and 2.26 respectively, the crown is weakly labiolingually compressed and moderately elongated, with a broad and rounded cross-section at its base.

In lateral view, the mesial and distal profiles are convex and concave, respectively. The crown is moderately recurved and its curvature is greater mesially than distally. The base of the crown is longer than the mid-crown mesiodistally.

In distal view, the mesial and distal profiles are curved towards the lingual side of the crown. The labial and lingual surfaces are mesiodistally convex with the enamel extending to the same level basally. The distal carina is centrally positioned on the distal margin of the crown and reaches the cervix. It does not show any serrations.

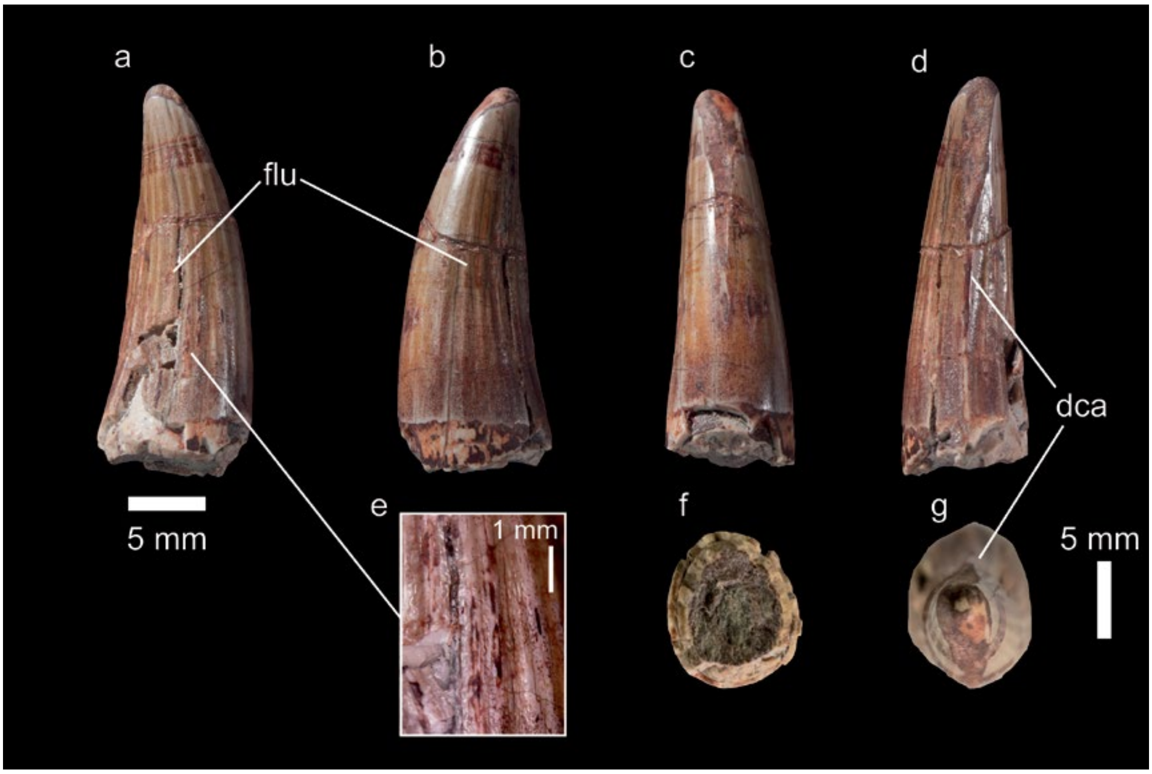


Fig. 5: Spinosaurinae? indet. HOC 17: a) lingual, b) labial, c) mesial, d) distal view. e) Enamel surface and ornamentation. f) basal view. g) apical views. *dca* distal carina, *flu* flutes.

In mesial view, the mesial surface is worn, and this precludes the recognition of a possible mesial carina. The mesial carina, if it was originally present, extended significantly (5.5 mm) above the cervix and was medially positioned. In apical view, the tip is slightly lingually oriented.

The cross-sections at the level of the cervix and the midcrown are elliptical to subcircular; the mesial margin is wider than the distal margin. Both labial and lingual surfaces are mesiodistally convex along the crown; mesial and distal margins are convex as well.

The distal carina is partially eroded, but the central part, which is better preserved, lacks denticles, suggesting that the distal carina is unserrated.

The apex of the crown has a spalled surface extending along the apical third of the crown on both the mesial and distal surfaces. Numerous flutes running apicobasally are visible on the lingual and labial sides of the crown. Five and eight flutes are present on the labial and lingual sides, respectively.

Some parts of the enamel are smooth due to erosion and wear. The preserved enamel surface texture corresponds to the veined texture described by Hendrickx *et al.,* (2015a). The texture is basoapically oriented in the middle of the crown but curves towards the carina at the distal margin. The enamel texture is best preserved between the apicobasal ridges delimiting each flute.

3.1.3.2 Discussion

The tooth has a combination of features seen in spinosaurid teeth such as a slight distal curvature, a subcircular cross-section, fluted enamel on both labial and lingual sides of the crown and a veined enamel texture. Spinosaurid teeth either have minute denticles or unserrated carinae (Charig and Milner, 1997; Sereno *et al.,* 1998; Ruiz-Omeñaca *et al.,* 2005; Canudo *et al.,* 2008a; Gasca *et al.,* 2008).

Some authors have pointed out the presence of a morphotype of spinosaurid tooth from the Barremian of Teruel Province with an unserrated mesial carina (Artoles Formation, Ruiz-Omeñaca *et al.,* 1998; El Castellar Formation, Gasca *et al.,* 2008). However, this cannot be established in the case of this tooth. The mesial carina, if present, was not reaching the cervix.

The presence of flutes is characteristic of spinosaurid teeth, although they are present in other taxa as well (e.g., *Coelophysis, Ceratosaurus, Masiakasaurus, Scipionyx*, and some dromaeosaurids; Madsen and Welles, 2000; Sampson *et al.,* 2001; Hendrickx, 2015). HOC 17 has flutes on both sides as in *Suchomimus, Spinosaurus* and *Siamosaurus* whereas *Baryonyx* tends to have flutes restricted to one side of the crown (Charig and Milner, 1997). The veined enamel texture (sensu Hendrickx *et al.,* 2015c) of the tooth characterizes spinosaurid teeth. It has been found in *Baryonyx, Suchomimus, Spinosaurus* and other spinosaurids (Canudo *et al.,* 2008a; Serrano-Martínez *et al.,* 2016; Hendrickx ,2015).

Spinosaurids are divided traditionally into two subfamilies, Baryonychinae and Spinosaurinae. There are various morphological differences between their teeth. Baryonychine teeth have serrated carinae with minute denticles, more labiolingually compressed teeth than spinosaurines and a more pronounced distal curvature of the crown (Charig and Milner, 1997; Canudo *et al.,* 2008a; Alonso and Canudo, 2016). Also, spinosaurine teeth have unserrated carinae, as exemplified by *Irritator, Angaturama* and *Spinosaurus* (Stromer, 1915; Kellner and Campos, 1996; Sues *et al.,* 2002). In general, all these differences are plesiomorphies in baryonychine teeth, or apomorphies in spinosaurine teeth.

The DFA analysis classifies HOC 17 as belonging to a member of Spinosaurinae (CD). Likewise, the cladistic analysis considers this morphotypeas the sister taxon of the group formed by *Spinosaurus* and *Irritator* (Appendix 4). The possible presence of spinosaurine spinosaurids in the Lower Cretaceous of the Iberian Peninsula has been proposed before (Sánchez- Hernández *et al.,* 2007; Alonso and Canudo, 2016), but the most common spinosaurid material belongs to Baryonychinae (Infante *et al.,* 2005; Canudo *et al.,* 2008a; Gasca *et al.*, 2008; Mateus *et al.,* 2011; Alonso and Canudo, 2016).

Given the combination of features and the results of the analyses here we consider tentatively this morphotype as Spinosaurinae? indet.

3.1.4 *Tetanurae cf. Carcharodontosauria indet.*

Material: HOC 19 and HOC 26, two shed teeth.

3.1.4.1 Description

The morphotype comprises two teeth lacking the root and the basalmost part of the tooth. The enamel surface is worn and shows microscratches. The shape of the teeth is the common blade-like morphology, with labiolingually compressed and distally curved crowns bearing serrated carinae (**Fig. 6**). The crown HOC 19 is the best-preserved tooth; it lacks the basal part, and the break reveals the dentine and a narrow pulp cavity filled with sediment. The apex and some areas of the labial and lingual surfaces lack the enamel cover, especially the lingual surface, which shows a longitudinal area from the basal part to the mid-crown where the enamel is missing.

The crown HOC 26 exhibits transverse breaks over its entire height: at least four large breaks plus minor fractures. The base is the most damaged region of the crown and some parts are missing. It also has a series of white marks which are more evident on the lingual surface of the crown. These marks were caused by the roots of modern plants that damaged the enamel.

HOC 19 and HOC 26 are medium-sized theropod teeth, with a preserved crown base length (CBL) of 14.8 and 16.2 mm respectively; a preserved crown base width (CBW) of 6.8 and 7.5 mm respectively; and preserved crown height (CH) of 39.1 and 50.6 mm respectively. All the crowns are strongly to moderately labiolingually compressed (CBR value around 0.4) and elongated (CHR around 2.6–3). The teeth have a narrow, teardrop-shaped cross-section at their bases.

In lateral view, the mesial and distal profiles are convex and concave, respectively. The mesial margins of the crowns are more recurved than the distal margins. The apices are acute, pointed and have spalled surfaces. The crowns have carinae on both mesial and distal margins, and the extension of these carinae varies: the mesial carina extends along two-thirds of the preserved crown height whereas the distal carina seems to reach the cervix.

In distal view, the distal carina is slightly displaced labially and bears serrations all along the crown. The labial and lingual surfaces are mesiodistally convex, with the lingual side more convex than the labial side, which is weakly mesiodistally convex, almost flattened. In mesial view, the mesial carina bears serrations and extends significantly above the cervix. The mesial carina of HOC 19 is placed slightly labially. On the other hand, the mesial carina of HOC 26 is placed labially at the tip but curves slightly towards the base, becoming centrally positioned. The labial surfaces of HOC 19 and HOC 26 are slightly sigmoid, with the basalmost part of the crowns and the apical part being convex and concave, respectively. The converse situation is found on the lingual surfaces, where the basal part is concave and the apical part is convex.

In apical view, the tip is distally positioned on the crown and slightly lingually oriented. Both the mesial and distal carinae are acute. In basal view, the cross-section of the crowns is lanceolate at the level of the cervix with a rounded and wide labial margin whereas the lingual margin is acute. The cross-section at the level of the mid-crown is lenticular with the mesial and distal margins both acute.

The mesial carinae of HOC 19 and HOC 26 have around 21–22 denticles per 5 mm at the mid-crown, respectively. The size of the denticles decreases towards the basalmost part of the crown and they display a regular variation in size, i.e. not sporadic or sudden. In lateral view, the denticles possess a subquadrangular outline, with the same basoapical and mesiodistal length. They are positioned perpendicularly to the carina.

The distal carinae of HOC 19 and HOC 31 have 18–19 denticles per 5 mm at the mid-crown, respectively, and the denticle size difference index (DSDI) has a value of around 1. The denticles also decrease in size towards the base, displaying a gradual variation. They are chisel-shaped and proximodistally subrectangular, with a mesiodistal axis that is greater than the apicobasal axis except in the apical denticles, which are subquadrangular in shape. The main axis of the denticles is perpendicular to the distal carina.

The external margin of the mesial and distal denticles is parabolic to semicircular and either symmetrically or asymmetrically convex; they do not hook towards the tooth apex. The lingual and labial surfaces of the denticles are convex. The interdenticular space between denticles is narrow and deeper in the distal denticles. There are short and basally inclined interdenticular sulci between the distal denticles; they are better seen at a low light angle.

The crown surface is covered with microscratches due to erosion and wear. The external enamel shows diagonally oriented marginal undulations which bend towards the tip of the crown near the carinae. They are abundant, and they are restricted to the carina. Where the carina is not present (e.g. the mesial margin of the basalmost part of the crown), the marginal undulations are absent. These wrinkles are clearly visible whereas the transverse undulations are better seen at certain angles. The transverse undulations are apically concave, curving apically as they approach the carina, and they completely cover the enamel surface of the crowns. The original enamel texture appears to be braided (*sensu* Hendrickx *et al.,* 2015c).

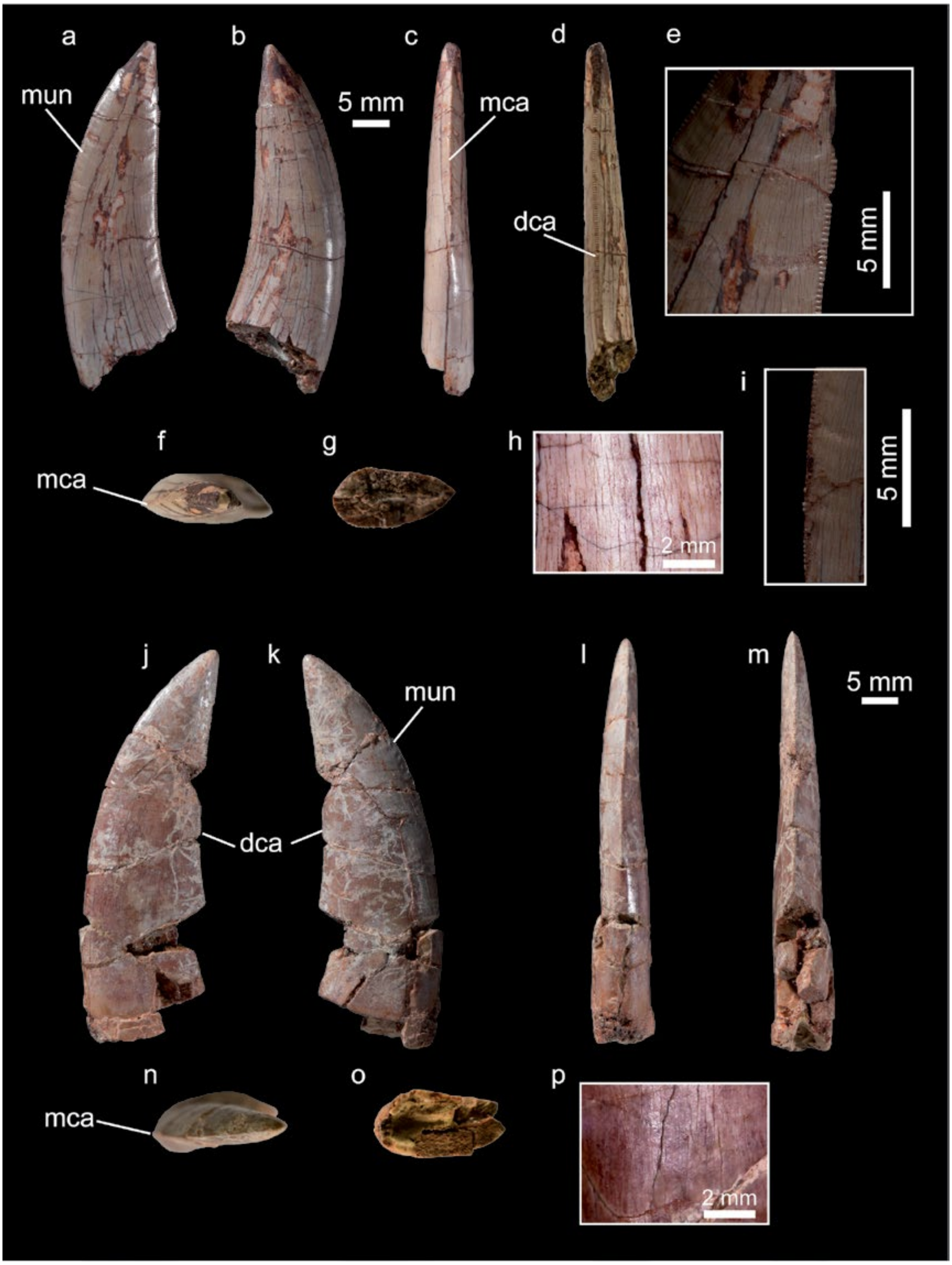


Fig. 6: Tetanurae cf. Carcharodontosauria indet. HOC 19 in a) labial, b) lingual, c) mesial, d) distal view. e) Undulations and denticles on the distal carina. f) Apical view, g) basal views, h) enamel surface, i) mesial carina. HOC 26 in j) labial, k) lingual, l) mesia, m) distal, n) apical, o) basal views, p) enamel surface. *dca* distal carina, *mca* mesial carina, *mun* marginal undulations.

3.1.4.2 Discussion

The teeth of this morphotype share traits commonly found in non-maniraptoriform tetanurans. They are strongly labiolingually compressed, as seen in the lateral dentition (Hendrickx *et al.,* 2015b). The mesial carina does not reach the cervix, the distal carina is slightly displaced labially, and they also have marginal and transverse undulations, interdenticular sulci, a braided enamel texture and a lenticular cross-section. Megalosauroids and allosauroids share these characteristics (Hendrickx, 2015; Hendrickx *et al.*, 2015b). A mesial carina that does not reach the cervix is seen in megalosaurids (Hendrickx *et al.,* 2015b), *Neovenator* (Hutt *et al.,* 1996), *Australovenator* (Hocknull *et al.,* 2009; White *et al.,* 2015), *Alioramus* (Brusatte *et al.*, 2012), Therizinosauria and Microraptorinae, and is also seen in *Acrocanthosaurus* and *Dromaeosaurus* (Hendrickx, 2015). The labial side of the teeth is weakly mesiodistally convex and comparatively flat. A surface centrally positioned on the crown roughly flattened on the labial side of lateral teeth is seen in non-abelisauroid ceratosaurs and neovenatorids (Hendrickx and Mateus, 2014b; Hendrickx, 2015); unlike non-abelisauroid ceratosaurs the mesial carina of this morphotype does not reach the cervix.

Teeth with a weak displacement of the distal carina are common in non-maniraptoriform theropods. Only a few clades such as Ceratosauridae, *Masiakasaurus*, *Allosaurus*, Tyrannosauroidea and *Dromaeosaurus* show a distal carina strongly deflected labially (Hendrickx, 2015). Another characteristic of HOC 19 and HOC 26 is the presence of transverse and marginal undulations, a widespread feature among theropods (Brusatte *et al.,* 2007). The braided texture of the enamel is also widespread and can be observed in megalosauroids, allosauroids, tyrannosauroids and basal ceratosaurians (Hendrickx, 2015).

DFA (CD) classifies HOC 19 and HOC 26 as *Erectopus*. *Erectopus* is a basal allosauroid from the Albian of France (Allain *et al.,* 2005). Some differences exist between this morphotype and the dentition of *Erectopus*: *Erectopus* has a concave surface on the lingual side adjacent to the distal carina (Hendrickx and Mateus, 2014b), the mesial carina reaches the cervix (Allain *et al.,* 2005) and the denticle density is slightly different. The cladistic analysis (Appendix 4) places HOC 19 in a polytomy with *Piatnitzkysaurus* and *Erectopus*. On the other hand, the cladistics analysis of HOC 26 recovers a polytomy at the base of Averostra. A reduced strict consensus was calculated using the pruning trees option in TNT. The pruning of HOC 26 from the consensus tree increased the resolution of the consensus (Appendix 4). HOC 26 is either recovered as the sister taxon of *Erectopus* or within Megalosauridae.

HOC 19 and HOC 26 share some traits with megalosaurids. The mesial carina does not reach the cervix, they are strongly to moderately labiolingually compressed, the enamel surface displays marginal and transverse undulations, and some of the denticle traits are relatively similar. In addition, a flattened labial surface is seen on *Erectopus*.

Despite these similarities some differences exist: *Erectopus* has a planar surface adjacent to the distal carina on the lingual margin of the crown and the mesial carina reaches the cervix. Besides, the labial surface of megalosaurids is not flattened (Hendrickx, 2015).

The presence of non-spinosaurid basal tetanurans is known for the deposits of the Lower Cretaceous of western Europe. Nevertheless, these are allosauroids related to Carcharodontosauria; if *Afrovenator* is of Jurassic age (Rauhut and López-Arbarello, 2009) then the youngest skeletal record of megalosaurids is *Torvosaurus* from the Kimmeridgian/Tithonian of Portugal and western USA (Hendrickx and Mateus, 2014a). The only tetanuran described from the Early Cretaceous of Spain, *Concavenator corcovatus* from the upper Barremian of Las Hoyas (Cuenca province), is a basal carcharodontosaurid (Ortega *et al.,* 2010). Another carcharodontosaurid specimen comes from other Barremian deposits in Teruel, where an isolated distal femur (Gasca *et al.,* 2014a) has been found, sharing affinities with *Acrocanthosaurus*. Recently, a single carcharodontosaurid theropod tooth from the Valanginian of Romania (Csiki-Sava *et al.,* 2016) has been proposed as the earliest evidence of Carcharodontosauridae in Europe. Carcharodontosaurid carcharodontosaurians are also found in Gondwanan deposits from the Early Cretaceous (Novas *et al.,* 2005; Fanti *et al.,* 2014), and in North America they are represented by the Albian genus *Acrocanthosaurus* (Sereno *et al.,* 1996; Harris, 1998; Brusatte and Sereno, 2008; Csiki-Sava *et al.,* 2016), becoming abundant and diverse in the course of the "middle" and Late Cretaceous (Csiki-Sava *et al.*, 2016). Non-carcharodontosaurid carcharodontosaurians are represented by *Neovenator* (Hutt *et al.,* 1996) from the Barremian Wealden of England, which shares the features seen in this morphotype.

Given the absence of non-spinosaurid megalosauroid theropods from the Early Cretaceous of the Iberian Peninsula, these teeth are here considered as belonging to an indeterminate Carcharodontosauria, pending the discovery of additional skeletal material to support this hypothesis.

4. DISCUSSION

The palaeobiodiversity of theropods from the Early Cretaceous of the Iberian Peninsula includes a broad set of neotheropods. The ceratosaur *Camarillasaurus cirugedae* (Sánchez-Hernández and Benton, 2014) has been described in the Barremian deposits of the Galve sub-basin. Among tetanurans there is a combination of basal and derived taxa. Basal tetanurans for which there is evidence include spinosaurids (Buffetaut, 2007; Canudo *et al.,* 2008a; Gasca *et al.,* 2008; Mateus *et al.,* 2011; Alonso and Canudo, 2016) and carcharodontosaurians such as *Concavenator corcovatus* (Ortega *et al.,* 2010), as well as other indeterminate carcharodontosaurids (Gasca *et al.,* 2014a). There is also evidence of derived tetanurans such as coelurosaurs, including ornithomimosaurs such as *Pelecanimimus* (Pérez-Moreno *et al.,* 1994), maniraptorans such as dromaeosaurids (i.e., Ruiz-Omeñaca *et al.,* 1996; Rauhut, 2002; Canudo *et al.,* 2010a) as well as birds (i.e., Sanz *et al.,* 1988). Thus the theropod fossil record from Barranco del Hocino-1 is congruent with the known record of theropods from the Early Cretaceous of the Iberian Peninsula. However, according to our phylogenetic analyses, these teeth would extend the non-spinosaurid megalosauroid lineage into the Early Cretaceous. HOC 19, HOC 24, HOC 26 and HOC 31 share some traits with some megalosauroids (e.g. a mesial carina that does not reach the cervix, they are strongly to moderately labiolingually compressed, the enamel surface displays marginal and transverse undulations, and some of the denticle traits are relatively similar).

Previous studies have supported the reliability of cladistics analyses applied to isolated teeth (e.g. Hendrickx and Mateus, 2014b; Csiki-Sava *et al.,* 2016). Nevertheless, it is interesting to point out that the state of preservation of Barranco del Hocino 1 teeth is deficient; partially explaining the results. The absence of relevant information about the crown and root could input a considerable amount of noise in our analyses.

In addition, the dataset does not include theropods from the Barremian of the Iberian Peninsula. It would be interesting to draw a comparison between Barranco del Hocino 1 morphotypes and theropods such as *Concavenator* (Ortega *et al.,* 2010). A comprehensive study of its dentition would probably improve the identification of isolated teeth from the Early Cretaceous of the Iberian Peninsula.

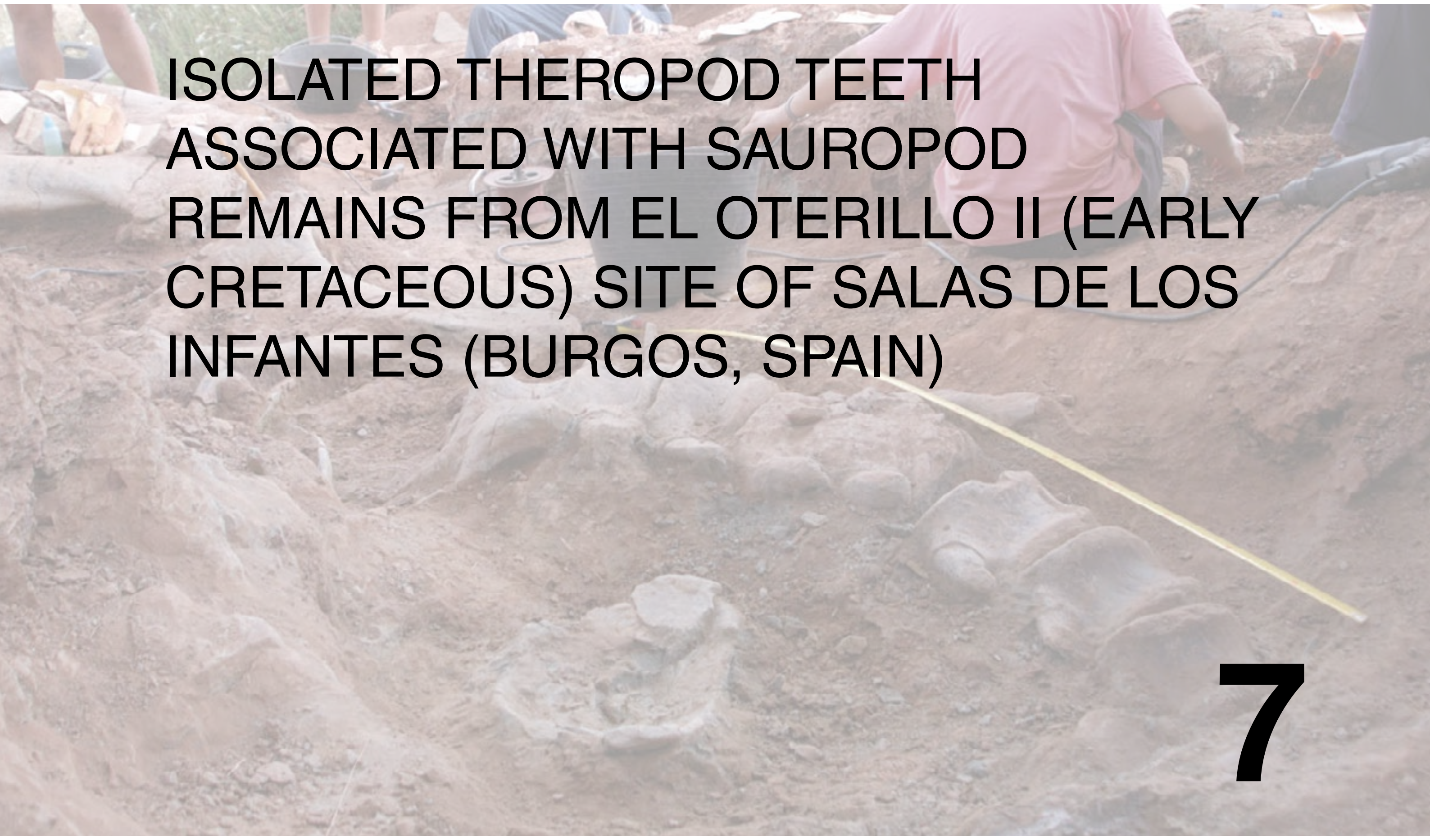
The association of spinosaurids and other basal tetanurans is also found in other places, such as the Wealden of England, which has *Baryonyx* (Charig and Milner, 1997) and *Neovenator* (Hutt *et al.,* 1996) and other indeterminate basal tetanurans (Benson *et al.,* 2009; Gasca *et al.,* 2014a). This association represents the megapredators of the epoch. These clades are also found in the north of Africa, where there are spinosaurine and baryonychine spinosaurids such as *Spinosaurus* from the Cenomanian of Egypt (Stromer, 1915) and *Suchomimus* from the Aptian/Albian of Niger (Sereno *et al.,* 1998) and carcharodontosaurians such as *Carcharodontosaurus* from the Cenomanian of Morocco and *Eocarcharia* from the Aptian/Albian of Niger (Brusatte and Sereno, 2007; Brusatte *et al.,* 2007; Sereno and Brusatte, 2008; Fanti *et al.,* 2014).

The absence of other theropod taxa in the Barranco del Hocino-1 fossil assemblage, especially smaller theropods, is remarkable. In contrast, other fossil sites in the Blesa Formation, such as La Cantalera-1, have evidence of the presence of small theropods. This may be explained by the taphonomic characteristics of the remains. Another explanation is the amount of sediment sampled. Small-sized teeth are usually recovered when screen-washing is carried out. Three tonnes of sediment have been screen-washed from the La Cantalera-1 site, whilst just a few kilograms have been screen-washed here at Barranco del Hocino-1. This bias could affect the palaeobiodiversity that comes to light.

Barranco del Hocino 1 shows similarities with other sites such as La Cantalera 1 site both in composition and formation. Fossil vertebrates are often worse preserved in Barranco del Hocino 1, this could be related to a prolongued subaerial exposition of these remains, and also to the effect of paedogenetic processes and scavenging. So far, theropods and crocodylomorphs are scarcer and less diverse than in La Cantalera 1. In addition we do not have evidence of other taxa such as sauropods, pterosaurs or mammals. Ostheichtian and testudines remains are scarce as seen in La Cantalera 1; a different situation is found in other barremian formations such as El Castellar Fm of the Galve and Peñagolosa subbasins (Gasca *et al.,* 2015).

5. CONCLUSIONS

Barranco del Hocino-1 is a new fossil site in the Oliete subbasin within the Maestrazgo Basin. Among the vertebrate fossils recovered from the site are remains from large-sized theropods which consist of isolated teeth. Four different morphotypes of theropod tooth have been identified. One morphotype has been assigned to Spinosauridae. The other morphotypes have been assigned to Tetanurae and one has been a tentatively attributed to Carcharodontosauria indet. in the light of the known record of basal tetanurans from the Barremian of the Iberian Peninsula and western Europe. These results represent a new contribution to our knowledge of the palaeobiodiversity and distribution of theropods from the Barremian of the Iberian Peninsula. They also provide further evidence of the palaeontological interest of this area.



ISOLATED THEROPOD TEETH ASSOCIATED WITH SAUROPOD REMAINS FROM EL OTERILLO II (EARLY CRETACEOUS) SITE OF SALAS DE LOS INFANTES (BURGOS, SPAIN)

7

1. INTRODUCTION

Several authors have pointed out the relationship between the carcasses of herbivorous dinosaurs and isolated theropod teeth (Buffetaut and Suteethorn, 1989; Maxwell and Ostrom, 1995; Canudo *et al.,* 2009; Canale *et al.,* 2014b). This usually includes the presence of a partially articulated individual dinosaur carcass and some isolated theropod teeth located close to the bone remains or concentrated in specific parts of the carcass (Corro, 1966; Buffetaut and Suteethorn, 1989; Maxwell and Ostrom, 1995; Jacobsen, 1998; Canudo *et al.,* 2009). The most parsimonious explanation seems to be that theropod dinosaurs fed on the herbivore carcass. In addition, tooth marks on the bone remains of herbivorous dinosaurs are well documented (Jacobsen, 1998; Paik *et al.,* 2011). El Oterillo II is a vertebrate site where a partially articulated individual titanosauriform sauropod, *Europatitan eastwoodi,* has been found. The fossil remains consist of a tooth, cervical, dorsal and caudal vertebrae, two scapulae, two ischia, two pubes (Torcida Fernández-Baldor, 2006; Pereda-Suberbiola *et al.,* 2012; Torcida Fernández-Baldor *et al.,* 2009, 2017), cervical and dorsal ribs, haemal arches, a coracoid and two metacarpals in association with isolated theropod and crocodylomorph teeth. The aim of this work is to study the palaeobiodiversity of the theropod teeth and to discuss their palaeoecological relationship with the carcass of the sauropod of El Oterillo II.

1.1 Institutional abbreviations

MDS Museo de Dinosaurios (Salas de los Infantes, Burgos, Spain).

2 MATERIALS AND METHODS

The fossils were recovered from excavation campaigns in 2004–2006 by the Colectivo Arqueológico y Paleontológico de Salas de los Infantes, with the corresponding permits from the Dirección General de Patrimonio of the regional government of Castilla y León (dossiers 307/04-BU; 257/05-BU; 262/06-BU). The recovered material is deposited in the Museo de Dinosaurios de Salas de los Infantes (Salas de los Infantes, Burgos, Spain). Observations were made with a stereomicroscope, and pictures taken with a Sony α200 digital camera. The teeth were measured with a Mitutoyo Digimatic Digital Calliper, Series Nº 500. Thirty theropod teeth (**CD**) from El Oterillo II were analysed during the course of this research.

In addition, bone remains from the sauropod dinosaur were studied to establish the possible presence of tooth marks.

2.1 Statistical analysis

Multivariate statistical analyses were performed in order to ascertain the variation among the theropod teeth from El Oterillo II site. The statistical analyses (discriminant function analyses) were performed using PAST v3.0 (Hammer et al. 2001) and SPSS 20.0 (SPSS Inc., Chicago, Illinois) on the dataset of Hendrickx *et al.* (2015b), which includes data from Farlow *et al.*(1991), Sankey *et al.,* (2002), Currie and Varrichio (2004), Sankey *et al. (*2005), Smith *et al.* (2005), Smith and Lamanna (2006), Smith and Dalla Vecchia (2006), Fanti and Therrien (2007), Sereno and Brusatte (2008), Longrich (2008), Sankey (2008), Hocknull *et al.* (2009), Molnar *et al.* (2009), Rauhut *et al.* (2010), Ösi *et al.* (2010), Larson and Currie (2013) and Hendrickx *et al.* (2015b); data from White *et al.* (2015) and Csiki-Sava *et al.* (2016) were also included. The dataset comprises 1022 teeth from different theropod taxa including El Oterillo II teeth. Discriminant function analysis DFA) was performed on the dataset. DFA is an ordination technique applied to previously identified data in order to find the best discriminant variables. It also has predictive power and is able to classify unknown data in the previously known groups (Hammer and Harper, 2006).

Due to their state of preservation, not all the teeth from El Oterillo II site were analysed; this was in order to avoid interference. Only MDS-OTII,73, MDS-OTII,78, MDSOTII, 82, MDS-OTII,91, MDS-OTII,92, MDS-OTII,99, MDS-OTII,100, MDS-OTII,101 and MDS-OTII,102 were included. The variables used are CBL, CBW, CH, AL, CBR, CHR, MC and DC. In order to better reflect a normal distribution all data were log-transformed (see rationalization in Samman *et al.,* 2005). When a character was absent or missing it was coded with a question mark. The dependent variable was not the species taxonomic level but a larger taxonomic unit (such as Megalosauridae or basal Tyrannosauroidea). The only exception was made with uncertain genera such as *Erectopus* or *Nuthetes* and Spinosauridae, which has been split into two different groups: Baryonychinae and Spinosaurinae.

The first analysis was conducted with PAST v3.0 using all the variables. Due to the low percentage of correctly identified teeth (<65%), some changes were made to the dataset. Firstly we differentiated absent data (anatomical traits not present in the specimen, coded as a zero) from missing data (traits that may be absent due to breakage, coded as a question mark). Secondly, the dataset was logtransformed using the formula *log* (1 + x), as seen in Gerke and Wings, (2016), to properly account for zero values. Third, we removed the variable AL from the dataset due to the large number of missing data. Finally, all the cases with remaining missing data were also removed from the dataset. The following analyses were performed with SPSS 20.0, using the stepwise method with Mahalanobis distance and using a within-group covariance matrix. SPSS allows better control of the statistical procedure. The SPSS analysis of the dataset without AL and missing data (901 teeth) returned a better percentage of correctly classified teeth (79.7%) (**Appendix A**). A third analysis was performed separating mesialmost and lateral teeth due to the pseudoheterodonty and differentiation between mesial and lateral dentition in theropods. The percentage of correctly classified teeth went down (74.6%). In order to avoid interference and overlapping between groups, and given the absence of mesialmost teeth from El Oterillo II site, the mesial teeth were removed from the dataset. A fourth SPSS analysis (777 teeth) showed an improvement in the percentage of teeth correctly classified (82.5%).

The presence of small groups affects the accuracy of DFA. In this case we maintained low-number groups due to the relevance of some of them for comparison with El Oterillo II morphotypes, even though this was at the expense of an improved analysis.

The analyses obtained functions that explain the variance of the dataset. The first and the second functions explain >90% of the variance (91.8% analysis without missing data; 90.8% analysis without missing data and without mesial dentition; separation between mesialmost and lateral teeth explains 88.1% of variance, CD). These canonical functions were used to produce a graphical representation of the relative positions of the teeth, creating a morphospace in a dispersion graph (**Fig.1**). The weight of each variable in the canonical functions is represented in CD.

2.2 Cladistic analysis

In addition to the statistical analyses, cladistic analyses were performed (Appendix 5) The supermatrix comprises 60 theropod taxa with 1972 characters from Xu *et al.,* (2009), Brusatte *et al.,* (2010), Martínez *et al.,* (2011), Senter *et al.,* (2011), Pol and Rauhut, (2012), Carrano *et al.,* (2012) and Hendrickx and Mateus, (2014b). 141 characters are tooth-based. The analysis was performed on TNT 1.1 (Goloboff et al. 2008) using the protocol described in Chapter 2 (Materials and Methods).

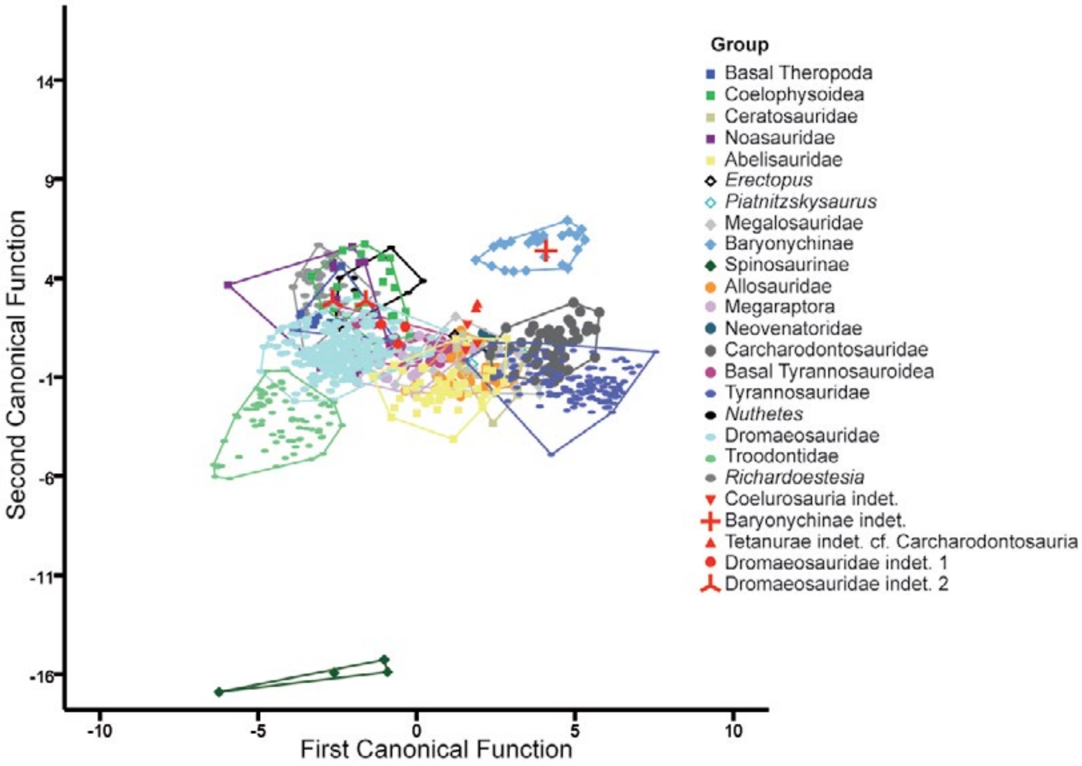


Fig. 1: DFA of 901 teeth dataset results, including El Oterillo II morphotypes (Coelurosauria indet., Baryonychinae indet., Tetanurae indet. cf. Carcharodontosauria, Dromaeosauridae indet. 1 and Dromaeosauridae indet. 2) and excluding AL and teeth with missing data. The first function explains the 63.4% of variance; the second canonical function explains the 28.4% of the variance.

2.3 Tooth mark analysis

In order to verify the presence of tooth marks on the sauropod carcass, various skeletal remains were studied, including dorsal and caudal vertebrae, haemal arches and autapodial elements. The distribution, morphology and abundance of the tooth marks were taken into account (Hunt *et al.,* 1994).

It is important to note that not all the bone remains were studied, so the interpretation of the results may lack important information about the type and distribution of the tooth marks. The conclusions derived from these observations should thus be taken with caution.

3 RESULTS

3.1 Systematic palaeontology

DINOSAURIA Owen 1842.
SAURISCHIA Seeley 1887.
THEROPODA Marsh 1881.
Theropoda indet.

Material Two teeth (MDS-OTII,88; MDS-OTII,89).

Description (after Hendrickx *et al.,* 2015c).

Two incomplete crowns that lack the basalmost part (**Fig. 2**). There are some horizontal fractures and parts of the enamel are missing. The carinae are damaged and MDS-OTII,88 lacks the mesial carina. The enamel surfaces have microscratches.

These are medium-sized, incomplete crowns with moderately compressed and distally curved ziphodont morphology. The CBR values are among the highest from El Oterillo II with the exception of spinosaurid teeth (0.6). Due to the absence of the basalmost part of the crown these values were not measured at the level of the cervix, so the real values of CBR could be slightly different. The absence of reliable values for these teeth makes it impossible to include them in the statistical analyses (CD). These teeth could represent mesial dentition. The elongation of the crown shows normal values according to Hendrickx and Mateus (2014b), but again this is not the real but the preserved elongation. The apex points towards the lingual side and seems to extend beyond the basal length of the crown. The mesial lateral profile of the crown is convex and the distal lateral profile is concave. The lingual surface is convex and the labial is almost planar.

MDS-OTII,89 has mesial and distal carinae. MDSOTII, 88 lacks the mesial carina. The carinae are well developed and serrated; the mesial carina is slightly twisted lingually and the distal carina of the teeth is strongly displaced labially. The distal carina seems to reach the cervix whereas the mesial carina does not extend along the whole mesial margin but finishes before the cervix. There are concave surfaces adjacent to the distal carinae, on the labial side of the crown. These surfaces are better developed toward the basal part of the preserved crowns. The preserved cross-section has a lanceolate-oval morphology, but this is not the cross-section at the level of the cervix.

Fig. 2: Theropoda indet. MDS-OTII,89: a) labial, b) lingual, c) mesial, d) distal, e) apical, f) basal views. g) detail of the denticles and the apex. MDSOTII, 88: h lingual, i labial, j mesial, k distal, l basal and m distal carina.

The distal carina of both teeth has 18 denticles per 5 mm, the largest denticles are located in the middle part of the carina. The denticles are chisel-shaped,they are proximodistally subrectangular and perpendicular to the carina. The external margin is symmetrically convex. The interdenticular space is broad, and the interdenticular slit is concave. There are interdenticular sulci on the distal margin on both the labial and lingual sides. The interdenticular sulci are straight, short and basally oriented.

There are spalled surfaces on the tips of the crowns. MDSOTII, 88 also has awear facet on the lingual surface. There are no flutes. The teeth have transversal undulations that cover the whole enamel surface and are visible at a certain angle. The enamel is polished and smooth but the original texture seems to be braided. The root is not preserved.

Discussion

The preserved crown base ratio (sensu Smith *et al.,* 2005) of these teeth is among the highest of the El Oterillo II teeth with the exception of the conical crowns of spinosaurids. The CBR does not exceed the 0.64 value proposed by Hendrickx (2015) as the most common value distinguishing mesial and lateral dentition. However, the basalmost parts of the teeth are not preserved, and its real value could well be greater.

Other interesting features of the teeth are the slightly twisted mesial carina, the distal carina that is deflected labially, and the concave surface adjacent to the carina. A distal carina that is strongly displaced labially appears in some basal theropods, ceratosaurids, tyrannosauroids, allosauroids, dromaeosaurids and troodontids (Hendrickx, 2015). Specifically, this deflection occurs in the mesial dentition of allosauroids, including carcharodontosaurids such as *Acrocanthosaurus* (Coria and Salgado, 1995) and *Mapusaurus* (Coria and Currie, 2006) and other possible carcharodontosaurians such as *Fukuiraptor* (Currie and Azuma, 2006; Hendrickx ,2015). It is also present in the mesialmost dentition of tyrannosauroids such as *Alioramus* and *Proceratosaurus*. *Allosaurus* (Hendrickx *et al.,* 2015b), ceratosaurids such as *Genyodectes* and dromaeosaurids such as *Dromaeosaurus* (Currie *et al.,* 1990) share this trait for the whole dentition. Another dromaeosaurid, *Deinonychus*, has this character in the mesial dentition only (Ostrom, 1969; Hendrickx, 2015).

The concave surface adjacent to the carina is also widespread among theropods. The mesial dentition of abelisaurids, *Allosaurus*, tyrannosauroids and some deinonychosaurs has concavities on the margins of the crowns (Smith, 2005, 2007; Hendrickx, 2015). In addition, the lateral dentition of basal theropods, ceratosaurids, neovenatorids and metriacanthosaurids may also have concave surfaces in the labiodistal part of the crowns (Rauhut, 2004; Azuma and Currie, 2000; Hendrickx, 2015).

The morphotype was not analysed with DFA due to the incompleteness of the tooth remains. The teeth were included in the cladistic analysis instead, coded separately as mesialmost and lateral dentition. The cladistic analysis (Appendix 5) recovered the teeth as mesial dentition in a polytomy with dromaeosaurids, *Piatnitzkysaurus*, *Erectopus, Dilophosaurus* and *Coelophysis*. A reduced strict consensus was calculated using the pruning trees option in TNT (Appendix 5), the morphotype being recovered either as the sister taxon of *Dilophosaurus* or within dromaeosaurids. According to a new cladistic analysis coding the teeth as lateral dentition, the morphotype corresponds to the sister taxon of *Dromaeosaurus*. Given the absence of relevant parts of the teeth, here we prefer to be cautious and consider this morphotype as Theropoda indet. The preserved measurements used in the cladistic analysis could deviate from the real measurements, and there could be relevant traits that are not preserved.

It cannot be ruled out that this morphotype represents a mesialmost morphotype related to other lateral tooth morphotypes from El Oterillo II site, such as Tetanurae indet. or Coelurosauria indet.

TETANURAE Gauthier 1986.
SPINOSAUROIDEA Stromer 1915.
Spinosauridae Stromer 1915.
Baryonychinae. Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson and Wilson, 1998.
Baryonychinae indet.

Material Five teeth (MDS-OTII,81; MDS-OTII,84; MDSOTII, 85; MDS-OTII,86; MDS-OTII,99).

Description

The teeth show different states of preservation. The majority of them are broken and incomplete, with the exception of MDS-OTII,99, which preserves the whole crown and some parts of the root (**Fig. 3**). Small fractures can be found on the enamel surface. The enamel is absent in some parts of the crown; the original enamel texture has been polished, probably due to abrasion. The enamel may show differences in polishing between different parts of the crown in these teeth. For instance, MDS-OTII,99 has more polished enamel on the apical, central and lingual parts of the crown. Usually, this polished enamel also shows microscratches on its surface.

The teeth show a curved distal profile with a slight tilt to the lingual surface. They are conidont crowns (sensu Hendrickx *et al.,* 2015c). The crown base ratio ranges between 0.6 and 0.8, typical of normal-subcircular crowns. The elongation of the crown (CHR around 2) shows normal values according to Hendrickx and Mateus (2014b). The apex of MDS-OTII,99 extends beyond the basal length. The mesial profile of the teeth in lateral view is convex and the distal profile is slightly concave, with the basalmost part almost straight. In distal view the mesial and distal profile are curved towards the lingual side. Both labial and lingual sides have convex surfaces. The enamel extension is similar on both sides.

The teeth have well-developed, serrated carinae on both the mesial and distal margins of the crown. Interestingly, the basal distal carina of MDS-OTII,99 is split, an unusual feature in theropods (Hendrickx, 2015). The carinae are located in central positions of the margins and reach the cervix. There are no adjacent surfaces or depressions on the basal part of the crowns. The cross-section of the crown at the level of the cervix is subcircular-elliptical; this is also the case at the level of the mid-crown. The carinae are densely serrated with minute denticles. MDS-OTII,99 has around 30 denticles per 5 mm. The state of preservation of the other crowns has prevented precise measurement, but there seem to be around 40 denticles per 5 mm, this higher number probably due to their small size. The DSDI values are around 0.9, which means that the denticles are similar in size in mesial and distal carinae. The denticles are small and may exhibit a sporadic variation in size along the carina, but generally they are bigger in the middle part. The denticles are subquadrangular and are located perpendicularly to the adjacent carina. The outline of the external margin of the denticle is symmetrically convex. The interdenticular space is shallow and narrow. The denticles have a diaphysis between them. The interdenticular slit is concave and shallow, and the denticles do not have interdenticular sulci.

MDS-OTII,99 and MDS-OTII,85 have a spalled surface on the apex of the crown. Wear facets have not been observed or are not preserved. The enamel surface bears flutes running apicobasally both on the lingual and labial sides. The number of flutes ranges between 5 and 9.

In addition to this ornamentation, MDS-OTII,99 has marginal and transversal enamel undulations. The undulations are scarce, around six per side, and extend horizontally except for the basal third of the crown. They are more easily visible at a certain angle. The enamel texture corresponds to the veined texture of Hendrickx *et al.,* (2015a). The texture is of an apical-adapical direction in the middle of the crown but curves toward the carinae at the margins.

The root is partially preserved in some of the teeth. The width is slightly greater than that of the crown and is of subcylindrical morphology. The surface of the root of MDS-OTII,99 has an ornamentation made up of undulations that are more visible on the lingual side. This tooth also has a small depression in this zone. The cross-section of the root is subcircular except for MDS-OTII,99, where the lingual depression makes the morphology slightly reniform. The dentine width of the root is about 4 mm.

Discussion

Spinosaurids have distinctive teeth with straight crowns or slight distal curvature, subcircular-elliptical cross-sections, fluted enamel, minute denticles or unserrated carinae, and a veined enamel texture (Charig and Milner, 1997; Sereno *et al.,* 1998; Sues *et al.,* 2002; Ruiz-Omeñaca *et al.,* 2005; Canudo *et al.*, 2008a; Hendrickx and Mateus, 2014b; Gasca *et al.,* 2008; Hendrickx *et al.,* 2015b; Serrano-Martínez *et al.*, 2016; Alonso and Canudo, 2016).

The spinosaurid teeth from El Oterillo II have a CBR greater than 0.64. CBR values higher than 0.64 are common for mesial teeth, which are broader than the lateral ones. This has been proposed as a dental feature by Hendrickx, (2015). Nevertheless, some clades have a CBR greater than 0.64 for non-mesial teeth, a feature seen in Allosauridae, Spinosauridae, Tyrannosauridae, Ornithomimosauria, Alvarezsauroidea and Therizinosauria (Hendrickx 2015).

The mesial carina reaches the cervix, a feature present in all theropod clades other than Megalosauridae and Therizinosauria. The presence of a mesial carina that reaches the cervix has been proposed as characteristic of all spinosaurids (Hendrickx *et al.,* 2015b) but some authors (Serrano-Martínez *et al.,* 2016) have noticed the occurrence of some spinosaurid teeth with mesial carinae that do not reach the cervix (CMP3-760, Canudo *et al.,* 2008a; Fig. 6), so there may be variation in this general trait. MDS-OTII,99 has an abnormal distal carina. A split mesial carina has been reported in tyrannosaurid theropods, A*llosaurus* and indeterminate carcharodontosaurids (Currie *et al.,* 1990; Erickson, 1995; Abler, 1997; Smith, 2005; Brusatte and Sereno, 2007; Candeiro and Tanke, 2008; Cillari, 2010; Hendrickx, 2015). The split mesial carina is common in Tyrannosauridae, as shown by Erickson (1995). This author also points to its possible causes: trauma, genetic factors and aberrant tooth replacement. This abnormal feature present in MDS-OTII,99 (given both its rarity and its location, the distal carina) seems to be the first evidence of the presence of this condition in Spinosauridae.

Fig. 3: Baryonychinae indet. MDS-OTII,99 in a) labial, b) lingual, c) mesial, d) distal, e) basal and f) enamel texture, marginal undulations and denticles on the distal carina.

More than 30 denticles per 5 mm are seen in non-tetanuran theropods, baryonychine spinosaurids and coelurosaurs. *Baryonyx* and *Suchomimus* have around 35 denticles per 5 mm (Hendrickx, 2015), values that are comparable to the teeth from El Oterillo II. The dental evolution of Spinosauridae seems to have resulted in robust crowns (Charig and Milner, 1997) with a reduction in the number of denticles in baryonychine spinosaurids, leading to unserrated crowns in Spinosaurinae (Charig and Milner, 1997; Buffetaut, 2011; Serrano-Martínez *et al.,* 2016). Other theropod taxa (*Ceratosaurus*, *Tyrannosaurus*) have carinae with a large number of denticles, but this is related to the great size of the crowns and the number of denticles per 5 mm is lower (Smith *et al.,* 2005; Hendrickx, 2015). The variation in denticle size along the carinae has been noted in the spinosaurids *Suchomimus* and *Baryonyx* and has been proposed as a feature of Baryonychinae (Mateus *et al.,* 2011; Hendrickx, 2015).

Fluted crowns are common in piscivorous tetrapods. The presence of flutes is characteristic of spinosaurid teeth, although they are also present in other taxa such as *Ceratosaurus* and some Dromaeosauridae (Madsen and Welles, 2000; Hendrickx and Mateus, 2014b). *Baryonyx* tends to have flutes restricted to one side of the crown (Charig and Milner, 1997), whereas *Suchomimus* shows flutes on both sides (Sereno *et al.,* 1998; Hendrickx, 2015).

Transverse and marginal undulations are a common feature of theropod teeth and have a widespread distribution among theropods (Brusatte *et al.,* 2007); they have been seen in spinosaurid theropods such as *Baryonyx*, *Irritator* and *Suchomimus* (Hendrickx, 2015) and in other indeterminate spinosaurid teeth (Canudo *et al.,* 2008a). The teeth studied here have a veined enamel texture (sensu Hendrickx *et al.,* 2015c). A veined enamel texture comprising alternating grooves and long sinuous ridges (Hendrickx *et al.,* 2015c) characterizes spinosaurid teeth; it has been found in *Baryonyx*, *Suchomimus*, *Spinosaurus* and other indeterminate spinosaurids (Canudo *et al.,* 2008a; Serrano-Martínez *et al.,* 2016).

This conjunction of dental features indicates that these teeth from El Oterillo II belong to Spinosauridae. The family Spinosauridae has been divided into two subfamilies: Baryonychinae and Spinosaurinae. Baryonychine teeth have an ornamentation based on ridges, a cross-section that is not as subcircular as in spinosaurine teeth, and a more pronounced distal curvature of the crown (Canudo *et al.,* 2008a; Alonso and Canudom 2016). Spinosaurine teeth also tend to have unserrated carinae, as in *Irritator*, *Angaturama* and *Spinosaurus* (Stromer, 1915; Kellner and Campos, 1996; Sues *et al.,* 2002; Hendrickx, 2015). In addition, the sporadic variation in size of denticles has been proposed as a feature of Baryonychinae (Mateus *et al.,* 2011).

DFA (CD) classifies MDS-OTII,99 as a member of the group Baryonychinae with 100% probability. The cladistic analysis (Appendix 5) places this morphotype as the sister taxon of a clade composed of all other spinosaurid theropods (S*pinosaurus, Irritator, Baryonyx* and *Suchomimus*). The teeth belonging to Baryonychinae indet. from El Oterillo II show no significant dissimilarity with respect to other baryonychines from the Iberian Peninsula (Torcida Fernández-Baldor *et al.,* 1997, 2003; Ruiz-Omeñaca *et al.,* 1998; Infante *et al.,* 2005; Canudo *et al.,* 2008a; Gasca *et al.,* 2008; Mateus *et al.,* 2011; Figueiredo *et al.,* 2015; Alonso and Canudo, 2016).

TETANURAE Gauthier 1986.

Tetanurae indet. cf. Carcharodontosauria.

Material Six teeth (MDS-OTII,75; MDS-OTII,77; MDS-OTII, 78; MDS-OTII,92; MDS-OTII,93; MDS-OTII,95).

Description

Four crown fragments and two teeth (MDS-OTII, 78 and MDS-OTII,92) belong to this morphotype. The two teeth are almost complete so the description is based on them. These teeth have horizontal fractures and are missing parts of the crown. Some areas lack enamel, and other parts of the teeth are broken or absent. The crowns have a labiolingually compressed and distally curved ziphodont morphology (**Fig. 4**).

Fig. 4: Tetanurae indet. cf. Carcharodontosauria. MDS-OTII,92 in a) labial, b) lingual, c) mesial, d) distal, e) basal views. f) detail of the apex and denticles of mesial and distal carinae. g) marginal undulations. MDS-OTII,78 in h) labial, i) lingual, j) mesial, k) distal and l) basal views, m) distal denticles.

The crowns are labiolingually compressed (CBR = 0.4) and moderately ellongated (CHR around 2.3). The apex is distally oriented and extends beyond the basal length. The mesial profile of the crown in lateral view is convex and the distal margin is concave. The distal profile of the crown is sigmoidal. The labial and lingual surfaces are convex; the enamel extension is similar on the lingual and labial sides.

The crowns have well-developed, serrated carinae on both margins. The distal carina is displaced labially. The distal carina reaches the cervix; the mesial carina extends along 2/3 of its margin, finishing before the cervix. The mesial carina is diagonally oriented and the distal carina is sigmoidal. The cross-section of the crowns is lanceolate at the level of the cervix and lenticular at the mid-level.

The crowns have a similar denticle number on both carinae, between 19 and 21 denticles per 5 mm. The DSDI has a value of around 1. The denticles show a regular variation in size and they are smaller at the apex and base and larger in the central area. The denticles are chisel-shaped and proximodistally subrectangular. They are perpendicularly positioned towards the carinae. The marginal contour of the denticle is convex and parabolic. The interdenticular space is broad and the diaphysis is not clearly visible due to the state of preservation. The interdenticular slit is concave. There are interdenticular sulci on both mesial and distal carinae; these are short, straight and basally inclined.

There are spalled surfaces on the apex of the crown. Wear facets are not observed and the teeth have no flutes. There are marginal and transversal undulations, which are abundant and horizontally oriented. They are more visible at a certain angle. The enamel texture is braided (sensu Hendrickx *et al.,* 2015c), and the braids are straight in the middle part of the crown and inclined towards the carina at the margin.

Some parts of the root are preserved. The root has a similar width to the crown and is labiolingually compressed. There is no constriction between the crown and the root. The root has depressions both on its labial and lingual sides, giving it a figure-eight-shaped cross-section. The dentine width in this part of the root has values around 1.6–1.9 mm.

Discussion

By comparison with the dental features proposed by Hendrickx (2015), these teeth have no basal constriction. The CBR is lower than 0.64, suggesting that they are lateral teeth due to their lateral compression. The crown height is less than 70 mm, and they are serrated both on mesial and distal carinae.

The mesial carina of this morphotype does not reach the cervix. This trait is seen in Megalosauridae (Hendrickx *et al.,* 2015b), *Eoraptor, Neovenator* (Hutt *et al.,* 1996), *Australovenator* (White *et al.,* 2015), basal tyrannosauroids such as *Alioramus* (Brusatte *et al.,* 2012), Therizinosauria and Microraptorinae, and it is also seen in *Acrocanthosaurus* and *Dromaeosaurus* (Hendrickx, 2015).

The distal carina of these teeth seems to be displaced labially. A strongly displaced distal carina has been observed in several theropod clades, such as Ceratosauridae, Allosauroidea and Tyrannosauroidea (Hendrickx, 2015). Nevertheless, this morphotype does not present the distal carina at the level of the labial margin. Teeth with a weak displacement of the distal carina have been identified in the whole dentition of Abelisauridae (Hendrickx and Mateus, 2014b) and Megalosauroidea and in the lateral dentition of Metriacanthosauridae, Neovenatoridae, Tyrannosauroidea and in neocoelurosaurs except *Dromaeosaurus* (Hendrickx, 2015). This weak displacement is more congruent with the morphotype's displacement.

Another significant characteristic of these teeth is the presence of transversal and marginal undulations, a widespread feature among non-neocoelurosaur averostrans (Brusatte *et al.,* 2007; Hendrickx and Mateus, 2014b). They also have interdenticular sulci, another trait present in nonneocoelurosaur averostrans. The braided texture of the enamel, present in non-neocoelurosaur neotheropods, can be observed in Megalosauroidea, Allosauroidea, Tyrannosauroidea and basal Ceratosauria (Hendrickx, 2015).

The characteristics seen in this morphotype are shared by many different theropod clades. Nevertheless, these traits are more specifically found in basal tetanurans such as megalosaurids or carcharodontosaurian theropods. The presence of non-spinosaurid basal tetanurans is known in the Early Cretaceous deposits of Western Europe (Hutt *et al.,* 1996; Pereda-Suberbiola *et al.,* 2012; Csiki-Sava *et al.,* 2016). The Iberian Peninsula record has one of the bestpreserved tetanurans of the Early Cretaceous, *Concavenator corcovatus* from the upper Barremian of Cuenca (Ortega *et al.,* 2010). Other evidence of carcharodontosaurian theropods comes from the Barremian deposits of Teruel (Gasca *et al.,* 2014a), where a distal femur with affinities to *Acrocanthosaurus* has been found.

Other carcharodontosaurian theropod remains have been found in the Weald of England, an example being *Neovenator*. Related theropods, such as *Fukuiraptor*, are represented in Asian sediments from this age (Azuma and Currie, 2000). The presence of carcharodontosaurid theropods in north Africa is also well-known (e.g. Fanti *et al.,* 2014).

The DFA analyses classify these teeth as *Erectopus* (41-50, 33.4-43.5 and 35.4-43.3% probability, CD). *Erectopus* is an enigmatic theropod with allosauroid affinities from the Lower Cretaceous (lower Albian) of France (Allain, 2005). Some differences exist between this morphotype and the dentition of *Erectopus*: the serrated mesial and distal carinae of *Erectopus* run along the entire margins; moreover, the denticle density is slightly different. Notably, the small size of the *Erectopus* group could have had a negative effect on the DFA analyses.

On the other hand, the cladistic analysis (Appendix 5) places this morphotype as the sister taxon of *Afrovenator* and includes it within the clade Megalosauridae. Despite the size differences, they share some features, including a mesial carina terminating well above the cervix, the presence of enamel undulations, short interdenticular sulci, similar CBR values and similar morphology (Hendrickx *et al.,* 2015b).

The traits present in this El Oterillo II morphotype show a variety of affinities with some of the basal tetanuran clades. Due to the degree of uncertainty, we attribute this morphotype to Tetanurae indet. cf. Carcharodontosauria, since the presence of megalosaurid theropods, unlike that of carcharodontosaurian theropods, is not known in the Barremian or Early Cretaceous of Spain. Megalosaurids are well-known in the Upper Jurassic of the Iberian Peninsula (e.g. Malafaia *et al.,* 2017c). However, the discrepancy with respect to the cladistic analysis suggests that this conclusion should be taken with caution until new material is found.

If these teeth belong to theropod dinosaurs other than carcharodontosaurid carcharodontosaurians, this means that the palaeobiodiversity of the theropods of the Early Cretaceous of Spain could be greater than previously thought (Gasca *et al.,* 2014a), including spinosaurids, diverse non-spinosaurid basal tetanurans such as carcharodontosaurids (Ortega *et al.,* 2010; Gasca *et al.,* 2014a) and other clades (Canudo *et al.,* 2006), ceratosaurs (Sánchez-Hernández and Benton, 2014) and different coelurosaurs such as ornithomimosaurs (Pérez-Moreno *et al.,* 1994), maniraptorans and birds (Sanz *et al.,* 1988; Lacasa-Ruiz, 1989; Sanz and Buscalioni, 1992; Sanz *et al.,* 1996; Sereno, 2000). Nevertheless, further work is required to find more diagnostic skeletal remains in order to clarify this question.

TETANURAE Gauthier 1986.
COELUROSAURIA von Huene 1914.
Coelurosauria indet.

Material One tooth (MDS-OTII,82).

Description

MDS-OTII,82 is an incomplete crown which lacks the apex and the basalmost part. The surface shows horizontal fractures. Some parts of the enamel are missing (**Fig. 5**).

MDS-OTII,82 is a labiolingually compressed (CBR=0.46), distally curved and moderatelly ellongated ziphodont crown (CHR = 1.85). The apex extends beyond the basal length. The mesial lateral profile of the crown is convex, and the distal lateral profile concave. The crown is slightly curved towards the lingual side in distal view. The labial and lingual surfaces are slightly convex; the preserved enamel shows a constant extension along the crown.

The distal carina is well developed and there is no mesial carina, and the possibility of its loss due to abrasion cannot be ruled out. The distal carina runs along the whole distal margin. The carina is strongly displaced labially. There are no concave surfaces adjacent to the carina, but there are shallow depressions both in the labial and basalmost lingual areas of the crown, conferring a figure-eight-shaped crosssection At the level of the mid-crown the cross-section is lanceolate. The distal carina has 15 denticles per 5 mm. The variation in size of the denticles along the carina is regular, with the larger denticles located in the middle part and decreasing in size towards the base. The denticles are chiselshaped and are proximodistally subrectangular. They are perpendicular to the carina. The exterior margin of the denticle is convex and parabolic. The interdenticular space is broad. The interdenticular slit is concave, and there are interdenticular sulci both on labial and lingual sides. The sulci are short, straight and inclined towards the base.

There is a possible wear facet on the lingual side of the crown. The exposed dentine shows diagonal scratches that are mesioapically-distobasally oriented. The crown has no flutes. There are abundant transversal and marginal undulations, horizontally oriented and with the concavity pointing to the apex. The undulations are visible at a certain angle and cover most of the enamel surface. The original enamel texture seems to be braided. This is difficult to assess due to the polished enamel and the microscratches that cover the tooth surface. The root is not preserved.

Fig. 5: Coelurosauria indet. MDS-OTII,82. a) labial, b) lingual, c) mesial, d) distal, e) basal view. f, g) Denticles and marginal enamel undulations of the distal carina. h) MDS-C15,7 in labial view. i) MDS-C15,6 in lingual view.

Discussion

This tooth has a series of interesting traits, most notably the figure-eight-shaped cross-section and the distal carina that is strongly displaced labially. This is not the only tooth from the Salas the los Infantes area with these features. Two other teeth from the Early Cretaceous have been recovered from the Tenadas de la Rosada site: MDS-C15,6 and MDS-C15,7 (Torcida Fernández-Baldor *et al.,* 2003) (**Fig.5**). The distal carina that is strongly displaced labially is seen in the whole dentition in ceratosaurids, allosaurids, tyrannosauroids and some dromaeosaurids (Hendrickx, 2015). The figure-of-eight shape is produced by the presence of two depressions in the basalmost part of the crown. This has been noted in the metriacanthosaurid *Sinraptor* (Hendrickx, 2015) and in coelurosaurian theropods. The figure eight- shaped cross-section is seen in *Berberosaurus* (Hendrickx and Mateus, 2014b), dromaeosaurids such as *Saurornitholestes* (Currie *et al.,* 1990; Sankey *et al.,* 2002), *Tsaagan* (Norell *et al.,* 2006), *Pyroraptor* (Allain and Taquet, 2000; Gianechini *et al.,* 2011, Hendrickx and Mateus, 2014b) and *Buitreraptor* (Gianechini *et al.,* 2011; Hendrickx and Mateus, 2014b), and other taxa such as *Richardoestesia* (Currie *et al.,* 1990) and troodontids such as *Byronosaurus* and *Xixiasaurus* (Hendrickx, 2015). Given the size of MDS-OTII,82, it is reasonable to look for another non-maniraptoran theropod as the possible owner. The lateral teeth of *Sinraptor* have a concave surface adjacent to the distal carina in the labiobasal part of the crown, which this morphotype does not possess. The figure-eight-shaped cross-section has been noted among the basal tyrannosauroids *Proceratosaurus* (Rauhut *et al.,* 2010) and *Alioramus* (Brusatte *et al.,* 2012; Hendrickx, 2015). Megaraptorans such as *Megaraptor*, *Orkoraptor* (Porfiri *et al.,* 2014) and *Australovenator* (White *et al.,* 2015) have been reported to share this trait for the lateral dentition. Unlike this morphotype, *Proceratosaurus* teeth show a significant difference in size between mesial and distal denticles (Rauhut *et al.,* 2010) (MDS-C15,7 preserves the mesial carina, which shows a similar number to the distal carina). This morphotype shows certain affinities with the teeth of *Alioramus altai*. The number of denticles is similar (14–15 denticles per 5 mm); the distal carina is deflected labially and the mesial carina lingually; and there are enamel undulations and interdenticular sulci (Brusatte *et al.,* 2012). Compared with *Alioramus*, the mesial carina is shorter.

The teeth from *Orkoraptor* and *Megaraptor* have strongly curved, low crowns and unserrated mesial carinae (Porfiri *et al.,* 2014) whereas this morphotype could have a denticulated mesial carina. The teeth from *Murusraptor* (Coria and Currie, 2016) also have a similar outline but the carinae are centrally positioned.

As seen in *Australovenator*, the morphotype from El Oterillo II could lack mesial denticles or have a reduced mesial carina; it also has transverse undulations and a similar number of denticles (around 15 per 5 mm) (White *et al.,* 2015). Despite these similarities some differences exist: The tooth from El Oterillo II does not show the lingual deviation of the distal carina and it has interdenticular sulci; marginal undulations of the enamel are also present.

DFA (CD) locates this morphotype within Megalosauridae (<47%). Given the poor results, this must be taken with caution. Megalosaurid teeth do not have the figure-eight-shaped cross-section, so this result could be a consequence of the size-dependent classification of this type of analysis. The cladistic analysis (Appendix 5) recovers the morphotype in a polytomy with tyrannosauroids, *Sinraptor, Piatnitzkysaurus* and *Erectopus*. The pruning of the morphotype from the consensus tree increased the resolution of the consensus (Appendix 5) and is either recovered as the sister taxon of *Piatnitzkysaurus*, as the sister taxon of *Sinraptor* or within tyrannosauroids. This morphotype lacks the concave surface adjacent to the distal carina that appears on *Sinraptor.* In addition, *Piatnitzkysaurus* and *Sinraptor* are Jurassic taxa, so here we consider that the most likely producer was an unknown coelurosaurian.

Given the uncertainty, this tooth has been classified as Coelurosauria indet. so as not to exclude the possibility of it being produced by a basal tyrannosauroid, a large maniraptoran or a megaraptorid theropod. The position of Megaraptora among theropods is currently a subject of discussion, with a suggested placement within Neovenatoridae or Tyrannosauroidea (Hendrickx *et al.,* 2015c). The phylogenetic analyses run by Coria and Currie, (2016) on two alternative data matrices based on the dataset of Carrano *et al.,* (2012) plus the modifications by Zanno and Makovicky, (2013), and the dataset of Novas *et al.,* (2013) plus the modifications by Porfiri *et al.,* (2014), show Megaraptora positioned within Neovenatoridae or as the sister group of Tyrannosauridae. Bell *et al.,* (2016) also state that the position of Megaraptora remains equivocal. Here we prefer to consider Megaraptora within Tyrannosauroidea in order to include all the possible owners of the morphotype within the clade Coelurosauria, as in the phylogeny of Hendrickx *et al.,* (2015c).

This morphotype could represent a singular taxon of coelurosaurian theropods from the Early Cretaceous of the Iberian Peninsula. The presence of basal tyrannosauroids is known in the deposits of the Upper Jurassic-Lower Cretaceous of Western Europe, especially England and Portugal (Hutt *et al.,* 2001), with genera such as *Proceratosaurus* and *Eotyrannus*. Megaraptorans have been found in Asia, Australia and South America (Bell *et al.,* 2016). The possible presence of these taxa opens a new scenario including more diverse theropods than previously thought. Nevertheless, new information is required to corroborate the distribution of these clades in the Early Cretaceous of the Iberian Peninsula.

TETANURAE Gauthier 1986.

COELUROSAURIA von Huene 1914.

MANIRAPTORA Gauthier 1986.

PARAVES Sereno 1997.

Dromaeosauridae Matthew and Brown 1922.

Dromaeosauridae indet. 1.

Material Three teeth (MDS-OTII,73; MDS-OTII,100; MDS-OTII,102).

Description

The crowns are well preserved. Some parts of the carinae and enamel are missing and they may bear horizontal fractures. The teeth have a ziphodont morphology; they are labiolingually compressed and distally curved (**Fig. 6**). The crowns are small (CH = 4–14 mm). The CBR values are around 0.5. The elongation of the crowns varies among weak-normal values according to Hendrickx and Mateus, (2014b) (CHR = 1.4–1.9). The crowns are curved and the apex extends beyond the basal length. The mesial lateral profile of the crowns is convex and the distal lateral profile is slightly concave, almost straight. The labial and lingual surfaces are convex. The distal profile is straight and the enamel shows a constant extension along the crown.

The teeth have mesial and distal carinae. The carinae are serrated and are located in central positions along the mesial and distal margins. The distal carina reaches the cervix, whereas the mesial carina only extends along the apical half of the crown. Carinae run along the tip of the crown. The outline of the teeth at the level of the cervix has a lanceolate morphology. The cross-section at the midlevel is lenticular.

The mesial carina has around 30–35 denticles per 5 mm, whereas the distal carina has 20 denticles per 5 mm. The mesial denticles are smaller (DSDI = 1.5–1.8) than the distal ones. The largest denticles on the mesial carina are located on the apex and decrease towards the base. The largest denticles on the distal carina are on the basalmost part of the crown. The variation in denticle size is regular. The denticles are chisel-shaped and are proximodistally subrectangular. The denticles are located perpendicular to the carina. The external margin has a convex outline. The interdenticular space is broad and the interdenticular slit is concave and shallow. There are no interdenticular sulci.

There are spalled surfaces on the tips of the crowns. MDS-OTII,102 also has a possible wear facet on the lingual side of the crown. There are some transversal undulations on the

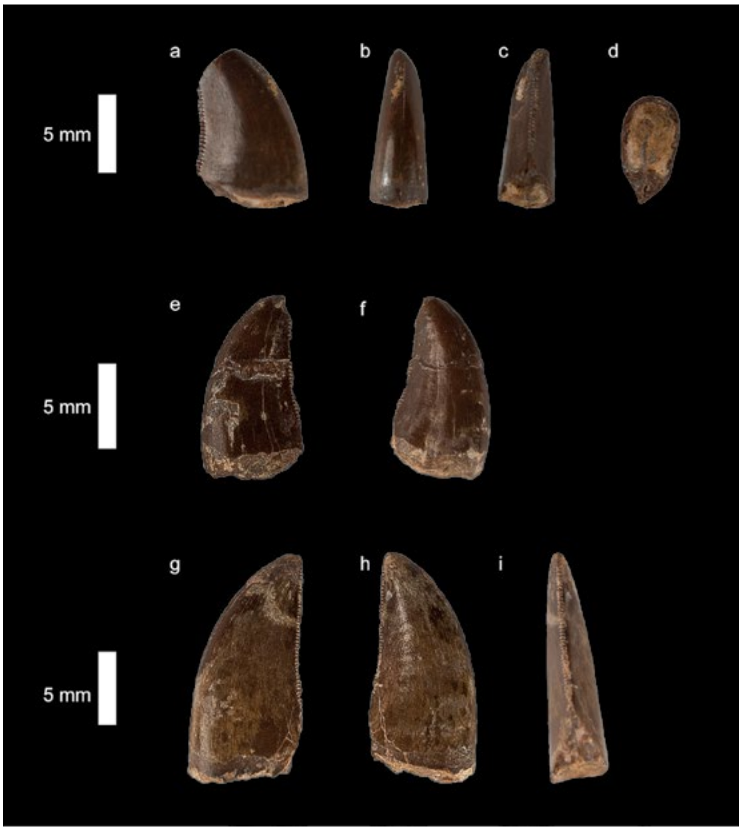


Fig. 6: Dromaeosauridae indet. 1. MDS-OTII,102 in a) lateral, b) mesial, c) distal and d) basal views. e, f) MDS-OTII,73 in lateral views. MDS-OTII,100 in g, h) lateral and i) distal view.

enamel surface. The undulations are horizontally oriented and are visible at a certain angle. The enamel texture is polished and smooth in some parts of the crown, but the original texture seems to be irregular. The root is not preserved.

Discussion

Small teeth size and high DSDI values have usually been considered typical of dromaeosaurid dentition. However, a DSDI greater than 1.2 is present in various clades of theropods, including Noasauridae, Piatnitzkysauridae, Tyrannosauroidea, Microraptorinae and Eudromaeosauria (Rauhut *et al.,* 2010; Hendrickx, 2015). The DFA (CD) with mesialmost dentition includes this morphotype (<50%) within Dromaeosauridae, with the exception of MDS-OTII,102, which is reclassified as a basal tyrannosauroid. This is not unusual, given the similarities that some tyrannosauroids and dromaeosaurids show in their dentition (Rauhut *et al.,* 2010; Hendrickx and Mateus, 2014b; Gerke and Wings, 2016). The DFA without the mesialmost dentition classified all the teeth as Dromaeosauridae (around 40% probability). The cladistic analysis (Appendix 5) likewise recovers the morphotype in a polytomy among other dromaeosaurids.

The presence of dromaeosaurid theropods in the Salas de los Infantes area has been cited before (Torcida Fernández-Baldor *et al.,* 2003). Theropod teeth from the Wealden facies of England have been attributed to dromaeosaurids (see for example Milner, 2002 and Sweetman, 2004). In the light of the convergence of results between the analyses, we thus classify the teeth as Dromaeosauridae indet.

Dromaeosauridae indet. 2.

Material Two teeth (MDS-OTII,91; MDS-OTII,101).

Description

The crowns are well preserved. Some parts of the carinae and enamel are missing. MDS-OTII,91 also lacks part of the base and apex. The crowns are small (4–8 mm). They have ziphodont morphology (**Fig.** 7). The CBR values are 0.4–0.5. The elongation of the crowns is normal (1.5-1.8). The crowns are distally curved with the apex extending beyond the basal length, and they are low and squat in appearance. The mesial lateral profile is convex, and the distal lateral profile slightly concave-almost straight. The labial and lingual surfaces are slightly convex. MDS-OTII,101 has serrated mesial and distal carinae. MDS-OTII,91 lacks the mesial carina. The carinae are located in central positions along the margins. The distal carina reaches the cervix but the mesial carina does not, for it only extends along the apical half of the crown. The carinae of MDS-OTII,101 cross the apex. The cross-section at the level of the cervix is figure-eight-shaped. At the level of the mid-crown the cross-section is lenticular.

These teeth have a large number of denticles along the carinae. The mesial carina has an estimated number of 45 denticles per 5 mm whereas the distal carina has 35 denticles per 5 mm. The largest denticles on the distal carina are located in the basalmost part, and the largest on the mesial carina are on the apex. The variation in size of the denticles is smooth and regular. The denticles have a chisel-shaped morphology, they are proximodistally subrectangular and they are located perpendicular to the carina. The external margin of the denticle is symmetrically convex. They have a broad interdenticular space; the interdenticular slit is concave and shallow. Interdenticular sulci have not been observed.

There are spalled surfaces on the tips of the crowns. The crowns also have transversal undulations on the surface of the basal and central areas; these are visible at a certain angle. The enamel texture of MDS-OTII,101 is smooth. MDS-OTII,91 has a braided enamel texture. The root is not preserved.

Fig. 7: Dromaeosauridae indet. 2. MDS-OTII,101 in a, b) lateral and c) basal view. MDS-OTII,101 in d, e) lateral, f) mesial, g) distal and h) basal view.

Discussion

As noted for the previous morphotype, the small size of the crowns and the high DSDI have often been considered dromaeosaurid characters. Nevertheless, these features are shared by other theropod groups (Rauhut *et al.,* 2010; Hendrickx and Mateus, 2014b). Unlike Dromaeosauridae indet.1, Dromaeosauridae indet. 2 possess a figure-eight-shaped cross-section, which is present in metriacanthosaurids, tyrannosauroids, *Berberosaurus*, megaraptorans and dromaeosaurids (Hendrickx, 2015).

The DFA analyses (CD) recover MDS-OTII,91 as belonging to *Richardoestesia* (51%, 50.9%, 59.8%) and MDS-OTII,101 as belonging to *Nuthetes* (44.9, 57 and 39.3%). *Richardoestesia* is a genus from the Late Cretaceous of North America (Currie *et al.,* 1990; Baszio 1997; Sankey *et al.,* 2002). Material from the Upper Jurassic of Portugal (Zinke, 1998; Hendrickx and Mateus, 2014b), the Lower Cretaceous of Spain (Rauhut, 2002), the Upper Cretaceous of Spain (Torices *et al.,* 2004, 2015) and the Upper Cretaceous of Romania (Codrea *et al.,* 2002; Weishampel *et al.,* 2010) has been referred to this taxon. MDS-OTII,91 shares the figure-eight-shaped cross-section, but the basal constriction is not observed. *Nuthetes* is a possible dromaeosaurid taxon from the Early Cretaceous of England (Milner, 2002). One tooth from the Lower Cretaceous deposits of France has been cited as *Nuthetes* sp. (Pouech *et al.*, 2006). These teeth share the small-sized crowns, which are strongly distally recurved, and smaller denticles on the mesial carina and the basal surfaces.

The cladistic analysis (Appendix 5) recovers these teeth in a polytomy with dromaeosaurids, *Compsognathus, Piatnitzkysaurus, Erectopus* and *Eodromaeus*. A reduced strict consensus was calculated using the pruning trees option in TNT. The new consensus recovers this morphotype as the sister taxon of *Eodromaeus* or within dromaeosaurids. We consider that it is unlikely that this morphotype was produced by a basal theropod so here we consider it as dromaeosaurid teeth. Given the similar morphologies among dromaeosaurid teeth, here we prefer not to assign this morphotype to a specific genus. Instead, we classify these teeth as Dromaeosauridae indet. The possibility that the difference between Dromaeosauridae indet.1 and Dromaeosauridae indet. 2 (the variation in cross-section) is due to variations in the position of the tooth row cannot be ruled out.

4 TOOTH MARKS

Some bones belonging to the El Oterillo II titanosauriform present unusual marks on their surface. Marks on the surface of bones are known among dinosaurs and they can be related to traumas, predation and scavenging. Marks due to predatory behaviour are difficult to prove, but sometimes it is possible to identify possible evidence in the fossil record (Carpenter, 1998; Canudo *et al.,* 2005b; Cruzado-Caballero, 2012; DePalma *et al.,* 2013). Hunt *et al.,* (1994) distinguish between the marks produced by predatory and scavenging behaviour. Multiple, related marks are typical of scavenging on a stationary carcass. Living organisms try to avoid bites and consequently the marks appear more isolated and separated from each other, due to the movement of the prey. Also scavenger animals try to eat first the parts with high concentrations of soft tissues.

Different bioerosion traces have been recognized on the titanosauriform bones (**Fig. 8**). The marks are scarce and have been identified on vertebral elements: a dorsal vertebra (MDS-OTII,1), a caudal vertebra (MDS-OTII,8) and a haemal arch (MDS-OTII,25). The dorsal vertebra MDSOTII, 1 has a few unusual marks. The most apparent is a subcircular mark (**Fig. 8a**) located on the left spinopostzygapophyseal lamina perpendicular to the surface. The orifice is 12-14 mm in diameter and about 10 mm in depth; it has parallel sides. Subcircular morphologies are often attributed to invertebrates (Britt *et al.,* 2008; Cruzado-Caballero, 2012). Another mark is located on the prezygapophysis. This mark (**Fig. 8b**) has furrow morphology. The furrow comprises an irregular trace, 20 mm in length, 4-7 mm in width, and 2-5 mm in depth. Interestingly, it remains isolated and there is no other evidence in the surrounding area. Other possible tooth marks are located on the distolateral part of the vertebral centrum, opposite the caudal surface. This area has two parallel grooves with v-shaped sections, both of them 21 cm long and 3 mm deep.

MDS-OTII,25 is a haemal arch. It has one trace (**Fig. 8c**), 24 mm long, 8 mm wide and 2 mm deep, located on the spine.

The caudal vertebra MDS-OTII,8 has five different marks. The first one (**Fig. 8d**) is located on the left lateral side of the vertebral centrum. The puncture is 15 mm in length and 8 mm in width. Interestingly, it has an oval outline. The preserved depth is 5 mm but the interior has been filled with sediment. The oval outline and dimensions are congruent with the cross-section of theropod teeth found in the site, specifically with basal tetanurans. Moreover, there is a set of furrows (**Fig. 8e**) located on the left lateral surface of the neural spine. The arrangement of the marks resembles the letter lambda (λ), with a long trace 45 mm in length and two related smaller traces of 25 and 17 mm. The width of the furrows is 5 mm and the section is u-shaped. These marks could have been produced by invertebrates. The lateral left side of the postzygapophysis also has a diagonally oriented furrow (**Fig. 8e**). This is 17 mm in length, 2 mm in width and 2 mm in depth.

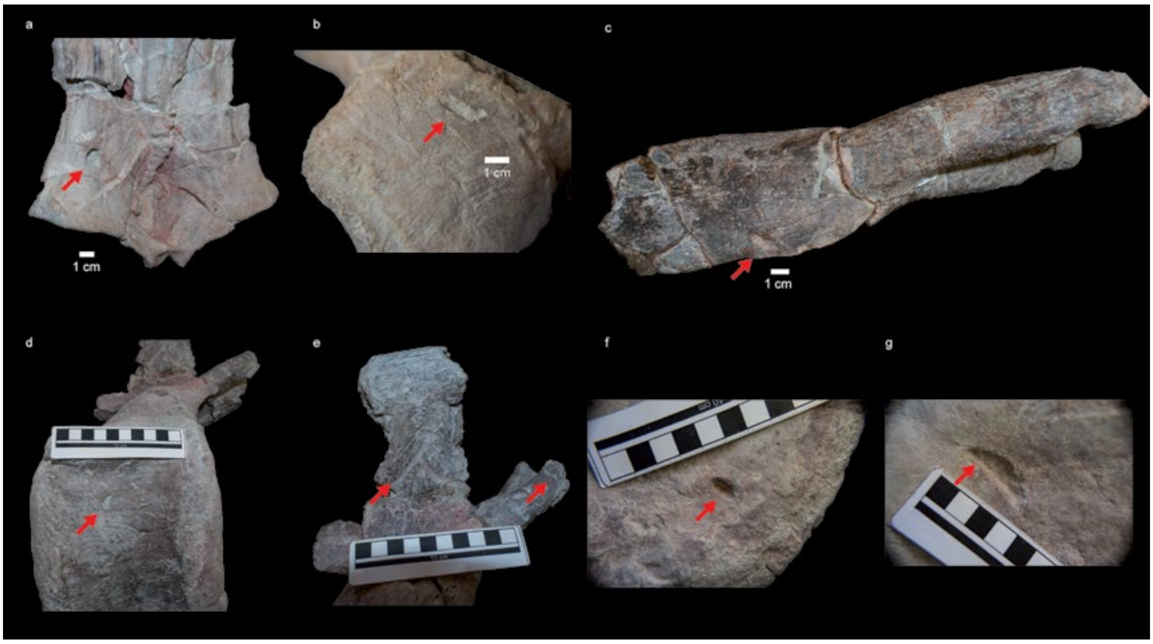


Fig. 8: Marks. a subcircular orifice on the left spinopostzygapophyseal lamina of MDS-OTII,1. b Furrow on the prezygapophysis of MDS-OTII,1. c Furrow on MDS-OTII,25. d Puncture on the left lateral side of the caudal vertebra MDS-OTII,8. e Furrows on the left lateral surface of the neural spine of MDS-OTII,8. f Puncture on the articular surface of MDS-OTII,8. g Possible mark on the articular surface of MDS-OTII,8.

The caudal surface of the centrum shows two additional marks. There is a puncture (**Fig. 8f**) in the lower right area, 18 mm in length and 6 mm in width. As in the other puncture, the interior is filled with sediment. The outline of the puncture is oval. Like the lateral mark, the morphology is congruent with some of the teeth recovered in this site. The upper left part of the caudal surface also has a furrow (**Fig. 8g**), which is diagonally oriented.

It is 36 mm in length, 12 mm in maximum width and 6.5 mm in depth. The right side of the furrow is convex and the left side is concave.

5 DISCUSSION

The feeding of theropod dinosaurs on carcasses has been proposed by some authors due to the accumulation of isolated teeth or the presence of tooth marks on the surface of the bones, specifically on sauropod remains (Buffetaut and Suteethorn, 1989; Chure *et al.,* 1998; Canudo *et al.,* 2009; Paik *et al.,* 2011; Canale *et al.,* 2014b) as well as other remains (Fiorillo, 1991; Currie and Jacobsen, 1995; Maxwell and Ostrom, 1995; Erickson and Olson, 1996; Jacobsen, 1998; Rogers *et al.,* 2003; Bell and Currie, 2010; De Valais *et al.,* 2012). Feeding seems the most parsimonious explanation for the accumulation of theropod teeth around the carcass.

Most of the teeth from El Oterillo II only preserve the crown or the crown and the basalmost part of the crown, and most likely represent shed teeth (Fiorillo and Currie, 1994). This is congruent with them being lost when processing food (Hendrickx *et al.,* 2015c).
The scarcity of tooth marks among the examined bones is remarkable. There are no multiple tooth marks as seen in other dinosaur bones (e.g. Erickson and Olson, 1996; Jacobsen, 1998; Paik *et al.,* 2011). A possible explanation is the presence of soft tissues when the scavenging was occurring, thus protecting the bone surface. Some of the tooth marks are located on articular surfaces, meaning that they could not have been made when the sauropod was alive and are not related to predatory behaviour. The presence of these traces on articular surfaces suggests that the feeding could have contributed to the partial disarticulation of the sauropod (Buffetaut and Suteethorn, 1989).

The sauropod remains are located on channel deposits, and the westbound trend and the accumulations of sand on the eastern part of the bones suggest the presence of water currents when the sauropod remains were deposited. The presence of water also influences the disarticulation of the titanosauriform dinosaur along with the theropods. The degree of disarticulation of the bones suggests that the channel was not a high-energy environment.

Another possible explanation for the presence of theropod teeth could be transport along the channel (Torcida Fernández-Baldor *et al.,* 2009). This could be congruent with the presence of quartzite clasts of similar size and density. In addition, Argast *et al.,* (1987) show that fossilized theropod teeth could resist long periods of transportinduced abrasion. However, a few points contradict this interpretation, at least for most of the teeth. The presence of well-preserved enamel textures in some of the teeth is not congruent with transport-induced abrasion. Further, a polished enamel surface does not necessarily mean that the tooth was transported; it could be caused by tooth wear (Hendrickx and Mateus, 2014b).

The experimental procedure of Argast *et al.,* (1987) provides an explanation for the presence of Tertiary theropod teeth but may not be applicable to the present case because the experiment was performed with fossilized teeth. Fossilized teeth may not actually be homologous to recent, fresh teeth due to the process of mineralization, which interferes with the physical properties of the teeth, hardening them. As mentioned above, the presence of shed teeth with herbivore remains produced by scavenging is not uncommon, and this is a simpler explanation than a casual accumulation around the sauropod carcass.

The presence of tooth marks reinforces the notion of scavenging by theropod dinosaurs. Some of the marks are similar to the outline of theropod teeth both in dimensions and morphology, and could be related to teeth similar to the Tetanurae and Coelurosauria morphotypes, attributed to medium-sized tetanurans.

Theropod teeth are distributed all over El Oterillo II site. There is a major accumulation in the southern part of the site. Most of the dromaeosaurid teeth are located in the northern part close to fragmented bone remains. A preferred orientation has not been recorded.

The scarcity of tooth marks on the bones is intriguing. A possible explanation is their rapid burial when the carcass was deposited, preventing a greater exploitation of the remains and a further disarticulation of the skeleton. The sudden burial of dinosaur remains has been proposed by Gianechini and De Valais, (2016) as a possible explanation of the semi-articulation of the remains of *Buitreraptor*.

6 CONCLUSIONS

Isolated theropod teeth related to a titanosauriform sauropod carcass have been studied. Six different morphotypes have been distinguished, including baryonychine spinosaurids, basal tetanurans, a singular tooth that could be related to basal coelurosaurian theropods, and two dromaeosaurid morphotypes. This is congruent with the known record of theropods from the Early Cretaceous of the Iberian Peninsula, represented by spinosaurids, carcharodontosaurians, ornithomimosaurians and maniraptorans such as dromaeosaurids and birds, as well as with the European Wealden record, with carcharodontosaurians such as *Neovenator* and tyrannosauroids such as *Eotyrannus*. The possibility of the presence of tyrannosauroids, represented by Coelurosauria indet., raises new questions about the distribution of these groups and points to a greater palaeobiodiversity of theropods than previously thought.

The relationship between the isolated theropod teeth and a sauropod carcass has been studied. Given the presence of shed teeth and tooth marks, the most probable explanation for the association seems to be the scavenging of the carcass by theropod dinosaurs. An exhaustive work identifying the tooth marks on the sauropod is required in order to understand this relationship more fully. The diversity of theropod tooth morphotypes suggests that a variety of different theropods exploited the sauropod remains.

CONCLUSIONES

8

1. Se han estudiado diez dientes aislados del Jurásico Superior (Kimmeridgiense) de la costa de los dinosaurios de Asturias, permitiendo la identificación de ocho morfotipos: Theropoda indet, Averostra indet. 1, 2 y 3; Abelisauridae? indet, y Megalosauridae indet. 1, 2 y 3. Este estudio representa una nueva contribución al conocimiento de los terópodos del Jurásico Superior de España.

2. Los dientes de Theropoda indet. y Averostra indet. pueden estar relacionados con terópodos de tamaño medio relacionados con allosauroideos o megalosauroideos.

3. Se plantea por vez primera la posible presencia de abelisáuridos en el Jurásico Superior de Asturias, grupo representado en otras áreas de la península ibérica como Portugal.

4. Se identifican tres morfotipos de dientes de gran tamaño relacionados con megaterópodos megalosáuridos, probablemente relacionados con *Torvosaurus* o similiares; un morfotipo de diente mesial y dos con dientes laterales. La presencia de grandes megalosáuridos en el Jurásico Superior de la península es conocida por otros restos esqueléticos y dientes aislados en Portugal, Asturias o la cordillera ibérica. La identificación de estos morfotipos supone la primera atribución de dientes aislados del Jurásico de Asturias a Megalosauridae tras un estudio estadístico y filogenético.

5. 17 dientes aislados atribuidos a terópodos espinosáuridos han sido estudiados en el yacimiento de La Cantalera 1, del Barremiense inferior de Teruel. Se han identificado dos morfotipos: Baryonychinae indet. y Spinosaurinae? indet.

6. Los dientes atribuidos a Baryonychinae indet. son muy similares a otros yacimientos del Cretácico Inferior de España salvo el tamaño. En tamaño y características son más parecidos a *Baryonyx* que a *Suchomimus*, lo que es congruente con la presencia de restos craneales atribuidos a *Baryonyx* en la península ibérica.

7. Los dientes tentativamente atribuidos a Spinosaurinae? indet. pueden suponer nueva evidencia en la presencia de este grupo en el Cretácico Inferior de la península. Hasta el momento, los restos atribuibles a este grupo son mucho más escasos que los de la subfamilia Baryonychinae.

8. El pequeño tamaño de los dientes de Baryonychinae indet. y Spinosaurinae? indet. de La Cantalera 1, junto al pequeño tamaño de restos de otros grupos como crocodilomorfos, puede suponer evidencia de un área de concentración de organismos de pequeño tamaño debido a las características del ecosistema.

9. Se han prospectado nuevas áreas de la Formación Blesa en el entorno de las localidades de Josa, Obón y Estercuel. En ésta última área se han determinado nuevos yacimientos cerca del yacimiento Barranco del Hocino 1. Se pone de manifiesto la riqueza fosilífera de la Formación Blesa, en particular de la secuencia superior, menos conocida.

10. Se ha estudiado un nuevo yacimiento localizado en el Barremiense de la Formación Blesa, Barranco del Hocino 1. Este yacimiento se formó en la secuencia superior de la formación en medios continentales aluviales, llanuras pobrementes drenadas y con presencias de agua dulce efímeras, condiciones similares a otros yacimientos de la Formación como La Cantalera 1.

11. Los restos fósiles de Barranco del Hocino 1 aparecen frecuentemente afectados por la meteorización, rotura y exposición subaérea, además de la acción de depredadores. Cuatro campañas de excavación (2015-2018), tres de ellas dirigidas por el doctorando, han permitido reconocer la diversidad de vertebrados tras recuperar unos 500 restos fósiles. La asociación está dominada por macrorrestos de dinsoaurios ornitópodos, junto a los que aparecen restos de dinosaurios tireóforos y dientes aislados de terópodo, junto a crocodilomorfos, testudines, peces óseos, numerosos coprolitos y cáscaras de huevo.

12. Se han estudiado seis dientes de terópodos de tamaño grande provenientes del yacimiento Barranco del Hocino 1. Se han identificado cuatro morfotipos: Un morfotipo de espinosáurido probablemente relacionado con Spinosaurinae, dos morfotipos de tetanuros indeterminados y un morfotipo de tetanuro basal probablemente relacionado con Carcharodontosauria, con similitudes a carcharodontosaurios de esta época como *Neovenator* del Barremiense de Reino Unido. Estos resultados ponen de manifiesto una paleobiodiversidad de terópodos mayor de la conocida, con varios espinosáuridos, carcharodontosaurios carcharodontosáuridos junto a neovenatóridos, y tetanuros derivados. La asociación es congruente con el registro de terópodos conocido del Cretácico Inferior de Europa occidental.

13. Se han estudiado dientes aislados provenientes del burgalés yacimiento de El

Oterillo II hallados en relación con la carcasa del saurópodo titanosauriforme *Europatitan eastwoodi*. Se han identificado seis morfotipos, incluyendo espinosáuridos de tipo barioniquino, tetanuros basales relacionados con Carcharodontosauria muy parecidos a los encontrados en Barranco del Hocino, un morfotipo atribuido a Coelurosauria indet. que puede representar la presencia de un tiranosauroideo o un maniraptor singular de gran tamaño; y dos morfotipos de dromeosáuridos indeterminados, de menor tamaño.

14. Debido a las características de la acumulación y la presencia de marcas de dientes en elementos vertebrales del saurópodo *Europatitan eastwoodi* se plantea la hipótesis del aprovechamiento de la carcasa del saurópodo por parte de un grupo diverso de terópodos tetanuros basales y derivados. La presencia de marcas en superficies articulares sugiere que los terópodos contribuyeron a la desarticulación del herbívoro.

15. La ausencia de marcas en abundancia en los restos óseos de *Europatitan* puede estar relacionado con un enterramiento rápido de los restos que impide un aprovechamiento más exhaustivo.

1. Ten isolated theropod teeth from the Late Jurassic (Kimmeridgian) of the dinosaur coast have been studied. Eight morphotypes have been identified: Theropoda indet., Averostra indet. 1, 2 and 3., Abelisauridae? indet. and Megalosauridae indet. 1, 2 and 3. This work represents a new contribution on the knowledge of the theropods from the Late Jurassic of Spain.

2. Theropoda indet. and Averostra indet. morphotypes could be related to medium-sized theropods close to Megalosauroidea or Allosauroidea.

3. The possible presence of abelisaurids during the Kimmeridgian of Asturias is proposed. This group appears on other areas such as the Late Jurassic of Portugal.

4. Three morphotypes of megatheropod teeth have been identified. They are probably related to megalosaurids close to *Torvosaurus* or related taxa. One morphotype comprises a mesial tooth and the other consist of lateral teeth. The presence of large megalosaurids in the Late Jurassic of the Iberian Peninsula is well-known; evidences include skeletal remains and isolated teeth from Portugal, Asturias and the Iberian Range. These morphotypes represent the first Asturias theropod teeth attribution to megalosaurid after statistic and philogenetic analyses.

5. 17 isolated spinosaurid teeth from La Cantalera 1 site (early Barremian, Teruel) have been studied. Two morphotypes have been identified: Baryonychinae indet. and Spinosaurinae? indet.

6. Except for their size, Baryonychinae indet. teeth from this site are similar to other material from the Early Cretaceous of Spain. They are more similar to *Baryonyx* than *Suchomimus*, which is congruent with the known record of craneal remains of the Iberian Peninsula that includes *Baryonyx* sp.

7. The teeth tentatively attributed to Spinosaurinae? indet. could support new evidence on the presence of this group during the Early Cretaceous of the Iberian Peninsula. So far, Spinosaurine remains are scarcer than baryonychines.

8. The small-sized teeth both from Baryonychinae and Spinosaurinae, and the small-sized remains from crocodylomorphs could be related to the characteristics that prevailed at La Cantalera-1 site, which allowed the concentration of small-sized organisms because the ecosystem could not sustain large vertebrates.

9. Prospection campaigns have been carried out around the localities of Josa, Obón and Estercuel. The latter revealed new fossiliferous sites in the area around Barranco del Hocino 1. This reveals the fossiliferous potential of the Blesa Formation, specifically the Upper Blesa sequence.

10. A new fossiliferous site from the Barremian of the Blesa Formation has been studied, Barranco del Hocino 1. The depositional environment is interpreted as an alluvial plain with evidence of shallow freshwater/palustrine episodes and the development of palaeosols, conditions that resemble those of La Cantalera 1 site.

11. The fossils have undergone intense breakage, abrasion and weathering, and also scavenging. Four fieldwork campaigns (2015-2018, three of them under the supervision of the PhD candidate) enabled us to recover roughly 500 fossil remains. The association is dominated by macroremains of ornithopod dinosaurs. In addition, ankylosaur bones, isolated theropod teeth, crocodylomorphs, testudines, fishes, coprolites and eggshells have been recovered.

12. Six teeth from large-bodied theropods have been studied. Four morphotypes have been identified: One spinosaurid morphotype probably related to Spinosaurinae, two morphotyes of indeterminate tetanurans and a basal tetanuran probably related to Carcharodontosauria. This morphotype resembles other carcharodontosaurians such as *Neovenator* from the Barremian of the United Kingdom. These results manifest a greater theropod paleobiodiversity than previously thought, including more than a single spinosaurid, carcharodontosaurid carcharodontosaurians along with neovenatorids, and a broad set of derived tetanurans. This assemblage is congruent with the known record of theropods from the Early Cretaceous of western Europe.

13. Isolated theropod teeth from El Oterillo II site (Burgos province) have been studied. These teeth have been found close to the sauropod *Europatitan eastwoodi* remains. Six morphotypes have been identified, including baryonychine spinosaurids, basal tetanurans probably close to Carcharodontosauria which resemble those from Barranco del Hocino

1, a morphotype attributed to Coelurosauria indet that could represent a singular big-sizedtyrannosauroid or maniraptoran; and two smaller dromaeosaurid morphotypes.

14. The accumulation traits and the presence of tooth marks on vertebral elements of *Europatitan eastwoodi* leads us to propose that the sauropod carcass was scavenged by a diverse group of basal and derived tetanurans. The presence of tooth marks on articular surfaces suggest that the theropods contributed to the partial disarticulation of the sauropod.

15. The scarcity of tooth marks on the bones could be explained by a rapid burial when the carcass was deposited, preventing a greater exploitation of the remains.

BIBLIOGRAFÍA

A

Abler, W. L. 1997. Tooth serrations in carnivorous dinosaurs. En P. J. Currie & K. Padian (Eds.), *Encyclopedia of dinosaurs (Vol. 8)*. San Diego: Academic Press.

Agnolín, F.L. y Novas, F.E. 2013. Avian Ancestors: A Review of the Phylogenetic Relationships of the Theropods Unenlagiidae, Microraptoria, Anchiornis and Scansoriopterygidae. En: Lohmann, G., Mysak, L.A., Notholt, J., Rabassa, J. y Unnithan (eds.), *Earth System Sicences- South America and the Southern Hemisphere*, Springer Verlag., Dordrecht, Heidelberg, New York, London.

Allain, R. 2005. The Enigmatic Theropod Dinosaur *Erectopus superbus* (Sauvage 1882) from the Lower Albian of Louppy-le-Château (Meuse, France). *The Carnivorous Dinosaurs* (September): 72-86.

Allain, R., y Taquet, P. 2000. A new genus of Dromaeosauridae (Dinosauria, Theropoda) from the Upper Cretaceous of France. *Journal of Vertebrate Paleontology*, 20(2), 404–407

Allain, R., Xaisanavong, T., Richir, P. y Khentavong, B. 2012. The first definitive Asian spinosaurid (Dinosauria: Theropoda) from the early cretaceous of Laos. *Naturwissenschaften* 99 (5): 369-377.

Alonso, A. y Canudo, J.I. 2016. On the spinosaurid theropod teeth from the early Barremian (Early Cretaceous) Blesa Formation (Spain). *Historical Biology* 28 (6): 823-834.

Alonso, A., Gasca, J.M., Navarro-Lorbés, P., Núñez-Lahuerta, C., Galán, J., Parrilla-Bel, J., Rubio, C. y Canudo, J.I. 2016. La asociación faunística de Barranco del Hocino 1, un nuevo yacimiento de vertebrados del Barremiense (Cretácico Inferior) de Teruel. *Cuadernos del Museo Geominero* 20: 303-307.

Alonso, A., Canudo, J.I., Torcida Fernández-Baldor, F. y Huerta, P. 2017. Isolated theropod teeth associated with sauropod remains from El Oterillo II (Early Cretaceous) site of Salas de los Infantes (Burgos, Spain). J*ournal of Iberian Geology* 43 (2): 193-215.

Alonso, A., Gasca, J.M., Navarro-Lorbés, P., Rubio, C. y Canudo, J.I. 2018. A new contribution to our knowledge of the large-bodied theropods from the Barremian of the Iberian Peninsula: the “Barranco del Hocino” site (Spain). *Journal of Iberian Geology* 44 (1): 7-23.

Alonso, J.L., Gallastegui, J., García-Ramos, J.C. y Poblet, J. 2009. Estructuras mesozoicas y cenozoicas relacionadas con la apertura y cierre parcial del Golfo de Vizcaya (Zona Cantábrica-Asturias). 6o Simposio sobre el Margen Ibérico Atlántico. Guía de Campo (May 2014): 18.

Amiot, R., Buffetaut, E., Lécuyer, C., Wang, X., Boudad, L., Ding, Z., Fourel, F., Hutt, S., Martineau, F., Medeiros, M.A., Mo, J., Simon, L., Suteethorn, V., Sweetman, S., Tong, H., Zhang, F. y Zhou, Z. 2010. Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods. *Geology* 38 (2): 139-142.

Antunes, M.T. y Mateus, O. 2003. Dinosaurs of Portugal. *Comptes Rendus Palevol* 2: 77-95.

Araujo, R., Castanhinha, R., Martins, R.M.S., Mateus, O., Hendrickx, C., Beckmann, F., Schell, N. y Alves, L.C. 2013. Filling the gaps of dinosaur eggshell phylogeny: Late Jurassic Theropod clutch with embryos from Portugal. *Scientific Reports* 3.

Arden, T.M.S., Klein, C.G., Zouhri, S. y Longrich, N.R. 2019. Aquatic adaptation in the skull of carnivorous dinosaurs (Theropoda: Spinosauridae) and the evolution of aquatic habits in spinosaurids. *Cretaceous Research* 93: 275-284.

Arenas, C., Piñuela, L. y García-Ramos, J.C. 2015. Climatic and tectonic controls on carbonate deposition in syn-rift siliciclastic fluvial systems: A case of microbialites and associated facies in the Late Jurassic. *Sedimentology* 62 (4): 1149-1183.

Argast, S., Farlow, J. O., Gabet, R. M., y Brinkman, D. L. 1987. Transport-induced abrasion of fossil reptilian teeth: implications for the existence of Tertiary dinosaurs in the Hell Creek Formation, Montana. *Geology,* 15(927), 930.

Arribas, J., Alonso, A., Mas, R., Tortosa, A., Rodas, M., Barrenechea, J.F., Alonso-Azcarate, J. y Artigas, R. 2003. Sandstone Petrography of Continental Depositional Sequences of an Intraplate Rift Basin: Western Cameros Basin (North Spain). *Journal of Sedimentary Research* 73 (2): 309-327.

Aurell, M., Meléndez, G., Olóriz, F., Bádenas, B., Caracuel, J.E., García-Ramos, J.C., Goy, A., Linares, A.,

Quesada, S., Robles, S., Rodríquez-Tovar, F.J., Rosales, I., Sandoval, J., Suárez de Centi, C., Tavera, J.M. y Valenzuela, M. 2002. Jurassic. In: Gibbons, W. y Moreno, T. (eds.), *The Geology of Spain*, 223-235. Geological Society, London.

Aurell, M., Bádenas, B., Canudo, J.I. y Ruiz-Omeñaca, J.I. 2004. Evolución tectosedimentaria de la Fm. Blesa (Cretácico Inferior) en el entorno del yacimiento de vertebrados de La Cantalera (Josa, Teruel). *Geogaceta* 35: 11-13.

Aurell, M., Soria, A.R., Bádenas, B., Liesa, C.L., Canudo, J.I., Gasca, J.M., Moreno-Azanza, M., Medrano-Aguado, E. y Meléndez, A. 2018. Barremian synrift sedimentation in the Oliete sub-basin (Iberian Basin, Spain): palaeogeographical evolution and distribution of vertebrate remains. *Journal of Iberian Geology* 44 (2): 285-308.

Austen, P.A. y Batten, D.J. 2018. English Wealden fossils: an update. *Proceedings of the Geologists' Association* 129(2): 171-201.

Averianov, A.O., Krasnolutskii, S.A. y Ivantsov, S. V. 2010. A new basal coelurosaur (Dinosauria: Theropoda) from the Middle Jurassic of Siberia. Proceedings of the Zoological Institute RAS 314 (1): 42-57.

Azuma, Y. y Currie, P.J. 2000. A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences* 37(12): 1735-1753.

B

Badiola, A., Canudo, J.I. y Cuenca-Bescós, G. 2008. New multituberculate mammals of the Hauterivian/Barremian transition of Europe (Iberian Peninsula). *Palaeontology* 51(6): 1455-1469.

Bakker, R.T. 1975. Dinosaur renaissance. *Scientific American* 58-74.

Bakker, R.T. 1986. *The Dinosaur Heresies. Vol. 91*. William Morrow, New York, .

Barco, J.L. y Ruiz-Omeñaca, J.I. 2001. Primeros dientes de terópodos (Dinosauria, Saurischia) en la Formación Villar del Arzobispo (Titónico-Berriasiense): yacimientos Cuesta Lonsal y Las Cerradicas 2 (Galve, Teruel). *Publicaciones del Seminario de Paleontologia de Zaragoza* 5: 247-254.

Barnolas, A. y Pujalte, V. 2004. La cordillera pirenaica. Definición, límites y división. En: Vera, J.A. (ed.), *Geología de España,* 884 pp. IGME.

Baron, M.G., Norman, D.B. y Barrett, P.M. 2017a. A new hypothesis of dinosaur relationships and early dinosaur evolution. *Nature* 543(7646): 501-506.

Baron, M.G., Norman, D.B. y Barrett, P.M. 2017b. Baron et al. reply. *Nature* 551: E4.

Barrett P.M., Benson R.B.J., Rich T.H., Vickers-Rich, P. 2011. First spinosaurid dinosaur from Australia and the cosmopolitanism of Cretaceous dinosaur faunas. *Biology Letters* 7(6):933–936. doi:10.1098/rsbl.2011.0466.

Barsbold, R. 1976. K evolyutsii i sistematike pozdnemezozoyskikh khishchnykh dinozavrov (The evolution and systematics of late Mesozoic carnivorous dinosaurs. *The Joint Soviet-Mongolian Paleontological Expedition Transactions* 3: 68-75.

Barsbold, R. y Perle, A. 1980. Segnosauria, a new infraorder of carnivorous dinosaurs. *Acta Palaeontologica Polonica* 25(2): 187-195.

Baszio, S. 1997. Systematic palaeontology of isolated dinosaur teeth from the latest Cretaceous of south Alberta, Canada. *Courier Forschungsinstitut Senckenberg,* 196, 33–77.

Bell, P.R., y Currie, P.J. 2010. A tyrannosaur jaw bitten by a confamilial: scavenging or fatal agonism? *Lethaia* 43(2): 278–281.

Bell, P.R., Cau, A., Fanti, F. y Smith, E.T. 2016. A large-clawed theropod (Dinosauria: Tetanurae) from the Lower Cretaceous of Australia and the Gondwanan origin of megaraptorid theropods. *Gondwana Research* 36: 473-487.

Benson, R.B.J. 2008. New information on *Stokesosaurus*, a tyrannosauroid (Dinosauria: Theropoda) from North America and the United Kingdom. *Journal of Vertebrate Paleontology* 28 (3): 732-750.

Benson, R.B.J., Brusatte, S.L., Hutt, S. y Naish, D. 2009. A new large basal tetanuran (Dinosauria: Theropoda) from the Wessex Formation (Barremian) of the Isle Of Wight, England. *Journal of Vertebrate Paleontology* 29 (2): 612-615.

Benson, R.B.J., Carrano, M.T. y Brusatte, S.L. 2010. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften* 97 (1): 71-78.

Bidar, A., Demay, L. y Thomel, G. 1972. *Compsognathus corallestris*, nouvelle espèce de dinosaurien théropode du Portlandien de Canjuers (sud-est de la France). *Annales du Musée d'Historie Naturelle de Nice* 1 (1): 1-34.

Bonaparte, J.F. 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétosauridés) du Jurassique Moyen de Cerro Cóndor (Chubut, Argentina). *Annales de Paleontologie* 72 (3): 247-289.

Bonaparte, J.F. y Powell, J.E. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina. *Mémoires de la Société Géologique de France, Nouvelle Série* 139 (470): 19-28.

Brink, K.S., Reisz, R.R., LeBlanc, a. R.H., Chang, R.S., Lee, Y.C., Chiang, C.C., Huang, T.D. y Evans, D.C. 2015. Developmental and evolutionary novelty in the serrated teeth of theropod dinosaurs. *Scientific Reports* 5: 12338.

Brink, K.S., Chen, Y., Wu, Y., Liu, W., Shieh, D., Huang, T.D., Sun, C. y Reisz, R.R. 2016. Dietary adaptions in the ultrastructure of dinosaur dentine. *Journal of The Royal Society Interface* 13 (December): 20160626.

Britt, B., Scheetz, R.D. y Dangerfield, A. 2008. A Suite of Dermestid Beetle Traces on Dinosaur Bone from the Upper Jurassic Morrison Formation, Wyoming. USA. *Ichnos* 15(2): 59-71.

Brusatte, S.L. 2016. Evolution: How some birds survived when all other dinosaurs died. *Current Biology* 26 (10): R415-R417.

Brusatte, S.L. y Sereno, P.C. 2007. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. *Journal of Vertebrate Paleontology* 27 (4): 902-916.

Brusatte, S. L. y Sereno, P. C. 2008. Phylogeny of Allosauroidea (Dinosauria: Theropoda): Comparative analysis and resolution. *Journal of Systematic Palaeontology,* 6(2): 155-182.

Brusatte, S.L. y Benson, R.B.J. 2013. The systematics of Late Jurassic tyrannosauroid theropods from Europe and North America. *Acta Palaeontologica Polonica* 58 (1): 47-54.

Brusatte, S.L., Benson, R.B.J., Carr, T.D., Williamson, T.E. y Sereno, P.C. 2007. The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology* 27 (4): 1052-1056.

Brusatte, S.L., Benson, R.B.J. y Hutt, S. 2008. The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden Group (Barremian) of the Isle of Wight. *Monograph of the Palaeontographical Society* 162 (631): 1-166.

Brusatte, S.L., Benson, R.B.J., Chure, D.J., Xu, X., Sullivan, C. y Hone, D.W.E. 2009. The first definitive carcharodontosaurid (Dinosauria: Theropoda) from Asia and the delayed ascent of tyrannosaurids. *Naturwissenschaften* 96 (9): 1051-1058.

Brusatte, S.L., Norell, M.A., Carr, T.D., Erickson, G.M., Hutchinson, J.R., Balanoff, A.M., Bever, G.S., Choiniere, J.N., Makovicky, P.J. y Xu, X. 2010a. Tyrannosaur paleobiology: New research on ancient exemplar organisms. *Science* 329 (5998): 1481-1485.

Brusatte, S.L., Nesbitt, S.J., Irmis, R.B., Butler, R.J., Benton, M.J. y Norell, M.A. 2010b. The origin and early radiation of dinosaurs. *Earth-Science Reviews* 101 (1-2): 68-100.

Brusatte, S.L., Carr, T.D. y Norell, M.A. 2012. The osteology of *Alioramus,* a gracile and long-snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. *Bulletin of the American Museum of Natural History*: 1-197.

Buckland, W. 1824. Notice on the Megalosaurus or great Fossil Lizard of Stonesfield. *Transactions of the Geological Society of London.* 21 (2): 390-396.

Buckley, L.G. 2009. Individual and ontogenetic variation in theropod dinosaur teeth: A case study of *Coelophysis bauri* (Theropoda: Coelophysoidea) and implications for identifying isolated theropod teeth (pp. 109). MSc. Dissertation, University of Alberta, Edmonton, Alberta, Canada.

Buckley, L.G., Larson, D.W., Reichel, M. y Samman, T. 2010. Quantifying tooth variation within a single population of Albertosaurus sarcophagus (Theropoda: Tyrannosauridae) and implications for identifying isolated teeth of tyrannosaurids. *Canadian Journal of Earth Sciences* 47 (9): 1227-1251.

Buffetaut, E. 2007. The spinosaurid dinosaur *Baryonyx* (Saurischia, Theropoda) in the Early Cretaceous of Portugal. *Geological Magazine*. 144(6): 1021–1025. doi:10.1017/S0016756807003883

Buffetaut, E. 2012. An early spinosaurid dinosaur from the Late Jurassic of Tendaguru (Tanzania) and the evolution of the spinosaurid dentition. *Oryctos* 10: 1-8.

Buffetaut E. y Ingavat R. 1986. Unusual theropod dinosaur teeth from the Upper Jurassic of Phu Wiang, northeastern Thailand. *Revue de Paléobiologie* 5(2): 217-220.

Buffetaut, E. y Suteethorn, V. 1989. A sauropod skeleton associated with theropod teeth in the Upper Jurassic of Thailand: remarks on the thaphonomic and palaeoecological significance of such associations. *Palaeogeography, Palaeoclimatology, Palaeoecolology,* 73, 77–83.

Buffetaut E. y Suteethorn V. 1999. The dinosaur fauna of the Sao Khua formation of Thailand and the beginning of the Cretaceous radiation of dinosaurs in Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology.* 150(1–2): 13-23. doi:10.1016/S0031-0182(99)00004-8

Buffetaut, E., Suteethorn, V. y Tong, H. 1996. The earliest known tyrannosaur from the Lower Cretaceous of Thailand. *Nature* 381 (6584): 689-691.

Buffetaut, E., Martill, D.M. y Escuillié, F. 2004. Pterosaurs as part of a spinosaur diet. *Nature* 430 (6995): 1 p following 33; discussion following 33.

Buscalioni, Á.D., Gasparini, Z., Pérez-Moreno, B.P. y Sanz, J.L. 1997. Argentinean theropods: first morphological analysis on isolated teeth. *Geological Society of Denmark, Online Series* 1: 1-5.

B**utler, R.J., Upchurch, P. y Norman, D.B. 2008.** The phylogeny of the ornithischian dinosaurs. *Journal of Systematic Palaeontology* 6 (1): 1-40.

C

Canale, J.I., Scanferla, C.A., Agnolín, F.L. y Novas, F.E. 2009. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften* 96 (3): 409-414.

Canale, J.I., Novas, F.E. y Pol, D. 2014a. Osteology and phylogenetic relationships of *Tyrannotitan chubutensis* Novas, de Valais, Vickers-Rich and Rich, 2005 (Theropoda: Carcharodontosauridae) from the Lower Cretaceous of Patagonia, Argentina. *Historical Biology* 00 (0): 1-32.

Canale, J. I., Carballido, J. L., Otero, A., Canudo, J. I., y Garrido, A. 2014b. Carcharodontosaurid teeth associated with titanosaur carcasses from the Early Cretaceous (Albian) of the Chubut Group, Chubut Province, Patagonia, Argentina (p. 23). Neuquén: *XXVIII Jornadas Argentinas de Paleontología de Vertebrados.*

Canale, J.I., Apesteguía, S., Gallina, P.A., Gianechini, F.A. y Haluza, A. 2017. The oldest theropods from the Neuquén Basin: Predatory dinosaur diversity from the Bajada Colorada Formation (Lower Cretaceous: Berriasian-Valanginian), Neuquén, Argentina. *Cretaceous Research* 71: 63-78.

Candeiro, C. R. A. y Tanke, D. H. 2008. A pathological Late Cretaceous carcharodontosaurid tooth from Minas Gerais, Brazil. *Bulletin of Geosciences,* 83(3): 351-354.

Candeiro, C.R.A., Currie, P.J., Candeiro, C.L. y Bergqvist, L.P. 2017. Tooth wear and microwear of theropods from the Late Maastrichtian Marília Formation (Bauru Group), Minas Gerais State, Brazil. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 106 (4): 229-233.

Canerot, J., Cugny, P., Pardo, G., Salas, R. y Villena, J. 1982. Ibérica Central y Maestrazgo. En: *El Cretácico de España*, 273-344. Universidad Complutense de Madrid, Madrid.

Canudo, J.I. 2007. Historia evolutiva de los terópodos no avianos. En: Sanz, J.L. (ed.), *Los dinosaurios en el Siglo XXI*, 241-263. Tusquets.

Canudo, J.I. y Ruiz-Omeñaca, J.I. 2003. Los restos directos de dinosaurios terópodos (excluyendo aves) en España. En: Canudo, J.I. y Ruiz-Omeñaca, J.I. (eds.), *Dinosaurios y otros reptiles mesozoicos de España*, 347-373. .

Canudo, J.I., Cuenca-Bescós, G. y Ruiz-Omeñaca, J.I. 1997a. Dinosaurios dromeosáuridos (Saurischia: Theropoda) en el Barremiense Superior (Cretácico Inferior) de Castellote, Teruel. *Geogaceta* 22: 8-11.

Canudo, J.I., Amo, O., Cuenca-Bescós, G., Meléndez, A., Ruiz-Omeñaca, J.I. y Soria, A.R. 1997b. Los vertebrados del Tithónico — Barremiense de Galve (Teruel, España). *Cuadernos de Geología Ibérica* 23: 209-241.

Canudo, J.I., Cuenca-Bescós, G. y Ruiz-Omeñaca, J.I. 1999. Dientes aislados de dinosaurios: su estudio. *VI Jornadas Aragonesas de Paleontología*: 217-246.

Canudo, J.I., Aurell, M., Barco, J.L., Cuenca-Bescós, G. y Ruiz-Omeñaca, J.I. 2005a. Los dinosaurios de la Formación Villar del Arzobispo (Titónico medio—Berriasiense inferior) en Galve (Teruel). *Geogaceta* 38: 39-42.

Canudo, J. I., Cruzado-Caballero, P. y Moreno-Azanza, M. 2005b. Possible theropod predation evidence in hadrosaurid dinosaurs from the Upper Maastrichtian (Upper Cretaceous) of Arén (Huesca, Spain). *Kaupia*, 14: 9-13.

Canudo, J.I., Ruiz-Omeñaca, J.I., Aurell, M., Barco, J.L. y Cuenca-Bescós, G. 2006. A megatheropod tooth from the late Tithonian - middle Berriasian (Jurassic-Cretaceous transition) of Galve (Aragón, NE Spain). *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 239 (1): 77-99.

Canudo, J.I., Gasulla, J.M., Gómez-Fernández, D., Ortega, F., Sanz, J.L. y Yagüe, P. 2008a. Primera evidencia de dientes aislados atribuidos a Spinosauridae (Theropoda) en el Aptiano inferior (Cretácico Inferior) de Europa: Formación Arcillas de Morella (España). *Ameghiniana* 45 (4): 649-662.

Canudo, J. I., Royo-Torres, R. y Cuenca-Bescós, G. 2008b. A new sauropod: *Tastavinsaurus sanzi* gen. et sp. nov. from the Early Cretaceous (Aptian) of Spain. *Journal of Vertebrate Paleontology* 28(3): 712-731.

Canudo, J. I., Filippi, L., Salgado, L., Garrido, A., Cerda, I., García, R., y Otero, A. 2009. Dientes de terópodos asociados con una carcasa de saurópodo en el Cretácico Superior (Formación Plottier) de Rincón de los Sauces (Patagonia, Argentina). En Colectivo Arqueológico y Paleontológico de Salas (Ed.), *Actas de las IV Jornadas Internacionales sobre Paleontologíade Dinosaurios y su Entorno* (pp. 321–330). Salas de los Infantes, Burgos

Canudo, J.I., Gasca, J.M., Aurell, M., Badiola, A., Blain, H.-A., Cruzado-Caballero, P., Gómez-Fernández, D., Moreno-Azanza, M., Parrilla, J., Rabal-Garcés, R. y Ruiz-Omeñaca, J.I. 2010a. La Cantalera: an Exceptional Window on the Vertebrate Biodiversity of the Hauterivian-Barremian transition in the Iberian Peninsula. *Journal of Iberian Geology* 36 (2): 205-224.

Canudo, J.I., Barco, J.L., Castanera, D. y Torcida Fernández-Baldor, F. 2010b. New record of a sauropod in the Jurassic-Cretaceous transition of the Iberian Peninsular (Spain): Palaeobiogeographical implications. *Palaontologische Zeitschrift* 84 (3): 427-435.

Canudo, J.I., Gasca, J.M., Moreno-Azanza, M. y Aurell, M. 2012. New information about the stratigraphic position and age of the sauropod Aragosaurus ischiaticus from the Early Cretaceous of the Iberian Peninsula. *Geological Magazine* 149 (02): 252-263.

Carpenter, K. 1998. Evidence of predatory behaviour by carnivorous dinosaurs. En Pérez-Moreno, B.P., Holtz., T. Jr., Sanz, J.L., y Moratalla, J.J. (Eds.), *Aspects of Theropod Paleobiology*. Gaia: Revista de Geociencias (pp. 135–144), vol 15. Lisbon: Museu Nacional de Historia Natural.

Carpenter, K. y Miles, C. 2005. New Small Theropod from the Upper Jurassic Morrison Formation of Wyoming. *The Carnivorous Dinosaurs*: 23-38.

Castanera, D., Vila, B., Razzolini, N.L., Santos, V., Pascual, C. y Canudo, J.I. 2014. Sauropod trackways of the Iberian Peninsula: palaeoetological and palaeoenvironmental implications. *Journal of Iberian Geology* 40 (1): 49-59.

Carr, T.D., Varricchio, D.J., Sedlmayr, J.C., Roberts, E.M. y Moore, J.R. 2017. A new tyrannosaur with evidence for anagenesis and crocodile-like facial sensory system. *Scientific Reports* 7 (October 2016): 44942.

Carrano, M.T. y Sampson, S.D. 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). J*ournal of Systematic Palaeontology* 6 (2): 183-236.

Carrano, M.T., Benson, R.B.J. y Sampson, S.D. 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 10 (2): 211-300.

Casal, G., Candeiro, C.R.A., Martínez, R., Ivany, E. y Ibiricu, L. 2009. Dientes de Theropoda (Dinosauria: Saurischia) de la Formación Bajo Barreal, Cretácico Superior, Provincia del Chubut, Argentina. *Geobios* 42 (5): 553-560.

Cau, A. 2018. The assembly of the avian body plan: A 160-million-year long process. *Bollettino della Societa Paleontologica Italiana* 57 (1): 1-25.

Cau, A., Beyrand, V., Voeten, D.F.A.E., Fernandez, V., Tafforeau, P., Stein, K., Barsbold, R., Tsogtbaatar, K., Currie, P.J. y Godefroit, P. 2017. Synchrotron scanning reveals amphibious ecomorphology in a new clade of bird-like dinosaurs. *Nature.*

Charig, A.J. y Milner, A.C. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum of London* 53 (1): 11-70.

Choiniere, J.N., Forster, C.A. y De Klerk, W.J. 2012. New information on *Nqwebasaurus thwazi*, a coelurosaurian theropod from the Early Cretaceous Kirkwood Formation in South Africa. *Journal of African Earth Sciences* 71-72: 1-17.

Choiniere, J.N., Xu, X., Clarck, J.M., Forster, C.A., Guo, Y. y Han, F. 2010. A Basal Alvarezsauroid Theropod from the Early Late Jurassic of Xinjiang, China. *Nature* 327 (5965): 571-574.

Chure, D.J. 1995. A reassessment of the gigantic theropod *Saurophagus maximus* from the Morrison Formation (Upper Jurassic) of Oklahoma, USA. *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers* (January 1995): 103–106.

Chure, D. J., Fiorillo, A. R. y Jacobsen, A. 1998. Prey bone utilization by predatory dinosaurs in the Late Jurassic of North America, with comments on prey bone use by dinosaurs throughout the Mesozoic. *Gaia,* 15, 227–232.

Cillari, A. 2010. Teeth of Theropoda (Dinosauria, Saurischia): morphology, function and classification. *Ph.D. Dissertation*. Sapienza Universita´ di Roma, p. 193.

Clack, J.A. 2012. *Gaining Ground: The Origin and Evolution of Tetrapods.* Indiana University Press, Bloomington, Indiana.

Clark, J.M., Maryanska, T. y Barsbold, R. 2004. Therizinosauroidea. En: Weishampel, D.B., Dodson, P. y Osmólska, H. (eds.), *The Dinosauria*, 151-164. University of California Press, Berkeley.

Clemente, P. 2010. Review of the Upper Jurassic-Lower Cretaceous stratigraphy in Western Cameros Basin, Northern Spain. *Revista de la Sociedad Geológica de España* 23 (3-4): 101-143.

Clemente, P. y Pérez-Arlucea, M. 1993. Depositional Architecfure of the Cuerda Del Pozo Formation, Lower Cretaceous of the Extensional. *Journal of Sedimentary Petrology* 63 (3): 437-452.

Cobos, A., Lockley, M.G., Gascó, F., Royo-Torres, R. y Alcalá, L. 2014. Megatheropods as apex predators in the typically Jurassic ecosystems of the Villar del Arzobispo Formation (Iberian Range, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 399: 31-41.

Codrea, V., Smith, T., Dica, P., Folie, A., García, G., Godefroit, P. 2002. Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the hateg Basin (Romania). *Comptes Rendus Palevol*, 1: 173-180.

Colbert, E.H. y Russell, D.A. 1969. The Small Cretaceous Dinosaur Dromaeosaurus. *American Museum Novitates* 2380: 50.

Cope, E.D. 1869. Synopsis of the exting Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society* 14: 1-252.

Cope, E.D. 1871. On the homologies of some of the cranial bones of the Reptilia, and on the systematic arrangement of the class. *Proceedings of the American Association for the Advancement of Science* 19: 194-247.

Coria, R. A. y Salgado, L. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* 377: 224-226.

Coria, R.A. y Currie, P.J. 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas* 28 (1): 71-118.

Coria, R.A. y Currie, P.J. 2016. A new megaraptoran dinosaur (Dinosauria, Theropoda, Megaraptoridae) from the late Cretaceous of Patagonia. *PLoS ONE* 11 (7): 1-53.

Cruzado-Caballero, P. 2012. Restos directos de dinosaurios hadrosáuridos (Ornithopoda, Hadrosauridae) del Maastrichtiense superior (Cretácico Superior) de Arén (Huesca). *Ph.D. Dissertation.* Universidad de Zaragoza, p. 411.

Csiki-Sava, Z., Brusatte, S.L. y Vasile, Ş. 2016. «*Megalosaurus* cf. *superbus*» from southeastern Romania: The oldest known Cretaceous carcharodontosaurid (Dinosauria: Theropoda) and its implications for earliest Cretaceous Europe-Gondwana connections. *Cretaceous Research* 60 (June): 221-238.

Csiki, Z., Vremir, M., Brusatte, S.L. y Norell, M.A. 2010. An aberrant island-dwelling theropod dinosaur from the Late Cretaceous of Romania. *Proceedings of the National Academy of Sciences* 107 (35): 15357-15361.

Cuenca-Bescós, G., Amo, O., Barco, J.L., Canudo, J.I., Royo-Torres, R. y Ruiz-Omeñaca, J.I. 1999. Dinosaurios de Aragón. *Zubía* 17: 235-257.

Currie, P.J. y Zhao, X. 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* 30 (10): 2037-2081.

Currie, P. J. y Jacobsen, A.R. 1995. An azhdarchid pterosaur eaten by a velociraptorine theropod. *Canadian Journal of Earth Sciences* 32: 922-925.

Currie, P.J. y Carpenter, K. 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda , Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous , Aptian) of Oklahoma , USA. *Geodiversitas* 22 (2): 207-246.

Currie, P. J. y Varrichio, D. J. 2004. A new dromaeosaurid from the Horseshoe Canyon Formation (upper Cretaceous) of Alberta, Canada. En Currie, P. J., Koppelhus, E. B., Shugar, M. A. y Wright, J.L. (Eds.). *Feathered dragons: studies on the transition from dinosaurs to birds* (pp. 112–132). Bloomington, Indiana: University Press.

Currie, P.J. y Azuma, Y. 2006. New speciments, including a growth series, of *Fukuiraptor* (Dinosauria, Theropoda) from the Lower Cretaceous Kitadani Quarry of Japan. *Journal of Paleontological Society of Korea* 22 (1): 173-193.

Currie, P.J., Rigby, J.K. y Sloan, R.E. 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. En: Carpenter, K. y Currie, P.J. (eds.), *Dinosaur Systematics: Perspectives and Approaches*, 107-125. Cambridge University Press.

D

D'Amore, D.C. 2009. A functional explanation for denticulation in theropod dinosaur teeth. *Anatomical Record* 292 (9): 1297-1314.

Dal Sasso, C. y Signore, M. 1998. Exceptional soft-tissue preservation in a theropod dinosaur from Italy. *Nature* 392 (6674): 383-387.

Dal Sasso C, Maganuco S, Buffetaut E. y Mendez MA. 2005. New information on the skull of the enigmatic theropod Spinosaurus with remarks on its size and affinities. Journal of Vertebrate Paleontology 25(4): 888-896.

De Valais, S., Apesteguı´a, S. y Garrido, A. C. 2012. Cretaceous Small scavengers: feeding traces in tetrapod bones from Patagonia, Argentina. *PLoS One* 7(1), e29841. doi:10.1371/ journal.pone.0029841.

del Corro, G. 1966. Un nuevo dinosaurio carnı´voro del Chubut (Argentina). Comunicaciones del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". Paleontología, 1, 1–4.

Delcourt, R. 2018. Ceratosaur palaeobiology: New insights on evolution and ecology of the southern rulers. Scientific Reports 8 (1): 1-12.

DePalma, R. A., Burnham, D. A., Martin, L. D., Rothschild, B. M. y Larson, P. L. 2013. Physical evidence of predatory behaviour in Tyrannosaurus rex. *Proceedings of the National Academy of Sciences* 110(31) :12560-12564. doi:10.1073/pnas.1216534110.

Dong, Z. 1984. A new theropod dinosaur from the Middle Jurassic of Sichuan Basin. *Vertebrata PalAsiatica* 22 (3): 213-218.

Dong, Z., Zhang, Y., Li, X. y Zhou, S. 1978. A new carnosaur from Yongchuan County, Sichuan Province. *Ke Xue Tong Bao [Science Newsletter]* 23 (5): 302-304.

E

Erickson, G.M. 1995. Split carinae on tyrannosaurid teeth and implicatinos of their development. *Journal of Vertebrate Paleontology* 15 (2): 268-274.

Erickson, G.M. 1996. Incremental lines of von Ebner in dinosaurs and the assessment of tooth replacement rates using growth line counts. *Proceedings of the National Academy of Sciences* 93 (December): 14623-14627.

Erickson, G.M. y Olson, K.H. 1996. Bite marks attributable to Tyrannosaurus rex: preliminary description and implications. *Journal of Vertebrate Paleontology* 16 (1): 175-178.

E**udes-Deslongchamps, J.-A. 1836.** Plusieurs parties d'un mémoire sur un très-grand animal fossile découvert, l'an dernier, dans les carrières de la Maladrerie à un quart de lieu de Caen. *Analyse des Travaux de la Société Pendant l'Année Académique* 1835–1836, Séance Publique de la Société Linnéenne de Normandie Tenue à Vire le 24 Mai 1836: 14-25.

Evers, S.W., Rauhut, O.W.M., Milner, A.C., McFeeters, B. y Allain, R. 2015. A reappraisal of the morphology and systematic position of the theropod dinosaur *Sigilmassasaurus* from the "middle" Cretaceous of Morocco. PeerJ 3: e1323.

F

Fanti, F. y Therrien, F. 2007. Theropod tooth assemblages from the Late Cretaceous maevarano Formation and the possible presence of dromaeosaurids in Madagascar. *Acta Palaeontologica Polonica* 52(1): 155-166.

Fanti, F., Cau, A., Martinelli, A. y Contessi, M. 2014. Integrating palaeoecology and morphology in theropod diversity estimation: A case from the Aptian-Albian of Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 410: 39-57.

Farlow, J.O., Brinkman, D.L., Abler, W.L. y Currie, P.J. 1991. Size, shape and serration density of theropod dinosaur lateral teeth. *Modern Geology* 16: 161-198.

Figueiredo, S., Figuti, L. y Rosina, P. 2015. Dinosaurs and other vertebrates from the papo-Seco Formation (Lower Cretaceous) of southern Portugal. *Journal of Iberian Geology* 41 (3): 301-314.

Fiorillo, A.R. 1991. Prey bone utilization by predatory dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 88 (3-4): 157-166.

Fiorillo, A.R. y Currie, P.J. 1994. Theropod teeth from the Judith River Formation (Upper Cretaceous) of south-central Montana. *Journal of Vertebrate Paleontology* 14 (1): 74-80.

Fitzinger, L. 1843. *Systema reptilium*. Fasciculus primus: Amblyglossae. Vienna, .

Foster, J.R. y Lucas, S.G. 2006. Paleontology and Geology of the Upper Jurassic Morrison Formation. N*ew Mexico Museum of Natural History & Science, Bulletin 36*, 1-249.

F**oth, C. y Rauhut, O.W.M. 2017.** Re-evaluation of the Haarlem *Archaeopteryx* and the radiation of maniraptoran theropod dinosaurs. *BMC Evolutionary Biology* 17 (1).

Fuentes Vidarte, C., Meijide Calvo, M., Izquierdo, L.A., Montero, D., Pérez, G., Torcida, F., Urién, V., Meijide Fuentes, F. y Meijide Fuentes, M. 1999. Restos fósiles de *Baryonyx* (Dinosauria, Theropoda) en el Cretácico Inferior de Salas de los Infantes (Burgos, España). *I Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno:* 349-359.

Fürsich, F.T., Werner, W., Delvene, G., García-Ramos, J.C., Bermúdez-Rochas, D.D. y Piñuela, L. 2012. Taphonomy and palaeoecology of high-stress benthic associations from the Upper Jurassic of Asturias, northern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 358-360: 1-18.

Furtado, M.R., Candeiro, C.R.A. y Bergqvist, L.P. 2013. Teeth of Abelisauridae and Carcharodontosauridae cf. (Theropoda, Dinosauria) from the Campanian-Maastrichtian Presidente Prudente Formation (Southwestern São Paulo State, Brazil). *Estudios Geológicos* 69 (1): 105-114.

G

Galton, P.M. y Jensen, J.A. 1979. A new large theropod dinosaur from the Upper Jurassic of Colorado. *Brigham Young University Geological Studies 26* (January 1979): 1–12.

García-Ramos, J.C. 1997. La sucesión Jurásica de la Cuenca Asturiana: Entorno paleogeográfico regional y relaciones Tectónica-Sedimentación. *Comunicaciones del IV Congreso del Jurásico de España:* 13-14.

García-Ramos, J.C. y Aramburu, C. 2010. V Congreso del Jurásico de España. *Guía de campo (Excursión B).* Las sucesiones litorales y marinas restringidas del Jurásico Superior. Acantilados de Tereñes (Ribadesella) y de la playa de La Griega (Colunga). En García-Ramos, J.C. y Aramburu, C. (eds.) Museo del Jurásico de Asturias, .

García-Ramos, J.C., Lires, J. y Piñuela, L. 2002. *Dinosaurios.* Rutas por el Jurásico de Asturias. La Voz de Asturias, Lugones, .

García-Ramos, J.C., Piñuela, L. y Lires, J. 2004. *Guía del Jurásico de Asturias.* Rutas por los yacimientos de huellas de dinosaurios. Zinco Comunicación, Gijón, .

García-Ramos, J.C., Piñuela, L. y Lires, J. 2006. *Atlas del Jurásico de Asturias.* Nobel, Oviedo, .

García-Ramos, J.C., Aramburu, C. y Piñuela, L. 2010. Las series fluviales del Jurásico Superior (Formación Vega). Descripción de la serie y ambientes sedimentarios. En: García-Ramos, J.C. (ed.), *V Congreso del Jurásico de España. Guía de campo, Excursión A*, 56-63. Museo del Jurásico de Asturias, Colunga.

Gasca, J.M. 2015. Aportaciones al conocimiento sobre los dinosaurios del Barremiense inferior (Cretácico Inferior) de Teruel, España: asociaciones fósiles, sistemática, paleobiodiversidad y afinidades paleobiogeográficas. *Tesis doctoral,* Universidad de Zaragoza, España, 170 pp.

Gasca, J.M., Moreno-Azanza, M. y Canudo, J.I. 2008. Dientes de dinosaurios terópodos espinosáuridos de la Formación El Castellar (Cretácico Inferior, Teruel). *Palaeontologica Nova SEPAZ* 8 (8): 233-234.

Gasca, J.M., Canudo, J.I. y Moreno-Azanza, M. 2009. Dientes aislados de dinosaurio de la Formación El Castellar en Miravete de la Sierra (Cretácico Inferior, Teruel, España). *Actas de Las IV Jornadas Internacinoales Sobre Paleontología de Dinosaurios y su Entorno*, Salas de Los Infantes (Burgos, Espana), 13-15 de Septiembre de 2007: 221-234.

Gasca, J.M., Moreno-Azanza, M. y Canudo, J.I. 2011. Dientes de dinosaurios en el Barremiense de Allepuz, Teruel. *Viajando a mundos pretéritos* 307: 145-155.

Gasca, J.M., Canudo, J.I. y Moreno-Azanza, M. 2014a. A large-bodied theropod (Tetanurae: Carcharodontosauria) from the Mirambel Formation (Barremian) of Spain. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 273 (1): 13-23.

Gasca JM, Canudo JI, Moreno-Azanza M. 2014b. On the Iberian iguanodont dinosaur diversity: new fossils from the lower Barremian, Teruel province, Spain. *Cretaceous Research* 50: 264-272. doi:10.1016/j.cretres.2014.05.009.

Gasca, J.M., Díaz-Martínez, I., Moreno-Azanza, M., Canudo, J.I. y Alonso, A. 2018. A hypertrophied ungual phalanx from the lower Barremian of Spain: Implications for the diversity and palaeoecology of Spinosauridae (Theropoda) in Iberia. *Cretaceous Research* 84: 141-152.

Gascó, F., Cobos, A., Royo-Torres, R., Mampel, L. y Alcalá, L. 2012. Theropod teeth diversity from the Villar del Arzobispo Formation (Tithonian-Berriasian) at Riodeva (Teruel, Spain). *Palaeobiodiversity and Palaeoenvironments* 92 (2): 273-285.

Gasulla, J.M., Ortega. F., Escaso, F. y Sanz J.L. 2006. Diversidad de terópodos del Cretácico Inferior (Fm. Arcillas de Morella, Aptiense) en los yacimientos del Mas de la Parreta (Morella, Castellón). En: Fernández-Martínez. E, (Ed). *Libro de resúmenesde las 22ª ̄Jornadasde la Sociedad Española de Paleontología*. León: Universidad de León; p. 117–118.

Gasulla, J. M., Escaso, F., Narváez, I., Ortega F., y Sanz, J. L. 2015. A new sail-backed styracosternan

(Dinosauria: Ornithopoda) from the Early Cretaceous of Morella, Spain. *PLoS One* 10(12): e0144167.

Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. En: Padian, K. (ed.), T*he Origin of Birds and the Evolution of Flight*, 1-55. .

Gauthier, J.A. 1994. The diversification of the amniotes. En: Prothero, D.R. y Schoch, R.M. (eds.), *Major features of vertebrate evolution,* 129-159. Paleontological Society, Knoxville.

Gerke, O. y Wings, O. 2016. Multivariate and cladistic analyses of isolated teeth reveal sympatry of theropod dinosaurs in the Late Jurassic of Northern Germany. *PLoS ONE* 11 (7): 1-52.

Gianechini, F.A. y De Valais, S. 2016. Bioerosion trace fossils on bones of the Cretaceous South American theropod *Buitreraptor gonzalezorum* Makovicky, Apesteguía and Agnolín, 2005 (Deinonychosauria). *Historical Biology* 28(4): 533-549.

Gianechini, F.A., Makovicky, P.J. y Apesteguía, S. 2011. The teeth of the unenlagiine theropod Buitreraptor from the Creta- ceous of Patagonia, Argentina, and the unusual dentition of the Gondwanan dromaeosaurids. *Acta Palaeontologica Polonica* 56(2): 279-290.

Gignac, P.M. y Erickson, G.M. 2017. The Biomechanics Behind Extreme Osteophagy in *Tyrannosaurus rex. Scientific Reports* 7 (1): 2012.

Gilmore, C.W. 1924. On T*roodon validus*, an orthopodous dinosaur from the Belly River Cretaceous of Alberta, Canada. *Department of Geology, University of Alberta Bulletin* 1: 1-43.

Godefroit, P., Cau, A., Dong-Yu, H., Escuillié, F., Wenhao, W. y Dyke, G. 2013. A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. *Nature* 498 (7454): 359-362.

Göhlich, U.B. y Chiappe, L.M. 2006. A new carnivorous dinosaur from the Late Jurassic Solnhofen archipelago. *Nature* 440 (7082): 329-332.

Goloboff, P.A. y Catalano, S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32: 221-238.

Goloboff, P.A., Farris, J.S. y Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24 (5): 774-786.

Gómez-Fernández, D., Canudo, J.I. y Cano-Llop, V. 2007. Cintura pelviana de un nuevo dinosaurio terópodo de la Formación Morella (Aptiense inferior) en Vallibona (Castellón). 3. *Jornadas de la Sociedad Española de Paleontologí*a: 96-97.

Goodrich, E.S. 1916. On the classification of the Reptilia. *Proceedings of the Royal Society of London* 89B: 261-276.

Grambast L. 1968. Evolution of the utricle in the charophyte genera *Perimneste* Harris and *Atopochara* Peck. *Journal of the Proceedings of the Linnean Society. Botany* 61 (384): 5-11. doi:10.1111/j.1095-8339.1968.tb00099.x.

Gutierrez, K. y Sheldon, N.D. 2012. Paleoenvironmental reconstruction of Jurassic dinosaur habitats of the Vega Formation, Asturias, Spain. *GSA Bulletin* 124: 596-610.

H

Hammer, Ø. y Harper, D.A.T. 2006. *Paleontological data analysis.* Blackwell, Oxford, .

Hammer, Ø., Harper, D.A.T. y Ryan, P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4 (1): 1-9.

Han, F., Clark, J.M., Xu, X., Sullivan, C., Choiniere, J.N. y Hone, D.W.E. 2011. Theropod teeth from the Middle-Upper Jurassic Shishugou Formation of northwest Xinjiang, China. *Journal of Vertebrate Paleontology* 31 (1): 111-126.

Harris, J.D. 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of natural History and Science Bulletin* 13: 1-75.

Harris, J.D., Lucas, S.G., Speilmann, J.A., Lockley, M.G., Milner, A.R.C. y Kirkland, J.I. 2006. The Triassic-Jurassic Terrestrial Transition: 37. En *Science*, N.M.M. of N.H. and (ed.) .

Hasegawa, Y., Buffetaut, E., Makoto, M. y Takakuwa, Y. 2003. A possible spinosaurid tooth from the Sebayashi Formation (Lower Cretaceous), Gunma, Japan. *Bulletin of Gunma Museum of Natural History* 7 (1): 1-5.

Hatcher, J.B. 1901. *Diplodocus* (Marsh): Its osteology, taxonomy, and probable habits, with a restoration of the skeleton. *Memoirs of the Carnegie Museum* 1: 1-63.

Henderson, D.M. 2018. A buoyancy, balance and stability challenge to the hypothesis of a semi-aquatic *Spinosaurus* Stromer, 1915 (Dinosauria: Theropoda). *PeerJ* 6: e5409.

Hendrickx, C. 2015. Evolution of Teeth and Quadrate in Non-avian Theropoda (Dinosauria: Saurischia), with the Description of *Torvosaurus* Remains from Portugal.Universidade Nova de Lisboa.

Hendrickx, C. y Mateus, O. 2014a. *Torvosaurus gurneyi* n. sp., the largest terrestrial predator from europe, and a proposed terminology of the maxilla anatomy in nonavian theropods. *PLoS ONE* 9 (3).

Hendrickx, C. y Mateus, O. 2014b. Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. *Zootaxa*, Vol. 3759.

Hendrickx, C., Hartman, S.A. y Mateus, O. 2015a. An Overview of Non-Avian Theropod Discoveries and Classification. *PalArch's Journal of Vertebrate Palaeontology* 12 (1): 1-73.

Hendrickx, C., Mateus, O. y Araújo, R. 2015b. The dentition of megalosaurid theropods. A*cta Palaeontologica Polonica* 60 (3): 627-642.

Hendrickx, C., Mateus, O. y Araújo, R. 2015c. A proposed terminology of theropod teeth (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology* 35 (5): e982797.

Hillson, S. 2005. *Teeth.* Cambridge University Press, Cambridge, .

Hocknull, S.A., White, M.A., Tischler, T. R., Cook, A.G., Calleja, N.D., Sloan, T. 2009. New mid-Cretaceous (Latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS One* 4 (7): e6190.

Holgado, B., Pêgas, R. V., Canudo, J.I., Fortuny, J., Rodrigues, T., Company, J. y Kellner, A.W.A. in press. On a new crested pterodactyloid from the Early Cretaceous of the Iberian Peninsula and the radiation of the clade Anhangueria. *Scientific Reports.*

Holtz, T.R. 2004. Tyrannosauroidea. En: Weishampel, D.B., Dodson, P. y Osmólska, H. (eds.), *The Dinosauria*, 111-136. University of California Press, Berkeley.

Holtz, T.R. 2012. Theropods. En: Brett-Surman, M.K., Holtz, T.R. y Farlow, J.O. (eds.), *The Complete Dinosaur*, 347-378. Indiana University Press, Bloomington, Indiana.

Holtz, T.R. 2017. Share names for dinosaur divisions. *Nature* 545: 30.

Holtz, T.R., Brinkman, D.L. y Chandler, C.L. 1998. Denticle morphometrics and a possibly omnivorous feeding habit for the theropod dinosaur *Troodon*. *Gaia* 166 (December): 159-166.

Holtz, T.R. y Osmólska, H. 2004. Saurischia. En: Weishampel, D.B., Dodson, P. y Osmólska, H. (eds.), *The Dinosauria*, 21-24. University of California Press, Berkeley.

Holtz, T.R., Molnar, R.E. y Currie, P.J. 2004. Basal Tetanurae. En: Weishampel, D.B., Dodson, P. y Osmólska, H. (eds.), *The Dinosauria*, 71-110. University of California Press, Berkeley.

Hone, D.W.E., Xu, X. y Wang, D.-Y. 2010. A probable baryonychine (Theropoda: Spinosauridae) tooth from the Upper Cretaceous of Henan province, China. *Vertebrata PalAsiatica* 48: 19-26.

Von Huene, F. 1914a. Beiträge zur geschichte der Archosaurier. *Geologie und Paläontologie Abhandlungen* 13 (7): 1-56.

Von Huene, F. 1914b. Über die Zweistätmmigkeit der Dinosaurier, mit Beiträgen zur Kenntnis einiger Schädek. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie Beilage-Band* 37: 577-589.

Von Huene, F. 1923. Carnivorous saurischia in Europe since the Triassic. *Bulletin of the Geological Society of America* 34: 449-458.

Von Huene, F. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. Vol. 4.

Hunt, A.P., Meyer, C.A., Lockley, M.G. y Lucas, S.G. 1994. Archaeology, toothmarks and sauropod dinosaur taphonomy. *Gaia*, 10, 225–231.

Hutt, S. 2001. A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. *Cretaceous Research* 22 (2): 227-242.

Hutt, S., Martill, D.M. y Barker, M.J. 1996. The first European allosaurid dinosaur (Lower Cretaceous, Wealden Group, England). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 10: 635-644.

Huxley, T.H. 1870. On the classification of the Dinosauria, with observations on the Dinosauria of the Trias. *Quarterly Journal of the Geological Society* 26: 32-51.

Hwang, S.H., Norell, M.A., Qiang, J. y Keqin, G. 2004. A large Compsognathid from the early cretaceous Yixian formation of China. *Journal of Systematic Palaeontology* 2 (1): 13-30.

I

Ibrahim, N., Sereno, P.C., Dal Sasso, C., Maganuco, S., Fabbri, M., Martill, D.M., Zouhri, S., Myhrvold, N. y Iurino, D.A. 2014. Semiaquatic adaptations in a giant predatory dinosaur. *Science* 345 (6204).

Infante, P., Canudo, J.I. y Ruiz-Omeñaca, J.I. 2005. Primera evidencia de dinosaurios terópodos en la Formación Mirambel (Barremiense inferior, Cretácico Inferior) en Castellote, Teruel. *Geogaceta* 38: 31-34.

J

Jacobsen, A.R. 1998. Feeding behaviour of carnivorous dinosaurs as determined by tooth marks on dinosaur bones. *Historical Biology* 13 (1): 17-26.

Janensch, W. 1920. Ueber Elaphrosaurus bambergi und die Megalosaurier aus den Tendaguru-Schichtend Deutsch-Ostafrikas. Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin: 225-235.

Janensch, W. 1925. Die Coelurosaurier und Theropoden der Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica, supplement VII* 1 (1): 1-100.

Ji, **Q., Ji, S. y Zhang, L. 2009.** First large tyrannosauroid theropod from the Early Cretaceous Jehol Biota in northeastern China. *Geological Bulletin of China* 28 (10): 1369-1374.

K

Kear, B.P., Rich, T.H., Vickers-Rich, P., Ali, M.A., Al-Mufarreh, Y.A., Matari, A.H., Al-Massari, A.M., Nasser, A.H., Attia, Y. y Halawani, M.A. 2013. First dinosaurs from Saudi Arabia. *PLoS ONE* 8 (12): e84041. doi:10. 1371/journal.pone.0084041

Kellner, A.W.A. y Campos, D.A. 1996. First early cretaceous theropod dinosaur from Brazil with comments on Spinosauridae. *Neues Jahrbuch für Geologie und Paläontologie -Abhandlungen* 199 (2): 151.

Kellner, A.W.A., Azevedo, S.A.K., Machado, E.B., de Carvalho, L.B. y Henriques, D.D.R. 2011. A new dinosaur (Theropoda, Spinosauridae) from the cretaceous (Cenomanian) Alcântara formation, Cajual Island, Brazil. *Anais da Academia Brasileira de Ciencias* 83 (1): 99-108.

Kirkland, J.I., Zanno, L.E., Sampson, S.D., Clark, J.M. y DeBlieux, D.D. 2005. A primitive therizinosauroid dinosaur from the Early Cretaceous of Utah. *Nature* 435 (5): 84-87.

De Klerk, W.J., Forster, C.A., Sampson, S.D., Chinsamy, A. y Ross, C.F. 2000. A new coelurosaurian dinosaur from the Early Cretaceous of South Africa. *Journal of Vertebrate Paleontology* 20 (2): 324-332.

Kneuper-Haack, F. 1966. Ostracoden as dem Wealden der Sierra de los Cameros. *Beihefte zum Geologischen Jahrbuch* 44: 165-209.

Kobayashi, Y. y Lü, J.-C. 2003. A new Ornithomimid Dinosaur with gregarious habits from Late Cretaceous of China. *Acta Paleontologica Polonica* 42 (2): 235-259.

Kurzanov, S.M. 1976. A new carnosaur from the Late Cretaceous of Nogon-Tsav, Mongolia. T*he Joint Soviet-Mongolian Paleontological Expedition Transactions* 3: 93-104.

L

Lacasa-Ruiz, A. 1989. Nuevo género de ave fósil del yacimiento neocomiense del Montsec (provincia de Lérida, España). *Estudios Geológicos* 45: 417-425.

Langer, M.C. 2003. The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquinz* (Late Triassic, Brazil). *PaleoBios* 23 (2): 1-40.

Langer, M.C., Abdala, F., Richter, M. y Benton, M.J. 1999. A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. *Comptes Rendus de l'Académie des Sciences* 329: 511-517.

Langer, M.C., Ezcurra, M.D., Rauhut, O.W.M., Benton, M.J., Knoll, F., McPhee, B.W., Novas, F.E., Pol, D. y Brusatte, S.L. 2017. Untangling the dinosaur family tree. *Nature* 551 (7678): E1-E3.

Langer, M.C., Ramezani, J. y Da Rosa, Á.A.S. 2018. U-Pb age constraints on dinosaur rise from south Brazil. *Gondwana Research* 57: 133-140.

Larson, D.W. y Currie, P.J. 2013. Multivariate Analyses of Small Theropod Dinosaur Teeth and Implications for Paleoecological Turnover through Time. *PLoS ONE* 8 (1).

Larson, D.W., Brown, C.M. y Evans, D.C. 2016. Dental disparity and ecological stability in bird-like dinosaurs prior to the end-cretaceous mass extinction. *Current Biology* 26 (10): 1325-1333.

Laurenti, J.N. 1768. Specimen Medicum, Exhibens Synopsin Reptilium Emendatam cum Experimentis circa Venena.

Laurin, M. y Anderson, J.S. 2004. Meaning of the name tetrapoda in the scientific literature: An exchange. *Systematic Biology* 53 (1): 68-80.

Lee, Y.N., Barsbold, R., Currie, P.J., Kobayashi, Y., Lee, H.J., Godefroit, P., Escuillié, F. y Chinzorig, T. 2014. Resolving the long-standing enigmas of a giant ornithomimosaur *Deinocheirus mirificus. Nature* 515 (7526).

Leidy, J. 1856. Notices of remains of extinct reptiles and fishes, discovered by Dr. F. V. Hayden in the bad lands of the Judith River, Nebraska Territory. *Proceedings of the Academy of Natural Sciences of Philadelphia* 8: 72-73.

Lepvrier, C. y Martínez-García, E. 1990. Fault development and stress evolution of the post-Hercynian Asturian Basin (Asturias and Cantabria, northwestern Spain). *Tectonophysics* 184 (3-4): 345-356.

Lindgren, J., Currie, P.J., Rees, J., Siverson, M., Lindström, S. y Alwmark, C. 2008. Theropod dinosaur teeth from the lowermost Cretaceous Rabekke Formation on Bornholm, Denmark. *Geobios* 41 (2): 253-262.

Lindoso, R.M., Medeiros, M.A., De Souza Carvalho, I. y Da Silva Marinho, T. 2012. *Masiakasaurus*-like theropod teeth from the Alcântara Formation, São Luís Basin (Cenomanian), northeastern Brazil. *Cretaceous Research* 36: 119-124.

Linnaeus, C. 1758. *Systema Naturae per Raegna Tria Naturae. Volume 1. Regnum Animale.* Trustees. British Museum (Natural History), London, .

Liyong, J., Jun, C. y Godefroit, P. 2012. A new basal Ornithomimosaur (Dinosauria: Theropoda) from the Early Cretaceous Yixian Formation, Northwest China. En: Godefroit, P. (ed.), *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*, 466-487. Indiana University Press, Bloomington, Indiana.

Loewen, M.A., Irmis, R.B., Sertich, J.J.W., Currie, P.J. y Sampson, S.D. 2013. Tyrant Dinosaur Evolution Tracks the Rise and Fall of Late Cretaceous Oceans. *PLoS ONE* 8 (11): e79420.

Longrich, N.R. 2008. Small theropod teeth from the Lance Formation of Wyoming, USA. En: Sankey, J.T. y Baszio, S. (eds.), *Vertebrate Microfossil Assemblages: Their Role in Paleoecology and Paleobiogeography.*, 135-158. Indiana University Press, Bloomington, Indiana..

López-Gómez, J., Arche, A. y Pérez-López, A. 2002. Permian and Triassic. En: *The Geology of Spain*, 185-222. .

Louchart, A. y Pouech, J. 2017. A tooth of Archaeopterygidae (Aves) from the Lower Cretaceous of France extends the spatial and temporal occurrence of the earliest birds. *Cretaceous Research* 73: 40-46.

Lozano, R.P., Delvene, G., Piñuela, L. y García-Ramos, J.C. 2016. Late Jurassic biogeochemical microenvironments associated with microbialite-coated unionids (Bivalvia), Asturias (N Spain).

Palaeogeography, Palaeoclimatology, Palaeoecology 443: 80-97.

Lü, J., Currie, P.J., Xu, L., Zhang, X., Pu, H. y Jia, S. 2013. Chicken-sized oviraptorid dinosaurs from central China and their ontogenetic implications. *Naturwissenschaften* 100 (2).

M

Madsen, J.H. 1974. A new theropod dinosaur from the Upper Jurassic of Utah. *Journal of Paleontology* 48 (1): 27-31.

Madsen, J.H. 1976a. A second new theropod dinosaur from the Late Jurassic of East Central Utah. *Utah Geology* 3 (1): 51-60.

Madsen, J.H. 1976b. *Allosaurus fragilis:* A revised osteology. *Utah Geological Survey, Miscellaneous Publication Bulletin* 1: 1-177.

Makovicky, P.J. y Norell, M.A. 2004. Troodontidae. En: Weishampel, D.B., Dodson, P. y Osmólska, H. (eds.), *The Dinosauria,* 184-195. University of California Press, Berkeley.

Makovicky, P.J., Kobayashi, Y. y Currie, P.J. 2004. Ornithomimosauria. En: Weishampel, D.B., Dodson, P. y Osmólska, H. (eds.), *The Dinosauria*, 137-150. University of California Press, Berkeley.

Malafaia, E., Mocho, P., Escaso, F. y Ortega, F. 2017a. A juvenile allosauroid theropod (Dinosauria, Saurischia) from the Upper Jurassic of Portugal. *Historical Biology* 29 (5): 654-676.

Malafaia, E., Escaso, F., Mocho, P., Serrano-Martínez, A., Torices, A., Cachão, M. y Ortega, F. 2017b. Analysis of diversity, stratigraphic and geographical distribution of isolated theropod teeth from the Upper Jurassic of the Lusitanian Basin, Portugal. *Journal of Iberian Geology* 43 (2): 257-291.

Malafaia, E., Mocho, P., Escaso, F. y Ortega, F. 2017c. New data on the anatomy of *Torvosaurus* and other remains of megalosauroid (Dinosauria, Theropoda) from the Upper Jurassic of Portugal. *Journal of Iberian Geology* 43 (1): 33-59. doi:10.1007/s41513- 017-0003-9.

Malafaia, E., Mocho, P., Escaso, F., Dantas, P. y Ortega, F. 2018a. Carcharodontosaurian remains (Dinosauria, Theropoda) from the Upper Jurassic of Portugal. *Journal of Paleontology*: 1-16.

Malafaia, E., Gasulla, J.M., Escaso, F., Narváez, I., Sanz, J.L. y Ortega, F. 2018b. New spinosaurid (Theropoda, Megalosauroidea) remains from the Arcillas de Morella Formation (upper Barremian) of Morella, Spain. *Cretaceous Research* 92: 174-183.

Maleev, E.A. 1955. New carnivorous dinosaurs from the Upper Cretaceous of Mongolia. *Doklady, Academy of Sciences USSR* 104 (5): 779-783.

Mantell, G. 1827. Illustrations of the geology of Sussex: a general view of the geological relations of the southeastern part of England, with figures and descriptions of the fossils of Tilgate Forest. London, .

Marsh, O.C. 1877. Notice of new dinosaurian reptiles from the Jurassic formation. *American Journal of Science and Arts* 14 (84): 514-516.

Marsh, O.C. 1878. Notice on new dinosaurian reptiles. *American Journal of Science and Arts* 15: 241-244.

Marsh, O.C. 1879. Notice of New Jurassic Reptiles. *American Journal of Science* 18 (108): 501-505.

Marsh, O.C. 1881. Principal characters of American Jurassic dinosaurs. Part V. T*he American Journal of Science and Arts* 3 (21): 417-423.

Marsh, O.C. 1884. Principal characters of American Jurassic dinosaurs, Part VIII, The Order Theropoda. *American Journal of Science* 27 (160): 329-340.

Marsh, O.C. 1889. Notice of gigantic horned Dinosauria from the Cretaceous. *American Journal of Science. Series 3* 38: 173-175.

Marsh, O.C. 1890. Description of new dinosaur reptiles. *The American Journal of Science, series 3* 39: 81-86.

Martill, D.M. y Hutt, S. 1996. Possible baryonychid dinosaur teeth from the Wessex Formation (Lower Cretaceous, Barremian) of the Isle of Wight, England. *Proceedings of the Geologists' Association* 107 (2): 81-84. doi:10.1016/ S0016-7878(96)80001-0.

Martill D.M., Cruickshank, A.R.I., Frey, E., Small, P. y Clarke, M. 1996. A new crested maniraptoran dinosaur from the Santana Formation (Lower Cretaceous) of Brazil. *Journal of the Geological Society* 153

(1): 5-8. doi:10.1144/gsjgs. 153.1.0005.

Martin, R.E. 1999. *Taphonomy: A Process Approach*. Cambridge University Press, Cambridge.

Martín-Closas, C. y Grambast-Fessard, N. 1986. Les Charophytes du Crétacé inférieur de la región du Maestrat (Chaîne ibérique-Catalanides, Espagne). *Paleobiologie Continentale* 15: 1-86.

Martin-Closas, C. y Alonso Millan, A. 1998. Estratigrafia y bioestratigrafia (Charophyta) del Cretacico inferior en el sector occidental de la cuenca de Cameros (Cordillera Iberica). *Revista de la Academia de Ciencias de Zaragoza* 11 (3-4): 253-269.

Martín-Closas, C. y Diéguez, C. 1998. Charophytes from the Lower Cretaceous of the Iberian ranges (Spain). Paleontology. Paleontology 41: 1133-1152.

Martínez, R., García-Ramos, J.C., Piñuela, L., Lires, J., Luna, M. y Veigas, D. 2000. Dientes de Theropoda (Dinosauria: Saurischia) del Jurásico Superior de Asturias, España. *I Congresso Ibérico de Paleontologia/XVI Jornadas de la Sociedad Española de Paleontología*: 109-110.

Martinez, R.N., Sereno, P.C., Alcober, O.A., Colombi, C.E., Renne, P.R., Montañez, I.P. y Currie, B.S. 2011. A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. *Science* 331 (6014): 206-210.

Maryańska, T., Osmólska, H. y Wolsan, M. 2002. Avialan status for Oviraptorosauria. *Acta Palaeontologica Polonica* 47 (1): 97-116.

Mas, R., García, A., Salas, R., Meléndez, A., Alonso, A., Aurell, M., Bádenas, B., Benito, M.I., Carenas, B., García-Hidalgo, J.F., Gil, J. y Segura, M. 2004. Segunda fase de rifting: Jurásico Superior-Cretácico Inferior. *Geología de España*: 503-510.

Mateus, O. 1998. *Lourinhanosaurus antunesi*, a new Upper Jurassic allosauroid (Dinosauria: Theropoda) from Lourinhã (Portugal). *Memórias da Academia de Ciências de Lisboa* 37: 111-124.

Mateus, O. 2006. Late Jurassic dinosaurs from the Morrison Formation (USA), the Lourinhã and Alcobaça Formations (Portugal), and the Tendaguru beds (Tanzania): a comparison. *New Mexico Museum of Natural History and Science Bulletin 36* (2003): 223-231.

Mateus, O., Walen, A. y Antunes, M.T. 2006. The large theropod fauna of the Lourinha Formation (Portugal) and its similarity to the Morrison Formation, with a description of a new species of *Allosaurus*. *New Mexico Museum of Natural History and Science Bulletin 36*: 123–129.

Mateus, O., Araújo, R., Natário, C. y Castanhinha, R. 2011. A new specimen of the theropod dinosaur *Baryonyx* from the early Cretaceous of Portugal and taxonomic validity of *Suchosaurus*. *Zootaxa* 68 (2827): 54-68.

Matthew, W.D. y Brown, B. 1922. The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. *Bulletin of the American Museum of Natural History* 46: 367-385.

Maxwell, W.D. y Ostrom, J.H. (1995). Taphonomy and paleobi- ological implications of Tenontosaurus-Deinonychus associations. *Journal of Vertebrate Paleontology* 15: 707–712.

Medrano-Aguado, E., Alonso, A., Pérez-Pueyo, M. y Canudo, J.I. 2018a. Primer resto poscraneal de Theropoda en la Formación Blesa (Barremiense). *XVI EJIP Conference Proocedings*: 1-4.

Medrano-Aguado, E., Parrilla-Bel, J., Alonso, A., Pérez-Pueyo, M., Galán, J., Canudo, J.I. y Aurell, M. 2018b. On the vertebrate palaeobiodiversity from the Middle Blesa Formation (Barremian) of Northeast Spain. *3rd IMERP conference proceedings*: 48.

Meyer, H. von. 1832. Paleologica zur Geschichte der Erde. Frankfurt am Main, .

Meyer, H. von. 1861. Vogel-Federn und Palpipes priscus von Solenhofen. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde* 561.

Milner, A.C. 2002. Theropod dinosaurs of the Purbeck Limestone Group, southern England. *Life and Environments in Purbeck Times* (1959): 191-201.

Modesto, S.P. y Anderson, J.S. 2004. The phylogenetic definition of Reptilia. *Systematic Biology* 53 (5): 815-821.

Molnar, R.E., Obata, I., Tanimoto, M. y Matsukawa, M. 2009. A tooth of *Fukuiraptor* aff. *F. kitaidaniensis* from the Lower Cretaceous Sebayashi Formation, Sanchu Cretaceous, Japan. *Bulletin of Tokyo Gakugei University, Division of Natural Sciences*, 61: 105-117.

Monroe, B.L. y Sibley, C.G. 1993. A world checklist of birds. Yale University Press, New Haven.

Moreno-Azanza, M., Canudo, J.I. y Gasca, J.M. 2014a. Spheroolithid eggshells in the Lower Cretaceous of Europe. Implications for eggshell evolution in ornithischian dinosaurs. *Cretaceous Research* 51: 75-87.

Moreno-Azanza, M., Canudo, J.I. y Gasca, J.M. 2014b. Unusual theropod eggshells from the Early Cretaceous Blesa Formation of the Iberian Range, Spain. *Acta Palaeontologica Polonica* 59 (4): 843-854.

Moreno-Azanza, M., Canudo, J.I. y Gasca, J.M. 2015. Enigmatic Early Cretaceous ootaxa from Western Europe with signals of extrinsic eggshell degradation. *Cretaceous Research* 56: 617-627.

Müller, R.T. y Dias-da-Silva, S. 2017. Taxon sample and character coding deeply impact unstable branches in phylogenetic trees of dinosaurs. *Historical Biology* 1-4.

Murat B. 1983. Contribution à l'étude stratigraphique, sédimentologique et tectonique du basin éocrétacé d'Oliete (Prov. de Teruel, Espagne) [*These Doct*]. [Toulouse]: Travaux du lab, Ge´ol. Sed. et. Paleont, Univ Paul Sabatier; p. 247.

N

Naish, D. y Sweetman, S.C. 2011. A tiny maniraptoran dinosaur in the Lower Cretaceous Hastings Group: Evidence from a new vertebrate-bearing locality in south-east England. *Cretaceous Research* 32 (4): 464-471.

Naish, D., Martill, D.M. y Frey, E. 2004. Ecology, systematics and biogeographical relationships of dinosaurs, including a new theropod, from the Santana Formation (?Albian, Early Cretaceous) of Brazil. *Historical Biology* 16 (2-4): 57-70.

Navarro-Lorbés, P. y Torices, A. 2018. Preliminary analysis of theropod teeth from «El Horcajo», Lower Cretaceous, La Rioja, Spain. Life finds a way. *XVI EJIP conference proceedings*: 83-88.

Nesbitt, S.J., Smith, N.D., Irmis, R.B., Turner, A.H., Downs, A. y Norell, M.A. 2009. A complete skeleton of a Late triassic Saurischian and the early evolution of dinosaurs. *Science* 326 (5959): 1530-1533.

Nesbitt, S.J., Sidor, C.A., Irmis, R.B., Angielczyk, K.D., Smith, R.M.H. y Tsuji, L.A. 2010. Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. *Nature* 464 (7285): 95-98.

Norell, M.A. y Makovicky, P.J. 2004. Dromaeosauria. En: Weishampel, D.B., Dodson, P. y Osmólska, H. (eds.), *The Dinosauria*, 196-209. University of California Press, Berkeley.

Norell, M.A., Clark, J.M., Turner, A.H., Makovicky, P.J., Barsbold, R. y Rowe, T. 2006. A new dromaeosaurdi theropod from Ukhaa Tolgod (Ömnögov, Mongolia). *American Museum Novitates* 3545: 1-51.

Norell, M.A., Makovicky, P.J., Bever, G.S., Balanoff, A.M., Clark, J.M., Barsbold, R. 2009. A review of the Mongolian Cretaceous dinosaur *Saurornithoides* (Troodontidae: Theropoda). *American Museum Novitates* 3654: 1-63.

Novas, F.E., De Valais, S., Vickers-Rich, P. y Rich, T.H. 2005. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften* 92 (5): 226-230.

Novas, F.E., Ezcurra, M.D. y Lecuona, A. 2008. *Orkoraptor burkei* nov. gen. et sp., a large theropod from the Maastrichtian Pari Aike Formation, Southern Patagonia, Argentina. *Cretaceous Research* 29 (3): 468-480.

Novas, F.E., Ezcurra, M.D., Chatterjee, S. y Kutty, T.S. 2010. New dinosaur species from the Upper Triassic Upper Maleri and Lower Dharmaram formations of Central India. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 101 (3-4): 333-349.

Novas, F.E., Agnolín, F.L., Ezcurra, M.D., Porfiri, J. y Canale, J.I. 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. *Cretaceous Research* 45: 174-215.

O

Ortega, F., Escaso, F., Gasulla, J.M., Dantas, P. y Sanz, J.L. 2006. Dinosaurios de la Península Ibérica. *Estudios Geológicos* 62 (1): 219-240. doi:10.3989/egeol. 0662122.

Ortega, F., Escaso, F. y Sanz, J.L. 2010. A bizarre, humped Carcharodontosauria (Theropoda) from the lower cretaceous of Spain. *Nature* 467 (7312): 203-206.

Osborn, H.F. 1903a. On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. *Science* 17 (424): 275-276.

Osborn, H.F. 1903b. *Ornitholestes hermanni*, a new compsognathoid dinosaur from the Upper Jurassic. *Bulletin of the American Museum of Natural History* XIX: 459-464.

Osborn, H.F. 1905. Tyrannosaurids and other Cretaceous carnivorous dinosaurs. *Bulletin of the American Museum of Natural History* 21: 191-226.

Osborn, H.F. 1906a. *Tyrannosaurus* and other cretaceous carnivorous dinosaurs. *Bulletin of the American Museum of Natural History* 21 (3): 259-265.

Osborn, H.F. 1906b. *Tyrannosaurus*, Upper Cretaceous carnivorous dinosaur. (Second communication). *Bulletin of the American Museum of Natural History* 22 (16): 281-296.

Osborn, H.F. 1924. Three new Theropoda, *Protoceratops* Zone, central Mongolia. *American Museum Novitates* (144): 1-12.

Ösi, A., Apesteguía, S. y Kowalewski, M. 2010. Non-avian theropod dinosaurs from the early Late Cretaceous of central Europe. *Cretaceous Research* 31 (3): 304-320.

Ostrom, J.H. 1969. Osteology of *Deinonychus antirrhopus,* an Unusual Theropod from the Lower Cretaceous of Montana. *Peabody Museum of Natural History* 30: 1-165.

Owen, R. 1842. Report on British Fossil Reptiles. Part II. *Report of the Eleventh Meeting of the British Association for the Advancement of Science*: 60-204.

Owen, R. 1854. On some fossil reptilian and mammalian remains from the Purbecks. *Quarterly Journal of the Geological Society of London* 10: 420-443.

Owen, R. 1876. Supplement (No. VII) to the Monograph on the Fossil Reptilia of the Wealden and Purbeck Formations. (*Poikilopleuron* and *Chondrosteosaurus*). *Palaeontographical Society Monograph* 30: 1-7.

P

Paik, I.S., Kim, H.J., Lim, J.D., Huh, M. y Lee, H. I. 2011. Diverse tooth marks on an adult sauropod bone from the Early Cretaceous, Korea: Implications in feeding behaviour of theropod dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 309: 342-346.

Park, E.-J., Yang, S.-Y. y Currie, P.J. 2000. Early Cretaceous dinosaur teeth of Korea. P*aleontological Society of Korea Special Publication* 4: 85-98.

Parrilla-Bel, J. y Canudo, J.I. 2015. On the presence of plesiosaurs in the Blesa Formation (Barremian) in Teruel (Spain). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 278 (2): 213-227.

Parrilla-Bel, J. y Canudo, J.I. 2018. New longirostrine crocodylomorph remains from the Blesa Formation (Barremian) in the Iberian Peninsula (Spain). *Journal of Iberian Geology* 44 (1): 55-66.

Parry, L.A., Baron, M.G. y Vinther, J. 2017. Multiple optimality criteria support Ornithoscelida. *Royal Society Open Science* 4 (10).

Parry, L.A., Baron, M.G. y Vinther, J. 2018. Correction to «Multiple optimality criteria support Ornithoscelida». *Royal Society Open Science* 5 (3): 180154.

Paul, G.S. 1988. *Predatory Dinosaurs of the World.* Simon & Schuster, New York.

Paul, G.S. 2002. *Dinosaurs of the Air*. John Hopkins University Press, Baltimore and London, .

Pereda-suberbiola, X., Ruiz-omeñaca, J.I., Canudo, J.I., Torcida, F. y Sanz, J.L. 2010. Dinosaur Faunas from the Early Cretaceous (Valanginian-Albian) of Spain. En: Godefroit, P. (ed.), B*ernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems*, 379-407. Indiana University Press.

Pereda-Suberbiola, X. y Ruiz-Omeñaca, J.I. 2005. Los primeros descubrimientos de dinosaurios en España. *Revista Española de Paleontología* X: 15-28.

Pereda-Suberbiola, X., Meijide, M., Torcida, F., Welle, J., Fuentes, C., Izquierdo, L.A., Montero, D., Pérez, G. y Urién, V. 1999. Espinas dermicas del dinosaurio anquilosaurio Polacanthus en las facies Weald de

Salas de los Infantes (Burgos, España). *Museum* 272: 267-272.

Pérez-Estaún, A., Bea, F., Bastida, F., Aurell, M., Martínez-Catalán, J.R., Martínez-Poyatos, D., Arenas, R., Díaz-García, A., Azor, A., Simancas, J.F. y González Lodeiro, F. 2004. La cordillera varisca europea: el macizo ibérico. En: Vera, J.A. (ed.), *Geología de España*, 21-25. IGME.

Pérez-Moreno, B.P., Sanz, J.L., Buscalioni, Á.D., Moratalla, J., Ortega, F. y Rasskin-Gutman, D. 1994. A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature* 370: 363-367.

Peyer, K. 2006. A reconsideration of *Compsognathus* from the Upper Tithonian of Canjuers, Southeastern France. *Journal of Vertebrate Paleontology* 26 (4): 879-896.

Platt, N.H. 1986. Sedimentology and tectonics of the Western Cameros Basin, Province of Burgos, N.Spain. *PhD dissertation.*

Platt, N.H. 1989. Continental sedimentation in an evolving rift basin: the Lower Cretaceous of the western Cameros Basin (northern Spain). *Sedimentary Geology* 64 (1-3): 91-109.

Platt, N.H. 1990. Basin evolution and fault reactivation in the western Cameros Basin, Northern Spain.165-175pp.

Plot, R. 1677. The Natural History of Oxfordshire, being an essay toward the Natural history of England.

Pol, D. y Rauhut, O.W.M. 2012. A middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. *Proceedings of the Royal Society B: Biological Sciences* 279 (1741): 3170-3175.

Porfiri, J.D., Novas, F.E., Calvo, J.O., Agnolín, F.L., Ezcurra, M.D. y Cerda, I.A. 2014. Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. *Cretaceous Research* 51: 35-55.

Porfiri, J.D., Juárez Valieri, R.D., Santos, D.D.D. y Lamanna, M.C. 2018. A new megaraptoran theropod dinosaur from the Upper Cretaceous Bajo de la Carpa Formation of northwestern Patagonia. *Cretaceous Research.* in press.

Pouech, J., Mazin, J.M. y Billon-Bruyat, J.P. 2006. Microvertebrate biodiversity from Cherves-de-Cognac (Lower Cretaceous, Berriasian: Charente, France). En: 9*th International symposium, mesozoic terrestrial ecosystems and Biota, Manchester, Abstracts and Proceedings*, pp 96-100.

Puértolas-Pascual, E., Canudo, J.I. y Rabal-Garcés, R. 2014. Revisión de la biodiversidad de los crocodilomorfos del yacimiento de La Cantalera en Teruel, España (Hauteriviense-Barremiense). In: Arreguín-Rodriguez, G., Colmenar, J., Díaz-Berenguer, E., Galán, J., Legarda-Lisarri, A., Parrilla-Bel, J., Puértolas-Pascual, E., Silva-Casal, R. (eds). *New insights on ancient life* 101-104.

Puértolas-Pascual, E., Canudo, J.I. y Rabal-Garcés, R. 2015. Exceptional crocodylomorph biodiversity of "La Cantalera" site (lower Barremian ; Lower Cretaceous) in Teruel , Spain. *Palaeontologia Electronica* 18.2.28A (June): 1-16.

R

Ramírez del Pozo, J. 1969. Bioestratigrafía y Paleogeografía del Jurásico de la costa asturiana (Zona de Oviedo-Gijón-Villaviciosa). *Boletín Geológico y Minero* 80 (4): 307-332.

Rauhut, O.W.M. 1995. Zur systematischen Stellung der afrikanische Theropoden Carcharodontosaurus Stromer 1931 und Bahariasaurus Stromer 1934. *Berliner geowissenschaftliche Abhandlungen* E16 (Gundo: 357-375.

Rauhut, O.W.M. 2000. The dinosaur fauna from the Guimarota mine. En: Martin, T. y Krebs, B. (eds.), *Guimarota a Jurassic Ecosystem*, 75-82. München.

Rauhut, O.W.M. 2002. Dinosaur teeth from the Barremian of Uña, Province of Cuenca, Spain. *Cretaceous Research* 23 (2): 255-263.

Rauhut, O.W.M. 2003. A tyrannosauroid dinosaur from the Upper Jurassic of Portugal. *Palaeontology* 46 (5): 903-910.

Rauhut, O.W.M. 2004. Provenance and anatomy of *Genyodectes serus*, a large toothed ceratosaur (Dinosauria: Theropoda) from Patagonia. *Journal of Vertebrate Paleontology* 24 (4): 773-779.

Rauhut, O.W.M. 2005. Osteology and relationships of a new theropod dinosaur from the Middle Jurassic of Patagonia. *Palaeontology* 48 (1): 87-110.

Rauhut, O.W.M. 2011. Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). *Special Papers in Palaeontology* (86): 195-239.

Rauhut, O.W.M. y Kriwet, J. 1994. Teeth of a big theropod dinosaur from Porto das Barcas (Portugal). *Berliner geowissenschaftliche Abhandlungen* (E) 13 (January 1994): 179-185.

Rauhut, O.W.M. y Werner, C. 1995. First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). *Paläontologische Zeitschrift* 69 (3-4): 475-489.

Rauhut, O.W.M. y López-Arbarello, A. 2009. Considerations on the age of the Tiouaren Formation (Iullemmeden Basin, Niger, Africa): Implications for Gondwanan Mesozoic terrestrial vertebrate faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 271: 259-267.

Rauhut, O.W.M. y Carrano, M.T. 2016. The theropod dinosaur Elaphrosaurus bambergi Janensch, 1920, from the Late Jurassic of Tendaguru, Tanzania. *Zoological Journal of the Linnean Society* 178 (3): 546-610.

Rauhut, O.W.M. y Pol, D. 2017. A theropod dinosaur from the Late Jurassic Cañadón Calcáreo Formation of central Patagonia, and the evolution of the theropod tarsus. *Ameghiniana* 54 (5): 539-566.

Rauhut, O.W.M., Milner, A.C. y Moore-Fay, S. 2010. Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society* 158 (1): 155-195.

Rauhut, O.W.M., Foth, C., Tischlinger, H. y Norell, M.A. 2012. Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. *Proceedings of the National Academy of Sciences* 109 (29): 11746-11751.

Rauhut, O.W.M., Hübner, T.R. y Lanser, K.-P. 2016. A new megalosaurid theropod dinosaur from the late Middle Jurassic (Callovian) of north-western Germany : Implications for theropod evolution and faunal turnover in the Jurassic. *Palaeontologia Electronica* 19.2.26A (August): 1-65.

Rauhut, O.W.M., Foth, C. y Tischlinger, H. 2018a. The oldest *Archaeopteryx* (Theropoda: Avialiae): a new specimen from the Kimmeridgian/Tithonian boundary of Schamhaupten, Bavaria. *PeerJ* 6.

Rauhut, O.W.M., Piñuela, L., Castanera, D., García-Ramos, J.C. y Sánchez Cela, I. 2018b. The largest European theropod dinosaurs: remains of a gigantic megalosaurid and giant theropod tracks from the Kimmeridgian of Asturias, Spain. *PeerJ* 6: e4963.

Rayfield, E.J., Milner, A.C., Xuan, V.B. y Young, P.G. 2007. Functional morphology of spinosaur «crocodile-mimic» dinosaurs. *Journal of Vertebrate Paleontology* 27 (4): 892-901.

Reichel, M. 2010. The heterodonty of *Albertosaurus sarcophagus* and *Tyrannosaurus rex*: biomechanical implications inferred through 3-D models. *Canadian Journal of Earth Sciences* 1261: 1253-1261.

Riveline, J., Berger, J.P., Feist, M., Martín-Closas, C., Schudack, M. y Soulié-Märsche, I. 1996. European Mesozoic-Cenozoic charophyte biozonation. *Bulletin de la Société Géologique de France* 167 (3): 453-468.

Reig, O.A. 1963. La presencia de dinosaurios saurisquios en los «estratos de Ischigualasto» (Mesotriásico Superior) de las provincias de San Juan y La Rioja (República Argentina). *Ameghiniana* 3 (1): 3-20.

Rogers, R.R., Krause, D.W. y Rogers, K.C. 2003. Cannibalism in the Madagascan dinosaur *Majungatholus atopus*. *Nature* 422: 515-518.

Rolando, A.M.A., Novas, F.E., Agnolín, F. (2019). A reanalysis of *Murusraptor barrosaensis* Coria & Currie (2016) affords new evidence about the phylogenetical relationships of Megaraptora. *Cretaceous Research*, in press.

Royo-Torres, R., Cobos, A. y Alcalá, L. 2009. Diente de un gran dinosaurio terópodo (Allosauroidea) de la Formación Villar del Arzobispo (Titónico-Berriasiense) de Riodeva (España). *Estudios Geológicos* 65 (1): 91-99.

Ruiz-Omeñaca, J.I. 2006. Restos directos de dinosaurios (Saurischia, Ornithischia) en el Barremiense (Creta´cico Inferior) de la Cordillera Ibérica en Aragón (Teruel, España) [*Tesis doctoral*]. Universidad de Zaragoza.

Ruiz-Omeñaca, J.I. 2011. *Delapparentia turolensis* nov. gen et sp., un nuevo dinosaurio iguanodontoideo (Ornithischia: Ornithopoda) en el Cretácico Inferior de Galve. *Estudios Geológicos* 67(1), 83–110.

Ruiz-Omeñaca, J.I. y Canudo, J.I. 2003. Un nuevo dinosaurio terópodo ("*Prodeinodon*" sp.) en el Cretácico Inferior de La Cantalera (Teruel). *Geogaceta* 34: 111-114.

Ruiz-Omeñaca, J.I., Canudo, J.I. y Cuenca-Bescós, G. 1995. Dientes de dinosaurios (Orntischia y Saurischia) del Barremiense superior (Cretácico inferior) de Vallipón (Castellote, Teruel). *Mas de las matas* 15: 59-103.

Ruiz-Omeñaca, J.I., Canudo, J.I. y Cuenca-Bescós, G. 1997a. Primera cita de dinosaurios barionícidos (Saurischia:Theropoda) en el Barremiense superior (Cretácico inferior) de Vallipón (Castellote, Teruel). *Mas de las Matas*: 201-223.

Ruiz-Omeñaca, J.I., Canudo, J.I. y Cuenca-Bescós, G. 1997b. Primera evidencia de un área de alimentación de dinosaurios herbívoros en el Cretácico Inferior de España (Teruel). *Monografía de la Academia de Ciencias Exactas, Física, Química y Naturales de Zaragoza*: 1-48.

Ruiz-Omeñaca, J.I., Canudo, J.I., Cruzado-Caballero, P., Infante, P. y Moreno-Azanza, M. 2005. Baryonychine teeth (Theropoda: Spinosauridae) from the Lower Cretaceous of La Cantalera (Josa, NE Spain). *Kaupia. Darmstädter Beiträger zur Naturgeschichte* 14: 59-63.

Ruiz-Omeñaca, J.I., Piñuela, L., García-Ramos, J.C. y Canudo, J.I. 2008. Dientes de dinosaurios carnívoros (Saurischia : Theropoda) del Jurásico Superior de Asturias. *Actas de Las IV Jornadas Internacinoales Sobre Paleontología de Dinosaurios y su Entorno, Salas de Los Infantes (Burgos, Espana), 13-15 de Septiembre de 2007:* 273-291.

Ruiz-Omeñaca, J.I., Piñuela, L., García-Ramos, J.C. y Canudo, J.I. 2009. Dientes de dinosaurios carnívoros (Saurischia : Theropoda) del Jurásico Superior de Asturias. *Actas del as IV Jornadas Internacinoales Sobre Paleontología de Dinosaurios y su Entorno, Salas de Los Infantes (Burgos, Espana), 13-15 de Septiembre de 2007*: 273-291.

Ruiz-Omeñaca, J.I., Piñuela, L. y García-Ramos, J.C. 2012a. Primera descripción de dientes de dinosaurios terópodos en la Formación Tereñes (Kimmeridgiense), Asturias. *Geogaceta* (52): 271-274.

Ruiz-Omeñaca, J.I., Canudo, J.I., Cuenca-Bescós, G., Cruzado-Caballero, P.L., Gasca, J.M. y Moreno-Azanza, M. 2012b. A new basal ornithopod dinosaur from the Barremian of Galve, Spain. *Comptes Rendus Paleovol* 11(6): 435-444.

Ruiz, J., Torices, A., Serrano, H. y López, V. 2011. The hand structure of *Carnotaurus sastrei* (Theropoda, Abelisauridae): Implications for hand diversity and evolution in abelisaurids. *Palaeontology* 54 (6): 1271-1277.

Russell, D.A. 1970. Tyrannosaurs from the Late Cretaceous of western Canada. *National Museum of Natural Sciences, Publications in Paleontology* 1: 1-34.

Russell, D.A. 1972. Ostrich Dinosaurs from the Late Cretaceous of Western Canada. *Canadian Journal of Earth Sciences* 9 (4): 375-402.

Russell, D.A. 1997. Therizinosauria. En: Currie, P.J. y Padian, K. (eds.), *Encyclopedia of Dinosaurs*, 729-730. Academic Press, San Diego.

S

Salas, R. y Casas, A. 1993. Mesozoic extensional tectonics, stratigraphy and crustal evolution during the Alpine cycle of the eastern Iberian basin. *Tectonophysics* 228 (1-2): 33-55.

Salas, R. y Guimerà, J. 1996. Main structural features of the Lower Cretaceous Maestrat Basin (Eastern Iberian Range). *Geogaceta* 20 (7): 1704-1706.

Salas, R., Guimerá, J., Mas, R., Martín-Closas, C., Meléndez, A. y Alonso, A. 2001. Evolution of the Mesozoic Central Iberian Rift System and its Cenozoic inversion (Iberian Chain). Peritethyan rift/wrench basins and passive margins. *Mémoires du Muséum National d'Histoire Naturelle* 186: 145-185.

Sales, M.A.F. y Schultz, C.L. 2017. Spinosaur taxonomy and evolution of craniodental features: Evidence from

Brazil. *PLoS ONE* 12 (11): 8-11.

Sales, M.A.F., Lacerda, M.B., Horn, B.L.D., De Oliveira, I.A.P. y Schultz, C.L. 2016. The «x» of the Matter: Testing the Relationship between Paleoenvironments and Three Theropod Clades. *PLoS ONE* 11 (2): e0147031.

Samman, T., Powell, G.L., Currie, P.J. y Hills, L. V. 2005. Morphometry of the teeth of western North American tyrannosaurids and its applicability to quantitative classification. *Acta Palaeontologica Polonica* 50 (4): 757-776.

Sampson, S.D., Carrano, M.T. y Forster, C.A. 2001. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. *Nature* 409 (6819): 504-506.

Sánchez-Hernández, B. y Benton, M.J. 2012. Filling the ceratosaur gap: A new ceratosaurian theropod from the Early Cretaceous of Spain. *Acta Palaeontologica Polonica* 59 (3): 581-600.

Sánchez-Hernández, B., Benton, M.J. y Naish, D. 2007. Dinosaurs and other fossil vertebrates from the Late Jurassic and Early Cretaceous of the Galve area, NE Spain. P*alaeogeography, Palaeoclimatology, Palaeoecology* 249 (1-2): 180-215.

Sánchez-Moya, Y. y Sopeña, A. 2004. El rift Mesozoico Europeo. En: Vera, J.A. (ed.), *Geología de España*, 484-485. IGME, Madrid.

Sankey, J.T. 2008. Diversity of latest Cretaceous (late Maastrichtian) small theropods and birds: teeth from the Lance and Hell Creek formations, USA. En: Sankey, J.T. y Baszio, S. (eds.), *Vertebrate Microfossil Assemblages: Their Role in Paleoecology and paleobiogeography.*, 117-134. Indiana University Press, Bloomington, Indiana.

Sankey, J.T., Brinkman, D.B., Guenther, M. y Currie, P.J. 2002. Small theropod and birth teeth from the Late Cretaceous (Late Campanian) Judith River Group, Alberta. J*ournal of Paleontology* 76 (4): 751-763.

Sankey, J.T., Standhart, B.R. y Schiebout, J.A. 2005. Theropod teeth from the Upper Cretaceous (Campanian-Maastrichtian), Big Bend National Park, Texas. En K. Carpenter (Ed.), *The Carnivorous Dinosaurs* (pp. 127–152). Bloomington: Indiana University Press.

Santafé, J. V, Casanovas, M.L., Sanz, J.L. y Calzada, S. 1982. Geología y Paleontología (Dinosaurios) de las Capas Rojas de Morella (Castellón, España). D*iputación Provincial de Castellón y Diputación de Barcelona*: 1-169.

Sanz, J.L. y Bonaparte, J.F. 1992. A New Order of Birds (Class Aves) from the Lower Cretaceous of Spain. In: Papers in avian paleontology honoring Pierce Brodkorb. *Natural History Museum of Los Angeles County Contributions in Science*, 36, 38-49. .

Sanz, J.L. y Buscalioni, A.D. 1992. A new bird from the Early Cretaceous of Las Hoyas, Spain, and the early radiation of birds. *Palaeontology* 35 (4): 829-845.

S**anz, J.L. Buscalioni, Á.D., Casanovas, M.L., y Santafé, J.V. 1987.** Dinosaurios del Cretácico Inferior de Galve (Teruel, España). *Estudios Geológicos Galve-Tremp*: 45-64.

Sanz, J.L., Bonaparte, J.F. y Lacasa, A. 1988. Unusual early Cretaceous birds from Spain. *Nature* 331: 433-435.

Sanz, J.L., Chiappe, L.M., Pérez-Moreno, B.P., Buscalioni, Á.D., Moratalla, J., Ortega, F. y Poyato-Ariza, F.J. 1996. An Early Cretaceous bird from Spain and its implications for the evolution of avian flight. *Nature* 382: 442-445.

Schudack, M.E. 1989. Charophytenflores aude den unterkretazischen Vertebraten-Fundschicten bei Galve und Uña (Ostspanien). *Berliner geowissenschaftliche Abhandlungen/ Reihe A, Geologie und Paläontologie* 106: 409-443.

Schudack, U. y Schudack, M. 2009. Ostracod biostratigraphy in the Lower Cretaceous of the Iberian chain (eastern Spain). *Journal of Iberian Geology* 35 (2): 141-168.

Seeley, H.G. 1887. On *Aristosuchus pusillus* (Owen), being further notes on the fossils described by Sir R. Owen as *Poikilopleuron pusillus*, Owen. *Quarterly Journal of the Geological Society of London* 43: 221-228.

Seeley, H.G. 1888. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London* 43 (258-265): 165-171.

Sellers, W.I., Pond, S.B., Brassey, C.A., Manning, P.L. y Bates, K.T. 2017. Investigating the running abilities of *Tyrannosaurus rex* using stress-constrained multibody dynamic analysis. *PeerJ* 5: e3420.

Senter, P., Kirkland, J.I., Bird, J. y Bartlett, J. A. 2011. A new troodontid theropod dinosaur from the lower Cretaceous of Utah. *PLoS One* 5(12): e14329.

Sereno, P.C. 1997. The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Sciences* 25: 435-489.

Sereno, P.C. 2000. *Iberomesornis romerali* (Ornithothoraces, Aves) re-evaluated as an enantiornithine bird. *Neues Jahrbuch fur Geologie und Paläontologie Abhandlungen*, 215, 365–395.

Sereno, P.C. 2005. Stem Archosauria - Taxon-Search. TaxonSearch Database for Suprageneric Taxa & Phylogenetic Definitions. Downloaded from http://www.taxonsearch.org/ .

Sereno, P.C. y Brusatte, S.L. 2008. Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz formation of Niger. *Acta Palaeontologica Polonica* 53: 15-46.

Sereno, P.C., Forster, C.A., Rogers, R.R. y Monetta, A.M. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature* 361: 64-66.

S**ereno, P.C., Beck, A.L., Dutheil, D.B., Gado, B., Larsson, H.C.E., Lyon, G.H., Marcot, J.D., Rauhut, O.W.M., Sadleir, R.W., Sidor, C.A., Varricchio, D.D., Wilson, G.P. y Wilson, J.A. 1998.** A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science* 282 (5392): 1298-1302.

Serrano-Brañas, C.I., Torres-Rodríguez, E., Reyes Luna, P.C., González, I. y González-León, C. 2014. Tyrannosaurid teeth from the Lomas Coloradas Formation, Cabullona Group (Upper Cretaceous) Sonora, México. *Cretaceous Research* 49: 163-171.

Serrano-Martínez, A., Ortega, F., Sciscio, L., Tent-Manclús, J.E., Fierro Bandera, I. y Knoll, F. 2015. New theropod remains from the Tiourarén Formation (?Middle Jurassic, Niger) and their bearing on the dental evolution in basal tetanurans. *Proceedings of the Geologists' Association* 126: 107-118.

Serrano-Martínez, A., Vidal, D., Sciscio, L., Ortega, F. y Knoll, F. 2016. Isolated theropod teeth from the Middle Jurassic of Niger and the early dental evolution of Spinosauridae. *Acta Paleontologica Polonica* 61 (2): 403-415.

Smith, J.B. 2005. Heterodonty in *Tyrannosaurus rex*: implications for the taxonomic and systematic utility of theropod dentitions. *Journal of Vertebrate Paleontology* 25 (4): 865-887.

Smith, J.B. 2007. Dental morphology and variation in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 27 (2): 103-126.

Smith, J.B. y Dodson, P. 2003. A Proposal for a Standard Terminology of Anatomical Notation and Orientation in Fossil Vertebrate Dentitions. *Journal of Vertebrate Paleontology* 23 (1): 1-12.

Smith, J.B. y Dalla Vecchia, F.M. 2006. An abelisaurid (Dinosauria: Theropoda) tooth from the Lower Cretaceous Chicla formation of Libya. *Journal of African Earth Sciences* 46: 240-244.

Smith, J.B. y Lamanna, M.C. 2006. An abelisaurid from the Late Cretaceous of Egypt: implications for theropod biogeography. *Naturwissenschaften*, 93, 242–245.

Smith, J.B., Vann, D.R. y Dodson, P. 2005. Dental morphology and variation in theropod dinosaurs: Implications for the taxonomic identification of isolated teeth. *Anatomical Record - Part A Discoveries in Molecular, Cellular, and Evolutionary Biology* 285 (2): 699-736.

S**oria, A.R. 1997.** La sedimentación en las cuencas marginales del surco ibérico durante el Cretácico Inferior y su control estructural. *Tesis doctoral*, Universidad de Zaragoza.

Soria, A.R., Martín-Closas, C., Meléndez, A., Meléndez, M.N. y Aurell, M. 1995. Estratigrafía del Cretácico inferior continental de la Cordillera Ibérica Central. *Estudios Geológicos* 51 (3-4): 141-152.

S**oto, M. y Perea, D. 2008.** A Ceratosaurid (Dinosauria , Theropoda) From the Late Jurassic – Early Cretaceous Of Uruguay. *Journal of Vertebrate Paleontology* 28 (2): 439-444.

Stevens, K.A. 2006. Binocular vision in theropod dinosaurs. *Journal of Vertebrate Paleontology* 26 (2): 321-330.

Stromer, E. 1915. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II Wirbeltier-Reste der Baharîje-Stufe (unterstes Cenoman). 3. Das Original des Theropoden Spinosaurus aegyptiacus nov. gen., nov. spec. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-physikalische Klasse* 28 (3): 1-32.

Stromer, E. 1931. Ergebnisse der Forschungreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharîjestufe (unterstes Cenoman). 10. Ein Skelett-Rest von Carcharodontosaurus nov. gen. *Abhandlungen der Bayerischen Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Abteilung. Neue Folfe* 9: 1-23.

Sues, H.D., Frey, E., Martill, D.M. y Scott, D.M. 2002. *Irritator challengeri,* a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology* 22 (3): 535-547.

Sues, H.D., Nesbitt, S.J., Berman, D.S. y Henrici, A.C. 2011. A late-surviving basal theropod dinosaur from the latest triassic of North America. *Proceedings of the Royal Society B: Biological Sciences* 278 (1723): 3459-3464.

Suñer, M. y Martín, M. 2009. Un nuevo yacimiento del tránsito Jurásico-Cretácico de Alpuente (Los Serranos, Valencia, España): Resultados preliminares. *Paleolusitana* 1: 441-447.

Sweetman, S.C. 2004. The first record of velociraptorine dinosaurs(Saurischia, Theropoda) from the Wealden(Early Cretaceous, Barremian) of southern England. *Cretaceous Research* 25 (3): 353-364.

T

Tavares, S.A.S., Ricardi Branco, F. y Santucci, R.M. 2014. Theropod teeth from the Adamantina Formation (Bauru Group, Upper Cretaceous), Monte Alto, São Paulo, Brazil. *Cretaceous Research* 50: 59-71.

Torcida Fernández-Baldor, F. 2006. Restos directos de dinosaurios en Burgos (Sistema Ibérico): un balance provisional. *Actas de las III Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*: 105-128

Torcida, F., Fuentes, C., Izquierdo, L.A., Montero, D. y Urién, V. 1997. Dientes de dinosaurios terópodos (cf. Baryonyx) en el *Weald* de Burgos (España). *Stvdia Geologica Salmanticensia* 33: 59-65.

Torcida Fernández-Baldor, F., Izquierdo Montero, L.Á., Huerta Hurtado, P., Montero Huerta, D., Pérez Martínez, G. y Pérez-Lorente, F. 2003. Dientes de dinosaurios (Theropoda, sauropoda), en el Cretácico inferior de Burgos (España). *Ciencias de la Terra* 26: 335-345.

Torcida Fernández-Baldor, F., Canudo, J.I., Huerta, P., Montero Huerta, D., Contreras, R., Pérez Martínez, G. y Urién Montero, V. 2009. Primeros Datos Sobre Las Vértebras Caudales Del Sauropodo De El Oterillo II (Fm. Castrillo De La Reina, Barremiense Superior-Aptiense Inferior, Salas De Los Infantes, Burgos, España). *IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno. Salas de los Infantes, Burgos*: 107-109.

Torcida Fernández-Baldor, F., Canudo, J.I., Huerta, P., Moreno-Azanza, M. y Montero, D. 2017. *Europatitan eastwoodi*, a new sauropod from the lower Cretaceous of Iberia in the initial radiation of somphospondylans in Laurasia. *PeerJ* 5: e3409.

Torices, A. 2007. Los dinosaurios terópodos del Cretácico Superior de la Cuenca Surpirenaica. Tesis doctoral. Universidad Complutense de Madrid, 409 pp.

Torices, A., Currie, P.J., Canudo, J.I. y Pereda-Suberbiola, X. 2013. Theropod Dinosaurs from the Upper Cretaceous of the South Pyrenees Basin of Spain. *Acta Palaeontologica Polonica* 60 (3): 611-626.

Torices, A., Wilkinson, R., Arbour, V.M., Ruiz-Omeñaca, J.I. y Currie, P.J. 2018. Puncture-and-Pull Biomechanics in the Teeth of Predatory Coelurosaurian Dinosaurs. *Current Biology* 28 (9): 1467-1474.e2.

Tsuihiji, T., Watabe, M., Tsogtbaatar, K., Tsubamoto, T., Barsbold, R., Suzuki, S., Lee, A.H., Witmer, L.M. y Ridgely, R.C. 2011. Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* (Theropoda , Tyrannosauridae) from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia. *Journal of Vertebrate Paleontology* 31 (3): 497-517.

Turner, A.H., Makovicky, P.J. y Norell, M.A. 2012. A Review of Dromaeosaurid Systematics and Paravian Phylogeny. *Bulletin of the American Museum of Natural History* 371 (371): 1-206.

V

Valenzuela, M., García-Ramos, J.C. y Suárez de Centi, C. 1986. The Jurassic sedimentation in Asturias (N Spain). *Trabajos de Geología, Univ. Oviedo* 16: 121-132.

Verdú, F. J., Godefroit, P., Royo-Torres, R., Cobos, A. y Alcalá, L. 2017. Individual variation in the postcranial skeleton of the Early Cretaceous Iguanodon bernissartensis (Dinosauria: Ornithopoda). *Cretaceous Research* 74: 65-86.

Viera, L. y Torres, J. 1995. Presencia de *Baryonyx walkeri* (Saurischia, Theropoda) en el Weald de La Rioja (España). Nota previa. M*unibe Ciencias Naturales* 57-61.

W

Walker, A.D. 1964. Triassic reptiles from the Elgin area: Ornithosuchus and the origin of Carnosaurs. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 248: 53-134.

Wang, S., Stiegler, J., Amiot, R., Wang, X., Du, G. hao, Clark, J.M. y Xu, X. 2017. Extreme Ontogenetic Changes in a Ceratosaurian Theropod. *Current Biology* 27 (1): 144-148.

Watson, D.M.S. 1957. On *Millerosaurus* and the early history of the sauropsid reptiles. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 240 (673): 325-400.

Weigert, A. 1995. Isolierte Zahne von cf *Archaeopteryx* sp. aus dem Oberen Jura der Kohlengrube Guimarota (Portugal). *Neues Jahrbuch für Geologie und Paläontologie*, Monatshefte 1995(9): 562-576.

Weishampel, D.A., Csiki, Z., Benton, M.J., Grigorescu, D. y Codrea, V. 2010. Palaeobiogeographic relationships of the Hateg biota-between isolation and innovation. *Palaeobiogeography, Palaeoclimatology, Palaeoecology* 293: 419-437.

White, M.A., Bell, P.R., Cook, A.G., Poropat, S.F. y Elliott, D.A. 2015. The dentary of *Australovenator wintonensis* (Theropoda, Megaraptoridae); implications for megaraptorid dentition. *PeerJ* 3: e1512.

Whitlock, J.A. y Richman, J.M. 2013. Biology of tooth replacement in amniotes. *International Journal of Oral Science* 5 (2): 66-70.

Williamson, T.E. y Brusatte, S.L. 2014. Small theropod teeth from the Late Cretaceous of the San Juan Basin, northwestern New Mexico and their implications for understanding latest Cretaceous dinosaur evolution. *PLoS ONE* 9 (4).

Witmer, L.M. y Ridgely, R.C. 2009. New insights into the brain, braincase, and ear region of tyrannosaurs (Dinosauria, Theropoda), with implications for sensory organization and behavior. *Anatomical Record* 292 (9): 1266-1296.

Wu, X.-C., Currie, P.J., Dong, Z., Pan, S. y Wang, T. 2009. A new theropod dinosaur from the Middle Jurasic of Lufeng, Yunnan, China. *Acta Geologica Sinica* 83 (1): 9-24.

X

Xu, X., Zhou, Z. y Wang, X. 2000. The smallest known nonavian theropod dinosaur. *Nature* 408: 705-708.

Xu, X., You, H., Du, K. y Han, F. 2011. An *Archaeopteryx*-like theropod from China and the origin of Avialae. *Nature* 475: 465.

Xu, X., Zhou, Z., Wang, X., Kuang, X., Zhang, F. y Du, X. 2003. Four-winged dinosaurs from China. *Nature* 421 (6921): 335-340.

Xu, X., Norell, M.A., Kuang, X., Wang, X., Zhao, Q. y Jia, C.K. 2004. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* 431: 680-684.

Xu, X., Clark, J.M., Mo, J., Choiniere, J.N., Forster, C.A., Erickson, G.M., Hone, D.W.E., Sullivan, C., Eberth, D.A., Nesbitt, S.J., Zhao, Q., Hernandez, R., Jia, C.K., Han, F.L. y Guo, Y. 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. *Nature* 459 (7249): 940-944.

Y

Yang, T.R. y Martin Sander, P. 2018. The origin of the bird's beak: New insights from dinosaur incubation periods. *Biology Letters* 14 (5).

Z

Zanno, L.E. y Makovicky, P.J. 2011. Herbivorous ecomorphology and specialization patterns in theropod dinosaur evolution. *Proceedings of the National Academy of Sciences* 108 (1): 232-237.

Zanno, L.E. y Makovicky, P.J. 2013. Neovenatorid theropods are apex predators in the Late Cretaceous of North America. *Nature communications* 4: 2827.

Zinke, J. 1998. Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). *Palaiontologische Zeitschrift* 72: 179-189.

ANEXO 1

A revision of the large-bodied theropod (Dinosauria: Saurischia) palaeobiodiversity from the Late Jurassic of Asturias (N Spain) on the basis of isolated teeth.

Morfotipo 1. Theropoda indet. MUJA 0856

Cladograma de consenso estricto de 8 árboles parsimoniosos al codificar como dentición lateral.

Codificación:

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Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7	+8
0	3578	3578	3578	3578	3578	3578	3578	3578	3724

Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.603

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.545


Strict consensus of 8 trees (0 taxa excluded)
Eoraptor
Herrerasaurus
Eodromaeus
Dilophosaurus
Coelophysis
MUJA 0856
Piatnitzkysaurus
Erectopus
Berberosaurus
Genyodectes
Ceratosaurus
Masiakasaurus
Noasaurus
Rugops
Majungasaurus
Kryptops
Skorpiovenator
Aucasaurus
Indosuchus
Abelisaurus
Spinosaurus
Irritator Angaturama
Suchomimus
Baryonyx
Eustreptospondylus
Dubreuillosaurus
Duriavenator
Afrovenator
Torvosaurus
Megalosaurus
Sinraptor
Allosaurus
Neovenator
Australovenator
Fukuiraptor
Eocarcharia
Acrocanthosaurus
Carcharodontosaurus
Mapusaurus
Giganotosaurus
Proceratosaurus
Eotyrannus
Raptorex
Tyrannosaurus
Alioramus
Compsognathus
Ornitholestes
Scipionyx
Erlikosaurus
Jianchangosaurus
Shuvuuia
Byronosaurus
Troodon
Zanabazar
Buitreraptor
Velociraptor
Tsaagan
Saurornitholestes
Richardoestesia_gil.
Dromaeosaurus
Bambiraptor

Posibles posiciones de Theropoda indet. 1., indicado por **a.**

Morfotipo 2. Averostra indet. 1. MUJA 0813

Cladograma de consenso estricto de 55 árboles parsimoniosos al codificar como dentición lateral.

Codificación:

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Tree lengths

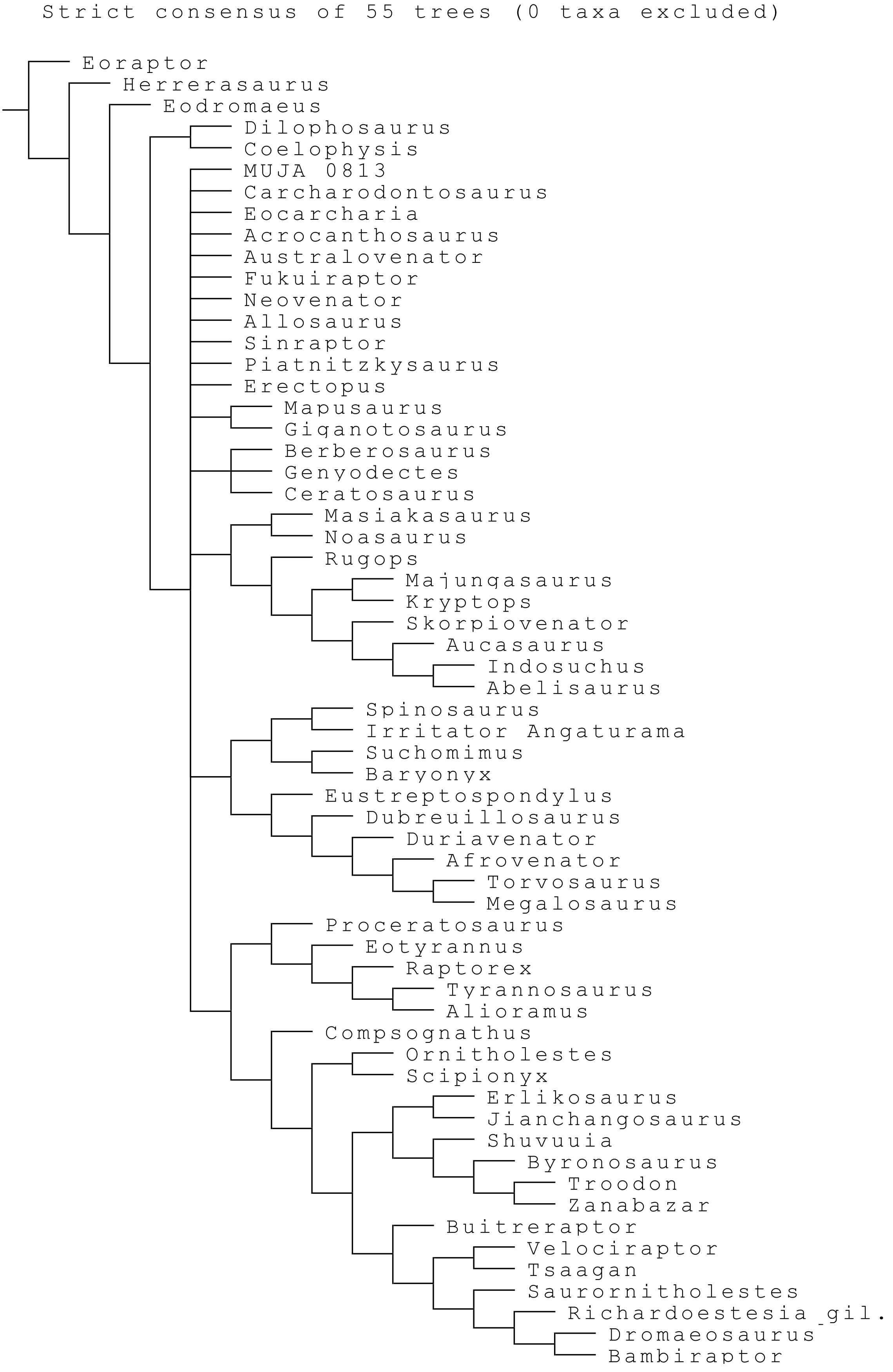
	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3578	3578	3578	3578	3578	3578	3578	3578	3578	3578
10	3578	3578	3578	3578	3578	3578	3578	3578	3578	3578
20	3578	3578	3578	3578	3578	3578	3578	3578	3578	3578
30	3578	3578	3578	3578	3578	3578	3578	3578	3578	3578
40	3578	3578	3578	3578	3578	3578	3578	3578	3578	3578
50	3578	3578	3578	3578	3578	4047				

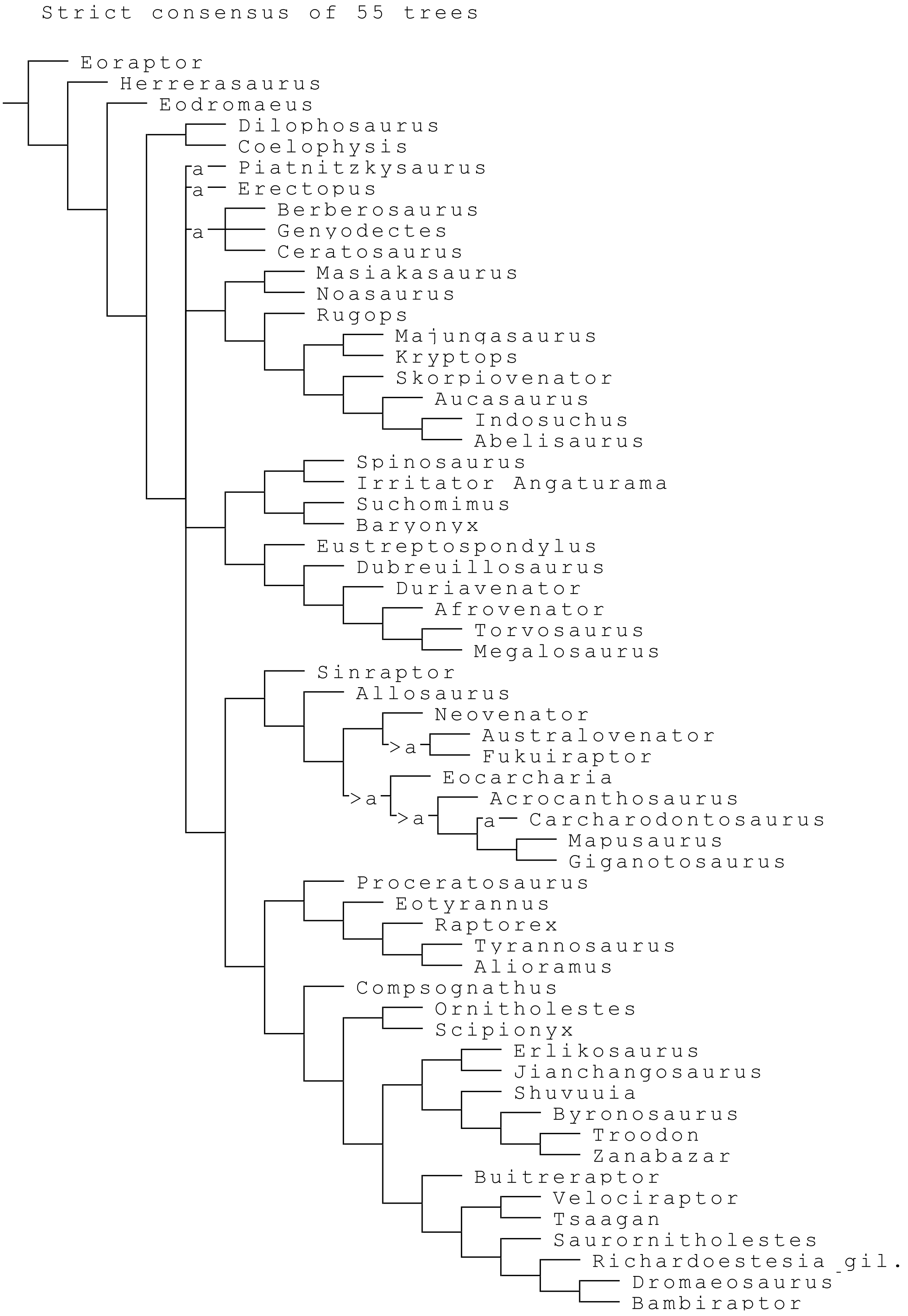
Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
10	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
20	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
30	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
40	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
50	0.568	0.568	0.568	0.568	0.568	0.502				

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
10	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
20	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
30	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
40	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
50	0.637	0.637	0.637	0.637	0.637	0.527				


Strict consensus of 55 trees (0 taxa excluded)
Eoraptor
Herrerasaurus
Eodromaeus
Dilophosaurus
Coelophysis
MUJA 0813
Carcharodontosaurus
Eocarcharia
Acrocanthosaurus
Australovenator
Fukuiraptor
Neovenator
Allosaurus
Sinraptor
Piatnitzkysaurus
Erectopus
Mapusaurus
Giganotosaurus
Berberosaurus
Genyodectes
Ceratosaurus
Masiakasaurus
Noasaurus
Rugops
Majungasaurus
Kryptops
Skorpiovenator
Aucasaurus
Indosuchus
Abelisaurus
Spinosaurus
Irritator Angaturama
Suchomimus
Baryonyx
Eustreptospondylus
Dubreuillosaurus
Duriavenator
Afrovenator
Torvosaurus
Megalosaurus
Proceratosaurus
Eotyrannus
Raptorex
Tyrannosaurus
Alioramus
Compsognathus
Ornitholestes
Scipionyx
Erlikosaurus
Jianchangosaurus
Shuvuuia
Byronosaurus
Troodon
Zanabazar
Buitreraptor
Velociraptor
Tsaagan
Saurornitholestes
Richardoestesia_gil.
Dromaeosaurus
Bambiraptor



Posibles posiciones de Averostra indet.1., indicado por **a.**

Morfotipo 3. Averostra indet. 2. MUJA 1218

Cladograma de consenso estricto de 20 árboles parsimoniosos al codificar como dentición lateral.

Codificación:

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Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3575	3575	3575	3575	3575	3575	3575	3575	3575	3575
10	3575	3575	3575	3575	3575	3575	3575	3575	3575	3575
20	4046									

Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
10	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
20	0.502									

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638
10	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638
20	0.527									

Strict consensus of 20 trees (0 taxa excluded)

Posibles posiciones de Averostra indet.2., indicado por **a.**

Morfotipo 4. Averostra indet. 3. MUJA 1018 y MUJA 4443

Cladograma de consenso estricto de 8 árboles parsimoniosos al codificar como dentición lateral.

Codificación:

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Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7	+8
0	3580	3580	3580	3580	3580	3580	3580	3580	3726

Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8
0	0.567	0.567	0.567	0.567	0.567	0.567	0.567	0.567	0.545

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.603

Strict consensus of 8 trees (0 taxa excluded)

Posibles posiciones de Averostra indet.3., indicado por **a**.

Morfotipo 5. Abelisauridae? indet. MUJA 1219

Cladograma de consenso estricto de 16 árboles parsimoniosos al codificar como dentición lateral.

Codificación:

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Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3584	3584	3584	3584	3584	3584	3584	3584	3584	3584
10	3584	3584	3584	3584	3584	3584	3727			

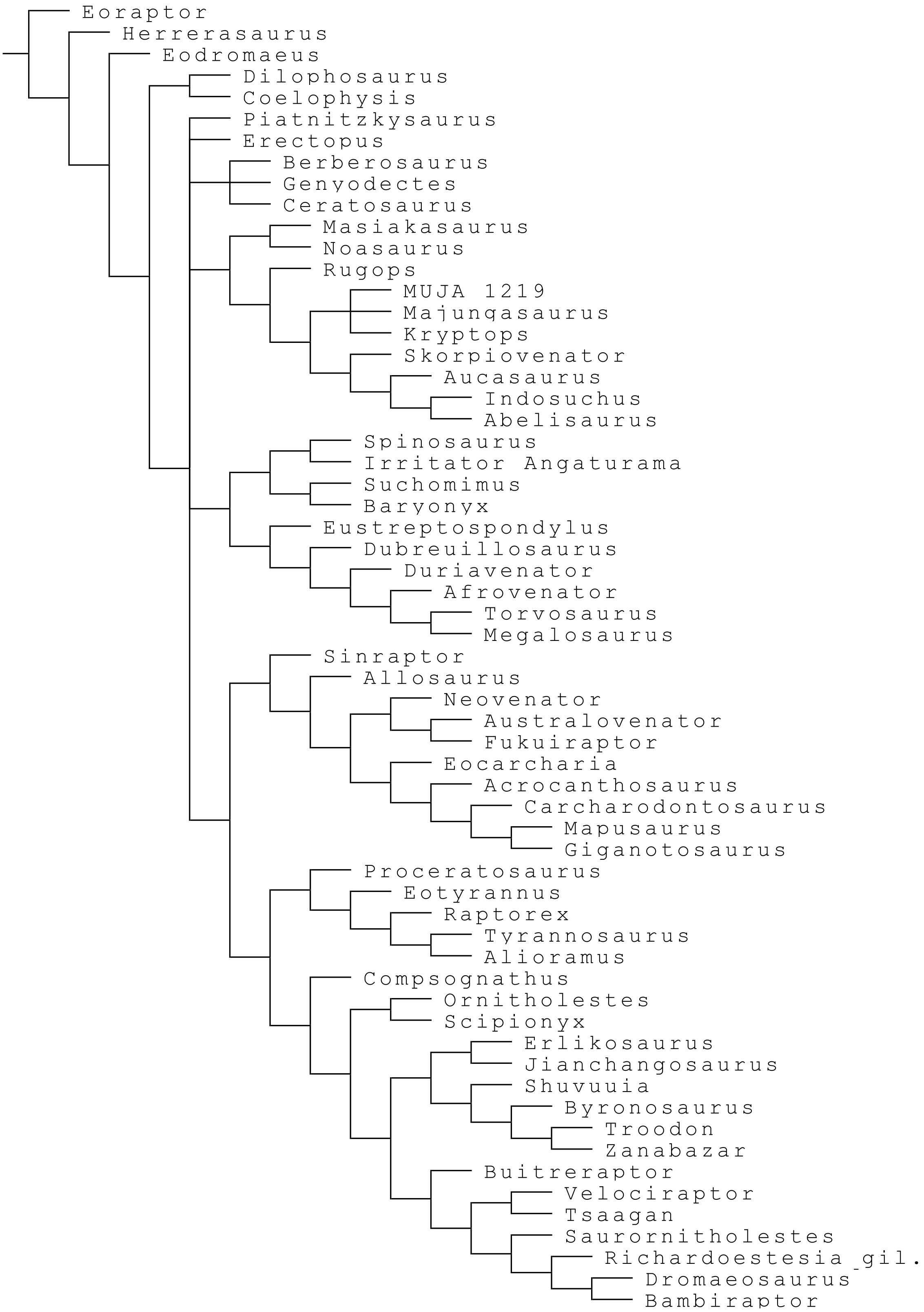
Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.567	0.567	0.567	0.567	0.567	0.567	0.567	0.567	0.567	0.567
10	0.567	0.567	0.567	0.567	0.567	0.567	0.545			

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
10	0.637	0.637	0.637	0.637	0.637	0.637	0.603			

Strict consensus of 16 trees (0 taxa excluded)



Morfotipo 6. Megalosauridae indet. 1. MUJA 4262

Cladograma de consenso estricto de 40 árboles parsimoniosos al codificar como dentición mesial.

Codificación:

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Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3573	3573	3573	3573	3573	3573	3573	3573	3573	3573
10	3573	3573	3573	3573	3573	3573	3573	3573	3573	3573
20	3573	3573	3573	3573	3573	3573	3573	3573	3573	3573
30	3573	3573	3573	3573	3573	3573	3573	3573	3573	3573
40	3724									

Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
10	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
20	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
30	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
40	0.545									

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638
10	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638
20	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638
30	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638
40	0.602									


Strict consensus of 40 trees (0 taxa excluded)
Eoraptor
Herrerasaurus
Eodromaeus
Dilophosaurus
Coelophysis
Piatnitzkysaurus
Erectopus
Berberosaurus
Genyodectes
Ceratosaurus
Masiakasaurus
Noasaurus
Rugops
Majungasaurus
Kryptops
Skorpiovenator
Aucasaurus
Indosuchus
Abelisaurus
Spinosaurus
Irritator Angaturama
Suchomimus
Baryonyx
Eustreptospondylus
Dubreuillosaurus
MUJA 4262
Torvosaurus
Megalosaurus
Duriavenator
Afrovenator
Sinraptor
Allosaurus
Neovenator
Australovenator
Fukuiraptor
Eocarcharia
Acrocanthosaurus
Carcharodontosaurus
Mapusaurus
Giganotosaurus
Proceratosaurus
Eotyrannus
Raptorex
Tyrannosaurus
Alioramus
Compsognathus
Ornitholestes
Scipionyx
Erlikosaurus
Jianchangosaurus
Shuvuuia
Byronosaurus
Troodon
Zanabazar
Buitreraptor
Velociraptor
Tsaagan
Saurornitholestes
Richardoestesia_gil.
Dromaeosaurus
Bambiraptor

Morfotipo 7. Megalosauridae indet. 2. MUJA 1226

Cladograma de consenso estricto de 16 árboles parsimoniosos al codificar como dentición lateral.

Codificación:

??2??100???00000???0
?331[01][01]00?100?00101001?220-100---
0020???
???
???
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???
???
????????????????????????????????

Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3577	3577	3577	3577	3577	3577	3577	3577	3577	3577
10	3577	3577	3577	3577	3577	3577	4268			

Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
10	0.568	0.568	0.568	0.568	0.568	0.568	0.477			

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
10	0.637	0.637	0.637	0.637	0.637	0.637	0.477			

Strict consensus of 16 trees (0 taxa excluded)

Posibles posiciones de Megalosauridae indet. 2., indicado por a.

Morfotipo 8. **Megalosauridae indet. 3. MUJA 1217 y MUJA 3697**

Cladograma de consenso estricto de 24 árboles parsimoniosos al codificar como dentición lateral.

Codificación:

??0?[12]0100001?00000??000441?[01]?1?10?00??010011[12]?0-10[01]0210020????????????????????0?0???

Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3579	3579	3579	3579	3579	3579	3579	3579	3579	3579
10	3579	3579	3579	3579	3579	3579	3579	3579	3579	3579
20	3579	3579	3579	3579	3727					

Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
10	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
20	0.568	0.568	0.568	0.568	0.546					

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
10	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
20	0.637	0.637	0.637	0.637	0.603					


Strict consensus of 24 trees (0 taxa excluded)
Eoraptor
Herrerasaurus
Eodromaeus
Dilophosaurus
Coelophysis
Piatnitzkysaurus
Erectopus
Berberosaurus
Genyodectes
Ceratosaurus
Masiakasaurus
Noasaurus
Rugops
Majungasaurus
Kryptops
Skorpiovenator
Aucasaurus
Indosuchus
Abelisaurus
Spinosaurus
Irritator Angaturama
Suchomimus
Baryonyx
Eustreptospondylus
Dubreuillosaurus
Duriavenator
MUJA 1217 3697
Torvosaurus
Megalosaurus
Afrovenator
Sinraptor
Allosaurus
Neovenator
Australovenator
Fukuiraptor
Eocarcharia
Acrocanthosaurus
Carcharodontosaurus
Mapusaurus
Giganotosaurus
Proceratosaurus
Eotyrannus
Raptorex
Tyrannosaurus
Alioramus
Compsognathus
Ornitholestes
Scipionyx
Erlikosaurus
Jianchangosaurus
Shuvuuia
Byronosaurus
Troodon
Zanabazar
Buitreraptor
Velociraptor
Tsaagan
Saurornitholestes
Richardoestesia_gil.
Dromaeosaurus
Bambiraptor

ANEXO 2

Alonso, A., Canudo, J.I. 2016. On the spinosaurid theropod teeth from the early Barremian (Early Cretaceous) Blesa Formation (Spain). *Historical Biology* 28(6), 823-834.

Historical Biology, 2015
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On the spinosaurid theropod teeth from the early Barremian (Early Cretaceous) Blesa Formation (Spain)

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Spinosaurids are one of the most abundant theropods from the Early Cretaceous of the Iberian Peninsula. The published fossil record consists mainly of teeth. A good example is La Cantalera-1 site in the Blesa Formation (Spain). This site represents a marshy environment with periodic droughts, resulting in a non-permanent body of water. Theropod dinosaur teeth are frequent. Seventeen spinosaurid teeth have been studied using qualitative and quantitative features, including a statistical analysis, in order to compare them with the known spinosaurid record from Spain. In La Cantalera-1 we recognise two different morphotypes: Baryonychinae indet. and Spinosaurinae? indet. Baryonychinae indet. was produced by baryonychines close to *Baryonyx*; teeth with similar morphology have been described in other sites from the Early Cretaceous of the Iberian Peninsula. Teeth tentatively attributed to Spinosaurinae? indet. were produced by spinosaurines close to *Spinosaurus*. This morphotype could provide new evidence of the presence of spinosaurines in the Early Cretaceous of the Iberian Peninsula. The small size of the teeth from La Cantalera-1 when compared with those from other sites is interpreted as the result of the conditions characteristic of the deposit area, which represents an ecosystem unable to sustain large-sized organisms.

Keywords: Spinosauridae; teeth; Lower Cretaceous; Blesa Fm.; Spain

1. Introduction

Spinosaurids are one of the most striking groups among the theropods, featuring an elongated, distinctive skull and conical teeth with fluted enamel and small denticles (Charig and Milner 1997; Sereno et al. 1998; Canudo et al. 2008; Buffetaut 2012). These characters have been interpreted as evidence of a dominant piscivorous tendency in their eating strategies, a hypothesis supported by several observations relating to features such as the skull morphology, stomach contents (Charig and Milner 1997), the oxygen isotopic composition of the bones (Amiot et al. 2010) and biomechanical data (Rayfield et al. 2007), though there is also evidence of spinosaurids feeding on other vertebrates such as pterosaurs (Buffetaut et al. 2004) and ornithopods (Charig and Milner 1997; Allain et al. 2012). Recently, Ibrahim et al. (2014) have shown a series of adaptations in *Spinosaurus* that fit with a semiaquatic lifestyle.

Spinosaurids had a wide distribution both in space and time during the Late Jurassic, the Early Cretaceous and the older part of the Late Cretaceous. It has been thought that the first reported spinosaurids appeared during the Late Jurassic (Buffetaut 2012) although new research suggests that early spinosaurids are Middle Jurassic in age (Serrano-Martínez et al. 2015). They became abundant in the Early Cretaceous, disappearing during the Late Cretaceous (Hone et al. 2010). Spinosaurid remains are mainly distributed in North Africa, Europe and South America although there is other evidence of them in Asia and Australia (Buffetaut and Ingavat 1986; Hasegawa et al. 2003; Barrett et al. 2011; Allain et al. 2012).

Most remains of the spinosaurids from the Iberian Peninsula are isolated teeth (Pereda-Suberbiola et al. 2012). The study of isolated theropod teeth is of particular interest because they are the most common fossilised remains. It is due to the resistance of the enamel and the constant replacement of the teeth during their lifetime (Currie et al. 1990; Torices-Hernández 2007).

La Cantalera-1 (= La Cantalera) is the site with the greatest vertebrate palaeobiodiversity in the early Barremian of the Iberian Peninsula. The fossil accumulation consists of teeth, postcranial remains, eggshells and coprolites; amphibians, a chelonian, a lizard, crocodylomorphs, pterosaurs, ornithopod dinosaurs, a thyreophoran, sauropods and theropods have been identified, as well as mammals (Badiola et al. 2008; Canudo et al. 2010; Gasca et al. 2014; Moreno-Azanza et al. 2014). La Cantalera-1 is the only site of the Blesa Formation with spinosaurid teeth (Ruiz-Omeñaca et al. 2005). In this context, the aim of the present article is to study the isolated spinosaurid teeth from the lower Barremian founded in this site.

1.1 Geographical and Geological context

La Cantalera-1 site is located in the NE of the Iberian Peninsula, near the village of Josa (Teruel) in the Iberian

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Range. The Iberian Basin of the NE of Spain was an intracratonic basin that developed during the Mesozoic extension (Salas et al. 2001). A rifting stage during the Early Cretaceous allowed the formation of numerous subsident areas in the Iberian Basin. Geologically, this site is located in the Mesozoic Oliete sub-basin, which forms part of the Cretaceous Maestrazgo basin. The Oliete sub-basin was formed during the second rifting stage that began in the Early Cretaceous, when the carbonate platform of the Iberian Basin was fractured due to its extension, creating several sub-basins (Soria de Miguel 1997; Salas et al. 2001). The Lower Cretaceous of the Oliete sub-basin is characterised by four mega-sequences: the Margas y Calizas de Blesa Formation; the Calizas de Alacón Formation; the Margas de Forcall Formation; and the Calizas de Oliete Formation (Soria de Miguel 1997).

The Blesa Formation lies over Jurassic units, such as the bioclastic limestones of the Barahona Formation (Pliensbachian), the marls of the Turmiel Formation (Toarcian), the Chelva Formation (Bathonian) and the Pozuel Formation (Kimmeridgian) (Aurell et al. 2004).

The Blesa Fm. can be divided into the lower and upper Blesa Fm. The lower part shows continental deposits whilst the upper part shows a coastal influence, with the presence of ostreids. The coastal lagoonal influence starts with a ferruginous and encrusted surface over lacustrine carbonate facies. This surface separates the lower and the upper Blesa Fm. La Cantalera-1 site is located within the base of the lower Blesa Fm. (Canudo et al. 2010).

Two different stages of tecto-sedimentary evolution are also recognised in the lower Blesa Fm. (Aurell et al. 2004). The first stage shows major subsidence due to normal faults, creating a small, isolated basin. During the second stage the basin increased in size, and homogeneous sediments were deposited. Palaeosols with ferruginous ooids and pisoids developed from the laterisation of clay sediment (Murat 1983; Aurell et al. 2004).

La Cantalera-1 site is located in the sediments of stage 1 of the lower Blesa Fm. (Figure 1). The fossil remains appear in grey clays characterised by the presence of charophytes, ostracods and gastropods. Some round edged of Jurassic limestones with invertebrate marine fossils such as brachiopods and ammonites are found as well. Clay-cemented nodules are interpreted as proof of the existence of palaeosols due to changes in the phreatic level. These facies are the result of deposits of distal-zone clays of alluvial fans (Canudo et al. 2010).

The invertebrates recognised in this site include freshwater gastropods such as Viviparidae indet. and Basommatophora indet. Other microfossils are also present, the most common being ostracods and charophytes. The ostracods include *Cypridea (Ulwellia) soriana* (Kneuper-Haack 1966), which appears in other sites of the Hauterivian–Barremian of the Iberian Peninsula. As regards charophytes, utricles and stems have been identified, mainly from clavatoraceans such as *Hemiclavator adnatus* (Martín-Closas and Grambast-Fessard 1986; Schudack 1989) and *Clavatoraxis* sp. (Martín-Closas and Diéguez 1998). The presence of oogonia from *Atopochara trivolvis triquetra* (Grambast 1968) in the site (Ruiz-Omeñaca et al. 1997) has traditionally allowed the site to be dated as upper Hauterivian–lower Barremian (Triquetra subzone). Recently, Canudo et al. (2012) have shown that this subzone marks the beginning of the Barremian by relating it to international scales; accordingly, La Cantalera-1 site belongs to the early Barremian. The charophyte association is biostratigraphically similar to the El Castellar Fm. of the Galve sub-basin (Canudo et al. 2010).

The charophytes and ostracods found at La Cantalera-1 are capable of inhabiting fresh and brackish waters, but viviparid gastropods are found exclusively in freshwater, so a continental saltwater environment can be ruled out. It is easy to find these gastropods in the Wealden facies, associated with bivalves such as *Anodonta, Eomiodon, Margaritifera, Teruella* and *Unio* (see references in Ruiz-Omeñaca et al. 1997) in freshwater sites. However, these bivalves are absent, and the site is interpreted in terms of a non-permanent body of water, because such bivalves are more sensitive to dry conditions than viviparid gastropods (Ruiz-Omeñaca et al. 1997).

La Cantalera-1 site is interpreted as having been deposited in a marshy environment with periodic droughts and surrounded by a Jurassic relief, resulting in a non-permanent body of water and a marshy vegetated area (Canudo et al. 2010).

1.2 *Institutional abbreviations*

MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza, Spain; UNIZAR, Universidad de Zaragoza, Zaragoza, Spain.

1.3 *Other abbreviations*

AL, apical length; CBL, crown base length; CBR, crown base ratio; CBW, crown base width; CH, crown height; DA, distoapical denticle density; DAVG, average distal denticle density; DB, distobasal denticle density; DC, distocentral denticle density; DSDI, denticle size density index; FESEM, field emission scanning electron microscope; MA, mesioapical denticle density; MAVG, average mesial denticle density; MC, mesiocentral denticle density; MB, mesiobasal denticle density.

2. Materials and methods

The fossils were recovered from surface prospections, excavation campaigns and the screen-washing of 3 tons of

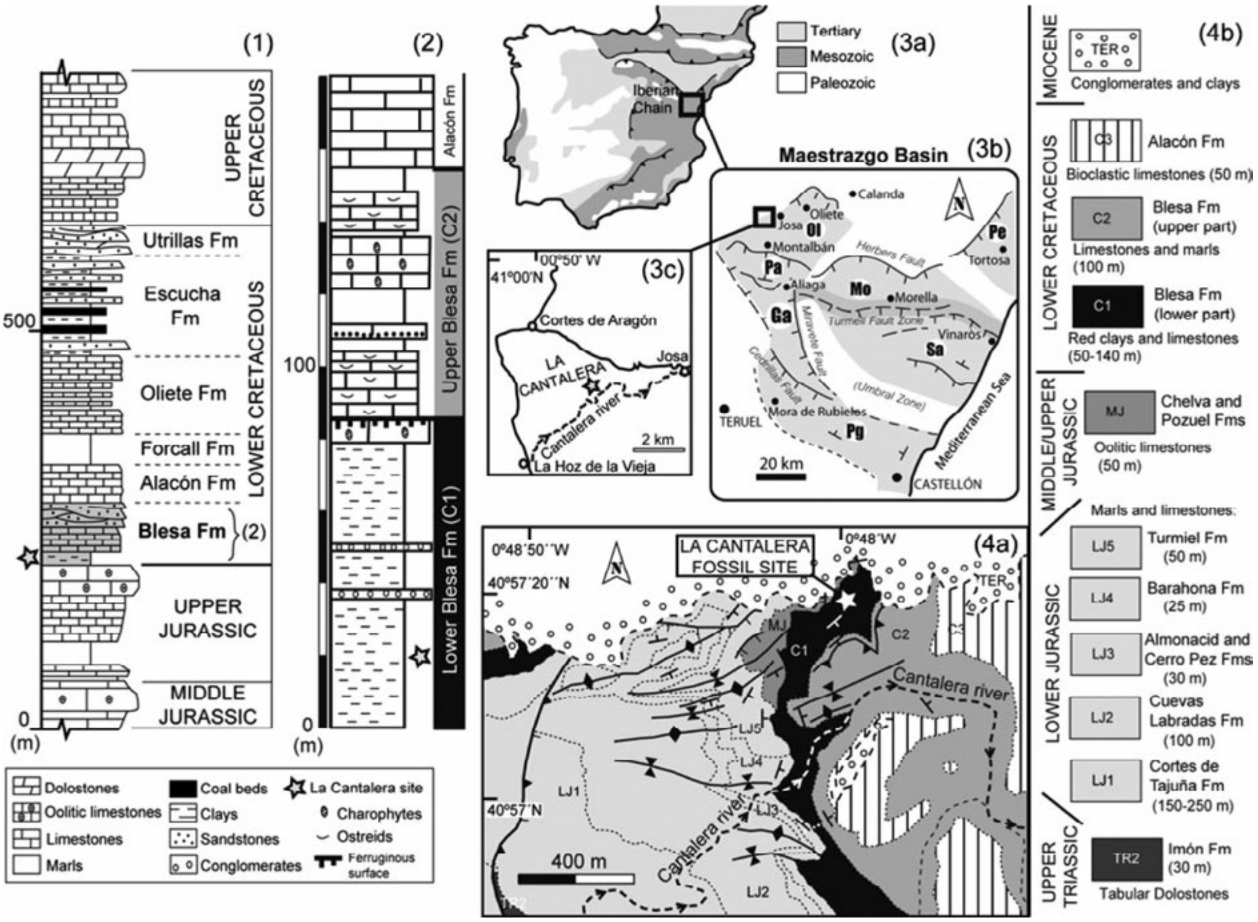

Figure 1. (Colour online) Geographical and geological context. Geographical and geological location of La Cantalera site (early Barremian). (1) Stratigraphical setting of the area. (2) Location of La Cantalera site within the Blesa Formation. (3) Geological context of the site. (3a) Geological map of the Iberian Peninsula. (3b) Location of palaeogeographic subbasins (Ol: Oliete, Pa: Las Parras, Ga: Galve, Mo: Morella; Pe: Perelló; Sa: Salzedella, Pg: Peñagolosa) within the Maestrazgo basin. (3c) Geographical location of La Cantalera site near Josa, Teruel. (4) Geological mapping of the area around La Cantalera (4a) with the local geological units (4b). From Canudo et al. (2010).

sediment, using a sieve with a 0.5 mm mesh. In addition, another 20 kg of sediment were screen-washed using a 0.150 mm mesh in order to get a representative sample of non-vertebrate microfossils (Ruiz-Omeñaca et al. 1997; Canudo et al. 2010). The recovered teeth show a variable state of preservation, with shed and functional teeth without evidence of transport.

Part of the material had previously been studied by electron microscopy in the FESEM service of UNIZAR. Other observations were made with an Olympus SZX7 zoom stereomicroscope with a KL1500 LCD lamp. Matrox Inspector 8.0 was used as imaging software. The teeth were measured with a Mitutoyo Digimatic Digital Caliper Series No 500 and Matrox Inspector 8.0 measurement tools. The measurements performed on scanning electron microscope images obtained in previous studies were conducted with ImageJ software.

Seventeen theropod (plus two crocodylomorph) teeth from La Cantalera have been analysed during the course of this research. Other teeth from the sites of Vallipón (Castellote) (Ruiz-Omeñaca et al. 1998) have been studied; data of spinosaurids from Iberia have also been included (Torcida et al. 1997; Torcida Fernández-Baldor et al. 2003; Infante et al. 2005; Sánchez-Hernández et al. 2007; Canudo et al. 2008; Gasca et al. 2008).

2.1 *Anatomical nomenclature*

Theropod teeth usually have ziphodont morphology (D'Amore 2009); they have a conical shape, labiolingually compressed and curved, with the apex of the crown facing distally. This general morphology may vary in some taxa. The anatomical nomenclature used in this work is mainly based on the recommendations of Smith and Dodson (2003) and Hendrickx et al. (2015). A theropod tooth is composed of a crown and a root; the junction between them is called the cervix. The top of the crown and the root is called the crown or root apex. Carinae are structures running apicobasally on the crown, usually on the edges, facing mesially or distally. Carinae can be denticulated, showing a serration formed by several denticles. Flutes are subparallel longitudinal grooves of similar width separated by straight and acute ridges on the crown. Longitudinal ridges are apicobasally long and narrow convexities. Crenulation is shallow and subtle apicobasal ornamentation. Enamel wrinkles are enamel undulations running mesiodistally. Enamel texture refers to the pattern on the crown surface (Hendrickx et al. 2015). The tooth surface facing outwards towards the lips is called labial. The opposite surface, which faces the sagittal midline of the skull, is called lingual, i.e. towards the tongue. The tooth surface close to the jaw symphysis is called mesial. The tooth surface close to the jaw articulation is called distal. Apical refers to the direction from the cervix to the crown apex. Basal refers to the direction from the apex to the cervix.

2.2 Morphometric nomenclature

The morphometric terminology (Figure 2) in the present work follows the terms and abbreviations used in Smith et al. (2005). The crown base length (CBL) is the mesiodistal length of the crown at the level of the cervix; the crown base width is the labiolingual width of the crown at the cervix level, perpendicular to CBL. The crown base ratio (CBR) is the ratio of CBW to CBL and shows the labiolingual compression; crown height (CH) is the basoapical extent of the distal margin of the crown, from the most distal point of the cervix to the most apical point of the apex. The crown height ratio (CHR) is the ratio of CH to CBL and shows the crown elongation (Hendrickx et al. 2015).

The apical length (AL) is the basoapical extent of the mesial margin of the crown. The mesial serration density is the number of denticles per mm on the mesial margin; initials change according to the position of the denticles (MA refers to mesioapical denticles per mm; MC, mesiocentral denticles per mm; MB, mesiobasal denticles per mm). The distal serration density is the number of denticles per mm on the distal margin (DA, distoapical denticles per mm; DC, distocentral denticles per mm; DB, distobasal denticles per mm). The average mesial serration density (MAVG) is the arithmetic mean of denticles per

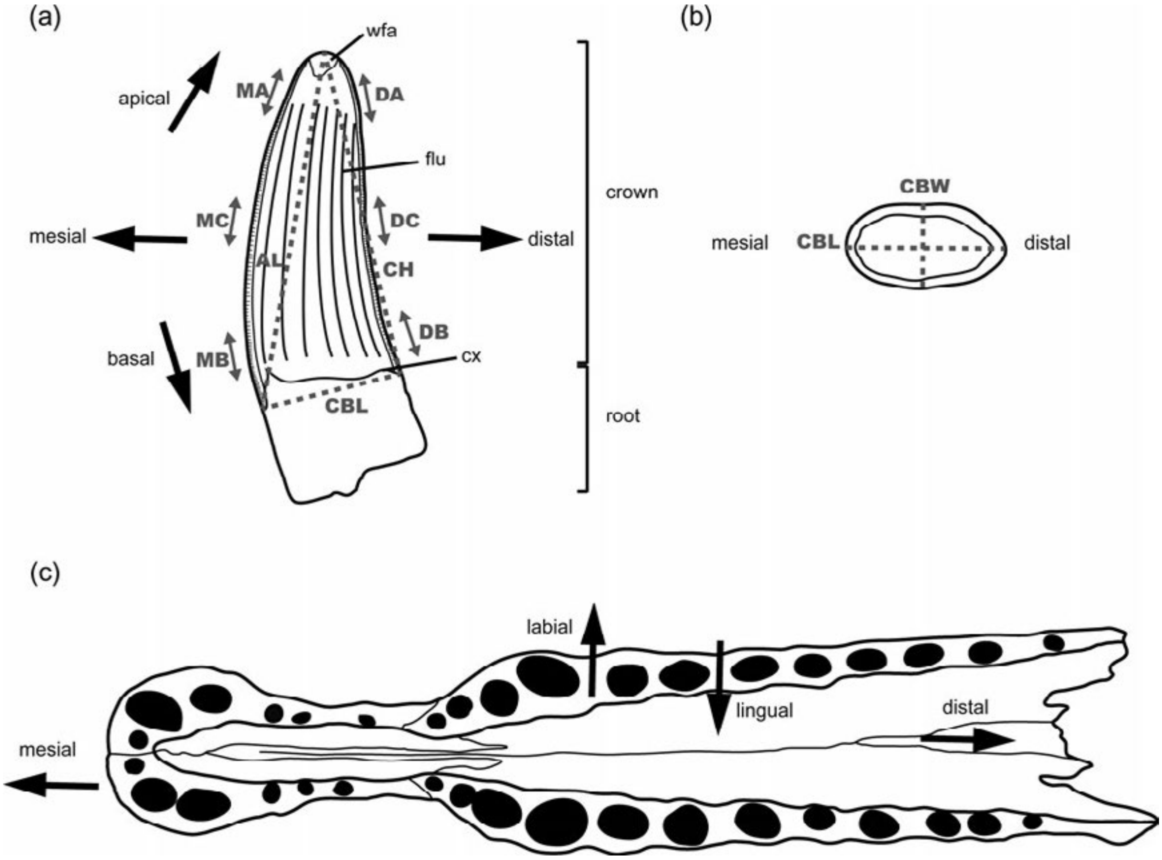

Figure 2. Positional and tooth nomenclature. (a) Spinosaurid tooth in lateral view. AL, Apical Length; CBL, Crown Base Length; CH, Crown Height; cx, cervix; flu, fluted enamel; DA, DC, DB, distal denticle density (apical, medial, basal); MA, MC, MB, mesial denticle density (apical, medial, basal); wfa, wear facet. (b) Cross-section of the tooth at the level of the cervix. CBW, Crown Basal Width; CBL, Crown Base Length. (c) Dorsal view of an upper jaw of *Spinosaurus*. Modified from Dal Sasso et al. (2005).

mm along the mesial carina (MA + MC + MB/3). The average distal serration density (DAVG) is the arithmetic mean of denticles per mm along the distal carina. The denticle size density index (DSDI), used by Rauhut and Werner (1995), shows the difference in size between the mesial and distal denticles and has been expressed in this work as the ratio of MAVG to DAVG.

2.3 *Qualitative features*

A number of qualitative features have been studied in this work in order to complement the morphometric information provided by measurements. The main such features are the shape of the tooth (Torices-Hernández 2007), the position of the mesial and distal carina (Currie et al. 1990; Torices-Hernández 2007), the morphology of the denticles (Currie et al. 1990, Torices-Hernández 2007), the cross-section of the crown and surface morphology (convex, plano-convex…), crown ornamentation, denticle position, the presence or absence of enamel wrinkles (Brusatte et al. 2007), the state of preservation of the tooth with observations on the presence/absence of broken root remains in order to identify whether it was a functional/shed tooth (Ruiz-Omeñaca and Canudo 2003), and the presence or absence of wear facets.

2.4 *Statistical analysis*

A statistical analysis has been performed in order to understand the variation among the spinosaurid teeth from La Cantalera-1 site. The analysis allows to draw a comparison between the data for these teeth and the morphometric data collected by other authors on spinosaurids from Iberia. Theropods from different parts of the world have also been included.

The statistical analysis was performed using PAST (Hammer et al. 2001) on numerical data collected by Smith et al. (2005), Canudo et al. (2008), Gasca et al. (2008), Torcida et al. (1997), Torcida Fernández-Baldor et al. (2003), Ruiz-Omeñaca et al. (1998), Infante et al. (2005), Sánchez-Hernández et al. (2007) and the measurements of the teeth from La Cantalera-1 taken by the authors.

In addition, morphometric data from crocodylomorph teeth were also included. The main reason was to use them as a control group in the analysis due to the similarity between spinosaurid and crocodylomorph teeth. The crocodylomorph teeth included in the analysis belong to Morphotype 1 of La Cantalera site crocodylomorphs (Puértolas-Pascual et al. 2014). This morphotype has usually been attributed to Goniopholididae, but it is also found in other neosuchians and heterodont crocodylomorphs.

When studying theropod teeth, it is common to log-transform the values in order to better reflect a normally distributed multivariate dataset (Smith et al. 2005; Kear et al. 2013; Larson and Currie 2013; Hendrickx et al. 2015; see justification in Samman et al. 2005). Here the values were not log-transformed, as the absence of mesial and distal denticles was taken into account. The absent data were coded with a zero value; the missing data were coded with a question mark.

A PCA analysis has been performed on the dataset, in order to reduce the original variables of the sample without losing information; the variables selected are CBL, CBW, CH, MAVG and DAVG. All measurements are expressed in mm. The dataset from Smith et al. (2005) has been included with the data for isolated teeth from the Iberian Chain. The aim is to check the validity of the morphotypes studied in the Systematic Palaeontology, and test whether the spinosaurids occupy the same region of the morphospace. A total of 119 teeth have been included. The measurements from Smith et al. (2005) included in this analysis comprise *Baryonyx, Suchomimus* (Spinosauridae), Carcharodontosauridae, Troodontidae, Dromaeosauridae and Ceratosauridae.

3. Systematic palaeontology

Clade DINOSAURIA Owen, 1842
Clade SAURISCHIA Seeley, 1887
Clade THEROPODA Marsh, 1881
Clade TETANURAE Gauthier, 1986
Superfamily SPINOSAUROIDEA Stromer, 1915
Family **Spinosauridae** Stromer, 1915
Subfamily **Baryonychinae** Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson and Wilson, 1998

3.1 *Baryonychinae indet*

3.1.1 *Material*

Thirteen teeth: CAN1 953, CAN1 957, CAN1 958, CAN1 959, CAN1 977, CAN1 983, CAN1 984, CAN 1 999, CAN1 1001, CAN1 1616, MPZ 97/468-CAN1 974, MPZ 2001/207 and MPZ 2001/208.

3.1.2 *Description*

Baryonychinae indet. teeth show a variable state of preservation (Figure 3). The mesial margin of the teeth is convex, while the distal margin is concave or straight. The cross-section varies between elliptical and subcircular. Crown height ranges from 6 to 28 mm. All teeth have mesial and distal carinae, but some teeth do not have serration on the mesial carina. Carinae are located on the mesiodistal axis of the crown and start close to the cervix. Denticles are chisel-shaped and their height and width vary between 0.1 and 0.12 mm. Denticle density per mm

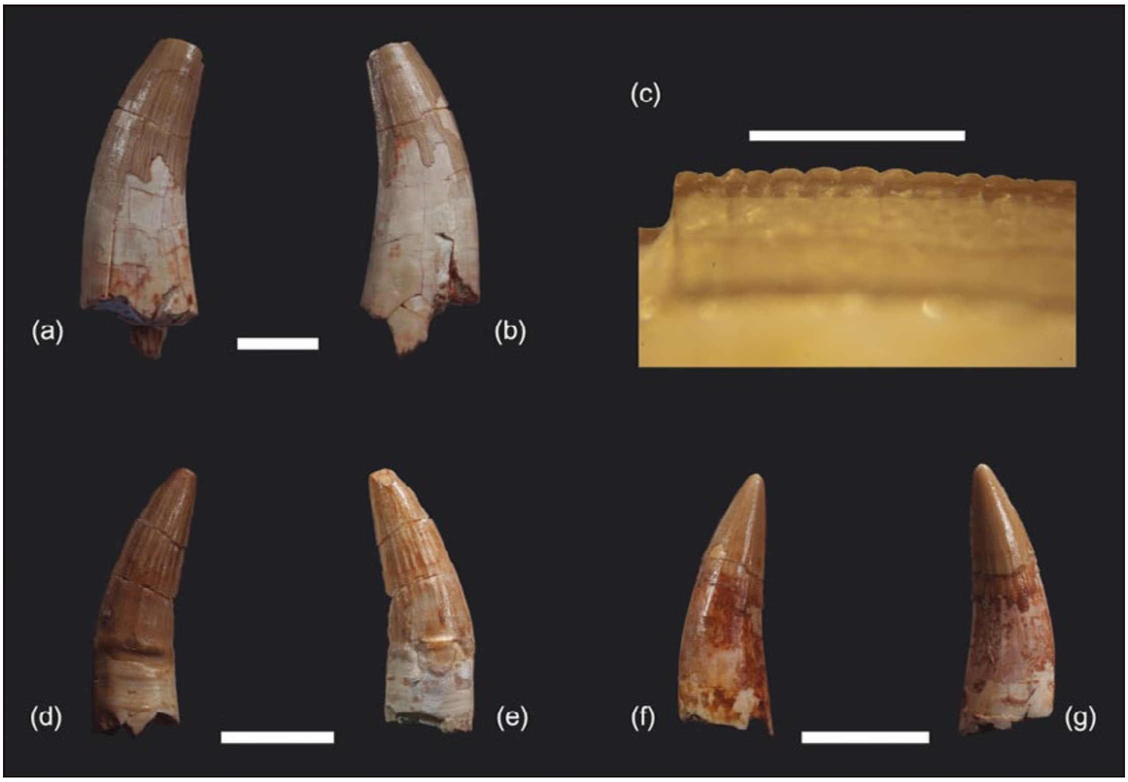

Figure 3. (Colour online) Baryonychinae teeth from La Cantalera-1 site in lingual (a, d, g) and labial (b, e, f) views, with detail of mesial denticles (c). (a–c) MPZ 2001/207; (d, e) MPZ 2001/208; (f, g) CAN1 957. Scale bar: 1 cm (a, b, d, g) or 1 mm (c).

ranges from 6 to 12. The denticle size density index values are close to one, so there is no difference between the mesial and the distal size of the denticles. The denticles are perpendicular to the margin of the teeth. Both faces of the teeth bear enamel ornamentation which consists of 6–7 ridges (on average) orientated apicobasally; the ridges do not reach the apex.

3.1.3 Discussion

Unlike other theropods, spinosaurid teeth have a subcircular-elliptical cross-section. The crown is usually straight, with very slight distal curvature. Spinosaurid teeth usually have fluted enamel and small denticles, and a veined enamel texture (Ruiz-Omeñaca et al. 2005; Gasca et al. 2008; Hendrickx et al. 2015). Baryonychine teeth have an ornamentation based on ridges, the cross-section is not as subcircular as in spinosaurine teeth, and the distal curvature is more pronounced than in Spinosaurinae (Canudo et al. 2008).

Previous papers (Canudo and Ruiz-Omeñaca 2003; Ruiz-Omeñaca 2006) have differentiated between two morphotypes of baryonychine spinosaurid teeth in the Barremian. The first morphotype includes all teeth with serration on the mesial and distal carina, and the second morphotype only has serration on the distal carina. Here we do not differentiate these morphotypes because sometimes the presence or absence of denticles on the mesial carina is difficult to determine due to the state of preservation of the teeth. In addition, this is the only difference between the morphotypes; they share all other features. There are no differences in size, denticle density per mm, ridges, enamel texture, etc. so we prefer to include them, for the moment, in a one morphotype in La Cantalera-1 site.

This morphotype of baryonychine teeth differs from that of other spinosaurids. *Baryonyx walkeri* teeth do not have fluted enamel on the labial surface (Charig and Milner 1997). *Ostafrikasaurus crassiserratus* teeth have larger denticles and, in consequence, a lower denticle density per mm (Buffetaut 2012). Asiatic forms such as *Siamosaurus suteethorni* have more ridges on the teeth surface (Buffetaut and Suteethorn 1999; Hasegawa et al. 2003). Other spinosaurids such as *Suchomimus tenerensis* (Sereno et al. 1998) have a microgranular ornamentation on the edges of the tooth; this ornamentation is absent in La Cantalera-1 site.

It is interesting to draw comparisons between the teeth from La Cantalera and other data from Spain. Baryonychine teeth from the early Aptian of the Morella Formation (Canudo et al. 2008) differ from this morphotype; the teeth from La Cantalera-1 lack the enamel wrinkles and microgranular ornamentation of these teeth. Teeth from El Castellar Fm. (Gasca et al. 2008) show more similarities with this morphotype. In addition, El Castellar Fm. is biostratigraphically similar to the Blesa Fm. spinosaurid teeth from Barremian-Aptian sites of the Wealden facies of Burgos (Torcida et al. 1997; Torcida Fernández-Baldor et al. 2003) have similar features both in terms of ridges and denticle density per mm. Teeth from the late Barremian of Vallipón (Ruiz-Omeñaca et al. 1998), early Barremian of Ladruñán (Infante et al. 2005) and some teeth from the late Hauterivian-early Barremian of Galve (Sánchez-Hernández et al. 2007) show a similar appearance to the remains from La Cantalera-1.

Subfamily **Spinosaurinae** Stromer, 1915

3.2 Spinosaurinae? indet

3.2.1 Material

Four teeth: CAN1 960, CAN1 968, CAN1 973 and CAN1 990.

3.2.2 Description

Spinosaurinae? indet. teeth show a variable state of preservation. The teeth have a convex mesial margin, while the distal margin is concave or straight. The teeth have a subcircular cross-section. Estimated crown height values range from 16 to 22 mm. The apex is pointing very slightly towards the distal margin. CHR values are high due to the elongation of the crowns. These teeth do not have carinae with the exception of CAN1 990, which has a distal carina without any serration (Figure 4). The teeth have ornamentation based on apicobasal crenulation, which is faint and shallow. This ornamentation is more subtle and numerous than the ridges of the Baryonychinae indet. morphotype.

3.2.3 Discussion

Four teeth have been tentatively attributed to Spinosaurinae on the basis of their features that do not fit in the

Figure 4. (Colour online) Spinosaurinae? indet. teeth from La Cantalera-1 (a–d) and Cerrada Roya sites (e, f), in labial (a, d), lingual (b, c, f), and distal (e) views. (a, b) CAN1 990; (c, d) CAN1 968; (e, f) MPZ 2014/444. Scale bar: 1 cm.

Baryonychinae subfamily. Spinosaurine teeth are usually less curved on the distal margin, ornamentation is less marked or absent, and the cross-section is heavily subcircular (Martill and Hutt 1996; Canudo et al. 2008; Fanti et al. 2014), though some spinosaurines such as *Irritator* (Sues et al. 2002) do not share these features. This morphotype can be hard to distinguish from crocodylomorph teeth. Crocodylomorph teeth have a lingual curvature, but the teeth from Spinosaurinae? indet. lack this trait.

The spinosaurine teeth from La Cantalera site differ from *Spinosaurus aegyptiacus* (Stromer, 1915). The holotype of *Spinosaurus* does not have fluted enamel (though other remains attributed to *Spinosaurus* do have some ornamentation), and the carinae are unserrated. *Irritator challengeri* (Martill et al. 1996) have teeth with serrated carinae and fluted enamel. *Oxalaia quilombensis* (Kellner et al. 2011) teeth have unserrated carinae and fluted enamel, and also enamel wrinkles that do not appear on the teeth from La Cantalera-1.

The ornamentation of the teeth from La Cantalera bears some similarities with Morphotype 5 reported by Fanti et al. (2014) from the Albian of Tunisia. These teeth have a faint and shallow crenulation along the tooth crown, extending neither straight nor parallel along the crown. However, the teeth from La Cantalera-1 belonging to Spinosaurinae? indet. seem to have a higher number of ornamentations than Morphotype 5 from North Africa, and there is no difference in number between the lingual and labial surfaces.

Another tooth, from the site of Cerrada Roya (Camarillas Formation, Barremian) (MPZ 2014/444) in Galve, has traits similar to the teeth from La Cantalera-1: the absence of carinae, a relatively straight crown, numerous and subtle crenulation, though it is more labiolingually compressed. However, this compression could be explained in terms of heterodonty, so we consider this tooth to belong to the same morphotype as the above.

Sánchez-Hernández et al. (2007) have also reported spinosaurine teeth from Galve, at the sites of Cerrada Roya and San Cristóbal. These teeth lack ornamentation with the exception of one tooth (MPG-SC 2), have both a mesial and distal unserrated carina (the ornamented tooth only has a distal carina), and the crown height ranges from 12 to 21 mm. It is possible that these teeth, though considered non-ornamented, may in fact have an ornamentation based on weak crenulation like the Cerrada Roya tooth (MPZ 2014/444) because they come from the same site. However, some differences exist. The teeth studied by Sánchez-Hernández et al. (2007) have an unserrated mesial and distal carina, absent in the teeth from La Cantalera-1 (with the exception of the distal carina of CAN1 990) and the Cerrada Roya MPZ tooth. Despite these differences, here we have considered all the teeth from Galve to belong to a single morphotype that also includes the Spinosaurinae? teeth from La Cantalera-1, due to the heterodonty present in theropods. Nevertheless, further studies are required in order to clarify this point.

4. Results

The principal component analysis shows the variation in the dataset in two axes or components (Figure 5). The first component (X-axis) explains 95.01% of the variance. The second component (Y-axis) explains only 2.44% of the variance. The first component loadings are CH, CBL and CBW; these variables show the size of the teeth. DAVG and MAVG load the second component and explain the denticle density of the teeth (Hendrickx et al. 2015). Quadrant 1 in the plot includes theropods with large teeth and a high denticle density. Quadrant 2 has theropods with small teeth and a high denticle density. Quadrant 3 shows theropods with small teeth with a low denticle density on the carinae, and quadrant 4 has large theropod teeth with a low denticle density.

The largest theropod teeth (belonging to *Suchomimus* and Carcharodontosauridae) are found in quadrants 1 and 4. Their positions on the Y-axis vary with the denticle density, which is higher in spinosaurids.

Baryonychine spinosaurids are located between quadrants 1 and 2. It is notable that the values for these baryonychine teeth lie in the area around *Baryonyx* values, while the *Suchomimus* values remain separate from them. The dataset from the Iberian Chain shows greater variation than the theropods in the Smith et al. (2005) dataset. The high range of variation of the Iberia dataset could be attributed to their origin in isolated teeth, unlike the data for the rest of the teeth. Data from isolated teeth may have a larger variation because they come from more different specimens. It is also notable that the state of preservation of isolated teeth has an effect when measuring and inferring data.

Ceratosauridae and Carcharodontosauridae are found in the 4th quadrant, which corresponds to medium–large sized teeth and a low denticle density.

Dromaeosaurid teeth are found between the 2nd and the 3rd quadrant. Small teeth with a low denticle density belonging to Troodontidae are located in the 3rd quadrant, close to the teeth from Spinosaurinae? indet. from Galve and La Cantalera-1 and Crocodylomorpha indet. teeth, with no denticles at all.

The baryonychine teeth from the Iberian Chain overlap. The teeth with the most similar values to the teeth from La Cantalera-1 site are from Vallipón, but these teeth are larger in size. The largest teeth from the Iberian Chain belong to the baryonychine spinosaurids of Burgos and the Morella Fm.

The teeth from La Cantalera-1 site are the smallest teeth among the baryonychine spinosaurids; only one of them is

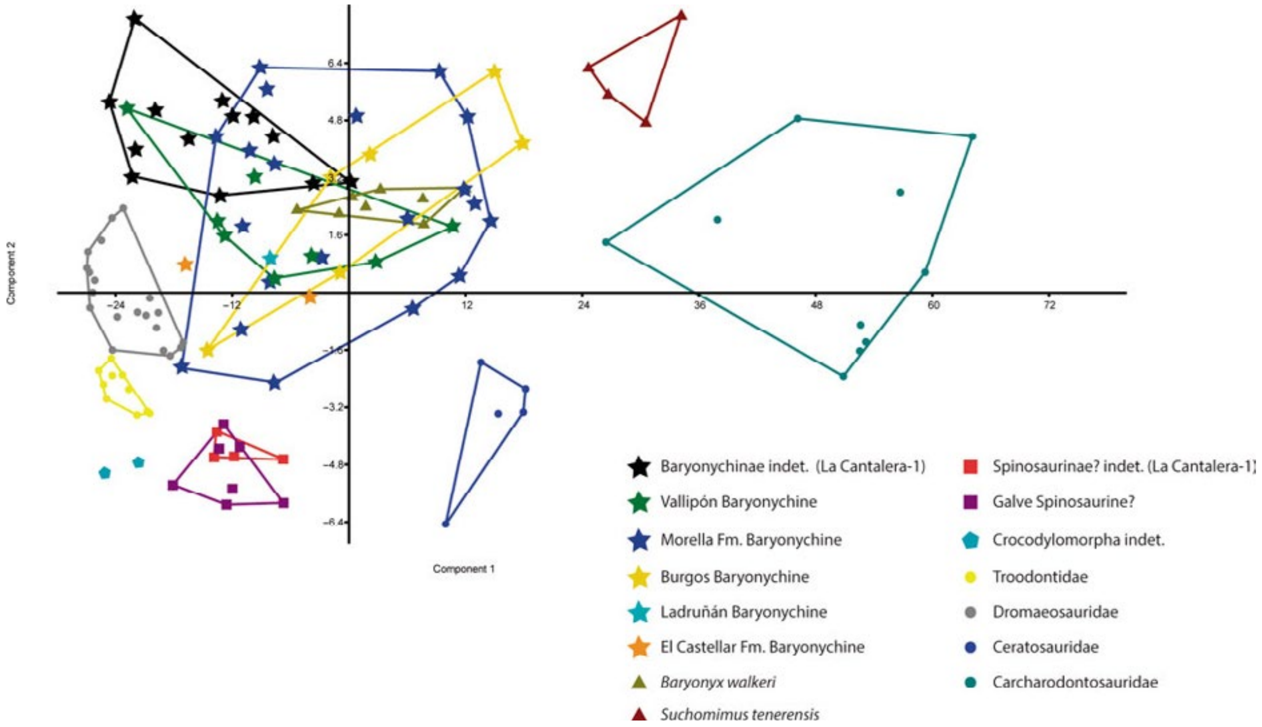

Figure 5. (Colour online) Principal component analysis plot using CBL, CBW, CH, MAVG and DAVG.

similar in size to *Baryonyx* teeth. The overall size is comparable with the data from dromaeosaurid, troodontid and other small theropod teeth. Other baryonychine spinosaurids do not share this feature and have large teeth, comparable with *Baryonyx.* Also remarkable is the grouping of the Spinosaurinae? indet. teeth of Galve and La Cantalera-1. Crocodylomorpha indet. teeth remain separate from those of Spinosaurinae? indet., the most similar teeth in the dataset.

5. Discussion

The grouping of baryonychine spinosaurids from the Iberian Chain around the *Baryonyx* values, as seen in the PCA analysis, suggests that they are closer to this dinosaur than to other baryonychine spinosaurids such as *Suchomimus tenerensis*. This is congruent with other fossil remains from the Iberian Chain, such as the mandibular fragment reported by Viera and Torres (1995) in La Rioja. This fragment was identified as a left maxilla belonging to *Baryonyx walkeri.* Postcranial remains attributed to baryonychine theropods have also been cited: a tibia (Gasulla et al. 2006) and cervical, dorsal and caudal vertebrae (Ortega et al. 2006). However, the tooth remains from the Iberian Peninsula do not have the same appearance as *B. walkeri* teeth from England; this is also seen in jaw fragments reported by Buffetaut (2007) from the Barremian of Portugal and attributed to *Baryonyx* sp. These fragments include some teeth that develop ornamentation both on the labial and lingual sides. It is possible that this difference between *B. walkeri* and other baryonychine teeth could be explained in terms of geographical variation, but in any case here we prefer to ascribe the teeth from La Cantalera site to Baryonychinae indet.

The possible presence of spinosaurine spinosaurids in the Early Cretaceous of Ibera is also of particular interest. The grouping of the teeth from La Cantalera-1 and Galve suggests that they belong to the same morphotype, as we proposed above. The separation between them and crocodylomorph teeth leads us to regard them as dinosaur teeth.

But are they really spinosaurine teeth? These teeth show a set of features that differ from the primitive condition in theropods. The primitive condition for theropod teeth is to be labiolingually compressed, with serrated carinae and the apex facing distally. Spinosaurinae? indet. teeth show scarce labiolingual compression, absent or unserrated carinae, and a relatively straight crown; these traits are considered present in spinosaurine spinosaurids by some authors (Martill and Hutt 1996; Canudo et al. 2008; Fanti et al. 2014). They also can lose ornamentation, which is congruent with the subtle ornamentation found on these teeth.

The derived features in these teeth lead us to rule out their attribution to other basal tetanurans which have primitive teeth. Other teeth with derived features can also be found in dinosaurs from the Early Cretaceous of the Iberian Peninsula, such as maniraptoran dinosaurs, but these have different traits in terms of shape, the presence or absence of denticles, carinae, DSDI, cross-section and size, so they can be ruled out. Other groups such as megalosaurids have mesial teeth with a rounded outline

(Hendrickx and Mateus 2014), but the teeth from La Cantalera-1 do not share their traits. Features such as the absence of lingual curvature, differences in ornamentation and divergent PCA results suggest that they do not belong to crocodylomorphs. We consider that the most probable producer of these teeth was a spinosaurine spinosaurid.

It is particularly remarkable that the teeth from La Cantalera are smaller than other spinosaurid teeth from Iberia. A taphonomic accumulation produced by transportation is ruled out due to the absence of evidence for the transport of the teeth. Other possibilities are the presence in La Cantalera-1 of small taxa and the presence of juvenile specimens. The latter appears to be the more plausible answer due to the presence of teeth with similar features in different parts of Iberia, such as the teeth from the Vallipón and Burgos sites. Nevertheless, further studies are required in order to answer this question.

Whatever the case, the spinosaurid teeth from La Cantalera-1 are small in size, though they are not the only fossil remains from this site with this trait. Other theropod teeth with different affinities such as Carcharodontosauridae? indet. teeth are small in size. The crocodylomorph teeth also show a small size, as reported by Puértolas-Pascual et al. (2014). Fossil remains from sauropods and ornithopods are also characterised by their small size in comparison with other sites in Iberia.

A possible explanation for such small-sized remains is attributable to the features of La Cantalera-1 site: a marshy environment with periodic droughts, surrounded by a Jurassic relief, resulting in a non-permanent body of water and a marshy vegetated area. This small lacustrine area has been interpreted as a feeding area for herbivore dinosaurs (Ruiz-Omeñaca et al. 1997). Moreover, the great biodiversity of vertebrates can be explained by the fact that palustrine areas tend to undergo an increase in organisms – especially during dry periods – due to the displacement of animals to flooded areas where food is found (Puértolas-Pascual et al. 2014). Here we propose that the small size of La Cantalera-1 site did not allow the presence of large animals, either crocodylomorphs or dinosaurs: the fact that large animals could not be sustained in the area led to the increased biodiversity of small-sized animals (juveniles and/or small taxa).

The lack of fish in La Cantalera-1 site implies that the spinosaurid theropods that have been found did not have a piscivorous diet. They probably had to feed on herbivore dinosaurs, smaller theropods such as maniraptorans, pterosaurs and other organisms found at the site (Ruiz-Omeñaca et al. 2005).

6. Conclusions

Two morphotypes of spinosaurid teeth have been recognised in the early Barremian of La Cantalera-1 site: Baryonychinae indet. and Spinosaurinae? indet.

Except for their size, the Baryonychinae indet. teeth are quite similar to those from other Iberian sites. The teeth from the Morella Fm. have microgranular ornamentation and enamel wrinkles that Baryonychinae indet. lacks, so it is probable that the Morella Fm. teeth belong to another baryonychine spinosaurid.

Baryonychine spinosaurids from Iberia are grouped closer to the values for *Baryonyx walkeri* than *Suchomimus tenerensis* in the PCA analysis. However, the Morella Fm. teeth share their microgranular ornamentation with *Suchomimus* (Canudo et al. 2008). We consider that all the baryonychine spinosaurids studied from the Iberian Peninsula with the exception of the Morella Fm. teeth are of a type closer to *Baryonyx walkeri*. This is congruent with the presence in Iberia of skull remains attributed to *Baryonyx walkeri* (Viera and Torres 1995).

Here we present new evidence that supports the idea of the presence of a spinosaurine spinosaurid in Iberia during the Early Cretaceous, as first proposed by Sánchez-Hernández et al. (2007). We have ruled out attribution to other theropods or crocodylomorphs, although we remain cautious due to the scarce fossil record known. Features of these teeth are similar to Morphotype 5 of Fanti et al. (2014), which has a different location both in space and time, tentatively assigned to cf. *Spinosaurus* sp. Nevertheless, Spinosaurinae? indet. does not fit exactly with any of the described spinosaurine teeth, so we regard them as belonging to an unknown spinosaurine spinosaurid, probably closer to *Spinosaurus* than any other member of Spinosaurinae. The presence of this spinosaurine is scarce when compared with its baryonychine relatives, which are present in abundance in the sites of the Iberian Chain. Teeth remains of Spinosaurinae? indet. are also less frequent than Baryonychinae indet. within La Cantalera-1 site.

Small-sized teeth both from Spinosaurinae and Baryonychinae have been observed. This small size has also been observed in other fossil remains belonging to other dinosaurs and crocodylomorphs, leading us to propose that the characteristics that prevailed at La Cantalera-1 site allowed the concentration of small-sized organisms because the ecosystem could not sustain large vertebrates.

Supplementary material

Supplementary material related to this article is available online.

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References

Allain R, Xaisanavong T, Richir P, Khentavong B. 2012. The first definitive asian spinosaurid (Dinosauria: Theropoda) from the Early Cretaceous of Laos. Naturwissenschaften. 99(5):369–377. doi:10.1007/s00114-012-0911-7.

Amiot R, Buffetaut E, Lécuyer C, Wang X, Boudad L, Ding Z, Zhou Z. 2010. Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods. Geology. 38(2):139–142. doi:10.1130/G30402.1.

Aurell M, Bádenas B, Canudo JI, Ruiz-Omeñaca JI. 2004. Evolución tectosedimentaria de la Fm. Blesa (Cretácico Inferior) en el entorno del yacimiento de vertebrados de La Cantalera (Josa, Teruel). Geogaceta. 35:11–13.

Badiola A, Canudo JI, Cuenca-Bescós G. 2008. New multituberculate mammals from the Hauterivian/Barremian transition of Europe (Iberian Peninsula). Paleontology. 51(6):1455–1469. doi:10.1111/j.1475-4983.2008.00822.x.

Barrett PM, Benson RBJ, Rich TH, Vickers-Rich P. 2011. First spinosaurid dinosaur from Australia and the cosmopolitanism of Cretaceous dinosaur faunas. Biol Lett. 7(6):933–936. doi:10.1098/rsbl.2011.0466.

Brusatte SL, Benson RBJ, Carr TD, Williamson TE, Sereno PC. 2007. The systematic utility of theropod enamel wrinkles. J Vert Paleontol. 27(4):1052–1056. doi:10.1671/0272-4634(2007)27[1052:TSUOTE]2.0.CO;2.

Buffetaut E. 2007. The spinosaurid dinosaur *Baryonyx* (Saurischia, Theropoda) in the Early Cretaceous of Portugal. Geol Mag. 144(6):1021–1025. doi:10.1017/S0016756807003883.

Buffetaut E. 2012. An early spinosaurid dinosaur from the Late Jurassic of Tendaguru (Tanzania) and the evolution of the spinosaurid dentition. Oryctos. 10:1–8.

Buffetaut E, Ingavat R. 1986. Unusual theropod dinosaur teeth from the Upper Jurassic of Phu Wiang, northeastern Thailand. Rev Paléobiol. 5(2):217–220.

Buffetaut E, Martill D, Escuillié F. 2004. Pterosaurs as part of a spinosaur diet. Nature. 429(6995):33. doi:10.1038/430033a.

Buffetaut E, Suteethorn V. 1999. The dinosaur fauna of the Sao Khua formation of Thailand and the beginning of the Cretaceous radiation of dinosaurs in Asia. Palaeogeogr Palaeoclimatol Palaeoecol. 150(1–2):13–23. doi:10.1016/S0031-0182(99)00004-8.

Canudo JI, Gasca JM, Aurell M, Badiola A, Blain H-A, Cruzado-Caballero P, Gómez-Fernández D, Moreno-Azanza M, Parrilla J, Rabal-Garcés R, Ruiz-Omeñaca JI. 2010. La Cantalera: an exceptional window onto the vertebrate biodiversity of the Hauterivian-Barremian transition in the Iberian Peninsula. J Iber Geol. 36(2):205–224. doi:10.5209/rev_JIGE.2010.v36.n2.8.

Canudo JI, Gasca JM, Moreno-Azanza M, Aurell M. 2012. New information about the stratigraphic postition and age of the sauropod *Aragosaurus ischiatus* from the Early Cretaceous of the Iberian Peninsula. Geol Mag. 149(2):252–263. doi:10.1017/S0016756811000732.

Canudo JI, Gasulla JM, Gómez-Fernández D, Ortega F, Sanz JL, Yagüe P. 2008. Primera evidencia de dientes aislados atribuidos a Spinosauridae (Theropoda) en el Aptiano inferior (Cretácico Inferior) de Europa: Formación Arcillas de Morella (España). Ameghiniana. 45(3):649–652.

Canudo JI, Ruiz-Omeñaca JI. 2003. Los restos directos de dinosaurios terópodos (excluyendo aves) en España. Dinosaurios y otros reptiles mesozoicos de España. 26:347–373.

Charig AJ, Milner AC. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. Bull Br Mus Nat Hist Geol. 53:11–70.

Currie PJ, Rigby JK, Sloan RE. 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: Carpenter K, Currie PJ, editors. Dinosaur systematics. Approaches and perspectives. Cambridge: Cambridge University Press; p. 107–125.

D'Amore DC. 2009. A functional explanation for denticulation in theropod dinosaur teeth. Anat Rec. 292(9):1297–1314. doi:10.1002/ar.20977.

Dal Sasso C, Maganuco S, Buffetaut E, Mendez MA. 2005. New information on the skull of the enigmatic theropod *Spinosaurus* with remarks on its size and affinities. J Vert Paleontol. 25(4):888–896. doi:10.1671/0272-4634(2005)025[0888:NIOTSO]2.0.CO;2.

Fanti F, Cau A, Martinelli A, Contessi M. 2014. Integrating palaeoecology and morphology in theropod diversity estimation: A case from the Aptian-Albian of Tunisia. Palaeogeogr Palaeoclimatol Palaeoecol. 410:39–57. doi:10.1016/j.palaeo.2014.05.033.

Gasca JM, Canudo JI, Moreno-Azanza M. 2014. On the Iberian iguanodont dinosaur diversity: new fossils from the lower Barremian, Teruel province, Spain. Cretaceous Res. 50:264–272. doi:10.1016/j.cretres.2014.05.009.

Gasca JM, Moreno-Azanza M, Canudo JI. 2008. Dientes de dinosaurios terópodos espinosáuridos de la Formación El Castellar (Cretácico Inferior, Teruel). Palaeontologica Nova SEPAZ. (8):233–234.

Gasulla JM, Ortega F, Escaso F, Sanz JL. 2006. Diversidad de terópodos del Cretácico Inferior (Fm. Arcillas de Morella, Aptiense) en los yacimientos del Mas de la Parreta (Morella, Castellón). In: Fernández-Martínez E, editor. Libro de resúmenes de las 22ª Jornadas de la Sociedad Española de Paleontología. León: Universidad de León; p. 117–118.

Gauthier JA. 1986. Saurischian monophyly and the origin of birds. In: Padian K, editor. The origin of birds and the evolution of flight. Memoirs of the California academy of sciences, Vol. 8. San Francisco, CA: California Academy of Sciences; p. 1–55.

Grambast L. 1968. Evolution of the utricle in the charophyte genera *Perimneste* Harris and *Atopochara* Peck. J Proc Linn Soc Bot. 61(384):5–11. doi:10.1111/j.1095-8339.1968.tb00099.x.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontol Electron. 4(1):1–9.

Hasegawa Y, Buffetaut E, Makoto M, Yuji T. 2003. A possible spinosaurid tooth from the Sebayashi formation (Lower Cretaceous), Gunma, Japan. Bull Gunma Mus Nat His. 7:1–5.

Hendrickx C, Mateus O. 2014. Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. Zootaxa. 3759(1):1–74. doi:10.11646/zootaxa.3759.1.1.

Hendrickx C, Mateus O, Araújo R. 2015. The dentition of megalosaurid theropods. Acta Palaeontol Pol. doi:10.4202/app.00056.2013

Hone DWE, Xu W, Wang DY. 2010. A probable baryonychine (Theropoda: Spinosauridae) tooth from the Upper Cretaceous of Henan Province, China. Vertebrat. PalAsiatic. 1:19–26.

Ibrahim N, Sereno PC, Dal Sasso C, Maganuco S, Fabbri M, Martill DM, Zouhri S, Myhrvold N, Iurino DA. 2014. Semiaquatic adaptations in a giant predatory dinosaur. Science. 345(6204):1613–1616. doi:10.1126/science.1258750.

Infante P, Canudo JI, et al. 2005. Primera evidencia de dinosaurios terópodos en la Formación Mirambel (Barremiense inferior, Cretácico Inferior) en Castellote, Teruel. Geogaceta. 38:31–34.

Kear BP, Rich TH, Vickers-Rich P, Ali MA, Al-Mufarreh YA, Matari AH, Al-Massari AM, Nasser AH, Attia Y, Halawani MA. 2013. First dinosaurs from Saudi Arabia. PLoS ONE. 8(12):e84041. doi:10.1371/journal.pone.0084041.

Kellner AW, Azevedo SA, Machado EB, Carvalho LBD, Henriques DD. 2011. A new dinosaur (Theropoda, Spinosauridae) from the Cretaceous (Cenomanian) Alcântara Formation, Cajual Island, Brazil. An Acad Bras Ciênc. 83(1):99–108.

Kneuper-Haack F. 1966. Ostracoden aus dem Wealden der Sierra de los Cameros. Geol Jb. 44:165–209.

Larson Derek WDW, Currie Philip JPJ, Evans Alistair Robert, Larson DW, Currie PJ. 2013. Multivariate analyses of small theropod dinosaur teeth and implications for paleoecological turnover through time. PLoS ONE. 8(1):e54329–14. doi:10.1371/journal.pone.0054329.

Marsh OC. 1881. Principal characters of American Jurassic dinosaurs, part V. Am J Sci Arts. 3(21):417–423.

Martill DM, Cruickshank ARI, Frey E, Small P, Clarke M. 1996. A new crested maniraptoran dinosaur from the Santana Formation (Lower

Cretaceous) of Brazil. J Geol Soc. 153(1):5–8. doi:10.1144/gsjgs.153.1.0005.

Martill DM, Hutt S. 1996. Possible baryonychid dinosaur teeth from the Wessex Formation (Lower Cretaceous, Barremian) of the Isle of Wight, England. Proc Geol Assoc. 107(2):81–84. doi:10.1016/S0016-7878(96)80001-0.

Martín-Closas C, Diéguez C. 1998. Charophytes from the Lower Cretaceous of the Iberian ranges (Spain). Paleontology. 41: 1133–1152.

Martín-Closas C, Grambast-Fessard N. 1986. Les Charophytes du Crétacé inférieur de la región du Maestrat (Chaîne ibérique-Catalanides, Espagne). Paleobiol Continentale. 15:1–86.

Moreno-Azanza M, Canudo JI, Gasca JM. 2014. Unusual theropod eggshells from the Early Cretaceous Blesa Formation of the Iberian range, Spain. Acta Palaeontol Pol. 59(4):843–854.

Murat B. 1983. Contribution à l'étude stratigraphique, sédimentologique et tectonique du basin éocrétacé d'Oliete (Prov. de Teruel, Espagne) [These Doct]. [Toulouse]: Travaux du lab, Géol. Sed. et. Paleont, Univ Paul Sabatier; p. 247.

Ortega F, Escaso F, Gasulla JM, Dantas P, Sanz JL. 2006. Dinosaurios de la Península Ibérica. Estud Geol. 62(1):219–240. doi:10.3989/egeol.0662122.

Owen R. 1842. Reporto n British fossil reptiles, part II. In: Murray J, editor. Report of the eleventh meeting of the British association for the advancement of science, *London*. p. 60–204.

Pereda-Suberbiola X, Ruiz-Omeñaca JI, Canudo JI, Torcida F, Sanz JL. 2012. Dinosaur faunas from the Early Cretaceous (Valanginian-Albian) of Spain. In: Godefroit P, editor. Bernissart Dinosaurs and early Cretaceous terrestrial ecosystems. Bloomington: Indiana University Press; p. 379–407.

Puértolas-Pascual E, Canudo JI, Rabal-Garcés R. 2014. Revisión de la biodiversidad de los crocodilomorfos del yacimiento de La Cantalera en Teruel, España (Hauteriviense-Barremiense). In: Arreguín-Rodríguez G, Colmenar J, Díaz-Berenguer E, Galán J, Legarda-Lisari A, Parrilla-Bel J, Puértolas-Pascual E, Silva-Casal R, editors. New insights on ancient life. Boltaña: UCM-Departamento de Paleontologia; p. 101–104.

Rauhut OWM, Werner C. 1995. First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). Paläont Z. 69:475–489.

Rayfield EJ, Milner AC, Xuan VB, Young PG. 2007. Functional morphology of spinosaur 'crocodile-mimic' dinosaurs. J Vert Paleontol. 27(4):892–901. doi:10.1671/0272-4634(2007)27[892:FMOSCD]2.0.CO;2.

Ruiz-Omeñaca JI. 2006. Restos directos de dinosaurios (Saurischia, Ornithischia) en el Barremiense (Cretácico Inferior) de la Cordillera Ibérica en Aragón (Teruel, España) [Tesis doctoral]. Universidad de Zaragoza.

Ruiz-Omeñaca JI, Canudo JI. 2003. Un nuevo dinosaurio terópodo ("*Prodeinodon*" sp.) en el Cretácico Inferior de La Cantalera (Teruel). Geogaceta. 34:111–114.

Ruiz-Omeñaca JI, Canudo JI, Cuenca-Bescós G. 1997. Primera evidencia de un área de alimentación de dinosaurios herbívoros en el Cretácico Inferior de España (Teruel). Monogr Acad Ci Exact Fís Quím Nat Zaragoza. 1–48.

Ruiz-Omeñaca JI, Canudo JI, Cuenca-Bescós G. 1998. Primera cita de dinosaurios barioníćidos (Saurischia: Theropoda) en el Barremiense superior (Cretácico Inferior) de Vallipón (Castellote, Teruel). Mas de las Matas. 17:201–223.

Ruiz-Omeñaca JI, Canudo JI, Cruzado-Caballero P, Infante P, Moreno-Azanza M. 2005. Baryonychine teeth (Theropoda: Spinosauridae) from the Lower Cretaceous of La Cantalera (Josa, NE Spain). Kaupia. 14:59–63.

Salas R, Guimerà J, Más R, Martín-Closas C, Meléndez A, Alfonso A. 2001. Evolution of the Mesozoic central Iberian Rift System and its Cainozoic inversion (Iberian Chain). Mém Mus Natl Hist Nat. 186: 145–185.

Samman T, Powell GL, Currie PJ, Hills LV. 2005. Morphometry of the teeth of western North American tyrannosaurids and its applicability to quantitative classification. Acta Palaeontol Pol. 50(4):757–776.

Sánchez-Hernández B, Benton MJ, Naish D. 2007. Dinosaurs and other fossil vertebrates from the Late Jurassic and Early Cretaceous of the Galve area, NE Spain. Palaeogeogr Palaeoclimatol Palaeoecol. 249:180–215.

Schudack ME. 1989. Charophytenflores aude den unterkretazischen Vertebraten-Fundschicten bei Galve und Uña (Ostspanien). Berl Geowiss Abh Reihe A. 106:409–443.

Seeley HG. 1887. On the classification of the fossil animals commonly named Dinosauria. Proc R Soc Lond. 43(258–265):165–171. doi:10.1098/rspl.1887.0117.

Sereno PC, Beck AL, Dutheil DB, Larsson HCE, Lyon GH, Marcot JD, Rauhut OWM, Sadleir RW, Sidor CA, Varrichio DD, et al. 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. Science. 282(5392):1298–1302. doi:10.1126/science.282.5392.1298.

Serrano-Martínez A, Ortega F, Sciscio L, Tent-Manclús JE, Fierro Bandera I, Knoll F. 2015. New theropod remains from the Tiourarén Formation (?Middle Jurassic, Niger) and their bearing on the dental evolution in basal tetanurans. Proc Geol Assoc. 126:107–118.

Smith JB, Dodson P. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. J Vert Paleontol. 23(1):1–12. doi:10.1671/0272-4634(2003)23[1:APFAST]2.0.CO;2.

Smith JB, Vann DR, Dodson P. 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. Anat Rec. 285A:69–736.

Soria de Miguel AR. 1997. La sedimentación en las cuencas marginales del Surco Ibérico durante el Cretácico Inferior y su control estructural [Tesis doctoral]. Universidad de Zaragoza.

Stromer E. 1915. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharîje-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. Abandl d bayr Akad d Wissensch II Kl. 28(3):1–31.

Sues HD, Frey E, Martill DM, Scott DM. 2002. *Irritator challengeri,* a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. J Vert Paleontol. 22(3):535–547. doi:10.1671/0272-4634(2002)022[0535:ICASDT]2.0.CO;2.

Torcida F, Fuentes C, Izquierdo LA, Montero D, Urién V. 1997. Dientes de dinosaurios terópodos (cf. *Baryonyx*) en el Weald de Burgos (España). Stvdia Geologica Salmanticensia. 33(4):59–65.

Torcida Fernández-Baldor FT, Izquierdo Montero LA, Huerta Hurtado p, Montero Huerta D, Pérez Martínez G. 2003. Dientes de dinosaurios (Theropoda, Sauropoda) en el Cretácico Inferior de Burgos (España). In: IER, editor. Dinosaurios y otros Reptiles Mesozoicos en España. Instituto de Estudios Riojanos, Logroño; p. 335–346.

Torices-Hernández A. 2007. Los dinosaurios terópodos del Cretácico Superior de la Cuenca Surpirenaica. [Tesis]. Universidad Complutense de Madrid p. 409 pp.

Viera LI, Torres JA. 1995. Presencia de *Baryonyx walkeri* (Saurischia, Theropoda) en el Weald de La Rioja (España). Nota previa Munibe. 47:53–56.

ANEXO 3

Alonso, A., Gasca, J.M., Navarro-Lorbés, P., Núñez-Lahuerta, C., Galán, J., Parrilla-Bel, J., Rubio, C., Canudo, J.I. 2016. La asociación faunística de Barranco del Hocino 1, un nuevo yacimiento de vertebrados del Barremiense (Cretácico Inferior) de Teruel. *Cuadernos del Museo Geominero* 20, 303-307.

G. Meléndez, A. Núñez y M. Tomás (eds.). Actas de las XXXII Jornadas de la Sociedad Española de Paleontología.
Cuadernos del Museo Geominero, nº 20. Instituto Geológico y Minero de España, Madrid, 2016. ISBN 978-84-9138-016-0.

LA ASOCIACIÓN FAUNÍSTICA DE BARRANCO DEL HOCINO 1, UN NUEVO YACIMIENTO DE VERTEBRADOS DEL BARREMIENSE (CRETÁCICO INFERIOR) DE TERUEL

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RESUMEN

El yacimiento de "Barranco del Hocino 1" es nueva localidad de vertebrados fósiles hallada en la Formación Blesa (Barremiense) cerca de la población de Estercuel (Teruel, España). Una campaña de trabajo de campo ha permitido la recuperación de un centenar de restos óseos y dientes correspondientes a dinosaurios ornitópodos, tireóforos y terópodos, junto a restos de crocodilomorfos, peces óseos, quelonios, además de coprolitos y cáscaras de huevo. Este nuevo yacimiento representa una contribución significativa sobre la diversidad de vertebrados en el Barremiense inferior de Teruel y la formación de yacimientos de vertebrados en la Subcuenca de Oliete.

Palabras clave: Estercuel, Formación Blesa, Dinosauria, Crocodilomorpha, paleobiodiversidad.

ABSTRACT

Here we present "Barranco del Hocino 1", a new vertebrate locality from the Blesa Formation (Barremian), near the town of Estercuel (Teruel, Spain). One campaign of fieldwork has enabled us to recover one hundred of osteological remains. They include ornithopod, thyreophoran and theropod dinosaur postcranial remains and isolated teeth, as well as those of crocodylomorphs, chelonians and osteichthyes. Coprolites and eggshell fragments are also present. This new vertebrate fossil site represents a significate contribution on the vertebrate diversity in the lower Barremian of Teruel and the formation of vertebrate sites in Oliete Sub-Basin.

Key words: Estercuel, Blesa Formation, Dinosauria, Crocodilomorpha, paleobiodiversity.

INTRODUCCIÓN

La parte oriental de la Cuenca del Maestrazgo (subcuenca de Oliete, Teruel) presenta una secuencia de sedimentos continentales en facies Weald donde se conocen pocos yacimientos de vertebrados fósiles, aunque alguno de ellos como

La Cantalera-1 (Josa) es uno de los que presenta una mayor paleobiodiversidad de dinosaurios y crocodilomorfos del Barremiense inferior de la Península Ibérica (Canudo *et al.*, 2010; Puértolas *et al.*, 2015; Alonso y Canudo, 2016). Además hay otros puntos y áreas con fósiles de vertebrados en esta subcuenca, pero en general son descubrimientos aislados (Gasca, 2015; Parrilla-Bel y Canudo, 2015). Sin embargo hay amplias áreas de sedimentos en facies Weald en esta parte de la Cuenca del Maestrazgo en el que no se ha encontrado hasta ahora restos de vertebrados como es el entorno de Estercuel. En este contexto, el objetivo de este trabajo es presentar por primera vez la asociación fósil del yacimiento Barranco del Hocino 1.

LOCALIZACIÓN GEOGRÁFICA Y GEOLÓGICA

El yacimiento del Barranco del Hocino 1 se encuentra en el término municipal de Estercuel, provincia de Teruel, España. Geológicamente se sitúa en el sector meridional de la subcuenca de Oliete, una de las subcuencas que componen la cuenca cretácica del Maestrazgo. El afloramiento del yacimiento se sitúa en la parte media de la Formación Blesa, de edad Barremiense (Canudo *et al.*, 2010).

La sección del Barranco del Hocino se sitúa en una sucesión estratigráfica de niveles de lutitas y margas multicolores con indicios de paleosuelos que alternan con calizas grises bioturbadas, correspondientes a depósitos aluviales y lacustres someros. El nivel fosilífero consiste en lutitas grises con moteado rojo, verde y amarillento, con presencia de bioturbación (trazas de invertebrados), nódulos de carbonato y calcretas. El contenido fósil consiste en vertebrados, moluscos bivalvos, gasterópodos, ostrácodos y carofitas. El paleoambiente se interpreta como una llanura aluvial con exposición área, episodios palustres y desarrollo de paleosuelos.

RESULTADOS

La campaña de trabajo de campo de 2015 ha permitido la recolección superficial de unos 100 restos fósiles de vertebrados. El yacimiento de Barranco del Hocino 1 es una acumulación de huesos desarticulados y fragmentados, muchos de ellos inidentificables. Los restos fósiles se encuentran dispersos en una amplia área que se extiende lateralmente una decena de metros, sin encontrarse en una acumulación significativa en las partes excavadas.Los huesos presentan alto grado de fracturación y meteorización y abrasión variable. Algunas superficies de hueso presentan marcas de dientes. La asociación fósil está dominada por macrorrestos de ornitópodos. En menor medida aparecen restos dérmicos de anquilosaurios, dientes de terópodosy restos de microvertebrados (dientes de crocodilomorfos y de peces osteíctios), fragmentos de placas de tortugas, coprolitos de tamaño medio-pequeño y cáscaras de huevo (Figura 1).

Parte del material ha sido obtenido mediante el lavado y tamizado de sedimento del yacimiento. Se han lavado 10 kilos de material utilizando una luz de malla de 0.5 mm. Además parte del material ha sido lavado empleando un tamiz de luz de malla 0.100 mm para obtener una muestra representativa de microfósiles aparte de los restos de vertebrados.

Dinosaurios

Ornithopoda

Los restos de dinosaurios ornitópodos son los más abundantes dentro de yacimiento de Barranco del Hocino 1, relacionados con iguanodontios estiracosternos. Se han encontrado restos craneales y postcraneales fragmentarios y desarticulados. Destaca por su conservación un yugal, pero también han aparecido restos de vértebras dorsales, sacras y caudales, fragmentos de costillas y de huesos largos y elementos autopodiales.También son frecuentes los dientes mudados muy similares a los que se encuentran en el yacimiento de la Cantalera-1 (Canudo *et al.*, 2010)

Thyreophora

Los restos de dinosaurios tireóforos están representados por fragmentos de osteodermos y dos espinas *dérmicas* bastante completas. Su morfología y tamaño son similares a los restos de anquilosaurios de la Cantalera-1 (Canudo *et al.*, 2010).

Theropoda

Las coronas incompletas y aisladas de dinosaurios terópodos son relativamente abundantes en el yacimiento. Los dientes recuperados hasta el momentoson detetanuros de tamaño pequeño a grande. Se han identificado dientes de espinosáurido de tipo barioniquino, con dientes cónicos y ornamentados con crestas longitudinales en las caras labial y lingual similares a los de la Cantalera-1 (Alonso y Canudo, 2016). Se ha reconocido otra morfología más plesiomórfica, con dientes zifodontos y aplastados labiolingualmente, con carenas serradas y ornamentación compuesta por ondulaciones transversales y marginales (*sensu* Hendrickx *et al*., 2015). Estos dientes han sido atribuido a Carcharodontosauridae indet. (Alonso *et al.,* 2016).

Crocodilomorfos

Además de los dinosaurios se han hallado restos de crocodilomorfos en el yacimiento de Barranco del Hocino 1. Hasta el momento se han recuperado dientes aislados de pequeño tamaño. Se han diferenciado dos morfotipos. El primero corresponde a dientes cónicos, de sección circular, con crestas longitudinales en ambas caras y curvados labiolingualmente. Este tipo de dientes ha sido atribuido tradicionalmente a los Goniopholididae. Morfol**ó**gicamente son similares a los dientes de Goniopholididae? de otros yacimientos de la Formación Blesa como La Cantalera-1 (Puértolas-Pascual *et al*., 2015).

El segundo morfotipo presenta dientes de pequeño tamaño, lanceolados, comprimidos labiolingualmente, con carenas y ornamentados con crestas longitudinales que divergen hacia los márgenes. Este morfotipo es similar a la de otros crocodilomorfos atoposáuridos de la Formación Blesa (Puértolas-Pascual *et al*., 2015).

Figura 1. Restos del Barranco del Hocino 1. A) HOC 32. Coprolito. B, C) HOC 12 y HOC 6. Pollex y diente de iguanodontio estiracosterno. D, E) HOC 26 y HOC 17. Diente de terópodo carcharodontosáurido y espinosáurido. F, G) HOC 33, HOC 34.Fragmentos de placa de tortuga.H) HOC 1. Yugal de iguanodontio. I) HOC 21. Fragmento de osteodermo de anquilosaurio. J) HOC 16. Vértebra caudal de iguanodontio con marcas de dientes. K) HOC 27. Espina dérmica de anquilosaurio.

DISCUSIÓN Y CONCLUSIONES

El yacimiento del Barranco del Hocino presenta bastante similitud con otros de la Formación Blesa como La Cantalera-1 (Canudo *et al.*, 2010) tanto en su composición, como en su formación. El ambiente de depósito corresponde a medios continentales aluviales, en llanuras pobremente drenadas y con presencia de masas de agua dulce efímeras. Estas afinidades geológicas se traducen también en el similar contexto de formación de los yacimientos de vertebrados con acumulación atricional de los restos biológicos. Los restos fósiles de vertebrados están frecuentemente peor conservados en Barranco del Hocino 1 que los de La Cantalera-1, esto podría relacionarse con una exposición subaérea más prolongada de los huesos y/o mayor alteración por procesos pedogénicos, además de la acción de predadores. Por otra parte, aparentemente el contenido y diversidad en microvertebrados es menor en Barranco del Hocino 1.

Salvando las diferencias en el tamaño de muestra entre los yacimientos estudiados de la Formación Blesa (en La Cantalera-1 se ha lavado toneladas de sedimento, Canudo *et al.*, 2010), la fauna de dinosaurios es similar, con gran abundancia de restos de dinosaurios ornitópodos, algunas evidencias de tireóforos y terópodos tetanuros. Por otra parte, terópodos y crocodilomorfos no muestran hasta el momento tanta variedad como en La Cantalera-1 (Canudo *et al.,* 2010; Puértolas-Pascual *et al.*, 2015). Hasta el momento no se han hallado evidencias de otros grupos como dinosaurios saurópodos, pterosaurios o mamíferos descritos en La Cantalera-1. Los restos de osteíctios y quelonios son escasos en el Barranco del Hocino-1, similar a La Cantalera-1, lo que les diferencia de formaciones barremienses como la formación El Castellar que aflora en otras subcuencas (Galve y Peñagolosa) de la Cuenca del Maestrazgo (Gasca, 2015).

No obstante, nuevas campañas de trabajo serán necesarias para comprender con mayor profundidad la paleobiodiversidad de vertebrados del yacimiento y complementar el conocimiento de la presencia de taxones y distribución en esta área de la subcuenca de Oliete.

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REFERENCIAS

Alonso, A., Canudo, J.I. 2016. On the spinosaurid theropod of Blesa Formation from the Early Barremian (Early Cretaceous, Spain). *Historical Biology*, 28(6), 823-834.

Alonso, A., Gasca, J.M., Navarro-Lorbés, P., Rubio, C. y Canudo, J.I. 2016. Isolated theropod teeth from the Barremian (Early Cretaceous) site of Barranco del Hocino 1 (Estercuel, Teruel, Spain). *1st IMERP/XIV EJIP conference proceedings,* Alpuente, 46.

Canudo, J.I., Gasca, J.M., Aurell, M., Badiola, A., Blain, H.-A., Cruzado-Caballero, P., Gómez-Fernández, D., Moreno-Azanza, M., Parrilla, J., Rabal-Garcés, R. y Ruiz-Omeñaca, J.I. 2010. La Cantalera: an exceptional window onto the vertebrate biodiversity of the Hauterivian-Barremian transition in the Iberian Peninsula. *Journal of Iberian Geology,* 36 (2), 205-224.

Gasca, J.M. 2015. *Aportaciones al conocimiento sobre los dinosaurios del Barremiense inferior (Cretácico Inferior) de Teruel, España: asociaciones fósiles, sistemática, paleobiodiversidad y afinidades paleobiogeográficas.* Tesis doctoral, Universidad de Zaragoza, España, 170 pp.

Hendrickx, C., Mateus, O. y Araújo, R. 2015. A proposed terminology of theropod teeth (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology,* 35 (5), e1512.

Parrilla-Bel, J. y Canudo, J.I. 2015. On the presence of plesiosaurs in the Blesa Formation (Barremian) in Teruel (Spain). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* 278(2), 213-227.

Puértolas-Pascual, E., Rabal-Garcés, R. y Canudo, J.I. 2015. Exceptional crocodylomorph biodiversity of "La Cantalera" site (lower Barremian; Lower Cretaceous) in Teruel, Spain. *Palaeontologia Electronica,* 18.2.28A (2), 1-16.

ANEXO 4

Alonso, A., Gasca, J.M., Navarro-Lorbés, P., Rubio, C., Canudo, J.I. 2018. A new contribution to our knowledge of the large bodied theropods from the Barremian of the Iberian Peninsula: the "Barranco del Hocino" site (Spain). *Journal of Iberian Geology* 44(1), 7-23.

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RESEARCH PAPER

A new contribution to our knowledge of the large-bodied theropods from the Barremian of the Iberian Peninsula: the "Barranco del Hocino" site (Spain)

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Abstract

Introduction Barranco del Hocino-1 is a new fossil site located near Estercuel, Teruel province, Spain. The fossil site is located geologically within the Oliete sub-basin, in the Blesa Formation (Barremian in age). Barranco del Hocino-1 shows a diverse assemblage of tetrapod vertebrates similar to other sites in the Blesa Formation.
Materials and methods Six isolated teeth belonging to Theropoda have been found. A study of their qualitative and quantitative characters, along with statistical (DFA) and cladistic analyses, enable us to identify four different dental morphotypes.
Results These morphotypes belong to separate tetanuran theropod taxa. One is related to Spinosauridae. The other morphotypes show affinities with non-spinosaurid tetanurans, probably related to Carcharodontosauria.
Conclusions The results are congruent with the known theropod record of the Iberian Peninsula and western Europe. This work is a new contribution to what is known of the palaeobiodiversity and distribution of large-bodied theropods from the Barremian of the Iberian Peninsula.

Keywords Lower Cretaceous · Blesa Formation · Theropoda · Dinosaur teeth · Spain

Resumen

Introducción Barranco del Hocino-1 es un nuevo yacimiento localizado en el entorno de Estercuel, provincial de Teruel (España). Geológicamente se sitúa en la Formación Blesa (subcuenca de Oliete) de edad Barremiense. El yacimiento presenta una asociación diversa de vertebrados similar a otros de la misma formación.
Materiales y métodos Se han encontrado seis dientes aislados de dinosaurios terópodos. Mediante el estudio de los caracteres cualitativos y cuantitativos junto con el uso de análisis estadístico multivariante (DFA) y análisis cladístico se han podido identificar cuatro morfotipos diferentes.
Resultados Los morfotipos identificados pertenecen a diferentes grupos de tetanuros basales. Uno de los morfotipos está relacionado con Spinosauridae, mientras que el resto presentan afinidades con tetanuros no espinosáuridos, posiblemente relacionados con el clado Carcharodontosauria.
Conclusiones Los resultados son coherentes con el registro de terópodos conocido tanto en la península ibérica y Europa Occidental durante el Cretácico Inferior. El hallazgo supone una nueva contribución al conocimiento de la paleobiodiversidad y distribución de grandes terópodos del Barremiense de la península ibérica.

Palabras clave Cretácico Inferior · Formación Blesa · Theropoda · Dientes de dinosaurio · España

1 Introduction

The presence of dinosaur remains is well-known in the Early Cretaceous sediments of the Iberian Peninsula (e.g., Pereda-Suberbiola et al. 2012). These include theropods, sauropods (basal macronarians, titanosauriforms and rebbachisaurid diplodocoids), thyreophorans and ornithopods

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(iguanodontoids, dryosaurids and basal euornithopods). The Cretaceous Maestrazgo Basin, located in the Iberian Range, has yielded some of the most remarkable examples of these faunas. Particularly noteworthy within this record are dinosaurs such as the sauropods *Aragosaurus* and *Tastavinsaurus* (Sanz et al. 1987; Canudo et al. 2008b) and the ornithopods *Gideonmantellia*, *Delapparentia* (which has been recently proposed as belonging to *Iguanodon* sp.) and *Morelladon* (Ruiz-Omeñaca 2011; Ruiz-Omeñaca et al. 2012; Gasulla et al. 2015; Verdú et al. 2017), as well as a single theropod taxon, *Camarillasaurus* from the Barremian of Teruel (Sánchez-Hernández and Benton 2014). However, isolated tetanuran theropod teeth and theropod eggshells are also relatively abundant (Ruiz-Omeñaca et al. 1996; Infante et al. 2005; Sánchez-Hernández et al. 2007; Moreno-Azanza et al. 2014).

The Oliete sub-basin, situated in the northwestern part of the Maestrazgo Basin, presents a Wealden facies where just a few vertebrate fossil localities are known. The geological formations of this sub-basin have an enormous potential to add to what is known of the Barremian vertebrate faunas of the Iberian Peninsula. A good example is La Cantalera 1 (= La Cantalera) site, which has provided the most diverse assemblage of tetrapods (amphibians, squamates, mammals, crocodylomorphs and dinosaurs) from the early Barremian of the Iberian Peninsula (Badiola et al. 2008; Canudo et al. 2010; Puértolas-Pascual et al. 2015; Alonso and Canudo 2016). So far, isolated vertebrate remains (ornithopod dinosaurs, plesiosaurs) have also been found in other parts of the sub-basin (fossiliferous sites from Obón and Josa, Gasca et al. 2014a; Parrilla-Bel and Canudo 2015).

Recently, the amateur palaeontologist Juan Rubio found a new Wealden outcrop in the sub-basin. No vertebrate remains were reported here until the discovery of the locality of Barranco del Hocino-1 (Alonso et al. 2016). Three fieldwork campaigns (in 2015, 2016 and 2017) enabled us to recover roughly 250 bone remains, revealing the vertebrate palaeodiversity of the site. The fossil locality of Barranco del Hocino-1 is a bonebed composed of disarticulated elements with a notable degree of breakage and incompleteness. The fossil association is dominated by isolated macroremains of ornithopod dinosaurs. In addition, ankylosaur bones, theropod teeth, scarce microvertebrate remains (crocodylomorph and osteichthyan teeth), turtle shell fragments, coprolites and eggshells are also present (Alonso et al. 2016). The aim of the current paper is to give first insights into the theropod fauna from this site.

1.1 Geographical and geological setting

The Barranco del Hocino-1 fossil site is located within the municipality of Estercuel, Teruel province, Spain. Geologically, this fossil locality (Fig. 1) is situated in the middle part of the Blesa Formation. The Early Cretaceous of the Iberian Range in the eastern part of the province of Teruel forms part of the Maestrazgo Basin, which is further divided into seven sub-basins (Salas et al. 2001). One of these is the Oliete sub-basin, where the Barranco del Hocino-1 site is located. This site is an outcrop of the continental facies from the middle part of the Blesa Formation. This geological unit comprises a lower part with alluvial to lacustrine sedimentation, followed by an upper part with two episodes of coastal lagoonal influence in the Josa area (Canudo et al. 2010). In the Estercuel area, it has not yet been possible to recognize the level that separates these two episodes.

The presence of charophyte oogonia attributed to *Atopochara trivolvis triquetra* in the lower part of the Blesa Formation indicates an early Barremian age (Riveline et al. 1996; Canudo et al. 2010; see discussion in Canudo et al. 2012). For the present, we date Barranco del Hocino-1 (upper part of the Blesa Formation) as Barremian in age, pending a more precise evaluation of the age.

The layer of Barranco del Hocino-1 lies within a stratigraphic succession of marly/lutitic levels, where palaeosols alternate with burrowed grey limestone beds. The fossiliferous bed consists of grey lutites with red, green and yellowish mottling, with the presence of bioturbation (invertebrate traces), carbonate nodules and calcrete. The fossil content consists of vertebrates, bivalves and gastropods, along with microfossil remains. Among the microfossils, ostracods and charophytes form the major bioclastic part of the residue from the 50-µm sieve. The depositional environment is interpreted as an alluvial plain with evidence of shallow freshwater/palustrine episodes and the development of palaeosols. Fossil remains are found dispersed over an area that extends laterally about ten metres. The bones have undergone intense breakage, abrasion and weathering; some of them bear tooth traces on the bone surface as well.

2 Materials and methods

The fossils were recovered during the fieldwork campaign of 2015 carried out by the Aragosaurus-IUCA research team (University of Zaragoza). The material recovered is provisionally housed in the Natural History Museum of the University of Zaragoza ("Museo de Ciencias Naturales de la Universidad de Zaragoza", Spain). Observations were made with a stereomicroscope. The teeth were measured with a Mitutoyo Digimatic Digital Calliper, Series No. 500. Six theropod teeth (Supplementary appendix A) from Barranco del Hocino-1 were analysed during the course of this research.

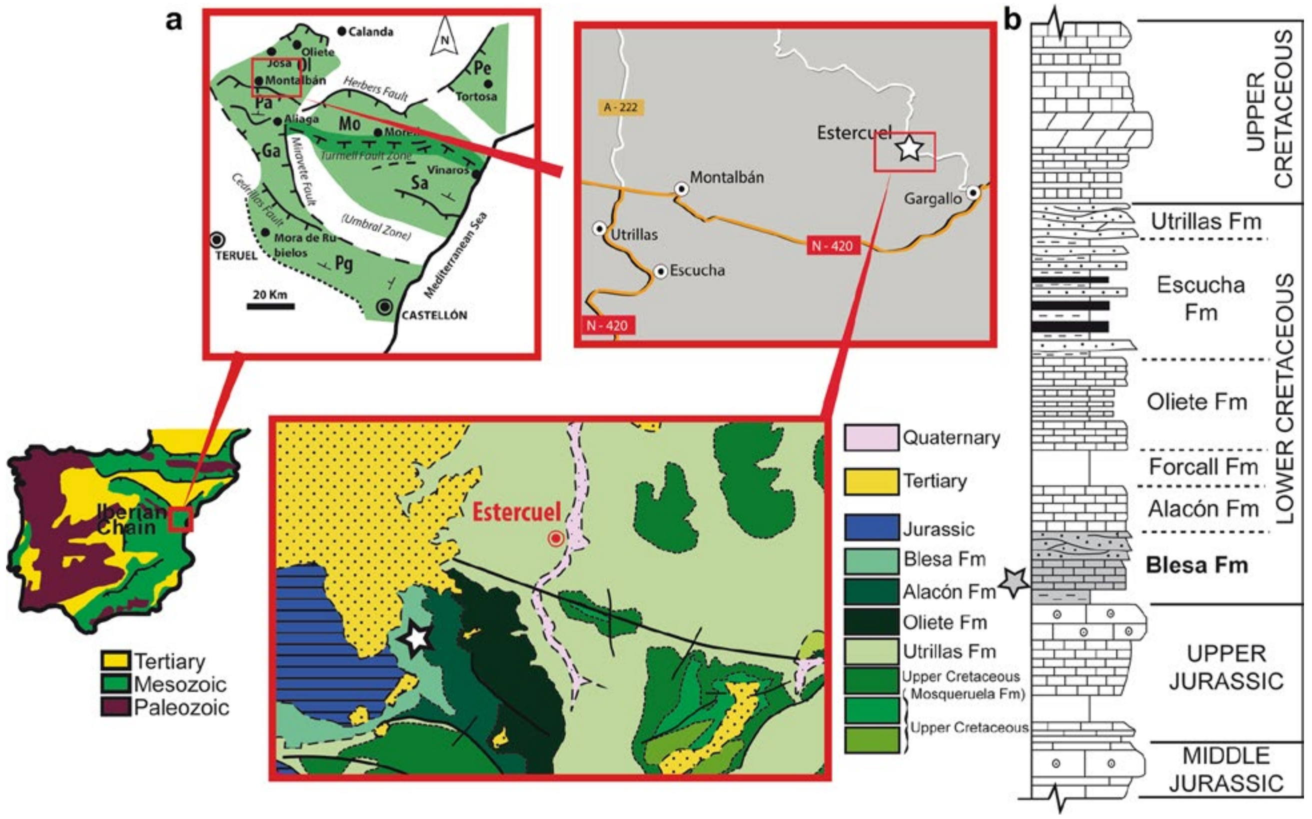

Fig. 1 **a** Geographical and geological setting of Barranco del Hocino-1 site. **b** Stratigraphical setting of the Blesa Formation, from Canudo et al. (2010)

2.1 Anatomical nomenclature

The anatomical nomenclature used in this work follows the recommendations provided by Smith and Dodson (2003) and Hendrickx et al. (2015a). Each tooth includes a crown made of a layer of dentine covered by a layer of enamel, and a root consisting of dentine only. The cervix marks the transition between the crown and root. The top of the crown and root are called the crown or root apices, respectively. The mesial and distal edges of the tooth crown are commonly marked by apicobasally extended crests called carinae. The carinae may bear elaborate serrations known as denticles. Dental ornamentations, such as enamel undulations, flutes, grooves, ridges and depressions are often present on the crown surface. The pattern of the enamel surface is called the enamel texture (Hendrickx et al. 2015a).

The surface of the tooth facing outwards towards the lips is referred to as labial; the opposite surface facing the sagittal midline of the skull is called lingual. The surface closer to the jaw symphysis is called mesial, and the surface facing the jaw articulation is called distal. Basal refers to the direction from the apex to the cervix. Apical refers to the direction from the cervix to the apex.

2.2 Morphometric nomenclature

The morphometric terminology used in this work (Fig. 2) follows the terminology and abbreviations used in Smith et al. (2005) and Hendrickx et al. (2015a). AL: apical length, the basoapical extent of the mesial margin of the crown. CBL: crown base length, the mesiodistal length of the crown at the level of the cervix. CBR: crown base ratio (CBW/CBL), a measure of the lingual compression. CBW: crown base width, the labiolingual width of the crown at the cervix level, perpendicular to CBL. CH: crown height, the basoapical extent of the distal margin of the crown from the most distal point of the cervix to the most apical point of the apex. CHR: crown height ratio (CH/CBL), a measure of the crown elongation. DC: distocentral denticle density, the number of denticles per 5 mm on the distal carina at mid-crown. DSDI: denticle size density index (MC/DC), introduced by Rauhut and Werner (1995), expressing the difference in size between the mesial and distal denticles. MC: mesiocentral denticle density, the number of denticles per 5 mm on the mesial carina at mid-crown.

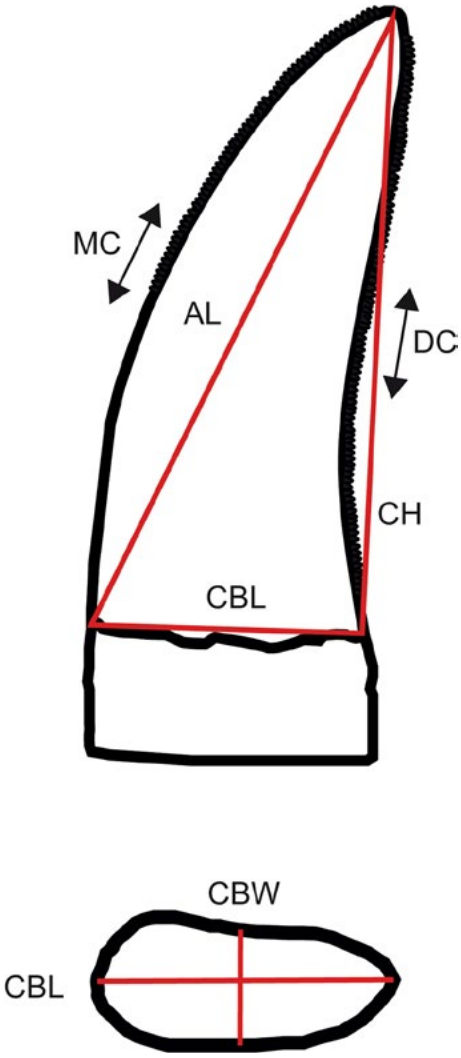

Fig. 2 DFA variables. *AL* apical length, *CBL* crown base length, *CBW* crown base width, *CH* crown height, *DC* distocentral denticle density, *MC* mesiocentral denticle density

2.3 Qualitative and other features

Qualitative features of the teeth were studied in order to complement the morphometric information provided by measurements. These dental features include the shape of the tooth (Torices et al. 2015), the presence and characteristics of the mesial and distal carinae (Currie and Sloan 1990; Hendrickx 2015), the morphology of the denticles (Currie and Sloan 1990; Torices et al. 2015; Hendrickx et al. 2015a), the crown cross-section at the crown base, the crown ornamentations (Hendrickx 2015) and the preservation of the tooth.

2.4 Statistical analysis

A discriminant function analysis (DFA) was carried out using PAST3 (Hammer et al. 2001) on the dataset of Hendrickx et al. (2015b); data from White et al. (2015) and Csiki-Sava et al. (2016) were also included. The dataset contains 1015 teeth from different theropod clades and taxa, as well as the Barranco del Hocino-1 teeth: basal saurischians (*Eoraptor*), basal theropods (*Ischisaurus* = *Herrerasaurus, Eodromaeus*), non-averostran neotheropods (*Coelophysis*, *Liliensternus*, *Dilophosaurus*), Ceratosauridae (*Genyodectes*, *Ceratosaurus*), Noasauridae (*Noasaurus*, *Masiakasaurus*), Abelisauridae (*Abelisaurus*, *Rugops*, *Indosuchus*, *Majungasaurus*, *Aucasaurus*, *Skorpiovenator*, *Carnotaurus*), the possible metriacanthosaurid *Erectopus*, Piatnitzkysauridae (*Piatnitzkysaurus*), Megalosauridae (*Afrovenator*, *Duriavenator*, *Megalosaurus*, *Dubreuillosaurus*, *Torvosaurus*), Baryonychinae (*Baryonyx*, *Suchomimus),* Spinosaurinae (*Irritator*, *Spinosaurus*), Allosauridae (*Allosaurus*), Neovenatoridae (*Neovenator*), Carcharodontosauridae (*Acrocanthosaurus*, *Eocarcharia*, *Carcharodontosaurus*, *Giganotosaurus*, *Mapusaurus*), Megaraptora (*Australovenator*, *Fukuiraptor*, *Aerosteon*), non-tyrannosaurid Tyrannosauroidea (*Eotyrannus*, *Raptorex*), Tyrannosauridae (*Alioramus, Gorgosaurus*, *Daspletosaurus*, *Albertosaurus*, *Tyrannosaurus*), the possible dromaeosaurid *Nuthetes*, Dromaeosauridae (*Bambiraptor*, *Deinonychus*, *Dromaeosaurus*, *Velociraptor*, *Saurornitholestes*, *Atrociraptor*, *Zapsalis*), Troodontidae (*Troodon*, *Zanabazar*, *Pectinodon*), and *Richardoestesia*. The analysis performed was a discriminant function analysis (DFA). DFA is an ordination technique applied to previously identified data in order to find the best discriminant variables. It also has predictive power and is able to classify unknown data in the previously known groups (Hammer and Harper 2006).

The variables used are CBL, CBW, CH, AL, MC and DC. Absent data were coded as a question mark and missing values were estimated with a mean value for that measurement from across the sample. To better reflect a normal distribution, all the data were log-transformed (see Samman et al. 2005). In order to avoid interference and overlapping between groups, and given the absence of mesial teeth from Barranco del Hocino 1 site, the mesial teeth were removed from the dataset.

The presence of small groups affects the accuracy of the analysis; in this case we maintained low number groups due to the relevance of some of them from comparison with Barranco del Hocino 1 morphotypes, even though this was at the expense of an improved analysis.

Also, we maintained isolated teeth that have been identified on generic level, for the same reason as above. Ideally, the dataset would consist of non-isolated teeth. Nonetheless, some taxa include isolated teeth; the relevance of those groups leads us to do not exclude the specimens.

The DFA of the 860 remaining teeth returned 70.99% correctly classified teeth (Supplementary appendix A).

The functions obtained explain the variance of the dataset. The first and the second functions explain 80.58% of the variance (Supplementary appendix A). These canonical functions can be used to create a plot showing the graphical representation of the morphospace occupied by the teeth in a dispersion graph (Fig. 3). The weight of each variable in the canonical functions can be found in Supplementary appendix A.

2.5 Cladistic analysis

Cladistic analyses have been used by some authors to evaluate the phylogenetic position of isolated theropod teeth. The teeth from Barranco del Hocino-1 were analysed using the supermatrix of Hendrickx and Mateus (2014b), with the modifications proposed by Gerke and Wings (2016). The supermatrix includes 60 theropod taxa with 1972 characters. Of these 1972 characters, 141 characters are dentition-based features. The analysis was carried with TNT 1.5 (Goloboff and Catalano 2016) using the "Traditional search" with 1000 replications, keeping 10 trees per replication. The protocol of Hendrickx and Mateus (2014b) and Gerke and Wings (2016) was performed as well, using the "New Technology Search", selecting "Sectorial Search", "Ratchet", "Drift" and "Tree fusing", and stabilizing the consensus trees twice with a factor of 75, followed an additional round of TBR using. Both analyses produced the same results.

3 Results

3.1 Systematic palaeontology

TETANURAE Gauthier, 1986

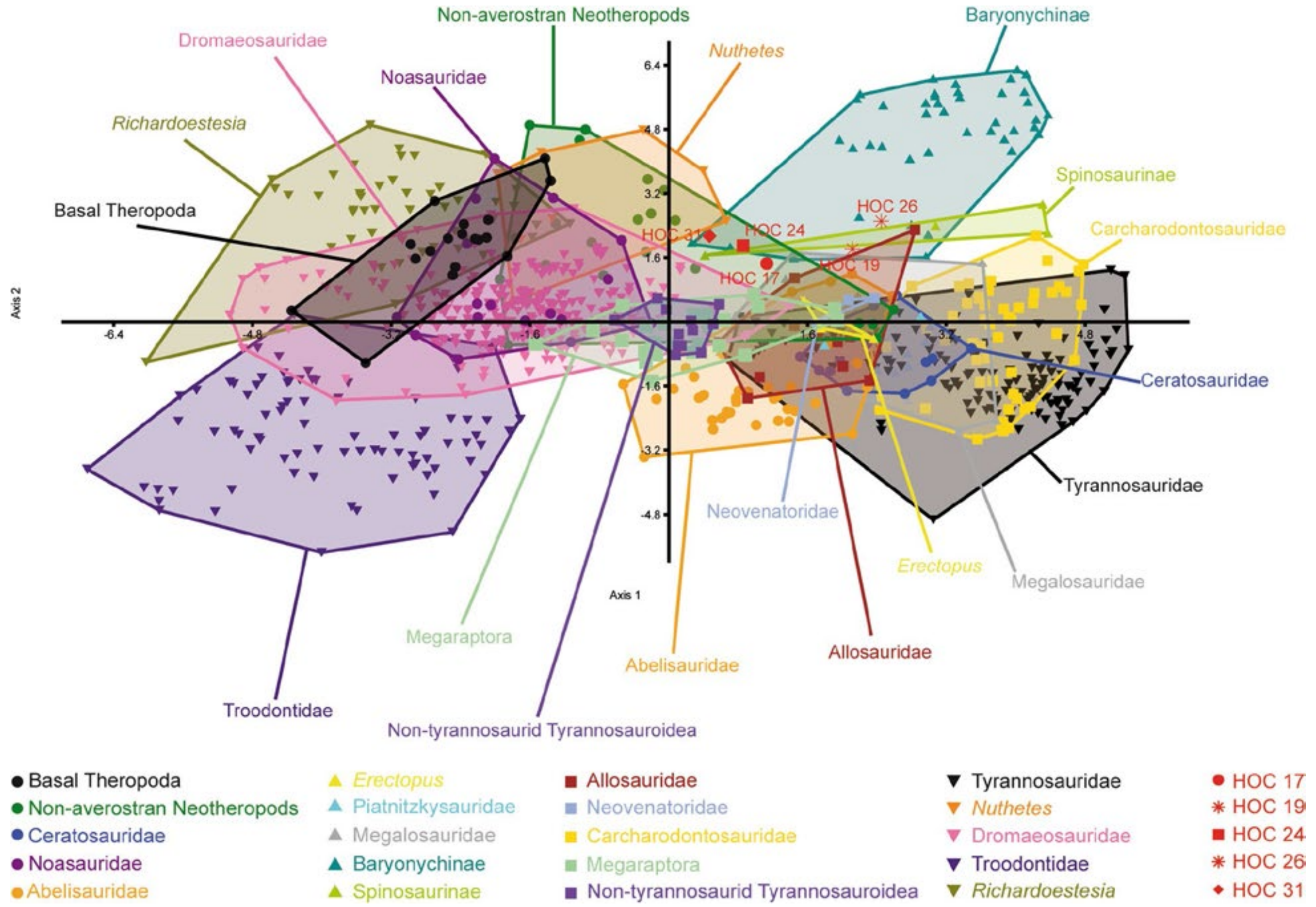

Fig. 3 Results of the DFA conducted on a dataset of 1015 teeth, including Barranco del Hocino-1 teeth. The first function explains the 56.86% of variance; the second canonical function explains the 23.72% of the variance

3.1.1 Tetanurae indet. 1

Material: One shed tooth (HOC 24).

3.1.1.1 Description This morphotype includes one tooth lacking the apex and a small part of the base (Fig. 4). The enamel surface is worn, show microstratches and the lingual area has some white marks on its apical and central regions that were caused by the roots of modern plants. The tooth is ziphodont, with a labiolingually compressed and a distally curved crown. The tooth crown also bears serrations but lacks a few denticles on the mesial and distal carina.

A transverse break is located at the mid-crown. Another break affects the lowermost part of the lingual surface, where a small fragment was detached from the crown. In basal view the tooth crown reveals the pulp cavity.

HOC 24 is a medium-sized theropod tooth, with a crown base length (CBL) of 9.43 mm, crown base width (CBW) of 5.63, and preserved crown height (CH) of 14.32 mm. The estimated value of the crown height (CH) is 20.2 mm. With a CBR and a CHR of 0.6 and 2.15 respectively, the crown is moderately labiolingually flattened and moderately elongated, with an ovoid cross-section at its base.

The mesial and distal profiles are convex and concave, respectively. The mesial margin of the tooth crown is more recurved than the distal margin; the crown has carinae on both mesial and distal margins. The mesial carina extends from the apex to the basal third of the crown, finishing well above the cervix. On the other hand, the distal carina extends along the entire distal margin. In addition, the labial surface adjacent to the distal carina is flattened.

The mesial carina bears denticles and is centrally positioned. The labial surface is slightly basoapically sigmoid with the basal part of the crown convex and the apical part concave. The lingual surface, however, seems to remain basoapically convex.

In distal view, the distal carina is displaced labially and bears denticles all along the edge. The labial and lingual surfaces are mesiodistally convex, with the lingual side more convex than the labial side.

In apical view, the tooth crown has a lenticular cross-section and both the mesial and distal carinae are acute. In basal view, the cross-section of the crown is oval and slightly lanceolate whereas the cross-section at the level of the mid-crown is lenticular.

The mesial carina preserves nine denticles per 2 mm (around 22.5 denticles per 5 mm). In lateral view, the apicobasal axis of the denticles is greater than the mesiodistal axis, giving them an apicobasally subrectangular outline. The external margin of the denticles is parabolic.

The distal carina has around 20 denticles per 5 mma at the mid-crown. The denticles gradually decrease in size towards

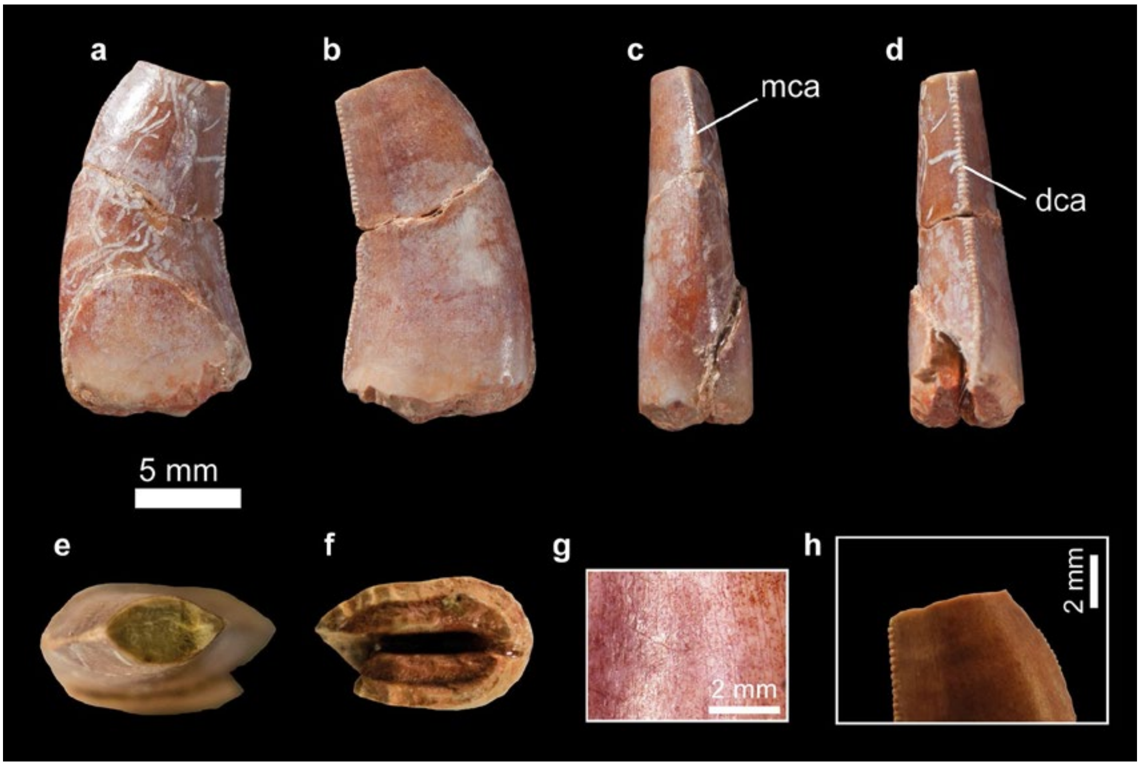

Fig. 4 Tetanurae indet. 1. HOC 24. **a** Lingual, **b** labial, **c** mesial, **d** distal, **e** apical, **f** basal views. **g**, **h** Enamel surface and denticles. *dca* distal carina, *mca* mesial carina

its base. Morphologically, they are chisel-shaped and the mesiodistal axis of the denticles is greater than the apicobasal length, which give them a subrectangular outline. The denticles are positioned perpendicularly to the carina and the external margin is parabolic to semicircular. In addition, the outline of the denticles is either symmetrically or asymmetrically convex. The interdenticular space between denticles is narrow and deeper in the distal denticles. The distal carina shows interdenticular sulci diagonally oriented basally towards the base of the tooth crown. They are short and are better seen at low light angle.

The crown surface is covered with microscratches on both lingual and labial sides due to wear and erosion. The surface also displays marginal undulations, which are short and are better seen at certain angles. In addition there are transverse undulations covering the complete surface of the crown; they are apically concave and they curve towards the apex as they approach the carina. The enamel texture is braided (sensu Hendrickx et al. 2015a).

3.1.1.2 Discussion HOC 24 is a moderately compressed crown, suggesting that it is a lateral tooth. This tooth is different from other theropod clades. Coelophysids and compsognathids have small crowns bearing minute denticles (Buckley 2009; Hendrickx and Mateus 2014b). The dentition of abelisaurid theropods is usually squat, weakly recurved and some of them have hooked denticles and the mesial carina reaches the cervix (Hendrickx et al. 2015b) whereas non-abelisaurid ceratosaurs have a mesial carina that extends at a certain distance from the cervix. HOC 24 is also clearly different from the conidont teeth with apicobasal enamel flutes, minute denticles and deeply veined enamel texture of spinosaurids (Charig and Milner, 1997; Canudo et al. 2008a; Hendrickx and Mateus 2014b). In addition, it does not possess the thickened and incrassate crowns of derived tyrannosauroids (Brusatte et al. 2010; Csiki-Sava et al. 2016) and it is significantly different from troodontids, therizinosaurs, ornithomimosaurs, alvarezsauroids, oviraptorosaurs or avialans, which have small, conical, folidont and/or unserrated crowns. When serrated, the carinae bear either particularly large, often hooked denticles, or minute serrations (Pérez-Moreno et al. 1994; Norell et al. 2009; Hendrickx and Mateus 2014b; Hendrickx et al. 2015b; Csiki-Sava et al. 2016).

One of the most striking features of this morphotype is a mesial carina that does not reach the cervix. This trait is seen in basal theropods such as *Eoraptor*, non-spinosaurid megalosauroids and most piatnitzkysaurid mesial and lateral teeth (Hendrickx et al. 2015b), neovenatorids (Hutt et al. 1996), carcharodontosaurids such as *Acrocanthosaurus,* megaraptorans (White et al. 2015), therizinosaurs, dromaeosaurids and microraptorans (Hendrickx 2015). The presence of transverse and marginal undulations is common among non-neocoelurosaur averostrans (Brusatte et al. 2007, Hendrickx and Mateus 2014b).

A slightly concave or planar surface adjacent to the distal carina is seen among non-neocoelurosaur theropods. The slightly concave or planar surface is observable in *Skorpiovenator*, *Erectopus*, *Piatnitzkysaurus*, *Afrovenator*, *Sinraptor*, *Neovenator*, *Fukuiraptor* and *Australovenator,* as well as *Coelophysis*, *Dilophosaurus* and *Ceratosaurus* (Hendrickx 2015).

DFA (Supplementary appendix A) classifies HOC 24 as a member of the group Neovenatoridae. The cladistic analysis (Supplementary appendix B) recovers HOC 24 as a tyrannosauroid.

This tooth shows some differences with respect to Tetanurae indet. 2 and Tetanurae cf. Carcharodontosauria indet. (see below). The tooth has a thicker cross-section and the general shape of the crown is more squat. It also possesses a planar surface adjacent to the distal carina. Despite this, they share some common features, including the presence of transverse and marginal undulations, a relatively similar denticle density, a mesial carina that does not reach the cervix and a distal carina that is displaced labially. The differences between the morphotypes could be explained by ontogenetic variation, different tooth positions, or the presence of two different taxa.

Given the incompleteness of the tooth crown here we prefer to be cautious and consider this morphotype as Tetanurae indet.

3.1.2 Tetanurae indet. 2

Material: HOC 31, a shed tooth.

3.1.2.1 Description The morphotype comprises one tooth lacking the root and part of the base (Fig. 5). The enamel surface is worn and shows microscratches. The tooth is ziphodont, with a labiolingually compressed and curved crown. The tooth crown has transverse breaks and the basalmost part is broken; this is the most damagead area. In basal view, it reveals a pulp cavity filled with sediment.

HOC 31 is a medium-sized theropod tooth, with a preserved crown base length (CBL) of 8.75 mm, a preserved crown base width (CBW) of 4.2 mm, and preserved crown height (CH) of 25.2 mm. The tooth crown is strongly labiolingually compressed (CBR around 0.4) and elongated (CHR around 2.8).

In lateral view, the mesial margin of the tooth crown is convex, while the distal margin is concave. The mesial margin is more recurved than the distal margin. The apex is acute and has spalled surfaces both on labial and lingual sides. The tooth crown has mesial and distal carinae, and the mesial carina terminates well above the cervix whereas the distal carina extends on the whole crown.

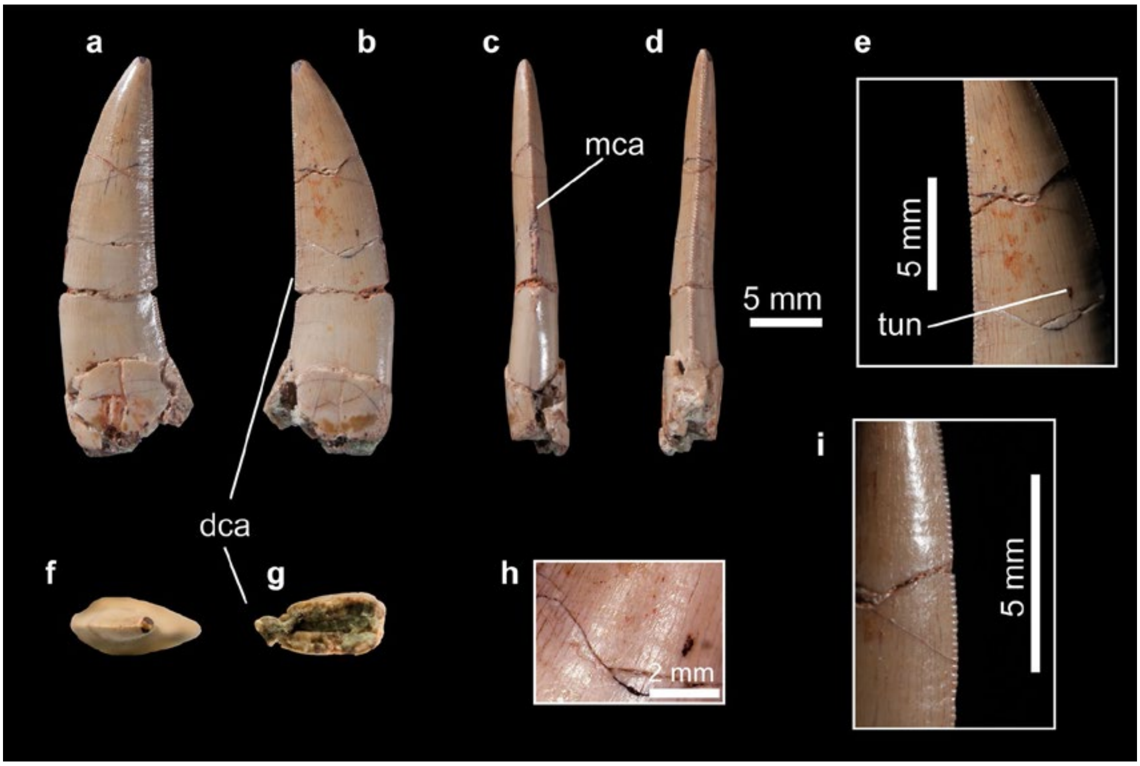

Fig. 5 Tetanurae indet. 2. HOC 31 in **a** labial, **b** lingual, **c** mesial, **d** distal view. **e** Detail of undulations, mesial and distal carinae. **f** Apical, **g** basal views. **h** Enamel surface, **i** mesial carina

In mesial view, the mesial carina bears denticles and is located on the mesiodistal axis of the crown. The labial surface of HOC 31 is slightly sigmoid basoapically, with the basalmost part of the crown convex whereas the apical part is concave.

In distal view, the distal carina bears serrations as well and is very slightly displaced labially. The labial and lingual surfaces of the tooth crown are weakly mesiodistally convex.

In apical view, the tip is distally positioned on the crown. In basal view, the cross-section of the crown is lanceolate at the level of the cervix with the mesial surface being broader than the distal surface. The cross section at the level of the mid-crown is lenticular with the mesial and distal margins both acute.

The mesial carina has 24 denticles per 5 mm at the mid-crown. The denticles display a gradual variation in size towards the basalmost part of the crown. The mesial denticles have the same basoapical and mesiodistal length which give them a subquadrangular shape. The external margin of the denticles is parabolic.

The distal carina has 20 denticles per 5 mm at the mid-crown, and the denticle size density index (DSDI) is 1.2. The denticles are perpendicular to the distal margin of the tooth. The denticles decrease in size towards the base, displaying a gradual variation. The distocentral denticles are subquadrangular. There is, however, variation in shape: the distobasal denticles are proximodistally subrectangular. The main axis of the denticles is perpendicular to the mesial carina and the external margin of the denticles is parabolic to semicircular; they are either symmetrically or asymmetrically convex. The space between denticles is narrow and deeper in the distal denticles. There are interdenticular sulci; they are short, basally inclined and they are present on the distal margin.

The crown surface is worn and is covered with micro-scratches probably due to wear and erosion. The enamel surface displays horizontally oriented marginal undulations which bend towards the tip of the crown near the mesial and distal carinae. In addition, there are horizontally oriented transverse undulations, which are apically concave, and they curve apically as they approach the carinae. The transverse undulations completely cover the enamel surface of the tooth crown.

The original enamel texture appears to be braided (sensu Hendrickx et al. 2015a).

3.1.2.2 Discussion This tooth share traits commonly found in non-maniraptoriform tetanurans. HOC 31 is strongly labiolingually compressed, the mesial carina does not reach the cervix, the distal carina is slightly displaced labially, and it also has transverse and marginal undulations, interdenticular sulci, a braided enamel texture and a lenticular cross-section. However, the tooth crown shows some differences with respect to Tetanurae cf. Carcharodontosauria indet. (see below). The DSDI is 1.2 and the distocentral denticles are subquadrangular instead of proximodistally subrectangular. The labial and lingual surfaces are similarly mesiodistally convex instead of a lingual surface more mesiodistally convex in shape.

DFA analysis (Supplementary appendix A) classifies this tooth as *Erectopus*. The cladistic analysis (Supplementary appendix B) recovers a polytomy at the base of Averostra. A reduced strict consensus was calculated using the pruning trees option in TNT (Supplementary appendix B), resulting in the pruning of HOC 31. It is recovered either as the sister taxon of Averostra, as the sister taxon of *Dubreuillosaurus*, as the sister taxon of *Piatnitzkysaurus* or as the sister taxon of Spinosauridae.

The difference in size between the mesial and distal denticles in this morphotype is remarkable. This character is present in the lateral dentition of noasaurids such as *Noasaurus* and *Masiakasaurus*¸ piatnitzkysaurids such as *Marshosaurus* and *Piatnitzkysaurus,* non-tyrannosaurid Tyrannosauroidea such as *Proceratosaurus* (Rauhut et al. 2010), *Dilong, Guanlong, Eotyrannus* and *Xiongguanlong*,. Dromaeosaurids such as *Velociraptor* and *Deinonychus* show this condition as well (Hendrickx 2015).

Despite the similarity between Tetanurae cf. Carcharodontosauria indet. (see below) and this tooth, the high denticle size index (DSDI) and the absence of this feature in allosauroids leads us to consider this morphotype as another morphotype of Tetanurae indet. However, we do not exclude that the differences between this morphotype and Tetanurae cf. Carcharodontosauria indet. could be explained by ontogenetic variation, different tooth positions, or the presence of two different taxa. New discoveries are required to resolve this issue.

TETANURAE Gauthier, 1986
MEGALOSAUROIDEA Fitzinger, 1843
Spinosauridae Stromer, 1915
Spinosaurinae Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson and Wilson, 1998

3.1.3 Spinosaurinae indet.

Material: HOC 17, HOC 28, two shed teeth.

3.1.3.1 Description HOC 17 is a conical tooth from a theropod dinosaur preserving most of the crown and a small part of the root (Fig. 6). The enamel shows small fractures, and some parts are missing. A transverse break is located at the end of the apical third. The lingual surface has a damaged area in its basal region, which is lacking

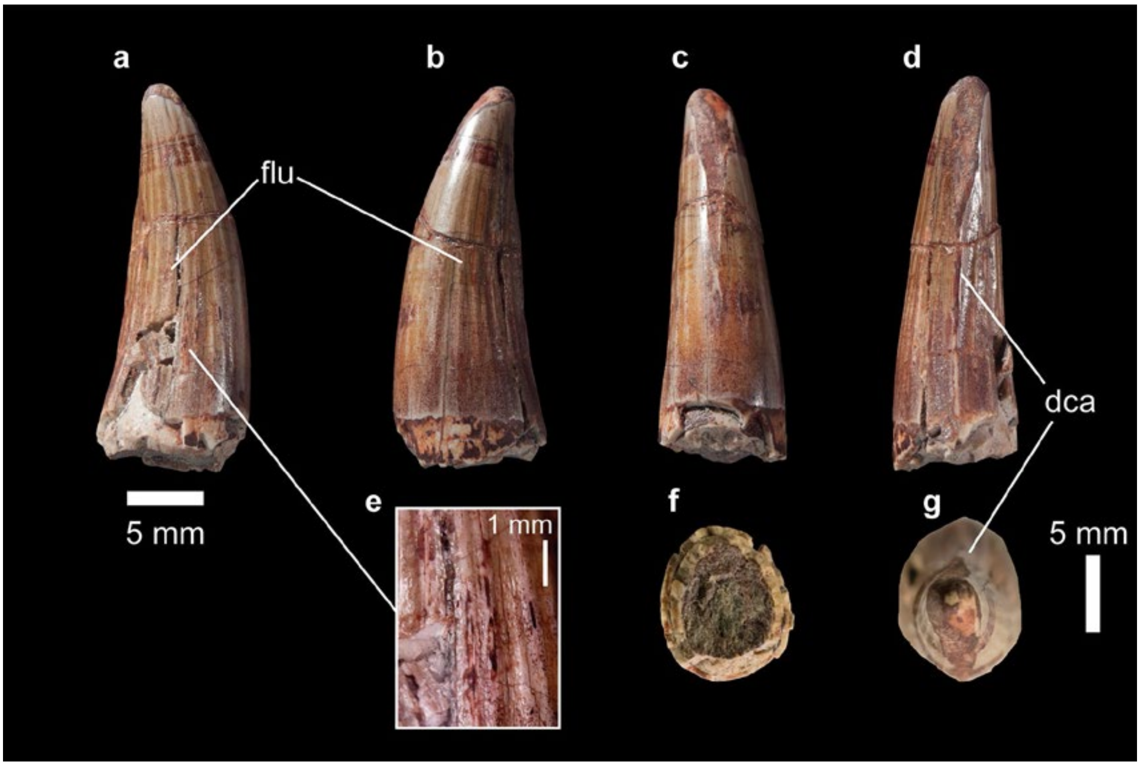

Fig. 6 Spinosaurinae indet. HOC 17: **a** lingual, **b** labial, **c** mesial, **d** distal view. **e** Enamel surface and ornamentation. **f** Basal view. **g** Apical views. *dca* distal carina, *flu* flutes

fragments of the crown. The surface is also covered with microscratches, and some parts of the original enamel texture are worn, possibly due to abrasion. HOC 28 is a poorly preserved theropod tooth fragment but here it is considered to represent the same morphotype as HOC 17 because of its general similarity and the presence of longitudinal flutes along the crown. Therefore, the description of this morphotype is based on the better-preserved tooth, HOC 17.

HOC 17 is a medium-sized tooth from a theropod dinosaur, with a crown base length (CBL) of 10.27 mm, crown base width (CBW) of 8.61 mm, and crown height (CH) of 23.25 mm. The tooth is conidont (sensu Hendrickx et al. 2015a). With a CBR and a CHR of 0.8 and 2.26 respectively, the crown is weakly labiolingually compressed and moderately elongated, with a broad and rounded cross-section at its base.

In lateral view, the mesial and distal profiles are convex and concave, respectively. The crown is moderately recurved and its curvature is greater mesially than distally. The base of the crown is longer than the mid-crown mesiodistally.

In distal view, the mesial and distal profiles are curved towards the lingual side of the crown. The labial and lingual surfaces are mesiodistally convex with the enamel extending to the same level basally. The distal carina is centrally positioned on the distal margin of the crown and reaches the cervix. It does not show any serrations.

In mesial view, the mesial surface is worn, and this precludes the recognition of a possible mesial carina. The mesial carina, if it was originally present, extended significantly (5.5 mm) above the cervix and was medially positioned. In apical view, the tip is slightly lingually oriented.

The cross-sections at the level of the cervix and the mid-crown are elliptical to subcircular; the mesial margin is wider than the distal margin. Both labial and lingual surfaces are mesiodistally convex along the crown; mesial and distal margins are convex as well.

The distal carina is partially eroded, but the central part, which is better preserved, lacks denticles, suggesting that the distal carina is unserrated.

The apex of the crown has a spalled surface extending along the apical third of the crown on both the mesial and distal surfaces. Numerous flutes running apicobasally are visible on the lingual and labial sides of the crown. Five and eight flutes are present on the labial and lingual sides, respectively.

Some parts of the enamel are smooth due to erosion and wear. The preserved enamel surface texture corresponds to the veined texture described by Hendrickx et al. (2015a). The texture is basoapically oriented in the middle of the crown but curves towards the carina at the distal margin. The enamel texture is best preserved between the apicobasal ridges delimiting each flute.

3.1.3.2 Discussion The tooth has a combination of features seen in spinosaurid teeth such as a slight distal curvature, a subcircular cross-section, fluted enamel on both labial and lingual sides of the crown and a veined enamel texture. Spinosaurid teeth either have minute denticles or unserrated carinae (Charig and Milner 1997; Sereno et al. 1998; Ruiz-Omeñaca et al. 2005; Canudo et al. 2008a; Gasca et al. 2008).

Some authors have pointed out the presence of a morphotype of spinosaurid tooth from the Barremian of Teruel Province with an unserrated mesial carina (Artoles Formation, Ruiz-Omeñaca et al. 1998; El Castellar Formation, Gasca et al. 2008). However, this cannot be established in the case of this tooth. The mesial carina, if present, was not reaching the cervix.

The presence of flutes is characteristic of spinosaurid teeth, although they are present in other taxa as well (e.g., *Coelophysis, Ceratosaurus, Masiakasaurus, Scipionyx,* and some dromaeosaurids; Hendrickx 2015). HOC 17 has flutes on both sides as in *Suchomimus*, *Spinosaurus* and *Siamosaurus* whereas *Baryonyx* tends to have flutes restricted to one side of the crown (Charig and Milner 1997; Hendrickx 2015). The veined enamel texture (sensu Hendrickx et al. 2015a) of the tooth characterizes spinosaurid teeth. It has been found in *Baryonyx*, *Suchomimus*, *Spinosaurus* and other spinosaurids (Canudo et al. 2008a; Serrano-Martínez et al. 2016; Hendrickx 2015).

Spinosaurids are divided traditionally into two subfamilies, Baryonychinae and Spinosaurinae. There are various morphological differences between their teeth. Baryonychine teeth have serrated carinae with minute denticles, more labiolingually compressed teeth than spinosaurines and a more pronounced distal curvature of the crown (Charig and Milner 1997; Canudo et al. 2008a; Alonso and Canudo 2016). Also, spinosaurine teeth have unserrated carinae, as exemplified by *Irritator*, *Angaturama* and *Spinosaurus* (Stromer, 1915; Kellner and Campos 1996; Sues et al. 2002). In general, all these differences are plesiomorphies in baryonychine teeth, or apomorphies in spinosaurine teeth.

The DFA analysis classifies HOC 17 as belonging to a member of Spinosaurinae (Supplementary appendix A). Likewise, the cladistic analysis considers this morphotype as the sister taxon of the group formed by *Spinosaurus* and *Irritator* (Supplementary appendix B). The possible presence of spinosaurine spinosaurids in the Lower Cretaceous of the Iberian Peninsula has been proposed before (Sánchez-Hernández et al. 2007; Alonso and Canudo 2016), but the most common spinosaurid material belongs to Baryonychinae (Infante et al. 2005; Canudo et al. 2008a; Gasca et al. 2008; Mateus et al. 2011; Alonso and Canudo 2016).

Given the combination of features and the results of the analyses here we consider this morphotype as Spinosaurinae indet.

TETANURAE Gauthier, 1986

3.1.4 Tetanurae cf. Carcharodontosauria indet.

Material: HOC 19 and HOC 26, two shed teeth.

3.1.4.1 Description The morphotype comprises two teeth lacking the root and the basalmost part of the tooth. The enamel surface is worn and shows microscratches. The shape of the teeth is the common blade-like morphology, with labiolingually compressed and distally curved crowns bearing serrated carinae (Fig. 7). The crown HOC 19 is the best-preserved tooth; it lacks the basal part, and the break reveals the dentine and a narrow pulp cavity filled with sediment. The apex and some areas of the labial and lingual surfaces lack the enamel cover, especially the lingual surface, which shows a longitudinal area from the basal part to the mid-crown where the enamel is missing.

The crown HOC 26 exhibits transverse breaks over its entire height: at least four large breaks plus minor fractures. The base is the most damaged region of the crown and some parts are missing. It also has a series of white marks which are more evident on the lingual surface of the crown. These marks were caused by the roots of modern plants that damaged the enamel.

HOC 19 and HOC 26 are medium-sized theropod teeth, with a preserved crown base length (CBL) of 14.8 and 16.2 mm respectively; a preserved crown base width (CBW) of 6.8 and 7.5 mm respectively; and preserved crown height (CH) of 39.1 and 50.6 mm respectively. All the crowns are strongly to moderately labiolingually compressed (CBR value around 0.4) and elongated (CHR around 2.6–3). The teeth have a narrow, teardrop-shaped cross-section at their bases.

In lateral view, the mesial and distal profiles are convex and concave, respectively. The mesial margins of the crowns are more recurved than the distal margins. The apices are acute, pointed and have spalled surfaces. The crowns have carinae on both mesial and distal margins, and the extension of these carinae varies: the mesial carina extends along two-thirds of the preserved crown height whereas the distal carina seems to reach the cervix.

In distal view, the distal carina is slightly displaced labially and bears serrations all along the crown. The labial and lingual surfaces are mesiodistally convex, with the lingual side more convex than the labial side, which is weakly mesiodistally convex, almost flattened.

In mesial view, the mesial carina bears serrations and extends significantly above the cervix. The mesial carina of HOC 19 is placed slightly labially. On the other hand, the mesial carina of HOC 26 is placed labially at the tip but curves slightly towards the base, becoming centrally positioned. The labial surfaces of HOC 19 and HOC 26 are slightly sigmoid, with the basalmost part of the crowns and the apical part being convex and concave, respectively. The converse situation is found on the lingual surfaces, where the basal part is concave and the apical part is convex.

In apical view, the tip is distally positioned on the crown and slightly lingually oriented. Both the mesial and distal carinae are acute. In basal view, the cross-section of the crowns is lanceolate at the level of the cervix with a rounded and wide labial margin whereas the lingual margin is acute. The cross-section at the level of the mid-crown is lenticular with the mesial and distal margins both acute.

The mesial carinae of HOC 19 and HOC 26 have around 21–22 denticles per 5 mm at the mid-crown, respectively. The size of the denticles decreases towards the basalmost part of the crown and they display a regular variation in size, i.e. not sporadic or sudden. In lateral view, the denticles possess a subquadrangular outline, with the same basoapical and mesiodistal length. They are positioned perpendicularly to the carina.

The distal carinae of HOC 19 and HOC 31 have 18–19 denticles per 5 mm at the mid-crown, respectively, and the denticle size difference index (DSDI) has a value of around 1. The denticles also decrease in size towards the base, displaying a gradual variation. They are chisel-shaped and proximodistally subrectangular, with a mesiodistal axis that is greater than the apicobasal axis except in the apical denticles, which are subquadrangular in shape. The main axis of the denticles is perpendicular to the distal carina.

The external margin of the mesial and distal denticles is parabolic to semicircular and either symmetrically or asymmetrically convex; they do not hook towards the tooth apex. The lingual and labial surfaces of the denticles are convex. The interdenticular space between denticles is narrow and deeper in the distal denticles. There are short and basally inclined interdenticular sulci between the distal denticles; they are better seen at a low light angle.

The crown surface is covered with microscratches due to erosion and wear. The external enamel shows diagonally oriented marginal undulations which bend towards the tip of the crown near the carinae. They are abundant, and they are restricted to the carina. Where the carina is not present (e.g. the mesial margin of the basalmost part of the crown), the marginal undulations are absent. These wrinkles are clearly visible whereas the transverse undulations are better seen at certain angles. The transverse undulations are apically concave, curving apically as they approach the carina, and they completely cover the enamel surface of the crowns.

The original enamel texture appears to be braided (sensu Hendrickx et al. 2015a).

3.1.4.2 Discussion The teeth of this morphotype share traits commonly found in non-maniraptoriform tetanurans. They are strongly labiolingually compressed, as seen in the lateral

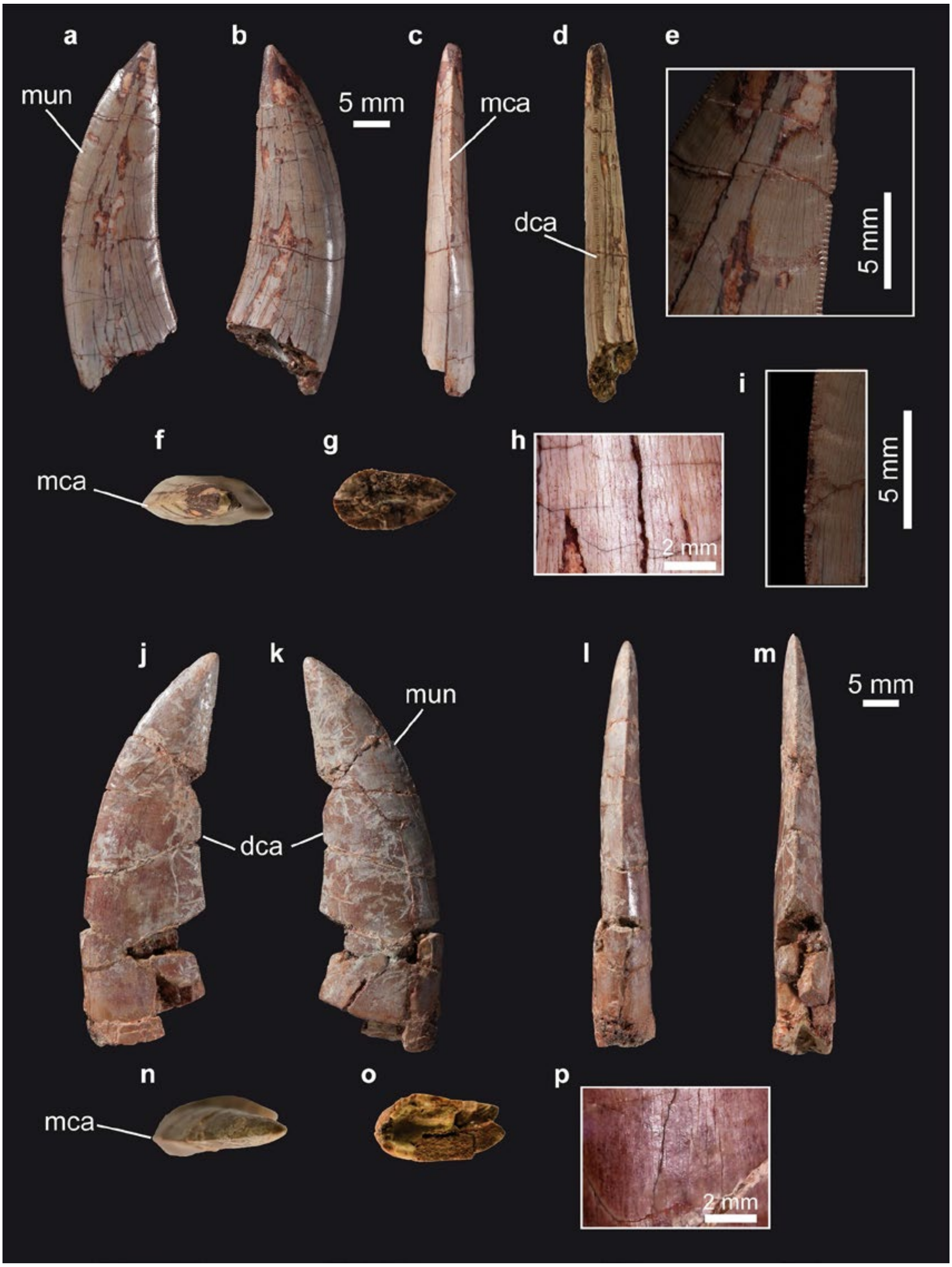

Fig. 7 Tetanurae cf. Carcharodontosauria indet. HOC 19 in **a** labial, **b** lingual, **c** mesial, **d** distal view. **e** Undulations and denticles on the distal carina. **f** Apical view, **g** basal views, **h** enamel surface, **i** mesial carina. HOC 26 in **j** labial, **k** lingual, **l** mesia, **m** distal, **n** apical, **o** basal views, **p** enamel surface. *dca* distal carina, *mca* mesial carina, *mun* marginal undulations

dentition (Hendrickx et al. 2015b). The mesial carina does not reach the cervix, the distal carina is slightly displaced labially, and they also have marginal and transverse undulations, interdenticular sulci, a braided enamel texture and a lenticular cross-section. Megalosauroids and allosauroids share these characteristics (Hendrickx 2015; Hendrickx et al. 2015b). A mesial carina that does not reach the cervix is seen in megalosaurids (Hendrickx et al. 2015b), *Neovenator* (Hutt et al. 1996), *Australovenator* (Hocknull et al. 2009; White et al. 2015), *Alioramus* (Brusatte et al. 2012), Therizinosauria, and Microraptorinae, and is also seen in *Acrocanthosaurus* and *Dromaeosaurus* (Hendrickx 2015). The labial side of the teeth is weakly mesiodistally convex and comparatively flat. A surface centrally positioned on the crown roughly flattened on the labial side of lateral teeth is seen in non-abelisauroid ceratosaurs and neovenatorids (Hendrickx and Mateus 2014b; Hendrickx 2015); unlike non-abelisauroid ceratosaurs the mesial carina of this morphotype does not reach the cervix.

Teeth with a weak displacement of the distal carina are common in non-maniraptoriform theropods. Only a few clades such as Ceratosauridae, *Masiakasaurus*, *Allosaurus,* Tyrannosauroidea and *Dromaeosaurus* show a distal carina strongly deflected labially (Hendrickx 2015). Another characteristic of HOC 19 and HOC 26 is the presence of transverse and marginal undulations, a widespread feature among theropods (Brusatte et al. 2007). The braided texture of the enamel is also widespread and can be observed in megalosauroids, allosauroids, tyrannosauroids and basal ceratosaurians (Hendrickx 2015).

DFA (Supplementary appendix A) classifies HOC 19 and HOC 26 as *Erectopus*. *Erectopus* is a basal allosauroid from the Albian of France (Allain et al. 2005). Some differences exist between this morphotype and the dentition of *Erectopus*: *Erectopus* has a concave surface on the lingual side adjacent to the distal carina (Hendrickx and Mateus 2014b), the mesial carina reaches the cervix (Allain et al. 2005) and the denticle density is slightly different. The cladistic analysis (Supplementary appendix B) places HOC 19 in a polytomy with *Piatnitzkysaurus* and *Erectopus.* On the other hand, the cladistics analysis of HOC 26 recovers a polytomy at the base of Averostra. A reduced strict consensus was calculated using the pruning trees option in TNT. The pruning of HOC 26 from the consensus tree increased the resolution of the consensus (Supplementary appendix B). HOC 26 is either recovered as the sister taxon of *Erectopus* or within Megalosauridae.

HOC 19 and HOC 26 share some traits with megalosaurids. The mesial carina does not reach the cervix, they are strongly to moderately labiolingually compressed, the enamel surface displays marginal and transverse undulations, and some of the denticle traits are relatively similar. In addition a flattened labial surface is seen on *Erectopus.* Despite these similarities some differences exist: *Erectopus* has a planar surface adjacent to the distal carina on the lingual margin of the crown and the mesial carina reaches the cervix. Besides, the labial surface of megalosaurids is not flattened (Hendrickx 2015).

The presence of non-spinosaurid basal tetanurans is known for the deposits of the Lower Cretaceous of western Europe. Nevertheless, these are allosauroids related to Carcharodontosauria; if *Afrovenator* is of Jurassic age (Rauhut and López-Arbarello 2009) then the youngest skeletal record of megalosaurids is *Torvosaurus* from the Kimmeridgian/Tithonian of Portugal and western USA (Hendrickx and Mateus 2014a). The only tetanuran described from the Early Cretaceous of Spain, *Concavenator corcovatus* from the upper Barremian of Las Hoyas (Cuenca province), is a basal carcharodontosaurid (Ortega et al. 2010). Another carcharodontosaurid specimen comes from other Barremian deposits in Teruel, where an isolated distal femur (Gasca et al. 2014b) has been found, sharing affinities with *Acrocanthosaurus.* Recently, a single carcharodontosaurid theropod tooth from the Valanginian of Romania (Csiki-Sava et al. 2016) has been proposed as the earliest evidence of Carcharodontosauridae in Europe. Carcharodontosaurid carcharodontosaurians are also found in Gondwanan deposits from the Early Cretaceous (Novas et al. 2005; Fanti et al. 2014), and in North America they are represented by the Albian genus *Acrocanthosaurus* (Sereno et al. 1996; Harris 1998; Brusatte and Sereno 2008; Csiki-Sava et al. 2016), becoming abundant and diverse in the course of the "Middle" and Late Cretaceous (Csiki-Sava et al. 2016). Non-carcharodontosaurid carcharodontosaurians are represented by *Neovenator* (Hutt et al. 1996) from the Barremian Wealden of England, which shares the features seen in this morphotype.

Given the absence of non-spinosaurid megalosauroid theropods from the Early Cretaceous of the Iberian Peninsula, these teeth are here considered as belonging to an indeterminate Carcharodontosauria, pending the discovery of additional skeletal material to support this hypothesis.

4 Discussion

The palaeobiodiversity of theropods from the Early Cretaceous of the Iberian Peninsula includes a broad set of neotheropods. The ceratosaur *Camarillasaurus cirugedae* (Sánchez-Hernández and Benton, 2014) has been described in the Barremian deposits of the Galve sub-basin. Among tetanurans there is a combination of basal and derived taxa. Basal tetanurans for which there is evidence include spinosaurids (Buffetaut 2007; Canudo et al. 2008a; Gasca et al. 2008; Mateus et al. 2011; Alonso and Canudo 2016) and carcharodontosaurians such as *Concavenator corcovatus* (Ortega et al. 2010), as well as other indeterminate carcharodontosaurids (Gasca et al. 2014b). There is also evidence of derived tetanurans such as coelurosaurs, including ornithomimosaurs such as *Pelecanimimus* (Pérez-Moreno et al. 1994), maniraptorans such as dromaeosaurids (i.e., Ruiz-Omeñaca et al. 1996; Rauhut 2002; Canudo et al. 2010) as well as birds (i.e., Sanz et al. 1988). Thus the theropod fossil record from Barranco del Hocino-1 is congruent with the known record of theropods from the Early Cretaceous of the Iberian Peninsula. However, according to our phylogenetic analyses, these teeth would extend the non-spinosaurid megalosauroid lineage into the Early Cretaceous. HOC 19, HOC 24, HOC 26 and HOC 31 share some traits with some megalosauroids (e.g. a mesial carina that does not reach the cervix, they are strongly to moderately labiolingually compressed, the enamel surface displays marginal and transverse undulations, and some of the denticle traits are relatively similar).

Previous studies have supported the reliability of cladistics analyses applied to isolated teeth (e.g. Hendrickx and Mateus 2014b; Csiki-Sava et al. 2016). Nevertheless, it is interesting to point out that the state of preservation of Barranco del Hocino 1 teeth is deficient; partially explaining the results. The absence of relevant information about the crown and root could input a considerable amount of noise in our analyses.

In addition, the dataset does not include theropods from the Barremian of the Iberian Peninsula. It would be interesting to draw a comparison between Barranco del Hocino-1 morphotypes and theropods such as *Concavenator* (Ortega et al. 2010). A comprehensive study of its dentition would probably improve the identification of isolated teeth from the Early Cretaceous of the Iberian Peninsula.

The association of spinosaurids and other basal tetanurans is also found in other places, such as the Wealden of England, which has *Baryonyx* (Charig and Milner 1997) and *Neovenator* (Hutt et al. 1996) and other indeterminate basal tetanurans (Benson et al. 2009; Gasca et al. 2014b). This association represents the megapredators of the epoch. These clades are also found in the north of Africa, where there are spinosaurine and baryonychine spinosaurids such as *Spinosaurus* from the Cenomanian of Egypt (Stromer, 1915) and *Suchomimus* from the Aptian/Albian of Niger (Sereno et al. 1998) and carcharodontosaurians such as *Carcharodontosaurus* from the Cenomanian of Morocco and *Eocarcharia* from the Aptian/Albian of Niger (Brusatte and Sereno 2007; Brusatte et al. 2007; Sereno and Brusatte 2008, Fanti et al. 2014).

The absence of other theropod taxa in the Barranco del Hocino-1 fossil assemblage, especially smaller theropods, is remarkable. In contrast, other fossil sites in the Blesa Formation, such as La Cantalera-1, have evidence of the presence of small theropods. This may be explained by the taphonomic characteristics of the remains. Another explanation is the amount of sediment sampled. Small-sized teeth are usually recovered when screen-washing is carried out. Three tonnes of sediment have been screen-washed from the La Cantalera-1 site, whilst just a few kilograms have been screen-washed here at Barranco del Hocino-1. This bias could affect the palaeobiodiversity that comes to light.

5 Conclusions

Barranco del Hocino-1 is a new fossil site in the Oliete subbasin within the Maestrazgo Basin. Among the vertebrate fossils recovered from the site are remains from large-sized theropods which consist of isolated teeth. Four different morphotypes of theropod tooth have been identified. One morphotype has been assigned to Spinosauridae. The other morphotypes have been assigned to Tetanurae and one has been a tentatively attributed to Carcharodontosauria indet. in the light of the known record of basal tetanurans from the Barremian of the Iberian Peninsula and western Europe. These results represent a new contribution to our knowledge of the palaeobiodiversity and distribution of theropods from the Barremian of the Iberian Peninsula. They also provide further evidence of the palaeontological interest of this area.

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References

Allain, R. (2005). The enigmatic theropod dinosaur Erectopus superbus (Sauvage 1882) from the Lower Albian of Louppy-le-Chateau. In Carpenter, K. (Ed.), *The carnivorous dinosaurs* (pp. 72–86). Bloomington, Indiana: Indiana University Press.

Alonso, A., & Canudo, J. I. (2016). On the spinosaurid theropod teeth from the early Barremian (Early Cretaceous) Blesa Formation (Spain). *Historical Biology, 28*(6), 823–834.

Alonso, A., Gasca, J. M., Navarro-Lorbés, P., Núñez-Lahuerta, C., Galán, J., Parrilla-Bel, J., et al. (2016). La asociación faunística de Barranco del Hocino 1, un nuevo yacimiento de vertebrados del Barremiense (Cretácico Inferior) de Teruel. *Cuadernos del Museo Geominero, 20,* 303–307.

Badiola, A., Canudo, J. I., & Cuenca-Bescós, C. (2008). New multituberculate mammals from the Hauterivian/Barremian transition of Europe (Iberian Peninsula). *Palaeontology, 51*(6), 1455–1469.

Benson, R. B., Brusatte, S. L., Hutt, S., & Naish, D. (2009). A new large basal tetanuran (Dinosauria: Theropoda) from the Wessex Formation (Barremian) of the isle of Wight, England. *Journal of Vertebrate Paleontology, 29*(2), 612–615.

Brusatte, S. L., Benson, R. B., Carr, T. D., Williamson, T. E., & Sereno, P. C. (2007). The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology, 27,* 1052–1056.

Brusatte, S. L., Carr, T. D., & Norell, M. A. (2012). The osteology of *Alioramus,* a gracile and long-snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. *Bulletin of the American Museum of Natural History, 366,* 1–197.

Brusatte, S. L., Norell, M. A., Carr, T. D., Erickson, G. M., Hutchinson, J. R., Balanoff, A. M., et al. (2010). Tyrannosaur paleobiology: New research on ancient exemplar organisms. *Science, 329,* 1481–1485.

Brusatte, S. L., & Sereno, P. C. (2007). A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. *Journal of Vertebrate Paleontology, 27*(4), 902–916.

Brusatte, S. L. & Sereno, P. C. (2008). Phylogeny of Allosauroidea (Dinosauria: Theropoda): Comparative analysis and resolution. *Journal of Systematic Palaeontology, 6*(2), 155–182.

Buffetaut, E. (2007). The spinosaurid dinosaur *Baryonyx* (Saurischia, Theropoda) in the Early Cretaceous of Portugal. *Geological Magazine, 144*(6), 1021–1025.

Buckley, L. G. (2009). *Individual and ontogenetic variation in theropod dinosaur teeth: A case study of Coelophysis bauri (Theropoda: Coelophysoidea) and implications for identifying isolated theropod teeth* (pp. 109). MSc. Dissertation, University of Alberta, Edmonton, Alberta, Canada.

Canudo, J. I., Gasca, J. M., Aurell, M., Badiola, A., Blain, H.-A., Cruzado-Caballero, P., et al. (2010). La Cantalera: An exceptional window onto the vertebrate biodiversity of the Hauterivian–Barremian transition in the Iberian Peninsula. *Journal of Iberian Geology, 36*(2), 205–224.

Canudo, J. I., Gasca, J. M., Moreno-Azanza, M., & Aurell, M. (2012). New information about the stratigraphic position and age of the sauropod *Aragosaurus ischiaticus* from the Early Cretaceous of the Iberian Peninsula. *Geological Magazine, 149*(2), 252–263.

Canudo, J. I., Gasulla, J. M., Gómez-Fernández, D., Ortega, F., Sanz, J. L., & Yagüe, P. (2008a). Primera evidencia de dientes aislados atribuidos a Spinosauridae (Theropoda) en el Aptiano inferior (Cretácico Inferior) de Europa: Formación Arcillas de Morella (España). *Ameghiniana, 45*(3), 649–652.

Canudo, J. I., Royo-Torres, R., & Cuenca-Bescós, G. (2008b). A new sauropod: *Tastavinsaurus sanzi* gen. et sp. nov. from the Early Cretaceous (Aptian) of Spain. *Journal of Vertebrate Paleontology, 28*(3), 712–731.

Charig, A. J., & Milner, A. C. (1997). *Baryonyx walkeri,* a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum of London, 53,* 11–70.

Csiki-Sava, Z., Brusatte, S. L., & Vasile, S. (2016). "*Megalosaurus* cf. *superbus*" from southeastern Romania: The oldest known Cretaceous carcharodontotosaurid (Dinosauria: Theropoda) and its implications for earliest Cretaceous Europe-Gondwana connections. *Cretaceous Research, 60,* 221–238.

Currie, P. J., Rigby, J. K. J., & Sloan, R. E. (1990). Theropod teeth from the Judith River Formation of southern Alberta, Canada. In K. Carpenter & P. J. Currie (Eds.), *Dinosaur systematics: Approaches and perspectives* (pp. 107–125). New York: Cambridge University Press.

Fanti, F., Cau, A., Martinelli, A., & Contessi, M. (2014). Integrating palaeoecology and morphology in theropod diversity estimation: A case from the Aptian-Albian of Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology, 410,* 39–57.

Gasca, J. M., Canudo, J. I., & Moreno-Azanza, M. (2014a). On the Iberian iguanodont dinosaur diversity: New fossils from the lower Barremian, Teruel province, Spain. *Cretaceous Research, 50,* 264–272.

Gasca, J. M., Canudo, J. I., & Moreno-Azanza, M. (2014b). A large-bodied theropod (Tetanurae: Carcharodontosauria) from the Mirambel Formation (Barremian) of Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 273*(1), 13–23.

Gasca, J. M., Moreno-Azanza, M., & Canudo, J. I. (2008). Dientes de dinosaurios terópodos espinosáuridos de la Formación El Castellar (Cretácico Inferior, Teruel). *Palaeontologica Nova SEPAZ, 8,* 233–234.

Gasulla, J. M., Escaso, F., Narváez, I., Ortega, F., & Sanz, J. L. (2015). A new sail-backed styracosternan (Dinosauria: Ornithopoda) from the Early Cretaceous of Morella, Spain. *PLoS One, 10*(12), e0144167.

Gauthier, J. A. (1986). Saurischian monophyly and the origin of birds. In K. Padian (Ed.), *The origin of birds and the evolution of flight. Memoirs of the California Academy of Sciences* (Vol. 8, pp. 1–55). San Francisco: California Academy of Sciences.

Gerke, O., & Wings, O. (2016). Multivariate and cladistic analyses of isolated teeth reveal sympatry of theropod dinosaurs in the Late Jurassic of northern Germany. *PLoS One, 11*(7), e0158334.

Goloboff, P. A., & Catalano, S. A. (2016). TNT versión 1.5, including a full implementation of phylogenetic morphometrix. *Cladistics, 32,* 221–238. https://doi.org/10.1111/cla.12160.

Hammer, Ø., & Harper, D. A. T. (2006). *Paleontological data analysis* (p. 351). Oxford: Blackwell.

Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). Past: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica, 4*(1), 1–9.

Harris, J. D. (1998). A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of natural History and Science Bulletin, 13,* 1–75.

Hendrickx, C. (2015). Evolution of Teeth and Quadrate in Non-avian Theropoda (Dinosauria: Saurischia), with the Description of *Torvosaurus* Remains from Portugal. Ph.D. Dissertation. Universidade Nova de Lisboa, p. 646.

Hendrickx, C., & Mateus, O. (2014a). *Torvosaurus gurneyi* n. sp., the largest terrestrial predator from Europe, and a proposed terminology of the maxilla anatomy in nonavian theropods. *PLoS One, 9*(3), e88905. https://doi.org/10.1371/journal.pone.0088905.

Hendrickx, C., & Mateus, O. (2014b). Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. *Zootaxa, 3759*(1), 1–74.

Hendrickx, C., Mateus, O., & Araújo, R. (2015a). A proposed terminology of theropod teeth (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology, 35*(5), e982797.

Hendrickx, C., Mateus, O., & Araújo, R. (2015b). The dentition of megalosaurid theropods. *Acta Palaeontologica Polonica, 60*(3), 627–642.

Hocknull, S. A., White, M. A., Tischler, T. R., Cook, A. G., Calleja, N. D., Sloan, T., et al. (2009). New mid-Cretaceous (Latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS One, 4*(7), e6190.

Hutt, S., Martill, D. M., & Barker, M. J. (1996). The first European allosauroid dinosaur (Lower Cretaceous, Wealden Group, England. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 10,* 635–644.

Infante, P., Canudo, J. I., & Ruiz-Omeñaca, J. I. (2005). First evidence of theropod dinosaurs from the Mirambel Formation (Lower Barremian, Lower Cretaceous) from Castellote, Teruel. *Geogaceta, 38,* 31–34.

Kellner, A. W. A., & Campos, D. A. (1996). First early Cretaceous theropod dinosaur from Brazil with comments on Spinosauridae. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 199*(2), 151–166.

Mateus, O., Araújo, R., Natário, C., & Castanhinha, R. (2011). A new specimen of the theropod dinosaur *Baryonyx* from the early Cretaceous of Portugal and taxonomic validity of *Suchosaurus*. *Zootaxa, 2827,* 54–68.

Moreno-Azanza, M., Canudo, J. I., & Gasca, J. M. (2014). Unusual theropod eggshells from the Early Cretaceous Blesa Formation of the Iberian Range, Spain. *Acta Paleontologica Polonica, 59*(4), 843–854.

Norell, M. A., Makovicky, P. J., Bever, G. S., Balanoff, A. M., Clark, J. M., Barsbold, R., et al. (2009). A review of the Mongolian Cretaceous dinosaur *Saurornithoides* (Troodontidae: Theropoda). *American Museum Novitates, 3654,* 1–63.

Novas, F. E., de Valais, S., Vickers-Rich, P. A., & Rich, T. H. (2005). A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften, 92,* 226–230.

Ortega, F., Escaso, F., & Sanz, J. L. (2010). A bizarre, humped Carcharodontosauria (Theropoda) from the lower Cretaceous of Spain. *Nature, 467*(7312), 203–206.

Parrilla-Bel, J., & Canudo, J. I. (2015). On the presence of plesiosaurs in the Blesa Formation (Barremian) in Teruel (Spain). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 278*(2), 213–227.

Pereda-Suberbiola, X., Ruiz-Omeñaca, J. I., Canudo, J. I., Torcida, F., & Sanz, J. L. (2012). Dinosaur faunas from the Early Cretaceous (Valanginian-Albian) of Spain. In P. Godefroit (Ed.), *Bernissart dinosaurs and early Cretaceous terrestrial ecosystem* (pp. 379–407). Bloomington: Indiana University Press.

Pérez-Moreno, B. P., Sanz, J. L., Buscalioni, A. D., Moratalla, J. J., Ortega, F., & Rasskin-Gutman, D. (1994). A unique multitoothed ornithomimosaur dinosaur from the lower Cretaceous of Spain. *Nature, 370,* 363–367.

Puértolas-Pascual, E., Rabal-Garcés, R., & Canudo, J. I. (2015). Exceptional crocodylomorph biodiversity of "La Cantalera" site (lower Barremian; Lower Cretaceous) in Teruel, Spain. *Palaeontologia Electronica, 18*(2), 1–16.

Rauhut, O. W. M. (2002). Dinosaur teeth from the Barremian of Uña, Province of Cuenca, Spain. *Cretaceous Research, 23*(2), 255–263.

Rauhut, O. W. M., & López-Arbarello, A. (2009). Considerations on the age of the Tiouaren Formation (Iullemmeden Basin, Niger, Africa): Implications for Gondwanan Mesozoic terrestrial vertebrate faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology, 271,* 259–267.

Rauhut, O. W. M., Milner, A. C., & Moore-Fay, S. (2010). Cranial osteology and phylogenetic position of the theropod dinosaur Proceratosaurus bradleyi (Woolward, 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society, 158*, 155–195.

Rauhut, O. W. M., & Werner, C. (1995). First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). *Paläontologische Zeitshrift, 69,* 475–489.

Riveline, J., Berger, J. P., Feist, M., Martín-Closas, C., Schudack, M., & Soulié-Märsche, I. (1996). European Mesozoic-Cenozoic charophyte biozonation. *Bulletin de la Société géologique de France, 167*(3), 453–468.

Ruiz-Omeñaca, J. I. (2011). *Delapparentia turolensis* nov. gen et sp., un nuevo dinosaurio iguanodontoideo (Ornithischia: Ornithopoda) en el Cretácico Inferior de Galve. *Estudios Geológicos, 67*(1), 83–110.

Ruiz-Omeñaca, J. I., Canudo, J. I., & Cuenca-Bescós, G. (1996). Dientes de dinosaurios (Ornitischia y Saurischia) del Barremiense superior (Cretácico inferior) de Vallipón (Castellote, Teruel). *Mas de las Matas, 15,* 59–103.

Ruiz-Omeñaca, J. I., Canudo, J. I., & Cuenca-Bescós, G. (1998). Primera cita de dinosaurios barionícidos (Saurischia: Theropoda) en el Barremiense superior (Cretácico Inferior) de Vallipón (Castellote, Teruel). *Mas de las Matas, 17,* 201–223.

Ruiz-Omeñaca, J. I., Canudo, J. I., Cuenca-Bescós, G., Cruzado-Caballero, P. L., Gasca, J. M., & Moreno-Azanza, M. (2012). A new basal ornithopod dinosaur from the Barremian of Galve, Spain. *Comptes Rendus Paleovol, 11*(6), 435–444.

Ruiz-Omeñaca, J. I., Cruzado-Caballero, P., Infante, P., & Moreno-Azanza, M. (2005). Baryonychine teeth (Theropoda: Spinosauridae) from the lower Cretaceous of La Cantalera (Josa, NE Spain). *Kaupia, 14,* 59–63.

Salas, R., Guimerà, J., Más, R., Martín-Closas, C., Meléndez, A., & Alonso, A. (2001). Evolution of the Mesozoic central Iberian Rift System and its Cainozoic inversion (Iberian Chain). *Mémoires du Muséum Nationale de l'Histoire Naturelle, Paris, 186,* 145–185.

Samman, T., Powell, G. L., Currie, P. J., & Hills, L. V. (2005). Morphometry of the teeth of western North American tyrannosaurids and its applicability to quantitative classification. *Acta Palaeontologica Polonica, 50,* 757–776.

Sánchez-Hernández, B. R., & Benton, M. (2014). Filling the ceratosaur gap: A new ceratosaurian theropod from the Early Cretaceous of Spain. *Acta Palaeontologica Polonica, 59*(3), 581–600.

Sánchez-Hernández, B., Benton, M. J., & Naish, D. (2007). Dinosaurs and other fossil vertebrates from the Late Jurassic and Early Cretaceous of the Galve area, NE Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology, 249,* 180–215.

Sanz, J. L., Bonaparte, J. F., & Lacasa, A. (1988). Unusual Early Cretaceous birds from Spain. *Nature, 331,* 433–435.

Sanz, J.L., Buscalioni, A.D., Casanovas, M.L., Santafé, J.V. (1987). Dinosaurios del Cretácico Inferior de Galve (Teruel, España). *Estudios geológicos.* Volumen extraordinario Galve-Tremp, pp. 45–64.

Sereno, P. C., Beck, A. L., Dutheil, D. B., Larsson, H. C. E., Lyon, G. H., Marcot, J. D., et al. (1998). A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science, 282*(5392), 1298–1302.

Sereno, P. C., & Brusatte, S. L. (2008). Basal abelisaurid and carcharodontosaurid theropods from the lower Cretaceous Elrhaz Formation of Niger. *Acta Palaeontologica Polonica, 53*(1), 15–46.

Sereno, P. C., Dutheil, D. B., Iarochene, M., Larsson, H. C. E., Lyon, G. H., Magwene, P. M., et al. (1996). Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science, 272,* 986–991.

Serrano-Martínez, A., Vidal, D., Sciscio, L., & Ortega, F. (2016). Isolated theropod teeth from the Middle Jurassic of Niger and the early dental evolution of Spìnosauridae. *Acta Palaeontologica Polonica, 61*(2), 403–415.

Smith, J. B., & Dodston, P. (2003). A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology, 23*(1), 1–12.

Smith, J. B., Vann, D. R., & Dodson, P. (2005). Dental morphology and variation in theropod dinosaurs: Implications for the taxonomic identification of isolated teeth. *The Anatomical Record, 285A,* 699–736.

Stromer, E. (1915). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharîje-Stufe (unterstes Cenoman). 3. Das Original des Theropoden

Spinosaurus aegyptiacus nov. gen., nov. spec. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathemtatisch-physikalische Klasse, 28*(3), 1–32.

Sues, H. D., Frey, E., Martill, D. M., & Scott, D. M. (2002). *Irritator challengeri,* a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology, 22*(3), 535–547.

Torices, A., Currie, P., Canudo, J. I., & Pereda Suberbiola, X. (2015). Theropod dinosaurs from the Upper Cretaceous of the South Pyrenees Basin of Spain. *Acta Paleontologica Polonica, 60*(3), 611–626.

Verdú, F. J., Godefroit, P., Royo-Torres, R., Cobos, A., & Alcalá, L. (2017). Individual variation in the postcranial skeleton of the Early Cretaceous *Iguanodon bernissartensis* (Dinosauria: Ornithopoda). *Cretaceous Research, 74,* 65–86.

White, M. A., Bell, P. R., Cook, A. G., Poropat, S. F., & Elliott, D. A. (2015). The dentary of *Australovenator wintonensis* (Theropoda, Megaraptoridae); implications for megaraptorid dentition. *PeerJ, 3,* e1512.

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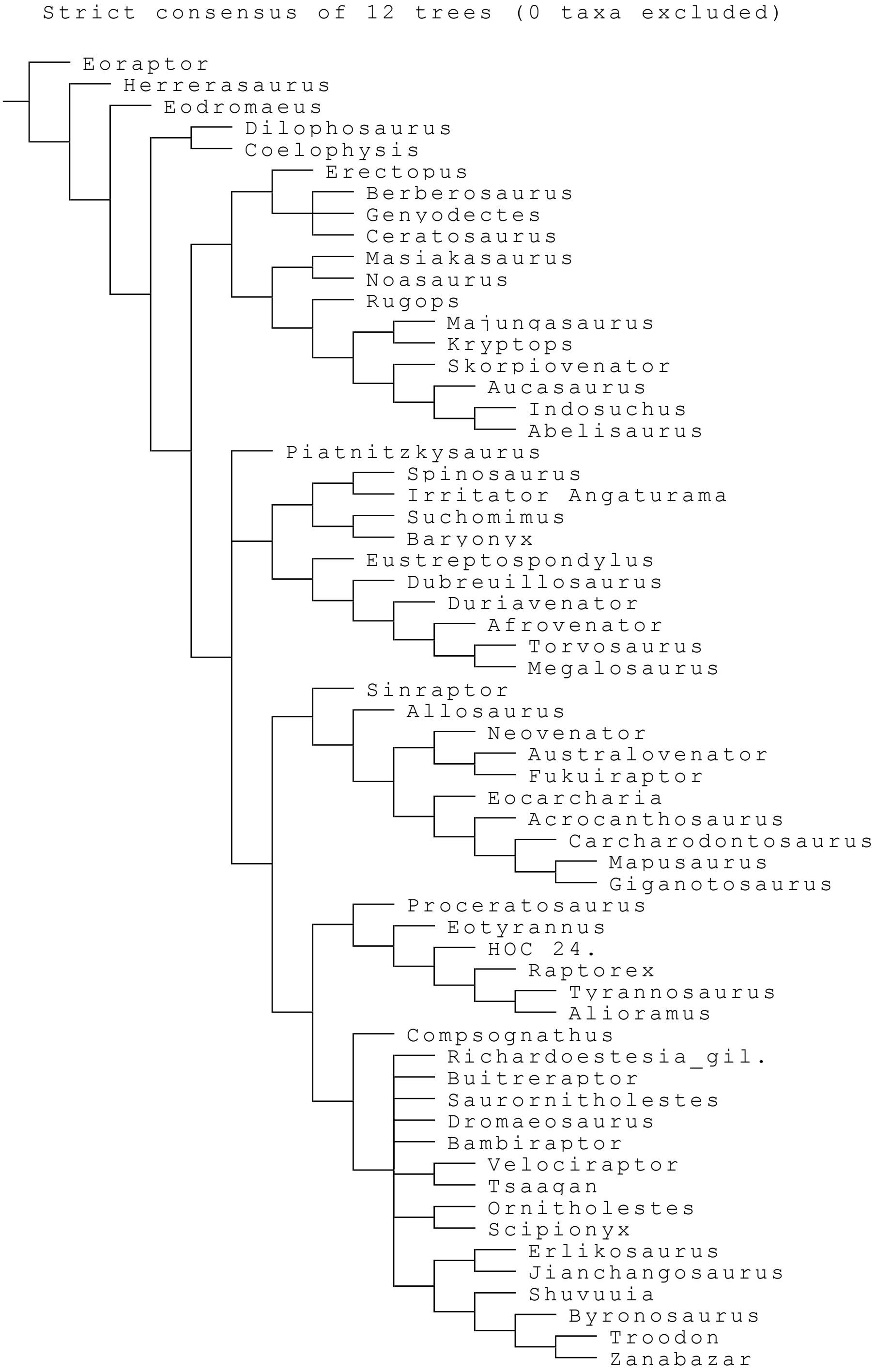
Appendix B. Results from the cladistic analysis and character codings of the morphotypes

HOC 24

??1110001 1?0000000?012
211[01]0[02]0100?0-?0?0?00110-101020001????????????????????????



HOC 24. Strict consensus cladogram of 12 parsimonious trees.

Consistency index.

0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
0.568	0.568	0.548							

Retention index.

0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
0.637	0.637	0.607							

Tree lengths.

3577	3577	3577	3577	3577	3577	3577	3577	3577	3577
3577	3577	3705							

HOC 31

??10200001?0000000?002
21[01]00[02]100000-0022000110-111020001????????????????????????

HOC 31. Strict consensus cladogram of 10 parsimonious trees.

Consistency index.

0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
0.532									

Retention index.

0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
0.581									

Tree lengths.

3578	3578	3578	3578	3578	3578	3578	3578	3578	3578
3817									

HOC 31. Reduced strict consensus cladogram. All possible positions of HOC 31. a: HOC 31.

HOC 17

???0?121100000???0101000--??-?-?-???--?-----?--220-0---0031???????????????????????

HOC 17. Strict consensus cladogram of 8 parsimonious trees.

Consistency index.

0.569	0.569	0.569	0.569	0.569	0.569	0.569	0.569	0.547

Retention index.

0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.605

Tree lengths.

3574	3574	3574	3574	3574	3574	3574	3574	3716

HOC 19

???10200101?0000000?012
21[01][01]0[02]110000-?0?0?00110-111121001????????????????????????

HOC19. Strict consensus cladogram of 14 parsimonious trees.

Consistency index.

0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
0.568	0.568	0.568	0.568	0.538					

Retention index.

0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
0.637	0.637	0.637	0.637	0.591					

Tree lengths.

3580	3580	3580	3580	3580	3580	3580	3580	3580	3580
3580	3580	3580	3580	3775					

HOC 19. Reduced strict consensus cladogram. All possible positions of HOC 19. a: HOC 19.

HOC 26

??10200101?0000000?002
21[01][01]0[02]110000-10100001?0-111121001????????????????????????

HOC 26. Strict consensus cladogram of 16 parsimonious trees.

Consistency index.

0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
0.568	0.568	0.568	0.568	0.568	0.568	0.525			

Retention index.

0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
0.568	0.568	0.568	0.568	0.568	0.568	0.525			

Tree lengths.

3580	3580	3580	3580	3580	3580	3580	3580	3580	3580
3580	3580	3580	3580	3580	3580	3873			

HOC 26. Reduced strict consensus cladogram. All possible positions of HOC 26. a: HOC 26.

ANEXO 5

Alonso, A., Canudo, J.I., Torcida Fernández-Baldor, F., Huerta, P. 2017. Isolated theropod teeth associated with sauropod remains from El Oterillo II (Early Cretaceous) site of Salas de los Infantes (Burgos, Spain). *Journal of Iberian Geology* 43(2), 193-215.

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RESEARCH ARTICLE

Isolated theropod teeth associated with sauropod remains from El Oterillo II (Early Cretaceous) site of Salas de los Infantes (Burgos, Spain)

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Abstract

Introduction The relationship between dinosaur carcasses and isolated theropod teeth is well known in the fossil record. The usual explanation is that theropod dinosaurs fed on the herbivore carcass. Other evidence is provided by theropod tooth marks on the surface of herbivore skeletal remains. In this work we study isolated theropod teeth and the tooth marks in evidence on the bones of the sauropod from El Oterillo II (Salas de los Infantes, Spain, Lower Cretaceous). Theropod and crocodylomorph teeth have been found in relationship with the sauropod carcass. The fossils lie on channel lag deposits composed of sandstones with quartzite gravel.

Materials and methods Thirty theropod teeth have been studied using qualitative features, statistical and cladistics analysis in addition to the tooth marks present on the vertebrae.

Results The morphology of the theropod teeth has revealed greater palaeobiodiversity in these faunas than previously known, including baryonychine spinosaurids, basal tetanurans, dromaeosaurids and a singular coelurosaurian. The presence of tooth marks and isolated theropod teeth in close relationship with the sauropod carcass could also provide new evidence of the scavenging of theropod dinosaurs on the sauropods of this age and location.

Conclusions Six morphotypes of theropod teeth have been distinguished; the combination of basal and derived tetanurans is congruent with the known record from the Early Cretaceous of the Iberian Peninsula. The most probable explanation for the association of isolated theropod teeth and sauropod remains is the scavenging of the carcass by theropod dinosaurs.

Keywords Lower Cretaceous · Sauropoda · Theropoda · Teeth · Palaeocology · Spain

Resumen

Introducción La relación entre carcasas de dinosaurios herbívoros y dientes aislados de terópodos es conocida en el registro fósil. La explicación más habitual es la alimentación de los dinosaurios terópodos de la carcasa del dinosaurio herbívoro. Otras evidencias de predación o carroñeo provienen de las marcas de dientes preservadas en diferentes partes de los huesos de los dinosaurios herbívoros. En este trabajo se estudian los dientes aislados de dinosaurios terópodos y las marcas de dientes encontradas en los huesos del saurópodo de Oterillo II (Salas de los Infantes, España, Cretácico Inferior). Estos

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dientes, además de crocodilomorfos se han encontrado en relación con la carcasa del saurópodo. Los restos fósiles aparecen en el fondo de un relleno de canal constituido por areniscas con cantos cuarcíticos de tamaño grava.

Materiales y métodos Se han estudiado 30 dientes aislados de terópodos utilizando caracteres cualitativos, análisis estadístico y análisis cladístico, junto a las marcas de dientes presentes en las vértebras del saurópodo.

Resultados La morfología de los dientes de terópodo ha revelado una mayor paleobiodiversidad de estas faunas de lo conocido previamente, incluyendo espinosáuridos barioniquinos, tetanuros basales, dromeosáuridos y un singular coelurosaurio. Además, la existencia de marcas de dientes y dientes aislados en relación con la carcasa de saurópodo puede suponer una nueva evidencia del carroñeo de dinosaurios terópodos en saurópodos para esta edad en la peninsula ibérica.

Conclusiones Se han distinguido seis morfotipos de dientes de terópodo; la combinación de tetanuros basales y derivados es congruente con el registro fósil conocido en el Cretácico Inferior de la peninsula ibérica. La explicación más probable de la asociación de dientes aislados de terópodos y los restos de saurópodo es el carroñeo de la carcasa por parte de los dinosaurios terópodos.

Palabras clave Cretácico Inferior · Sauropoda · Theropoda · Dientes · Paleoecología · España

1 Introduction

Several authors have pointed out the relationship between the carcasses of herbivorous dinosaurs and isolated theropod teeth (Buffetaut and Suteethorn 1989; Maxwell and Ostrom 1995; Canudo et al. 2009; Canale et al. 2014). This usually includes the presence of a partially articulated individual dinosaur carcass and some isolated theropod teeth located close to the bone remains or concentrated in specific parts of the carcass (Corro 1996; Buffetaut and Suteethorn 1989; Maxwell and Ostrom 1995; Jacobsen 1998; Canudo et al. 2009). The most parsimonious explanation seems to be that theropod dinosaurs fed on the herbivore carcass. In addition, tooth marks on the bone remains of herbivorous dinosaurs are well documented (Jacobsen 1998; Paik et al. 2011).

El Oterillo II is a vertebrate site where a partially articulated individual titanosauriform sauropod has been found. The fossil remains consist of a tooth, cervical, dorsal and caudal vertebrae, two scapulae, two ischia, two pubes (Torcida Fernández-Baldor 2006; Torcida Fernández-Baldor et al. 2009; Pereda-Suberbiola et al. 2012), cervical and dorsal ribs, haemal arches, a coracoid and two metacarpals in association with isolated theropod and crocodylomorph teeth. The aim of this work is to study the palaeobiodiversity of the theropod teeth and to discuss their palaeoecological relationship with the carcass of the sauropod of El Oterillo II.

1.1 Geographical and Geological setting

El Oterillo II site is located in Burgos, northern Spain, 6.5 km to the NW of Salas de los Infantes (Fig. 1). The site is located in the Castrillo de la Reina Fm. of the western Cameros Basin, which has a basin-fill history from Upper Jurassic to Lower Cretaceous (Platt 1986, 1990; Martín-Closas and Alonso-Millán 1998; Mas et al. 2004; Salas et al. 2001). The Castrillo de la Reina Fm. (Clemente and Pérez Arlucea 1993) is composed of red mudstones, sandstones and conglomerates which are interpreted as a fluvial system that drained the basin towards the northeast. This unit is upper Barremian-lower Aptian in age according to biostratigraphic studies (Martín-Closas and Alonso-Millán 1998; Schudack and Schudack 2009).

The dinosaur bones appears at the top of a 0.5 m-thick sandstone bed with channel geometry. The sandstone bed is reddish-brown in colour and passes upwards into grey-blue colours at the top of the bed as the grain size decreases and passes into mudstones. The bones are partially articulated and have been assigned to a sauropod dinosaur (Torcida Fernández-Baldor et al. 2009). The teeth appear very close to the bones, on a channel reactivation surface with a lag deposit composed of quartzite clasts (1–2.5 cm in diameter). Palaeocurrents measured in the channel fill indicate westward directions, although the preferred teeth orientation has not been detected.

1.2 Institutional abbreviations

MDS Museo de Dinosaurios (Salas de los Infantes, Burgos, Spain).

2 Materials and methods

The fossils were recovered from excavation campaigns in 2004–2006 by the Colectivo Arqueológico y Paleontológico de Salas de los Infantes, with the corresponding permits from the Dirección General de Patrimonio of the regional government of Castilla y León (dossiers 307/04-BU; 257/05-BU; 262/06-BU). The recovered material is deposited in the Museo de Dinosaurios de Salas de los Infantes (Salas de los Infantes, Burgos, Spain). Observations were made with a stereomicroscope, and pictures taken with a Sony α200 digital camera. The teeth were measured with a Mitutoyo Digimatic Digital Calliper, Series No 500. Thirty theropod teeth (Appendix A) from El

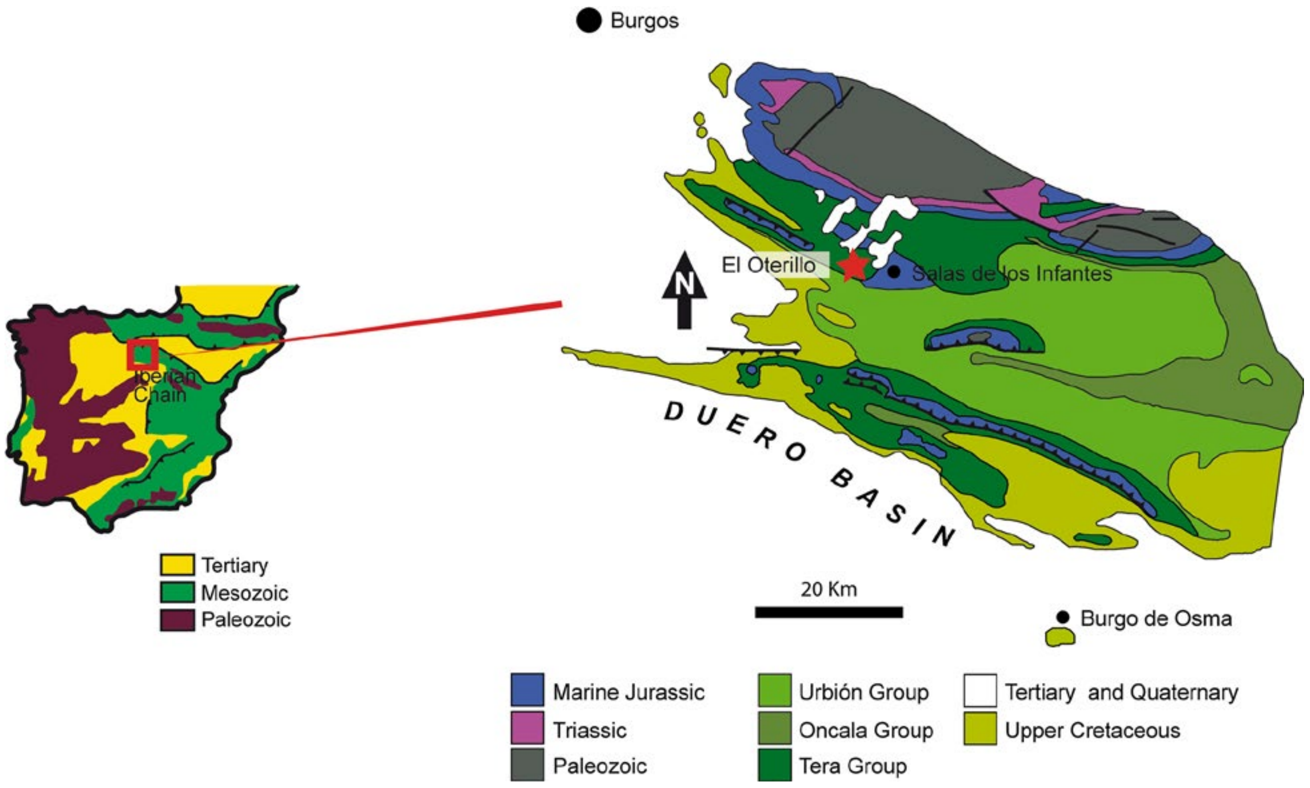

Fig. 1 Geographical and geological setting of El Oterillo II site

Oterillo II were analysed during the course of this research. In addition, bone remains from the sauropod dinosaur were studied to establish the possible presence of tooth marks.

2.1 Anatomical nomenclature

The anatomical nomenclature used in this work is mainly based on the recommendations of Smith and Dodson (2003) and Hendrickx et al. (2015a) (Fig. 2). A theropod tooth is composed of a crown, made of dentine and covered by enamel, and a root, made of dentine. The junction between them is called the cervix. The top of the crown and root are called the crown or root apex. Usually, theropod teeth have structures on their edges running apicobasally along the crown called carinae. These may be denticulated, i.e. with a serration consisting of denticles. Other features commonly present on theropod teeth are marginal and transversal undulations of the enamel, flutes, depressions and surfaces. The enamel texture refers to the pattern of the enamel surface (Hendrickx et al. 2015a).

Theropod teeth come in a variety of shapes and sizes. The most usual shape of the crown is the ziphodont morphology (D'Amore 2009), which is labiolingually compressed and distally curved. The surface of the tooth facing outwards towards the lips is called labial; the opposite surface facing the sagittal midline of the skull is called lingual. The surface that is close to the jaw symphysis is called mesial, and the opposite one facing the jaw articulation is called distal. Apical refers to the direction from the cervix to the crown apex. Basal refers to the direction from the apex to the cervix (Hendrickx et al. 2015a).

2.2 Morphometric nomenclature

The morphometric terminology used in this work follows the terms and abbreviations used in Smith et al. (2005) and Hendrickx et al. (2015a). The mesiodistal length of the crown at the level of the cervix is called the crown base length (CBL). The labiolingual width of the crown at the cervix level, perpendicular to CBL, is called the crown base width (CBW). The ratio of CBW to CBL is the crown base ratio (CBR) and shows the labiolingual compression. The basoapical extent of the distal margin of the crown from the most distal point of the cervix to the most apical point of the apex forms the crown height (CH). As a measure of the crown elongation the crown height ratio (CHR) has been proposed and is the ratio of CH to CBL.

The basoapical extent of the mesial margin of the crown is the apical length (AL). The mesial serration density is the number of denticles per 5 mm on the mesial margin (MC). The distal serration density is the number of denticles per 5 mm on the distal margin (DC). The denticle size

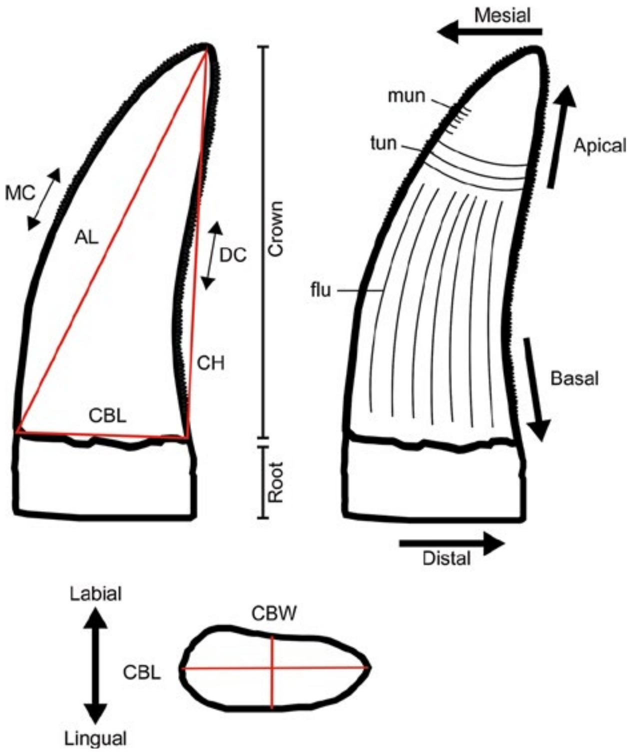

Fig. 2 Anatomical nomenclature and DFA variables. *AL* apical length, *CBL* crown base length, *CBW* crown base width, *CH* crown height, *DC* distocentral denticle density, *flu* flutes, *MC* mesiocentral denticle density, *mun* marginal undulations, *tun* transversal undulations

density index (DSDI), used by Rauhut and Werner (1995), expresses the difference between the mesial and distal denticles (Fig. 2).

2.3 Qualitative and other features

In order to complement the morphometric information provided by measurements, a number of qualitative features were studied. These features include the shape of the tooth (Torices 2007), the presence, position and development of the mesial and distal carinae (Currie et al. 1990; Torices 2007; Hendrickx et al. 2015a), the denticle morphology (Currie et al. 1990; Torices 2007; Hendrickx et al. 2015a), the cross-section of the crown, the crown ornamentation, enamel texture (Hendrickx et al. 2015a), enamel undulations (Brusatte et al. 2007; Hendrickx 2015a) and the preservation of the tooth.

2.4 Statistical analysis

Multivariate statistical analyses were performed in order to ascertain the variation among the theropod teeth from El Oterillo II site. The statistical analyses (discriminant function analyses) were performed using PAST v3.0 (Hammer et al. 2001) and SPSS 20.0 (SPSS Inc., Chicago, Illinois) on the dataset of Hendrickx et al. (2015b), which includes data from Farlow et al. (1991), Sankey et al. (2002), Currie and Varricchio (2004), Sankey et al. (2005), Smith et al. (2005), Smith and Lamanna (2006), Smith and Dalla Vecchia (2006), Fanti and Therrien (2007), Sereno and Brusatte (2008), Longrich (2008), Sankey (2008), Hocknull et al. (2009), Molnar et al. (2009), Rauhut et al. (2010), Ösi et al. (2010), Larson and Currie (2013) and Hendrickx et al. (2015b); data from White et al. (2015) and Csiki-Sava et al. (2016) were also included. The dataset comprises 1022 teeth from different theropod taxa including El Oterillo II teeth (see Table 1). Discriminant function analysis (DFA) was performed on the dataset. DFA is an ordination technique applied to previously identified data in order to find the best discriminant variables. It also has predictive power and is able to classify unknown data in the previously known groups (Hammer and Harper 2006).

Due to their state of preservation, not all the teeth from El Oterillo II site were analysed; this was in order to avoid interference. Only MDS-OTII,73, MDS-OTII,78, MDS-OTII,82, MDS-OTII,91, MDS-OTII,92, MDS-OTII,99, MDS-OTII,100, MDS-OTII,101 and MDS-OTII,102 were included. The variables used are CBL, CBW, CH, AL, CBR, CHR, MC and DC. In order to better reflect a normal distribution all data were log-transformed (see rationalization in Samman et al. 2005). When a character was absent or missing it was coded with a question mark. The dependent variable was not the species taxonomic level but a larger taxonomic unit (such as Megalosauridae or basal Tyrannosauroidea) as listed above (Table 1). The only exception was made with uncertain genera such as *Erectopus* or *Nuthetes* and Spinosauridae, which has been split into two different groups: Baryonychinae and Spinosaurinae.

The first analysis was conducted with PAST v3.0 using all the variables. Due to the low percentage of correctly identified teeth (<65%), some changes were made to the dataset. Firstly we differentiated absent data (anatomical traits not present in the specimen, coded as a zero) from missing data (traits that may be absent due to breakage, coded as a question mark). Secondly, the dataset was log-transformed using the formula $log\ (1 + x)$, as seen in Gerke and Wings (2016), to properly account for zero values. Third, we removed the variable AL from the dataset due to the large number of missing data. Finally, all the cases with remaining missing data were also removed from the dataset. The following analyses were performed with SPSS 20.0, using the stepwise method with Mahalanobis distance and using a within-group covariance matrix. SPSS allows better control of the statistical procedure. The SPSS analysis of the dataset without AL and missing data (901 teeth) returned a better percentage of correctly classified

Table 1 Theropod taxa used in this study

Group	Taxa	Group	Taxa
Basal Saurischians	*Eoraptor*	Allosauridae	*Allosaurus*
Basal Theropods	*Ischisaurus*	Neovenatoridae	*Neovenator*
	Eodromaeus	Carcharodontosauridae	*Acrocanthosaurus*
Coelophysoidea	*Coelophysis*		*Eocarcharia*
	Liliensternus		*Carcharodontosaurus*
	Dilophosaurus		*Giganotosaurus*
Ceratosauridae	*Genyodectes*		*Mapusaurus*
	Ceratosaurus	Megaraptora	*Australovenator*
	Berberosaurus		*Fukuiraptor*
Noasauridae	*Noasaurus*		*Aerosteon*
	Masiakasaurus	Basal Tyrannosauroidea	*Eotyrannus*
Abelisauridae	*Abelisaurus*		*Raptorex*
	Rugops		*Alioramus*
	Indosuchus	Tyrannosauridae	*Gorgosaurus*
	Majungasaurus		*Daspletosaurus*
	Aucasaurus		*Albertosaurus*
	Skorpiovenator		*Tyrannosaurus*
	Carnotaurus	*Nuthetes*	*Nuthetes*
Erectopus	*Erectopus*	Dromaeosauridae	*Bambiraptor*
Piatnitzkysauridae	*Piatnitzkysaurus*		*Deinonychus*
Megalosauridae	*Afrovenator*		*Dromaeosaurus*
	Duriavenator		*Velociraptor*
	Megalosaurus		*Saurornitholestes*
	Dubreillosaurus		*Atrociraptor*
	Torvosaurus		*Zapsalis*
Spinosauridae	*Baryonyx*	Troodontidae	*Troodon*
	Suchomimus		*Zanazabar*
	Irritator		*Pectinodon*
	Spinosaurus	*Richardoestesia*	*Richardnes tesia*

teeth (79.7%) (Appendix A). A third analysis was performed separating mesialmost and lateral teeth due to the pseudoheterodonty and differentiation between mesial and lateral dentition in theropods. The percentage of correctly classified teeth went down (74.6%). In order to avoid interference and overlapping between groups, and given the absence of mesialmost teeth from El Oterillo II site, the mesial teeth were removed from the dataset. A fourth SPSS analysis (777 teeth) showed an improvement in the percentage of teeth correctly classified (82.5%).

The presence of small groups affects the accuracy of DFA. In this case we maintained low-number groups due to the relevance of some of them for comparison with El Oterillo II morphotypes, even though this was at the expense of an improved analysis.

The analyses obtained functions that explain the variance of the dataset. The first and the second functions explain >90% of the variance (91.8% analysis without missing data; 90.8% analysis without missing data and without mesial dentition; separation between mesialmost and lateral teeth explains 88.1% of variance, Appendix A). These canonical functions were used to produce a graphical representation of the relative positions of the teeth, creating a morphospace in a dispersion graph (Fig. 3). The weight of each variable in the canonical functions is represented in Appendix A.

2.5 Cladistic analysis

In addition to the statistical analyses, cladistic analyses were performed (Appendix B) using the supermatrix of Hendrickx and Mateus (2014) with the modifications proposed by Gerke and Wings (2016). The supermatrix comprises 60 theropod taxa with 1972 characters from Xu et al. (2009), Brusatte et al. (2010), Martínez et al. (2011), Senter et al. (2011), Pol and Rauhut (2012), Carrano et al. (2012) and Hendrickx and Mateus (2014). 141 characters are tooth-based. The analysis was performed on TNT 1.1

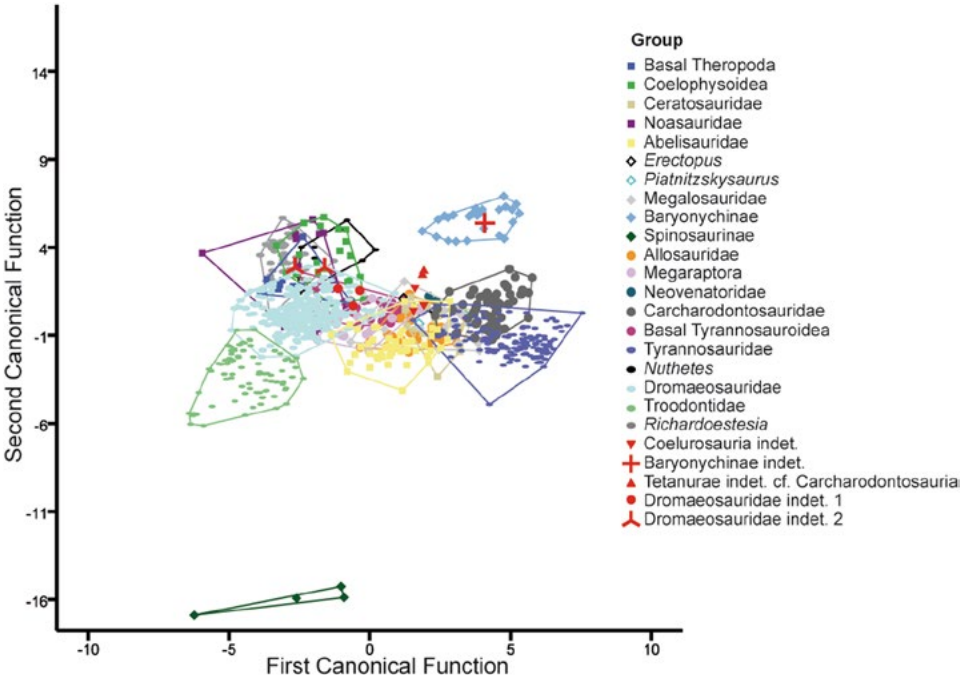

Fig. 3 DFA of 901 teeth dataset results, including El Oterillo II morphotypes (Coelurosauria indet., Baryonychinae indet., Tetanurae indet. cf. Carcharodontosauria, Dromaeosauridae indet. *1* and Dromaeosauridae indet. *2*. and excluding AL and teeth with missing data. The first function explains the 63.4% of variance; the second canonical function explains the 28.4% of the variance

(Goloboff et al. 2008) using the protocol described by Hendrickx and Mateus (2014) and Gerke and Wings (2016). Seven different cladograms were obtained with this analysis. The cladistic analysis (Appendix B) classifies the morphotypes as a combination of basal tetanurans (Baryonychinae, Megalosauridae) and derived tetanurans (Tyrannosauroidea, Dromaeosauridae).

2.6 Tooth mark analysis

In order to verify the presence of tooth marks on the sauropod carcass, various skeletal remains were studied, including dorsal and caudal vertebrae, haemal arches and autapodial elements. The distribution, morphology and abundance of the tooth marks were taken into account (Hunt et al. 1994).

It is important to note that not all the bone remains were studied, so the interpretation of the results may lack important information about the type and distribution of the tooth marks. The conclusions derived from these observations should thus be taken with caution.

3 Results

3.1 Systematic palaeontology

DINOSAURIA Owen 1842.
SAURISCHIA Seeley 1887.
THEROPODA Marsh 1881.
Theropoda indet.

Material Two teeth (MDS-OTII,88; MDS-OTII,89).

Description (after Hendrickx et al. 2015a).

Two incomplete crowns that lack the basalmost part (Fig. 4). There are some horizontal fractures and parts of the enamel are missing. The carinae are damaged and MDS-OTII,88 lacks the mesial carina. The enamel surfaces have microscratches.

These are medium-sized, incomplete crowns with moderately compressed and distally curved ziphodont morphology. The CBR values are among the highest from El Oterillo II with the exception of spinosaurid teeth (0.6). Due to the absence of the basalmost part of the crown these values were not measured at the level of the cervix, so the real values of CBR could be slightly different. The absence of reliable values for these teeth makes it impossible to include them in the statistical analyses (Appendix A). These teeth could represent mesial dentition. The elongation of the crown shows normal values according to Hendrickx and Mateus (2014), but again this is not the real but the preserved elongation. The apex points towards the lingual side and seems to extend beyond the basal length of the crown. The mesial lateral profile of the crown is convex and the distal lateral profile is concave. The lingual surface is convex and the labial is almost planar.

MDS-OTII,89 has mesial and distal carinae. MDS-OTII,88 lacks the mesial carina. The carinae are well developed and serrated. The mesial carina is slightly twisted lingually and the distal carina of the teeth is strongly displaced labially. The distal carina seems to reach

Fig. 4 Theropoda indet. MDS-OTII,89: **a** labial, **b** lingual, **c** mesial, **d** distal, **e** apical, **f** basal views. **g** detail of the denticles and the apex. MDS-OTII,88: **h** lingual, **i** labial, **j** mesial, **k** distal, **l** basal and **m** distal carina

the cervix. The mesial carina does not extend along the whole mesial margin but finishes before the cervix. There are concave surfaces adjacent to the distal carinae, on the labial side of the crown. These surfaces are better developed toward the basal part of the preserved crowns. The preserved cross-section has a lanceolate-oval morphology, but this is not the cross-section at the level of the cervix.

The distal carina of both teeth has 18 denticles per 5 mm. The largest denticles are located in the middle part of the carina. The denticles are chisel-shaped and are proximodistally subrectangular. They are perpendicular to the carina. The external margin is symmetrically convex. The interdenticular space is broad, and the interdenticular slit is concave. There are interdenticular sulci on the distal margin on both the labial and lingual sides. The interdenticular sulci are straight, short and basally oriented.

There are spalled surfaces on the tips of the crowns. MDS-OTII,88 also has a wear facet on the lingual surface. There are no flutes. The teeth have transversal undulations that cover the whole enamel surface and are visible at a certain angle. The enamel is polished and smooth but the original texture seems to be braided. The root is not preserved.

Discussion The preserved crown base ratio (sensu Smith et al. 2005) of these teeth is among the highest of the El Oterillo II teeth with the exception of the conical crowns of spinosaurids. The CBR does not exceed the 0.64 value proposed by Hendrickx (2015) as the most common value distinguishing mesial and lateral dentition. However, the basalmost parts of the teeth are not preserved, and its real value could well be greater.

Other interesting features of the teeth are the slightly twisted mesial carina, the distal carina that is deflected labially, and the concave surface adjacent to the carina. A distal carina that is strongly displaced labially appears in some basal theropods, ceratosaurids, tyrannosauroids, allosauroids, dromaeosaurids and troodontids (Hendrickx 2015). Specifically, this deflection occurs in the mesial dentition of allosauroids, including carcharodontosaurids such as *Acrocanthosaurus* (Coria and Salgado 1995) and *Mapusaurus* (Coria and Currie 2006) and other possible carcharodontosaurians such as *Fukuiraptor* (Currie and Azuma 2006; Hendrickx 2015). It is also present in the mesialmost dentition of tyrannosauroids such as *Alioramus* and *Proceratosaurus*. *Allosaurus* (Hendrickx et al. 2015b), ceratosaurids such as *Genyodectes* and dromaeosaurids such as *Dromaeosaurus* (Currie et al. 1990) share this trait for the whole dentition. Another dromaeosaurid, *Deinonychus*, has this character in the mesial dentition only (Ostrom 1969; Hendrickx 2015).

The concave surface adjacent to the carina is also widespread among theropods. The mesial dentition of abelisaurids, *Allosaurus*, tyrannosauroids and some deinonychosaurs has concavities on the margins of the crowns (Smith 2005, 2007; Hendrickx 2015). In addition, the lateral dentition of basal theropods, ceratosaurids, neovenatorids and metriacanthosaurids may also have concave surfaces in the labiodistal part of the crowns (Rauhut 2004; Azuma and Currie 2000; Hendrickx 2015).

The morphotype was not analysed with DFA due to the incompleteness of the tooth remains. The teeth were included in the cladistic analysis instead, coded separately as mesialmost and lateral dentition. The cladistic analysis (Appendix B) recovered the teeth as mesial dentition related to Dromaeosauridae. According to a second cladistic analysis coding the teeth as lateral dentition, the morphotype corresponds to the sister taxon of *Dromaeosaurus*. Given the absence of relevant parts of the teeth, here we prefer to be cautious and consider this morphotype as Theropoda indet. The preserved measurements used in the cladistic analysis could deviate from the real measurements, and there could be relevant traits that are not preserved.

It cannot be ruled out that this morphotype represents a mesialmost morphotype related to other lateral tooth morphotypes from El Oterillo II site, such as Tetanurae indet. or Coelurosauria indet.

TETANURAE Gauthier 1986.
SPINOSAUROIDEA Stromer 1915.
Spinosauridae Stromer 1915.
Baryonychinae.
Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson and Wilson, 1998.
Baryonychinae indet.

Material Five teeth (MDS-OTII,81; MDS-OTII,84; MDS-OTII,85; MDS-OTII,86; MDS-OTII,99).

Description The teeth show different states of preservation. The majority of them are broken and incomplete, with the exception of MDS-OTII,99, which preserves the whole crown and some parts of the root (Fig. 5). Small fractures can be found on the enamel surface. The enamel is absent in some parts of the crown. The original enamel texture has been polished, probably due to abrasion. The enamel may show differences in polishing between different parts of the crown in these teeth. For instance, MDS-OTII,99 has more polished enamel on the apical, central and lingual parts of the crown. Usually, this polished enamel also shows microscratches on its surface.

The teeth show a curved distal profile with a slight tilt to the lingual surface. They are conidont crowns (sensu Hendrickx et al. 2015a). The crown base ratio ranges between 0.6 and 0.8, typical of normal-subcircular crowns. The elongation of the crown (CHR around 2) shows normal values according to Hendrickx and Mateus (2014). The apex of MDS-OTII,99 extends beyond the basal length. The mesial profile of the teeth in lateral view is convex and the distal profile is slightly concave, with the basalmost part almost straight. In distal view the mesial and distal profile are curved towards the lingual side. Both labial and lingual sides have convex surfaces. The enamel extension is similar on both sides.

The teeth have well-developed, serrated carinae on both the mesial and distal margins of the crown. Interestingly, the basal distal carina of MDS-OTII,99 is split, an unusual feature in theropods (Hendrickx 2015). The carinae are located in central positions of the margins and reach the cervix. There are no adjacent surfaces or depressions on the basal part of the crowns. The cross-section of the crown at the level of the cervix is subcircular-elliptical. This is also the case at the level of the mid-crown. The carinae are densely serrated with minute denticles. MDS-OTII,99 has around 30 denticles per 5 mm. The state of preservation of the other crowns has prevented precise measurement, but there seem to be around 40 denticles per 5 mm, this higher number probably due to their small size. The DSDI values are around 0.9, which means that the denticles are similar in size in mesial and distal carinae. The denticles are small and may exhibit a sporadic variation in size along the carina, but generally they are bigger in the middle part. The denticles are subquadrangular and are located perpendicularly to the adjacent carina. The outline of the external margin of the denticle is symmetrically convex. The interdenticular space is shallow and narrow. The denticles have a diaphysis between them. The interdenticular slit is concave and shallow, and the denticles do not have interdenticular sulci.

MDS-OTII,99 and MDS-OTII,85 have a spalled surface on the apex of the crown. Wear facets have not been observed or are not preserved. The enamel surface bears flutes running apicobasally both on the lingual and labial sides. The number of flutes ranges between 5 and 9.

In addition to this ornamentation, MDS-OTII,99 has marginal and transversal enamel undulations. The undulations are scarce, around six per side, and extend horizontally except for the basal third of the crown. They are more easily visible at a certain angle. The enamel texture corresponds to the veined texture of Hendrickx et al. (2015a). The texture is of an apical-adapical direction in the middle of the crown but curves toward the carinae at the margins.

The root is partially preserved in some of the teeth. The width is slightly greater than that of the crown and is of subcylindrical morphology. The surface of the root of MDS-OTII,99 has an ornamentation made up of undulations that are more visible on the lingual side. This tooth also has a small depression in this zone. The cross-section of the root is subcircular except for MDS-OTII,99, where the lingual depression makes the morphology slightly reniform. The dentine width of the root is about 4 mm.

Discussion Spinosaurids have distinctive teeth with straight crowns or slight distal curvature, subcircular-elliptical cross-sections, fluted enamel, minute denticles or unserrated carinae, and a veined enamel texture (Charig and Milner 1997; Sereno et al. 1998; Sues et al. 2002; Ruiz-

Fig. 5 Baryonychinae indet. MDS-OTII,99 in **a** labial, **b** lingual, **c** mesial, **d** distal, **e** basal and **f** enamel texture, marginal undulations and denticles on the distal carina

Omeñaca et al. 2005; Canudo et al. 2008; Hendrickx and Mateus 2014; Gasca et al. 2008; Hendrickx et al. 2015b; Serrano-Martínez et al. 2016; Alonso and Canudo 2016).

The spinosaurid teeth from El Oterillo II have a CBR greater than 0.64. CBR values higher than 0.64 are common for mesial teeth, which are broader than the lateral ones. This has been proposed as a dental feature by Hendrickx (2015). Nevertheless, some clades have a CBR greater than 0.64 for non-mesial teeth, a feature seen in Allosauridae, Spinosauridae, Tyrannosauridae, Ornithomimosauria, Alvarezsauroidea and Therizinosauria (Hendrickx 2015).

The mesial carina reaches the cervix, a feature present in all theropod clades other than Megalosauridae and Therizinosauria. The presence of a mesial carina that reaches the cervix has been proposed as characteristic of all spinosaurids (Hendrickx et al. 2015b) but some authors (Serrano-Martínez et al. 2016) have noticed the occurrence of some spinosaurid teeth with mesial carinae that do not reach the cervix (CMP3-760, Canudo et al. 2008; Fig. 6), so there may be variation in this general trait.

MDS-OTII,99 has an abnormal distal carina. A split mesial carina has been reported in tyrannosaurid theropods, *Allosaurus* and indeterminate carcharodontosaurids (Currie et al. 1990; Erickson 1995; Abler 1997; Smith 2005; Brusatte and Sereno 2007; Candeiro and Tanke 2008; Cillari 2010; Hendrickx 2015). The split mesial carina is common in Tyrannosauridae, as shown by Erickson (1995). This author also points to its possible causes: trauma, genetic factors and aberrant tooth replacement. This abnormal feature present in MDS-OTII,99—given both its rarity and its location, the distal carina—seems to be the first evidence of the presence of this condition in Spinosauridae.

More than 30 denticles per 5 mm are seen in non-tetanuran theropods, baryonychine spinosaurids and coelurosaurs. *Baryonyx* and *Suchomimus* have around 35 denticles per 5 mm (Hendrickx 2015), values that are comparable to the teeth from El Oterillo II. The dental evolution of Spinosauridae seems to have resulted in robust crowns (Charig and Milner 1997) with a reduction in the number of denticles in baryonychine spinosaurids, leading

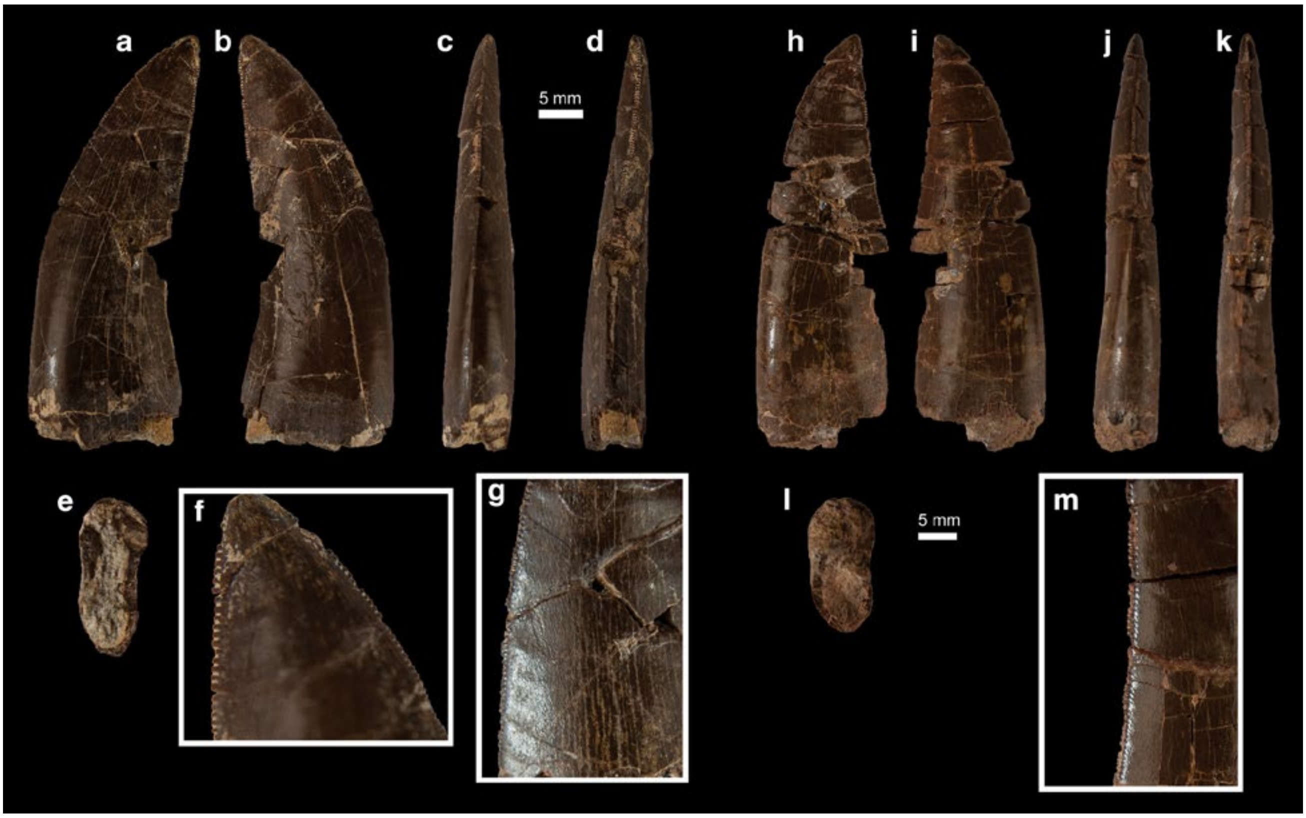

Fig. 6 Tetanurae indet. cf. Carcharodontosauria. MDS-OTII,92 in **a** labial, **b** lingual, **c** mesial, **d** distal, **e** basal views. **f** Detail of the apex and denticles of mesial and distal carinae. **g** Marginal undulations. MDS-OTII,78 in **h** labial, **i** lingual, **j** mesial, **k** distal and **l** basal views, **m** Distal denticles

to unserrated crowns in Spinosaurinae (Charig and Milner 1997; Buffetaut 2011; Gianechini et al. 2011; Serrano-Martínez et al. 2016). Other theropod taxa (*Ceratosaurus*, *Tyrannosaurus*) have carinae with a large number of denticles, but this is related to the great size of the crowns and the number of denticles per 5 mm is lower (Hendrickx 2015). The variation in denticle size along the carinae has been noted in the spinosaurids *Suchomimus* and *Baryonyx* and has been proposed as a feature of Baryonychinae (Mateus et al. 2011; Hendrickx 2015).

Fluted crowns are common in piscivorous tetrapods. The presence of flutes is characteristic of spinosaurid teeth, although they are also present in other taxa such as *Ceratosaurus* and some Dromaeosauridae (Hendrickx and Mateus 2014). *Baryonyx* tends to have flutes restricted to one side of the crown (Charig and Milner 1997), whereas *Suchomimus* shows flutes on both sides (Hendrickx 2015).

Transverse and marginal undulations are a common feature of theropod teeth and have a widespread distribution among theropods (Brusatte et al. 2007); they have been seen in spinosaurid theropods such as *Baryonyx*, *Irritator* and *Suchomimus* (Hendrickx 2015) and in other indeterminate spinosaurid teeth (Canudo et al. 2008). The teeth studied here have a veined enamel texture (sensu Hendrickx et al. 2015a). A veined enamel texture comprising alternating grooves and long sinuous ridges (Hendrickx et al. 2015a) characterizes spinosaurid teeth; it has been found in *Baryonyx*, *Suchomimus*, *Spinosaurus* and other indeterminate spinosaurids (Canudo et al. 2008; Serrano-Martínez et al. 2016).

This conjunction of dental features indicates that these teeth from El Oterillo II belong to Spinosauridae. The family Spinosauridae has been divided into two subfamilies: Baryonychinae and Spinosaurinae. Baryonychine teeth have an ornamentation based on ridges, a cross-section that is not as subcircular as in spinosaurine teeth, and a more pronounced distal curvature of the crown (Canudo et al. 2008; Alonso and Canudo 2016). Spinosaurine teeth also tend to have unserrated carinae, as in *Irritator*, *Angaturama* and *Spinosaurus* (Stromer 1915; Kellner and Campos 1996; Sues et al. 2002; Hendrickx 2015). In addition, the sporadic variation in size of denticles has been proposed as a feature of Baryonychinae (Mateus et al. 2011).

DFA (Appendix A) classifies MDS-OTII,99 as a member of the group Baryonychinae with 100% probability. The cladistic analysis places this morphotype as the sister taxon of a clade composed of all other spinosaurid theropods (*Spinosaurus*, *Irritator*, *Baryonyx* and *Suchomimus*). The teeth belonging to Baryonychinae indet. from El Oterillo II show no significant dissimilarity with respect to other baryonychines from the Iberian Peninsula (Torcida Fernández-Baldor et al. 1997, 2003; Ruiz-Omeñaca et al. 1998; Infante et al. 2005; Canudo et al. 2008; Gasca et al. 2008; Mateus et al. 2011; Figuereido et al. 2015; Alonso and Canudo 2016).

TETANURAE Gauthier 1986.
Tetanurae indet. cf. Carcharodontosauria.

Material Six teeth (MDS-OTII,75; MDS-OTII,77; MDS-OTII,78; MDS-OTII,92; MDS-OTII,93; MDS-OTII,95).

Description Four crown fragments and two teeth (MDS-OTII,78 and MDS-OTII,92) belong to this morphotype. The two teeth are almost complete so the description is based on them. These teeth have horizontal fractures and are missing parts of the crown. Some areas lack enamel, and other parts of the teeth are broken or absent.

The crowns have a labiolingually compressed and distally curved ziphodont morphology (Fig. 6). The crowns have normal CBR values for lateral teeth (CBR = 0.4) according to Hendrickx and Mateus (2014). The elongation of the crowns is normal, lying between 2.3 and 2.4. The apex is distally oriented and extends beyond the basal length. The mesial profile of the crown in lateral view is convex and the distal margin is concave. The distal profile of the crown is sigmoidal. The labial and lingual surfaces are convex. The enamel extension is similar on the lingual and labial sides.

The crowns have well-developed, serrated carinae on both margins. The distal carina is displaced labially. The distal carina reaches the cervix; the mesial carina extends along 2/3 of its margin, finishing before the cervix. The mesial carina is diagonally oriented and the distal carina is sigmoidal. The cross-section of the crowns is lanceolate at the level of the cervix and lenticular at the mid-level.

The crowns have a similar denticle number on both carinae, between 19 and 21 denticles per 5 mm. The DSDI has a value of around 1. The denticles show a regular variation in size. They are smaller at the apex and base and larger in the central area. The denticles are chisel-shaped and proximodistally subrectangular. They are perpendicularly positioned towards the carinae. The marginal contour of the denticle is convex and parabolic. The interdenticular space is broad and the diaphysis is not clearly visible due to the state of preservation. The interdenticular slit is concave. There are interdenticular sulci on both mesial and distal carinae; these are short, straight and basally inclined.

There are spalled surfaces on the apex of the crown. Wear facets are not observed and the teeth have no flutes. There are marginal and transversal undulations, which are abundant and horizontally oriented. They are more visible at a certain angle. The enamel texture is braided (sensu Hendrickx et al. 2015a), and the braids are straight in the middle part of the crown and inclined towards the carina at the margin.

Some parts of the root are preserved. The root has a similar width to the crown and is labiolingually compressed. There is no constriction between the crown and the root. The root has depressions both on its labial and lingual sides, giving it a figure-eight-shaped cross-section. The dentine width in this part of the root has values around 1.6–1.9 mm.

Discussion By comparison with the dental features proposed by Hendrickx (2015), these teeth have no basal constriction. The CBR is lower than 0.64, suggesting that they are lateral teeth due to their lateral compression. The crown height is less than 70 mm, and they are serrated both on mesial and distal carinae.

The mesial carina of this morphotype does not reach the cervix. This trait is seen in Megalosauridae (Hendrickx et al. 2015b), *Eoraptor, Neovenator* (Hutt et al. 1996), *Australovenator* (White et al. 2015), basal tyrannosauroids such as *Alioramus* (Brusatte et al. 2012), Therizinosauria and Microraptorinae, and it is also seen in *Acrocanthosaurus* and *Dromaeosaurus* (Hendrickx 2015).

The distal carina of these teeth seems to be displaced labially. A strongly displaced distal carina has been observed in several theropod clades, such as Ceratosauridae, Allosauroidea and Tyrannosauroidea (Hendrickx 2015). Nevertheless, this morphotype does not present the distal carina at the level of the labial margin. Teeth with a weak displacement of the distal carina have been identified in the whole dentition of Abelisauridae (Hendrickx and Mateus 2014) and Megalosauroidea and in the lateral dentition of Metriacanthosauridae, Neovenatoridae, Tyrannosauroidea and in neocoelurosaurs except *Dromaeosaurus* (Hendrickx 2015). This weak displacement is more congruent with the morphotype's displacement.

Another significant characteristic of these teeth is the presence of transversal and marginal undulations, a widespread feature among non-neocoelurosaur averostrans (Brusatte et al. 2007; Hendrickx and Mateus 2014). They also have interdenticular sulci, another trait present in non-neocoelurosaur averostrans. The braided texture of the enamel, present in non-neocoelurosaur neotheropods, can be observed in Megalosauroidea, Allosauroidea, Tyrannosauroidea and basal Ceratosauria (Hendrickx 2015).

The characteristics seen in this morphotype are shared by many different theropod clades. Nevertheless, these traits are more specifically found in basal tetanurans such as megalosaurids or carcharodontosaurian theropods. The presence of non-spinosaurid basal tetanurans is known in the Early Cretaceous deposits of Western Europe (Hutt et al. 1996; Pereda-Suberbiola et al. 2012; Csiki-Sava et al. 2016). The Iberian Peninsula record has one of the best-preserved tetanurans of the Early Cretaceous, *Concavenator corcovatus* from the upper Barremian of Cuenca (Ortega et al. 2010). Other evidence of carcharodontosaurian theropods comes from the Barremian deposits of Teruel (Gasca et al. 2014), where a distal femur with affinities to *Acrocanthosaurus* has been found.

Other carcharodontosaurian theropod remains have been found in the Weald of England, an example being *Neovenator*. Related theropods, such as *Fukuiraptor*, are represented in Asian sediments from this age (Azuma and Currie 2000). The presence of carcharodontosaurid theropods in north Africa is also well-known (e.g. Fanti et al. 2014).

The DFA analyses classify these teeth as *Erectopus* (41–50, 33.4–43.5 and 35.4–43.3% probability, Appendix A). *Erectopus* is an enigmatic theropod with allosauroid affinities from the Lower Cretaceous (lower Albian) of France (Allain 2005). Some differences exist between this morphotype and the dentition of *Erectopus*: the serrated mesial and distal carinae of *Erectopus* run along the entire margins; moreover, the denticle density is slightly different. Notably, the small size of the *Erectopus* group could have had a negative effect on the DFA analyses.

On the other hand, the cladistic analysis (Appendix B) places this morphotype as the sister taxon of *Afrovenator* and includes it within the clade Megalosauridae. Despite the size differences, they share some features, including a mesial carina terminating well above the cervix, the presence of enamel undulations, short interdenticular sulci, similar CBR values and similar morphology (Hendrickx et al. 2015b).

The traits present in this El Oterillo II morphotype show a variety of affinities with some of the basal tetanuran clades. Due to the degree of uncertainty, we attribute this morphotype to Tetanurae indet. cf. Carcharodontosauria, since the presence of megalosaurid theropods, unlike that of carcharodontosaurian theropods, is not known in the Barremian or Early Cretaceous of Spain. Megalosaurids are well-known in the Upper Jurassic of the Iberian Peninsula (e.g. Malafaia et al. 2017). However, the discrepancy with respect to the cladistic analysis suggests that this conclusion should be taken with caution until new material is found.

If these teeth belong to theropod dinosaurs other than carcharodontosaurid carcharodontosaurians, this means that the palaeobiodiversity of the theropods of the Early Cretaceous of Spain could be greater than previously thought (Gasca et al. 2014), including spinosaurids, diverse non-spinosaurid basal tetanurans such as carcharodontosaurids (Ortega et al. 2010; Gasca et al. 2014) and other clades (Canudo et al. 2006), ceratosaurs (Sánchez-Hernández and Benton 2014) and different coelurosaurs such as ornithomimosaurs (Pérez-Moreno et al. 1994), maniraptorans and birds (Sanz et al. 1988; Lacasa-Ruiz 1989; Sanz and Buscalioni 1992; Sanz et al. 1996; Sereno 2000). Nevertheless, further work is required to find more diagnostic skeletal remains in order to clarify this question.

TETANURAE Gauthier 1986.
COELUROSAURIA von Huene 1914.
Coelurosauria indet.

Material One tooth (MDS-OTII,82).

Description MDS-OTII,82 is an incomplete crown which lacks the apex and the basalmost part. The surface shows horizontal fractures. Some parts of the enamel are missing (Fig. 7).

MDS-OTII,82 is a labiolingually compressed (CBR = 0.46) and distally curved ziphodont crown. The compression is typical for lateral teeth. The values for the elongation of the crown are normal according to Hendrickx and Mateus (2014) (CHR = 1.85). The apex extends beyond the basal length. The mesial lateral profile of the crown is convex, and the distal lateral profile concave. The crown is slightly curved towards the lingual side in distal view. The labial and lingual surfaces are slightly convex. The preserved enamel shows a constant extension along the crown.

The distal carina is well developed. There is no mesial carina, and the possibility of its loss due to abrasion cannot be ruled out. The distal carina runs along the whole distal margin. The carina is strongly displaced labially. There are no concave surfaces adjacent to the carina, but there are shallow depressions both in the labial and basalmost lingual areas of the crown, conferring a figure-eight-shaped cross-section. At the level of the mid-crown the cross-section is lanceolate. The distal carina has 15 denticles per 5 mm. The variation in size of the denticles along the carina is regular, with the larger denticles located in the middle part and decreasing in size towards the base. The denticles are chisel-shaped and are proximodistally subrectangular. They are perpendicular to the carina. The exterior margin of the denticle is convex and parabolic. The interdenticular space is broad. The interdenticular slit is concave, and there are interdenticular sulci both on labial and lingual sides. The sulci are short, straight and inclined towards the base.

There is a possible wear facet on the lingual side of the crown. The exposed dentine shows diagonal scratches that are mesioapically-distobasally oriented. The crown has no flutes. There are abundant transversal and marginal undulations, horizontally oriented and with the concavity pointing to the apex. The undulations are visible at a certain angle and cover most of the enamel surface. The original enamel texture seems to be braided. This is

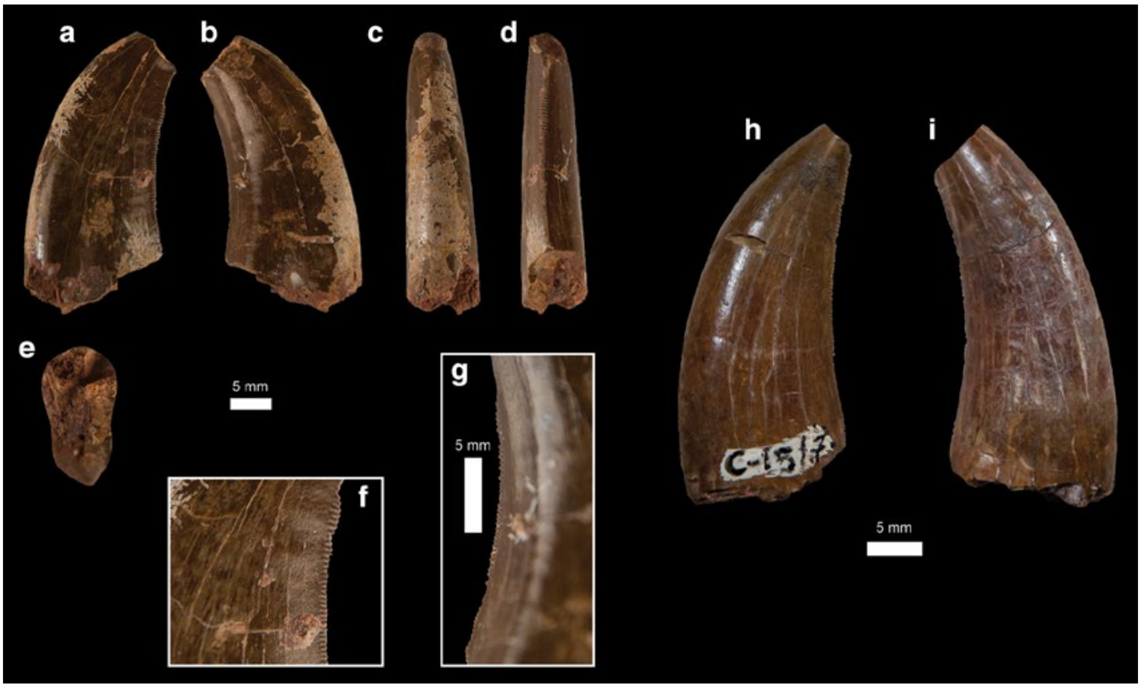

Fig. 7 Coelurosauria indet. MDS-OTII,82. **a** labial, **b** lingual, **c** mesial, **d** distal, **e** basal view. **f**, **g** Denticles and marginal enamel undulations of the distal carina. **h** MDS-C15,7 in labial view. **i** MDS-C15,6 in lingual view

difficult to assess due to the polished enamel and the microscratches that cover the tooth surface. The root is not preserved.

Discussion This tooth has a series of interesting traits, most notably the figure-eight-shaped cross-section and the distal carina that is strongly displaced labially. This is not the only tooth from the Salas the los Infantes area with these features. Two other teeth from the Early Cretaceous have been recovered from the Tenadas de la Rosada site: MDS-C15,6 and MDS-C15,7 (Torcida Fernández-Baldor et al. 2003) (Fig. 7). The distal carina that is strongly displaced labially is seen in the whole dentition in ceratosaurids, allosaurids, tyrannosauroids and some dromaeosaurids (Hendrickx 2015). The figure-of-eight shape is produced by the presence of two depressions in the basalmost part of the crown. This has been noted in the metriacanthosaurid *Sinraptor* (Hendrickx 2015) and in coelurosaurian theropods. The figure-eight-shaped cross-section is seen in possible ceratosaurids such as *Berberosaurus* (Hendrickx and Mateus 2014), dromaeosaurids such as *Saurornitholestes* (Currie et al. 1990; Sankey et al. 2002; Hendrickx and Mateus 2014), *Tsaagan* (Norell et al. 2006), *Pyroraptor* (Allain and Taquet 2000; Gianechini et al. 2011, Hendrickx and Mateus 2014) and *Buitreraptor* (Gianechini et al. 2011; Hendrickx and Mateus 2014), and other taxa such as *Richardoestesia* (Currie et al. 1990) and troodontids such as *Byronosaurus* and *Xixiasaurus* (Hendrickx 2015). Given the size of MDS-OTII,82, it is reasonable to look for another non-maniraptoran theropod as the possible owner. The lateral teeth of *Sinraptor* have a concave surface adjacent to the distal carina in the labiobasal part of the crown, which this morphotype does not possess. The figure-eight-shaped cross-section has been noted among the basal tyrannosauroids *Proceratosaurus* (Rauhut et al. 2010) and *Alioramus* (Brusatte et al. 2012; Hendrickx 2015). Megaraptorans such as *Megaraptor*, *Orkoraptor* (Porfiri et al. 2014) and *Australovenator* (White et al. 2015) have been reported to share this trait for the lateral dentition. Unlike this morphotype, *Proceratosaurus* teeth show a significant difference in size between mesial and distal denticles (Rauhut et al. 2010) (MDS-C15,7 preserves the mesial carina, which shows a similar number to the distal carina). This morphotype shows certain affinities with the teeth of *Alioramus altai*. The number of denticles is similar (14–15 denticles per 5 mm); the distal carina is deflected labially and the mesial carina lingually; and there are enamel undulations and interdenticular sulci (Brusatte et al. 2012). Compared with *Alioramus*, the mesial carina is shorter.

The teeth from *Orkoraptor* and *Megaraptor* have strongly curved, low crowns and unserrated mesial carinae (Porfiri et al. 2014) whereas this morphotype could have a denticulated mesial carina. The teeth from *Murusraptor* (Coria and Currie 2016) also have a similar outline but the carinae are centrally positioned.

As seen in *Australovenator*, the morphotype from El Oterillo II could lack mesial denticles or have a reduced mesial carina; it also has transverse undulations and a similar number of denticles (around 15 per 5 mm) (White et al. 2015). Despite these similarities some differences exist: The tooth from El Oterillo II does not show the lingual deviation of the distal carina and it has interdenticular sulci; marginal undulations of the enamel are also present.

DFA (Appendix A) locates this morphotype within Megalosauridae (<47%). Given the poor results, this must be taken with caution. Megalosaurid teeth do not have the figure-eight-shaped cross-section, so this result could be a consequence of the size-dependent classification of this type of analysis. The cladistic analysis (Appendix B) recovers the morphotype within Tyrannosauroidea close to basal tyrannosauroids.

Given the uncertainty, this tooth has been classified as Coelurosauria indet. so as not to exclude the possibility of it being produced by a basal tyrannosauroid, a large maniraptoran or a megaraptorid theropod. The position of Megaraptora among theropods is currently a subject of discussion, with a suggested placement within Neovenatoridae or Tyrannosauroidea (Hendrickx et al. 2015c). The phylogenetic analyses run by Coria and Currie (2016) on two alternative data matrices based on the dataset of Carrano et al. (2012) plus the modifications by Zanno and Makovicky (2013), and the dataset of Novas et al. (2013) plus the modifications by Porfiri et al. (2014), show Megaraptora positioned within Neovenatoridae or as the sister group of Tyrannosauridae. Bell et al. (2016) also state that the position of Megaraptora remains equivocal. Here we prefer to consider Megaraptora within Tyrannosauroidea in order to include all the possible owners of the morphotype within the clade Coelurosauria, as in the phylogeny of Hendrickx et al. (2015c).

This morphotype could represent a singular taxon of coelurosaurian theropods from the Early Cretaceous of the Iberian Peninsula. The presence of basal tyrannosauroids is known in the deposits of the Upper Jurassic-Lower Cretaceous of Western Europe, especially England and Portugal (Hutt et al. 2001), with genera such as *Proceratosaurus* and *Eotyrannus*. Megaraptorans have been found in Asia, Australia and South America (Bell et al. 2016). The possible presence of these taxa opens a new scenario including more diverse theropods than previously thought. Nevertheless, new information is required to corroborate the distribution of these clades in the Early Cretaceous of the Iberian Peninsula.

TETANURAE Gauthier 1986.
COELUROSAURIA von Huene 1914.
MANIRAPTORA Gauthier 1986.
PARAVES Sereno 1997.
Dromaeosauridae Matthew and Brown 1922.
Dromaeosauridae indet. 1.

Material Three teeth (MDS-OTII,73; MDS-OTII,100; MDS-OTII,102).

Description The crowns are well preserved. Some parts of the carinae and enamel are missing. They may bear horizontal fractures. The teeth have a ziphodont morphology; they are labiolingually compressed and distally curved (Fig. 8). The crowns are small (CH = 4–14 mm). The CBR values are around 0.5. The elongation of the crowns varies among weak-normal values according to Hendrickx and Mateus (2014) (CHR = 1.4–1.9). The crowns are curved and the apex extends beyond the basal length. The mesial lateral profile of the crowns is convex and the distal lateral profile is slightly concave, almost straight. The labial and lingual surfaces are convex. The distal profile is straight. The enamel shows a constant extension along the crown.

The teeth have mesial and distal carinae. The carinae are serrated and are located in central positions along the mesial and distal margins. The distal carina reaches the cervix, whereas the mesial carina only extends along the apical half of the crown. Carinae run along the tip of the crown. The outline of the teeth at the level of the cervix has a lanceolate morphology. The cross-section at the mid-level is lenticular.

The mesial carina has around 30–35 denticles per 5 mm, whereas the distal carina has 20 denticles per 5 mm. The mesial denticles are smaller (DSDI = 1.5–1.8) than the distal ones. The largest denticles on the mesial carina are located on the apex and decrease towards the base. The largest denticles on the distal carina are on the basalmost part of the crown. The variation in denticle size is regular. The denticles are chisel-shaped and are proximodistally subrectangular. The denticles are located perpendicular to the carina. The external margin has a convex outline. The interdenticular space is broad and the interdenticular slit is concave and shallow. There are no interdenticular sulci.

There are spalled surfaces on the tips of the crowns. MDS-OTII,102 also has a possible wear facet on the lingual side of the crown. There are some transversal undulations on the enamel surface. The undulations are horizontally oriented and are visible at a certain angle. The enamel texture is polished and smooth in some parts of the crown, but the original texture seems to be irregular. The root is not preserved.

Discussion Small teeth size and high DSDI values have usually been considered typical of dromaeosaurid dentition. However, a DSDI greater than 1.2 is present in various clades of theropods, including Noasauridae, Piatnitzkysauridae, Tyrannosauroidea, Microraptorinae and Eudromaeosauria (Hendrickx 2015). The DFA (Appendix A) with mesialmost dentition includes this morphotype

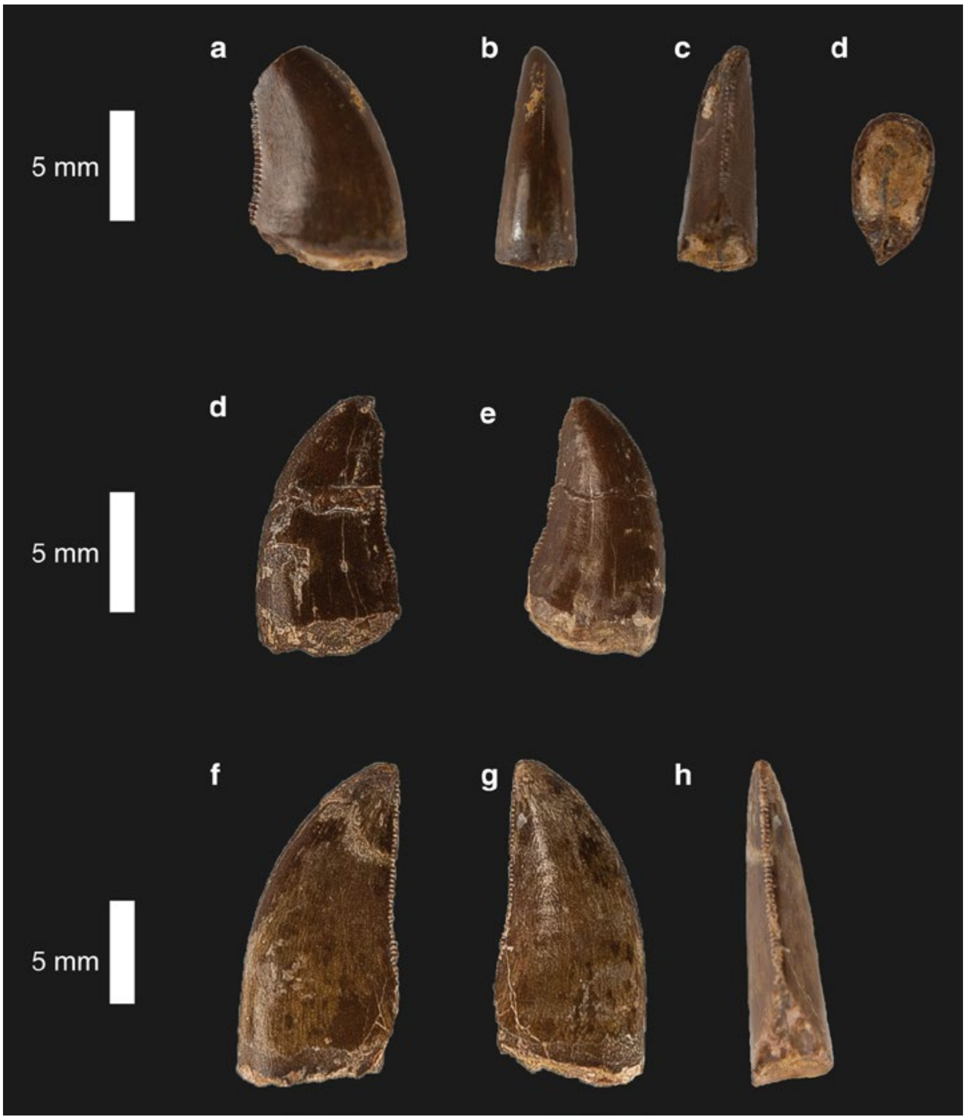

Fig. 8 Dromaeosauridae indet. 1. MDS-OTII,102 in **a** lateral, **b** mesial, **c** distal and **d** basal views. **d**, **e** MDS-OTII,73 in lateral views. MDS-OTII,100 in **f**, **g** lateral and **h** distal view

(<50%) within Dromaeosauridae, with the exception of MDS-OTII,102, which is reclassified as a basal tyrannosauroid. This is not unusual, given the similarities that some tyrannosauroids and dromaeosaurids show in their dentition (Rauhut et al. 2010; Hendrickx and Mateus 2014; Gerke and Wings 2016). The DFA without the mesialmost dentition classified all the teeth as Dromaeosauridae (around 40% probability). The cladistic analysis (Appendix B) likewise recovers the morphotype within Dromaeosauridae, as the sister taxon of *Dromaeosaurus.*

The presence of dromaeosaurid theropods in the Salas de los Infantes area has been cited before (Torcida Fernández-Baldor et al. 2003). Theropod teeth from the Wealden facies of England have been attributed to dromaeosaurids (see for example Milner 2002 and Sweetman 2004). In the light of the convergence of results between the analyses, we thus classify the teeth as Dromaeosauridae indet.

Dromaeosauridae indet. 2.

Material Two teeth (MDS-OTII,91; MDS-OTII,101).

Description The crowns are well preserved. Some parts of the carinae and enamel are missing. MDS-OTII,91 also lacks part of the base and apex. The crowns are small (4–8 mm). They have ziphodont morphology (Fig. 9). The CBR values are 0.4–0.5. The elongation of the crowns is normal (1.5–1.8). The crowns are distally curved with the apex extending beyond the basal length, and they are low and squat in appearance. The mesial lateral profile is convex, and the distal lateral profile slightly concave-almost straight. The labial and lingual surfaces are slightly convex. MDS-OTII,101 has serrated mesial and distal carinae. MDS-OTII,91 lacks the mesial carina. The carinae

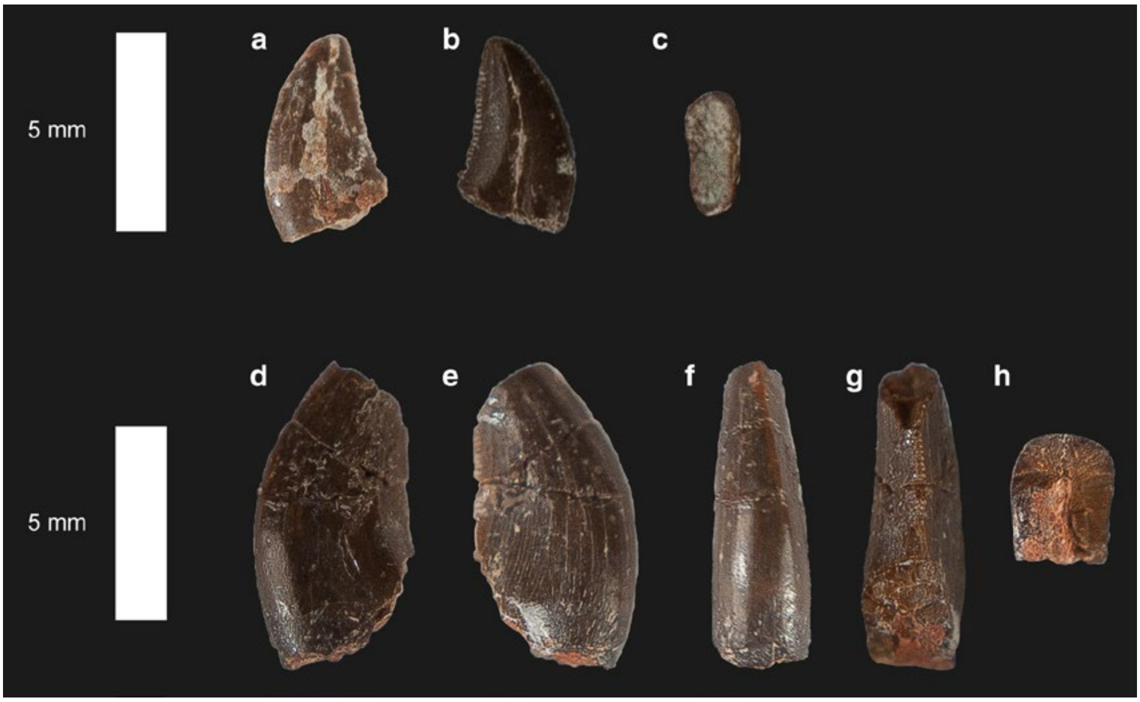

Fig. 9 Dromaeosauridae indet. 2. MDS-OTII,101 in **a**, **b** lateral and **c** basal view. MDS-OTII,101 in **d**, **e** lateral, **f** mesial, **g** distal and **h** basal view

are located in central positions along the margins. The distal carina reaches the cervix but the mesial carina does not, for it only extends along the apical half of the crown. The carinae of MDS-OTII,101 cross the apex. The cross-section at the level of the cervix is figure-eight-shaped. At the level of the mid-crown the cross-section is lenticular.

These teeth have a large number of denticles along the carinae. The mesial carina has an estimated number of 45 denticles per 5 mm. The distal carina has 35 denticles per 5 mm. The largest denticles on the distal carina are located in the basalmost part, and the largest on the mesial carina are on the apex. The variation in size of the denticles is smooth and regular. The denticles have a chisel-shaped morphology and are proximodistally subrectangular. The denticles are located perpendicular to the carina. The external margin of the denticle is symmetrically convex. They have a broad interdenticular space. The interdenticular slit is concave and shallow. Interdenticular sulci have not been observed.

There are spalled surfaces on the tips of the crowns. The crowns also have transversal undulations on the surface of the basal and central areas; these are visible at a certain angle. The enamel texture of MDS-OTII,101 is smooth. MDS-OTII,91 has a braided enamel texture. The root is not preserved.

Discussion As noted for the previous morphotype, the small size of the crowns and the high DSDI have often been considered dromaeosaurid characters. Nevertheless, these features are shared by other theropod groups (Rauhut et al. 2010; Hendrickx and Mateus 2014). Unlike Dromaeosauridae indet.1, Dromaeosauridae indet. 2 possess a figure-eight-shaped cross-section, which is present in metriacanthosaurids, tyrannosauroids, *Berberosaurus*, megaraptorans and dromaeosaurids (Hendrickx 2015).

The DFA analyses (Appendix A) recover MDS-OTII,91 as belonging to *Richardoestesia* (51%, 50.9%, 59.8%) and MDS-OTII,101 as belonging to *Nuthetes* (44.9, 57 and 39.3%). *Richardoestesia* is a genus from the Late Cretaceous of North America (Currie et al. 1990; Baszio 1997; Sankey et al. 2002). Material from the Upper Jurassic of Portugal (Zinke 1998; Hendrickx and Mateus 2014), the Lower Cretaceous of Spain (Rauhut 2002), the Upper Cretaceous of Spain (Torices et al. 2004; 2015) and the Upper Cretaceous of Romania (Codrea et al. 2002; Weishampel et al. 2010) has been referred to this taxon. MDS-OTII,91 shares the figure-eight-shaped cross-section, but the basal constriction is not observed. *Nuthetes* is a possible dromaeosaurid taxon from the Early Cretaceous of England (Milner 2002). One tooth from the Lower Cretaceous deposits of France has been cited as *Nuthetes* sp. (Pouech et al. 2006). These teeth share the small-sized crowns, which are strongly distally recurved, and smaller denticles on the mesial carina and the basal surfaces.

The cladistic analysis (Appendix B) recovers these teeth within Dromaeosauridae, again as the sister taxon of *Dromaeosaurus*. Given the similar morphologies among dromaeosaurid teeth, here we prefer not to assign this morphotype to a specific genus. Instead, we classify these teeth as Dromaeosauridae indet. The possibility that the difference between Dromaeosauridae indet.1 and Dromaeosauridae indet. 2 (the variation in cross-section) is due to variations in the position of the tooth row cannot be ruled out.

4 Tooth marks

Some bones belonging to the El Oterillo II titanosauriform present unusual marks on their surface. Marks on the surface of bones are known among dinosaurs and they can be related to traumas, predation and scavenging. Marks due to predatory behaviour are difficult to prove, but sometimes it is possible to identify possible evidence in the fossil record (Carpenter 1998; Canudo et al. 2005; Cruzado-Caballero 2012; DePalma et al. 2013). Hunt et al. (1994) distinguish between the marks produced by predatory and scavenging behaviour. Multiple, related marks are typical of scavenging on a stationary carcass. Living organisms try to avoid bites and consequently the marks appear more isolated and separated from each other, due to the movement of the prey. Also scavenger animals try to eat first the parts with high concentrations of soft tissues.

Different bioerosion traces have been recognized on the titanosauriform bones (Fig. 10). The marks are scarce and have been identified on vertebral elements: a dorsal vertebra (MDS-OTII,1), a caudal vertebra (MDS-OTII,8) and a haemal arch (MDS-OTII,25). The dorsal vertebra MDS-OTII,1 has a few unusual marks. The most apparent is a subcircular mark (Fig. 10a) located on the left spinopostzygapophyseal lamina perpendicular to the surface. The orifice is 12–14 mm in diameter and about 10 mm in depth; it has parallel sides. Subcircular morphologies are often attributed to invertebrates (Britt et al. 2008; Cruzado-Caballero 2012). Another mark is located on the prezygapophysis. This mark (Fig. 10b) has furrow morphology. The furrow comprises an irregular trace, 20 mm in length, 4–7 mm in width, and 2–5 mm in depth. Interestingly, it remains isolated and there is no other evidence in the surrounding area. Other possible tooth marks are located on the distolateral part of the vertebral centrum, opposite the caudal surface. This area has two parallel grooves with v-shaped sections, both of them 21 cm long and 3 mm deep.

MDS-OTII,25 is a haemal arch. It has one trace (Fig. 10c), 24 mm long, 8 mm wide and 2 mm deep, located on the spine.

The caudal vertebra MDS-OTII,8 has five different marks. The first one (Fig. 10d) is located on the left lateral

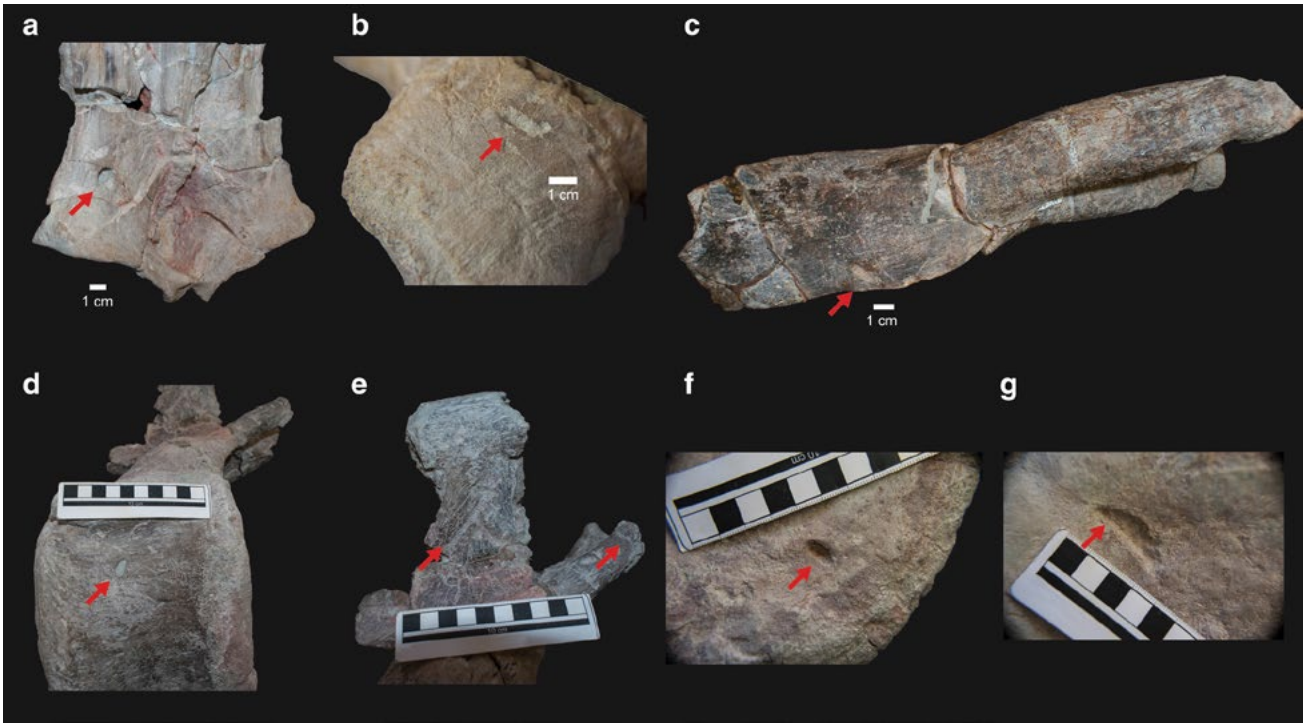

Fig. 10 Marks. **a** subcircular orifice on the left spinopostzygapophyseal lamina of MDS-OTII,1. **b** Furrow on the prezygapophysis of MDS-OTII,1. **c** Furrow on MDS-OTII,25. **d** Puncture on the left lateral side of the caudal vertebra MDS-OTII,8. **e** Furrows on the left lateral surface of the neural spine of MDS-OTII,8. **f** Puncture on the articular surface of MDS-OTII,8. **g** Possible mark on the articular surface of MDS-OTII,8

side of the vertebral centrum. The puncture is 15 mm in length and 8 mm in width. Interestingly, it has an oval outline. The preserved depth is 5 mm but the interior has been filled with sediment. The oval outline and dimensions are congruent with the cross-section of theropod teeth found in the site, specifically with basal tetanurans. Moreover, there is a set of furrows (Fig. 10e) located on the left lateral surface of the neural spine. The arrangement of the marks resembles the letter lambda (λ), with a long trace 45 mm in length and two related smaller traces of 25 and 17 mm. The width of the furrows is 5 mm and the section is u-shaped. These marks could have been produced by invertebrates. The lateral left side of the postzygapophysis also has a diagonally oriented furrow (Fig. 10e). This is 17 mm in length, 2 mm in width and 2 mm in depth.

The caudal surface of the centrum shows two additional marks. There is a puncture (Fig. 10f) in the lower right area, 18 mm in length and 6 mm in width. As in the other puncture, the interior is filled with sediment. The outline of the puncture is oval. Like the lateral mark, the morphology is congruent with some of the teeth recovered in this site. The upper left part of the caudal surface also has a furrow (Fig. 10g), which is diagonally oriented. It is 36 mm in length, 12 mm in maximum width and 6.5 mm in depth. The right side of the furrow is convex and the left side is concave.

5 Discussion

The feeding of theropod dinosaurs on carcasses has been proposed by some authors due to the accumulation of isolated teeth or the presence of tooth marks on the surface of the bones, specifically on sauropod remains (Buffetaut and Suteethorn 1989; Chure et al. 1998; Canudo et al. 2009; Paik et al. 2011; Canale et al. 2014) as well as other remains (Fiorillo 1991; Currie and Jacobsen 1995; Maxwell and Ostrom 1995; Erickson and Olson 1996; Jacobsen 1998; Rogers et al. 2003; Bell and Currie 2010; De Valais et al. 2012). Feeding seems the most parsimonious explanation for the accumulation of theropod teeth around the carcass.

Most of the teeth from El Oterillo II only preserve the crown or the crown and the basalmost part of the crown, and most likely represent shed teeth (Fiorillo and Currie 1994). This is congruent with them being lost when processing food (Hendrickx et al. 2015a).

The scarcity of tooth marks among the examined bones is remarkable. There are no multiple tooth marks as seen in other dinosaur bones (e.g. Erickson and Olson 1996; Jacobsen 1998; Paik et al. 2011). A possible explanation is the presence of soft tissues when the scavenging was occurring, thus protecting the bone surface. Some of the tooth marks are located on articular surfaces, meaning that they could not have been made when the sauropod was alive and are not related to predatory behaviour. The presence of these traces on articular surfaces suggests that the feeding could have contributed to the partial disarticulation of the sauropod (Buffetaut and Suteethorn 1989).

The sauropod remains are located on channel deposits, and the westbound trend and the accumulations of sand on the eastern part of the bones suggest the presence of water currents when the sauropod remains were deposited. The presence of water also influences the disarticulation of the titanosauriform dinosaur along with the theropods. The degree of disarticulation of the bones suggests that the channel was not a high-energy environment.

Another possible explanation for the presence of theropod teeth could be transport along the channel (Torcida Fernández-Baldor et al. 2009). This could be congruent with the presence of quartzite clasts of similar size and density. In addition, Argast et al. (1987) show that fossilized theropod teeth could resist long periods of transport-induced abrasion. However, a few points contradict this interpretation, at least for most of the teeth. The presence of well-preserved enamel textures in some of the teeth is not congruent with transport-induced abrasion. Further, a polished enamel surface does not necessarily mean that the tooth was transported; it could be caused by tooth wear (Hendrickx and Mateus 2014).

The experimental procedure of Argast et al. (1987) provides an explanation for the presence of Tertiary theropod teeth but may not be applicable to the present case because the experiment was performed with fossilized teeth. Fossilized teeth may not actually be homologous to recent, fresh teeth due to the process of mineralization, which interferes with the physical properties of the teeth, hardening them. As mentioned above, the presence of shed teeth with herbivore remains produced by scavenging is not uncommon, and this is a simpler explanation than a casual accumulation around the sauropod carcass.

The presence of tooth marks reinforces the notion of scavenging by theropod dinosaurs. Some of the marks are similar to the outline of theropod teeth both in dimensions and morphology, and could be related to teeth similar to the Tetanurae and Coelurosauria morphotypes, attributed to medium-sized tetanurans.

Theropod teeth are distributed all over El Oterillo II site. There is a major accumulation in the southern part of the site. Most of the dromaeosaurid teeth are located in the northern part close to fragmented bone remains. A preferred orientation has not been recorded.

The scarcity of tooth marks on the bones is intriguing. A possible explanation is their rapid burial when the carcass was deposited, preventing a greater exploitation of the remains and a further disarticulation of the skeleton. The sudden burial of dinosaur remains has been proposed by Gianechini and De Valais (2016) as a possible explanation of the semi-articulation of the remains of *Buitreraptor*.

6 Conclusions

Isolated theropod teeth related to a titanosauriform sauropod carcass have been studied. Six different morphotypes have been distinguished, including baryonychine spinosaurids, basal tetanurans, a singular tooth that could be related to basal coelurosaurian theropods, and two dromaeosaurid morphotypes. This is congruent with the known record of theropods from the Early Cretaceous of the Iberian Peninsula, represented by spinosaurids, carcharodontosaurians, ornithomimosaurians and maniraptorans such as dromaeosaurids and birds, as well as with the European Wealden record, with carcharodontosaurians such as *Neovenator* and tyrannosauroids such as *Eotyrannus*. The possibility of the presence of tyrannosauroids, represented by Coelurosauria indet., raises new questions about the distribution of these groups and points to a greater palaeobiodiversity of theropods than previously thought.

The relationship between the isolated theropod teeth and a sauropod carcass has been studied. Given the presence of shed teeth and tooth marks, the most probable explanation for the association seems to be the scavenging of the carcass by theropod dinosaurs. An exhaustive work identifying the tooth marks on the sauropod is required in order to understand this relationship more fully. The diversity of theropod tooth morphotypes suggests that a variety of different theropods exploited the sauropod remains.

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References

Abler, W. L. (1997). Tooth serrations in carnivorous dinosaurs. In P. J. Currie & K. Padian (Eds.), *Encyclopedia of dinosaurs* (Vol. 8). San Diego: Academic Press.

Allain, R. (2005). The enigmatic theropod dinosaur *Erectopus superbus* (Sauvage, 1882) from the Lower Albian of Louppy-le-Chateau (Meuse, France). In K. Carpenter (Ed.), *The carnivorous dinosaurs* (pp. 72–86). Bloomington, Indiana: Indiana University Press.

Allain, R., & Taquet, P. (2000). A new genus of Dromaeosauridae (Dinosauria, Theropoda) from the Upper Cretaceous of France. *Journal of Vertebrate Paleontology, 20*(2), 404–407.

Alonso, A., & Canudo, J. I. (2016). On the spinosaurid theropod teeth from the early Barremian (Early Cretaceous) Blesa Formation (Spain). *Historical Biology, 28*(6), 823–834. doi:10.1080/08912963.2015.1036751.

Argast, S., Farlow, J. O., Gabet, R. M., & Brinkman, D. L. (1987). Transport-induced abrasion of fossil reptilian teeth: implications for the existence of Tertiary dinosaurs in the Hell Creek Formation, Montana. *Geology, 15*(927), 930.

Azuma, Y., & Currie, P. J. (2000). A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences, 37,* 1735–1753.

Baszio, S. (1997). Systematic palaeontology of isolated dinosaur teeth from the latest Cretaceous of south Alberta, Canada. *Courier Forschungsinstitut Senckenberg, 196,* 33–77.

Bell, P. R., Cau, A., Fanti, F., & Smith, E. T. (2016). A large-clawed theropod (Dinosauria: Tetanurae) from the Lower Cretaceous of Australia and the Gondwanan origin of megaraptorid theropods. *Gondwana Research, 36,* 473–487.

Bell, P. R., & Currie, P. J. (2010). A tyrannosaur jaw bitten by a confamilial: scavenging or fatal agonism? *Lethaia, 43*(2), 278–281.

Britt, B., Scheetz, R. D., & Dangerfield, A. (2008). A Suite of Dermestid Beetle Traces on Dinosaur Bone from the Upper Jurassic Morrison Formation, Wyoming. *USA. Ichnos, 15*(2), 59–71.

Brusatte, S. L., Benson, R. B., Carr, T. D., Williamson, T. E., & Sereno, P. C. (2007). The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology, 27*(4), 1052–1056.

Brusatte, S. L., Carr, T. D., & Norell, M. A. (2012). The osteology of *Alioramus,* a gracile and long-snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. *Bulletin of the American Museum of Natural History, 366,* 1–197.

Brusatte, S. L., Norell, M. A., Carr, T. D., Erickson, G. M., Hutchinson, J. R., Balanoff, A. M., et al. (2010). Tyrannosaur paleobiology: new research on ancient exemplar organisms. *Science, 329*(5998), 1481–1485.

Brusatte, S. L., & Sereno, P. C. (2007). A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revisión of the genus. *Journal of Vertebrate Paleontology, 27*(4), 902–916.

Buffetaut, E. (2011). An early spinosaurid dinosaur from the Late Jurassic of Tendaguru (Tanzania) and the evolution of the spinosaurid dentition. *Oryctos, 10,* 1–8.

Buffetaut, E., & Suteethorn, V. (1989). A sauropod skeleton associated with theropod teeth in the Upper Jurassic of Thailand: remarks on the thaphonomic and palaeoecological significance of such associations. *Palaeogeography, Palaeoclimatology, Palaeoecolology, 73,* 77–83.

Canale, J. I., Carballido, J. L., Otero, A., Canudo, J. I., & Garrido, A. (2014). *Carcharodontosaurid teeth associated with titanosaur carcasses from the Early Cretaceous (Albian) of the Chubut Group, Chubut Province, Patagonia, Argentina* (p. 23). Neuquén: XXVIII Jornadas Argentinas de Paleontología de Vertebrados.

Candeiro, C. R. A., & Tanke, D. H. (2008). A pathological Late Cretaceous carcharodontosaurid tooth from Minas Gerais, Brazil. *Bulletin of Geosciences, 83*(3), 351–354.

Canudo, J. I., Cruzado-Caballero, P., & Moreno-Azanza, M. (2005). Possible theropod predation evidence in hadrosaurid dinosaurs from the Upper Maastrichtian (Upper Cretaceous) of Arén (Huesca, Spain). *Kaupia, 14,* 9–13.

Canudo, J. I., Filippi, L., Salgado, L., Garrido, A., Cerda, I., García, R., & Otero, A. (2009). Dientes de terópodos asociados con una carcasa de saurópodo en el Cretácico Superior (Formación Plottier) de Rincón de los Sauces (Patagonia, Argentina). In Colectivo Arqueológico y Paleontológico de Salas (Ed.), Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno (pp. 321–330). Salas de los Infantes, Burgos

Canudo, J. I., Gasulla, J. M., Gómez-Fernández, D., Ortega, F., Sanz, J. L., & Yagüe, P. (2008). Primera evidencia de dientes aislados atribuidos a Spinosauridae (Theropoda) en el Aptiano inferior (Cretácico Inferior) de Europa: formación Arcillas de Morella (España). *Ameghiniana, 45*(3), 649–652.

Canudo, J. I., Ruiz-Omeñaca, J. I., Aurell, M., Barco, J. L., & Cuenca-Bescós, G. (2006). A megatheropod tooth from the late Tithonian-lower Berriasian (Jurassic-Cretaceous transition) of Galve (Aragon, NE Spain). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 239*(1), 77–99.

Carpenter, K. (1998). Evidence of predatory behaviour by carnivorous dinosaurs. In Pérez-Moreno, B.P., Holtz., T. Jr., Sanz, J.L., & Moratalla, J.J. (Eds.), *Aspects of Theropod Paleobiology. Gaia: Revista de Geociencias* (pp. 135–144), vol 15. Lisbon: Museu Nacional de Historia Natural.

Carrano, M. T., Benson, R. B. J., & Sampson, S. D. (2012). The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology, 10*(2), 211–300.

Charig, A. J., & Milner, A. C. (1997). *Baryonyx walkeri,* a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum of London, 53,* 11–70.

Chure, D. J., Fiorillo, A. R., & Jacobsen, A. (1998). Prey bone utilization by predatory dinosaurs in the Late Jurassic of North America, with comments on prey bone use by dinosaurs throughout the Mesozoic. *Gaia, 15,* 227–232.

Cillari, A. (2010). Teeth of Theropoda (Dinosauria, Saurischia): morphology, function and classification. Ph.D. Dissertation. Sapienza Universitá di Roma, p. 193.

Clemente, P., & Pérez Arlucea, M. (1993). Depositional architecture of the Cuerda del Pozo Formation, Lower Cretaceous of the extensional Cameros Basin, north-central Spain. *Journal of Sedimentary Petrology, 63*(3), 437–452.

Codrea, V., Smith, T., Dica, P., Folie, A., García, G., Godefroit, P., et al. (2002). Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the hateg Basin (Romania). *Comptes Rendus Palevol, 1,* 173–180.

Coria, R. A., & Currie, P. J. (2006). A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas, 28*(1), 71–118.

Coria, R. A., & Currie, P. J. (2016). A new megaraptoran dinosaur (Dinosauria, Theropoda, Megaraptoridae) from the Late Cretaceous of Patagonia. *PLoS One, 11*(7), e0157973. doi:10.1371/journal.pone.0157973.

Coria, R. A., & Salgado, L. (1995). A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature, 377,* 224–226.

Cruzado-Caballero, P. (2012). Restos directos de dinosaurios hadrosáuridos (Ornithopoda, Hadrosauridae) del Maastrichtiense superior (Cretácico Superior) de Arén (Huesca). Ph.D. Dissertation. Universidad de Zaragoza, p. 411.

Csiki-Sava, Z., Brusatte, S. L., & Vasile, S. (2016). "*Megalosaurus* cf. *superbus*" from southeastern Romania: the oldest known Cretaceous carcharodontotosaurid (Dinosauria: Theropoda) and its implications for earliest Cretaceous Europe-Gondwana connections. *Cretaceous Research, 60,* 221–238.

Currie, P. J., & Azuma, Y. (2006). New specimens, including a growth series, of *Fukuiraptor* (Dinosauria, Theropoda) from the Lower Cretaceous Kitadani Quarry of Japan. *Journal of the Paleontological Society of Korea, 22*(1), 173–193.

Currie, P. J., & Jacobsen, A. R. (1995). An azhdarchid pterosaur eaten by a velociraptorine theropod. *Canadian Journal of Earth Sciences, 32,* 922–925.

Currie, P. J., Rigby, J. K., Jr., & Sloan, R. E. (1990). Theropod teeth from the Judith River Formation of southern Alberta, Canada. In K. Carpenter & P. J. Currie (Eds.), *Dinosaur Systematics: perspectives and approaches* (Vol. 8, pp. 107–125). New York: Cambridge University Press.

Currie, P. J., & Varrichio, D. J. (2004). A new dromaeosaurid from the Horseshoe Canyon Formation (upper Cretaceous) of Alberta, Canada. In Currie, P. J., Koppelhus, E. B., Shugar, M. A. and Wright, J.L. (Eds.). *Feathered dragons: studies on the transition from dinosaurs to birds* (pp. 112–132). Bloomington, Indiana: University Press.

D'Amore, D. C. (2009). A functional explanation for denticulation in theropod dinosaur teeth. *The Anatomical Record, 292,* 1297–1314.

De Valais, S., Apesteguía, S., & Garrido, A. C. (2012). Cretaceous Small scavengers: feeding traces in tetrapod bones from Patagonia, Argentina. *PLoS One, 7*(1), e29841. doi:10.1371/journal.pone.0029841.

del Corro, G. (1966). Un nuevo dinosaurio carnívoro del Chubut (Argentina). Comunicaciones del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia*". Paleontología, 1,* 1–4.

DePalma, R. A., Burnham, D. A., Martin, L. D., Rothschild, B. M., & Larson, P. L. (2013). Physical evidence of predatory behaviour in *Tyrannosaurus rex*. *Proceedings of the National Academy of Sciences, 110*(31), 12560–12564. doi:10.1073/pnas.1216534110.

Erickson, G. M. (1995). Split carinae on tyrannosaurid teeth and implications of their development. *Journal of Vertebrate Paleontology, 15*(2), 268–274.

Erickson, G. M., & Olson, K. H. (1996). Bite marks attributable to *Tyrannosaurus rex:* preliminary description and implications. *Journal of Vertebrate Paleontology, 16*(1), 175–178. doi:10.1080/02724634.1996.10011297.

Fanti, F., Cau, A., Martinelli, A., & Contessi, M. (2014). Integrating palaeoecology and morphology in theropod diversity estimation: A case from the Aptian-Albian of Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology, 410*,39–57

Fanti, F., & Therrien, F. (2007). Theropod tooth assemblages from the Late Cretaceous maevarano Formation and the possible presence of dromaeosaurids in Madagascar. *Acta Palaeontologica Polonica, 52*(1), 155–166.

Farlow, J. O., Brinkman, D. L., Abler, W. L. , Currie, P. J. (1991). Size, shape, and serration density of theropod dinosaur lateral teeth. *Modern Geology 16*, 161–198.

Figuereido, S., Rosina, P., & Figuti, F. (2015). Dinosaurs and other vertebrates from the Papo-Seco Formation (Lower Cretaceous) of southern Portugal. *Journal of Iberian Geology, 41*(3), 301–314.

Fiorillo, A. R. (1991). Prey bone utilization by predatory dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology, 88,* 157–166.

Fiorillo, A. R., & Currie, P. J. (1994). Theropod teeth from the Judith River formation (Upper Cretaceous) of south-central Montana. *Journal of Vertebrate Paleontology, 14*(1), 74–80.

Gasca, J. M., Canudo, J. I., & Moreno-Azanza, M. (2014). A large-bodied theropod (Tetanurae: Carcharodontosauria) from the Mirambel Formation (Barremian) of Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 273*(1), 13–23.

Gasca, J. M., Moreno-Azanza, M., & Canudo, J. I. (2008). Dientes de dinosaurios terópodos espinosáuridos de la Formación El Castellar (Cretácico Inferior, Teruel). *Palaeontologica Nova SEPAZ, 8,* 233–234.

Gauthier, J. A. (1986). Saurischian monophyly and the origin of birds. In K. Padian (Ed.), *The origin of birds and the evolution of flight.*

Memoirs of the California Academy of Sciences (Vol. 8, pp. 1–55). San Francisco: California Academy of Sciences.

Gerke, O., & Wings, O. (2016). Multivariate and cladistic analyses of isolated teeth reveal sympatry of theropod dinosaurs in the late jurassic of northern germany. *PLoS One, 11*(7), e0158334. doi:10.1371/journal.pone.0158334.

Gianechini, F. A., & De Valais, S. (2016). Bioerosion trace fossils on bones of the Cretaceous South American theropod *Buitreraptro gonzalezorum* Makovicky, Apesteguía and Agnolín, 2005 (Deinonychosauria). *Historical Biology, 28*(4), 533–549.

Gianechini, F. A., Makovicky, P. J., & Apesteguía, S. (2011). The teeth of the unenlagiine theropod *Buitreraptor* from the Cretaceous of Patagonia, Argentina, and the unusual dentition of the Gondwanan dromaeosaurids. *Acta Palaeontologica Polonica, 56*(2), 279–290.

Goloboff, P. A., Farris, J. S., & Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics, 24*(5), 774–786. doi:10.1111/j.1096-0031.2008.00209.x.

Hammer, Ø., & Harper, D. A. T. (2006). *Paleontological data analysis* (p. 351). Oxford: Blackwell.

Hammer, O., Harper, D. A. T., & Ryan, P. D. (2001). PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica, 4*(1), 1–9.

Hendrickx, C. (2015). Evolution of Teeth and Quadrate in Non-avian Theropoda (Dinosauria: Saurischia), with the Description of Torvosaurus Remains from Portugal. Ph.D. Dissertation. Universidade Nova de Lisboa, p. 646.

Hendrickx, C., & Mateus, O. (2014). Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. *Zootaxa, 3759*(1), 1–74.

Hendrickx, C., Mateus, O., & Araújo, R. (2015a). A proposed terminology of theropod teeth (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology*. doi:10.1080/02724634.2015.982797.

Hendrickx, C., Mateus, O., & Araújo, R. (2015b). The dentition of megalosaurid theropods. *Acta Palaeontologica Polonica, 60*(3), 627–642.

Hendrickx, C., Hartmann, S. A., & Mateus, O. (2015c). An overview of non-avian theropod discoveries and classification. *PalArch's Journal of Vertebrate Palaeontology, 12*(1), 1–73.

Hocknull, S. A., White, M. A., Tischler, T. R., Cook, A. G., Calleja, N. D., Sloan, T., et al. (2009). New mid-Cretaceous (Latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS One, 4*(7), e6190.

Hunt, A. P., Meyer, C. A., Lockley, M. G., & Lucas, S. G. (1994). Archaeology, toothmarks and sauropod dinosaur taphonomy. *Gaia, 10,* 225–231.

Hutt, S., Martill, D. M., & Barker, M. J. (1996). The first European allosauroid dinosaur (Lower Cretaceous, Wealden Group, England. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 10,* 635–644.

Hutt, S., Naish, D., Martill, D. M., Barker, M. J., & Newbery, P. (2001). A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 1996,* 635–644.

Infante, P., Canudo, J. I., & Ruiz-Omeñaca, J. I. (2005). First evidence of theropod dinosaurs from the Mirambel Formation (Lower Barremian, Lower Cretaceous) from Castellote, Teruel. *Geogaceta, 38,* 31–34.

Jacobsen, A. R. (1998). Feeding behaviour of carnivorous dinosaurs as determined by tooth marks on dinosaur bones. *Historical Biology, 13,* 17–26.

Kellner, A. W. A., & Campos, D. A. (1996). First early cretaceous theropod dinosaur from Brazil with comments on Spinosauridae. *Neues Jahrbuch für Geologie und Paläontologie —Abhandlungen, 199*(2), 151.

Lacasa-Ruiz, A. (1989). Nuevo género de ave fósil del yacimiento neocomiense del Montsec (provincia de Lérida, España). *Estudios Geológicos, 45,* 417–425.

Larson, D. W., & Currie, P. J. (2013). Multivariate analyses of small theropod dinosaur teeth and implications for paleoecological turnover through time. *PLoS One, 8*(1), e54329.

Longrich, N. (2008). A new, large ornithomimid from the Cretaceous Dinosaur Park Formation of Alberta, Canada: implications for the study of dissociated dinosaur remains. *Palaeontology, 51*(4), 983–997.

Malafaia, E., Mocho, P., Escaso, F., & Ortega, F. (2017). New data on the anatomy of Torvosaurus and other remains of megalosauroid (Dinosauria, Theropoda) from the Upper Jurassic of Portugal. *Journal of Iberian Geology, 43*(1), 33–59. doi:10.1007/s41513-017-0003-9.

Marsh, O. C. (1881). Principal characters of American Jurassic dinosaurs, part V. *American Journal of Sciences and Arts, 3*(21), 417–423.

Martín-Closas, C., & Alonso-Millán, A. (1998). Estratigrafía y bioestratigrafía (Charophyta) del Cretácico Inferior en el sector occidental de la Cuenca de Cameros (Cordillera Ibérica). *Revista de la Sociedad Geológica de España, 11,* 253–269.

Martínez, R. N., Sereno, P. C., Alcober, O. A., Colombi, C. E., Renne, P. R., Montañez, I. P., et al. (2011). A Basal dinosaur from the dawn of the dinosaur era in Southwestern Pangaea. *Science, 331*(6014), 206–210.

Mas, R., García, A., Salas, R., Meléndez, A., Alonso, A., Aurell, M., et al. (2004). Segunda fase de rifting: Jurásico Superior-Cretácico Inferior. In W. Gibbons & M. T. Moreno (Eds.), *The Geology of Spain* (pp. 503–510). London: Geological Society.

Mateus, O., Araújo, R., Natário, C., & Castanhinha, R. (2011). A new specimen of the theropod dinosaur *Baryonyx* from the early Cretaceous of Portugal and taxonomic validity of *Suchosaurus*. *Zootaxa, 2827,* 54–68.

Matthew, W. D., & Brown, B. (1922). The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. *Bulletin of the American Museum of Natural History, 46*(6), 285–367.

Maxwell, W. D., & Ostrom, J. H. (1995). Taphonomy and paleobiological implications of Tenontosaurus-Deinonychus associations. *Journal of Vertebrate Paleontology, 15,* 707–712.

Milner, A. C. (2002). Theropod dinosaurs of the Purbeck limestone group, Southern England. *Special Papers in Palaeontology, 68,* 191–202.

Molnar, R. E., Obata, I., Tanimoto, M., & Matsukawa, M. (2009). A tooth of *Fukuiraptor* aff. *F. kitaidaniensis* from the Lower Cretaceous Sebayashi Formation, Sanchu Cretaceous, Japan. *Bulletin of Tokyo Gakugei University, Division of Natural Sciences, 61,* 105–117.

Norell, M. A., Clark, J. M., Turner, A. H., Makovicky, P. J., Barsbold, R., & Rowe, T. (2006). A new dromaeosaurdi theropod from Ukhaa Tolgod (Ömnögov, Mongolia). *American Museum Novitates, 3545,* 1–51.

Novas, F. E., Agnolín, F. L., Ezcurra, M. D., Porfiri, J., & Canale, J. I. (2013). Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia. *Cretaceous Research, 45,* 174–215.

Ortega, F., Escaso, F., & Sanz, J. L. (2010). A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. *Nature, 467*(7312), 203–206.

Ösi, A., Apesteguía, S., & Kowalewski, M. (2010). Non-avian theropod dinosaurs from the early Late Cretaceous of central Europe. *Cretaceous Research, 31*(3), 304–320.

Ostrom, J. H. (1969). Osteology of *Deinonychus antirrhopus,* an unusual theropod from the Lower Cretaceous of Montana. *Peabody Museum of Natural History Bulletin, 30,* 1–165.

Owen, R. (1842). Report on British fossil reptiles, part II. In Murray J. (Ed.), *Report on the eleventh meeting of the British association for the advancement of science*. (pp. 60–204), London.

Paik, I. S., Kim, H. J., Lim, J. D., Huh, M., & Lee, H. I. (2011). Diverse tooth marks on an adult sauropod bone from the Early Cretaceous, Korea: Implications in feeding behaviour of theropod dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology, 309,* 342–346.

Pereda-Suberbiola, X., Ruiz-Omeñaca, J. I., Canudo, J. I., Torcida, Fernández-Baldor F., & Sanz, J. L. (2012). Dinosaur Faunas from the Early Cretaceous (Valanginian-Albian) of Spain. In P. Godefroit (Ed.), *Bernissart dinosaurs and early Cretaceous terrestrial ecosystem* (pp. 379–407). Bloomington: Indiana University Press.

Pérez-Moreno, B. P., Sanz, J. L., Buscalioni, A. D., Moratalla, J. J., Ortega, F., & Rasskin-Gutman, D. (1994). A unique multi-toothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature, 370,* 363–367.

Platt, N.H. (1986). Sedimentology and tectonics of the western Cameros basin. Province of Burgos, Northern Spain. PhD Thesis Thesis, University of Oxford, p. 125.

Platt, N. H. (1990). Basin evolution and fault reactivation in the western Cameros Basin, Northern Spain. *Journal of the Geological Society, 147*(1), 165–175.

Pol, D., & Rauhut, O. W. M. (2012). A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. *Proceedings of the Royal Society B, 279,* 3170–3175.

Porfiri, J. D., Novas, F. E., Calvo, J. O., Agnolín, F. L., Ezcurra, M. D., & Cerda, I. A. (2014). Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. *Cretaceous Research, 51,* 35–55.

Pouech, J., Mazin, J.M., & Billon-Bruyat, J.P. (2006). Microvertebrate biodiversity from Cherves-de-Cognac (Lower Cretaceous, Berriasian: Charente, France). In :9th International symposium, mesozoic terrestrial ecosystems and Biota, Manchester, Abstracts and Proceedings, pp 96-100.

Rauhut, O. W. M. (2002). Dinosaur teeth from the Barremian of Uña, Province of Cuenca. *Spain. Cretaceous Research, 23*(2), 255–263.

Rauhut, O. W. M. (2004). Provenance and anatomy of *Genyodectes serus,* a large-toothed ceratosaur (Dinosauria: Theropoda) from Patagonia. *Journal of Vertebrate Paleontology, 24*(4), 894–902.

Rauhut, O. W. M., Milner, A. C., & Moore-Fay, S. (2010). Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society, 158,* 155–195.

Rauhut, O. W. M., & Werner, C. (1995). First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). *Paläontologische Zeitshrift, 69,* 475–489.

Rogers, R. R., Krause, D. W., & Rogers, K. C. (2003). Cannibalism in the Madagascan dinosaur *Majungatholus atopus*. *Nature, 422,* 515–518.

Ruiz-Omeñaca, J. I., Canudo, J. I., & Cuenca-Bescós, G. (1998). Primera cita de dinosaurios barionícidos (Saurischia: Theropoda) en el Barremiense superior (Cretácico Inferior) de Vallipón (Castellote, Teruel). *Mas de las Matas, 17,* 201–223.

Ruiz-Omeñaca, J. I., Cruzado-Caballero, P., Infante, P., & Moreno-Azanza, M. (2005). Baryonychine teeth (Theropoda: Spinosauridade) from the Lower Cretaceous of La Cantalera (Josa, NE Spain). *Kaupia, 14,* 59–63.

Salas, R., Guimerá, J., Mas, R., Martín-Closas, C., Meléndez, A., & Alonso, A. (2001). Evolution of the Mesozoic Central Iberian Rift system and its Cainozoic inversion (Iberian chain). In P. A. Ziegler, W. Cavazza, A. H. F. Robertson, & S. Crasquin-Soleau (Eds.), *Peri-Tethys Memoir: 6, Peri-Thetyan Rift/. Wrench basins and passive margins* (pp. 145–185). Paris: Mémoires du Muséum national d'histoire naturelle. Muséum national d'histoire naturelle.

Samman, T., Powell, G. L., Currie, P. J., & Hills, L. V. (2005). Morphometry of the teeth of western North American tyrannosaurids and its applicability to quantitative classification. *Acta Palaeontologica Polonica, 50,* 757–776.

Sánchez-Hernández, B. R., & Benton, M. (2014). Filling the ceratosaur gap: a new ceratosaurian theropod from the Early Cretaceous of Spain. *Acta Palaeontologica Polonica, 59*(3), 581–600.

Sankey, J. T. (2008). Diversity of latest Cretaceous (Late Maastrichtian) small theropods and birds: teeth from the Lance and Hell Creek formations, USA. In J. T. Sankey & S. Baszio (Eds.), *Vertebrate microfossil assemblages: their role in paleoecology and paleobiogeography* (pp. 117–134). Bloomington: Indiana University Press.

Sankey, J. T., Brinkman, D. B., Guenther, M., & Currie, P. J. (2002). Small theropod and bird teeth from the Late Cretaceous (Late Campanian) Judith River Group, Alberta. *Journal of Paleontology, 76,* 751–763.

Sankey, J. T., Standhart, B. R., & Schiebout, J. A. (2005). Theropod teeth from the Upper Cretaceous (Campanian-Maastrichtian), Big Bend National Park, Texas. In K. Carpenter (Ed.), *The carnivorous dinosaurs* (pp. 127–152). Bloomington: Indiana University Press.

Sanz, J. L., Bonaparte, J. F., & Lacasa, A. (1988). Unusual early Cretaceous birds from Spain. *Nature, 331,* 433–435.

Sanz, J. L., & Buscalioni, A. D. (1992). A new bird from the Early Cretaceous of Las Hoyas, Spain, and the early radiation of birds. *Palaeontology, 35*(4), 829–845.

Sanz, J. L., Chiappe, L. M., Pérez-Moreno, B. P., Buscalioni, A. D., Moratalla, J. J., Ortega, F., et al. (1996). An early Cretaceous bird from Spain and its implications for the evolution of avian flight. *Nature, 382*(6590), 442–445.

Schudack, U., & Schudack, M. (2009). Ostracod biostratigraphy in the Lower Cretaceous of the Iberian chain (eastern Spain). *Journal of Iberian Geology, 35*(2), 141–168.

Seeley, H. G. (1887). On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London, 43*(258–265), 165–171. doi:10.1098/rspl.1887.0117.

Senter, P., Kirkland, J. I., Bird, J., & Bartlett, J. A. (2011). A new troodontid theropod dinosaur from the lower Cretaceous of Utah. *PLoS One, 5*(12), e14329.

Sereno, P. C. (1997). The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Sciences, 25*(1), 435–489.

Sereno, P. C. (2000). *Iberomesornis romerali* (Ornithothoraces, Aves) re-evaluated as an enantiornithine bird. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 215,* 365–395.

Sereno, P. C., Beck, A. L., Dutheil, D. B., Larsson, H. C. E., Lyon, G. H., Marcot, J. D., et al. (1998). A long-snouted predatory dinosaur from Africa and the evolution of Spinosaurids. *Science, 282*(5392), 1298–1302.

Sereno, P. C., & Brusatte, S. L. (2008). Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz formation of Niger. *Acta Palaeontologica Polonica, 53,* 15–46.

Serrano-Martínez, A., Vidal, D., Sciscio, L., & Ortega, F. (2016). Isolated theropod teeth from the Middle Jurassic of Niger and the early dental evolution of Spìnosauridae. *Acta Palaeontologica Polonica, 61*(2), 403–415.

Smith, J. B. (2005). Heterodonty in *Tyrannosaurus rex*: implications for the taxonomic and systematic utility of theropod dentitions. *Journal of Vertebrate Paleontology, 25*(4), 865–887.

Smith, J. B. (2007). Dental morphology and variation in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology, 27*(2), 103–126.

Smith, J. B., & Dalla Vecchia, F. M. (2006). An abelisaurid (Dinosauria: Theropoda) tooth from the Lower Cretaceous Chicla formation of Libya. *Journal of African Earth Sciences, 46,* 240–244.

Smith, J. B., & Dodson, P. (2003). A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology, 23*(1), 1–12.

Smith, J. B., & Lamanna, M. C. (2006). An abelisaurid from the Late Cretaceous of Egypt: implications for theropod biogeography. *Naturwissenschaften, 93,* 242–245.

Smith, J. B., Vann, D. R., & Dodson, P. (2005). Dental morphology and variation in theropod dinosarurs: implications for the taxonomic identification of isolated teeth. *The Anatomical Record, 285A,* 699–736.

Stromer, E. (1915). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharîje-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathemtatisch-physikalische Klasse, 28*(3), 1–32.

Sues, H. D., Frey, E., Martill, D. M., & Scott, D. M. (2002). *Irritator challengeri,* a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology, 22*(3), 535–547. doi:10.1671/0272-4634(2002)022[0535:ICASDT]2.0.CO;2.

Sweetman, S. C. (2004). The first record of velociraptorine dinosaurs (Saurischia, Theropoda) from the Wealden (Early Cretaceous, Barremian) of southern England. *Cretaceous Research, 25*(3), 353–364.

Torcida Fernández-Baldor, F., Izquierdo Montero, L. A., Huerta-hurtado, P., Montero Huerta, D., & Pérez Martínez, G. (2003). Dientes de dinosaurios (Theropoda, Sauropoda), en el Cretácico Inferior de Burgos (España). In F. Pérez-Lorente (Ed.), *Dinosaurios y otros reptiles mesozoicos en España* (pp. 335–346). Logroño: Universidad de la Rioja.

Torcida Fernández-Baldor, F. (2006). Restos directos de dinosaurios en Burgos (Sistema Ibérico): un balance provisional. *Actas de las III Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*. In Colectivo Arqueológico y Paleontológico de Salas (Ed.) (pp 105-128), Salas de los Infantes: Colectivo Arqueológico y Paleontológico de Salas.

Torcida Fernández-Baldor, F., Canudo, J.I., Huerta, P., Izquierdo Montero, L.A., Montero Huerta, D., Contreras Izquierdo, R., Pérez Martínez, G., & Urién Montero, V. (2009). Primeros datos sobre las vértebras caudales del saurópodo de El Oterillo II (Formación Castrillo de la Reina, Barremiense superior-Aptiense, Cretácico Inferior, Salas de los Infantes, España). In: Colectivo Arqueológico y Paleontológico de Salas, (Ed.), *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno* (pp. 311–318). Salas de los Infantes: Colectivo Arqueológico y Paleontológico de Salas.

Torcida Fernández-Baldor, F., Fuentes, C., Izquierdo, L. A., Montero, D. M., & Urién, V. (1997). Dientes de dinosaurios terópodos (cf. Baryonyx) en el Weald de Burgos (España). *Stvdia Geologica Salmanticensia, 33,* 59–65.

Torices, A. (2007). Los dinosaurios terópodos del Cretácico Superior de la CuencSurpirenaica. *Ph.D Dissertation*. Universidad Complutense de Madrid. pp 409.

Torices, A., Currie, P. J., Canudo, J. I., & Pereda-Suberbiola, X. (2015). Theropod dinosaurs from the Upper Cretaceous of the South Pyrenees Basin of Spain. *Acta Palaeontologica Polonica, 6*(3), 611–626.

Torices, A., Ruiz-Omeñaca, J. I., Canudo, J. I., & López-Martínez, N. (2004). Nuevos datos sobre los dinosaurios terópodos (Saurischia: Theropoda) del Cretácico Superior de los Pirineos Sur Centrales (Huesca, Lleida). *Geo-Temas, 6*(5), 71–74.

von Huene, F. R. (1914). Beiträge zur geschichte der Archosaurier. *Geologie und Paläontologie Abhandlungen, 13*(7), 1–56.

Weishampel, D. A., Csiki, Z., Benton, M. J., Grigorescu, D., & Codrea, V. (2010). Palaeobiogeographic relationships of the Hateg biota-between isolation and innovation. *Palaeobiogeography, Palaeoclimatology, Palaeoecology, 293,* 419–437.

White, M. A., Bell, P. R., Cook, A. G., Poropat, S. F., & Elliott, D. A. (2015). The dentary of *Australovenator wintonensis* (Theropoda, Megaraptoridae); implications for megaraptorid dentition. *PeerJ, 3,* e1512. doi:10.7717/peerj.1512.

Xu, X., Clarck, J. M., Mo, J., Choiniere, J., Forster, C. A., Erickson, G. M., et al. (2009). A Jurassic ceratosaur from China helps clarify avian digital homologies. *Nature, 459,* 940–944.

Zanno, L. E., & Makovicky, P. J. (2013). Neovenatorid theropods are apex predators in the Late Cretaceous of North America. *Nature Communications, 4,* 2827. doi:10.1038/ncomms3827.

Zinke, J. (1998). Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). *Paläontologische Zeitshrift, 72*(1), 179–189.

Morfotipo 1. **Theropoda indet.**

Cladograma de consenso estricto de 40 árboles parsimoniosos al codificar como dentición lateral.

Codificación:

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Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3576	3576	3576	3576	3576	3576	3576	3576	3576	3576
10	3576	3576	3576	3576	3576	3576	3576	3576	3576	3576
20	3576	3576	3576	3576	3576	3576	3576	3576	3576	3576
30	3576	3576	3576	3576	3576	3576	3576	3576	3576	3576
40	3841									

Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
10	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
20	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
30	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
40	0.529									

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
10	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
20	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
30	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
40	0.575									


Strict consensus of 40 trees (0 taxa excluded)
Eoraptor
Herrerasaurus
Eodromaeus
Dilophosaurus
Coelophysis
Piatnitzkysaurus
Erectopus
Berberosaurus
Genyodectes
Ceratosaurus
Masiakasaurus
Noasaurus
Rugops
Majungasaurus
Kryptops
Skorpiovenator
Aucasaurus
Indosuchus
Abelisaurus
Spinosaurus
Irritator Angaturama
Suchomimus
Baryonyx
Eustreptospondylus
Dubreuillosaurus
Duriavenator
Afrovenator
Torvosaurus
Megalosaurus
Sinraptor
Allosaurus
Neovenator
Australovenator
Fukuiraptor
Eocarcharia
Acrocanthosaurus
Carcharodontosaurus
Mapusaurus
Giganotosaurus
Proceratosaurus
Eotyrannus
Raptorex
Tyrannosaurus
Alioramus
Compsognathus
Richardoestesia_gil.
Buitreraptor
Saurornitholestes
Bambiraptor
Morphotype 1
Dromaeosaurus
Velociraptor
Tsaagan
Ornitholestes
Scipionyx
Erlikosaurus
Jianchangosaurus
Shuvuuia
Byronosaurus
Troodon
Zanabazar

Morfotipo 1. Theropoda indet.

Cladograma de consenso estricto de 38 árboles parsimoniosos al codificar como dentición lateral.

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Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3576	3576	3576	3576	3576	3576	3576	3576	3576	3576
10	3576	3576	3576	3576	3576	3576	3576	3576	3576	3576
20	3576	3576	3576	3576	3576	3576	3576	3576	3576	3576
30	3576	3576	3576	3576	3576	3576	3576	3576	4425	

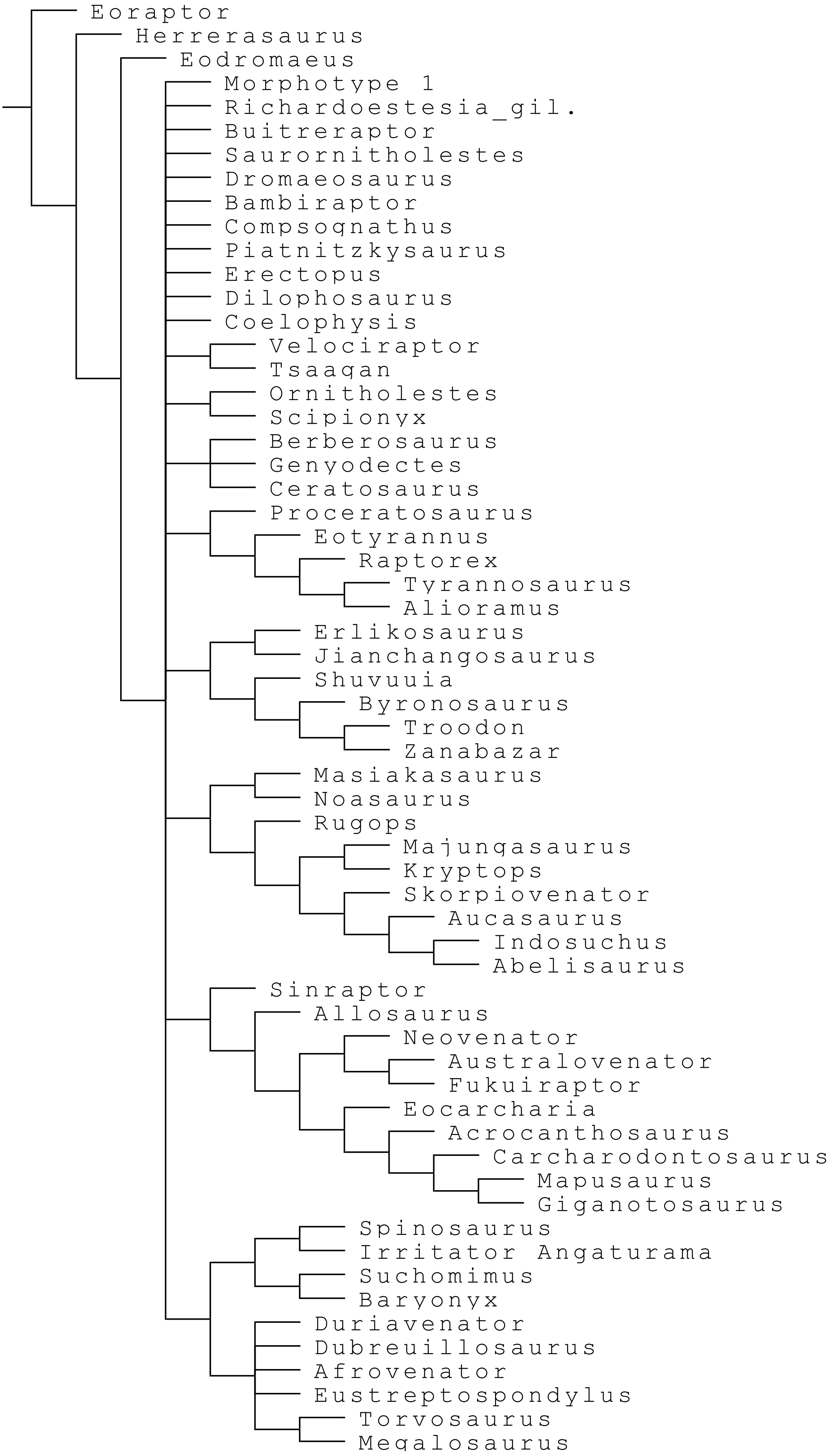
Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
10	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
20	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
30	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.459	

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
10	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
20	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
30	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.438	

Strict consensus of 38 trees (0 taxa excluded)



Posibles posiciones de Morfotipo 1 al ser codificado como dentición mesial, indicado por **a.**

Morfotipo 2. **Baryonychinae indet.**

Cladograma de consenso estricto de 38 árboles parsimoniosos al codificar como dentición lateral.

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Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3580	3580	3580	3580	3580	3580	3580	3580	3580	3580
10	3580	3580	3580	3580	3580	3580	3580	3580	3580	3580
20	3580	3580	3580	3580	3580	3580	3580	3580	3580	3580
30	3580	3580	3580	3580	3580	3580	3580	3580	3769	

Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
10	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
20	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
30	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.539	

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
10	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
20	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
30	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.593	

Strict consensus of 38 trees (0 taxa excluded)

Morfotipo 3. **Tetanurae indet cf. Carcharodontosauria**

Cladograma de consenso estricto de 7 árboles parsimoniosos al codificar como dentición lateral.

Codificación:
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Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7
0	3583	3583	3583	3583	3583	3583	3583	3762

Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7
0	0.567	0.567	0.567	0.567	0.567	0.567	0.567	0.540

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.595

Strict consensus of 7 trees (0 taxa excluded)

Morfotipo 4. **Coelurosauria indet.**

Cladograma de consenso estricto de 26 árboles parsimoniosos al codificar como dentición lateral.

Codificación:
??1[01]100?03?[01]0000000012[23]10000010000-100001?110-1110200010??

Tree lengths

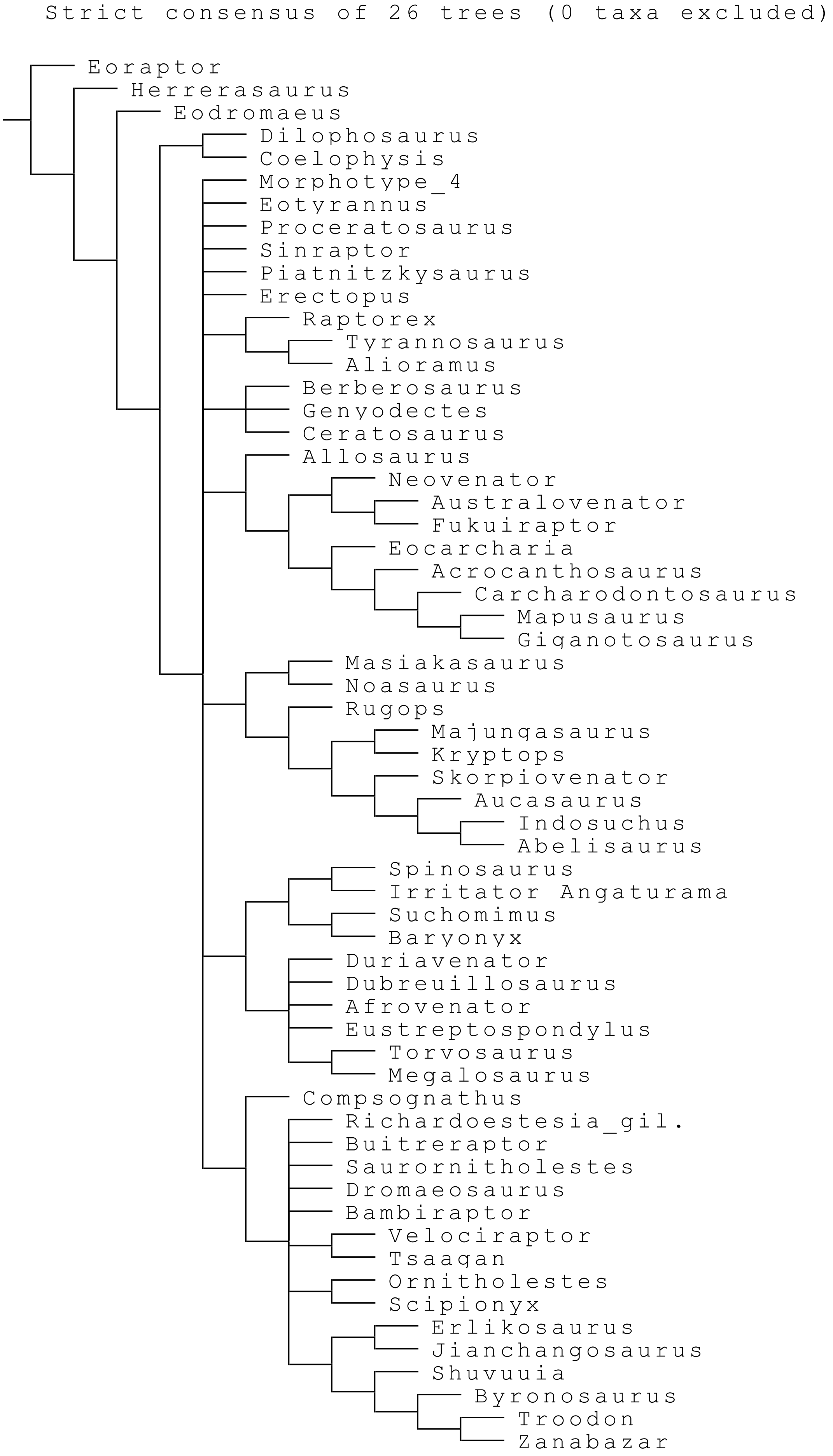
	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3578	3578	3578	3578	3578	3578	3578	3578	3578	3578
10	3578	3578	3578	3578	3578	3578	3578	3578	3578	3578
20	3578	3578	3578	3578	3578	3578	4017			

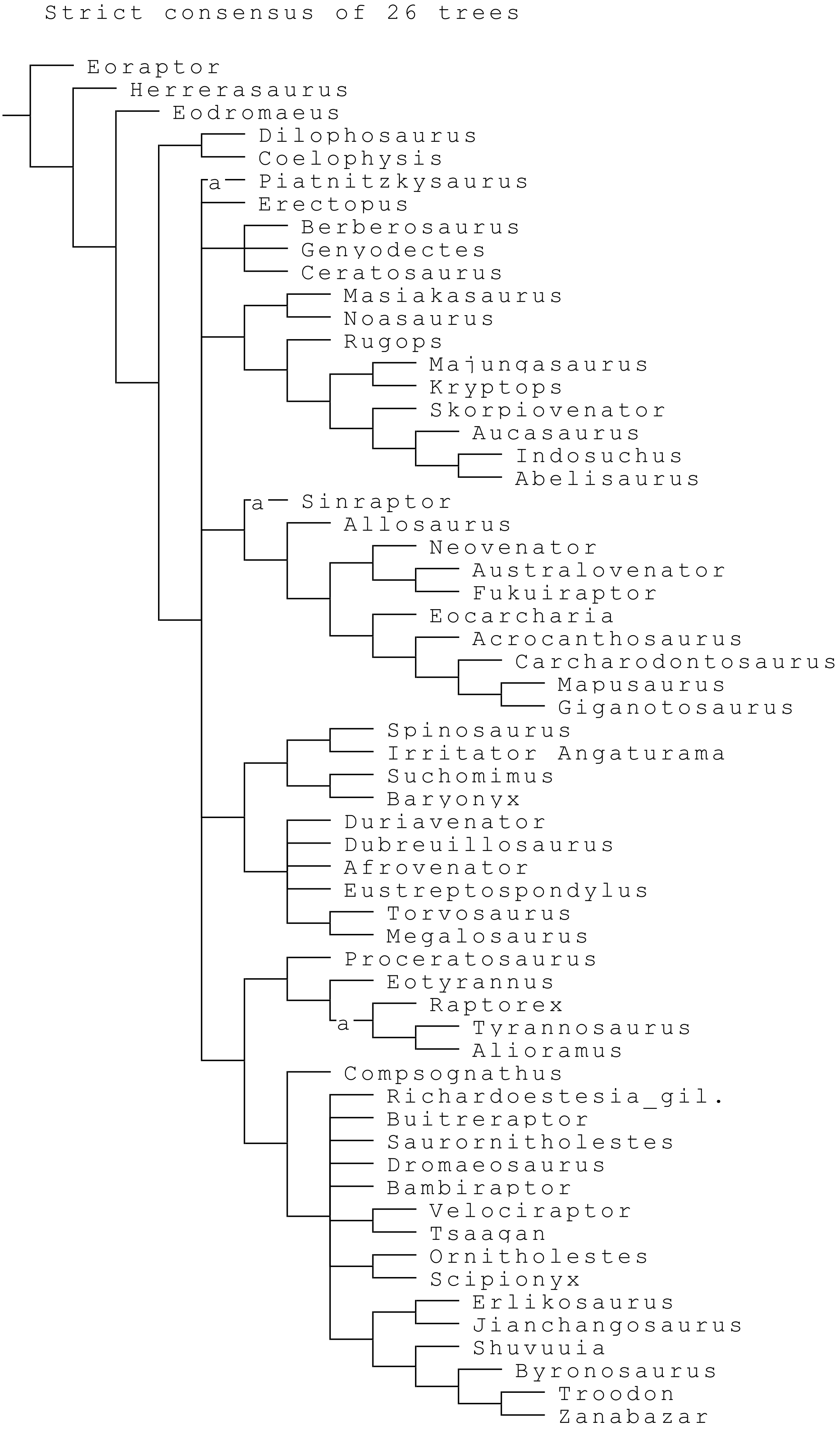
Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
10	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
20	0.568	0.568	0.568	0.568	0.568	0.568	0.506			

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
10	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
20	0.637	0.637	0.637	0.637	0.637	0.637	0.534			


Strict consensus of 26 trees (0 taxa excluded)
Eoraptor
Herrerasaurus
Eodromaeus
Dilophosaurus
Coelophysis
Morphotype_4
Eotyrannus
Proceratosaurus
Sinraptor
Piatnitzkysaurus
Erectopus
Raptorex
Tyrannosaurus
Alioramus
Berberosaurus
Genyodectes
Ceratosaurus
Allosaurus
Neovenator
Australovenator
Fukuiraptor
Eocarcharia
Acrocanthosaurus
Carcharodontosaurus
Mapusaurus
Giganotosaurus
Masiakasaurus
Noasaurus
Rugops
Majungasaurus
Kryptops
Skorpiovenator
Aucasaurus
Indosuchus
Abelisaurus
Spinosaurus
Irritator Angaturama
Suchomimus
Baryonyx
Duriavenator
Dubreuillosaurus
Afrovenator
Eustreptospondylus
Torvosaurus
Megalosaurus
Compsognathus
Richardoestesia_gil.
Buitreraptor
Saurornitholestes
Dromaeosaurus
Bambiraptor
Velociraptor
Tsaagan
Ornitholestes
Scipionyx
Erlikosaurus
Jianchangosaurus
Shuvuuia
Byronosaurus
Troodon
Zanabazar



a) Posibles posiciones de Coelurosauria indet.

Morfotipo 5. **Dromaeosauridae indet . 1.**

Cladograma de consenso estricto de 56 árboles parsimoniosos al codificar como dentición lateral.

Codificación:
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Tree lengths

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3575	3575	3575	3575	3575	3575	3575	3575	3575	3575
10	3575	3575	3575	3575	3575	3575	3575	3575	3575	3575
20	3575	3575	3575	3575	3575	3575	3575	3575	3575	3575
30	3575	3575	3575	3575	3575	3575	3575	3575	3575	3575
40	3575	3575	3575	3575	3575	3575	3575	3575	3575	3575
50	3575	3575	3575	3575	3575	3575	3841			

Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
10	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
20	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
30	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
40	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
50	0.568	0.568	0.568	0.568	0.568	0.568	0.529			

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638
10	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638
20	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638
30	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638
40	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638	0.638
50	0.638	0.638	0.638	0.638	0.638	0.638	0.575			


Strict consensus of 56 trees (0 taxa excluded)
Eoraptor
Herrerasaurus
Eodromaeus
Dilophosaurus
Coelophysis
Piatnitzkysaurus
Erectopus
Berberosaurus
Genyodectes
Ceratosaurus
Masiakasaurus
Noasaurus
Rugops
Majungasaurus
Kryptops
Skorpiovenator
Aucasaurus
Indosuchus
Abelisaurus
Spinosaurus
Irritator Angaturama
Suchomimus
Baryonyx
Eustreptospondylus
Dubreuillosaurus
Duriavenator
Afrovenator
Torvosaurus
Megalosaurus
Sinraptor
Allosaurus
Neovenator
Australovenator
Fukuiraptor
Eocarcharia
Acrocanthosaurus
Carcharodontosaurus
Mapusaurus
Giganotosaurus
Proceratosaurus
Eotyrannus
Raptorex
Tyrannosaurus
Alioramus
Compsognathus
Morphotype 5
Richardoestesia_gil.
Buitreraptor
Saurornitholestes
Dromaeosaurus
Bambiraptor
Velociraptor
Tsaagan
Ornitholestes
Scipionyx
Erlikosaurus
Jianchangosaurus
Shuvuuia
Byronosaurus
Troodon
Zanabazar

Morfotipo 6. Dromaeosauridae indet . 2.

Cladograma de consenso estricto de 57 árboles parsimoniosos al codificar como dentición lateral.

Codificación:
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0000000110000110000-1102010000-100---
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Tree lengths

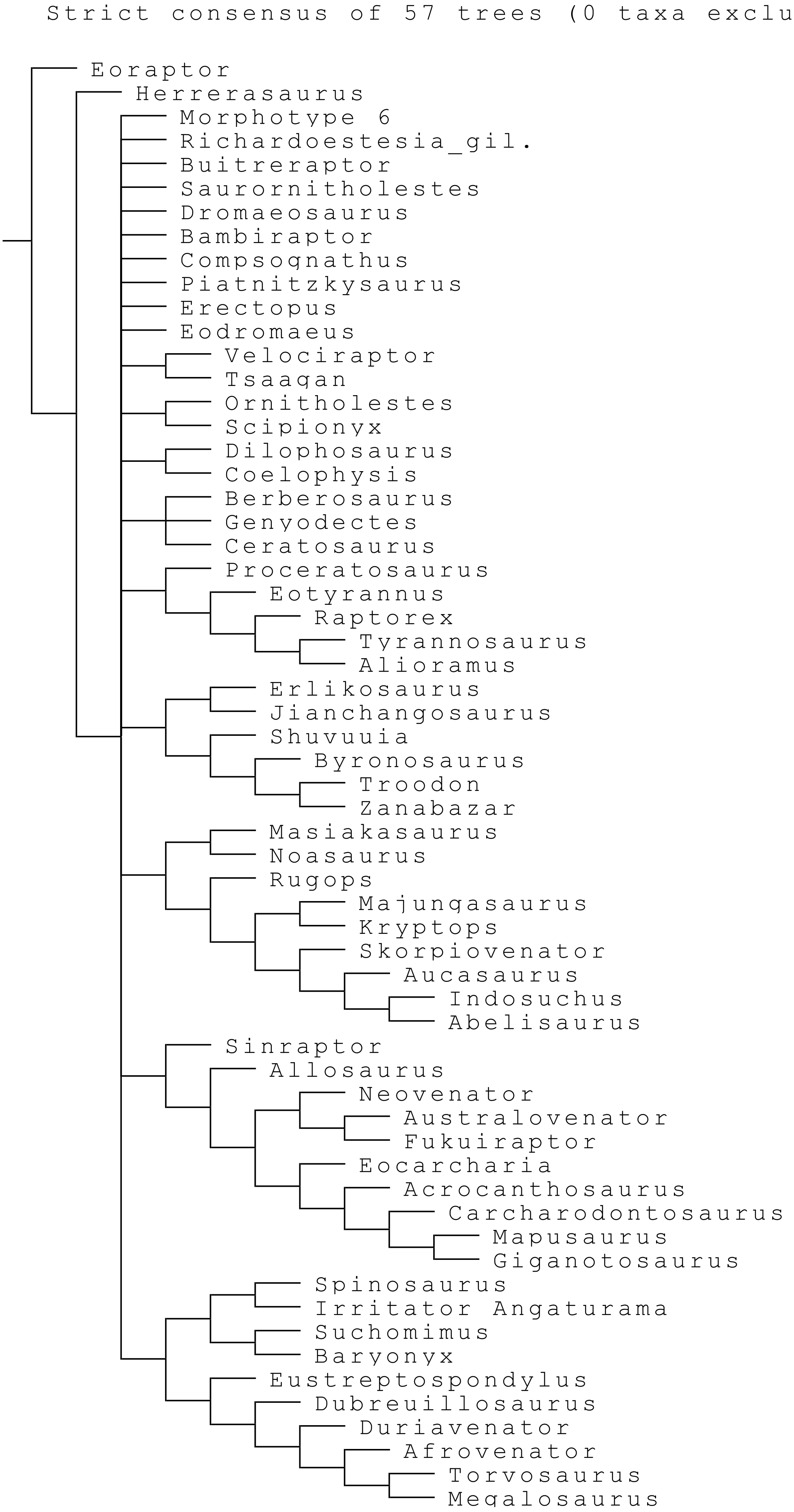
	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	3577	3577	3577	3577	3577	3577	3577	3577	3577	3577
10	3577	3577	3577	3577	3577	3577	3577	3577	3577	3577
20	3577	3577	3577	3577	3577	3577	3577	3577	3577	3577
30	3577	3577	3577	3577	3577	3577	3577	3577	3577	3577
40	3577	3577	3577	3577	3577	3577	3577	3577	3577	3577
50	3577	3577	3577	3577	3577	3577	3577	4329		

Consistency index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
10	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
20	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
30	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
40	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.568
50	0.568	0.568	0.568	0.568	0.568	0.568	0.568	0.469		

Retention index

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
10	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
20	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
30	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
40	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.637
50	0.637	0.637	0.637	0.637	0.637	0.637	0.637	0.461		


Strict consensus of 57 trees (0 taxa excluded)
Eoraptor
Herrerasaurus
Morphotype 6
Richardoestesia_gil.
Buitreraptor
Saurornitholestes
Dromaeosaurus
Bambiraptor
Compsognathus
Piatnitzkysaurus
Erectopus
Eodromaeus
Velociraptor
Tsaagan
Ornitholestes
Scipionyx
Dilophosaurus
Coelophysis
Berberosaurus
Genyodectes
Ceratosaurus
Proceratosaurus
Eotyrannus
Raptorex
Tyrannosaurus
Alioramus
Erlikosaurus
Jianchangosaurus
Shuvuuia
Byronosaurus
Troodon
Zanabazar
Masiakasaurus
Noasaurus
Rugops
Majungasaurus
Kryptops
Skorpiovenator
Aucasaurus
Indosuchus
Abelisaurus
Sinraptor
Allosaurus
Neovenator
Australovenator
Fukuiraptor
Eocarcharia
Acrocanthosaurus
Carcharodontosaurus
Mapusaurus
Giganotosaurus
Spinosaurus
Irritator Angaturama
Suchomimus
Baryonyx
Eustreptospondylus
Dubreuillosaurus
Duriavenator
Afrovenator
Torvosaurus
Megalosaurus

a) Posibles posiciones de Dromaeosauridae indet. 2

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