X Jornadas Internacionales sobre Paleontología de DINOSAURIOS y su entorno

10th Symposium about Dinosaurs Palaeontology and their Environment

ABSTRACTS BOOK
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Programa/Schedule

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The rich history but the poor fate of Crocodylians

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Keywords: Phylogenetics, Macroevolution, Macroecology, Disparity, crown Crocodylia, stem Crocodylia

Introduction

Since the early 2000s, research on fossil crocodilians has significantly increased, challenging outdated neo-Darwinian beliefs that regarded living crocodilians as "living fossils." This growing body of research has provided a more integrative view of the functional and locomotor innovations of crocodylomorphs, highlighting that the baseline dichotomy in Archosauria-divided into two main lineages, Pan-Crocodylia and Pan-Aves-reflects a shared ancestry characterized by significant locomotor innovations, particularly driven by the hindlimb complex. (Gauthier et al., 2011). Recent studies show that contemporary crocodilians exhibit multifaceted locomotion behaviors—comparable to those of birds—including belly sliding, sprawling runs, high walks, gallops, and suspended paces. These findings challenge the notion that crocodilians are less mobile than their avian relatives. Furthermore, they reveal shared traits in internal anatomy, respiratory physiology, reproductive strategies, parental care, and limb development between crocodilians and birds (Brazaitis & Watanabe, 2011; McCartney et al., 2021). As a result, both extant groups now serve as valuable models for reconstructing the paleobiology of other archosaurs, including dinosaurs.

According to the Paleobiology Database, the peak in crocodyliform species richness occurred during the Turonian–Maastrichtian interval (see also Mannion et al., 2015). Interestingly, during this interval, species from all clades (Notosuchia + (non-Euschia Neosuchia + (Stem-Crocodylia, + Crown Group Crocodylia))) converged in shared biogeographic areas. One such example is the Tremp Formation, which includes the sebecid *Ogresuchus furatus*, the Neosuchia-non-Eusuchian *Sabresuchus*, members of the Crocodylia stem-group Allodaposuchidae, and partial evidence of Gavialoidea representing the crown-group Crocodylia (Sellés, et al., 2020; Pérez-Pueyo, et al., 2021).

In terms of diversity, Crocodylia experienced two major peaks: one during the Paleocene and a more pronounced one in the mid to late Miocene (De Celis et al., 2019). Phylogenetic data suggests that the rate of species generation per million years, based on the temporal spreading of crocodylomorph clades, does not differ greatly among them. However, the crown group Crocodylia shows an elevated rate—up to approximately one species per million years. Estimates based on combined morphological and molecular data place the origin of Crocodylia between 100 and 81 million years ago (Darlim-Oliveira, 2023), during the Cenomanian to Santonian stages. A nearly synchronous divergence of the main lineages—Crocodyloidea, Alligatoroidea, and Gavialoidea—complicates efforts to reconstruct the biogeography and ecological characteristics of their last common ancestor, especially considering the presence of three distinct habitat preferences: terrestrial, semi-aquatic, and marine. Despite its rich fossil record, and the existence of 25 extant species, explaining the evolutionary history and diversification of Crocodylia remains a considerable scientific challenge.

Explaining the clade Crocodylia

A review of the existing literature on the evolutionary explanations of Crocodylia reveals a lack of a fully resolved and cohesive framework. Broadly, four major approaches can be identified: the constructional-deductive approach, the reductionist phylogenetic approach, macroevolutionary dynamic models, and the macroecological perspective.

The constructional approach, as exemplified by the crocodylian bracing system (Salisbury et al., 2006), assumes that the mechanical loads generated during high-walk locomotion affect the neck, vertebral column, and dermal armor. This system is thought to function optimally in a tetraserial dermal shield configuration—characterized by isolated scutes, a discontinuous nuchal shield, and procoelous vertebrae. However, this model shows inconsistencies when variations of the system are examined across stem-group taxa (i.e., non-crocodylian eusuchians), raising questions about its general applicability.

The reductionist phylogenetic approach highlights the difficulty of drawing evolutionary conclusions amidst conflicting hypotheses of crocodylian relationships (Turner, 2015). The stem group exhibits remarkable phenotypic variation, combining both primitive and derived traits. This has complicated the diagnosis of Crocodylia, resulting in ambiguous synapomorphy optimizations (see Salisbury et al., 2006; Rio & Mannion, 2021). Consequently, cladistics has not yielded a clear understanding of Crocodylia's evolutionary trajectory, prompting debate over whether the crown group represents a genuine evolutionary innovation or whether the origin of Eusuchia itself should be the focus (Brochu et al, 2009).

Some researchers have approached this issue by analyzing cranial disparity across Crocodyliformes, using phylogenetically corrected methods. Their findings suggest that modern crocodylians exhibit lower cranial disparity compared to their Cretaceous predecessors (Wilberg, 2017). In our investigation, we aim to address this question by comparing the morphological disparity between crown and stem-group members. Specifically, we explore which anatomical components of the facial skeleton and splanchnocranium may have contributed to evolutionary innovations in Crocodylia. Preliminary results indicate that different allometric patterns and the involvement of the jugal–quadratojugal complex underlies crown-group innovations.

It is evident that macroevolutionary-dynamic models have exposed intriguing evolutionary correspondences between biotic and abiotic parameters, looking for adaptative and selective forces to be contrasted with the phylogenetic pattern. This has positively resulted (i.e., body size and physiology) particularly for the marine crocodylians. Nevertheless, these models leave numerous questions unanswered due to the questionable representativeness of the data sampled, the limited number of abiotically determined parameters used (temperature or latitude), and the paucity of organismal values represented (size, few physiological variables, and resumed lifestyles). Interestingly, size and even diversity seem not to be strongly correlated either to temperature or latitudinal distribution in the semiaquatic groups (Godoy et al., 2019; de Celis et al., 2019).

The fourth point concerns macroecological approaches and evolutionary innovations. These approaches are characterized by the search for statistical relationships that explain the distribution of biodiversity from historical and geographical perspectives.

The goal is to incorporate multilevel processes to uncover the non-random origins of species within major clades across time and space. Although the results from these approaches may be statistically less robust than those derived from macroevolutionary dynamics, they tend to be more predictive due to their multilevel nature. We applied a variation partitioning function to divide the variation of a response variable among several explanatory datasets. By analyzing rostral shape, rostral structural performance, geographical range, and body size within a phylogenetic framework, we estimated the plausible evolutionary trajectories of crocodyloids and alligatoroids.

The results show that Alligatoroidea exhibit strong phylogenetic inertia, with a high degree of morphological integration between the rostrum and the postrostral area. The species segregate into phylogenetically discrete groups. In contrast, the skulls of Crocodyloidea display lower morphological integration, with the rostrum acting as a more independent structure. This region shows weak covariation with the postrostrum and a high degree of evolvability, with patterns of variation linked to environmental factors (Piras et al., 2009; 2014; see also Felice et al., 2021). Predictive models suggest that global climate change will have a greater impact on Crocodyloidea, promoting shifts in rostral traits and altering species' geographical distributions as they track favorable environmental conditions. In contrast, Alligatoroidea, due to the tightness to their ecosystems, its diversity and vicariance patterns likely share the fate of those wetlands and freshwater environments where historically they lived.

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Qué nos dice el registro de Patagonia sobre la evolución de los Eusauropoda (Jurásico Temprano-límite K/Pg)

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Palabras clave: Saurópodos, Jurásico, Cretácico, Evolución, Patagonia

Introducción

Los dinosaurios eusaurópodos fueron, sin duda, el grupo de herbívoros con mayor éxito evolutivo a lo largo de todo el Mesozoico, siendo el clado de dinosaurios más diverso y con mayor distribución geográfica. A pesar de mostrar un mismo plan corporal básico (cuadrúpedos de cuello y cola largos), los eusaurópodos poseen una amplia variedad de adaptaciones y una gran diversidad taxonómica. La Patagonia Argentina, con un extenso registro que va desde el Jurásico Temprano hasta el límite K/Pg., es la región geográfica que mayor información ha brindado acerca de la diversidad, anatomía, evolución y paleoecología de este linaje de dinosaurios.

El registro patagónico de Eusauropoda podría dividirse en cuatro momentos principales. Los dos primeros, representados en la Cuenca Cañadón Asfalto (provincia del Chubut), corresponden al Jurásico Temprano (Formación Cañadón Asfalto) y al Jurásico Tardío (Formación Cañadón Calcáreo). Los otros dos corresponden al Cretácico "medio", Aptiense-Turoniense (Patagonia Norte y Central) y al Cretácico Tardío, Campaniense-Maastrichtiense (con registros a lo largo de toda la Patagonia).

En esta contribución se mencionarán algunos de los principales hallazgos realizados durante los últimos 15 años en las provincias de Chubut y Neuquén, y sus implicancias en el desarrollo del conocimiento sobre este diverso y exitoso grupo de dinosaurios. Estos avances fueron realizados por los diferentes grupos de investigación liderados por parte de los autores firmantes.

Jurásico

La Formación Cañadón Asfalto (Toarciense, 179-178 Ma) aflora en el centro de la provincia del Chubut. Los primeros hallazgos en esta unidad fueron realizados por José Bonaparte en los años 70, cuando dio a conocer el primer registro de fauna continental jurásica para América del Sur. Los trabajos en el área fueron retomados 30 años más tarde por Oliver Rauhut y posteriormente por Diego Pol, y continúan actualmente. En el año

2007, se comenzó con la apertura de un nuevo *bonebed* en el que se recuperaron, al menos, tres ejemplares de un nuevo Eusaropoda: *Bagualia alba* Pol et al., 2020. *Bagualia*, con una masa corporal en el orden de las 7 toneladas, representa el eusaurópodo más antiguo registrado hasta el momento, y la especie más completa recuperada en esta unidad, permitiendo analizar las primeras etapas evolutivas del grupo. El esqueleto postcraneano de *Bagualia* presenta todas las características propias de los eusauropódos, incluyendo un alargamiento en el cuello, la presencia de neumaticidad en el esqueleto axial, cinturas robustas, y miembros columnares. Su cráneo alto y robusto, proporcionalmente pequeño, con narinas externas retraídas, fenestra antorbital reducida, mandíbulas en forma de U, y una reducción en el número de dientes (los cuales poseen una marcada oclusión corona-corona y esmalte grueso), constituyen innovaciones evolutivas claramente vinculadas a un cambio en la dieta. A su vez, el análisis del endocráneo muestra una marcada reducción del lóbulo floculonodular del cerebelo, una marcada hipertrofia de la glándula pituitaria, y canales semicirculares del oído interno algo más cortos y robustos respecto a formas basales de cuerpo pequeño. Estas características endocraneanas podrían indicar que *Bagualia* poseía poca agilidad para mover la cabeza y el cuello, así como para los movimientos oculares en respuesta a estímulos externos. Las adaptaciones craneanas, dentales y apendiculares de *Bagualia* estarían relacionadas con su estilo de vida, caracterizado por un cuadrupedalismo obligado con miembros columnares y una alimentación masiva de vegetación alta en fibra, en respuesta a la crisis del Toarciense y a un marcado cambio ambiental y florístico bien documentado en Patagonia.

Los trabajos en el Jurásico Superior (Formación Cañadón Calcáreo; Kimeridgiense-Titoniense) comenzaron en la década del 90 con una serie de exploraciones llevadas adelante por Thomas Rich (Museum Victoria, Australia) desde el Museo Paleontológico Egidio Feruglio de Trelew. Los mismos resultaron en el descubrimiento de *Tehuelchesaurus benitezi* Rich et al., 1999, en un primer momento considerado como una forma basal de Eusauropoda emparentada con los Mamenchisauridae asiáticos. *Tehuelchesaurus* representa uno de los dinosaurios gigantes más antiguos de América del Sur, con una masa corporal estimada en 40 toneladas, cercana a la masa estimada para grandes saurópodos como *Giraffatitan*, aunque considerablemente menor que la estimada para los grandes titanosaurios del Cretácico. Estudios posteriores indicaron que se trataría de una forma de Macronaria, cercana al origen de los Titanosauriformes, vinculada a formas coetáneas de América del Norte, como *Camarasaurus*, aunque de mayor tamaño (Carballido et al., 2011). Estudios recientes (e.g., Mannion et al., 2019) han recuperado a *Tehuelchesaurus* como un Turiasauria, un grupo de eusaurópodos basales con distribución en América del Norte, Europa y África.

De la misma unidad se ha descripto el dicraeosáurido *Brachytrachelopan mesai* Rauhut et al., 2001, un diplodocoideo que no habría superado las 10 toneladas y cuya principal característica es su cuello relativamente corto. Las diferencias morfológicas entre *Tehuelchesaurus* y *Brachytrachelopan*, y sus respectivos linajes, parecerían estar marcando una clara partición vertical del nicho ecológico.

Durante los últimos años se han realizado numerosos trabajos de campo en la Formación Cañadón Calcáreo, que han dado como resultado dos nuevas formas de saurópodos. Una de ellas, estrechamente relacionada con *Tehuelchesaurus*, preserva, además de vértebras dorsales, varios elementos cervicales, que indican la presencia de un cuello elongado, aunque no en la medida de otros linajes como Mamenchisauridae o Brachiosauridae. La segunda forma, a su vez, presenta una serie de características

anatómicas extremadamente similares a lo que originalmente fue descripto como *Janenschia* (actualmente dividido en *Janenschia*, *Tendaguria* y *Wamweracaudia*). El estudio de estas dos nuevas formas no sólo ampliará la diversidad para el Jurásico Tardío de Patagonia, sino que además podría brindar valiosa información anatómica que permitiría ampliar el conocimiento sobre la evolución temprana de los Macronaria, y eventualmente confirmar la presencia de mamenchisáuridos en América del Sur.

Cretácico

El Cretácico "medio" está muy bien representado en Patagonia, con unidades que van desde el Aptiense al Cenomaniense (e.g., formaciones Cerro Barcino, Rayoso, Lohan Cura, Candeleros, Huincul). La fauna de esta edad se encuentra representada por un único linaje de saurópodos diplodocoideos, los Rebbachisauridae, y por formas intermedias de Macronaria: los Somphospondyli.

Los rebaquisáuridos muestran en Patagonia Norte una increíble diversidad taxonómica, no registrada en otras regiones del mundo. A pesar de esta gran diversidad, hay numerosos aspectos anatómicos, evolutivos y paleobiológicos de este grupo que son aún muy poco conocidos, aunque los avances y descubrimientos de los últimos años han comenzado a arrojar algo de luz sobre los mismos.

Lavocatisaurus agrioensis Canudo et al., 2018 es, hasta el momento, el único taxón de América del Sur con suficiente material craneano como para analizar diferentes aspectos, no sólo anatómicos sino también paleoecológicos, y poder ser comparado con el taxón africano *Nigersaurus*. El estudio de *Lavocatisaurus* ha permitido reconocer características únicas para los Rebbachisauridae, como la presencia de una gran fenestra preantorbital en el maxilar, yugal elongado, desplazamiento anterior de la fenestra infratemporal, articulación del yugal con el escamoso que deja al postorbital fuera de la fenestra, y la pronunciada fosa en el margen lateral del dentario. En base a la reconstrucción tridimensional de su cráneo, se puede observar que el hocico de *Lavocatisaurus* presenta una morfología intermedia entre aquella de los flagelicaudados y la de *Nigersaurus*, ubicando a los rebaquisáuridos como animales generalistas que se alimentaban de los estratos más bajos de la vegetación. Su abundancia en el norte de Patagonia sugiere una preferencia por ambientes abiertos, semidesérticos, coincidiendo con la presencia de un gran desierto que se extendería hasta el Sur de Brasil.

Los sonfospondílidos del Cretácico "medio" estarían representados en Patagonia por formas basales (no-titanosaurios), y los primeros registros claros de titanosaurios en esta parte del continente. Dentro de las formas basales se encuentra *Chubutisaurus insignis* Del Corro, 1975 (Carballido et al., 2011), de unas 30 toneladas de peso. Colectado con metodologías poco ortodoxas, como la utilización de dinamita, *Chubutisaurus* es reconocido por materiales apendiculares, algunos elementos dorsales y centros caudales anfipláticos. Actualmente es considerado como una de las formas de Somphospondyli más cercana al origen de los titanosaurios.

Con excepción de *Ninjatitan*, del Valanginiense, *Patagotitan mayorum* Carballido et al., 2017 representa el registro más antiguo de Titanosauria en Patagonia. Con una masa corporal del orden de las 65 toneladas, y una longitud estimada en 35 metros, *Patagotitan* es actualmente considerado uno de los animales terrestres más grandes que haya existido. La posición filogenética de este gigante, próxima a otros gigantes patagónicos como *Puertasaurus* o *Argentinosaurus*, indica la existencia de un grupo endémico de titanosaurios gigantes que habría habitado la Patagonia desde finales del Cretácico Temprano hasta finales del Cretácico Tardío. La presencia de, al menos, seis ejemplares en tres niveles diferentes, indica que *Patagotitan* retornaba al área repetidamente, en un

patrón de comportamiento conocido como “fidelidad al sitio”. Si bien actualmente no puede confirmarse este comportamiento, ni conocerse las causas de esas acumulaciones de esqueletos, la gran cantidad de dientes de terópodos carcarodontosáuridos (alrededor de 80) hallados en la excavación, y el estadio ontogenético de los ejemplares (adultos jóvenes), permitiría descartar que se tratara de un sitio de caza, y plantea otro escenario en donde estos grandes carnívoros se estarían alimentando de las carcasas de los ejemplares hallados.

Las faunas de saurópodos del Cretácico Tardío (Coniaciense-Maastrichtiense) de Patagonia son claramente diferentes a las registradas en el Cretácico Temprano y “medio”. En efecto, a partir del Turoniense, los rebaquisáuridos desaparecen del registro y los titanosaurios pasan a ser el único clado de Eusauropoda presente en los ecosistemas.

El registro de saurópodos del Cretácico más tardío (Campaniense-Maastrichtiense) de Patagonia Norte es abundante. Hasta hace poco tiempo, era muy poco lo que se conocía de Patagonia Central (Provincia del Chubut). Sin embargo, las investigaciones realizadas en los últimos años están comenzando a mostrar, por primera vez, una diversidad similar a la de otras áreas, como la Cuenca Neuquina.

Los trabajos de campo llevados a cabo en la Formación La Colonia resultaron en la descripción de un nuevo titanosaurio, *Titanomachia gimenezi* Pérez Moreno et al., 2024. A pesar de estar representado por material fragmentario, *Titanomachia* es claramente recuperado como un Saltasauroidea cercano a los saltasaurinos, un grupo de titanosaurios con miembros robustos y cuellos relativamente cortos y tamaños pequeños (la masa corporal de *Titanomachia* se estima en el orden de las 7 toneladas). Este es, hasta el momento, el único taxón de titanosaurios publicado para el Cretácico más alto de Patagonia Central, aunque en trabajos recientes llevados a cabo en la Formación Lefipan (considerada como un equivalente lateral a la Formación la Colonia) se recuperó una nueva forma de titanosaurio. Este ejemplar, del que se preservan vértebras cervicales posteriores y caudales anteriores y medias, es recuperado como un aeolosaurino, cercano al género *Aeolosaurus*. Los aeolosaurinos son, al igual que los saltasauroideos más anidados, animales de tamaño pequeño a moderado, pero con un plan corporal ligeramente diferente, con miembros más gráciles y cuellos más alargados, diferencias que parecen indicar una partición de nichos entre ambos clados, aunque el ingreso de los hadrosaurios a esta parte del continente podría haber marcado una competencia directa por la ocupación del espacio.

El registro patagónico de los eusaurópodos permite reconstruir la historia evolutiva de este grupo desde lo anatómico y estrictamente filogenético hasta algunos de los aspectos paleoecológicos más relevantes. Claramente, la escasa cantidad de restos craneanos limita el conocimiento de muchos de estos aspectos.

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A multidisciplinary approach to investigating early branching sauropodomorph growth and development

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The End-Triassic Extinction saw the disappearance of ~76% of Earth's terrestrial and marine species. Sauropodomorph dinosaurs appeared unaffected by the event and remained the dominant herbivorous organisms in most terrestrial ecosystems (Bordy et al. 2020). Several factors play a role in a species' ability to thrive in post-extinction periods when reproductive pressure is increased. These include faster incubation periods, developmental plasticity, eggshell structure, and rapid growth rates (Chapelle et al. 2021; Chapelle et al. 2025; Erickson et al. 2017; Wiemann et al. 2018). The study of reproductive biology in dinosaurs is hindered by the lack of ontogenetic series of species, especially embryonic material. The Early Jurassic sauropodomorph *Massospondylus carinatus* is the most abundant dinosaur species from southern Africa, with hundreds of specimens ranging in size from embryos to adults referred to the taxon since its description in 1854 (Figure 1) (Barrett & Chapelle 2024, Barrett et al. 2019; Owen 1854; Viglietti et al. 2020). Close to 100 fossil eggs and over a dozen fossil embryos attributed to *Massospondylus* have been recovered from the Rooidraai site in South Africa's upper Elliot Formation (uEF), making it one of the oldest known dinosaur nesting sites globally (Kitching 1979). Unlike other uEF localities dominated by large sauropodomorph remains, Rooidraai preserves a diverse assemblage of small vertebrate fossils, but few have been studied due to difficulties preparing small, easily damaged bone from a hard matrix.

Using a multidisciplinary approach including micro-computed tomography (CT) scanning, synchrotron radiation CT scanning (SRμCT), digital retrodeformation, geometric morphometrics and osteohistology, we re-assessed longstanding hypotheses regarding the identity and growth strategies of *Massospondylus carinatus* and their implications in the macroevolution of dinosaurs. This approach has allowed us to reveal previously unknown aspects of *Massospondylus carinatus*' ontogeny, including the development of its inner ear, the changes in its skull shape during growth, its locomotory posture, its growth strategies, and the investigation of its embryonic anatomy (Chapelle et al. 2022; Chapelle & Choiniere 2018; Chapelle et al. 2020; Chapelle et al. 2019; Neenan et al. 2018). We also reveal a rich vertebrate diversity including theropods, sauropodomorphs, ornithischians, small-bodied cynodonts, and several small-bodied "protosuchian" crocodyliforms at the Rooidraai nesting site, elucidating a previously unknown taxonomic diversity and ecosystem assembly, and providing insights into an undersampled and poorly understood post-end Triassic Extinction small-bodied fauna.

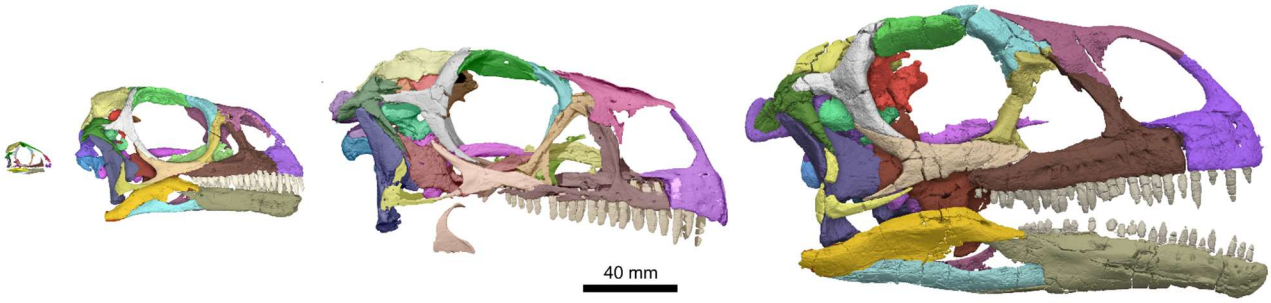

Figure 1: Growth series of *Massospondylus carinatus* skulls (from left to right: BP/1/5347a, BP/1/4376, BP/1/5241, BP/1/4934).

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Fossils that speak: uncovering pathologies in the history of life

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The study of paleopathologies is a discipline within paleontology which focuses are researching the origin of injuries, traumas, and diseases recorded in fossil organisms, whether through their hard parts or impressions of body parts (Bicknell & Holland, 2020; Mathias et al., 2016; Razzolini et al., 2016). From the data obtained by studying these pathological fossils, it is possible to make inferences about the evolutionary history of diseases, as well as conduct paleobiological studies—such as assessing recovery capacity after injury or illness—and paleoecological analyses, examining how these conditions influenced relationships between individuals or species within their ecosystems (Rothschild & Martin, 2006; Rothschild et al., 2012; Cruzado-Caballero et al., 2021).

Cases such as the impact fractures recorded in theropods, which reveal the risks associated with hunting, or the cancer observed in the foot of *Bonapartesaurus* (Fig. 1), illustrate different aspects of behaviour and health in fossil organisms (Rothschild, 2009; Cruzado-Caballero et al., 2021). Furthermore, bone pathologies allow us to explore key moments in the evolution of vertebrates. An example for this is the study of bones of early tetrapods from the Carbonifer period, such as *Ossinodus,* which shows evidence of a healed fracture. These data help us better understand the transition from aquatic to terrestrial environments, as well as the temporal, biogeographical, and physiological contexts in which terrestriality evolved in vertebrates (Bishop et al., 2015).

In recent decades, the use of various techniques from other disciplines, such as medical —histological sections or computed tomography imaging (Fig. 1C)—has made it possible to obtain increasingly comprehensive data to improve the diagnosis of paleopathologies and paleobiological and paleoecological inferences (Aureliano et al., 2020). In this context, paleohistological data reveal the presence of pathological tissue, which appears as rapidly growing bone characterized by a predominance of primary over secondary osteons, radially oriented canals, high reticular vascularization, and a high density of resorption cavities (Aureliano et al., 2020; Bertozzo et al., 2024). Histological sections allow for the detection of alterations in growth patterns and cellular distribution in bone tissue, as well as in the processes of bone formation and resorption (Chinsamy and Tumarkin-Deratzian, 2009; Cerda et al., 2014). However, the main drawback of this technique is that it requires the destruction of part of the fossil specimen.

Computed tomography offers the significant advantage of being a non-destructive technique. It allows for the generation of a sequence of images throughout the entire scanned bone, revealing its internal structure in grayscale (Fig. 1D). This tool not only enables the visualization of areas of bone resorption and the identification of pathological tissue (periosteal reaction), but also facilitates the diagnosis of multiple pathologies through the examination of serial images (Rothschild & Martin, 2006). Among the conditions that can be detected are osteosarcomas, fractures, developmental disorders, infections, and enthesophytes, among others. For instance, in the case of an osteosarcoma,

hypodense or radiolucent areas (darker regions) are observed, corresponding to neoplastic or resorbed tissue (Rothschild & Martin, 2006). In contrast, enthesophytes are characterized by the presence of highly dense pathological tissue formations (brighter areas; Anné et al., 2016). It is also possible to distinguish the external cortical layer of healthy bone, which appears as a radiopaque (white) line embedded between the healthy bone and the periosteal reaction in pathological specimens (Anné et al., 2015).

Once a pathology has been diagnosed in a fossil, various paleobiological inferences can be made, such as those related to individual and population health, the prevalence of certain diseases within specific taxonomic groups, or even the healing processes involved (Rothschild, 2009; Straight et al., 2009; Cruzado-Caballero et al., 2023). Additionally, the study of these alterations allows researchers to formulate paleoethological hypotheses about the organism's life experiences, including interactions with other individuals or with the environment. For example, certain types of fractures may be associated with behaviors such as intraspecific combat or accidental injuries, while healed bite marks may indicate encounters with predators (De Palma et al., 2013; Cruzado-Caballero et al., 2021; Arbour et al., 2022). Similarly, some pathologies related to repetitive microtrauma, such as enthesophytes, may be linked to recurring mechanical stress (Anné et al., 2016). From a functional perspective, these lesions can also reveal possible biomechanical limitations, either due to pain—such as in the case of fractures or arthropathies—or due to restricted range of motion caused by infections, developmental diseases, or osteomyelitis (Martinelli et al., 2015; Cruzado-Caballero et al., 2020; Bertozzo et al., 2021). Finally, certain types of pathologies may reflect particular paleoenvironmental conditions, such as saline stress (Petit & Khalloufi, 2012).

In summary, the study of paleopathologies not only expands our understanding of the evolution of diseases, but also allows for a reinterpretation of the fossil record from an integrative perspective—one that encompasses biological, ecological, and ethological aspects—offering a more dynamic and comprehensive view of the history of life on Earth.

Figure 1. Foot of the hadrosaurid *Bonapartesaurus*. A–B) Images of the foot showing the metatarsal of digit II (indicated by the arrow) with a bone overgrowth caused by the presence of an osteosarcoma; C) histological section of the pathological tissue, with red arrows indicating the boundary between healthy and pathological bone; D) CT scan image.

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Dinosaur tracks and locomotion

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Keywords: Footprint, track, locomotion, biomechanics, trackway, simulation

Abstract

The record of dinosaur tracks is almost as old as the record of their bones. The earliest reconstructions of dinosaurs from their skeletons were as slow, sprawling, lumbering reptilian creatures. But the first dinosaur tracks described - by Edward Hitchcock (Hitchcock 1836, 1841, 1858) in the 1830's 40's and 50's - were attributed to large, upright, agile birds (Hitchcock 1836). Given many of Hitchcock's tracks are now interpreted to have been made by theropods, it seems that ichnology, not osteology, offered the earliest accurate glimpse into how dinosaurs truly lived and moved.

Figure 1- Some of Hitchcock's tracks, housed today in the Beneski Museum of Natural History

Since their first discovery, tracks and trackways have offered a complimentary and parallel source of information about dinosaurs. Rarely found in the same rocks as osteological material, and always preserved *in situ*, tracks offer useful information about biogeographical distributions, palaeoenvironment, and palaeoecology (Falkingham 2014). They also provide an intimate record of dinosaur movement, and from this record we can reconstruct locomotor capabilities.

A track is a three-dimensional volumetric shape, the morphology of which is resultant from the interaction between an autopod (foot) and the substrate (Allen 1989; Manning 2004; Milàn *et al.* 2004). The substrate may react differently depending on grain size, water content, or composition, all of which are linked to the palaeoenvironment. The foot has a morphology that affects the shape of the track, and the foot interacts via motions (kinematics) and forces (kinetics) that move the sediment (Falkingham 2014).

As an animal moves over compliant, plastically deformable substrates, it leaves behind tracks, multiple of which form trackways. The footfall patterns can be informative as to gross locomotion, including gait (Henderson 2006; Lallensack & Falkingham 2022) and speed (Alexander 1976). Individual tracks can provide more specific and precise information about the foot anatomy and movement of the trackmaker (Falkingham *et al.* 2020; Turner *et al.* 2020).

However, recovering this information with confidence is not trivial, for a multitude of reasons. Trackmaker identification is notoriously difficult, especially in groups with conservative foot morphology such as theropods. Precise foot fall positions

can be hidden by overprinting, or by formational changes along a trackway resulting from spatial heterogeneity of the substrate. Feet can sink to variable depths, deforming or penetrating surface and sub-surface sediment layers, making identification of surface tracks and undertracks difficult.

The last two decades have seen considerable advances in computational techniques across vertebrate ichnology, and wider palaeontology. This has included rapid improvements in digitization technology (Matthews *et al.* 2006; Falkingham 2012), to the point that most people now carry a high-resolution scanning device in their pocket (that also happens to make phone calls). Tracks can now be accurately recorded and shared with collaborators and the broader community as a matter of course, something that was previously difficult due to their *in situ* nature. Those digitized tracks can provide inputs to new simulation techniques including finite element analysis (Falkingham *et al.* 2009; Schanz *et al.* 2016) and the discrete element method (Falkingham & Gatesy 2014; Falkingham *et al.* 2020), to 'reverse engineer' track formation and recover details about foot anatomy and motion, or about the track forming process more generally.

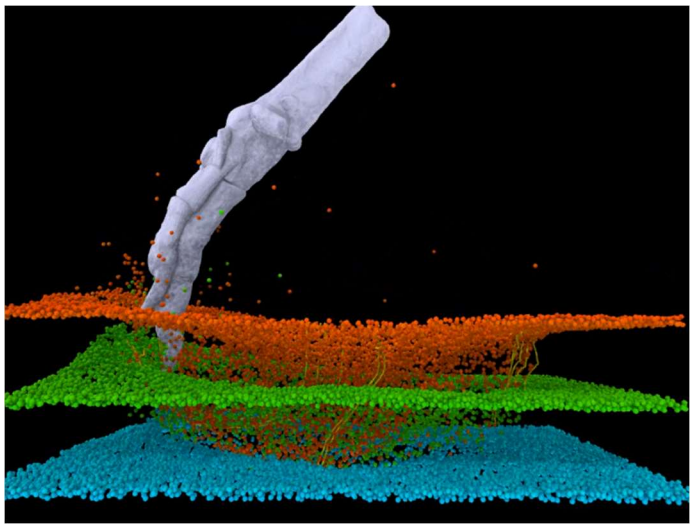

Figure 2 - Computational methods such as the discrete element method enable complex modelling of the foot-sediment interaction

However, even with these new tools at our disposal, it has become more evident than ever that our palaeontological hypotheses must be grounded in the world of the living. Just as for rocks "the present is the key to the past," so too is it the case for biology. In order to be confident in our interpretations of extinct life, we must study similar phenomena – in this case the track forming process and movement over deformable substrates – in extant taxa (Falkingham & Gatesy 2014; Turner *et al.* 2020; Prescott *et al.* 2025). By combining traditional ichnological methods with cutting edge technology *and* comparative study, we can shed new light on the lives of dinosaurs and other extinct animals.

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Geological stories and dinosaurs of the Iberian Basin

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Keywords: **Dinosauria, *Aragosaurus*, Maestrazgo, Cameros, Spain, Cretaceous, Mesozoic.**

Introduction

Within Spain, the fossil record of the Iberian Basin has provided the first reports of dinosaurs (see Pereda-Suberbiola and Ruiz-Omeñaca, 2005), the first described dinosaur species (Sanz et al., 1987), and some of the Mesozoic vertebrate sites with the greatest paleobiodiversity (e.g., Buscalioni et al., 2008; Canudo et al., 2010).

Mesozoic sedimentation in the Iberian Basin took place within an intraplate extensional tectonic framework related to Tethys and Central Atlantic spreading (Salas and Casas, 1993). Two main rift stages (Late Permian to Hettangian and Late Jurassic to Early Cretaceous) followed by their subsequent postrift phases have been recognized (Salas et al., 2001). Later on, the latest Cretaceous onset of Africa-Europe-Iberia convergence had impact in the interior areas of northeast Iberia, with the progressive inversion and contractive deformation of the Mesozoic Iberian basin rift system giving rise to the alpine Iberian Ranges (e.g., Álvaro et al., 1979).

Aspects such as tectonics, climate, and sea level changes have influenced the evolution of the sedimentary record and paleogeography of the Iberian Basin. They also influence the dinosaur fossil record. The latter is also affected by the evolutionary history and paleobiogeography of Dinosauria. All of this leads us to find in the Iberian Basin geological units and periods that are especially interesting for dinosaur paleontology. Likewise, the study of the dinosaur record of the Iberian Basin and the need to contextualize findings and faunal associations have contributed to the advancement of our knowledge of geological history, with notable cases, such as those reviewed in this contribution.

Concluding remarks

There have been cases in which the study of dinosaurs and fossil assemblages in the Iberian Basin have contributed to improving our understanding of regional geology. There are even dinosaurs that have changed history (geologically):

The scientific discussion about the age and geological context of the dinosaur *Aragosaurus* (e.g. Royo-Torres et al., 2009; Aurell et al., 2016) has led to a redefinition of the geological history of an entire sub-basin on the western margin of the Maestrazgo Basin (Teruel province). This has implications for the reconstruction of the paleobiodiversity of Late Jurassic-Early Cretaceous fossil assemblages and the regional tecto-sedimentary evolution, including the definition of new lithostratigraphic units.

The integrated study of the stratigraphic, paleoenvironmental context and vertebrate record (bones, ichnites, eggshells) of some Early Cretaceous units of Maestrazgo (Aurell et al., 2016; Gasca et al., 2017) and Cameros (Aurell et al., 2021;

Pinilla-Serrano and Gasca, 2025) has allowed us to characterize the influence of synsedimentary tectonics on the basin fill and facies distribution. It also shows how these, in turn, determine the presence of vertebrate fossils and their type of preservation.

The stratigraphic, sedimentological and paleontological characterization of the successions recorded during the initial stages of development of the Montalbán subbasin (Teruel province) has had major implication to understand the latest Cretaceous palaeogeographic evolution of northeast Iberia (Aurell et al., 2022). Sedimentation during the Campanian-Maastrichtian was irregularly distributed in the interior areas of the Iberian basin, with a patchy distribution of the subsiding continental-dominated areas. In all the latest Cretaceous continental subbasins of the Iberian basin, dinosaur fossil sites including abundant titanosaurs and ornithopods are concentrated in a relatively narrow timespan from late Campanian to earliest Maastrichtian.

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Comunicaciones/Comunications

Paleontología Social, 20 años de retrospectiva

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Palabras clave: Paleontología social, Divulgación, Discapacidades, Exclusión social, Revisión sistemática

Introducción

Paleontología social es un término creado en 2004 en el yacimiento de Somosaguas, Madrid por Torices et al. (2004) para agrupar todas las actividades relacionadas con la paleontología destinadas a sectores de la población que normalmente no tienen acceso a ellas. Esto incluye personas con discapacidades o en riesgo de exclusión social. Más de 20 años después, este término se ha extendido más allá de sus orígenes llegando a diferentes partes del mundo como Italia, Chile etc, incluyendo diferentes tipos de actividades de divulgación.

Metodología

Se ha realizado una revisión sistemática para localizar todos los artículos realizados sobre paleontología social utilizando las pautas PROSPERO [International Prospective Register of Systematic Reviews]. La revisión se ha registrado en OSF [Open Science Framework]. Se han utilizado cuatro bases de datos en esta revisión sistemática. [PubMed, Web of Science, Google Scholar y Dialnet]. Los criterios de inclusión fueron: 1- Trabajos sobre sobre actividades paleontológicas centradas en poblaciones que normalmente no tendrían acceso a actividades más tradicionales.2- Resúmenes en inglés o español. 3- Todas las edades y géneros están incluidos. Tras definir los criterios de inclusión se buscaron los "meshterms" apropiados para realizar las búsquedas, además de definir las palabras clave que se iban a utilizar para las búsquedas. La literatura gris también se ha incluido en esta revisión sistemática mediante búsquedas en diversos repositorios de tesis doctorales. Un diagrama PRISMA se ha utilizado para mostrar el proceso de cribado y selección.

Resultados

La búsqueda inicial proporcionó cuarenta trabajos de los cuales, solo diez trabajos cumplieron los criterios de exclusión. Ocho de los trabajos consistían en descripciones narrativas de actividades realizadas con personas con discapacidades. Uno de los estudios incluía una evaluación con encuestas de satisfacción. Por último, la búsqueda de literatura gris encontró una tesis sin publicar de Brasil. La mayoría de los estudios se habían realizado dentro de la Península Ibérica con algunas excepciones como trabajos en Chile, Italia y Brasil.

Conclusiones

El concepto de paleontología social se ha utilizado extensamente en el área geográfica donde se originó, pero hay una notable falta de evaluación rigurosa de estas actividades en términos de satisfacción de los participantes y cumplimiento de objetivos

didácticos. Publicar y evaluar actividades específicamente diseñadas para incluir a comunidades que no tienen acceso a actividades de divulgación tradicionales es esencial para proporcionar una educación paleontológica inclusiva.

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Palaeobiodiversity of Crocodylomorpha (Neosuchia) from the Lower Cretaceous of the Cameros Basin: dental crocodylomorph diversity from the Enciso Group, La Rioja

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Keywords: Early Cretaceous, Iberian range, La Rioja, Teeth, Goniopholididae, Bernissartiidae

Introduction

Recent advances in the study of Crocodylomorpha diversity from the Lower Cretaceous of Europe have highlighted the importance of fossil records from the Iberian Peninsula (Puértolas-Pascual et al., 2015, Guilleume et al., 2020). This study presents a systematic study of crocodylomorph teeth from the Enciso Group (eastern Cameros Basin) of La Rioja, aiming to unravel the neosuchian palaeodiversity and distribution in latest Barremian–early Aptian continental environments of the Iberian Peninsula.

Geological and Geographical setting

Most of the herein analysed teeth were recovered near Igea (La Rioja, Spain). Geologically, the sites are located within the eastern Cameros Basin, specifically in the Enciso Group (DS7). The deposits of the Enciso Group have been interpreted as a siliciclastic-influence carbonate lacustrine and palustrine environment, including fluvial and deltaic episodes (Mas et al., 2011, Hernán, 2018) and the age is estimated from the latest Barremian to the early Aptian (Suarez-Gonzalez et al., 2013).

Methodology

The herein studied material comprises a set of 26 isolated teeth curated at the Centro de Interpretación Paleontológica de La Rioja in Igea (La Rioja, Spain). The teeth were studied using a binocular microscope NexiusZoom NZ.1902-PG and following the dental terminology proposed by Hendrickx *et al.* (2015) for theropod dinosaurs, which is also applicable to other archosaurs. The measurements were taken using a digital calliper *Filetta* KSD-150 and ImageJ v1.54 program.

Systematic Palaeontology

CROCODYLOMORPHA Walker, 1970 (*sensu* Clark, 1986)

MESOEUCROCODYLIA Whetstone and Whybrow, 1983 (*sensu* Benton & Clark, 1988)

NEOSUCHIA Benton and Clark, 1988

GONIOPHOLIDIDAE Cope, 1875

GONIOPHOLIDIDAE INDET.

Morphotype 1 (19 teeth; CPI 874, 1705, 1709, 1714 to 1716, 1774 to 1786, 391-1, 392-2 and 392-3, 392-4): The teeth grouped with morphotype 1 are conidont, display tall crowns (CH: 5–15 mm), slightly pointed and lingually inclined apices, and subcircular basal cross-sections. In distal view, the labial surface is strongly convex, and the lingual surface is slightly concave. Both mesial and distal carinae are present. These lack denticles and extend from the apex to the cervix. The enamel ornamentation consists of fine, sub-parallel longitudinal ridges on both surfaces, extending from the apex to the cervix. These ridges are more abundant and narrower on the lingual surface (15–20) compared to the labial surface (5–10).

Morphotype 2 (5 teeth; CPI 1706, 1708, 1782, 392-1 and 392-2): The teeth within Morphotype 2 are conidont and exhibit slender and elongated crowns (CH:10-20 mm), pointed and lingually tilted apices, and subcircular basal cross-sections. In distal view, the labial surface is convex and the lingual surface concave. The mesial and distal carinae are present and extend from the apex to the mid-crown. Both carinae are non-denticulated. Some longitudinal ridges are present on the enamel of both lingual and labial surfaces. These ridges extend from the apex to the cervix in all specimens, but in one (CPI 392-1), in which the ridges face at mid-crown. The number of ridges varies between the two surfaces, ranging from 10 to 15 on the lingual surface and from 9 to 13 on the labial surface.

BERNISSARTIIDAE Dollo, 1883

BERNISSARTIIDAE INDET.

Morphotype 3 (1 tooth; CPI 1710): This tooth displays a folidont crown morphology, with a triangular outline in labial and lingual views and a constriction at the level of the cervix. The crown is low (CH of 7 mm), with a pointed apex, which is lingually and slightly mesially-tilted. In distal view, the labial surface is convex, and the lingual surface is nearly straight. The basal cross-section is elliptical. Both mesial and distal carinae are present. They follow the curvature of the crown and lack denticles. The enamel ornamentation consists of 6 longitudinal ridges on both surfaces, extending from apex to the cervix.

Morphotype 4 (1 tooth; CPI 1711): The tooth included in Morphotype 4 is a molariform crown that has a bulbous shape, with a low, broad crown and a blunt apex. In lateral view, it presents an ellipsoidal outline with slight labiolingual constriction at the cervix. In distal view, the labial and lingual surface is convex. The basal cross-section is elliptical. The tooth lacks carinae, but it exhibits an enamel ornamentation, which is based on thin and evenly developed longitudinal ridges on both labial and lingual surfaces. On the labial surface 30 ridges are present whereas there are 35 on the lingual surface.

Discussion

The teeth analysed in this study exhibit significant morphological diversity, which can be attributed to variability within the different crocodylomorph groups. The teeth grouped within Morphotypes 1 and 2 are conidont, with high crowns, carinae lacking denticles, ornamentation based on longitudinal ridges, and pointed and lingually tilted apices. These features are shared with the dentition of Goniopholididae (Puértolas-Pascual et al., 2015, Guillaume et al., 2020). From those grouped within Morphotype 1 and 2 can be confidently assigned to Goniopholididae. Regarding the morphological differences between the morphotypes 1 and 2, the teeth belonging to Morphotype 2 exhibit a more elongated shape and circular cross-section. The variation in crown height

and overall shape can be caused by pseudoheterodonty and the position of the dental element along the jaw (López-Rojas et al., 2024). The tooth of Morphotype 3 is folidont, with a pointed apex, no denticles on either carinae, an ornamentation based on longitudinal ridges on both surfaces, extending from apex to the cervix and a constriction at the level of the cervix. These morphological features can be observed in the mesial teeth of the Bernissartiidae family (Martin et al., 2019). Hence this morphotype is assigned to this clade. Finally, the tooth of Morphotype 4 is molariform with a very low crown, blunt apex, a strong labiolingual constriction at the cervix and numerous longitudinal ridges on both surfaces. These features refer to it as a tooth of Bernissartiidae, from the most distal part of the jaws (Puertolas-Pascual et al., 2015). Such variation has been documented also in the complete skulls of the taxon *Bernissartia fagesii* (Martin et al., 2019). Therefore, it cannot be ruled out that these morphotypes do not belong to the same taxon. The fossil record of crocodylomorphs in the Iberian Peninsula throughout the Early Cretaceous shows a remarkable diversity, with representatives of families such as Bernissartiidae, Goniopholididae and Atoposauridae, found in sites from Barremian to the Aptian, formed in fluvio-deltaic and lacustrine environments (Puértolas-Pascual et al., 2015, Guillaume et al., 2020).

Conclusion

The herein studied tooth sample indicates, that at least two main crocodylomorph families are present in the uppermost Barremian–lower Aptian deposits of the Enciso Group, Igea area (La Rioja): Goniopholididae and Bernissartiidae. The Morphotypes 1 and 2 exhibit features consistent with Goniopholididae. The Morphotypes 3 and 4, which exhibit folidont and molariform crowns-types, respectively, are attributed to Bernissartiidae. Therefore, the preliminary revision of the dental material recovered from the Enciso Group is consistent with the other Iberian fossil records, due to similar clades being present in the different Iberian Lower Cretaceous basins.

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On the potential presence of 'pistosaurs' in the Middle Triassic of the Middle East

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Keywords: Makhtesh Ramon, Israel, Anisian, Ladinian, Eosauropterygia, Pistosauroidea.

Pistosauroids (Pistosauroidea, Eosauropterygia) are a monophyletic group of sauropterygians that include the well-known plesiosaurs (i.e., Plesiosauria) as well as other basal forms from the Triassic (Wang et al., 2019). This clade was the most successful among Sauropterygia considering that they were globally distributed and that their fossil record spans from the probably Lower Triassic (i.e., Olenekian) to the uppermost Cretaceous (i.e., Maastrichtian) (Bardet et al., 2014). The oldest record for Triassic pistosauroids probably occurs in the Lower Triassic, with the putative pistosauroid *Corosaurus alcovensis* Case, 1936, from the Olenekian of USA or, alternatively, with the pistosauroid *Kwangsisaurus orientalis* Rieppel, 1999, from the Olenekian or earliest Anisian of China; whereas the youngest record is represented by the plesiosaurian *Rhaeticosaurus mertensi* Wintrich, Hayashi, Houssaye, Nakajima, and Sander, 2017, from the Rhaetian (i.e., uppermost Triassic) of Germany. Most of these Triassic forms belong to the non-plesiosaur pistosauroids, with *Bobosaurus forojuliensis* Dalla Vecchia, 2006, from the Carnian (Upper Triassic) of Italy (Dalla Vecchia, 2017), having been hitherto considered as the youngest known representative (Benson et al., 2012; Wintrich et al., 2017). Non-plesiosaur pistosauroids are informally referred to as 'pistosaurs', previously considered to conform a monophyletic group (i.e., the Pistosauria *sensu* Rieppel, 2000) or, more recently, having been considered paraphyletic (Fabbri et al., 2013). 'Pistosaurs' remains have been recovered from USA (e.g., Case, 1936; Sander et al., 1997), China (e.g., Rieppel, 1999; Ma et al., 2015; Wang et al., 2019), Europe (e.g., Rieppel, 2000; Diedrich, 2013; Sander et al., 2013), and North Africa (e.g., Rieppel, 1997). Nonetheless, the knowledge about this group is relatively limited relative to other Triassic sauropterygians due to the incompleteness of their fossil record and the lack of well-preserved specimens (Wang et al., 2019). The most abundant and best-preserved 'pistosaur' material corresponds to that of *Yunguisaurus liae* Cheng, Sato, Wu, Li, 2006, from the Ladinian (Middle Triassic) of China (Wang et al., 2019), and *Pistosaurus longaevus* Meyer, 1839, from the Anisian (Middle Triassic) of Germany and Poland (Diedrich, 2013). In this sense, 'pistosaurs' have never been reported from any Middle East Triassic locality, where several other Triassic sauropterygian clades occur (i.e., Placodontia, Pachypleurosauria, Nothosauria, and Simosauridae) (Rieppel et al., 1999; Vickers-Rich et al., 1999; Kear et al., 2010; Cabezuelo-Hernández et al., 2024), especially in the Middle Triassic levels of Makhtesh Ramon (Negev, south Israel) (Rieppel et al., 1999). In this work, we present several unpublished vertebral remains from the Muschelkalk levels (Anisian or Ladinian) of Makhtesh Ramon. The vertebral material seems incompatible with any sauropterygian clade previously described in this region, but potentially akin to the non-plesiosaurian pistosauroids (i.e., 'pistosaurs'). We provide here both preliminary anatomical descriptions and a systematic study of this vertebral material, in addition to an anatomical comparative study with other 'pistosaurs'.

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Preliminary systematic discussion of the first remain of Sauropterygia from Almería (southeastern Spain)

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Keywords: Betic Cordillera, Middle Triassic, Eosauropterygia, Nothosauroidea, vertebral element.

Sauropterygia was a successful group of aquatic reptiles with a fossil record spanning from the Olenekian (i.e., Lower Triassic) to the Maastrichtian (i.e., uppermost Cretaceous) (Bardet et al., 2014). Triassic sauropterygians can be divided into two main groups: Placodontia (i.e., durophagous forms) and Eosauropterygia, which included the most derived forms (Rieppel, 2000). Eosauropterygia groups the pachypleurosaurs (i.e., Pachypleurosauria); the nothosauroids (i.e., Nothosauroidea), which includes nothosaurs (i.e., Nothosauria) and simosaurs (i.e., Simosauridae); and the pistosauroids (i.e., Pistosauroidea), which includes 'pistosaurs' (i.e., non-plesiosaur pistosauroids) and plesiosaurs (i.e., Plesiosauria) (Rieppel, 2000). With regards to the Spanish fossil record, all the main sauropterygian clades are represented, ranging from the Anisian (i.e., Middle Triassic; de Miguel Chaves et al., 2020) to the Maastrichtian (i.e., uppermost Cretaceous; Bardet et al., 2008; Pereda-Suberbiola et al., 2015). The Spanish Triassic sauropterygian record is mostly represented by fragmentary and/or isolated remains (Bardet et al., 2008) being only diagnostic at supraspecific or suprageneric level. These remains come from Middle (i.e., Anisian and Ladinian) to Upper Triassic (i.e., probably Rhaetian) outcrops of several localities (de Miguel Chaves et al., 2020; García-Ávila et al., 2021; Reolid et al., 2022). Nonetheless, several Spanish Triassic sauropterygian species have been identified, some of them being common faunal components of other European Triassic localities (i.e., *Lariosaurus balsami* Curioni 1847, *Nothosaurus* cf. *giganteus* Münster 1834, *Nothosaurus* cf. *mirabilis* Münster 1834; Rieppel, 2000; de Miguel Chaves et al., 2020); whereas others have been recognized as endemic Spanish forms (i.e., *Parahenodus atancensis* de Miguel Chaves, Ortega, Pérez-García, 2018a; *Paludidraco multidentatus* de Miguel Chaves, Ortega, Pérez-García, 2018b; *Hispaniasaurus cranioelongatus* Márquez-Aliaga, Klein, Reolid, Plasencia, Villena, Martínez-Pérez, 2017). In this context, most of the Spanish Triassic sauropterygian remains come from the central and northeastern areas of this country, where they are represented by placodonts, pachypleurosaurs, nothosaurs, simosaurs, and pistosauroids (de Miguel Chaves et al., 2020; and references therein). Conversely, sauropterygians remains in southern Spain are less abundant, having being recorded mostly from southeastern (i.e., Murcia, Jaén, Granada; de Miguel Chaves et al., 2020; and references therein), but also from southwestern Spain (i.e., Huelva; Reolid et al., 2022). Sauropterygians in southern Spain are represented by nothosaurs (i.e., *Nothosaurus* cf. *mirabilis*, *Nothosaurus* sp., Nothosauria indet.; de Miguel Chaves et al., 2020; and references therein), pachypleurosaurs (i.e., Pachypleurosauria indet.; de Miguel Chaves et al., 2020; and references therein), placodonts (i.e., Placodontia indet., Cyamodontoidea indet., Placochelyidae indet.; de Miguel Chaves et al., 2020; and references therein), a probable 'pistosaur' (Pérez-Valera et al. 2019; de Miguel Chaves et al., 2020), a probable simosaur (Reolid and Reolid, 2020), and a probable nothosaur or placodont (i.e., cf. *Nothosaurus*/cf. Cyamodontoidea; Reolid et al., 2022). We report here the first sauropterygian occurrence from the Triassic of Almería Province (southeastern Spain). It

corresponds to an almost complete neural arch found in Sierra de Gádor in the Betic Cordillera. It is attributable to Eosauropterygia based on the presence of accessory intervertebral articulations (i.e., zygosphene-zygantrum complex) and the expanded neural arch pedicels with butterfly-shaped articulation areas for the centrum (Rieppel, 2000). The medium-sized neural arch displays a relative tall neural spine and short transverse processes, indicating potential nothosauroid affinities. We provide here a detailed anatomical description and the systematic study of the unpublished neural arch from Almería, in addition to a comparative analysis with the vertebrae of Eosauropterygia.

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Nuevas icnitas de dinosaurio de la Formación Artoles (Cretácico Inferior) en la subcuenca de Galve (Cuenca del Maestrazgo, Teruel, España)

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Palabras clave: Ornitópodos, terópodos, contramoldes, icnodiversidad, Barremiense, Aliaga

Introducción

En la última década ha aumentado notablemente el número de yacimientos con icnitas de dinosaurio del Cretácico Inferior en las subcuencas de Galve y Peñagolosa (provincia de Teruel). En estas dos subcuencas del margen occidental de la Cuenca del Maestrazgo afloran diversas formaciones de edad Barremiense que están proporcionando una gran cantidad de datos sobre las icnoasociaciones de dinosaurios. Así, en las formaciones El Castellar (Castanera et al., 2022; García-Cobeña et al., 2023), Camarillas (Cobos y Gascó, 2012; Herrero et al., 2017; Cobos et al., 2018; García-Cobeña et al., 2023; 2024 y referencias) y Artoles (Cobos et al., 2016) se han descrito distintos yacimientos, en los que muchos de ellos destacan por contener icnitas conservadas como contramoldes.

El objetivo del presente trabajo es la descripción de un nuevo yacimiento de icnitas de dinosaurio, denominado El Cañizarejo, localizado en el término municipal de Aliaga (provincia de Teruel, España). El yacimiento se localiza en capas de la Formación Artoles, de edad Barremiense superior basal (Bover-Arnal et al., 2016) y lo componen al menos 4 niveles icnológicos diferentes. El yacimiento principal (EC1) se descubrió en el año 2020 y el trabajo de campo permitió identificar 2 niveles icnológicos más (EC2-EC3). Los tres niveles (EC1-EC3) se localizan en la carretera comarcal que une Aliaga y Camarillas (Teruel), mientras que EC4, se localiza un poco más al Norte en un pequeño barranco. La serie estratigráfica presenta un alto buzamiento y los niveles EC1-EC3 han aflorado como consecuencia de las obras de ensanchamiento de la carretera y la posterior erosión de los sedimentos menos competentes. Así, afloran superficies y secciones de niveles que contienen las icnitas, mostrando diferentes tipos de conservación entre los distintos horizontes.

Metodología

La metodología llevada a cabo durante la documentación de los yacimientos ha sido principalmente la toma de fotografías de los niveles que contienen las icnitas y de cada espécimen individualmente. Con esas fotografías se han realizado modelos 3D mediante técnicas de fotogrametría, con el *software* Agisoft Metashape. Sobre estos modelos 3D se han generado mapas de profundidad por colores con el *software* Cloud Compare. De las icnitas mejor conservadas se han obtenido una serie de parámetros siguiendo metodologías previas (ver Castanera et al., 2022 y referencias) como longitud y anchura de la icnita, longitud y anchura de los dedos, ángulos interdigitales (II-III, III-IV), y se han calculado la mesaxonia y la ratio longitud/anchura (FL/FW).

Resultados

El nivel EC1destaca por contener icnitas conservadas como contramoldes, la mayoría adheridas al techo del estrato inferior que son areniscas con *ripples*, con una gran superficie aflorante (algo más de 12 m^2). Las huellas están conservadas como epirelieves convexos, es decir como "pedestales" (Fig.1). Se han identificado un total de 8 icnitas, pero el número posiblemente aumentará con la erosión del nivel suprayacente, que ha permitido la identificación de nuevas icnitas en las sucesivas visitas. Entre ellas destaca un posible rastro formado por tres icnitas tridáctilas, de gran tamaño (FL > 35 cm) y caracterizadas por dedos robustos y baja mesaxonía. Estas características son propias de ornitópodos de tamaño mediano a grande. Además, hay al menos otros dos morfotipos de icnitas tridáctilas, ambas de tamaño medio (FL = 25-30 cm). Unas se caracterizan por su gracilidad, una ratio FL/FW muy alto y alta mesaxonía, caracteres de un productor terópodo. La presencia de garras y almohadillas interdigitales soportan esta atribución. El segundo morfotipo, se caracteriza por dedos robustos y redondeados y bajos valores de mesaxonía y FL/FW ratio, caracteres de icnitas de ornitópodo de tamaño medio.

Los niveles EC2 y EC3 corresponden a areniscas situadas estratigráficamente por debajo y se observan principalmente en sección en la base de los estratos (hiporelieves convexos). En ellos las icnitas se han conservado como contramoldes, que rellenan pisadas que se formaron en niveles lutíticos. Se han recuperado varios contramoldes que se encontraban en la cuneta rodados. Algunos de ellos son de gran tamaño y profundos y se observan estrías de deslizamientoe impresiones de las escamas de la piel. En EC2, además algunos se observan todavía *in situ*.

El nivel EC4 es una capa demargocaliza gris y es el único nivel que conserva icnitas como epirelieves cóncavos. Se ha identificado una icnita tridáctila de tamaño medio, caracterizada por un bajo FL/FW ratio y una mesaxonia media y unos dedos acuminados. Estos caracteres indican posiblemente un productor terópodo. Además, se han observado otras icnitas, no muy bien conservadas, someras e indeterminadas.

Discusión

De los cuatro niveles, EC1 es el más interesante tanto por la conservación de las icnitas como por la icnoasociación. El modo de conservación de las huellas como epirelieves convexos en EC1 es novedoso ya que apenas se conocen yacimientos en la península ibérica con esta particularidad (ej.: Cobos y Gascó, 2012; Huerta et al., 2012). Por el contrario, este tipo de conservación dificulta la clasificación icnotaxonómica, ya que se observa una gran variabilidad en la forma de las icnitas y en pocos casos se observa la vista plantar. Además, algunos parámetros son muy variables incluso entre icnitas del mismo rastro. En cualquier caso, los caracteres de las icnitas de ornitópodo (icnitas mesaxonicas, subsimétricas y con una longitud y anchura similar) los relacionan con la familia Iguanodontipodidae, y posiblemente con el icnogénero *Caririchnium*, caracterizado por un "talón" grande, ancho, redondeado y centrado (Díaz-Martínez et al., 2015). Este icnogénero es muy común en el Barremiense europeo, incluyendo las unidades barremienses de las subcuencas de Galve y Peñagolosa (Díaz-Martínez et al., 2015; Castanera et al., 2022; García-Cobeña et al., 2024). Estos últimos autores han diferenciado dos morfotipos (MOR1 y MOR2) cuyas principales diferencias son un dedo III más alargado y ancho en su parte proximal que los dedos II y IV, escotaduras pronunciadas en la parte proximal y una ligera mayor mesaxonia en el caso de las icnitas de MOR1. Por el contrario, las icnitas MOR2 tienen dedos proporcionalmente más anchos y robustos y dedos de una longitud más similar, con mesaxonia y FL/FW ratio más bajos. Los datos de las icnitas de ornitópodos de EC1, a pesar de la variabilidad, posiblemente

encajan mejor en este segundo morfotipo. En el caso de la icnita de terópodo de EC1, los altos valores de mesaxonia y de FL/FW ratio lo relacionan con la icnofamilia Grallatoridae (Melchor et al., 2019).

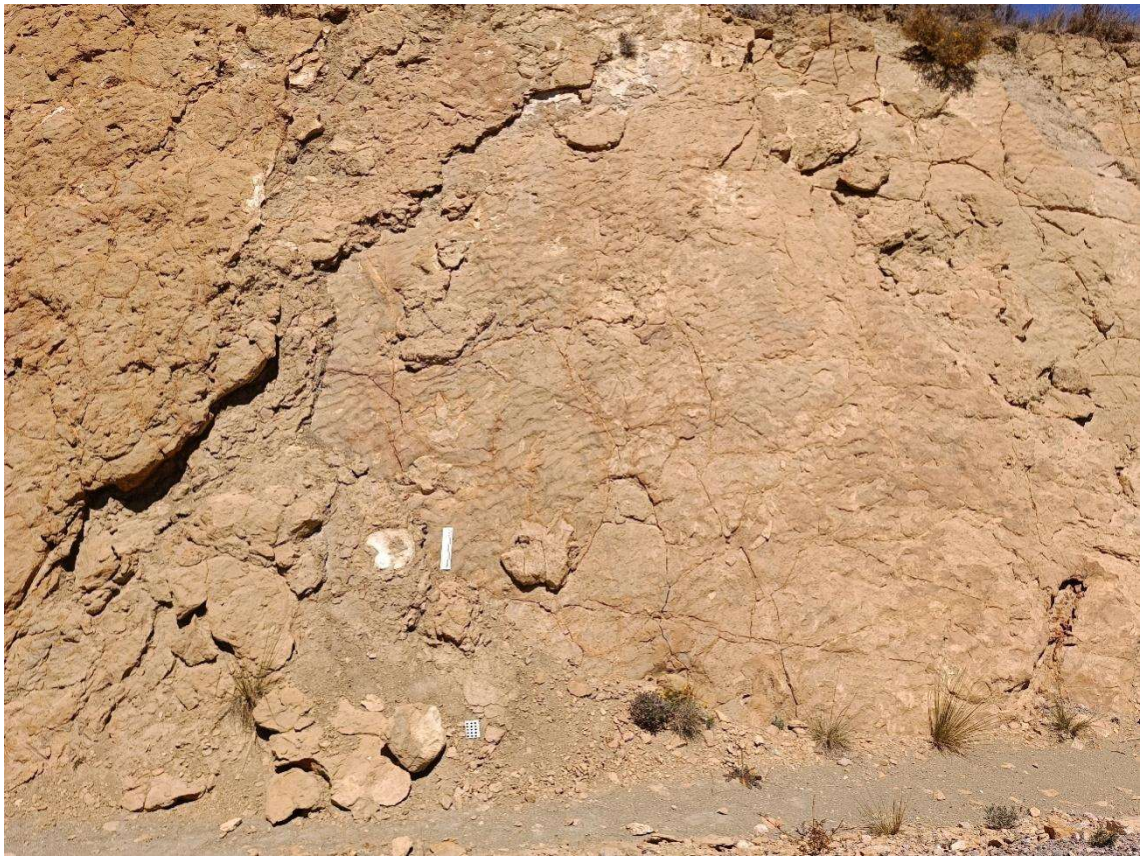

Figura 1.- Fotografía del nivel EC1, nótese el modo de conservación de la mayoría de icnitas como epirelieves convexos y el relleno de una icnita de ornitópodo (en color blanco) cuyo sedimento circundante todavía no se ha erosionado.

Las icnitas de ornitópodos de gran tamaño son con diferencia las más abundantes en las unidades barremienses de las subcuencas de Galve y Peñagolosa, aunque también hay representados otros grupos como terópodos, saurópodos y tireóforos (Cobos et al., 2016; 2018; Herrero et al., 2017; García-Cobeña et al., 2024).El nuevo yacimiento es de especial interés, particularmente el nivel EC1 que exhibe en una única superficie al menos dos icnotaxones diferentes. Esta icnoasociación no es común en el resto de los yacimientos barremienses de estas subcuencas, los cuales suelen estar dominados por un único icnotaxón (*Caririchnium*), atribuido a grandes ornitópodos.

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Conservación, restauración y preparación de yacimientos con icnitas de dinosaurios en la provincia de Teruel (España): 20 años de investigación y resultados

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Palabras clave: Dinosauria, yacimientos paleontológicos, huellas fósiles, intervención, patrimonio natural.

Introducción

La provincia de Teruel cuenta con un importante registro paleontológico de vertebrados continentales mesozoicos, en el que destacan varios yacimientos con icnitas de dinosaurios. Estos yacimientos, distribuidos por gran parte del territorio turolense, abarcan un amplio intervalo geocronológico, desde el Jurásico Superior hasta el Cretácico Superior, e incluyen una gran diversidad de morfotipos de icnitas (p. ej. Alcalá et al., 2014; Cobos et al., 2016; Mampel & Cobos 2022; Castanera et al., 2024; García-Cobeña et al., 2024). Trece de estos yacimientos han sido declarados con la máxima figura de protección, Bien de Interés Cultural (BIC) en la categoría de Conjunto de Interés Cultural Zona Paleontológica, por el Gobierno de Aragón (Cobos et al. 2018).

Desde hace más de veinte años, la Fundación Conjunto Paleontológico de Teruel-Dinópolis ha realizado un conjunto de actuaciones en estos yacimientos de icnitas, combinando, al margen de la investigación estrictamente paleontológica y geológica, intervenciones de conservación, restauración y preparación con planes museográficos y estrategias de puesta en valor para el desarrollo territorial (Cobos & Alcalá 2018; Cobos et al. 2020).

El objetivo de este estudio es analizar la evolución de los productos y tratamientos utilizados para la conservación de estos yacimientos, así como identificar los que ofrecen mejores resultados en términos de compatibilidad con el sustrato litológico y durabilidad en el tiempo.

Metodología

Todas las actuaciones realizadas en los yacimientos de icnitas de Teruel para minimizar los efectos de degradación se han regido por una metodología científica (Ballano et al. 2008), al amparo de criterios nacionales e internacionales como las Cartas de UNESCO, ICOM o el Proyecto COREMANS (Ministerio de Educación, Cultura y Deporte 2012) y por la normativa patrimonial vigente en España y Aragón (Ley 16/1985 del Patrimonio Histórico Español y Ley 3/1999 del Patrimonio Cultural Aragonés). Esta metodología se ha desarrollado de manera similar en otros territorios nacionales como La Rioja (Caro et al. 1998; Caro & Pavía 1998, 2001).

Por tanto, cada intervención ha respondido a un análisis individualizado de las condiciones geológicas, ambientales y estructurales del yacimiento. En este caso hay que destacar la elevada altitud de los afloramientos en la provincia de Teruel (en muchos casos por encima de los 1200 m s.n.m.) que ha condicionado la selección de algunos materiales y los tiempos de actuación. En general, todas las intervenciones directas sobre los

yacimientos se han basado en: (1) eliminación de derrubios y vegetación, (2) adhesión de fragmentos y escamas desprendidas, (3) relleno de fisuras y grietas, (4) gestión del agua para evitar escorrentías y acumulaciones y (5) consolidación estructural de los sustratos (p. ej. Ferrer-Ventura et al., 2019). Respecto a los productos utilizados (adhesivos, morteros, consolidantes e hidrofugantes) se han ido realizando ensayos preliminares tanto en laboratorio, utilizando cámaras de envejecimiento hasta condiciones extremas, como *in situ* comprobando la estabilidad de los productos en condiciones naturales.

Los trabajos de observación y selección de materiales llevados a cabo a lo largo de estos años, han permitido tener una visión global sobre las técnicas y productos más adecuados para la conservación, restauración y preparación de yacimientos de icnitas.

Resultados y discusión

Procesos de intervención continuados en el tiempo, como la eliminación periódica de la vegetación, la gestión eficaz de aguas superficiales y/o el sellado de grietas y fisuras, han demostrado ser decisivas en la ralentización de los procesos de alteración, al tiempo que contribuyen de forma sustancial a preservar la integridad del yacimiento y a mejorar la visualización de las icnitas.

Los adhesivos más adecuados para la estabilización de fragmentos y fijado puntual de elementos son los compuestos de naturaleza epoxídica bicomponente flexible. Estos han mostrado excelentes resultados de estabilidad frente al envejecimiento y la capacidad de adherencia en las variaciones térmicas y ambientales (características fundamentales en contextos de exposición a la intemperie).

Para el relleno de fisuras y grietas, los morteros formulados con cal natural de media dureza y áridos en proporción 1:3 han ofrecido resultados óptimos en todos los yacimientos. Este tipo de mortero presenta ventajas significativas en términos de compatibilidad físico-química con los sustratos litológicos, además de una elevada transpirabilidad y una buena resistencia a los agentes de alteración. En el caso de los morteros bastardos y de cemento, no se han detectado alteraciones físicas o mecánicas destacables durante el periodo de observación, lo que ha permitido confirmar su estabilidad inicial. No obstante, su uso queda desaconsejado debido a sus propiedades intrínsecas: alta rigidez, escasa transpirabilidad y una incompatibilidad progresiva con el sustrato pétreo, especialmente en contextos donde la porosidad y la humedad ambiental son factores condicionantes (Garate et al. 2002). Se recomienda, por tanto, la utilización preferente de morteros de cal hidráulica natural, que, si bien presentan una menor resistencia mecánica, ofrecen un equilibrio más favorable entre la funcionalidad, la compatibilidad litológica y la capacidad de respuesta ante agentes de deterioro.

En yacimientos con litologías calcáreas, los consolidantes más eficaces han sido aquellos formulados con nanopartículas de hidróxido de calcio, debido a su elevada compatibilidad, su capacidad de penetración capilar y su eficacia para reforzar estructuras debilitadas sin alterar la porosidad original del material. Los yacimientos con litologías silíceas han respondido favorablemente a la aplicación de consolidantes e hidrofugantes a base de compuestos de silicato, los cuales promueven una reestructuración interna eficaz y duradera sin inducir tensiones diferenciales ni alteraciones cromáticas graves.

Además, se ha observado que los yacimientos protegidos y cubiertos mediante techumbres presentan una menor tasa de degradación y requieren intervenciones menos frecuentes (Pavía et al. 2007), lo que avala la eficacia de estas estructuras como medida preventiva.

En definitiva, la eficiencia global de las acciones de conservación está determinada por tres aspectos clave: continuidad temporal en el mantenimiento, adecuación de las soluciones técnicas a cada caso y uso exclusivo de materiales compatibles con el soporte litológico.

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Update of the ankylosaurian Maastrichtian record from the Iberian southeastern Pyrenees

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Keywords: Dinosauria, Ornithischia, Thyreophora, Osteoderms, Western Europe, Late Cretaceous.

Introduction

Ankylosaurs are among the most distinctive herbivores of the Mesozoic Era. This clade of quadrupedal dinosaurs was unique in possessing a heavily armored shield made of osteodermal scutes and plates of various shapes and sizes. The ankylosaur fossil record spans the Middle Jurassic through the latest Cretaceous of primarily North America and Asia, along with more basally-branching representatives in the southern landmasses.

Although comparatively rare and fragmentary, the Late Cretaceous European record revealed a distinct diversity of ankylosaurs, predominantly represented by Polacanthidae and Struthiosauridae (*sensu* Raven et al., 2023). The better-known genus in the continent is *Struthiosaurus,* which includes the type species *S. austriacus* (Campanian of Austria), *S. languedocensis* (Campanian of France), and *S. transylvanicus* (lower Maastrichtian of Romania) (Ösi & Prondvai, 2013). The discovery of the basal nodosaurid *Hungarosaurus tormai* from the Santonian of Hungary further expanded the taxonomic diversity of European struthiosaurids (Ösi & Prondvai, 2013; Ősi, 2015).

Ankylosaur discoveries in the southeastern Pyrenees of northern Spain and southern France have further supported the presence of *Struthiosaurus* in western Europe (Pereda-Suberbiola, 1999; Garcia & Pereda-Suberbiola, 2003). In this region, the ankylosaur record is limited to a humerus (Martín Jiménez et al., 2017), two teeth (Álvarez-Sierra et al., 1994; López- Martínez et al., 2000; López-Martínez, 2003) and two osteoderms (Santafé et al., 1997; Castillo-Visa et al., 2022). The fragmentary nature of this record hinders its taxonomic identification (López-Martínez, 2003; Martín Jiménez et al., 2017; Castillo-Visa et al., 2022). Therefore, every new discovery of ankylosaurian material is potentially critical for advancing the taxonomic diversity and evolutionary biology of these animals in the European continent.

Here, we describe new ankylosaurian material from three Maastrichtian localities of the south-central Pyrenees of Lleida province, Catalonia, northeastern Spain, and discuss their taxonomic affinity and biostratigraphic implications.

Material

The study sample consists of five osteoderms. Three of them were collected at the lower Maastrichtian Fontllonga-6 locality (Fondevilla et al., 2019) in the eastern Àger syncline. Another osteoderm came from the lower Maastrichtian site of Vicari-4 (Fondevilla et al., 2019) in the eastern Tremp syncline. Finally, a fifth osteoderm was found at the upper Maastrichtian Molí del Baró-1 locality, also in the eastern Tremp

syncline (Marmi et al., 2016). All elements are housed at the Museu de la Conca Dellà (MCD, Isona, Pallars Jussà, Catalonia, Spain). The nomenclatural terminology follows Ösi & Makadi (2009) and Arbour et al. (2014).

Osteology

Fontllonga-6. The largest element preserves most of its anterior and posteromedial regions. The complete osteoderm may have been subsquared to subrectangular. The longer anteroposterior dimension exceeds 10 cm. The surface texture is smooth. The medial margin is dorsoventrally convex and mostly complete, albeit slightly abraded. A median keel is present on the posterior extent of the dorsal surface of the osteoderm. The dorsal margin of this keel is missing. It may have occupied an anteromedian pectoral or perhaps an undetermined sacral position on the dorsal surface of the body. This is estimated on the basis of the similar lateromedially expanded surface of the cervical plate-like osteoderm base observed in *Struthiosaurus* sp. of Laño (Pereda-Suberbiola, 1999), and the cervical and caudosacral plates of *Europelta* (Kirkland et al., 2013); and unlike those dermal armor morphotypes of other recognized body regions in *Europelta* (i.e., dorsal osteoderms. Kirkland et al., 2013).

With a preserved anteroposterior length of 6.5 cm, the second osteoderm is highly fragmentary, hindering an estimation of its position in the body. Notably, this element features a slightly curved keel, which is mostly eroded. The surface texture of the osteoderm is smooth.

The third osteoderm is also partially preserved, twice as broad as it is long. It measures 5.5 cm in lateromedial width. As the other osteoderms collected so far from this site, its surface texture is smooth. This element features a low and short, posteriorly projected median keel. The preserved overall proportions and the morphology of the median keel in this osteoderm are similar to some of the scutes of the Laño *Struthiosaurus* sp. (Pereda-Suberbiola, 1999). Consequently, this osteoderm likely originated from either the dorsal or the caudal region of the body.

Vicari-4. All that is left of this osteoderm are parts of its left anterolateral and posterior regions. The median keel is relatively short and located near the posterior end of the bone. It rises abruptly from the smooth dorsal surface of the element.

Molí del Baró-1. This site has provided at least five osteoderms. Of these, all but the element described here remain embedded in rock matrix and under preparation. The osteoderm is tear-shaped, longer than wide (~5cm in length). There is a relatively low, posteriorly raising median keel extending throughout the length of the element. This keel also becomes thicker near the posterior end of the osteoderm. The surface texture is ornamented with fine rugosities similar to that of struthiosaurids (Kirkland et al., 2013; Ösi et al., 2019). The overall shape and proportions of this osteoderm, along with the morphology of its median keel, indicates that this dermal bone would be likely positioned on the caudal region of the body (Pereda-Suberbiola, 1999).

Implications for western European ankylosaur taxonomy and biostratigraphy

The new osteoderm recovered at Molí del Baró-1 supports previous studies showing the presence of non-ankylosaurid ankylosaurs in the Maastrichtian of Western Europe. Further, the dermal bones from the other two localities show a smooth surface texture. This feature is commonly recognized (despite not unambiguously) in non-ankylosaurid ankylosaurs, with the exception of the ankylosaurid *Ankylosaurus* (Burns and Currie, 2014), which reinforces the idea of Ankylosauridae being absent in the region. Notably, the Fontllonga-6 and Molí del Baró-1 are the first localities in the region

providing multiple ankylosaurian elements in a single site, possibly representing a single individual in each locality. Further, the osteoderms found in Fontllonga-6 and the one in Vicari-4 are from different body regions, allowing for a more nuanced understanding of the morphological variation of these elements within a single individual.

Previous studies had documented the presence of ankylosaurs in the Iberian southeastern Pyrenees up to the early Maastrichtian, approximately until the faunal turnover when, as far as ornithischians is concerned, they appear to have been replaced by hadrosaurids (Vila et al., 2016). The new material extends the ankylosaur record in this region well into the late Maastrichtian. The precise and robust dating of the Molí del Baró-1 site (C29r; Vila et al., 2012) places this as the youngest record of ankylosaurs in Europe, with the clade having persisted until the K-Pg event. This finding adds to our current understanding of ankylosaurian resilience leading up to the end-Cretaceous extinction event.

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First reconstruction of the neurovascular network of the maxilla of *Iguanodon bernissartensis* from the Lower Cretaceous of Morella (Castellón, Spain)

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Keywords: Dinosauria, Styracosterna, computed tomography, Trigeminal nerve.

Introduction

The study of dinosaur neuroanatomy is a growing field. This field is mostly dominated by the study of the cavities of the central nervous system on the braincase. However the increasing study of the neurovascular cavities on the rostral bones in recent years is allowing a more thorough reconstruction of the neurovascular system (Rotatori et al., 2023).

The trigeminal nerve is the primary somatosensory nerve that can be identified in the rostral bones. It stems from the hindbrain and then divides into three main rostral divisions: the ophthalmic division (V1), the maxillary division (V2), and the mandibular division (V3). These branches with their corresponding arteries and veins run through bony canals in the nasal (V1), the maxilla (V2) and the dentary (v3) (Bouabdellah et al., 2022; Porter & Witmer, 2020). Its knowledge in Ornithopoda however, is so far limited to an indeterminate Dryosaurid (Roratori et al., 2023), the elasmarian *Galleonosaurus* (Herne et al., 2019), the non hadrosaurid Styracosterna *Fukuisaurus* and the Hadrosaurid *Edmontosaurus* (Kawabe & Hattori, 2021). We explore this neurovascular network in the maxillae of the non hadrosaurid Styracosterna *Iguanodon bernissartensis.*

Material and Methods

Two right maxillae (CMP11.1 and CMP11.2) retrieved from the upper Barremian "Arcillas de Morella" Formation at Morella (Castellón, Spain) were referred to the large-sized European ornithopod *Iguanodon bernissartensis* (Gasulla et al., 2014). To evaluate potential differences between these specimens and other dinosaurs, the maxillae were scanned using computed axial tomography (CT-scan).

Description of the maxillary canals

The maxillary canal of the best preserved CMP11.1 has a relatively large diameter and runs longitudinally through the maxilla dorsal and labial to the roots of the teeth. This main canal branches into secondary canals that exit the maxilla through two rows of foramina in the lateral surface. The secondary canals that exit through the ventral row of seven foramina form an obtuse angle with the posterior part of main maxillary canal. The second row of four foramina emerge lateral to the main canal with a close to 90 degree angle in dorsal or ventral view. Finally, the main canal exits through the anterior maxillary foramen without branching.

Preservation of the second maxilla CMP11.2 is not as good as CMP11.1 but it also shows the same structure: a large main maxillary canal and some ventral and lateral rows of foramina. A comparison with the trigeminal V2 branch from a braincase of a different individual also referrable to *I. bernissartensis* (Rodríguez-Barreiro et al., 2024) shows a

diameter very close to that of the posterior foramen in both maxillae, suggesting no drastic changes in the diameter of V2.

Discussion: Comparison with other ornithopods

The maxillary canal has been described only in a handful of non-avian dinosaurs (Bouabdellah et al., 2022), especially in theropods (Ibrahim et al., 2014; Paulina Carabajal et al., 2016; Barker et al., 2017; Porter & Witmer, 2020). But among the clade Ornithopoda this structure has only described before in *Galleonosaurus dorisae* a basal elasmarian ornithopod from the Barremian of Australia (Wonthaggi Formation) (Herne et al., 2019).

Both *Iguanodon* and *Galleonosaurus* share an obtuse angle of the secondary canals with the posterior portion of the main canal, however these secondary canals are noticeably longer in *Iguanodon*. Also, the number and distribution of the external foramina differ; in *Galleonosaurus* there is one predominant ventral row of foramina but in the anterior part of the maxilla the canal divides into multiple branches anterior to the antorbital fenestra (Herne et al., 2019; Bouabdellah et al., 2022). In *Iguanodon* the dorsal row of foramina is distributed in the anterior half of the bone, however in both taxa these dorsal foramina are located anterior to the ascending process of the maxilla. This suggests that the more spaced distribution in *Iguanodon* might be a product of the elongation of the anterior portion of the maxilla.

Conclusion

The dorsal alveolar canals in ornithopods are large and the secondary canals show a characteristic obtuse angulation which differs with the branching of these canals in other non-avian dinosaurs. The differences in the organization of the second dorsal row of secondary canals among ornithopods particularly the density, number of rows and position might be a product of the elongation of the preorbital region in Iguanodontia, absent in earlier branching ornithopods.

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New ichthyosaur remains from the Turmiel Formation (Lower Jurassic) of Ariño (Teruel, Spain)

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Keywords: Systematic, marine reptiles, Ichthyopterygia, Neoichthyosauria, cranial remains.

Introduction

Ichthyosaurs were a group of fully aquatic marine reptiles that lived from the Early Triassic to the Late Cretaceous, spanning a temporal range of approximately 145 million years and achieving a wide global distribution.

Despite their cosmopolitan distribution and abundance in Jurassic localities across Europe (often with exceptional preservation), the ichthyosaur record in the Iberian Peninsula, and especially in Spain, is generally scarce, isolated, and fragmentary. However, the southern paleogeographic position of Iberia relative to other European sites enhances the value of these discoveries. These findings extend and broaden the presence of this group of marine reptiles in the western Tethys region, reaching areas much farther south than their main areas of diversity and abundance, such as Central Europe.

Ichthyosaur remains in the Iberian Peninsula have been primarily found in Lower Jurassic deposits across several localities on the Portuguese Atlantic coast and in northern Spain, specifically in Asturias (Ruiz-Omeñaca et al., 2006; Pereda-Suberbiola et al., 2010; Pratas e Sousa et al., 2025). Several significant discoveries stand out, contributing to our understanding of the evolution and distribution of these marine reptiles in the proto-European Atlantic Ocean. These include *Gadusaurus aqualigneus*, a Neoichthyosaurian thunnosaurian from the Sinemurian (Pratas e Sousa et al., 2025), and the remains of a partial *Leptonectes* sp. skeleton found in the Pliensbachian of the Rodiles Formation, Asturias (Fernández et al., 2018). In addition, Triassic remains of an ichthyosauriform have been described in the Balearic Islands (Matamales-Andreu et al., 2020), an ichthyosaur in Manzanera, Teruel (Aragon) (de Miguel Chaves et al., 2015), and several vertebrae in the Toarcian of Alòs de Balaguer (Catalonia) (Chambers et al., 2012).

In this context, we present the first Jurassic ichthyosaur remains found in Aragon, significantly expanding the Iberian fossil record.

Geographical and Geological Setting

The remains came from two sites, Mas del Gato-1 and Mas del Gato-2, situated a few kilometres northwest of the town of Ariño, within the province of Teruel (Aragon, Spain), in the northeastern Iberian Peninsula.

Both localities are found within the Turmiel Formation, as defined by Goy et al. (1976). This formation's stratotype is located in the Mesa River valley in Guadalajara, Spain. The Turmiel Formation extends not only through that area but also into the Iberian Range of Teruel, and, in isolated occurrences, even into the Catalan Coastal Range. Its age is primarily Toarcian, though locally, its lower part can date to the late Pliensbachian,

and its upper part to the early Aalenian. Therefore, it represents the last Lower Jurassic unit present in the study area.

This formation is characterized by an alternation of marls and limestones (predominantly mudstone and, to a lesser extent, wackstone and packstone). It exhibits shallowing and deepening sequences, with sedimentation occurring in an outer shelf environment, below wave base. Occasionally, tempestite levels are observed, which can extend for several tens of kilometres. In the Ariño area, the Turmiel Formation can reach a thickness of up to 40 meters (Goy et al., 1997).

Material and methods

The material from the Mas del Gato-1 locality was recovered in the 1990s by José María Abad and subsequently donated to the Museo de Ciencias Naturales de la Universidad de Zaragoza. The remains, found disarticulated and fragmented, include: an incomplete skull; part of the appendicular skeleton, with several fragments of the pectoral girdle, an incomplete right forefin; a fragment of the left humerus; as well as various rib fragments. Given the preservation state of the remains and the presence of some external molds where the body fossil had been lost, they were scanned at the TESCAN MicroCT CoreTOM at CENIEH (National Center for Research on Human Evolution) in Burgos (Spain).

From the Mas del Gato-2 locality, two large posterior dorsal or anterior caudal vertebrae, a fragment of a third caudal vertebra, a phalanx, and a tooth fragment were recovered. This material was found and donated to the Museo de Ciencias Naturales de la Universidad de Zaragoza by the geologists María José Mayayo and Felipe Barbed.

Results and Discussion

The morphology of the reconstructed skull of Mas del Gato-1 features an elongated, narrow rostrum with numerous small, very similar conical teeth and aulacodont dental implantation. These characteristics allow the specimen to be assigned to an ichthyosaur within the Parvipelvia euichthyosaur clade (Maxwell & Cortés, 2020).

The morphology of the left forefin displays a humerus with only two facets for the radius and ulna, and a phalangeal count between 4 and 5 digits. This is a typical synapomorphy of ichthyosaurs belonging to the Neoichthyosauria clade up to the Middle Jurassic, at which point ichthyosaurs of this clade began to exhibit three facets on the humerus, a distinctive character of the Ophthalmosauridae family (Fischer et al., 2012). Therefore, the Mas del Gato-1 remains belong to a neoichthyosaur, likely from the Eurhinosauria clade or the families Ichthyosauridae or Stenopterygiidae, within Thunnosauria.

As for the remains of the Mas del Gato-2 locality, the vertebrae exhibit the typical biconcave disc morphology, with a length of 6–7 cm and a diameter of approximately 12–13 cm. Regarding the tooth fragment, it shows distinct striations. The material is highly fragmentary and does not present conclusive diagnostic characters. However, the size of the vertebrae and the tooth are comparable to remains described for the neoichthyosaur *Temnodontosaurus*, the only Toarcian genus that reached significantly large body sizes. Furthermore, longitudinal striation on the dental enamel is a character present in Triassic ichthyosaurs, but it tends to be reduced or absent in more derived clades. *Temnodontosaurus* is characterized by having teeth with distinct longitudinal striations.

Conclusions

The ichthyosaur remains from the Turmiel Formation (Toarcian) at the Ariño localities belong to the Neoichthyosauria clade. It is probable that they represent two distinct species: a small-sized thunnosaurian and a large-bodied ichthyosaur, whose remains are comparable to those of the genus *Temnodontosaurus*.

The co-occurrence of these two types of specimens within the same geological formation suggests an ecological niche partitioning, with each species likely exploiting distinct resources or employing varied hunting strategies. These discoveries not only confirm the presence of at least two ichthyosaur species in the Toarcian of the Iberian Range, but also provide crucial evidence for the presence of these Early Jurassic marine reptiles in the northeastern Iberian Peninsula.

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Dinosaurios en el aula: una unidad didáctica para desarrollar el pensamiento científico en el tercer ciclo de Educación Primaria

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Palabras clave: paleontología, aula, enseñanza, ciencias naturales.

Resumen

La enseñanza de las Ciencias Naturales en la etapa de Educación Primaria puede beneficiarse enormemente de propuestas que partan de los intereses del alumnado. En este contexto, los dinosaurios constituyen un recurso didáctico excepcional, al conectar con la curiosidad infantil y facilitar un acercamiento significativo a contenidos científicos (Royo-Torres et al., 2021). El fenómeno conocido como *dinomanía*, acuñado por Sanz (2000), refleja el impacto sociocultural que ejercen los dinosaurios en la infancia a través del cine, la literatura y los medios de comunicación. Aprovechar este interés permite introducir conceptos de biología, ecología, paleontología y geología de forma integrada, participativa y motivadora.

La unidad didáctica diseñada parte de esta premisa, con el objetivo de favorecer una actitud positiva hacia las ciencias y prevenir el rechazo que pueden generar estos contenidos si se presentan de forma descontextualizada. Aunque los dinosaurios son animales extintos, siguen despertando fascinación, pese a que el conocimiento general sobre ellos suele estar muy limitado. La propuesta busca ampliar esa visión y ofrecer una comprensión más rigurosa y amplia desde una perspectiva científica.

La unidad didáctica se delineó gracias a la realización del Trabajo de Fin de Grado de la primera autora. Las sesiones programadas y diseñadas realizaron en el contexto de un prácticum en el Colegio de Educación Infantil y Primaria Matilde de la Torre de Muriedas, en Cantabria. Durante el desarrollo de las sesiones la tutora se encontraba en el aula, y el alumnado se formaba por 22 alumnos y alumnas sin necesidades educativas especiales. Cada una de las sesiones realizadas, tuvo una duración de una clase (aproximadamente una hora).

La unidad se estructuró en tres bloques. El primero, "El medio a través de los dinosaurios", establece vínculos entre las referencias culturales del alumnado y los contenidos científicos, fomentando el pensamiento hipotético y argumentativo. La primera sesión consistió en la comparación de dibujos sobre los dinosaurios antes y después de realizar una puesta en común sobre conocimientos previos. La segunda sesión trató de conocer las distintas etapas geológicas donde vivieron los dinosaurios a través de una interpretación del propio alumnado. Por último, la tercera sesión consistió en relacionar diferentes dinosaurios con la fauna de la actualidad, realizando conexiones a

través de las características físicas y clasificando las diferentes clases de dinosaurios con material elaborado por la autora.

El segundo bloque, "Desaparición de los dinosaurios", se centró en la extinción. Partiendo de ideas previas para introducir contenidos científicos vinculados a problemáticas actuales mediante los Objetivos de Desarrollo Sostenible (ODS), se promueve el pensamiento crítico y el uso del método científico. Las sesiones comienzan por la elaboración de hipótesis y posterior investigación sobre las causas de las extinciones, relacionando la de los dinosaurios con las problemáticas actuales (ODS). La segunda actividad consistió en aprender sobre el proceso de fosilización y la realización de un fósil por el alumnado. Por último, se empleó el método científico para elaborar hipótesis sobre diferentes rastros de huellas.

El tercer bloque culminaba con una salida didáctica al Museo Jurásico de Asturias, donde, a través de un "diario del explorador" elaborado por el propio alumnado, se reforzaría y amplían los aprendizajes mediante la observación directa. Sin embargo, debido a cuestiones internas del centro de organización docente, no se pudo realizar este último bloque.

Los resultados derivados de esta propuesta sugieren que el uso de los dinosaurios como recurso educativo incrementa la motivación, la participación activa y la comprensión de contenidos científicos. Se confirma así que el acercamiento a las ciencias desde referentes cercanos puede contribuir al desarrollo del pensamiento crítico y de competencias científicas. La propuesta se fundamenta en teorías como el aprendizaje significativo y el enfoque constructivista, que promueven un rol activo del alumnado en la construcción del conocimiento (Piaget, 1972). De esta manera, se ha apreciado cómo el alumnado ha ido modificando su aprendizaje tras las puestas en común y la colaboración. Además, se destaca el valor de conectar los contenidos científicos con la realidad actual del alumnado, lo cual favorece no solo la comprensión, sino también la implicación emocional y ética con los problemas del mundo. Las actividades experienciales, como la de realizar sus propios dibujos, fósiles o hipótesis, consolidan los aprendizajes y fomentan la autonomía. No obstante, la aplicación de esta propuesta requiere una actitud docente flexible, capacidad de adaptación del currículo y formación en metodologías activas.

Como conclusión, este trabajo evidencia la necesidad y el valor de acercar las ciencias al alumnado de Primaria desde sus propios intereses. Formar desde la curiosidad y la motivación es una vía poderosa para construir aprendizajes duraderos y significativos. El reto del profesorado está en ampliar la mirada, abrir el currículo y permitir que la voz del alumnado tenga un papel activo en su propio proceso de aprendizaje.

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New Data on the Paleopathology of Sauropod Caudal Skeleton from the Upper Jurassic and Lower Cretaceous of Spain

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Keywords: Vertebrae, Haemal arch, Histology, Computed Tomography, *Europatitan*, *Demandasaurus*.

Introduction

The Sierra de la Demanda (Burgos) hosts an extensive and highly biodiverse dinosaur fossil record (Blázquez et al., 2024). Among its notable Sauropoda assemblage are Upper Jurassic and Lower Cretaceous macronarians and diplodocimorphs, exemplified by recently described taxa such as *Europatitan* and *Demandasaurus* (Torcida Fernández-Baldor et al., 2011, 2017, 2020, 2024). Furthermore, pathological alterations in the caudal vertebral series have been documented in the holotype material of these dinosaurs. In this study, we conducted a paleopathological assessment of bones belonging to three sauropod specimens recovered from the Sierra de la Demanda. Our aims were to apply paleohistology and computed tomography (CT) scans to describe observed lesions and propose differential and presumptive diagnoses for their etiology.

Materials and Methods

The studied specimens, comprising three distinct individuals (Fig. 1), were recovered from various sites within the western sector of the Cameros Basin and are deposited in the Museo de Dinosaurios de Salas de los Infantes (MDS). Those included: (i) MDS-VPCR,29, an anterior caudal vertebra of an indeterminate sauropod, from the Rupelo Formation (Tithonian, Upper Jurassic) at the Valdepalazuelos-Tenadas del Carrascal locality; (ii) MDS-OTII,5, consisting of two caudal vertebrae and a haemal arch fused, and MDS-OTII,6, an anterior caudal vertebra, are both referred to *Europatitan eastwoodi* and were recovered from the El Oterillo II site, within the Castrillo la Reina Formation (Barremian–Aptian, Lower Cretaceous); and (iii) MDS-RVII,23 and 232, two middle-posterior hemal arches from *Demandasaurus darwini*, also from the Castrillo la Reina Formation but recovered from the Tenadas de los Vallejos II site.

CT scans were performed at the Veterinary Hospital of the University of León, using GE Optima® CT540 model, 140 kV, auto amperage and 1.25 or 0.625 mm slice thickness. Histological thin sections were prepared at the University of Zaragoza (SAI) and the University of Salamanca and were studied and photographed at the Paleontology Laboratory of the University of León using a Leica® DMRBE microscope and a ZEISS® AxioCam MRc5 camera.

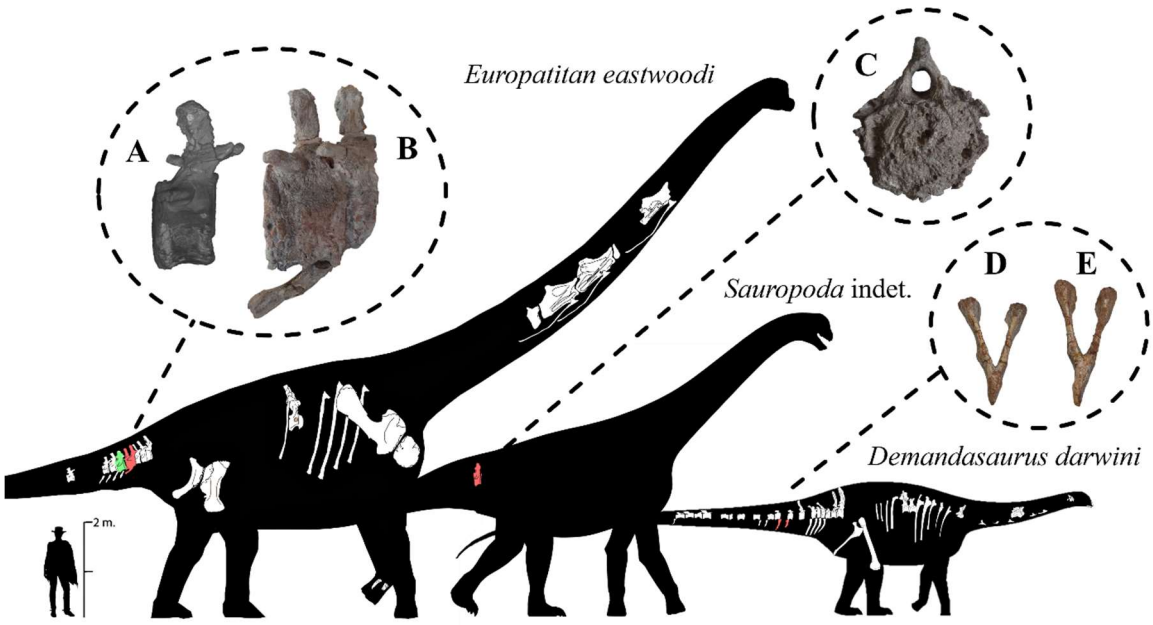

Figure 1. The fossil bones and sauropod specimens examined in this study are illustrated in the figures, with healthy material highlighted in green and pathological material in red. Specifically, *Europatitan eastwoodi* is represented by a healthy anterior caudal vertebra (A, MDS-OTII,6) and a pathological fused block (B, MDS-OTII,5). An anterior caudal vertebra from an indeterminate sauropod (C, MDS-VPCR 29) was also studied. Finally, *Demandasaurus darwini* is represented by two middle-posterior hemal arches (D, MDS-RVII,23 and E, MDS-RVII,232).

Results

Macroscopically and compared to a healthy vertebra (MDS-OTII,6), specimen MDS-OTII,5 clearly showed irregular bone overgrowth and marks corresponding with the left *longissimus caudae* muscle insertion site. This overgrowth created a single, fused mass by incorporating the hemal arch and affecting the lateral and ventral regions of the vertebral centra. Importantly, this periosteal reaction did not invade the medullary canal or involve other vertebral processes. CT imaging revealed a homogeneous internal bone structure, marked by a subtle radiolucent band dorsally at the vertebral junction. Subsequent histological analysis corroborated those findings, demonstrating irregular and disorganized bone tissue.

A smooth-surfaced bulge on the lateral side of the right haemal ramus was observed in haemal arches MDS-RVII,23 and MDS-RVII,232, corresponding with the insertion site of *caudofemoralis longus* muscle. CT scans revealed cortical bone thickening at these sites. Additionally, specimen MDS-RVII,232 presented several cystic cavities in its ventral ramus. Histological analysis was not conducted on these specimens.

The caudal vertebra MDS-VPCR,29 presented irregular-surfaced bone overgrowth affecting its posterior articular face and the lateral aspects of the centrum. Notably, this proliferation did not invade the medullary canal but formed channels on the lateral surfaces of the vertebral centrum for caudal blood vessels. CT scans showed a radiodense band consistent with the irregular growth surface, while histological sections demonstrate irregular and disorganized bone tissue.

Discussion

Lesions observed in the indeterminate sauropod specimen MDS-OTII,5 (consisting of two anterior caudal vertebrae and a hemal arch) were compatible with

various potential pathologies, including congenital alterations, hypervitaminosis A, infection, neoplasia, or chronic degenerative spondyloarthropathy, being the latter the most likely presumptive diagnosis (Craig et al., 2016). When referring to the haemal arches MDS-RVII,23 and MDS-RVII,232, the small pathological area was consistent with exostoses possibly caused by mechanical stress. Additionally, bone cysts or Brodie's abscesses (small foci of osteomyelitis) were observed (Craig et al., 2016). The caudal vertebra MDS-VPCR,29 exhibited lesions compatible with neoplasia, hypertrophic osteopathy, or chronic osteoarthritis (Craig et al., 2016).

Conclusion

The results from this study of Upper Jurassic and Lower Cretaceous sauropods from the Sierra de la Demanda enhance our understanding of the diverse lesions that affected the caudal region of these dinosaurs. The recognized lesions provide new insights into the vascular anatomy and muscular insertions in sauropod tails, as well as how these structures are affected by different pathological processes.

Acknowledgements

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Patologías craneales en terópodos: Caso de estudio *Murusraptor barrosaensis*

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Palabras claves: megaraptorido, fractura, infección piogénica, deformidad
Keywords: megaraptorid, fracture, pyogenic infection, deformity

Introducción

El registro de traumas y patologías óseas es particularmente abundante en dinosaurios mesozoicos, incluyendo a terópodos, saurópodos y ornitópodos (véase Cruzado-Caballero et al., 2020 y referencias allí citadas). Este tipo de evidencias son una herramienta clave para realizar inferencias paleobiológicas y paleoecológicas en faunas fósiles. El análisis de los procesos de curación nos permite estudiar el impacto que las lesiones tuvieron en sus relaciones intra e interespecíficas (Rothschild et al., 2012; Kappelman et al., 2016; entre otros). En el presente trabajo revisamos las patologías encontradas en el esqueleto del dinosaurio terópodo argentino *Murusraptor barrosaensis* Coria y Currie 2016 y proponemos posibles hipótesis para su origen.

Material y métodos

El material estudiado corresponde al esqueleto del megaraptorido del Coniaciense (Cretácico Superior) de Sierra Barrosa (Neuquén, Argentina) *Murusraptor*. Corresponde a ejemplar subadulto de unos 6 metros de largo, el cual presenta diversas patologías en huesos craneales (neurocráneo) y postcraneales (costillas dorsales de los lados derecho e izquierdo; Coria y Currie, 2016). El neurocráneo (incluyendo techo craneano) fue tomografiado en un hospital de Canadá (ver especificaciones en Paulina-Carabajal y Currie, 2017).

Descripción

El análisis macroscópico del neurocráneo determinó que las patologías se localizan en el lado posterior izquierdo y son las siguientes (Fig. 1 A-B): 1) una serie de aberturas irregulares en la cresta nucal del parietal; 2) pérdida de la mitad posterior del proceso paraoccipital del complejo exoccipital-opistótico izquierdo, cuyo extremo distal termina con un sobrecrecimiento de hueso patológico con una superficie irregular; 3) diversas malformaciones en la cara lateral del neurocráneo (lateroesfenoides, proótico y el opistótico-exoccipital y en menor grado el basiesfenoides); y 4) una distribución anómala de los forámenes neurovasculares y de las cavidades neumáticas internas del cráneo. Mientras que el análisis de los huesos postcraneales (costillas dorsales derechas 11, 15º a 17º, 19º y 20º, e izquierda 17º) hablan de una serie de fracturas de diferente

grado de gravedad, algunas de ellas con signos de infección asociada y otras ya curadas o en proceso de curación.

El análisis de las imágenes tomográficas del neurocráneo han revelado una marcada reacción periostal en el proceso paraoccipital izquierdo (Fig. 1 C-D), probablemente asociada a la formación de tejido calloso. Dicha reacción cubre parcialmente el lado medial del proceso, el cual presenta una morfología anómala con la porción distal conservada más ancha mediolateralmente que la del proceso derecho. Además, la superficie posterior del proceso izquierdo muestra una textura rugosa, con aspecto colifloriforme, y el tejido en esta zona patológica tiene una menor densidad, en las imágenes tomográficas, en comparación con el tejido sano.

El examen macroscópico y de las tomografías de los huesos patológicos y su estado de cicatrización no permiten afirmar que todas las lesiones fueran contemporáneas.

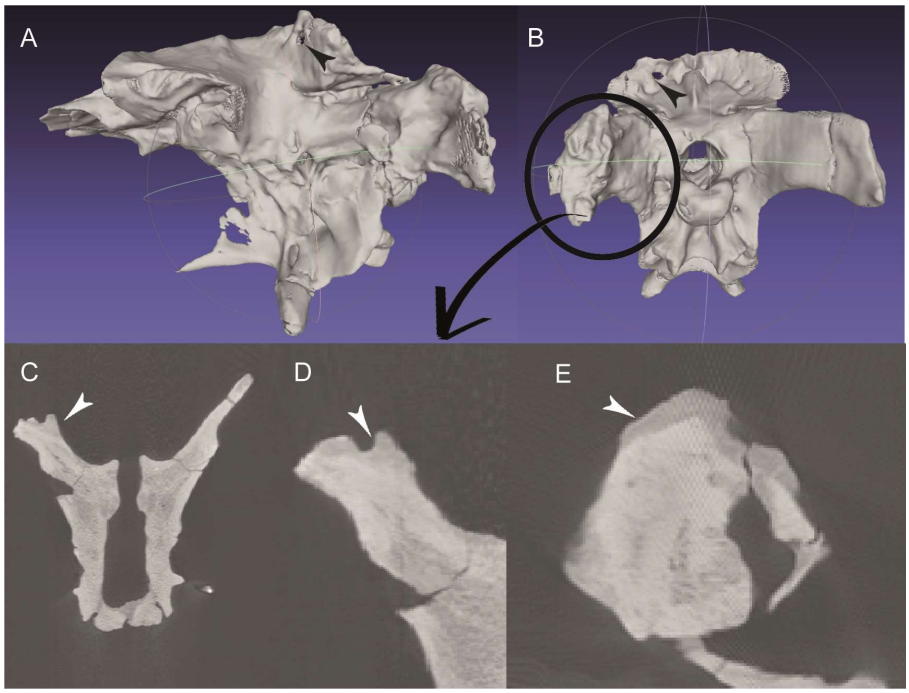

Figura 1. Reconstrucción 3D del neurocráneo de *Murusraptor*. A) vista lateral izquierda, B) vista posterior, C) imagen tomográfica del proceso paraoccipital en sección sagital, D) detalle de la reacción periostal del proceso paraoccipital en sección sagital y E) detalle de la reacción periostal del proceso paraoccipital en sección transversal. Flechas negras indican las aberturas patológicas y las flechas blancas indican la reacción periostal.

Diagnosis

Inicialmente, las aberturas anormales de la cresta nucal fueron interpretadas como marcas dentales provocadas por el ataque de otro dinosaurio terópodo, lo que posteriormente habría desencadenado una infección piogénica (productora de pus). Aquí proponemos dos posibles hipótesis nuevas, ambas vinculadas a un evento traumático, probablemente una mordida de un terópodo en la zona posterior del cráneo o el cuello. En el primer caso, la mordedura en la zona posterior del cráneo habría causado directamente la pérdida del proceso paraoccipital. En el segundo, una mordedura en el cuello habría generado una infección en los tejidos blandos de la zona, derivando en una osteomielitis crónica. Esta, a su vez, habría provocado la reabsorción ósea y, como consecuencia, la pérdida del proceso paraoccipital. En ambos casos, el desarrollo de una

infección piogénica significativa y la respuesta inflamatoria del tejido óseo explicarían la deformación en el lado izquierdo del neurocráneo, la distribución irregular de los forámenes neurovasculares y la presencia de cavidades de reabsorción en distintas áreas.

Implicaciones paleobiológicas

El registro de varias lesiones óseas con diferente grado de curación en el espécimen de *Murusraptor* nos sugiere que el individuo sufrió diversos episodios traumáticos a lo largo de su vida, muy probablemente debidas a su comportamiento depredador, pero también posiblemente a interacciones intraespecíficas (ej., luchas territoriales o durante la época de reproducción) o accidentes indeterminados.

El grado avanzado de curación de varias fracturas asociadas a las costillas dorsales nos sugiere que *Murusraptor* fue capaz de sobrevivir como mínimo varios meses hasta su total curación a pesar del dolor que estas debieron causarle (durante la respiración, desplazamientos o alimentación) y una posible reducción de su movilidad o funcionalidad torácica. Por otro lado, las patologías encontradas en el neurocráneo, caracterizadas por deformaciones y engrosamientos patológicos, podrían haber afectado funciones sensoriales relacionadas con el oído interno o el equilibrio, aunque esto no puede afirmarse con certeza.

Conclusiones

Los análisis realizados muestran evidencias de alteraciones óseas compatibles con patologías curadas o en proceso de curación, lo que sugiere que el animal pudo haber vivido durante un tiempo con una condición que habría afectado su desempeño biológico. No obstante, la información actualmente disponible no permite establecer un diagnóstico definitivo. Es necesario realizar estudios adicionales, incluyendo tomografías en las costillas, con el fin de afinar la diagnosis diferencial y evaluar con mayor precisión las posibles implicaciones paleobiológicas de estas lesiones.

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The dinosaur tracksite of Puente del Molino de Yera (Vega de Pas, Cantabria, Spain): new icnological evidence from continental Lower Cretaceous deposits in the Basque-Cantabrian Basin

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Keywords: Paleoichnology, ornithopod, theropod, Vega de Pas Formation, Hauterivian-Barremian.

Introduction

The Yera River (a tributary of the Pas River) is located in the municipality of Vega de Pas (Cantabria, northern Spain) and has yielded, to date, three significant dinosaur tracksites: Puente del Terrerón (VP4), Puente del Camino Viejo (VP3), and Puente del Molino de Yera (VP2). The latter is the largest and potentially most scientifically relevant outcrop, due to the abundance, preservation quality, and morphological diversity of its tracks, including possible trackways of bipedal dinosaurs.

Track preservation across the three sites is highly variable and strongly influenced by their position within the active riverbed, which results in severe weathering and hydrological erosion. Many of the footprints are continuously exposed to water flow, leading to their progressive degradation (Moratalla, 2004; Moratalla et al., 2007).

The dinosaur tracks are preserved in deposits of the Vega de Pas Formation, Basque-Cantabrian Basin, which dates to the Valanginian–Barremian and corresponds to a meandering fluvial system with extensive floodplains that grade eastward into a coastal lagoonal system (Villaro Formation) (e.g., Pujalte et al., 2004). The trackways are preserved in sandstones exhibiting parallel lamination, erosive bases, and ripple-marked upper surfaces—with asymmetrical ripples indicative of unidirectional currents, and occasionally symmetrical ripples associated with oscillatory flows. These deposits are interpreted as high-energy floodplain deposits, formed between sandy meandering channels during high-water (flood) events within the fluvial system. To date, vertebrate track records from the Lower Cretaceous of the Basque-Cantabrian Basin are extremely scarce, which underscores the paleontological significance of this study (e.g., Díaz-Martínez et al., 2022).

Description

The surface of this outcrop covers approximately 60 m², with a long and relatively narrow geometry (about 18 meters in length by 5 meters in width), and preserves two distinct ichnological horizons (Fig. 1). The lower level consists of a very fine- to fine-grained silty sandstone with well-preserved ripple marks on its surface. These ripples are characterized by low, parallel crests, likely heavily eroded, with an estimated wavelength of around 1.5 cm. Several footprint impressions are present on this level, some of which are incomplete. Most of the clearer tracks exhibit sub-elliptical outlines and vary in size:

five are small (approximately 10 cm in length), while others are three to four times larger. No clear digit impressions or internal structures are visible. In general, the footprints are very shallow, which—aside from a few exceptions—suggests they may be undertracks transmitted from the upper level, which represents the main ichnological surface and shows more extensive bioturbation.

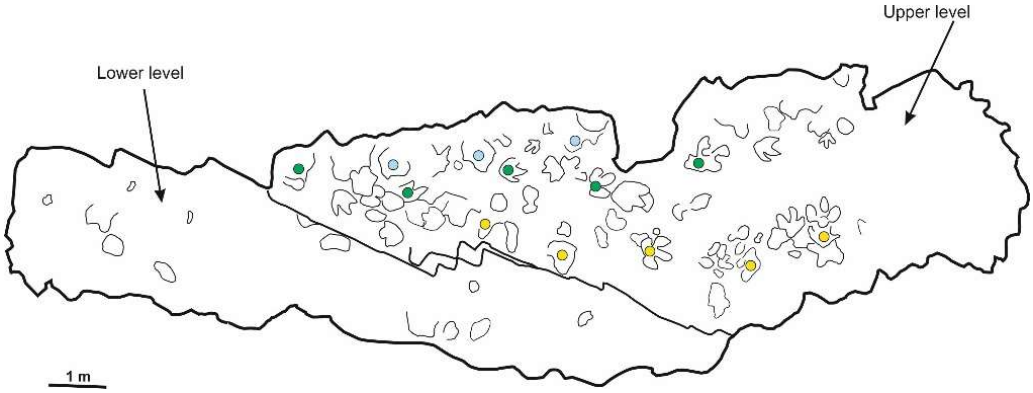

Fig. 1. General view of the Puente del Molino de Yera tracksite (Vega de Pas, Cantabria).

The main ichnological level is also composed of a fine-grained silty sandstone, but in this case, it is heavily bioturbated due to the high concentration of dinosaur tracks. The distribution of these tracks across the surface is relatively homogeneous, although a notable increase in track density is observed in the left and central sectors, where intense accumulations occur (Fig. 1). These dense clusters suggest multiple episodes of track superposition, which are clearly distinguishable in several instances. The tracks do not show any preferred orientation. Some of the larger footprints are incomplete, but most tracks on this level preserve well-defined digit impressions, a clearly outlined morphology, and in many cases are complete, displaying a characteristic tridactyl shape (Fig. 1). Additionally, a set of much smaller tracks—with sub-elliptical outlines similar to those described from the lower level—are also present. Based on these observations, we infer the presence of at least three distinct morphological track types.

Type 1

These are large-sized tracks (approximately 35–45 cm in length), with a well-defined outline and an overall sub-rounded morphology. The digits are short, broad, and robust, with the central digit displaying a U-shaped termination. The plantar surface is broad, and both the medial and lateral margins are either smooth or, when preserved, exhibit two well-marked and nearly symmetrical notches. In the best-preserved examples, the general morphology of the plantar surface shows a high degree of symmetry, due to the presence of two similarly developed notches on both sides of the track (Fig. 2). This symmetry is observable in many tracks across the outcrop, including some of the more poorly preserved specimens. The proximal margin (heel area) is relatively broad and open, typically with a clear outline that indicates a firm contact of the autopodium with the substrate. These tracks are nearly as wide as they are long, allowing their outline to be roughly inscribed within a circular shape (Fig. 2). Despite these consistent features, a significant degree of morphological variation is observed, likely due to the intense weathering that has affected most of the footprints. The combination of these morphological traits suggests that the tracks were most likely produced by medium- to large-sized ornithopod dinosaurs.

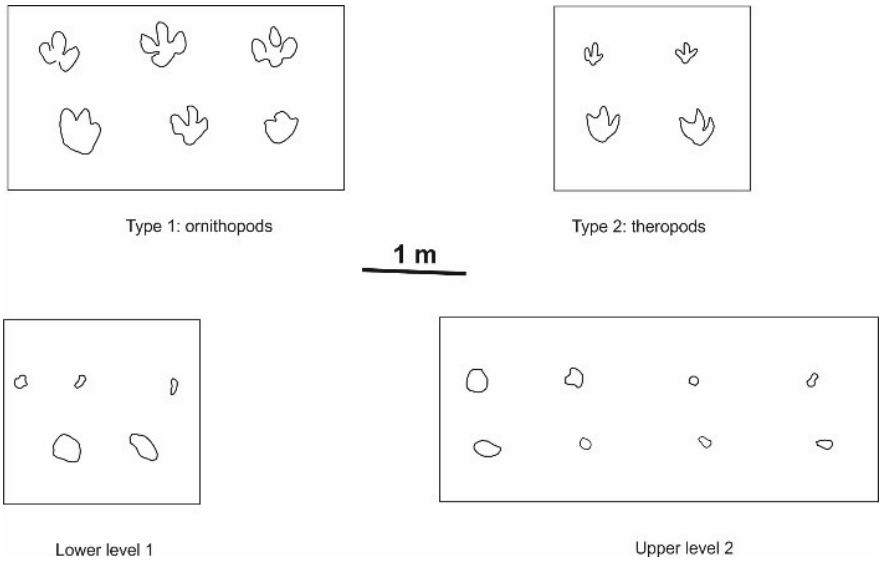

Fig. 2. Morphological ichnodiversity of the Puente del Molino de Yera tracksite (Vega de Pas, Cantabria).

Type 2

These tracks are smaller in size and exhibit a markedly asymmetrical morphology, primarily due to the presence of a medial notch, which is absent on the lateral side. The digits are significantly more elongated and asymmetric, with clear morphological differences between the medial and lateral digits (Fig. 2). The central digit (digit III) is V-shaped and, in some cases, displays a slight medial curvature. Unlike Type 1, the hypex regions (interdigital notches) are also asymmetrically arranged, with the medial hypex positioned more anteriorly than the lateral one. This overall morphology suggests that these tracks were likely produced by theropod dinosaurs, probably of a smaller size than those inferred for Type 1.

Type 3

The map shown in Figure 2 reveals the presence of a number of small-sized, sub-rounded tracks. However, most of these impressions are slightly elongated, resulting in a generally sub-elliptical outline. No digit impressions or internal anatomical structures are visible that would allow for a reliable ichnotaxonomic identification. Some tracks exhibit a sub-rounded shape, while most show a sub-elliptical morphology, with one end being slightly more pointed than the other. In few cases, the tracks display a slightly bilobed outline (Fig. 2), with two mildly asymmetric lobes. This morphology is of particular interest, as—in combination with their small size—it suggests a potential interpretation as manus tracks of ornithopod dinosaurs.

Trackways

The high density of footprints at the Puente del Molino de Yera site suggests the potential presence of trackways. Although several alignments of footprints of the same morphotype are observed, clear and continuous trackways are not unequivocally evident at this locality. Figure 3 presents a selection of the most apparent track alignments within the outcrop, with various potential trackways highlighted using colored circles (blue, yellow, and green).

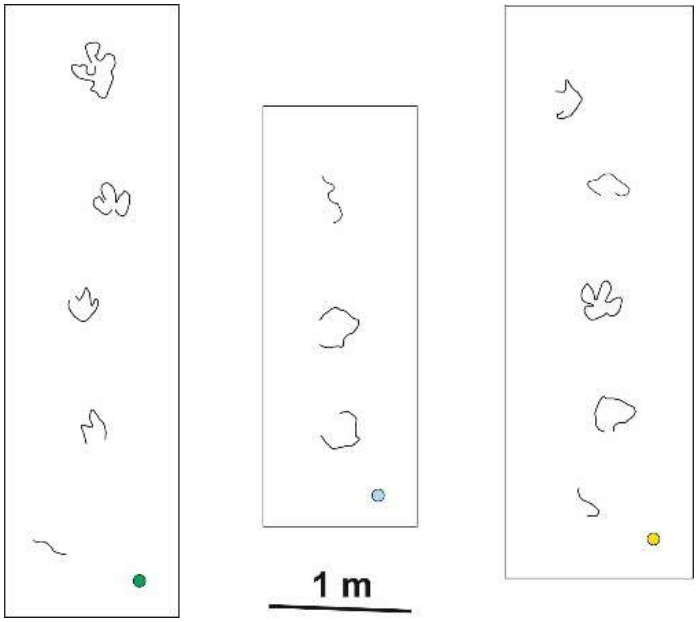

Fig. 3. Potential trackways at the Puente del Molino de Yera tracksite (Vega de Pas, Cantabria).

The trackway highlighted with green circles is composed of at least four medium-to-large tridactyl footprints, plus a possible partial footprint at the beginning of the trackway, which is considerably less well preserved. This potential trackway indicates clear bipedal locomotion, with relatively consistent step and stride lengths as well as a fairly constant pace angulation. The trackway marked with yellow circles exhibits a similar pattern, characterized by relatively consistent stride and step lengths following a mostly linear trajectory.

Conclusions

A new dinosaur tracksite from the Lower Cretaceous of the Basque-Cantabrian Basin is presented. Three distinct track morphotypes have been identified, attributed to theropod and large ornithopod dinosaurs. It is inferred that dinosaurs accessed these areas during low-water stages, when symmetric ripples formed, likely searching among the materials deposited by receding floodwaters. This ichnological record is especially significant due to the scarcity of dinosaur tracks in this basin, providing an important opportunity for comparative analysis with coeval tracksites from other regions.

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Tail tales: the biomechanical diversity of the caudal series of the Late Jurassic sauropods from Tendaguru (Tanzania)

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Keywords: Late Jurassic, Tendaguru, Tanzania, Sauropoda, Biomechanics, 3D musculoskeletal reconstruction.

Introduction

Both the scientific community and the general public no longer hold on to the outdated concept that sauropod dinosaurs were slow animals with an almost identical body plan across different clades. Furthermore, within the Sauropoda clade, we can find dwarf taxa (Díez Díaz et al., 2025; Navarro et al., 2022) and the largest animals that ever walked the earth (Carballido et al., 2017; Lacovara et al., 2014), as well as species with very peculiar anatomical characteristics (see e.g. Gallina et al., 2019; Salgado & Bonaparte, 1991; Sereno et al., 2007). This anatomical diversity may have been vital in defining patterns of behaviour, feeding and locomotion. In this project, we focus on the tails of sauropod dinosaurs and the differences we find in the taxa found in the Late Jurassic of Tendaguru (Tanzania).

The Tendaguru area is located in the southern coastal region of Tanzania (East Africa), ca. 60 km NW of the coastal town of Lindi. The age of the Tendaguru Formation ranges at least from the Callovian or middle Oxfordian to the Hauterivian or even Aptian (ca. 166 to 129 Ma) (but see Bussert et al., 2009). Six members constitute the Tendaguru Formation, and dinosaur remains have been discovered in three of them (from bottom to top): Lower Dinosaur Member (Callovian to middle Oxfordian), Middle Dinosaur Member (late Kimmeridgian), and Upper Dinosaur Member (Tithonian). The Tendaguru Formation was deposited in a marginal marine to continental setting with several marine transgression cycles, with the three Dinosaur Members representing tidal flat, lagoonal and coastal palaeoenvironments (Bussert et al., 2009). Sauropod remains have been recovered from all three of them, but the Upper Dinosaur Member is the one with the highest diversity. This project focuses on the articulated caudal series referred to the mamenchisaurid *Wamweracaudia keranjei*, the diplodocoid *Dicraeosaurus hansemanni*, and the titanosauriform *Giraffatitan brancai*.

We are analysing in detail the anatomy of these caudal series, collecting data to develop for the first time detailed biomechanical analyses of the axial skeleton of dinosaurs. These results will be highly useful for better understanding the locomotion and behaviour of these extinct animals.

Methodologies

This project consists of several steps, so we are following different methodologies and strategies, several of which are innovative in the study of dinosaurs. First, it is very important to be familiar with the workflow for performing biomechanical analyses so that each phase can be planned appropriately (Bishop et al., 2020; Falkingham, 2025). After digitising the caudal elements, the quality of the generated 3D models is assessed (i.e. error deletion, decimation) and retrodeformation techniques are used to reconstruct

specimens that are deformed or have missing elements (Demuth et al., 2022; DeVries et al., 2022; Tschopp et al., 2012).

With the final 3D caudal series, the Osteological and Cartilaginous Neutral Poses are assembled (ONP and CNP) (Stevens & Parrish, 1999; Taylor, 2014), and osteological Ranges of Motion (RoMs) analyses are carried out with different Centre of Rotation (CoR) locations, depending on the articular joint type (concavo-convex or amphicoelous).

Musculature and ligaments often leave characteristic traces (i.e. osteological correlates) on the bone surface of all vertebrates. Thanks to the Extant Phylogenetic Bracket method (Bryant & Russell, 1992; Witmer, 1995; Witmer, 1997), these correlates can be identified on the surface of the caudal vertebrae, assessing muscle origins and insertions, and later with this information, volumetric reconstructions of the muscles can be developed (Díez Díaz et al., 2020).

With the data collected, together with the material properties of both the bones and soft tissues, biomechanical analyses (e.g. multi-body dynamic locomotor simulations, Anderson et al., 2023) are being carried out, developing detailed simulations on how the sauropod tails could have moved. We are also following the Natural Frequency Method (van Bijlert et al., 2021), which uses the natural frequency of the vertical swaying of the tail to estimate the preferred step frequency and walking speed of the animal.

Analyses on the skeletal reconstructions

After calculating the RoMs, we can confirm that the choice of CNP and CoR, as well as whether or not to include the haemal arches in the analysis, will greatly influence the results obtained. As mentioned above, these data can influence the biomechanical simulations performed, so we emphasise the importance of clearly defining in the methodology how and why the parameters have been chosen.

In the case of the three Tendaguru sauropod taxa, significant anatomical variability can be observed in the anterior caudal vertebrae, and this is also reflected in the results obtained, showing different vertebral flexibility at the base of the tail.

The importance of the soft tissues

When dissections or in-vivo biomechanical experiments and analyses are not feasible, or when information on soft tissues is limited, as for extinct species, osteological limits can act as proxies to more accurately calculate RoMs. It can be assumed that these maximum osteological RoMs are reduced by the addition of soft tissue performance. Therefore, if the contact and disarticulation protocols of the osteological constraints are maintained in RoM analyses, they can be very useful for comparisons between extinct animals for which no information on their soft tissues is available.

Even so, in our project, we are analysing the osteological correlates present in the caudal vertebrae and haemal arches of several tails of extant crocodilians, as well as the serial variation in the intervertebral cartilage volume and ligament properties. All this information will be very useful for analysing the anatomical and mechanical properties of the Tendaguru sauropods in greater detail.

What do these differences and results imply for the Tendaguru dinosaur fauna?

As mentioned above, we have identified anatomical differences between the three sauropods, correlated with differences in their musculoskeletal reconstructions and locomotion. This variability is very interesting to assess, especially in an area where three large species coexisted, as there may have been competition for resources (even with

other herbivorous species present in the Upper Dinosaur Member, such as other sauropod taxa and the stegosaurid *Kentrosaurus aethiopicus*). Similarly, a more detailed analysis of all the information obtained can help us better understand migration patterns and speeds, while also assessing communication and defense hypotheses (Baron, 2021; Conti et al., 2022; Myhrvold & Currie, 1997).

Conclusion

Even though tails precede the evolution of paired appendages by ca. 200 million years (Donoghue & Keating, 2014; Schwaner et al., 2021), we are just starting to understand their function, development, and evolution. Because of the complexity of these segmented anatomical structures, the axial skeleton – and in particular the tail – are often ignored within musculoskeletal reconstructions and biomechanical analyses or simplified as stiff element (see e.g. Anderson et al., 2023; Sellers et al., 2013, 2017), making a greater focus toward paired appendage function.

With this project, apart from improving our understanding of the herbivorous faunas of Tendaguru and their relationship with the environment, we want to emphasise the importance of incorporating the axial skeleton (e.g. at least in segments, units or sections) into biomechanical analyses, which will help to perform more realistic simulations and more objective discussions.

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Los dinosaurios que no nos enseñaron. La extinción académica de la paleontología en las aulas

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Palabras Clave: Docencia, Didáctica, Environmental Learning, Aprendizaje, LOMLOE.

Introducción

El número de matriculados en estudios superiores de Geología ha disminuido en la última década, con caídas del 50-65%, dependiendo de la Comunidad Autónoma. La desaparición de contenido geológico del temario en Secundaria, no ayuda al respecto. Si echamos la vista atrás hasta la anterior Ley Orgánica LOMCE, ya se evidenciaba una reducción de la presencia de las ciencias geológicas. En 2017 el Ilustre Colegio Oficial de Geólogos ya advertía que los estudiantes finalizan esta etapa educativa sin una comprensión adecuada de los fenómenos geológicos. Esta desaparición genera una pérdida en el despertar de nuevas vocaciones, siendo difícil recuperarlas en etapas posteriores a la educación obligatoria (García Yelo *et al.*, 2022).

En la nueva Ley Orgánica LOMLOE, la asignatura de Biología y Geología se imparte sólo en 3 cursos en la ESO y uno en Bachillerato, siendo Geología optativa en segundo. La asignatura se enfoca en saberes sobre el cuerpo humano y la inmunidad (influenciados por la reciente pandemia global) y dejando el contenido geológico prácticamente en la dinámica interna y el relieve. Los términos "paleontología" o "dinosaurio" ni siquiera aparecen mencionados en el currículo. Brusi *et al.*, (2022) critican que la última responsabilidad sobre la geología quede en el docente, existiendo ya un documento denominado *"Alfabetización en Ciencias de la Tierra"*, desarrollado por Pedrinaci *et al*., (2013) como referente de qué enseñar, ignorado por LOMLOE.

Marco teórico

Los dinosaurios destacan como uno de los temas más populares en el imaginario colectivo (Mampel y Cortes, 2012) y uno de los más estimulantes desde el punto de vista científico (Schroeder *et al*., 2009). Ante esto, resulta pertinente cuestionarse por qué un tema que despierta tanto interés en el alumnado y que se alinea con los objetivos del currículo, tiende a ser ignorado en la clase de ciencias. Tradicionalmente, se ha tendido a establecer una separación entre los aspectos cognitivos y socioemocionales en el proceso de enseñanza-aprendizaje (García Bacete y Domènech Betoret, 1997), considerándose temas como los dinosaurios menos relevantes frente a contenidos teóricos o técnicos en ciencia (Mampel *et al*., 2015). No obstante, González *et al*. (1996) subrayan que existe una relación entre lo cognitivo y lo emocional, generando un entorno propicio, denominado *Environmental Learning*, que favorece la motivación para aprender.

Metodología

Cuando el alumnado lleva a cabo sus propias prácticas favorece el aprendizaje de la ciencia a través de la acción, es decir, *"aprenden ciencia haciendo ciencia"* (García-Carmona, 2021). Para ello, se han realizado una serie de talleres enfocados al alumnado en diferentes etapas de escolarización (Tabla 1).

	Tipo de Taller	Cantidad talleres		Edad	Institución de apoyo
Educación infantil	Fósiles de escayola	5		3-5 años	Centro de Interpretación Paleontológica de La Rioja
Educación primaria	Modelado de *Riojaventrix*	1		5-10 años	Centro de Interpretación Paleontológica de La Rioja
	Taller de marionetas	1		5-10 años	Centro de Interpretación Paleontológica de La Rioja
Atención a la diversidad: alumnado de altas capacidades	Evolución y anatomía comparada	2		5-10 años	Proyecto Eureka, Torrelodones (Madrid)
Educación secundaria	Icnología	ESO	3	14-15 años	Universidad de la Rioja
		Bachiller	1	16-17 años	

Tabla 1. Características de los talleres con respecto a las etapas escolares.

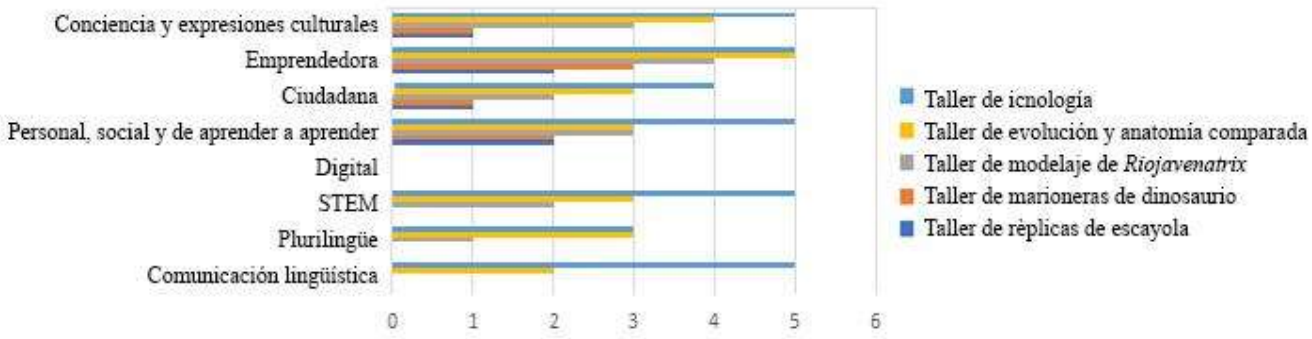

Figura 1. Relación entre Competencias Clave y talleres realizados.

Resultados y Conclusiones

El taller de icnología se presenta como el más completo y transversal en cuanto al desarrollo de competencias clave, influenciado por la edad y la madurez de los estudiantes a la hora de enfrentarlo. Aquellos enfocados al alumnado de altas capacidades destacan en las competencias STEM, Emprendedora y Conciencia y expresiones culturales, permitiendo trabajar contenidos paleontológicos al tiempo que se fomentó la creatividad y la capacidad de iniciativa. Aquellos enfocados a la educación primaria e infantil, presentan una incidencia más limitada y focalizada, fomentando la curiosidad científica y la expresión artística.

El desarrollo de estos talleres demuestra que los dinosaurios son útiles como recurso didáctico en todas las etapas académicas, además de que el interés espontáneo que despiertan, puede derivar en una motivación intrínseca hacia el aprendizaje (Royo-Torres *et al*., 2019). A través de estas dinámicas se introdujeron conceptos más complejos para los más pequeños, como el tiempo geológico, nomenclatura o evolución, como ya indicase Clauss (1993). Si bien para secundaria, se reforzaron nociones básicas de geología y se introdujo anatomía y filogenia. Los dinosaurios vienen a complementar el currículo académico y con su utilización no sólo se despiertan nuevas vocaciones científicas, sino que se impide una nueva extinción, académica en este caso.

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A large hadrosauriform dinosaur from the Early Cretaceous from the Sierra de la Demanda (Burgos, Spain)

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Key words: Ornithopod, femur, tibia, fibula, Barremian, Aptian

Abstract

In the Sierra de la Demanda (Burgos), various ornithopod remains have been found, ranging from basal forms to Hadrosauriformes, in sites such as La Solana, El Oterillo II, and Vegagete. This study presents a large individual, a styracosthernan ornithopod (MDS-TBM), from the La Tejera site (Castrillo de la Reina Formation, Upper Barremian–Lower Aptian), whose distal fluvial sediments contain red clays, sandstones, and conglomerates. During the 2007 and 2008 excavations campaigns, more than 200 fossils were recovered; the femur, tibia, fibula, several teeth, and a caudal vertebra are described here. Phylogenetic analysis was performed using the matrix of Madzia et al. (2021) and TNT software, and places the specimen in a basal position within Hadrosauriformes. Its dimensions exceed those of *Iguanodon bernissartensis*, which may represent one of the largest styracosthernans from the Iberian Peninsula and reinforces the hypothesis of high biodiversity and ecological diversification of the Early Cretaceous in the Cameros Basin.

In the Sierra de la Demanda (Burgos), numerous cranial and postcranial remains of ornithopods have been identified (Torcida Fernández-Baldor, 1996, 2006; Torcida Fernández-Baldor et al., 2006; Contreras-Izquierdo et al., 2009). Several sites, such as La Solana, Los Terreros-Altollano, El Oterillo II, and Vegagete, have yielded records of basal ornithopods, Iguanodontidae indet., Hadrosauriformes indet., and Rhabdodontomorpha (Ruiz-Omeñaca et al., 2009; Dieudonné et al., 2016; Torcida Fernández-Baldor et al., 2017; Escanero-Aguilar et al., 2024; Blázquez et al., 2024).

This study describes a large individual identified as a styracosternan ornithopod (MDS-TBM) from the site of La Tejera, located 2.2 km northeast of Barbadillo del Mercado (Burgos). La Tejera is in the Castrillo de la Reina Formation, in the western part of the Cameros Basin, of Upper Barremian-Lower Aptian age (Martín Closas and Alonso Millán, 1998), and its component materials are clays, sandstones, and, to a lesser extent, conglomerates. It is interpreted as part of a distal fluvial system, with meandering channels, over an extensive floodplain (Martín-Closas & Alonso-Millán, 1998).

During two fieldwork seasons (2007-2008), more than 200 vertebrate fossils were recovered. In this work, the elements corresponding to the right hind limb have been studied: femur (MDS-TBM,151), tibia (MDS-TBM,150) and fibula (MDS-TBM,26),

several dental pieces (MDS-TBM,3; 4; 5; 71; 152; 169), and a vertebral core (MDS-TBM,254). The material has been documented with photogrammetry. Phylogenetic analyses were carried out, using the modified matrix of Madzia et al. (2021), which includes a total of 76 taxa and uses 153 characters, of which 21 could be coded in the MDS-TBM specimen. Analyses were carried out with TNT software (Goloboff et al., 2003), setting the memory for 10,000 trees before running the analysis.

MDS-TBM,5 is a right maxillary tooth corresponding to a fragment of a badly worn dental crown. On the labial side it has a very prominent primary ridges, displaced distally, and two weak secondary carinas in the mesial half. Other teeth, MDS-TBM,3, MDS-TBM,71, and MDS-TBM,152, are from the right dentary, and MDS-TBM,4, from the left. Their crowns are broad, with a distally displaced primary ridge and two faint secondary ridges in the mesial half. The edge of the mandibular crowns has small denticles containing mamelons, up to seven per denticle. One crown fragment, MDS-TBM,169, has a different pattern: sub-mamelons are formed on each mamelon, a large central one and a small one on each side of it.

MDS-TBM,254 is a posterior caudal vertebra that preserves the vertebral centrum and the proximal part of the neural arch. The centrum is amphicelic, elongated and low, with hexagonal articular faces and a flat ventral surface.

The appendicular bones were recovered in a semi-articulated condition, well preserved, with evidence of fossil-diagenetic crushing, especially the diaphysis. MDS-TBM,151 is nearly complete, its total length is 114.15 cm. The diaphysis is slightly curved in anterior view and "S" shaped in medial view. The proximal end has prominent greater and lesser trochanters. The fourth trochanter is trapezoidal, located on the posteromedial border of the diaphysis. It has a longitudinal ridge running from the greater trochanter to the distal medial condyle. The distal end has asymmetric condyles. MDS-TBM,150 has a straight and elongated morphology, curving medially at the distal end. The cnemial crest is prominent, projecting anteriorly. The proximal end partially preserves the medial and lateral condyles, separated by a narrow intercondylar groove; the distal end is fragmented. MDS-TBM,26 is elongated and curved anteriorly distally, the distal end of which is not preserved. The proximal end is semilunar, slightly concave on the medial surface. The cranial process is projected anteriorly.

The studied remains of the MDS-TBM specimen present characteristics attributed to larger styracosternan ornithopods, such as *I. bernissartensis* and *I. galvensis*. The femur and tibia exceed the length of those of all the taxa compared, including the holotype of *I. bernissartensis*: the femur IRSNB 1534 has a length of 102 cm, compared to 114 cm for MDS-TBM,151 and could be considered the largest styracosternan described from the Iberian Peninsula. Phylogenetic analysis based on the matrix of Madzia et al. (2021) places MDS-TBM in a basal position within the Hadrosauriformes clade, although the low resolution of the analyses obtained highlights the need for further research. This study supports the hypothesis of high ornithopod diversity during the Lower Cretaceous of the Iberian Peninsula, particularly within the Cameros Basin. In this Basin, the coexistence of taxa of different sizes, as has also been recorded in the Maestrazgo Basin (Verdú et al., 2019; Gasulla et al., 2022), suggests ecological diversification and adaptation to different niches of these phytophagous dinosaurs within the same ecosystem.

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Dental topography and feeding behaviour in dinosaurs from Sierra de la Demanda (Burgos, Spain)

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Keywords: Dental complexity, Dinosauria, Diet, Paleoecology, Burgos.

Introduction

The Cuenca de Cameros is a sedimentary basin formed during the rifting period between the Oxfordian and the Upper Albian stages. Its extent covers parts of the present-day provinces of La Rioja, Soria, and Burgos. The basin is primarily composed of Mesozoic sedimentary infill overlying a Palaeozoic basement (Mas *et al.*, 2004). The Sierra de la Demanda (Burgos), located in the western part of the Cuenca de Cameros, is exceptionally rich in Mesozoic vertebrate fossil remains, particularly those of dinosaurs from Upper Jurassic and Lower Cretaceous deposits (Torcida Fernández-Baldor, 1996, 2006; Blázquez et al., 2024).

Teeth are the only skeletal elements in direct contact with the environment, making them valuable for studying morphology, development, and interactions with food mechanical properties through dental macrowear (Cuozzo & Sauther, 2012; Romero et al., 2022). In particular, the size and shape of dinosaur teeth reveal important features related to taxonomy, phylogenetic diversification (Smith et al., 2005; Datta et al., 2021; Ballell et al., 2022), and feeding strategies (Torices et al., 2018). However, the role of dental complexity in understanding functional adaptations and eco-feeding diversity in dinosaurs remains poorly understood.

This study investigates dental functional traits by means of 3D topographic techniques of carnivorous and herbivorous dinosaurs from the Sierra de la Demanda, near the locality of Salas de los Infantes (Burgos, Spain).

Materials and methods

A total of 29 well-preserved fossil teeth were analysed. The sample includes 8 theropod teeth and 3 belong to sauropods, all from the Valdepalazuelos–Tenadas del Carrascal site (Torrelara), within the Rupelo Formation, dating to the Tithonian stage of the Upper Jurassic. The remaining 18 teeth are from ornithopods and were recovered from several sites: La Solana (Cabezón de la Sierra), Tenada del Bardal (Hacinas), Vegagete, Camino de Salas a Villanueva (Villanueva de Carazo), El Peñascal (Salas de los Infantes), and Las Callejas–Arroyo del Cubillo (Cabezón de la Sierra), all located within the Castrillo de la Reina Formation, dated to the Upper Barremian–Lower Aptian (Lower Cretaceous) (Martín-Closas and Alonso Millán, 1998). The fossil remains were provided by the Museo de Dinosaurios de Salas de los Infantes (Burgos, Spain).

Polyurethane replicas were produced for each tooth using polyvinylsiloxane moulds (Galbany *et al.,* 2006). Tooth replicas were scanned using a Shining® 3D EINSCAN-SP structured light scanner to generate 3D models (.ply), which were then

post-processed in Geomagic Wrap® and MeshLab. The resulting dental models, standardized to 20,000 polygons, were analysed using MorphoTester (Winchester, 2016) to quantify occlusal relief (RFI), surface complexity (OPCR), and curvature (DNE).

To assess differences among the three groups (theropods, sauropods, and ornithopods) in topographic metrics (RFI, OPCR, and DNE) one-way analysis of variance (ANOVA) was performed, followed by Tukey's *post hoc* test. Statistical analyses were conducted using PAST 2.17® with a significance level of $\alpha = 0.05$.

Results and discussion

Theropod teeth exhibit significantly higher mean RFI values compared to both sauropods and ornithopods, with sauropods also displaying higher relief values than ornithopods (Figure 1A). In contrast, tooth complexity (OPCR) is lower in theropods than in the other groups, with sauropods showing the highest values, followed by ornithopods (Figure 1B). Tooth surface curvature (DNE) in theropods is greater than in ornithopods but lower than in sauropods. Overall, the topographic configuration of theropod teeth differs markedly from that of sauropods and ornithopods, which exhibit greater morphological similarity to each other.

These results reinforce the usefulness of dental complexity analysis in understanding feeding adaptations in dinosaurs. Our findings also raise new questions about dental morphological variability between carnivorous and herbivorous taxa, which should be further explored in relation to paleoecology and dietary versatility.

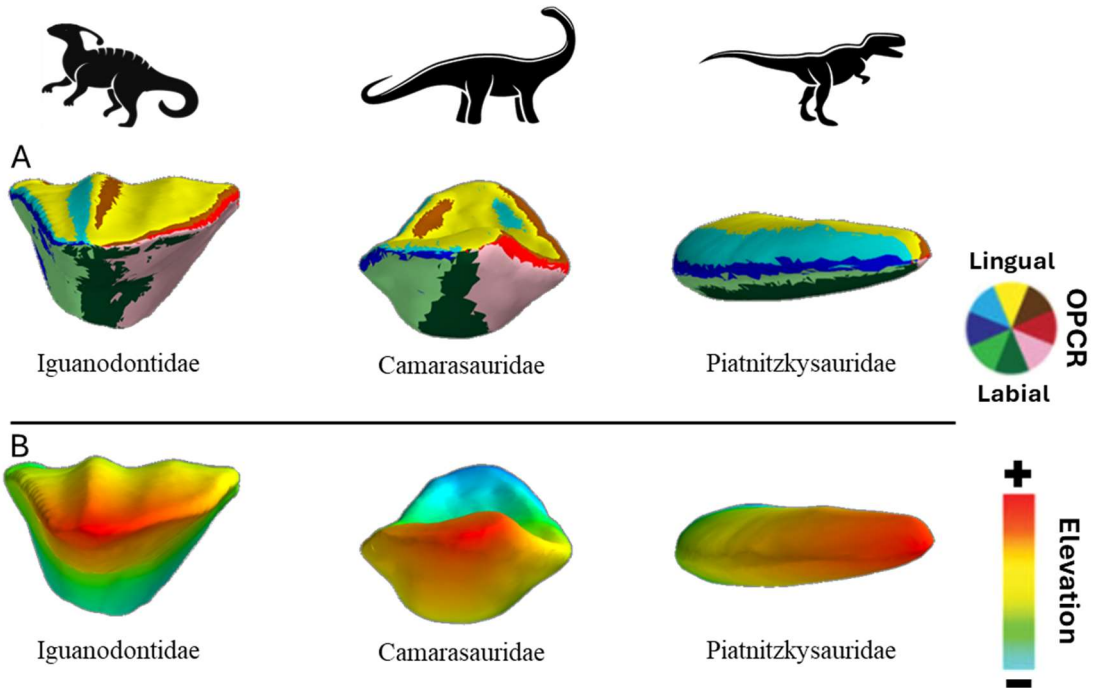

Figure 1: Occlusal views of representative tooth models depict topographic metrics: (A) complexity (OPCR) and (B) relief (RFI). OPCR maps display the orientation of the model's surface triangles, represented using a colour wheel. Elevation maps show higher and lower crown (warm and cool colours, respectively). Mesial is oriented to the left.

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Comparación entre la asociación macroflorística de Camino Fornons 3 del Maastrichtiense superior en la provincia de Huesca con otras floras contemporáneas de los Pirineos

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Palabras clave: Pirineos meridionales, Formación Tremp, ambiente transicional, macroflora, asociaciones florísticas, bioestratinomía

Introducción

El Maastrichtiense se caracterizó por ser una edad clave en la historia geológica de la Tierra, marcada por profundos cambios ambientales, y finalmente, por un impacto meteorítico, que culminaron en una de las mayores extinciones masivas conocidas, la extinción del límite Cretácico-Paleógeno (límite K/Pg). Este evento, ocurrido hace 66 millones de años, supuso la desaparición de numerosos grupos faunísticos, entre ellos los dinosaurios no avianos (Brusatte *et al.,* 2015). Sin embargo, además de afectar profundamente a la fauna, la flora también experimentó importantes transformaciones, aunque ninguno de los principales grupos de plantas presentes en el Maastrichtiense desapareció (Nichols y Johnson, 2008), y la recuperación de las asociaciones vegetales en el Paleoceno temprano fue rápida (Vajda y Bercovici, 2014). Sin embargo, el estudio de la vegetación durante el Maastrichtiense resulta complejo debido a la escasez y fragmentación del registro fósil de plantas correspondiente a esta etapa, en donde la mayor parte de la información de los afloramientos continentales procede de yacimientos situados en Norteamérica (Vajda y Bercovici, 2014).

En este contexto, los yacimientos del Cretácico Superior del Pirineo español adquieren una relevancia particular, ya que proporcionan un valioso testimonio delos ecosistemas terrestres del final del Cretácico. Los afloramientos transicionales y continentales de la Formación Tremp (Maastrichtiense), han aportado abundante material faunístico además de un registro paleobotánico de los más completos de la Península ibérica. Por ello, el estudio de las plantas fósiles del Pirineo español resulta esencial para comprender la dinámica ecológica y evolutiva de la flora previa al límite Cretácico-Paleógeno

Contexto geológico y metodología

El yacimiento de Camino Fornons 3 (Beranuy, Huesca, Pirineo aragonés) se localiza estratigráficamente en un nivel de lutitas margosas y limos de unos 2,10 m de espesor en la unidad 'Garumniense gris' de la Formación Tremp, que en la zona de Beranuy está datada como Maastrichtiense Superior (C29r), e interpretada como depósitos en un ambiente de bahía costera restringida o de zona proximal de *lagoon* (Martínez de Espronceda, et al., 2023). En este yacimiento se realizaron dos campañas de excavación en el año 2020 y 2022, en las que se recuperaron 131 muestras con fósiles vegetales procedentes de los 3 subniveles con registros macropaleobotánicos del yacimiento (CF3-7, CF3-12-INF y CF3-12-SUP). La preparación del material se realizó

en el laboratorio en seco debido a la matriz lutítica de las muestras, utilizando herramientas manuales finas y percutores de aire comprimido para limpiar los restos.

Resultados

Taxonómicos

En el yacimiento Camino Fornons 3 se han identificado restos vegetales fósiles correspondientes a tres grandes grupos: briofitas, gimnospermas y angiospermas. En todos los casos la clasificación ha estado limitada a nivel de género debido a la ausencia de cutículas preservadas. Las briofitas están representadas por *Marchantites sp.*, cuya morfología (talos dicótomos sin vena central y esporangios elíptico-circulares en el ápice) se asemeja a registros del Cretácico inferior de Asia (Li et al., 2014). En cuanto a las gimnospermas, se han identificado registros de coníferas con hojas falcadas y con venación simple pertenecientes a *Cunninghamites* sp. y un cono de morfología romboidal con escamas en disposición helicoidal asignado al mismo género. Se han identificado ejes de *Araucarites* sp. y tallos platíclados con venación paralela identificados como pertenecientes a *Frenelopsis* sp. En cuanto a las angiospermas, se identificaron hojas de dicotiledóneas de morfología espatulada y lanceolada, con al menos dos morfotipos diferenciados (tipos 1 y 2), que presentan venación pinnada o craspedódroma, además de hojas acintadas con márgenes dentados o enteros y venación paralela con conexiones transversales que se han asignado a monocotiledóneas del género *Pandanites* y a otros 3 morfotipos indeterminados), además de una flor de muy pequeño tamaño y afinidad indeterminada conservada con algunos pétalos en conexión.

Tafonómicos

Se han analizado los caracteres bioestratinómicos de los registros paleobotánicos en cada uno de los niveles estudiados del yacimiento, teniendo en cuenta la síntesis de análisis y conclusiones tafonómicas sobre plantas fósiles recogidas en Martín-Closas y Gomez (2004). Así, se han estudiado el tamaño, la morfología, el estado de fragmentación de los restos, y su orientación, para interpretar los procesos tafonómicos que afectaron a los restos vegetales antes de su enterramiento, observándose variaciones significativas entre los diferentes niveles y los taxones presentes.El nivel CF3-7 muestra fragmentos heterométricos, angulosos, y de pequeño tamaño de hojas de angiospermas, dispuestos sin una orientación preferente, que indica un depósito en un ambiente de alta energía con transporte turbulento. En CF3-12-INF, los restos son de tamaño medio, y con cierta orientación, incluyendo fragmentos de hojas de angiospermas de morfología lanceolada y fragmentos de ramas de coníferas, que indicarían condiciones de una moderada energía del medio. Finalmente, CF3-12-SUP presenta tapices de briofitas, registros de hojas de angiospermas de mayor tamaño y en ocasiones completas, así como ramas multidivididas de coníferas que no presentan una orientación preferente, indicando una baja energía del medio y la proximidad del área de producción de los restos respecto a la zona de depósito.

Interacciones

Se identificaron diferentes daños foliares sobre hojas de angiospermas como resultado de la interacción entre plantas e insectos, los cuales fueron clasificados siguiendo las determinaciones del compendio de Labandeira et al., (2007). En la muestra CF3-12-13A se observó un daño tipo DT-15 (alimentación en margen) con una escisión semilunar cerca de la vena principal. Por su parte, en CF3-12-INF se detectaron orificios tipo DT-148 (alimentación en orificios) y un daño no identificado que podría corresponder bien a agallas (DT-11) o a marcas por ataque fúngico.

Discusión

Hasta el momento solo se conocían yacimientos con restos de macroflora del Maastrichtiense en el Pirineo catalán, pero no en el Pirineo aragonés. Se ha comparado el material estudiado con los yacimientos maastrichtienses de Molí del Baró-1 (Marmi et al*.,* 2016) y Zona de Isona (Marmi et a*l.,* 2014), ambos en el Pirineo catalán. Los tres yacimientos muestran asociaciones vegetales diversas, tanto con similitudes como diferencias que reflejan la complejidad de las comunidades de la época. En los tres yacimientos se identifican gimnospermas, y angiospermas tanto monocotiledóneas como dicotiledóneas, aunque con proporciones variables según la localización. Molí del Baró-1 destaca por un claro predominio de angiospermas, con monocotiledóneas (Familias Arecaceae, Typhaceae) y eudicotiledóneas específicas, además de restos de ámbar y de carbón. Por su parte, la Zona de Isona presenta un equilibrio mayor entre gimnospermas coníferas (géneros *Brachyphyllum, Cunninghamites* y *Frenelopsis*) y una amplia diversidad de angiospermas eudicotiledóneas y monocotiledóneas (géneros *Pandanites* y *Sabalites* entre otros*)*. Camino Fornons 3 es menos diverso, aunque presenta registros de hepáticas y tres géneros de gimnospermas coníferas (*Cunninghamites, Araucarites y Frenelopsis*), pero las angiospermas están menos representadas con dos morfotipos de hojas asignadas a dicotiledoneas y otros 4 a monocotiledóneas (*Pandanites* y otros tres morfotipos indeterminados).

Los tres yacimientos evidencian ambientes cálidos-templados con distintas influencias en cuanto al medio sedimentario: fluvial de llanura de inundación, concretamente en el contexto de ríos meandriformes intercalados con depósitos de llanuras de inundación, correspondiente a la parte superior de la "unidad roja inferior" en el yacimiento Molí del Baró-1; un ambiente aluvial-lacustre en el caso de la Zona de Isona, en el Garummiense gris, y, un ambiente de *lagoon*-fluvial en Camino Fornons 3. La comparación refleja la transición evolutiva hacia floras dominadas por angiospermas en el Cretácico superior, especialmente patente en Molí del Baró-1. La presencia común de monocotiledóneas como *Sabalites* o *Pandanites* indica una amplia dispersión y adaptación ecológica de estos taxones. Las gimnospermas, aunque en declive, mantienen relevancia en la Zona de Isona y Camino Fornons 3. Por su parte, la elevada diversidad y morfología foliar en la Zona de Isona sugiere un ecosistema complejo y especializado.

En conjunto, estas asociaciones ilustran la coexistencia de comunidades vegetales con distintos grados de complejidad y predominio a nivel taxonómico, reflejando la dinámica evolutiva y ambiental propia del final del Mesozoico, con angiospermas en consolidación, diversificación y expansión, así como otros grupos relictos de gimnospermas mesozoicas persistentes.

Conclusiones

El yacimiento de Camino Fornons 3 en la provincia de Huesca muestra representantes de la mayoría de los principales grupos vegetales del Cretácico superior del Pirineo, aunque su variedad taxonómica resulta inferior en comparación con la observada en los otros dos yacimientos analizados. Esta diferencia podría ser debida bien a factores ambientales o bioestratinómicos, o bien a la cantidad de material recuperado hasta el momento, ya que los yacimientos del Pirineo catalán han sido objeto de un mayor número de intervenciones que han permitido la recuperación de abundantes restos paleobotánicos. No obstante, y pese a esta limitación, el yacimiento Camino Fornons 3 es de notable relevancia, tanto por su diversidad y por la conservación de los registros,

así como por su potencial científico, para el conocimiento de la paleobotánica del Maastrichtiense en la Península Ibérica.

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Ontogenetic Insights into the Iberian Pleurosternid *Toremys cassiopeia*: New Specimens from the lower Albian of Ariño (Spain)

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Keywords: Testudinata, Paracryptodira, Spanish record, Intraspecific variation, Shell development

Pleurosternidae is a clade of freshwater paracryptodiran turtles recorded from the Kimmeridgian (Upper Jurassic) to the Albian (Lower Cretaceous) in North America and Europe (Gaffney, 1979; Brinkman, 2000; Pérez-García, 2017). Despite recent advances in their taxonomy and diversity—particularly in the Iberian Peninsula with the description of *Selenemys lusitanica* (Pérez-García & Ortega, 2011), *Riodevemys inumbragigas* (Pérez-García et al., 2015a), *Toremys cassiopeia* (Pérez-García et al., 2015b), and *Pleurosternon moncayensis* (Pérez-García et al., 2022) —ontogenetic trajectories within the group are still poorly understood. Our knowledge of intraspecific variation within this lineage also remains relatively limited, with the notable exception of *Pleurosternon bullockii*, which has been recently investigated in detail (Guerrero & Pérez-García, 2021a, 2021b, 2021c). This lack of data has contributed to persistent ambiguities in the anatomical interpretation and phylogenetic placement of several pleurosternid taxa (e.g., Lapparent de Broin & Murelaga, 1999; Milner, 2004).

Toremys cassiopeia was described from the lower Albian bonebed of Ariño (Teruel, Spain), and represents the stratigraphically youngest known pleurosternid worldwide. Thus, it is currently the only pleurosternid taxon confirmed beyond the Berriasian extending the stratigraphic range of the group. Until now, *T. cassiopeia* was only known from adult or subadult specimens, limiting developmental interpretations.

In this context, this study presents shells and shells remains of nine unpublished specimens of *T. cassiopeia* from the same Albian bonebed (i.e., from the type locality of the taxon), representing different ontogenetic stages, including several identifiable as juveniles. These specimens offer, for the first time in the Iberian record, a detailed ontogenetic series for a pleurosternid turtle. The comparative analysis of juvenile and adult morphologies provides critical insights into developmental changes in shell architecture and diagnostic traits across ontogeny. These results contribute to refining the diagnosis of *T. cassiopeia* and clarifying its intraspecific variability across ontogeny. Furthermore, the ontogenetic patterns observed are compared with those recently documented for *Pleurosternon bullockii*, from the British Berriasian record (Guerrero & Pérez-García, 2021a, 2021b), providing a broader evolutionary and paleobiogeographic framework for understanding developmental trends within Pleurosternidae.

Thus, by documenting ontogenetic patterns in *T. cassiopeia*, this study also emphasizes the need to take growth-related variation into account within the systematic frameworks of fossil turtles—an essential step toward resolving long-standing taxonomic uncertainties within Pleurosternidae.

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Appendicular skeleton of the Upper Cretaceous turtle from Brazil *Bauruemys elegans* (Podocnemididae, Pleurodira)

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Keywords: Testudines, Pectoral girdle, pelvic girdle, femur, tibia

The studies of fossil turtles are normally focused on the shell and the skull. Thus, the appendicular skeleton is unknown for most fossil species (Gaffney et al., 2011). *Bauruemys elegans* is a podocnemidid turtle (Testudines, Pleurodira) described in the Upper Cretaceous (Turonian-Santonian) Adamantina Formation of Brazil (Suarez, 1969). In Suarez (1969), the original publication where the taxon was described, the carapace, the plastron and the skull were characterised. All of them being part of the holotype (for a discuss about it see Gaffney et al., 2011, and the references there), which also included both femora, coracoid and scapula, but they are not described or figured in that publication, and they remain unpublished (Suarez, 1969).

Although some studies of this species were subsequently published (Kischlat, 1994; Romano and Azevedo, 2007; Mariani and Romano, 2017; Sena et al., 2024; Oliveira and Romano, 2007), no appendicular elements have been so far figured or described. In the list of specimens that could be referred to this species elaborated by Gaffney et al. (2011) in the revision of the podocnemidid turtles, they noted that, in addition to the appendicular skeleton of the holotype, some other specimens also preserve elements of the appendicular skeleton. However, these elements were neither figured or described, and they remain unpublished.

We present here the first detail description of some elements of the appendicular skeleton of *Bauruemys elegans*. We characterised some elements of scapular and pelvic girdles, but also others of the limbs. These remains belonging to a partial unpublished individual of the species, deposited in the Muséum national d'Histoire naturelle of Paris (France). We compare these bones with those of other podocnemidids turtles, including both extinct and extant taxa.

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New fossil remains of an ornithopod dinosaur from the Lower Cretaceous of Ladruñán (Teruel province, Spain)

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Keywords: Barremian, Maestrazgo Basin, Ornithopoda, Iguanodontia, Styracosterna, Osteology.

Abstract

This study consists in the morphological characterization of an ornithopod dinosaur specimen from the Pepe paleontological site, situated in the upper part of the Barremian Mirambel Formation. This site is located in the Ladruñán anticline in the NE of the Iberian Peninsula (Maestrazgo basin, province of Teruel). The remains are found in anatomical relation and well preserved and include both axial and appendicular remains such as vertebrae, an ischium and two pubes. The pelvic girdle is the most taxonomically informative element recovered. The osteological description and taxonomic approach carried out in this work suggest that this specimen was a member of the clade Styracosterna, having some affinities with Iberian members of this clade, such as *Iguanodon*, *Mantellisaurus* and *Morelladon*.

Introduction

In recent years, up to eight species of ornithopod dinosaurs have been reported from the Lower Cretaceous of the Iberian Peninsula. *Magnamanus soriaensis* (Fuentes-Vidarte *et al*., 2016) was found in rocks from the Hauterivian-Barremian transition. *Delapparentia turolensis* (Gasca et *al*., 2015), *Portellsaurus sosbaytani* (Santos-Cubedo *et al*., 2021), *Iguanodon galvensis* (Verdú *et al*., 2017) and *Iguanodon bernissartensis* (Norman, 1980) are recorded during the Barremian. The latter taxon also is appearing in rocks from the upper Barremian and coinciding with the presence of species such as *Morelladon beltrani* (Gasulla *et al*., 2015) and *Mantellisaurus atherfieldensis* (Norman, 2014). Finally, *Proa valdearinnoensis* (McDonald *et al*., 2012b) is found at the lower Albian.

In this work, a partial ornithopod skeleton coming from the Teruel province (Spain) is studied. We carry out an osteological description of the fossil remains and compare their anatomical features with other taxa within Iguanodontia.

Geographical and geological setting

The fossil remains were recovered from the "Pepe" site, located near the village of Ladruñán (Castellote municipality), Teruel province, Spain.

Geologically, this site belongs to the eastern domain of the Iberian Range, an Alpine structure with NW-SE direction, formed by the inversion of the Jurassic-Cretaceous sedimentary basin (Álvaro *et al*., 1979). In addition, "Pepe" site is situated in the Ladruñán anticline (Morella subbasin, Maestrazgo Basin), where outcrops rocks with ages between Late Jurassic and Late Cretaceous.

Specifically, Pepe site is located within the Mirambel Formation, a continental unit which encompass alluvial plain and lacustrine deposits of Barremian age. This stratigraphic unit is a 200 m-thick succession that alternates carbonated facies interpreted as lacustrine-palustrine deposits with terrigenous facies interpreted as alluvial plain deposits (Gasca *et al*., 2017). "Pepe" is located in the upper part of the Mirambel Formation, and the fossil-bearing layer is a red-purple lutitic interval affected by pedogenic processes.

Material

The studied bones were excavated in several campaigns from 2009 to 2011 and are currently housed at the Museo de Ciencias Naturales de la Universidad de Zaragoza. The ornithopod fossil remains included in the study are a neural arch of a cervical vertebra (MPZ 2025/13), a caudal vertebra (MPZ 2025/14), an ischium (MPZ 2025/06) and two pubes (MPZ 2025/05 and MPZ 2025/07).

Osteological description and discussion

The ornithopod from Pepe possesses several characteristics that allow it to be included within the group of iguanodontian ornithopods and that make it similar to those in the Styracosterna clade.

Concerningt the cervical vertebrae, MPZ 2025/11 is similar to the neural cervical arches of *Iguanodon bernissartensis*, although it differs from the latter in that its neural spine is taller and curved posteriorly. MPZ 2025/14 fits within the general morphology of this type of vertebra (platycoelous) in Styracosterna iguanodontian taxa.

Regarding pelvic girdle, the preserved portion of the ischium MPZ 2025/06, it largely resembles *Morelladon*, with a straight ischial shaft like some taxa such as *Altirhinus* (Norman, 1998), *Barilium* (Norman, 2011), *Bayannurosaurus* (Xu *et al*., 2018), *Ouranosaurus* (Bertozzo *et al*., 2017), *Proa*, *Eolambia* (McDonald *et al*., 2012a) and *Mantellisaurus*, unlike *Hypselospinus* (Norman, 2015), *Iguanodon* and *Delapparentia*. This feature allows this ornithopod to be assigned within the Styracosterna clade. Furthermore, the morphology of the section of the ischial shaft changes along its length, a feature that is not observed in other ankylopollexian ornithopods, where this section has a "D" shape as in *Iguanodon*.

The pubes MPZ 2025/05 and MPZ 2025/07 have a similar morphology of pubes of *I. bernissartensis* and *I. galvensis*, with a dorsoventrally expanded prepubic blade and with its dorsal edge more curved than the ventral one, as occurs in *Eolambia*, *Lanzhousaurus* or *Mantellisaurus* and which differs greatly from *Iguanacolossus* (McDonald *et al*., 2010), *Bayannurosaurus*, *Magnamanus* and *Proa*. In addition, the dorsal margin of the prepubic blade is concave, another characteristic in the Styracosterna clade. Furthermore, the prepubic shaft is dorsoventrally compressed in its midsection, as in *Iguanodon*, *Eolambia*, *Altirhinus*, *Bayannurosaurus*, and *Delapparentia*, among others.

The study of the skeletal remains of the specimen from Pepe allows it to resemble other taxa recorded on the Iberian Peninsula in Barremian deposits, such as *Morelladon* and *Mantellisaurus*, with notable differences from some taxa, such as *I. galvensis*, *I. bernissartensis*, and *Delapparentia*, and with few morphological similarities with other Iberian taxa like *Proa* and *Magnamanus*. Nevertheless, the differences observed with all of the aforementioned taxa, does not allow to exclude the hypothesis of the specimen from Pepe represents a new taxon closely related to other coeval iguanodontids.

Conclusions

A partial skeleton of an ornithopod has been studied and shows several diagnostic features of Styracosterna clade, for example, the morphology of its ischial shaft and the concave dorsal margin of the prepubic blade. Compared to other Iberian styracosternan ornithopods, the Pepe specimen shares the general morphology of its pubis with *Iguanodon* and also the possession of a dorsoventrally expanded prepubic blade. Furthermore, the dorsal region of the prepubic blade projects dorsally, as in *Mantellisaurus*. It also has a dorsoventrally compressed prepubic shaft in its mid-area, a feature it shares with Iguanodon and *Delapparentia*. Finally, the ischial shaft is straight, matching with *Mantellisaurus* and *Morelladon*. Further research is needed to elucidate if the specimen from Pepe represents a new taxon for the Lower Cretaceous or is one of the closely related species described in the Iberian Peninsula.

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New evidences of Diplodocoid Dinosaurs remains (Sauropoda) from the Upper Jurassic in Eastern Iberia

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Keywords: Diplodocidae, Eusauropoda, Villar del Arzobispo Fm, Alpuente, Spain.

The Mesozoic sedimentary basins in the Iberian Peninsula are home to numerous vertebrate taxa, highlighting non-avian dinosaur remains (Alcalá *et al*., 2018). Many of them are recorded from the Jurassic and Cretaceous successions in the Iberian System, which includes the Cameros, Maestrazgo and South-Iberian (or Ibero-Levantine) basins. The last one, at the eastern part of the Mesozoic Iberian Trough, comprises the Villar del Arzobispo Fm, which presents a chronostratigraphical record comprised between the Kimmeridgian and the Barremian stages (Mas *et al*., 1984, 2004; Santisteban & Santos-Cubedo, 2010, Campos-Soto *et al*., 2019).

The known sauropod fossil remains from Villar del Arzobispo Fm include turiasaurids such as *Losillasaurus giganteus* and *Turiasaurus riodevensis*, Titanosauriformes and Diplodocoidea (Royo-Torres *et al*., 2021; Suñer, 2023), being the latter poorly recorded in the South-Iberian basin.

The municipality of Alpuente (Los Serranos region, province of Valencia, Spain) has a large number of fossil sites, and over the past few years, the Paleontological Museum of Alpuente has been carrying out a review of these known sites in order to catalog, know the state of preservation and make a heritage assessment of them. One of these sites has been the focus of a non-published master's degree final project and the present study.

In this study**,** we present a preliminary revision of the La Cañadilla fossil site, located near the village of Alpuente (province of Valencia, Spain). A stratigraphic and petrographic study was performed. After fossil preparation, a preliminary systematic study was carried out. Finally, a heritage assessment has been applied using two models for paleontological and geological heritage management: the IELIG (the acronym in Spanish for the Spanish Inventory of Sites of Geological Interest developed by the IGME), and FOPALI (the management tool developed by Fundación Cidaris and the Museo Paleontológico de Elche).

The La Cañadilla fossil site is part of the siliciclastic facies of Villar del Arzobispo Fm (Kimmeridgian-Tithonian) (Mas *et al.*, 1984, 2004; Campos-Soto *et al.*, 2016, 2019). It contains features of a deltaic plain-like parasequence similar to those seen in other areas of Los Serranos (Santisteban & Santos-Cubedo, 2010). To date, sediments washed and sieved have not yielded additional results.

The fossil collection from the La Cañadilla site is composed of 11 remains in different preservational stages, from which 9 were properly identified. It includes a partial dental crown with “foil-like” or “pencil-like” morphology, two proximal dorsal ribs fragments and other rib fragments, a vertebral centrum that lacks the neural arch, and two nearly complete haemal arches. Some of them show features similar to those seen in

Diplodocoidea, corroborated by this first approach by preliminary morphometric analysis.

The heritage assessment indicates that the La Cañadilla outcrop holds high scientific value. These preliminary results highlight the need for further research, which is likely to yield additional data and enable comparisons with coeval faunal assemblages from other regions.

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Marcas de dientes en una vértebra caudal de Titanosauria del Campaniense superior de Allueva (Teruel)

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Palabras clave: Campaniense superior, Sauropoda, Theropoda, Crocodylomorpha.

Introducción

Las marcas de dientes en las vértebras caudales de saurópodos titanosaurios representan una línea de evidencia significativa en estudios paleoecológicos, ya que aportan datos directos sobre las interacciones tróficas entre grandes dinosaurios herbívoros y sus potenciales depredadores durante el Mesozoico. Estas marcas, que incluyen impresiones dentarias, surcos, fracturas (curadas o patológicas) y otras modificaciones óseas, permiten inferencias sobre aspectos del comportamiento, la biomecánica defensiva y la dinámica ecológica de estos taxones. En el presente estudio se analiza una vértebra caudal (CLT-36) de un titanosaurio procedente del Campaniense superior del yacimiento de Cañalatorre (Allueva, Teruel), la cual presenta evidencias compatibles con actividad predatoria o carroñera. En este trabajo, se discuten las características morfológicas de las marcas de CLT-36 y se evalúan posibles agentes productores en el contexto faunístico regional.

El yacimiento de Cañalatorre se ubica en la subcuenca de Montalbán (Teruel, noreste de la península ibérica), una cuenca intramontañosa de origen cenozoico. Desde el punto de vista estratigráfico, se enmarca en la Formación Allueva, una unidad del Campaniense medio a superior, caracterizada por depósitos de origen continental. Dicha formación ha sido subdividida en cuatro subunidades litológicas. El yacimiento de Cañalatorre, localizado a la subunidad A2, está compuesto por dos niveles margosos superpuestos: el inferior, de tonalidad grisácea, presenta restos fósiles fragmentarios y dispersos; mientras que el superior corresponde a un depósito tipo *bone-bed* de color más oscuro, con una notable biodiversidad de vertebrados (Torromé et al., 2024).

Los fósiles recuperados en Cañalatorre están asociados a un paleoambiente lacustre, correspondiente a zonas distales de un sistema aluvial (Aurell et al., 2022). En la superficie del yacimiento se han identificado 3 centros vertebrales caudales, morfológica y dimensionalmente compatibles entre sí, que se hallaban en asociación espacial, aunque sin conexión anatómica, lo que sugiere una posible pertenencia a un mismo individuo.

Descripción

El ejemplar CLT-36 corresponde a una vértebra caudal media casi completa. Solo se conserva la parte anterior del arco neural, el cual muestra una orientación predominantemente horizontal. Las prezigapófisis se encuentran fracturadas, mientras que las postzigapófisis no se han conservado. Los restos de saurópodos recuperados en el yacimiento de Cañalatorre se atribuyen a Titanosauria (Aurell et al., 2022), en base a varias características presentes en CLT-36: el centro vertebral, que en este caso muestra

compresión dorsoventral, es procélico, y el arco neural situado en una posición marcadamente anterior respecto al cuerpo vertebral. La cara articular anterior es cóncava, mientras que la cara articular posterior es convexa. La ausencia de espina neural y de procesos transversos de CLT-36, junto con las proporciones del centro y la disposición del arco neural, sugieren que se trata de una vértebra perteneciente a la región media o distal de la cola, donde estas estructuras tienden a reducirse o desaparecer en muchos titanosaurios.

CLT-36 presenta múltiples marcas y alteraciones morfológicas. En su superficie ventral se observan cinco orificios cónicos localizados en la parte anterior izquierda. El más proximal al borde anterior del centro es el de menor diámetro y muestra una depresión que lo divide en dos partes, una morfología que también se repite en el orificio más distal, el único que no se encuentra alineado con los demás. También existen tres surcos rectos de marcada profundidad y 3 cm de longitud, con dirección anteroposterior y sección transversal en forma de U en la parte central de esta superficie. El centro vertebral tiene una fractura de morfología triangular que ha hecho desaparecer una gran parte del mismo. En el interior de la rotura, en la superficie posterior del centro vertebral, se identifican dos surcos curvados bien definidos: el mayor mide aproximadamente 4 cm de longitud por 1,5 cm de anchura, y el menor 3,5 cm de longitud por 1 cm de anchura.

Discusión y conclusiones

La morfología de las estructuras que presenta CLT-36 sugiere que son modificaciones óseas de origen biogénico, posiblemente relacionadas con procesos de depredación o carroñeo. El tejido óseo es una fuente de nutrientes, por lo que una gran variedad de animales lo incluyen en sus dietas de forma habitual en los ecosistemas actuales (McHugh et al., 2020). En el Campaniense superior, la península ibérica y Francia formaban parte de isla iberoarmoricana. Su fauna de dinosaurios estaba compuesta fundamentalmente por titanosaurios, anquilosaurios, rabdodóntidos entre los fitófagos y abelisaurios, dromaeosaurios entre los carnívoros, además de crocodilomorfos entre los grandes predadores (Csiki-Sava et al., 2015).

Los terópodos presentan una dentición afilada, comprimida y curvada diseñada para cortar carne, no para triturar huesos (Drumheller et al., 2020). Los abelisaurios, principales carnívoros del entorno (Canudo et al*.,* 2005), poseían dientes similares a cuchillas y su comportamiento alimenticio probablemente evitaba el contacto con huesos (Therrien et al*.,* 2005). Los dromaeosaurios, aunque podían generar fuerzas de mordida altas, muestran patrones de marcas similares a las de otros terópodos y diferentes a las de la vértebra estudiada (Torices et al., 2018).

Durante el Campaniense superior, los restos de crocodilomorfos son particularmente abundantes en el dominio iberoarmoricano y corresponden a taxones que presentan adaptaciones ecológicas similares a las de crocodilos actuales (Puértolas-Pascual et al., 2016). Las mordeduras de estos animales sobre restos óseos generan modificaciones que incluyen punciones cónicas y hoyos circulares, fosas y surcos de sección transversal en forma de U, variantes bisectadas de las anteriores, marcas en forma de “gancho” (con morfología en J o en L) y fracturas asociadas (Drumheller et al., 2020).

CLT-36 presenta un conjunto de marcas que encajan dentro de esta última tipología: se observan múltiples hoyos y punciones circulares, dos de ellos bisectados, así como tres surcos lineales profundos cuya sección transversal presenta un perfil en U. Estas características son congruentes con las marcas producidas por los dientes cónicos y no serrados de crocodilomorfos, lo que permite proponer a un miembro de este clado como posible agente productor de las alteraciones observadas en el CLT-36.

La distribución, morfología y profundidad de las marcas observadas en la vértebra caudal de titanosaurio CLT-36 aportan información clave para su interpretación tafonómica. Estas marcas se concentran en la región posterior del centro vertebral, una zona anatómicamente más accesible para la mordida, lo cual sugiere una acción dirigida al aprovechamiento de tejidos blandos residuales. La profundidad de algunas de las punciones indica una interacción intensa, compatible con un comportamiento de consumo más que con manipulación incidental.

En un escenario de depredación activa, se esperaría encontrar marcas más curvadas, resultado de la lucha y el movimiento del animal vivo, así como una distribución más aleatoria o extendida de las mismas (Drumheller et al., 2020). Asimismo, otras regiones anatómicas, como las costillas o los huesos de las extremidades, habrían sido más atractivas desde el punto de vista nutricional. La ausencia de remodelado óseo indica que las lesiones no fueron sufridas en vida, lo que refuerza la hipótesis de un consumo *post mortem*. Además, el estado de desarticulación del material es consistente con patrones de manipulación asociados al carroñeo (Hone y Tanke, 2015).

Este hallazgo constituye una valiosa evidencia de interacción ecológica entre grandes saurópodos y crocodilomorfos durante el Campaniense superior. La identificación de un crocodilomorfo como probable agente productor de las marcas en CLT-36 sugiere que estos arcosaurios desempeñaban un papel más activo en las redes tróficas de lo que tradicionalmente se ha asumido, siendo potenciales carroñeros oportunistas e incluso depredadores facultativos de dinosaurios.

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Ampliación del registro de *Hadrosauropodus* en la Formación Yacoraite (Maastrichtiano–Daniano), noroeste argentino: nuevos aportes desde el sitio Huichaira

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Introducción

La Formación Yacoraite constituye una unidad del Maastrichtiano ampliamente distribuida dentro del sistema de la Cuenca Salta en el noroeste argentino, reconocida por su notable registro fósil y por una historia deposicional compleja (Turner, 1959). Sus principales depocentros comprenden las subcuencas de Tres Cruces (Jujuy), Sey (Catamarca), Lomas de Olmedo, Metán, Alemanía y El Rey (Salta) (Marquillas et al., 2005). La unidad es normalmente interpretada como un mar epicontinental, dominado por acción del oleaje y subordinadamente por procesos mareales, con fluctuaciones eustáticas que habrían modificado reiteradamente este entorno, generando un mosaico variable de facies marinas someras, peritidales y marginales continentales en los distintos depocentros (Marquillas et al., 2005, 2007, 2011). En particular, en la subcuenca de Tres Cruces, algunos autores han propuesto un ambiente marino restringido (Cónsole-Gonella et al., 2017; Villafañe et al., 2021, 2022), mientras que otros trabajos documentan una incursión marina en el contacto basal con la Formación Lecho (Astini et al., 2020; Coppa Vigliocco et al., 2024).

La presencia de huellas de grandes ornitópodos del Cretácico Superior, y en particular pertenecientes a *Hadrosauropodus*, ha sido ampliamente documentada en depósitos de Laurasia. En América del Norte, el icnogénero *Hadrosauropodus* ha sido identificado en múltiples unidades del Campaniano–Maastrichtiano (Lockley et al., 2003; McCrea et al., 2014; Enriquez et al., 2022). También existen reportes relevantes en Asia oriental, como en las formaciones Zhutian y Shaxian de China (Xing et al., 2009, 2017; Niu y Xing, 2023), y en Europa occidental, especialmente en la Formación Tremp de los Pirineos (Vila et al., 2013).

En cambio, la evidencia de *Hadrosauropodus* en el hemisferio sur se limitaba a un solo registro en la Formación Yacoraite, en la localidad de Maimará, quebrada de Humahuaca, provincia de Jujuy, Argentina (Díaz-Martínez et al., 2016). Recientemente, un nuevo hallazgo ha sido descrito en la zona de Huichaira, cercano a la localidad previa. En esta contribución se describe, analiza e interpreta este material asignado al icnogénero de *Hadrosauropodus*, sumándose al registro previamente conocido.

Desarrollo

El nivel icnofosilífero contiene 25 huellas tridáctilas distribuidas sobre una superficie de aproximadamente 10 m² inmediatamente por encima del contacto con la Formación Lecho, en la base de Formación Yacoraite. Se identifican huellas aisladas y tres cortas rastrilladas (Fig. 1). Dos de ellas (rastrilladas 1 y 2) pertenecen al icnogénero *Hadrosauropodus*, quedando asignado con dudas como *H*. isp. mientras que la tercera (rastrillada 3) corresponde a huellas son vinculadas a terópodos, sin asignación icnotaxonómica cierta. Las huellas miden en promedio 32,3 cm de largo y 19,9 cm de ancho, siendo generalmente más largas que anchas. Las impresiones asignadas a *Hadrosauropodus* exhiben su morfología característica: simetría tridáctila, dígitos anchos con terminaciones romas, y un "talón" bilobulado, correspondiente a la almohadilla metatarsofalángica. Los ángulos de divergencia promedio entre las improntas de los dígitos son de 33,8° entre los II–III, 32,4° entre III–IV y 66,2° entre II–IV. La mayoría de las huellas presenta rebabas de desplazamiento de barro poco marcados y contornos mal definidos. Las rastrilladas 2 y 3 muestran orientación noreste (20–30°), con longitudes de paso que varían entre 148 y 207 cm. Algunas impresiones presentan posibles huellas de manos asociadas, con dimensiones de entre 10 y 13 cm de largo (Fig. 2).

Desde el punto de vista estratigráfico, el hallazgo en la base de la formación sugiere que la dispersión de estos grandes ornitópodos en la región se dio en fases tempranas de la transgresión marina registrada para la Formación Yacoraite.

El hallazgo de *Hadrosauropodus* isp. en Huichaira constituye la segunda localidad confirmada para este icnogénero en la Formación Yacoraite y en el hemisferio sur, reforzando la hipótesis de una dispersión de hadrosáuridos hacia Sudamérica durante el -Campaniano-Maastrichtiano (Rozadilla et al 2021). Su posición basal dentro de la unidad carbonática destaca además la relevancia del sitio para futuras reconstrucciones paleoecológicas y biogeográficas de los ecosistemas marginales andinos del Cretácico Superior.

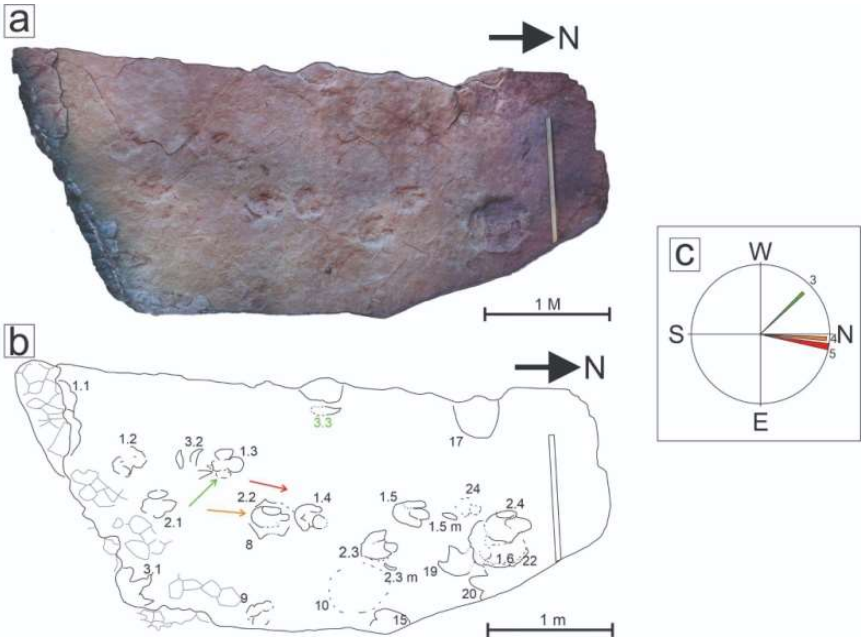

Figura 1: Imagen de la superficie portadora en el icnositio Huichaira. El norte está indicado por la flecha negra. b) Mapa interpretativo de la laja con huellas, con las pistas individuales y las rastrilladas etiquetadas. Los contornos sólidos representan huellas bien preservadas; los contornos punteados indican huellas mal

preservadas o incompletas. Las rastrilladas están codificadas por colores: rastrilladas de hadrosáuridos en rojo y naranja (1 y 2, respectivamente), y rastrillada de terópodo en verde (3). c) Diagrama de rosas que muestra la orientación de las rastrilladas, lo que sugiere una dirección de movimiento predominantemente hacia el norte.

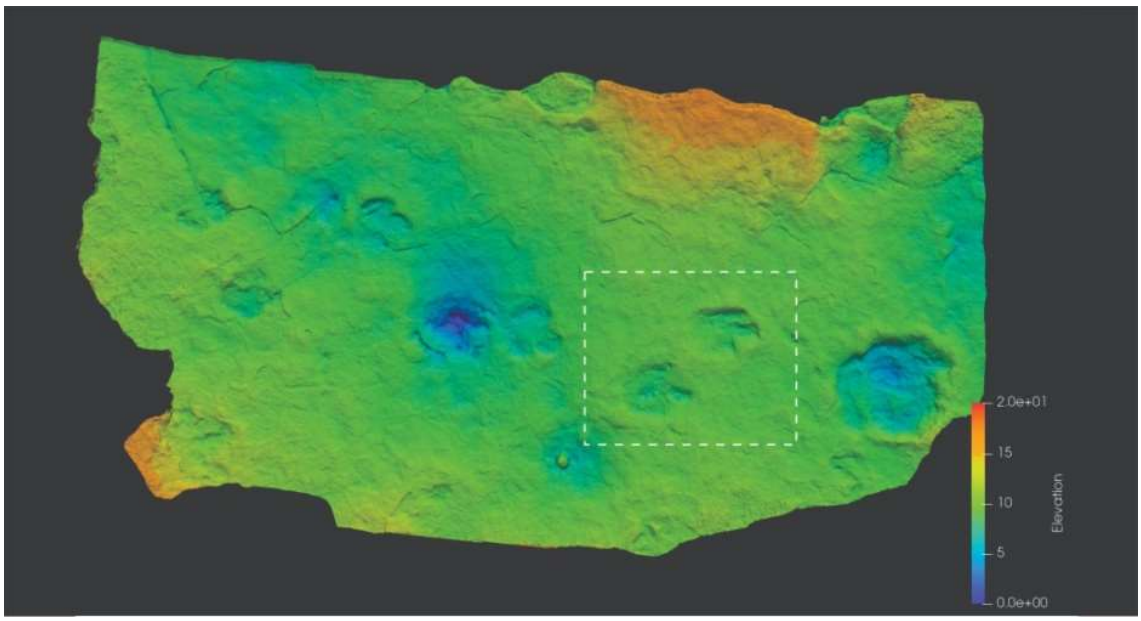

Figura 2: Mosaico fotogramétrico de la principal superficie portadora de huellas, que muestra las icnitas de Huichaira, codificado por colores. El recuadro punteado indica el sector con impresiones que conservan rasgos morfológicos mejor definidos.

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Dientes aislados de dinosaurios terópodos del yacimiento de Lo Hueco (Cretácico Superior. Cuenca, España)

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Los depósitos del Cretácico Superior europeo han proporcionado un abundante registro de dinosaurios y otros vertebrados continentales debido al descubrimiento de un gran número de yacimientos en las últimas décadas (e.g., Pereda-Suberbiola, 2009; Riera et al., 2019; Ősi et al., 2012; Ortega et al., 2015; Csiki et al., 2015, Pereda-Suberbiola et al., 2015; Canudo et al., 2016; Pérez-García et al., 2016, 2020; Isasmendi et al., 2022, 2024; Malafaia et al., 2025). Desafortunadamente, el registro de dinosaurios terópodos en estos niveles es relativamente escaso y compuesto mayormente por material fragmentario, complicando la comprensión de la historia evolutiva de estas faunas durante la última parte del Mesozoico en Europa (Malafaia et al. 2023).

El yacimiento de Lo Hueco (Fuentes, Cuenca) fue descubierto en 2007 en niveles atribuidos al Campaniense superior-Maastrichtiense inferior de la Formación Villalba de la Sierra, en el dominio suribérico de la Cordillera Ibérica (Ortega et al., 2015). Este yacimiento ha proporcionado uno de los registros más abundantes de la fauna de vertebrados continentales del Cretácico Superior del suroeste de Europa (Mocho et al., 2024). El registro de dinosaurios terópodos en este yacimiento está representado por escaso material postcraneal aislado, atribuido preliminarmente a abelisáuridos y maniraptores, incluyendo eudromeosaurios dromeosaurinos y velociraptorinos, y avialanos (Ortega et al., 2021; Ortega et al., 2022; Malafaia et al., 2023) y a un gran número de dientes aislados, asignados preliminarmente a diferentes clados de Maniraptora.

Los dientes aislados suelen ser los restos mejor conservados y más abundantes de terópodos gracias a la dureza del esmalte, lo cual facilita su preservación, y al continuo reemplazamiento de sus dientes a lo largo de la vida del individuo (Torices et al., 2015)

Se han estudiado 150 dientes aislados de terópodos provenientes de dicha localidad, en primer lugar, desde un enfoque cualitativo, mediante la comparación de sus caracteres morfológicos y, posteriormente desde un enfoque cuantitativo, realizando análisis multivariantes y cladísticos. Los resultados obtenidos de dichos análisis conjuntamente permitieron asignar el material dental principalmente a cf. Velociraptorinae indet., cf. Dromaeosaurinae indet., cf. *Paronychodon*, cf. *Richardoestesia*, cf. *Pyroraptor olympius* y a un terópodo indeterminado. Este conjunto faunístico presenta una estrecha similitud y es consistente con los documentados en otras localidades ibéricas y europeas del Cretácico Superior (Company et al., 2009; Torices et al., 2015; Pereda-Suberbiola et al., 2015; Ősi et al., 2019), proporcionando un contexto preciso de la composición y diversidad de los terópodos en el yacimiento. Este patrón sugiere que las faunas de terópodos europeos podrían haber experimentado escasas modificaciones a lo largo de las últimas etapas del Cretácico. Estos hallazgos respaldan investigaciones previas y contribuyen a una mejor comprensión de la composición y la

historia evolutiva de los terópodos europeos a finales del Mesozoico (Malafaia et al., 2023). Las diferencias en los resultados de los análisis cladísticos respecto a los análisis multivariantes para la clasificación de varios de los dientes de Lo Hueco pueden deberse a la falta de información en nuestra base de datos, ya que todos ellos son dientes aislados y algunos están parcialmente rotos. A ello hay que sumarle el alto grado de homoplastia que presentan los dientes de terópodos y la falta de conocimiento sobre la variación morfológica y/u ontogenética intraespecífica. (Smith y Dalla Vecchia, 2006; Rauhut, 2011; Serrano-Martínez et al., 2015; Hendrickx et al., 2020). Sin embargo, el uso conjunto de técnicas multivariantes y análisis cladísticos nos permite sugerir la presencia de ciertos taxones y evaluar la similitud entre los especímenes.

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Preliminary study on pelvic ossification in an ornithopod dinosaur from Ladruñán (Teruel, Spain)

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Keywords: Iguanodontia, osteohistology, myology, locomotion, ischium.

Abstract

This study presents an osteohistological analysis of a partially preserved ischium (MPZ 2025/06) from an iguanodontian dinosaur recovered in the Barremian levels of the Mirambel Formation (Teruel, Spain). The thin section reveals marked cortical remodelling and high compactness, comparable to another coeval specimen of similar ontogenetic stage (MPZ 2024/94). Despite morphological differences, both ischia show a similar distribution of tissue fronts, suggesting limited interspecific histovariability between them. The asymmetric microanatomy identified (ventromedial expansion of the medullary cavity and dorsolateral thickening of compact tissue) correlates with muscle distribution inferred from previous reconstructions. These features support a biomechanical origin for the extreme remodelling seen in the ischium and highlight the value of histology in testing locomotor hypotheses in ornithopods.

Introduction

Ornithopod dinosaurs are a notable case study in palaeohistology, as the abundance of specimens has enabled a reasonable understanding of their development (Woodward *et al*., 2015). However, questions remain, such as the origin of unusual appendicular microstructures possibly linked to ontogenetic and locomotor changes (Hübner, 2012). Due to intraskeletal histovariability, a broader approach is needed, including postcranial elements potentially influenced by biomechanical factors (Maidment *et al*., 2014). This study analyses an iguanodontian ischium and compares it with that of a previously studied specimen that showed high compactness and remodelling. The aim is to improve the understanding of the pelvic microanatomy and its biomechanics in Iguanodontia.

Geological Setting

The ischium analysed belongs to a partial skeleton recovered by the Aragosaurus research team in Pepe site, near the town of Ladruñán (northeastern Teruel Province, Spain). The Pepe site lies in the uppermost levels of the Barremian Mirambel Formation, in the Morella sub-basin (Maestrazgo Basin). This unit comprises lutites, sandstones and limestones corresponding to alluvial and shallow lacustrine facies (Gasca *et al*., 2017). The fossil-bearing layer occurs in the upper part of a terrigenous alluvial interval composed of reddish to purplish mudstones, interpreted as floodplain deposits.

Material and Methods

The material consists of an incomplete ischium attributed to Iguanodontia indet. The element (MPZ 2025/06) and its thin section (MPZ 2025/06-L1) are housed in the Museo de Ciencias Naturales de la Universidad de Zaragoza. The section was taken from the proximal ischial shaft, offset from the ossification centre, which limits the skeletochronological record but enables comparison with a previously studied specimen. The 70–100 µm section was prepared at the Servicio General de Apoyo a la Investigación (UNIZAR) following standard procedures (Cerda *et al*., 2020). It was examined using an Olympus BX53M petrographic microscope at IUCA-UNIZAR, with high-resolution images obtained via an Olympus DP27 camera and OLYMPUS *Stream Basic* software. A CT scan was performed using a Zeiss Metrotom 800 G3/225 kV system and *ZEISS METROTOM OS* software (4 merge, 2103 µA, 400 ms exposure, 3 mm Cu filter) to analyse ossification patterns along the proximal plate near the cut point. Images were processed to enhance porosity detection, and compactness was assessed using *Fiji* with the *BoneJ* plug-in. Histological terminology follows de Buffrénil and Quilhac (2021).

Results

Morphological description

MPZ 2025/06 is a left ischium that preserves part of the ischial shaft, the base of the obturator process, and a fragment of the iliac peduncle. It has a preserved anteroposterior length of 392 mm and a maximum dorsoventral height of 153 mm. The lateral surface is slightly concave dorsoventrally and convex anteroposteriorly. The medial surface is flat dorsoventrally and anteroposteriorly concave from the base of the obturator process towards the anterior part. The ischial shaft is straight, expands lateromedially, and progressively compresses dorsoventrally as it lengthens. The obturator process is narrow and quadrangular in shape. The iliac peduncle widens anteriorly at its dorsal margin, becoming much thicker and possessing a triangular cross-section.

Osteohistological description

The sample exhibits cortical thickening in the dorsolateral area and a ventromedial expansion of the medullary cavity (Fig. 1A). The cavity contains large resorption chambers that inhibit trabecular bone formation, although porosity decreases medially. In the dorsolateral area, some resorption clusters are unusually developed and separated from the cavity by a band of compact tissue. The cortical region is filled with Haversian tissue, including up to three generations of secondary osteons in the most remodelled areas (Fig. 1B). In contrast, the ventral subperiosteum preserves a small portion of extracellular matrix with a woven-parallel complex, simple canals, and primary osteons arranged longitudinally. Sharpey's fibres are present, along with two lines of arrested growth (LAG) and four more peripheral LAG clusters with narrower spacing. CT data show a similar ossification pattern throughout the bone, although the available resolution does not confirm whether Haversian development matches that observed in the thin section.

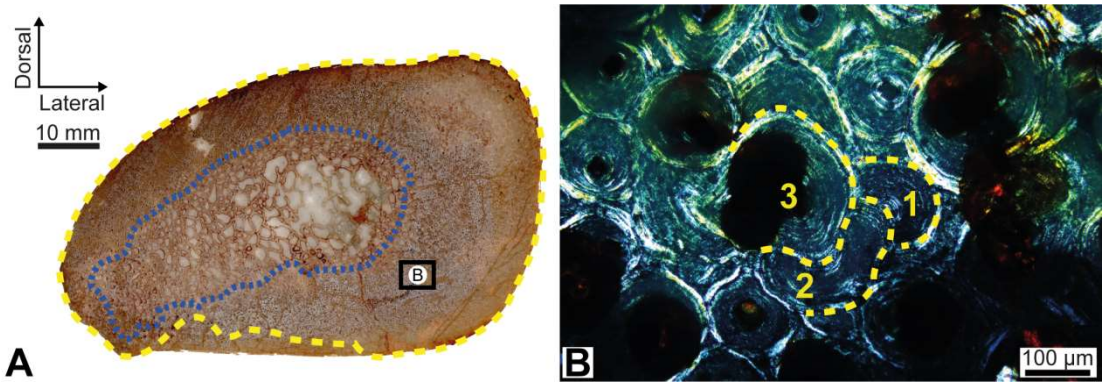

Figure 1. MPZ 2025/06-L1. A) Distribution of the medullary cavity and the resorption front (blue), and the Haversian substitution front (yellow). B) Magnification of the framed area in A under crossed Nicols: Haversian tissue with three generations of secondary osteons.

Discussion

Previous assessments based on two dorsal ribs indicate that the specimen was sexually mature but had not yet reached full skeletal maturity (Maíllo *et al*., 2023). The ischium shows extensive Haversian tissue, which could suggest an advanced ontogenetic stage. However, the preserved LAGs disperse similarly to those in the ribs, indicating that remodelling was driven by factors unrelated to late-stage skeletal maturity. Possible causes include biomechanical stress from active muscle insertions or changes in load distribution, both especially relevant in ornithopods transitioning between bipedal and quadrupedal locomotion (Maidment *et al*., 2014). The degree of remodelling and compactness in MPZ 2025/06 is comparable to that of another ischium (MPZ 2024/94-L1) from a coeval iguanodontian of similar ontogenetic stage, found at the nearby Azud Aliaga site (Aliaga, Teruel Province) (Maíllo *et al*., 2025) (Fig. 2). Despite differences in section morphology, both show a comparable distribution of tissue fronts, suggesting minimal interspecific variability in ischial histology.

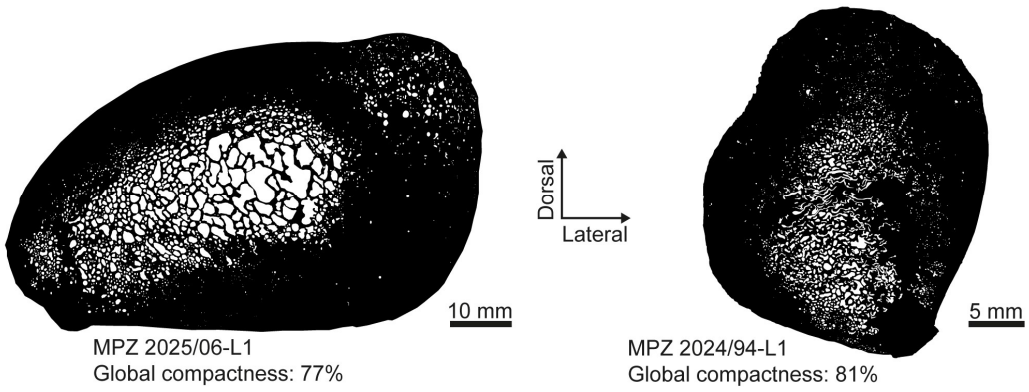

Figure 2. Distribution of compact tissue (black) and porosity (white) in each sample.

The tissue distribution in both specimens aligns with the muscular reconstruction proposed by Maidment *et al*. (2014) for the pelvic girdle and its influence on hindlimb moment arms in quadrupedal ornithopods. Both ischia show ventromedial expansion of the medullary cavity and narrowing of compact tissue in that area. This drift correlates with the lower medial rotator moment arms. Similarly, dorsolateral thickening of compact tissue and increased Haversian density in that region may reflect interaction with pelvic

abductors and the *femorotibialis internus*, which originates on the dorsal surface of the ischium. If so, its involvement at the proximal margin of the ischial shaft should be reflected in the proximal plate's microstructure, with denser Haversian tissue proximally that decreases distally as the bone extends away from the muscle. Although we lack CT scans of the ischial shaft to confirm if this ossification persists as the influence of muscle diminishes, available data show that the distribution of the medullary cavity and the compact tissue is maintained throughout the proximal plate. This may indicate either proximally focused remodelling, driven by stress of the above-mentioned muscles and the primary ossification centre (near the shaft-acetabulum junction), decreasing distally as their influence wanes; or a uniform remodelling along the shaft, maintained by a larger sustained loading and tail muscle input that helps distribute mass evenly. Distinguishing between these will require further histological sampling along the bone.

Conclusions

Our preliminary results suggest that the ischial microstructure of Early Cretaceous iguanodontids from the Maestrazgo Basin shows minimal interspecific variability. Its asymmetric microanatomy, marked by ventromedial expansion of the medullary cavity and dorsolateral thickening of compact bone, aligns with associated musculature and suggests that the remodelling is primarily driven by biomechanical factors. Histology thus provides a useful complement to myological analysis, allowing the testing of locomotor inferences. Considering these results, further histological sampling of ornithopod pelvic bones is key to better understanding their palaeoecology and development.

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Taphonomic insights from a corroded maxilla of a hatchling *Allosaurus* from the Upper Jurassic of Guimarota (Portugal)

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Keywords: Kimmeridgian, Lusitanian Basin, Leiria, Dinosauria, Paleoecology

Introduction

The Guimarota coal mine, located in the Leiria region on the western margin of the Lusitanian Basin (Portugal), is one of the most significant Upper Jurassic microvertebrate localities. It is particularly renowned for its exceptional fossil record of early branching mammalians (e.g. Krebs, 2000; Martin, 2001, 2013). However, the site has also yielded a diverse assemblage of other vertebrates, including dinosaurs (primarily represented by isolated teeth), actinopterygians, amphibians, lepidosaurs, turtles, crocodyliforms, and pterosaurs (e.g. Broschinski, 2000; Gassner, 2000; Kriwet, 2000; Wiechmann, 2000; Wiechmann and Gloy, 2000; Caldwell et al., 2015). An abundant and diverse assemblage of theropod dinosaurs, mainly represented by isolated teeth, was recovered from this locality. These have been interpreted as possibly belonging to *Ceratosaurus* and *Allosaurus*, as well as various coelurosaur clades, including tyrannosauroids (some possibly referable to *Aviatyrannis*), potential *Compsognathus*, *Dromaeosaurus*, *Paronychodon*, *Richardoestesia*, indeterminate troodontids, and several specimens first attributed to *Archaeopteryx* (Zinke and Rauhut, 1994; Zinke, 1998; Rauhut, 2000, 2003). A few non-dental theropod remains have been also described, including a small maxilla interpreted as belonging to a hatchling *Allosaurus* individual and, a set of pelvic elements described as the new tyrannosauroid species *Aviatyrannis jurassica* (Rauhut, 2003; Rauhut & Fechner, 2005).

A review of the theropod fossil record from Guimarota revealed notable taphonomic features. These include enamel-free patches on some isolated teeth, interpreted as marks produced by foraging mollusks (Maggia et al., 2005,) and a corrosion pattern on the hatchling *Allosaurus* individual, consistent with digestion-related damage.

Geological context of the Guimarota fossil site

The vertebrate-bearing strata at the Guimarota fossil site consist of two lignite coal layers intercalated within marly limestones (Zinke, 1998), which belong to the Alcobaça Formation (Fig. 1) and are dated to the early Kimmeridgian (Helmdach, 1971; Schudack 2000a, b). This sedimentary sequence represents the deposits of a lagoon with abundant vegetation, comparable to modern tropical mangrove forests (e.g. Helmdach, 1971; Van Erve and Mohr, 1988; Gloy, 2000; Schudack, 2000a; Schwarz, 2002).

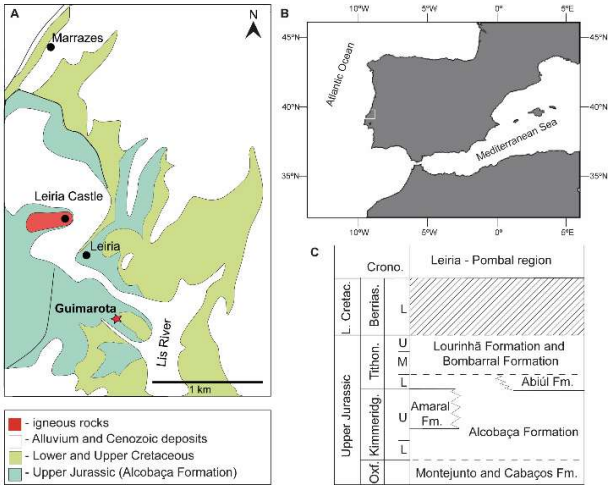

Figure 1.- Geographic and geologic context of the Guimarota fossil site. A, simplified geologic map showing the position of Guimarota. B, geographic map of the Iberian Peninsula. The white rectangle indicates the region of Leiria on the central-west coast of Portugal. C, simplified stratigraphy of the Upper Jurassic and Lower Cretaceous sequences in the region of Pombal-Leiria based on Kullberg et al. (2013) and Fürsich et al. (2021).

Material and Methods

The studied material consists of an isolated maxilla (MG 27804; former inventory number IPFUB Gui Th 4), interpreted as belonging to a hatchling *Allosaurus* individual, collected in the Kimmeridgian Guimarota fossil site (Leiria, Portugal). The specimen is housed in the paleontological collections of the Museu Geológico, Laboratório Nacional de Energia e Geologia of Lisbon. High-resolution photographs of the specimen were obtained using a Leica Stereomicroscope M165 equipped with a Leica Z6 AP0 zoom system (zoom range: x0.57 and x3.6), connected to a Leica DMC4500 Camera. Additionally, the specimen was analysed using a HITACHI™ S3700N Scanning Electronic Microscope (SEM) equipped with a Bruker™ Xflash 5010 SDD Energy Dispersive Spectrometry (EDS) detector.

Description and discussion

The maxilla is nearly complete preserving thirteen alveoli with eight erupted teeth. The lateral surface of the maxilla is relatively well preserved, but the anterior part of the medial surface along the alveolar margin is mostly missing, exposing the tooth roots between the third and seventh alveoli. The tips of most tooth crowns have lost their enamel, exposing underlying dentine with a wavy and somewhat polished texture (Fig. 2). The transition between the enamel-free apex and the basal section of the crown, where enamel is still preserved, is marked by a nearly straight, smoothed margin that is consistently positioned at approximately the same level across all affected teeth.

The enamel loss at the crown tips and the wavy aspect of the exposed dentine in MG 27804 closely resemble decalcification patterns documented in experimental studies by Smith et al. (2021) on lizards ingested by ferrets. No known diagenetic process selectively removes tooth enamel while leaving dentine intact (Fisher, 1981). Although enamel loss due to decalcification by plant acids has also been identified in the fossil record, such processes typically affects both enamel and dentine, producing pitted or vermiform surface textures (Fisher, 1981). Similarly, corrosion marks caused by soil biological activity or immersion in acidic water have been described, but these generally affect all exposed surfaces uniformly (Fernández-Jalvo and Andrews, 2016).

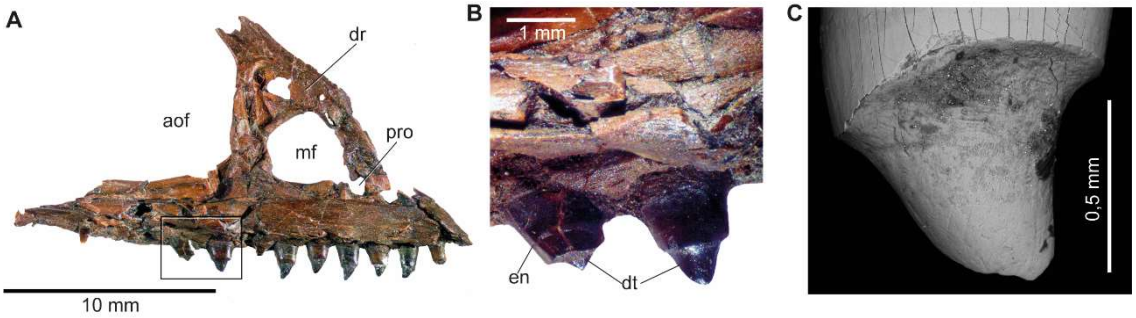

Figure 2.- *Allosaurus* maxilla from Guimarota (MG 27804), showing the enamel-free apices on all preserved teeth. A, lateral view of the maxilla; B, close-up of teeth from the posterior section; C, detail of the tooth crown tip observed under SEM. Abbreviations: aof, antorbital fenestra; dr, dorsal recess; dt, dentine; en, enamel; mf, maxillary fenestra; pro, promaxillary fenestra.

Conclusion

The corrosion pattern identified in the *Allosaurus* maxilla from Guimarota is consistent with digestion marks, and the loss of enamel at the tips of the crows suggests that this process occurred while the teeth were still embedded in the maxilla and partially protected by the gingiva, most probably indicating that this specimen represents an egested rather than completely digested remain. This study represents the first identification of digestion marks in a Late Jurassic theropod dinosaur. By drawing attention to these corrosion patterns, future research may uncover additional examples, further expanding our understanding of trophic interactions in Mesozoic ecosystems.

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The Caminonegro site (Allueva Fm., middle-upper Campanian): paleoological assemblage, sedimentary environment and genesis

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Introduction

Recent charophyte biostratigraphy and magnetostratigraphy studies in Paleocene units of the Montalbán subbasin, Teruel, (units M1-M2; Pérez *et al.,* 1983), motivated by the discovery of dinosaur remains, have allowed a chronostratigraphic reassignment of these units to the Late Cretaceous (Aurell *et al.,* 2022). This allowed the definition of a new geological unit, the Allueva Formation, with a sedimentary association characteristic of an alluvial system in mid-distal areas (Aurell *et al.,* 2022; Torromé *et al.,* 2024). Numerous and diverse paleontological sites have been found along its outcrops. One of these sites, near the villages of Allueva and Bea, is Caminonegro site (middle-late Campanian), which is notable for its content of vertebrate microfossils, especially eggshell fragments.

Methodology

A 58-meter-thick stratigraphic section was realized in the Allueva Fm, including Caminonegro site outcrop, to contextualize the site in the sedimentary environment. 25 sediment samples were taken along its length to describe the rock facies. An additional 94 kg of sediments were collected in the Caminonegro site in order to analyze its palaeontological record.

The sample was dried at room temperature for 48 hours and then bathed in a 5% hydrogen peroxide solution. The resulting mud was sieved through mesh sizes of 2, 1, and 0.5 mm. The remains retained on the sieves were dried, packaged, labeled, and sorted to separate the micropaleontological remains (bone fragments, teeth, eggshells, charophytes, gastropods, plant remains, and microbial structures). The eggshells found in the +2 mm sample were studied using Secondary Electron images acquired with a MERLIN FESEM and 30 μm thick thin sections observed in an Olympus petrographic microscope.

Sedimentary environment

In the facies analysis, seven lithofacies were identified that are consistent with an alluvial system: massive conglomerates with erosive bases, laminated sandstones, fossiliferous marls, mudstone limestones, wackestone limestones, packstone limestones with oncoids, and carbonate microconglomerates. These are laterally related in mid-distal areas of the alluvial system, where the coarse-grain detrital facies represent the paleochannels that furrowed the floodplains of the system (e.g. Nichols and Fisher, 2007).

The limestones and marls association formed in lacustrine-palustrine environments as suggested by the identified sedimentary structures (brecciation, mudcracks, bioturbation and fenestral porosity) that indicate a marsh environment with shallow water bodies and constant variations in lake level (e.g. Alonso-Zarza and Tanner, 2010). This interpretation is further supported by the identification of the association of *Lychnus sp.* and charophytes, that has been commonly associated to lacustrine environments at the end of the Cretaceous (e.g. Freytet and Plaziat, 1982; Torromé *et al.,* 2023).

The formation of the Caminonegro site is associated with both the detrital input from the alluvial streams and the carbonate fraction derived from precipitation of $CaCO_3$-rich meteoric waters (e.g. Alonso-Zarza and Tanner, 2010). The fossil content of the deposit is notable for bone fragments, fish and crocodylomorph teeth, plant remains, charophytes, gastropods and eggshells. The weathering of the fossil remains indicates transport to the lacustrine system, making it an allochthonous fossil assemblage, along with the remains of organisms that inhabited the lake areas, such as charophytes, gastropods, fish and crocodylomorphs.

Fossil and paleoological assemblage

A total of 281 eggshell fragments were identified and classified into three oofamilies: Krokolithidae, Prismatoolithidae, and Spheroolithidae.

Krokolithidae eggshells are calcite eggshells with three structural layers, with an inner layer formed by microcrystalline basal protuberances with accessory crystals forming a rosette, and a continuous layer with a tabular, book-like ultrastructure, are diagnostic characters of the oofamily, along with the block extinction in crossed nicoles. The Krokolithidae eggshells can be related to the crocodylomorph teeth present at the site, with bulbous (globidont) and conical morphologies, which, in the absence of a detailed study on the remains, are tentatively assigned to cf. *Acynodon* (Hylaeochampsidae) and Allodaposuchidae indet. respectively (Blanco *et al.,* 2020). Thus, it can be deduced that these two genera that would inhabit the lacustrine areas of the outcrop would be the animals that produce the Krokolithidae eggshells.

Prismatoolithidae eggshells show 2 structural layers, with a lower mammillary layer in a ratio with respect to the continuous prismatic layer of 1:6, together with an external surface with dispersituberculate ornamentation formed by irregular nodes with pore openings in some of them, are diagnostic characters of the oogenus *Pseudogeckoolithus*. Choi *et al.* (2020) relates the *Pseudogeckoolithus* eggshells with maniraptoran theropod dinosaurs through the EBSD study technique, focused on the crystallography of calcite prisms. In Caminonegro site there is an absence of fossil remains (teeth and bones) of these dinosaurs, as in the Allueva Fm., highlighting these eggshells as the first fossil remains of this group of animals in the Campanian of the Iberian range.

Spheroolithidae eggshells show a single calcite layer with a spherulitic structure featuring sagenotuberculate ornamentation and a protocanaliculate pore system, features diagnostic of the this oofamily. The Caminonegro site contains few centimeter-sized fossil remains, with a tooth of an indeterminate Rhabdodontidae standing out, along with isolated bone remains from the Allueva Fm. The Spheroolithidae shells, which are generally attributed to hadrosauroids (Horner and Weishampel, 1988), a group of animals belonging to the Maastrichtian that replaced the rhabdodontids (Fondevilla *et al.,* 2019), are here related to Rhabdodontidae in the absence of other preserved ornithopods.

The Caminonegro oological assemblage can be compared with other eggshell paleoassemblages from the Upper Cretaceous of Iberia. In Blasi 2 (Arén, Huesca), upper Maastrichtian age, eggshells of Spheroolithidae, Prismatoolithidae, Krokolithidae and Testudoolithidae are recognized (Pérez-Pueyo *et al.,* 2021). Similar associations have been described in several localities of the Pyrenees, including Fontllonga 6 (where the holotype of *Pseudogeckoolithus* is located) (Vianey-Liaud and López-Martínez, 1997). Other localities, such as Poyos (Guadalajara), upper Maastrichtian, most of the Localities of the Tremp Formation (late Campanian-Maastrichtian, Selles *et al.,* 2013; Sanz *et al.,* 1995), and Loarre, (late Campanian-early Maastrichtian, Moreno-Azanza *et al.,* 2022), are dominated by sauropod related ootaxa (Fusioolithidae and Megaloolithidae).

The absence of sauropod-related eggshells in Caminonegro, despite titanosaurian sauropod bones being abundant in the Allueva Fm (Aurell *et al.,* 2022) requires further examination.

In one hand, recent studies have confirmed that sauropods inhabited coastal and lowland environments, but preferred the last, in a proportion of 1 to 4 (Vázquez *et al.,* 2025). On the other hand, sauropod eggshell fragments are typically centimetric in size, several orders of magnitude larger than the largest fragment recovered in Caminonegro. Further research is needed to confirm in the total absence of these otherwise conspicuous fossils in allochthonous assemblages like Caminonegro site is a true palaeoecological signal or a taphonomic bias. In any case, the lack of sauropod-related oological remains in an alluvial environment supports the hypothesis of sauropods been selective for their nesting sites.

These results enhance the vertebrate fossil record of the Allueva Fm, previously limited to the skeletal remains of titanosaur and ornithopod dinosaurs along with crocodylomorphs (Aurell *et al.,* 2022), identifying the presence of theropod dinosaurs in the ecosystem for the first time.

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Analysis of the morphological variability of the inner ear in the extinct bothremydid turtles

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Introduction

Bothremydidae was a successful lineage of turtles within the Crown-group Pleurodira. Their representatives were widely distributed on most continents of both northern and southern hemispheres, and they were recognized from the Albian (Early Cretaceous) to the Eocene at least. All extant species of Pleurodira live in freshwater environments. However, the bothremydids occupied a wide range of aquatic habitats, not being limited to continental environments (Gaffney et al., 2006). Thus, the representatives of Cearachelyini and most members of Bothremydini were identified as freshwater turtles, while the representatives of Taphrosphyini and Nigeremydini, and also some species of Bothremydini (as the Maastrichtian *Zolhafah bella*), were recognized as marine forms. The proposed lifestyle for most bothremydid taxa is generally based on the interpretation of the sedimentary environments in which they were found. However, some anatomical modifications were identified as marine adaptations convergent with those observed in extant cryptodiran sea turtles, as the high-domed skulls or the elongated limb bones. The scarce neuroanatomical information available for Bothremydidae has not allowed to quantify modifications of the cranial cavities related to a particular lifestyle. Nevertheless, modifications in the endosseous labyrinth in response to adaptations for life in marine environments have been observed for different groups of reptiles. Thus, some groups of sauropterygians highly adapted to pelagic marine environments, such as plesiosaurs and sea cryptodiran turtles, have labyrinths with relatively short and wide semicircular canals. In contrast, Triassic sauropterygians adapted to coastal areas and marine crocodiles have relatively more elongated and narrow canals (Neenan et al., 2017).

Methodology

In this work, the inner ear of different lineages of bothremydid turtles were analyzed with the aim of identifying differences in this element related to adaptations to life in diverse aquatic environments. As in previous works on neuroanatomy of turtles, the analysis of the endosseous labyrinths of the bothremydids studied here was carried out using three-dimensional reconstructions generated from high-resolution CT-scan images. These virtual models have also been compared with those of other forms of turtles (both extant and extinct pleurodires and cryptodires) to identify modifications due to adaptation to different habitats. Relative measurements of the height and length of the semicircular canals have been used to identify these differences.

Results and discussion

Although neuroanatomical studies are still relatively scarce for Bothremydidae, they provide valuable information on the modifications in the inner ears of this lineage. Although, in general terms, some previous studies have not revealed a direct relationship between the morphology of the inner ear and the lifestyle of the turtles (Evers et al., 2022), the endosseous labyrinths within Bothremydidae exhibit morphological differences across the lineages within this group. Bothremydid taxa identified as freshwater forms (i.e., Cearachelyini and most of Bothremydini) showed relatively elongated and narrow semicircular canals with a ratio between the length and the height above 2.20 (Martín-Jiménez & Pérez-García, 2021; 2022). However, the ratios measured for other taxa (i.e., the Bothremydini *Zolhafah bella*, Taphrosphyini, and Nigeremydini) are below 2.00, reflecting relatively anteroposteriorly shorter and dorsoventrally higher semicircular canals in the endosseous labyrinth (Martín-Jiménez & Pérez-García, 2025). Comparison with both freshwater and marine turtle forms (both pleurodires and cryptodires) allows to identify morphological differences in the inner ears of bothremydids. This analysis provides new neuroanatomical evidence that confirms the previously proposed lifestyles for the different lineages within Bothremydidae.

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The dinosaur postcranial fossils of the La Cantalera-1 site (Barremian, Lower Cretaceous) in Josa (Teruel, Spain)

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Introduction

La Cantalera-1 site was discovered in the 1990s in the locality of Josa (Teruel, Aragón, Spain). Since then, thousands of fossils remain have been recovered, most of them replaced teeth from vertebrates, predominantly ornithopod dinosaurs (Canudo et al. 2010). This outcrop is located in the basal levels of the lower sequence of the Blesa Formation, the unit that marks the beginning of Cretaceous sedimentation in the Oliete sub-basin (Maestrazgo Basin). The site is found in a level of red clays representing deposits from distal alluvial to palustrine mudflat, with local sheet flood and debris flow deposits (Aurell et al. 2018).

The presence of *Atopochara trivolvis triquetra* has allowed to date the site as Early Barremian (Aurell et al. 2018). Canudo et al. (2010) conducted an initial review of the vertebrate palaeobiodiversity at the site through the study of isolated teeth, identifying 31 different taxa. This biodiversity has been further expanded through the continued analysis of isolated teeth from various groups, such as ornithopods (Gasca et al. 2014), crocodylomorphs (Puértolas-Pascual et al. 2015), and theropods (Alonso & Canudo, 2016). In addition, more than 10 different ootaxa have been described, two of which were first defined at this site (Moreno-Azanza et al. 2014).

Despite the numerous studies carried out on this paleontological site, the majority of non-dental bones from macrovertebrates remain unexamined. Most of the material are small, broken and difficult to assign fragments of bones. Despite this, a significant portion of these remains belong to axial skeleton bones of ornithopod dinosaurs, although fossils of sauropods, ankylosaurs, and, to a lesser extent, theropods have also been recovered.

Material and Methods

All the material described is housed at the Museum of Natural Sciences of the University of Zaragoza. Most of the remains were recovered during excavation campaigns carried out in the 1990s and in 2002. Some fossils were discovered by amateur collectors and donated to the museum, while others were excavated using a grid-based collection methodology, in which sediment was gathered in bags for later washing. As a result, the exact provenance of most fossils within the site is unknown, and for others, only the grid square is known, but not the precise position within it. This makes it impossible to assign most of the fossils to the same skeleton, making it difficult to determine the number of individuals or taxa.

Results and discussion

Thyreophora

Several fragments of the dermal skeleton and some complete osteoderms have been recovered and identified. Most of the material has previously been reviewed by

Parrilla-Bel & Canudo (2017) and Perales-Gogenola et al. (2019). Both studies agree in assigning the material to a Polacanthinae, although the presence of two different taxa cannot be ruled out. Specimen CAN1-724 is a fragment of a vertebral centrum. The dimensions of the articular surface—wider than tall, heart-shaped, and concave—are consistent with the anterior to middle caudal vertebrae of ankylosaurid dinosaurs. This morphology can be observed in *Polacanthus*, *Panoplosaurus*, *Europelta* and *Gastonia* (Raven et al. 2020 and references therein). CAN1-724 may be related to Polacanthinae and could represent the second caudal vertebra identified at the site

Ornithopoda

Most of the recovered and assignable macrovertebrate fossils correspond to ornithopod dinosaur bones. Several dorsal and caudal vertebrae have been recovered, as well as some nearly complete ribs. Regarding the appendicular skeleton, a scapula, two tibiae, a fibula, and an ungual phalanx from ornithopod dinosaurs have been identified. Most of these fossils were found isolated at the site, and some show evidence of deformation or compression—such as the scapula—while others are in excellent condition. All the recovered ornithopod vertebrae share characters related with the Styracosterna clade. The absence of pleurocoels and the amphiplatyan or platycoelous vertebral centra with a sinuous suture with the neural arch are features typical of ornithopod dinosaurs (Norman, 2004). Additionally, the caudal vertebrae exhibit lateral ridges on the centra, a trait commonly observed in iguanodontians (Norman, 2004). The recovered middle to posterior caudal vertebrae exhibit consistent morphology and size, with four of them preserved in articulation. These vertebrae represent the only evidence of anatomically connected material found at the La Cantalera-1 site. The presence of two tibiae and one fibula of markedly different sizes indicates the presence of three different ornithopods at the site. This variation may be due to different ontogenetic stages (hatchling, juvenile, and adult) or to the presence of distinct taxa (hypsilophodontids, and medium and large-sized styracosternans).

Sauropoda

The sauropod material has been recently reviewed by Medrano-Aguado et al. (2023). It consists of several tooth crowns and two vertebrae. The tooth crowns are associated with the asian clade Euhelopodidae, as they exhibit a bulge on the lingual surface—a feature considered a synapomorphy of the group. The vertebrae display typical characteristics of somphospondylan sauropods, which is consistent with the dental assignment.

Theropoda

This is the least represented group at the site in terms of identifiable non-dental remains. Only a single ungual phalanx fragment has been tentatively assigned to Theropoda indet. It is an elongated, straight, pointed phalanx with a subtriangular cross-section, taller than it is wide. The proximal end is missing, but a rounded cavity can be seen inside the phalanx. It features a deep, rounded lateral groove, which is much less pronounced on the medial side. This phalanx differs markedly from those of ornithischian and sauropod dinosaurs. Among theropods, ornithomimosaurs may possess relatively straight manual ungual phalanges (Cuesta et al. 2022), making them a possible source of this fossil, especially since they have already been identified in the Barremian of the Iberian Peninsula. However, it cannot be ruled out that the specimen belongs to a hypsilophodontid ornithopod, whose ungual phalanges differ from those of styracosternan ornithopods and whose teeth have already been found at the La Cantalera-

1 site. The ungual phalanges of hypsilophodontids are characterized by their slenderness and well-defined grooves (Galton, 1975). The extreme slenderness of this phalanx appears to be more consistent with theropod dinosaurs, suggesting that this could be the first postcranial remain of this group recovered from the La Cantalera-1 site.

Conclusions

Most previous research at the La Cantalera-1 site have focused on assessing the diversity of various vertebrate groups based on isolated teeth, which represent the most abundant fossil elements at the site. As shown in this brief review of the postcranial elements, the remains of medium-sized ornithopods are particularly abundant at the site, whereas those of other vertebrate groups are comparatively scarce. The discovery

of caudal vertebrae preserved in anatomical articulation, along with additional elements attributable to a medium-sized styracosternan ornithopod, supports the presence of a partially disarticulated skeleton at the site. Despite the large number of fossils recovered from La Cantalera-1, the site remains far from exhausted. Future excavations are likely to yield diagnostically informative postcranial elements that will enhance species-level identifications, as well as isolated remains of vertebrate groups currently underrepresented in the Barremian fossil record of the Iberian Peninsula.

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Descripción de nuevos rastros de dinosaurio del Yacimiento de Valdecevillo (Grupo Enciso, Cuenca de Cameros) y el impacto de la tectónica en su morfología

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Palabras clave: icnitas, Aptiense, terópodo, deformación

En este estudio, se presenta la descripción de un par de nuevos grupos de icnitas de dinosaurios del Cretácico Inferior localizados en el yacimiento de Valdecevillo (La Rioja), distribuidos en 2 rastros, uno de 6 huellas y otro de 4 huellas, siendo notable de estos rastros la importante deformación sufrida en los mismos derivada posiblemente de procesos tectónicos.

El yacimiento de Valdecevillo se encuentra ubicado en las afueras de la localidad de Enciso, a unos 2 kilómetros al sur del mismo, localizado en la comunidad autónoma de La Rioja en la región septentrional de la Península Ibérica. A nivel geológico, los rastros se encuentran en rocas pertenecientes a la Cuenca de Cameros (Mas et al., 2003), dentro de la cual, los rastros se encuentran en el Grupo Enciso, una unidad compuesta principalmente por una alternancia de lutitas y areniscas datando del Aptiense inferior (Cretácico Inferior) (Mas et al., 2003).

Ambos rastros se encuentran sobre la superficie de un estrato ubicado por encima del denominado "Sector superior" del yacimiento de Valdecevillo, el cual posee, entre otras, las primeras huellas de saurópodo descritas en La Rioja (Pérez-Lorente et al., 2001). La litología es de calizas con textura *mudstone* de color grisáceo, no presenta estructuras sedimentarias y contiene otros ocho rastros de icnitas de dinosaurio, aparte de los dos descritos en este trabajo.

El denominado Rastro 1 está formado por 6 huellas tridáctilas en dirección N208ºE, comenzando con una huella correspondiente al pie derecho. Este rastro continúa durante las 5 huellas siguientes sin pérdida de ningún elemento del rastro y manteniendo una dirección constante. Las huellas presentan una longitud media de 42 centímetros y una separación entre huellas que aumenta sutilmente a lo largo del rastro, indicando un pequeño incremento en la velocidad del animal. Estas huellas han sido interpretadas como pertenecientes a un posible terópodo de tamaño medio basándose en caracteres como la presencia de impresiones de garras (especialmente visibles en la primera huella del rastro), impresiones del talón en forma de V y ángulos interdigitales amplios (Rubio-Nieto et al. 2023), aunque estos últimos no se corresponden con los de un dinosaurio de estas características.

Por otro lado, el Rastro 2 se encuentra conformado por una sucesión de 4 huellas en dirección N109ºE, comenzando con una icnita correspondiente al pie izquierdo. Este rastro mantiene la dirección y preserva todas las huellas individuales, aunque con estados de preservación variable y con tendencia a empeorar en las regiones anteriores del rastro. Las huellas del Rastro 2 presentan una longitud media de 48 centímetros sin contar con

que en algunas huellas la marca del metatarso hace que su longitud llegue a los 61 centímetros. De forma similar a lo observado en el primer rastro, estas huellas se caracterizan también por ser tridáctilas, con impresiones de garras. En este caso los ángulos interdigitales son reducidos y las impresiones del talón están marcadas en forma de V, indicando un posible productor terópodo.

Debido a la tectónica implicada en la zona, es probable que cada uno de los rastros sufriera dos tipos de deformaciones diferenciadas. El Rastro 1 se encuentra deformado de forma dúctil y compresiva, en dirección próxima-distal, mientras que el Rastro 2 sufre de una deformación frágil en forma de falla. Se han realizado dos fotogrametrías, una sobre la icnita del Rastro 1 que se encuentra más afectada y otra sobre las dos icnitas del Rastro 2, que están implicadas en la zona de la falla.

La deformación hallada en el Rastro 1 se aprecia de mejor forma en la pisada I (Fig. 1). Esta presenta una compresión próximo-distal que genera que la relación longitud/anchura sea >1 y que los ángulos interdigitales se vean agrandados, lo cual no se ajusta a los parámetros de huellas de dinosaurio terópodo.

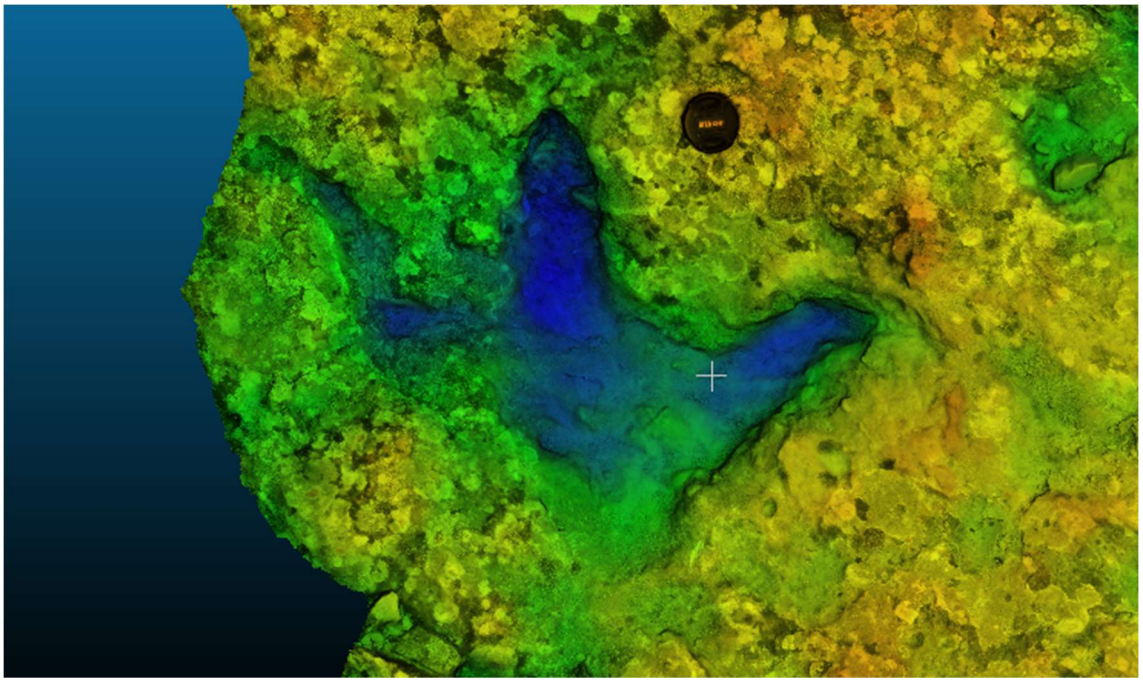

Fig. 1. Mapa de profundidad sobre la pisada I del Rastro 1. Se aprecian los caracteres afectados por la deformación, como el ángulo interdigital y la relación longitud/anchura. Longitud de la huella: 42 cm.

El Rastro 2 no parece presentar importantes deformaciones derivadas de procesos tectónicos en las pisadas II, III y IV. La pisada I resulta notable por estar dividida por una falla. La falla en cuestión se trata de una falla normal, presentando una dirección de N 20ºE y un salto de falla vertical de 5 a 7 cm. La pisada se encuentra atravesada transversalmente por la falla, dejando las regiones distales de los dígitos II, III y IV en el bloque hundido y el talón y regiones proximales de los dígitos en el bloque levantado. Los elementos a ambos lados de la falla son interpretados como pertenecientes a la misma huella en el mismo nivel, dada la litología de las superficies, la aparente continuidad de los dígitos a ambos lados de la falla y la profundidad de la huella, siendo comparable a ambos lados de la falla.

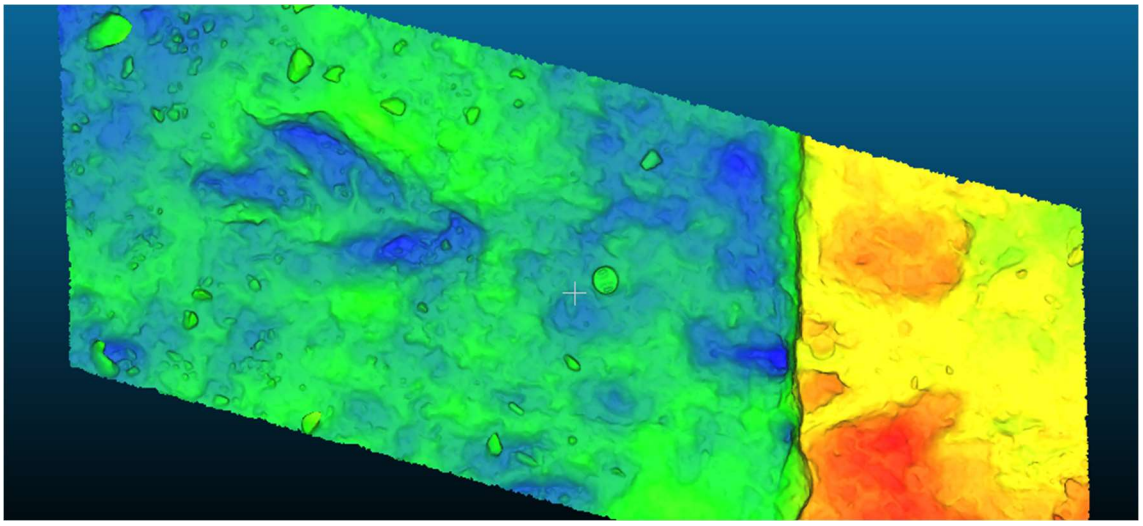

Fig. 2. Mapa de calor de las icnitas del Rastro 2. Se aprecia en colores cálidos el bloque levantado con la pisada I cortada por la falla. A la izquierda de la imagen se aprecia la pisada II con la marca pronunciada del metatarso. Longitud de la huella izquierda: 61 cm.

Es evidente que algunos caracteres permiten asignar con más probabilidad las icnitas al grupo de los dinosaurios terópodos, sin embargo, algunas de estas características se ven afectadas por una tectónica compresiva que en algunos casos podría obstaculizar en un mayor grado el estudio de icnitas.

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Portugal, the nesting ground of the Late Jurassic

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Introduction

Eggs and nests remain as relatively rare findings in the Pre-Cretaceous fossil record (Stein et al., 2019). Despite egg-laying amniotes appearing and diversifying long before the beginning of the Mesozoic, mineralized shelled eggs, those more susceptible of fossilization, appeared independently in the main clades of amniotes only at the end of the Triassic or beginning of the Jurassic (Norell et al., 2020). Earliest mineralized eggshells from dinosaurs are Sinemurian-Pliensbachian in age (Norell et al., 2020; Reisz et al., 2005), while the first testudines eggs date from the Bathonian (Buckman, 1860). Crocodylomorphs, despite having a huge Jurassic diversity and disparity, have a very scarce record of fossil eggs, with the first report on the Kimmeridgian (Russo et al., 2017). This poor record contrasts with the high abundance of Cretaceous localities with testudines, crocodylomorphs, pterosaur and dinosaur eggs that have been reported from all over the world (Carpenter, 1999 and references within). In this work we highlight the exception that proves the rule, the Jurassic coast of Portugal, where a handful of localities in the vicinities of Lourinhã and Leiria have provided an unrivaled record of eggshell fragments, eggs, clutches and embryos of testudines, crocodylomorphs and dinosaurs, dating from the Kimmeridgian to the earliest Tithonian.

Geological setting

The Lusitanian Basin is a large Mesozoic extensional structure at the western Iberian margin. The basin was formed as result of the extensional processes related to the North Atlantic opening, with four marked rift phases from the late Triassic to the early Cretaceous (Kullberg, 2000 and references within) In the central-western area, four depressions called Consolação, Bombarral-Alcobaça, Arruda and Turcifal sub-basins filled with syn-rift sedimentary successions of marine and continental deposits during the late Kimmeridgian, a shift from mixed marine environments (Consolação Fm., Abadia Fm. or Alcobaça Fm.) to more terrestrial (Lourinhã fm.) characterized all four sub-basins. These transitional environments have produced a plethora of vertebrate fossils, with an extensive record of osteological, ichnological and oological remains (Castanera et al., 2020; Mateus et al., 2017; Mocho et al., 2017).

Paleoological record

Testudines. Eggshells have a single report from the Jurassic of Portugal, being described by Kohring (1990) in the Guimarota Mine, from Leiria. Kohring described thin 150 μm shell fragments with aragonitic radial ultrastructure and a subtle compactituberculated ornamentation that he referred to the testudoid morphotype, using the morphotype as a parataxonomic rank. He then referred these eggshells to cryptodiran turtles, based on the fossil record of the Guimarota Mine. These eggshells have taller than wide aragonitic eggshell units, so are most likely attributable to Testudoolithidae, and the extremely thin eggshell probably is enough to erect a new ootaxon. Nevertheless, the materials studied by Kohring never returned to Portugal with the rest of the materials currently housed in the Museu Geológico de Lisboa and can be considered lost. Furthermore, the Guimarota Mine level KM11 of the Alcobaça formation is no longer accessible.

Crocodylomorphs. Portugal has the oldest record of crocodylomorph eggs, with the holotype of *Krokolithes dinophilus* having been described in the locality of Paimogo (Russo et al., 2017). These authors erected a new oospecies based on materials from the type locality and a series of other coeval localities in the Lourinhã formation. The diagnosis is based on a relatively large ellipsoidal egg with a relatively thin crocodyloid eggshell. This combination of features is diagnostic for the holotype egg, but difficult the attribution of most of the fragmentary referred material. In addition, the eggshells are largely recrystallized and the quality of the thin sections figured is not adequate.

Russo et al. (2017) described a second ootaxon, *Suchoolithus portucalensis* based on a clutch of 13 small eggs from Cambelas (Torres Vedras). The diagnostic characters include a small ellipsoid egg with ornamented eggshell surfaces and shell units wider than taller. Authors also refer to a lack of interstices at the base of the shell units. Again, the thin sections provided difficult the identification of the described characters, but the unusual ornamentation on a crocodylomorph egg, coupled with the small egg size and unusually thin eggshell render this oogenus and oospecies easily diagnosable. In his PhD thesis, Castanhinha (2014) studied the same clutch and performed a propagation phase contrast X-ray synchrotron microtomography scan of one egg, stating the presence of a well-developed *in ovo* crocodylomorph embryo, confirming the crocodylomorph affinity of *Suchoolithus*.

In addition, Krokolithidae are the most abundant eggshells in the sampled microfossil vertebrate assemblages. These fragments are sub-millimetric, caramel colored, of thin eggshells (100 to 200 microns), smooth to slightly ornamented, and show typical crocodylomorph eggshell organization under the Scanning Electron Microscope (SEM). The lack of complete eggs hinders the identification of the diagnostic characters of *K. dinophilus*, but smooth or slightly undulated eggshells are much more frequent than those with dispersituberculated ornamentation, suggesting that *Krokolithes* is more abundant than *Suchoolithus* in these localities.

Dinosaurs. The first reports of dinosaur eggshells from Portugal date from the first years of the 1990's. Dantas et al. (1991, 1992) presented two meeting abstracts describing several localities in the vicinity of Lourinhã (Peralta, Paimogo and Valmitão beaches). In these outcrops the authors describe spherulithic eggshells that they tentatively assigned to Megaloolithidae, an oofamily associated with sauropod dinosaurs. In addition, they describe a dinosaur prismatic eggshell from Peralta that is described as very similar to the eggshells with obliquoprismatic morphotype from USA that later will be named *Preprismatoolithus coloradoensis* (Hirsch, 1994). It is noteworthy that Kohring (Kohring,

1993) describes spherulitic eggshells from the near beach of Porto Dinheiro (Porto "Pinheiro") that are similar to those described by Dantas et al (1991, 1992) in Peralta and Valmitão, which were collected between 1959 and 1982, but remained unidentified. Kohring (1993) agrees with the identification of the eggshells as spherulithic but proposes a more accurate Dendroolithidae (=Phaceloolithidae) affinity, an oofamily that has been related to both theropod and sauropod dinosaurs.

Since these first findings, several localities with dinosaur eggshells, eggs and clutches have been identified in the Jurassic coast of Portugal (e.g. Ribeiro et al., 2013a, b), but only eggshell ootaxa have been identified. The spherulithic eggshells have been reported in several additional localities, with the most spectacular specimen being a partial clutch with associated *Torvosaurus* embryonic material from Porto das Barcas (Araújo et al., 2013). Similar eggshell fragments are omnipresent in microfossil vertebrate assemblages, characterized by a spherulithic morphotype and sagenotuberculated ornamentation, although when heavily eroded they can be easily misidentified as megaloolithid eggshells. Another important occurrence is a sandstone block from Porto das Barcas containing two elongated partial eggs (Ribeiro et al., 2013). Concerning the prismatic eggshells, they are characterized by an oblicuoprismatic morphotype, with two layered eggshells with wide shell units and obliquocanaliculated pore system, probably belonging to an unnamed oospecies of *Preprismatoolithus*. The most significant specimen is the "Paimogo clutch" a taphonomic assemblage of over 80 eggs, some with embryos, formed by the washing of several dinosaur clutches (Ezquerro et al., 2024; Fernandes et al., 2021; MATEUS, 1997). Additional important specimens include the Peralta nest, a collection of over 60 complete to collapsed eggs collected in four jackets in one of the outcrops originally described by (Dantas et al., 1992) currently under study. Finally, in 2019, a large jacket containing two to three small, seemingly individualized but in close proximity clutches was excavated in the beach of Canhiçal by our team and is currently under study. This vast collection of eggshells allowed establishing a faster and less destructive sampling protocol for geochemical analysis, ultimately providing more reliable paleoenvironmental reconstructions (Coimbra et al., 2023)

Meaningful absences. It is noteworthy that, despite sauropods being the most ubiquitous dinosaur fossils in the Lourinhã Fm, no sauropod eggshells or eggs have been identified in Portugal. Ongoing research on the eggshell of early-diverging sauropodomorphs suggests that their eggshell is poorly mineralized, regarded as soft by some authors (Norell et al., 2021). Jurassic and Early Cretaceous sauropod eggshells are significantly thinner than their late Jurassic equivalents. The lack of sauropod eggshell in the Lourinhã Fm. represents evidence of ecological behavior of Jurassic sauropod nesting elsewhere, far from the alluvial flats, or it is caused by a taphonomic bias. The lack of ornithischian eggshells predating the Cretaceous is a global enigma that it is also observed in the Jurassic of Portugal.

Conclusion

In the last 40 years, the Jurassic coast of Portugal has produced the second oldest Testudines' eggshells, the two oldest instances of Crocodylomorpha eggshells, the oldest crocodylomorph embryos, and two of the oldest theropod embryos, together with several clutches of crocodylomorphs and dinosaurs. Nowadays, it remains as an unrivaled window to Amniotes' reproduction during the final millions of years of the Jurassic.

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Evolución de la falange ungueal II en Maniraptoriformes (Dinosauria, Theropoda): una aproximación mediante morfometría geométrica 2D

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Palabras clave: Maniraptoriformes, Garra podal, Captura de presa, Morfometría geométrica 2D, Filomorfoespacios. Macroevolución
Keywords: Maniraptoriformes, Pedal claw, Prey capture, 2D Geometric morphometrics, Phylomorphospaces, Macroevolution.

Introducción

Los maniraptoriformes (Dinosauria, Theropoda) son un grupo que ha explorado una gran cantidad de adaptaciones anatómicas de sus ungueales hacia funciones muy diferentes respecto a la mayoría de terópodos no Maniraptoriformes (Lautenschlager, 2014; Qin et al., 2023). Uno de los elementos anatómicos que presenta más diversidad morfológica es la falange ungueal del dedo II posterior, especialmente con el desarrollo de la "garra asesina" o "garra de hoz" en algunos dromaeosauridos (Bishop, 2019). Aunque llamativa, la mayoría de estudios en profundidad se han concentrado en la morfología de las falanges ungueales anteriores en Theropoda (ej., Lautenschlager, 2014; Qin et al., 2023), mientras que las ungueales posteriores sólo han sido estudiadas en taxones o comparativas concretas (ej., Fowler et al., 2011). Resulta especialmente interesante abordar el ungueal II posterior, conociendo su particular morfología en algunos clados de Maniraptoriformes.

Métodos

Se ha procedido al estudio en contexto filogenético de la falange ungueal II posterior de 55 taxonespertenecientes al orden Theropoda. De esta muestra, 46 taxones pertenecen a Maniraptoriformes no avialae, 5 taxones basales pertenecientes al grupo avialae y 4 taxones de terópodos no maniraptoriformes como grupo externo. Dentro de Maniraptoriformes no avianos se encuentran representantes de los subclados Ornithomimosauria, Therizinosauria, Alvarezsauroidea, Oviraptorosauria, Dromaeosauridae y Troodontidae. Para cuantificar la morfología de la falange ungueal II posterior se muestrearon landmarks 2D y se analizaron mediante morfometría geométrica. En la toma de datos, se emplearon imágenes en vista lateral de publicaciones previas o reconstrucciones digitales 3D disponibles. Se muestrearon 3 landmarks y 3 curvas de semilandmarks que definen el perímetro de la garra con un total de 30 semilandmark muestreados. Para la comparativa de la morfología de las falanges ungueales del pie se muestrearon las longitudes métricas de las falanges ungueales de dedo II, III y IV posteriores, así como el metatarsal II posterior como aproximación al desarrollo del grado de cursorialidad del taxón (ver Fowler et al. 2011). La longitud de las ungueales se obtuvo mayoritariamente de la digitalización mediante ImageJ de imágenes previamente publicadas, con algunas excepciones obtenidas directamente de tablas de datos morfométricos proporcionadas por otros autores. Debido a la variabilidad de criterios en la toma de longitud de las ungueales, se decidió unificar el criterio en la medición consistente en la longitud medida entre la punta de la garra y el punto superior

de la curvatura exterior del ungueal, siguiendo el recorrido de dicha curvatura. Para la comparativa evolutiva se polarizaron los análisis con la topología propuesta en la filogenia más reciente e inclusiva de Theropoda (Cau, 2024), podada a los taxones muestreados para este estudio y estimándose la edad de sus ramas mediante el método de mínimo-máximo de edad. Se realizó un análisis de componentes principales (PCA) sobre las coordenadas tras el análisis generalizado Procrustes. Se obtuvieron un total de 53 componentes principales (PC en adelante) que capturan toda la variación morfológica de la muestra, de los cuales los 2 primeros PC resumen el 63,01% de la varianza muestral.

Resultados

En el PCA sobre las coordenadas procrustes, el PC1 (que muestra el 43.01% de la varianza total) proyecta los ejemplares de ungueal con un tubérculo flexor más amplio y marcado dorsoventralmente, ligeramente más corto proximodistalmente y con una faceta articular de mayor hendidura y de menor excentricidad hacia valores negativos de PC1. Hacia valores positivos de PC1 se observa un incremento en el arco de la curvatura dorsal de la ungueal, una faceta articular más amplia y más excéntrica, y es menos apuntada distalmente. También se observa una superficie ventral menos arqueada en toda su extensión, aspecto reforzado por la mayor amplitud proximodistal del tubérculo flexor hacia valores positivos de PC1. El PC2 (que muestra 20.94% de la varianza total) resume una forma del ungueal con un tubérculo flexor más alargado dorsoventralmente y prominente proximalmente, una faceta articular de menor hendidura y curvatura, así como una región superior proximal menos protuberante en valores negativos de PC2. Para valores positivos de PC2, se observa cómo la región distal de la curvatura externa presenta un arqueamiento más pronunciado a la vez que lo hace la superficie ventral. Se observa un tubérculo flexor más corto dorsoventralmente y contraído proximodistalmente. La faceta articular presenta una mayor hendidura y menor excentricidad, con un extremo proximal de mayor prominencia.

Se realizaron análisis de regresión entre las longitudes de los diferentes elementos anatómicos. Las correlaciones consistieron en la relación entre la longitud del ungueal II respecto a sus homólogos de los dígitos III, IV y el Mt II. Se observa un incremento del tamaño de la falange ungueal II respecto la III y la IV en Maniraptoriformes más derivados. Por otra parte, las correlaciones entre las ungueales y el Mt II revelaron una tendencia a la disminución de la longitud MtII respecto a las falanges ungueales a lo largo de Maniraptoriformes.

Se obtuvieron proporciones entre las ungueales II y III-IV respectivamente. Se observó una clara separación en la proporción en ambos índices casi exclusiva de Maniraptoriformes derivados (Dromaeosauridae, Troodontidae y Avialae basales). El resto de los representantes de otros clados quedan por debajo de valores umbral. No obstante, existen una cantidad notable de taxones pertenecientes a Avialae basal muy por debajo de los valores umbral.

Discusión

Se observa una tendencia a la ocupación de los valores negativos de PC1 e intermedios a positivos de PC2 desde los Maniraptoriformes más basales a los más derivados. Paraves ocuparía una región nueva del morfoespacio respecto al resto de terópodos no paravianos muestreado, con la morfología característica de “garra en hoz”. Una vez ocupada esta zona del morfoespacio, los taxones de Averaptora (Troodontidae y Avialae basales) se representan entre los valores negativos de PC1 y centrales de PC2 expandiéndose hacia valores que representan la morfología plesiomórfica de Maniraptoriformes, aunque ligeramente proyectados a valores negativos de PC1. No

obstante, los datos actuales no permiten comprobar si existe una convergencia evolutiva o reversión entre la morfología de la falange ungueal II posterior de Paraves derivados y terópodos no paravianos.

Otro aspecto notable de la adquisición de la morfología característica de "garra de hoz" entre dromaeosauridos es el incremento de tamaño y desarrollo de unas falanges no ungueales del dedo II posterior más robustas (ej., Fowler 2011). Nuestros resultados indican que Dromaeosauridae y Troodontidae presentan una ungueal II posterior ligeramente más desarrollada que el resto de las falanges ungueales posteriores. En relación a ello, considerando las claras adaptaciones depredadoras de estos subclados y la disminución de la cursorialidad respecto a terópodos más basales, las proporciones del ungueal novedoso podrían indicar un cambio en la estrategia de depredación hacia el acecho en el que el ungueal II hipertrofiado podría tener un papel relevante. No así los taxones representantes de Avialae, que mantienen la morfología novedosa, aunque casi estrictamente en proporción de tamaño similar a las falanges ungueales posteriores de otros terópodos no paravianos. Esto apoya la hipótesis de morfología común en Paraves de la falange ungueal II y la adquisición de la hipertrofia del ungueal II relacionada con un mecanismo de depredación muy específico.

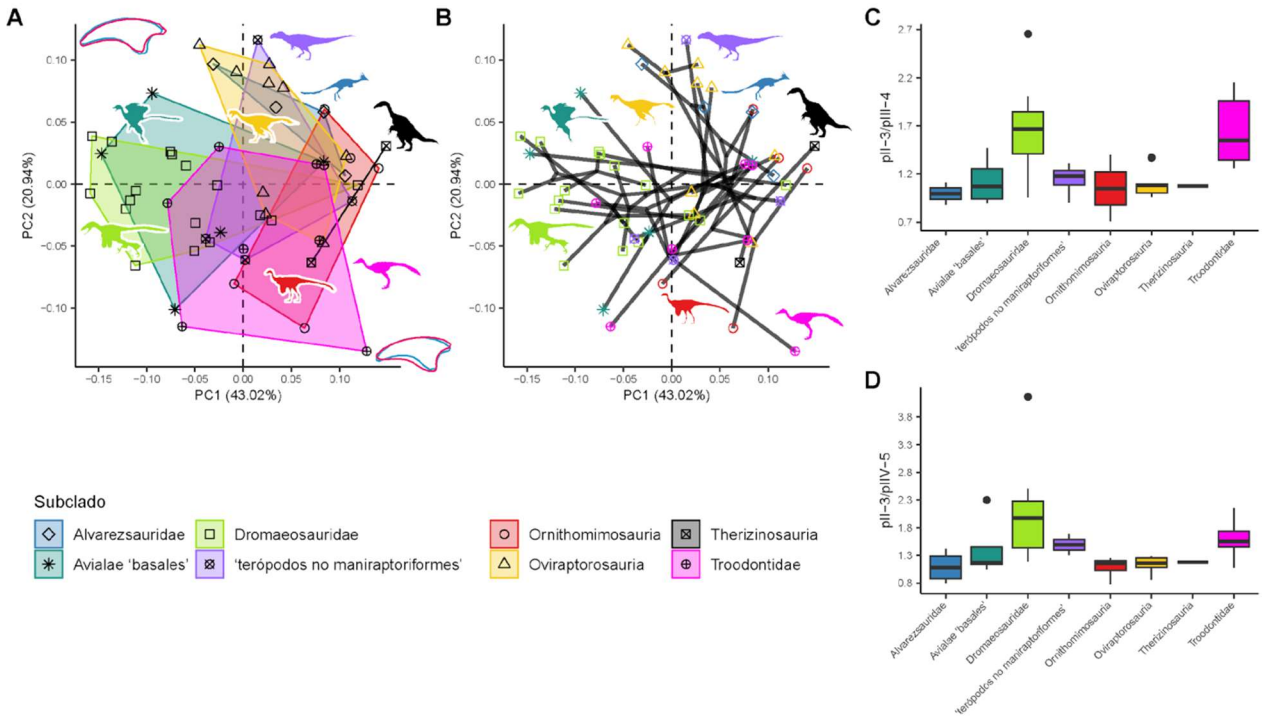

Figura 1.- Resultados de los PCA de forma de las ungueales posteriores en Maniraptoriformes. A PC1-PC2 del ungueal II posterior. B. Filomorfoespacio. C. Proporción longitud del ungueal pII-3/pIII-4. D. Proporción longitud pII-3/pIV-5.

Conclusiones

Los análisis mediante morfometría geométrica permiten observar el desarrollo de una nueva morfología innovadora de la falange ungueal II posterior en Paraves mientras que Maniraptoriformes no paravianos retienen morfologías muy similares a otros terópodos no maniraptoriformes. Una vez desarrollada esta morfología de hoz, algunos miembros más derivados del subclado Paraves exhiben una morfología plesiomórfica de la ungueal II posterior. La hipertrofia de la morfología de hoz podría estar relacionada

con hábitos predatorios innovadores de algunos subclados de Paraves (Dromaeosauridae y Troodontidae). Esta especialización se ve reflejada en un desarrollo proporcionalmente mayor del ungueal II posterior respecto a sus homólogos III y IVen taxones de Paraves adaptados a la depredación. La morfología novedosa continúa presente en Paraves no depredadores como carácter plesiomórfico, exhibiendo una similitud morfológica con terópodos noparavianos.

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Revisiting the Igea hypsilophodontid (Dinosauria, Ornithopoda) from the Lower Cretaceous Olivan Group of La Rioja

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Keywords: Oliván Group, Cameros Basin, Hypsilophodontidae, small ornithopod, Aptian

Introduction

The Monte Quemado specimen is a fragmentary dinosaur skeleton with elements from every anatomical region, probably a single individual due lack of duplicity of the elements and constant size and preservation. It was found in the Monte Quemado area, Igea municipality, almost in the soil surface due to erosion of red-brownish mudstone layers (Torres & Viera, 1994). The outcrops belong to the base of the Oliván Group, Aptian, Lower Cretaceous (Suarez-Gonzalez et al., 2014) unlike other bone remains found in the area coming from the Enciso Group outcrops. The specimen was found in 1985 and can be considered one of the oldest putative dinosaur fossil discoveries of La Rioja (Torres & Viera, 1994); it corresponds unambiguously to a small-sized ornithischian dinosaur. In recent years, the exact location has been determined, and re-excavation of the fossil site is underway. The fieldworks have allowed to retrieve several fragmentary fossils that unambiguously pertain to and complete elements of the 1985 skeleton (Páramo et al., 2023), increasing the information from this individual. It was initially referred as a specimen of *Hypsilophodon foxii* (Torres & Viera, 1994), but this referral is disputed with the new information available about small-sized ornithischian dinosaurs (Páramo et al., 2023; see Ruiz-Omeñaca, 2001). Also, the 'hypsilophodontid' dinosaurs are disputed as a natural group as many of the taxa referred to Hypsilophodontidae have been found to pertain to either less deeply-branched non-ornithopod Pyrodontia (Fonseca et al., 2024) or to deeply-branched ornithopods like Elasmaria or Dryosauridae (e.g., Boyd, 2015; Dieudonné et al., 2021; Madzia et al., 2021).

The redescription of the specimen is important to assess its taxonomical status, and to increase our information about these elusive herbivorous dinosaurian faunas of the Lower Cretaceous of Cameros Basin. In this study we will also assess if it can be referred to as an actual hypsilophodontoid ornithopod and the presence of this group in the Aptian of the Iberian Peninsula.

Methodology

The studied specimen is a fragmentary, partly articulated skeleton of a small ornithischian dinosaur. The 1985 specimen is pending restoration of the newly found fossils. Bone fragments recovered from the 2021-2022 fieldworks were not still attached together, instead, only digitally mounted or photographed. Appendicular elements were digitally mounted in anatomical position after 3D digitizing via stereophotogrammetry. In order to assess dental information from the skull specimens, the premaxillary,

maxillary and dentary specimens were digitized via CT-scan. A preliminary phylogenetic analysis was carried out following Fonseca et al. (2024) without pruning the unstable taxa except for *Paraeisactus*. Instead, we want to assess the cladistic relationships with other Iberian specimens like the 'Vegagete ornithopod' (Dieudonné et al., 2016), so it was retained in our analyses. The data matrix was analysed in TNT 1.6 (Goloboff et al., 2008).

Systematic Palaeontology

ORNITHISCHIA Seeley, 1888

ORNITHOPODA Huxley, 1870

HYPSILOPHODONTIDAE Dollo, 1882 (sensu Madzia et al. 2021)

HYPSILOPHODONTIDAE INDET.

A small ornithischian dinosaur with fragmentary premaxilla without the rostral and much of the surrounding narial fenestra. It exhibits the usual basal ornithopod single layer of evenly-placed, slightly-pseudoheterodont teeth with straight crowns. It exhibits a fossa-like contact between the maxilla-premaxilla contact but without a marked hiatus. Much of the axial skeleton is lost but the vertebrae present elongated amphicoelous centra along the neck. These vertebrae lean slightly to anterior with a lower neural canal than the posterior articular face. The anterior caudal vertebrae do not exhibit a transverse process within the centrum nor the neurocentral suture.

The scapular girdle and the anterior limb are incomplete, but exhibit a slightly robust forelimb. The incomplete coracoid has a short sternal process. The humeral head is prominent and the only part of the proximal end that it is preserved. It lacks any medial groove and it is rather continuous with the shaft. The ulna and radius lack also great portions of the shaft but the articular ends are preserved. The ulna has a bulbous olecranon process that is not separated or forming a great dome above the surface of the proximal end. The distal end of the radius is mediolaterally-wider than the ulnar distal end.

The pubis lacks much of the proximal part and any information from the prepubis. The shaft is rod-like posteriorly with a retroverted process running parallel with the ischium until the end, but without fusion or co-ossification with the latter. The ischium has a well-developed, mediolaterally wide ilium process and the flange-like anteroproximal step indicates the presence of a wide acetabular surface. Only part of the distal ischial blade is preserved and is a mediolaterally-wide and anteroposteriorly-thin lamina without signs of co-ossification neither with the ischium, nor a wide spatulate-like fusion with the other ischium, nor a 'pes'-like morphology. The distal femur is anteroposteriorly-wide with a well-developed tibial process and a slightly ventrally-bevelled surface. The tibia is long, with an anteroposteriorly-wide proximal end. It exhibits an overhanging lateral process. The distal end is mediolaterally compressed, but much larger than the fibula. The fibula has a triangularly-shaped proximal end, slightly arched but it is not possible to determine if its anterior edge is tapering. The astragalus is triangle-shaped both in distal view and the anterior ascending process. The latter exhibit a small, triangle-shaped 'tooth'. The calcaneum is bean-like without a greatly-developed dorsal flange in lateral view.

The pes lacks most of the metatarsals and any of the fragmentary bones can be referred to as tarsals. It exhibits an unfused metatarsal I and the associated, unfused phalanx. The pedal phalanges are slightly robust but without being completely

proximodistally-compressed between them, nor exhibiting a hove-like morphology. There phalanges exhibit extensor pits and several of them have extensor processes.

Discussion

The Monte Quemado specimen shares the slightly curved tooth roots of ornithopod ornithischians. It has many similarities with *Hypsilophodon* and *Gideonmantellia*, including the astragalar 'tooth' in the ascending process, an unambiguous synapomorphy of the Hypsilophodontidae (following Fonseca et al., 2024; Madzia et al., 2021). It lacks any maxillary hiatus nor the fused tibiotarsus or rod-like astragal process to be considered an heterodontosaurid. The Monte Quemado specimen exhibits, however, several differences with *Hypsilophodon* and *Gideonmantellia*, including a tibial lateral flange. The distal bevelling of the femur end is shared with rhabdodontomorph ornithopods, but lacks any of the key synapomorphies to be referred to this group. Also, while it exhibits the lack of carinae in some premaxillary teeth like in less deeply-branched iguanodontians, it lacks the absence of differences between tooth primary and secondary ridges as in rhabdodontomorphs. The shaft of the femur remains sub-circular as in non-rhabododontomorph ornithopods (Dieudonné et al. 2021). While the overall hindlimb proportions remain gracile, the pes is slightly more compact than in other hypsilophodontids. The phylogenetic analyses recovered a single group with Monte Quemado specimen, *Gideonmantellia* and *Hypsilophodon*, further supporting its attribution to a later, potential new form of Early Cretaceous Hypsilophodontidae.

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Scientifically Accurate Reconstruction of *Concornis lacustris*, an Enantiornithine Bird from Las Hoyas (Early Cretaceous, Cuenca)

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Keywords: Early Cretaceous, Spain, Enantiornithes, Aves, Palaeoart, Sculptural Reconstruction

Introduction

The palaeontological site of Las Hoyas (Early Cretaceous, Cuenca, Spain) is renowned for its exceptional degree of preservation and is classified as a Konservat-Lagerstätte. It has yielded fossils of notable international significance, characterised by the uniqueness and quality of their preservation, even providing detailed information of soft tissues (including at the cellular level). Among the most important findings are remains belonging to various dinosaur groups, with particular emphasis on those of the most diverse and abundant Early Cretaceous birds, the Enantiornithes. This site was one of the first to provide information about this group, establishing it as a globally important palaeontological locality.

Concornis lacustris, one of the most significant birds from Las Hoyas and one of the most iconic in the Spanish fossil record, is reconstructed at life size in this study, detailing the reconstruction process. A combination of digital and traditional sculpting techniques was employed to achieve a scientifically accurate representation. The reconstruction was based on the description of the holotype (MUPA-LH-2814; Sanz et al., 1995), using the preserved osteology supplemented by anatomical references from other enantiornithine birds. In gathering this supplementary information, the degree of skeletal preservation was prioritised over phylogenetic criteria, given the historical instability of the systematic position of *C. lacustris* in several phylogenetic analyses published over the past decades (e.g., Sanz et al., 1995; Mayr, 2017; Chiappe et al., 2024).

The method used corresponds to the so-called "reverse dissection", which involves reconstructing the anatomy of palaeobiological entities from the skeleton outward—a technique popularised by palaeoartists such as Mauricio Antón (Antón & Turner, 1997).

Materials and Methods

The right appendicular skeleton (almost complete), the pectoral and pelvic girdles (partially complete), and part of the axial skeleton (dorsal vertebrae, ribs, and fragments of the synsacrum) were reconstructed based on the description of *Concornis lacustris* in Sanz et al. (1995). We used the Figure 3 of this publication as the basis for life-sized digital modelling of the preserved skeletal elements, using Blender software (Fig. 1A).

To complete the postcranial skeleton, we used the holotype of *Rapaxavis pani* (DNHM D2522; O'Connor et al., 2011), one of the most osteologically complete and best-preserved enantiornithines. This specimen was proportionally scaled to match the estimated size of *C. lacustris*, enabling us to complete the digits II and III of the foot, and the axial skeleton (Fig. 1B).

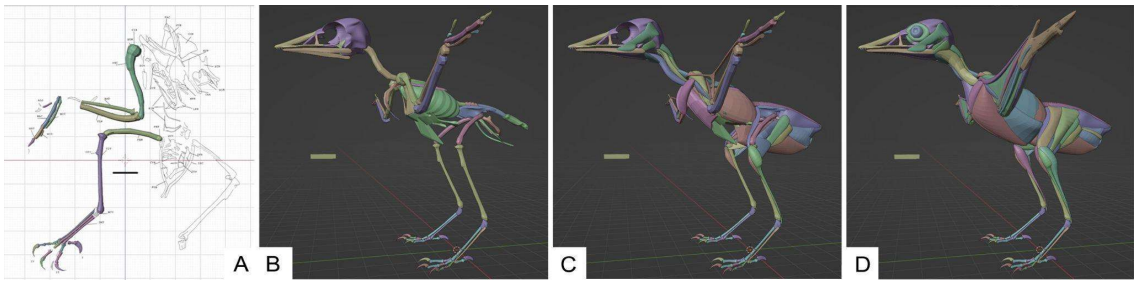

Figure 1: Anatomical reconstruction process. Scale bars = 10 mm. (A) Modelling based on the figure 3 from Sanz et al. (1995). (B) Skeletal reconstruction of *C. lacustris*. (C and D) Myological reconstruction of *C. lacustris*. (A) Modified from fig. 3 in Sanz et al. (1995). (B, C and D) Original work.

Regarding the skull, cranial elements from two other enantiornithines were used: the mandibular unit and the premaxilla of a new enantiornithine species from Las Hoyas (MUPA-LH-13240; Nebreda et al., in review), which is equivalent in size to *C. lacustris*; and the skull of *Navaornis hestiae* (MPM-200-1; Chiappe et al., 2024), currently the best three-dimensionally preserved enantiornithine skull known. The latter was dimensionally adjusted to tentatively integrate the dimensions of MUPA-LH-13240 (Fig. 1B).For the myological and integumentary reconstruction, various sources were consulted (e.g. Baumel et al., 1993; Navalón et al., 2015; Mayr, 2017; Liu et al., 2019), which enabled the inference of the main areas of muscular origin and insertion. These were digitally represented at different levels of depth (Fig. 1C and D).

Feather coverage was based on exceptionally preserved fossils such as *Protopteryx fengningensis* (STM7-143; O'Connor et al., 2020), which provided information about the number and morphology of the remiges (Fig. 2A), and various specimens from the Jehol biota (Foth and Rauhut, 2020), which served as references for the covert feathers. Given that body morphology in birds differs significantly when they are covered by dense plumage, the volume occupied by feathers was tentatively modelled by observing small passerines and comparing them with the aforementioned works (Fig. 2B).

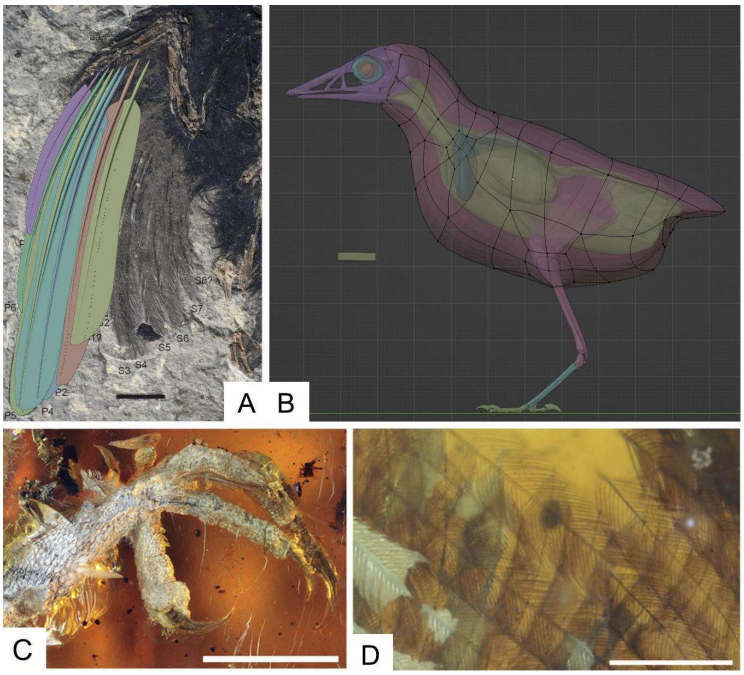

Figure 2: Integument reconstruction process and materials used as reference. (A) Morphological fitting of remiges in STM7-143. Scale bar = 10 mm. (B) Estimated volume of covert feathers on reconstructed anatomy. Scale bar = 10 mm. (C) Detail of the foot of HPG-15-1. Scale bar = 1 mm. (D) Detail of pigment structure and distribution in the feathers of HPG-15-1. Scale bar = 0.5 mm. (A) Modified from O'Connor et al. (2020). (B) Original work. (C and D) Taken from Xing et al. (2017).

Results

The reconstruction of the podotheca was based on specimen HPG-15-1 (Xing et al., 2017), an exceptionally well-preserved enantiornithine chick preserved in amber (Fig. 2C). Plumage colouration was interpreted based on studies of enantiornithines also preserved in amber, as well as melanocytes from avian fossils (e.g. Xing et al., 2017, 2020; Fig. 2D).

A complete digital model of the skeletal and myological anatomy of *C. lacustris* was produced, along with a volumetric estimation of feather coverage. Based on these elements, a sculptural pose was defined, depicting this small Mesozoic bird in the moment just before perching, with one limb resting on a branch of *Frenelopsis* sp. (a cheirolepidiaceous conifer from Las Hoyas; Poyato-Ariza & Buscalioni, 2016).

The model was 3D printed using FDM technology with PLA filament (Fig. 3A). The covert feathers were then hand-sculpted with epoxy putty (Fig. 3B), 3D-printed remiges were incorporated, and additional details were added using nylon thread to simulate filamentous feathers (Fig. 3C and D). The sculpture was finally polychromed in oil paint, based on colouration patterns from avian fossils (Xing et al., 2017, 2020).

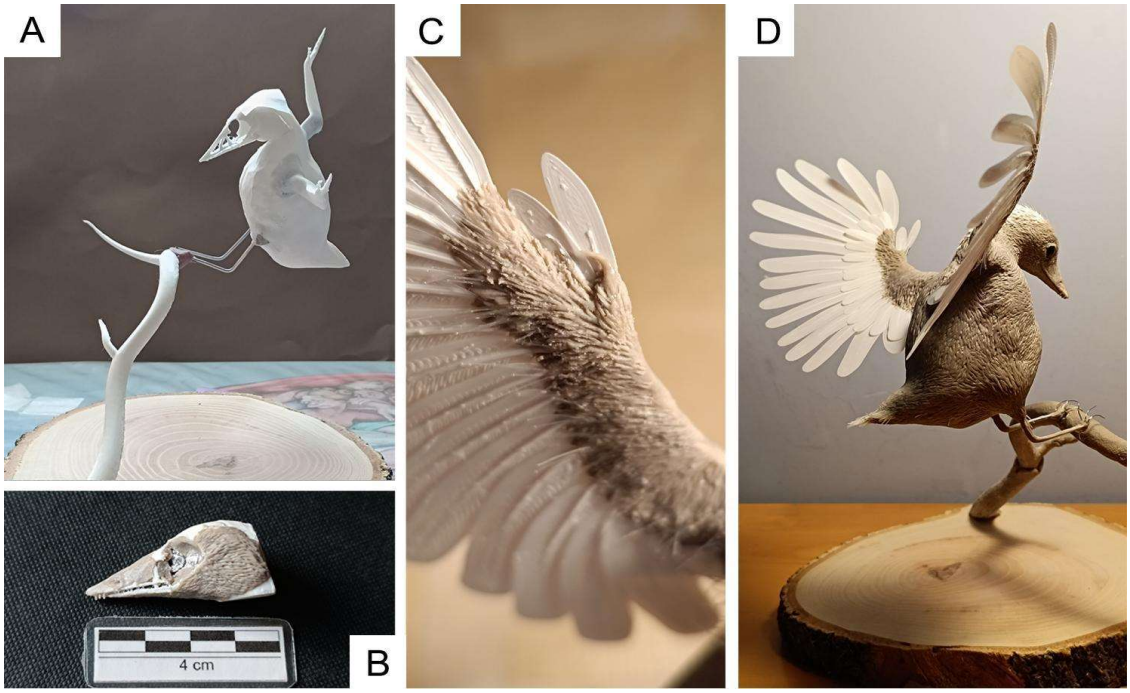

Figure 3: Physical reconstruction process. (A) 3D-printed digital reconstruction model. (B) Modelling process using epoxy putty over the 3D print. (C and D) Modelling with integrated 3D-printed feathers and nylon detailing. (A–D) Original work.

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The second individual of Pleurosternidae from the Tithonian Barrihonda-El Humero site (Riodeva, Teruel)

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Keywords: Testudinata, Paracryptodira, Upper Jurassic, Iberian Ranges, Spanish record

One of the main lineages of stem turtles (i.e., Testudinata not attributable to the crown group Testudines) identified in the Iberian record is that of Paracryptodira (Pérez-García, 2017). In this region, it is exclusively represented by members of the Pleurosternidae. Pleurosternidaeis the only group of freshwater turtles identified in the Upper Jurassic record of both North America and Europe (Pérez-García and Ortega, 2011), showing a relatively high diversity in both regions. The North American record of this lineage is restricted to the Upper Jurassic. However, Pleurosternidae shows a notably wider temporal distribution in Europe, surviving at least until the last stage of the Lower Cretaceous (i.e., the Albian) (Pérez-García et al., 2015a).

The information on the European members of Pleurosternidae was, until a few years ago, very limited. However, recent studies and, especially, the description of several new forms, allowed improving the knowledge on the diversity, systematic, and stratigraphic and palaeobiogeographic distributions of the forms that inhabited this continent (see Pérez-García et al., 2021, and references therein). Although several forms are currently known for the Spanish record, the first described there was *Riodevemysinumbra gigas* (Pérez-García et al., 2015b). It comes from the Kimmeridgian or Tithonian Barrihonda-El Humero fossil site, located in Riodeva, in the Teruel Province (South Iberian Basin)(Campos-Soto et al. 2019). Other vertebrates found at this site include the sauropod *Turiasaurus* (Royo-Torres et al., 2006), the stegosaurid*Dacentrurus* (Cobos et al., 2010), and the ornithopod*Oblitosaurus* (Sánchez Fenollosa et al., 2023).

Riodevemysinumbragigas was defined by a partial skeleton of an adult individual, including the almost complete shell, as well as several bones of the scapular and pelvic girdles. No other specimen has been attributed to it so far.

An unpublished partial skeleton of a turtle from the type locality of *Riodevemys inumbragigas* is presented here. It corresponds to a juvenile individual. Its attribution to Pleurosternidae is justified here. In fact, it is probably attributable to *Riodevemys inumbragigas*. However, differences in several shell characters relative to the holotype of this species are recognized. The possibility that some of these differences are due to ontogeny, but others to individual variability, are evaluated here considering the intraspecific variability known for Pleurosternidae (Guerrero and Pérez-García, 2021a, 2021b).

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Shell anatomy of the pleurodiran turtle *Teneremys lapparenti*, from the Aptian of Gadoufaoua (Niger)

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Keywords: Testudines, Pelomedusoides, Lower Cretaceous, Illumeden Basin, Sahara Desert.

One of the most relevant fossil localities for understanding the Lower Cretaceous vertebrate record of the African continent is Gadoufaoua. This region is located in the Illumeden Basin, in the central region of Niger (Ténéré Desert, south-central region of the Sahara Desert) (Broin, 1980; Lapparent de Broin, 2000a). The fossil remains come from Aptian levels. Several lineages have been found there, including the identification of several pleurodiran turtles (Broin,1980; Pérez-García, 2019a). This represents the oldest documented synchronistic and sympatric presence of several pleurodiran representatives in Africa, as well as one of the oldest globally (Pérez-García, 2019b). The first study of this turtle fauna was published in the early 1980s. Broin (1980) documented the presence of at least three taxa. One of them, attributed to the new turtle *Taquetochelys decorata*, was recognized as belonging to the extinct lineage Araripemydidae. The other two turtles from Gadoufaoua were identified as belonging to 'Pelomedusidae (s.l.)', a term used by her to group the podocnemidids, the pelomedusids, and the bothremydids, but not the araripemydids nor the chelids. One of them was defined as a new species, *Teneremys lapparenti*, but the other was referred to as *Platycheloides* cf. *nyasae* (Broin, 1980).

Taquetochelys decorata is the only species of Araripemydidae identified in Africa. Both its cranial and postcranial anatomy are well-known, so that it represents one of the best characterized Cretaceous pleurodiran turtles (see Pérez-García, 2019a; and references therein). Almost 40 years after the study of Broin (1980), the shell from Gadoufaoua attributed by her to *Platycheloides* cf. *nyasae*, as well as other shells and carapacial remains corresponding to the same species, were detailed studied (see Pérez-García, 2019b). They were attributed to a new taxon, *Francemys gadoufaouaensis*, exclusive to that locality. This turtle was recognized as a representative of Pelomedusoides closely related to Podocnemidoidea, but not attributable to this clade or to any of the families so far defined.

Teneremys lapparenti was defined by a shell fragment (preserving the partial carapace but a very small area of the plastron) associated with a skull (partially visible only in ventral view). An isolated nuchal plate was tentatively attributed to it (Broin, 1980). New information relative to the cranial anatomy of *Teneremys lapparenti* was subsequently provided (see Lapparent de Broin, 2000b), but not on its shell. Since *Francemys gadoufaouaensis* is only known from the shell, new data on this anatomical region in *Teneremys lapparenti* would be vital for comparing both taxa and, consequently, for better understanding how the successful radiation experienced by the Pelomedusoides in northern Gondwana during the Aptian-Cenomanian interval occurred (see Pérez-García, 2019b). In fact, the scarce shell information currently available on *Teneremys lapparenti* allows to recognize that it shares several derived characters in relation to other forms of Pelomedusoides with *Francemys gadoufaouaensis*, to which it may be closely related.

Abundant shell remains from Gadoufaoua compatible with *Teneremys lapparenti*, including several relatively complete shells, are available for study. This material is presented here. Thanks to the analysis of these fossils, some preliminary conclusions related to the diversity and disparity of Pelomedusoides during the Early Cretaceous, as well as concerning the precise phylogenetic position of the representatives from Gadoufaoua, are proposed.

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A las puertas del centenario de la primera cita de restos de dinosaurios en Soria: una actualización del contexto geológico del yacimiento de "Los Caños"

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Palabras clave: Soria, Cretácico Inferior, Formación Golmayo, Clemente Sáenz, Royo Gómez, Cuenca de Cameros, paleoambientes.

Introducción

En 2026 se cumplirán 100 años de la primera cita de restos de dinosaurios en la provincia de Soria (España), correspondiente al yacimiento clásico de "Los Caños" (Royo y Gómez, 1926a, 1926b). Estas reseñas fueron escritas por el pionero de la paleontología de dinosaurios en España D. José Royo Gómez (Pereda-Suberbiola et al., 2010). Pese a ser un yacimiento con 100 años de historia la bibliografía científica existente es escasa, sin que se haya analizado al detalle el contexto paleoambiental de los hallazgos más tempranos de dinosaurios sorianos. En este trabajo se presenta una actualización del contexto estratigráfico y paleoambiental del yacimiento de Los Caños, en el término municipal de Golmayo, próximo a la capital de Soria.

Historia y Antecedentes

En 1917 el geólogo soriano Clemente Sáenz descubre los primeros restos de dinosaurios en las cercanías de la ciudad de Soria, en el yacimiento de "Los Caños". Estos restos fueron entregados al ya mencionado José Royo Gómez, en 1926, siendo descritos en una serie de publicaciones (Royo y Gómez, 1926a, 1926b, 1927, 1928) donde se citan por primera vez restos directos de dinosaurios en Soria. Tras su estudio, los fósiles fueron enviados al Museo Nacional de Ciencias Naturales en Madrid, aunque en la actualidad permanecen perdidos (Fuentes Vidarte et al., 2003).

En décadas posteriores se llevan a cabo más prospecciones que aportan más restos fragmentarios de diferentes vertebrados (Sáenz Garcia, 1932, 1955; Bataller, 1960; Buscalioni, 1986), destacando los de un pequeño ornitópodo, atribuido al género *Hypsilophodon* (Sanz et al., 1992; Sanz & Moratalla, 1993), descubierto en 1981 por el geólogo Esteban Arlegui. Estos restos se encuentran actualmente en el Museo del Instituto Geominero de España en Madrid (Fuentes Vidarte et al., 2022).

En la década de los 2000, Carolina Fuentes y Manuel Meijide, junto a sus hijos, realizan grandes descubrimientos en el entorno de la ciudad de Soria y la localidad de Golmayo (Fuentes Vidarte et al., 2022). Realizan nuevas prospecciones en "Los Caños" recuperando gran cantidad de restos aislados, donde se incluyen nuevos fragmentos atribuidos a un pequeño ornitópodo similar al ya descrito y dientes de terópodo. Además, realizan una recopilación de todo el registro fósil de este yacimiento hasta la fecha (Fuentes-Vidarte et al., 2003). De manera reciente, parte de estos restos han sido incluidos y revisados en un estudio sobre terópodos de la Formación Golmayo (Isasmendi et al., 2025).

Contexto Geológico: La Formación Golmayo

La Formación Golmayo (Clemente y Alonso, 1990) es una sucesión sin-rift de carácter fluvial y lacustre subordinado que aflora únicamente en el Sector de Soria, (SE de la Cuenca de Cameros). Se le estima una edad Hauteriviense tardío-Barremiense temprano (Martín-Closas & Alonso Millán, 1998) y forma parte del Grupo Urbión (SD6) (Mas et al., 2002). Esta unidad es relevante por su contenido en fósiles de vertebrados, destacando holotipos de algunos dinosaurios como *Magnamanus soriaensis* (Fuentes Vidarte. et al., 2016) o *Soriatan golmayensis* (Royo-Torres et al., 2017), ambos procedentes del yacimiento de "Zorralbo I".

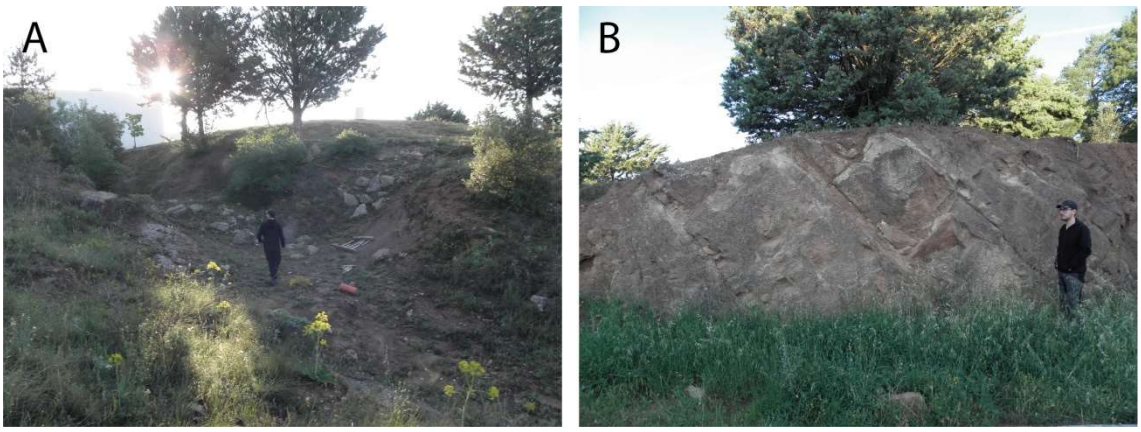

Figura 1. Depósitos fluviales de la Formación Golmayo (Cretácico Inferior, Soria). A) Foto general del "Los Caños" ("Caño II"). B) Barras de migración lateral (*point bars*).

Resultados: Análisis estratigráfico y sedimentológico

A partir del análisis estratigráfico y sedimentológico se ha establecido un modelo diferenciando dos estadios evolutivos para la Formación Golmayo. En el estadio 1 (Golmayo inferior) alternan etapas (1.1) de dominio de ambientes fluviales de baja pendiente y sinuosidad, y ambientes lacustres asociados y etapas (1.2) con dominio de canales fluviales algo más sinuosos y con llanura lutítica asociada. El estadio 2 (Golmayo superior) está representado por sistemas fluviales meandriformes, de alta sinuosidad y mayor energía.

Evaluando el potencial fosilífero de esta unidad, las facies finas asociadas a la llanura aluvial y a ambientes lacustres son las más favorables para contener fósiles de vertebrados, siendo más frecuentes en la unidad Golmayo inferior.

El yacimiento de "Los Caños" se ubica en el estadio 2 (Golmayo superior) en el tramo inferior donde dominan areniscas y conglomerados intercaladas tramos lutíticos intercalados (Fig. 1A). Es el yacimiento más alto estratigráficamente, en torno al metro 860 en la serie local de la Formación Golmayo del entorno de los Caños y la "vía verde". En este tramo dominan las facies de canal, intercaladas con algunos tramos lutíticos de llanura de inundación. Estos canales pasan lateralmente a cuerpos con estratificación inclinada de gran extensión, interpretándose como canales de tipo meandriformes asociados a barras de migración lateral *(point bars)* (Fig. 1B).

Estas facies en general presentan unas condiciones menos adecuadas para preservación de restos de vertebrados, en comparación con las facies de los yacimientos

en la Golmayo Inferior. Esto explicaría la preservación de los fósiles siendo mayormente restos aislados y con indicios de transporte.

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First evidence of a sauropod tooth from the fossil site of Cantera Carcalín, Buñol (Valencia, Spain)

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Keywords: Archosaurs, Dinosauria, Sauropoda, Tooth, Titanosauriformes

Introduction

The Eastern Iberian Peninsula is a key region for the study of dinosaur diversity and the organisms that coexisted with them. The most well-known discoveries are concentrated in the central and northeastern areas of the Valencian Community, such as the Serranía region and Benagéber, among many others. However, other significant Mesozoic outcrops are located toward the outermost foothills of the Iberian Range. Among these, the Cantera Carcalín fossil site, dating to the Late Jurassic, stands out. Despite its potential, the Mesozoic fossil localities of Buñol remained largely unexplored for years. Recent projects and studies have continued to gather data on the fossils and the paleoenvironment of the site. This paper presents the first evidence of a sauropod dinosaur from this locality, contributing new data on the diversity of dinosaurs.

Material and methods

Here we describe MGUV-40299, a isolated tooth, found in Cantera Carcalín fossil site, housed at the *Museu de la Universitat de València d'Història Natural* (Fig. 1). The terminology used for the descriptions follows the framework proposed by Mocho et al., 2017.

Description

MGUV-40299 are 25 '48 mm in height and 7' 33 mm in width. The tooth crown exhibits an apical wear facet (awf) on the lingual view and lacks any denticles on the lateral, apical, or mesial margins. On the mesial side, in labial view, a non-denticulate carina can be observed, which fades toward the apex, and is followed by a very slight lingual groove (lig) on lingual view also with a labial ridge (lar). The cross section of the tooth is cylindrical to circular from mid-crown toward the root. The apical region displays a smooth and polished surface, lacking the slight striations observed in the mesial region closer to the root. Toward the base, enamel striations become apparent, with some enamel structures discernible on the lateral sides of the mesial region, both in labial and lingual views. These structures gradually fade as they approach the apex of the tooth crown, a feature previously described in teeth with similar morphologies (Mocho et al., 2017, Saleiro & Tschopp, 2025). The tooth crown is slightly convex along the apicobasal axis on the basal surface, while the lingual surface displays a more pronounced convexity. A slight torsion relative to the central axis of the tooth can be observed in both labial and lingual views.

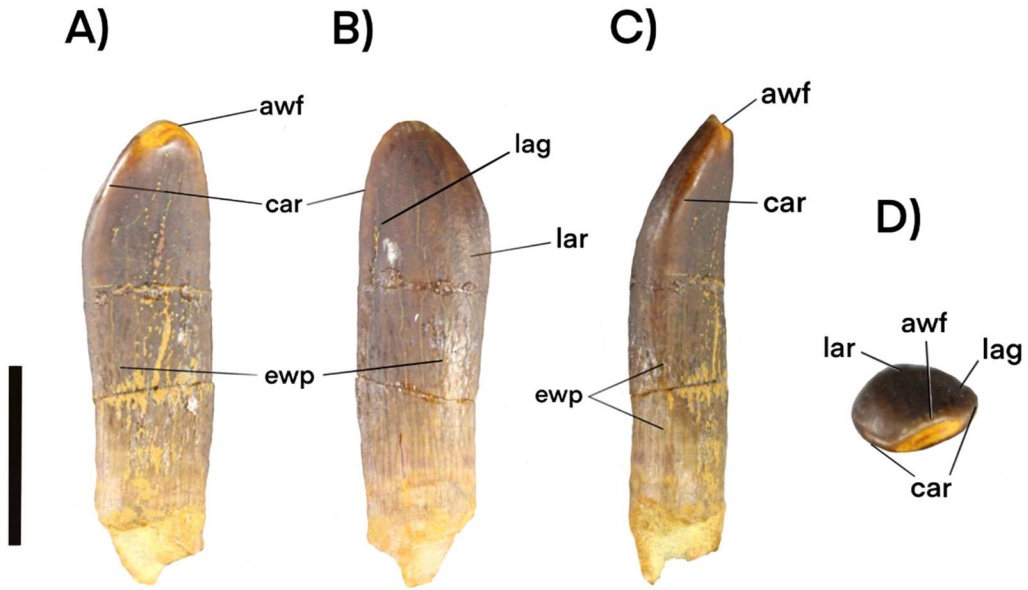

Fig.1: MGUV-40299 in lingual (A), labial (B) and apical (C) views. Scale bar equals 1 cm. *Abbreviations*: awf, apical wear facet; car, carina; lag, labial groove; lar, labial ridge; ewp, enamel wrinkle pattern.

Comparisons

Some features, such as the presence of an "V" apical wear facet (awf) at the coronal apex, its axial torsion degree, and slight expansion, suggest that the specimen can be attributed to the *compressed cone-chisel-shape* morphology (Buffetaut et al., 2006; Mocho et al., 2017), but axial torsion degree is also observed in some *peg-shaped* teeth. (Saleiro & Tschopp, 2025; Figueiredo et al., 2023). *Compressed cone-chisel-shape* teeth are commonly associated with Titanosauriformes group, such as *Giraffatitan brancai*, *Brachiosaurus altithorax*, *Abydosaurus mcinthosi*, and other sauropod teeth described in the Iberian Peninsula, including those found in Portugal associated with *Lusotitan atalaiensis*, and the interior region of the Valencian Community (Jensen, 1987; Paul, 1988; Casanovas, Santafé & Santiesteban, 1993; Chure et al., 2010; Mocho et al., 2017). There are also features present in some specimens belonging to the Macronarian group, excluding Titanosauriformes, with taxa such as *Europasaurus holgeri*, and some basal Titanosauriformes like *Voivouira damparensis* (Sander et al., 2006; Mannion et al., 2017). The presence of non-denticulate carina on the lateral margins, the degree of torsion relative to the tooth´s central axis, the overall size of the specimen, and the weak development of labial grooves and ridges suggests a relatively posterior position within the maxilla. These features are typically associated with teeth located in this region of the jaw in sauropod dinosaurs. This could be supported by the slender morphology of the tooth, wich resembles the C2 and C3 morphotypes proposed by Mocho et al. 2017, and differs from other morphotypes associated with Titanosauriformes wich tend to be larger, with a accused degree of torsion, more robust in shape, and with a denticulate lateral carina (Mocho et al., 2017; Bindellini & Sasso, 2019). However, it is important to consider the morphological variation within the dentition of these animals, as the wear patterns can vary depending on the tooth's position within the jaw. Therefore, this potential bias must be taken into account when determining certain morphological characters and their placement within the dental formula. The SI value is 3.4, falling

within the range associated to Titanosauriformes (2.7 - 3.3 by Mocho et al. 2017; 2-3.5 by Saleiro & Tschopp, 2025), supporting a possible affinity with this group.

Discussion

Paleontological studies conducted in nearby areas have revealed the presence of turiasaurian sauropods, such as *Losillasaurus,* as well as basal macronarians, including members of the Camarasauridae, primarily within the sediments of the Villar del Arzobispo Formation in various localities. In contrast, the Hoya de Buñol-Chiva region remains poorly documented, complicating efforts to establish a clear geochronological framework for the recovered fossils. Ruiz-Omeñaca et al. (2010) reported the presence of theropod allosauroids and teleosaurid thalattosuchians, including *Machimosaurus sp*., from the Cantera Carcalín fossil site. These remains were attributed to the Late Jurassic (Kimmeridgian–Tithonian) and assigned to the Higueruelas Oncolitic Limestone Formation.

Conclusions

Specimen MGUV-40299 can be classified as a *compressed cone-chisel-shaped* tooth, exhibiting some of the synapomorphies of macronarian Titanosauriformes sauropods. The tooth described in this study likely represents the first direct evidence of sauropod dinosaurs from the Hoya de Buñol-Chiva region, thereby expanding the known record of sauropod dental remains in the eastern Iberian Peninsula.

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New data on dwarf crocodylomorphs (Atoposauridae) from the Upper Jurassic of Portugal

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Keywords: Upper Jurassic, Portugal, Crocodylomorpha, Neosuchia, Lourinhã Formation, Kimmeridgian-Tithonian.

Introduction

The Lourinhã Formation (Late Jurassic, Kimmeridgian–Tithonian) in western Portugal is one of the richest fossil-bearing units of this age in Europe, particularly known for its exceptional vertebrate record. This formation has yielded abundant remains of dinosaurs, mammals, turtles, and pterosaurs, but also preserves a notably diverse assemblage of crocodylomorphs. Within the Lusitanian Basin, crocodylomorph fossils have been recovered from both macrofossil sites and microvertebrate assemblages, spanning a wide range of body sizes, morphologies, and ecological adaptations. Notably, the Guimarota lignite mine (further north, in the Alcobaça Formation, near the city of Leiria) produced *Knoetschkesuchus guimarotae*, originally described as *Theriosuchus guimarotae* (Schwarz et al., 2017), one of the best-known atoposaurids from the Iberian Peninsula, as well as the medium-sized goniopholidid *Goniopholis baryglyphaeus* (Schwarz, 2002). Additional taxa such as *Lisboasaurus estesi* and *Lusitanisuchus mitracostatus*, small mesoeucrocodylians of uncertain affinities, were originally identified as anguimorph lizards or even maniraptoran theropods, but were later reassigned to Crocodylomorpha (Buscalioni et al., 1996; Schwarz & Fechner, 2004). These taxa, known from Guimarota and possibly Lourinhã, further highlight the taxonomic and ecological diversity of crocodylomorphs in the Portuguese Upper Jurassic.

In the Lourinhã area specifically, some neosuchian taxa have been described based on more complete material. These include *Ophiussasuchus paimogonectes* (López-Rojas et al., 2024), a newly described goniopholidid skull from Paimogo beach. In addition, postcranial material and isolated teeth from Valmitão and other localities have been attributed to several taxa, including *Lusitanisuchus*, Atoposauridae, Goniopholididae, Bernissartiidae, and undetermined mesoeucrocodylians, suggesting a higher diversity than previously recognized based on skeletal remains alone (Guillaume et al., 2020). Despite this diversity, the record of atoposaurids in the Lourinhã Formation remains sparse and fragmentary, mostly limited to isolated teeth and cranial fragments recovered from microvertebrate-rich layers. These small-sized remains from dwarf crocodylomorphs are crucial for understanding the evolutionary history of Atoposauridae and their phylogenetic and biogeographic patterns in western Europe. The present study

contributes new data to this group, based on previously undescribed material from three fossiliferous sites, Zimbral, Porto das Barcas, and Peralta Sul, located along the coastal cliffs of Lourinhã. The specimens under study comprise ML2631, a skull table that was preserved in a nodule from Zimbral; ML2322, a partial skeleton including cranial elements from Porto das Barcas; and ML2688, an articulated partial skeleton preserving most of the posterior body region, from Peralta Sul. All three specimens were prepared at the Museu da Lourinhã laboratory. Since portions of the surrounding rock matrix could not be removed mechanically, they were micro-CT scanned at the Micronsense facilities (Leiria, Portugal) to reveal hidden anatomical features and allow the digital reconstruction of internal bony cavities.

Geological and geographical settings

The crocodylomorph fossil material comes from coastal outcrops in western Portugal, near the town of Lourinhã (Lisboa district, Oeste region), where Upper Jurassic strata of the Lusitanian Basin are well exposed. The Lusitanian Basin is a Mesozoic rift basin developed along the western margin of the Iberian Plate during the opening of the North Atlantic, and it preserves a thick sedimentary succession spanning from the Late Triassic to the Late Cretaceous. During the Late Jurassic, the basin experienced an active rifting phase associated with syn-sedimentary faulting and the development of nested sub-basins, such as Consolação, where the studied outcrops are located. This phase led to marked lateral facies changes and the accumulation of thick continental successions dominated by fluvial and deltaic systems (e.g., Taylor et al., 2014; and references therein).

All the specimens described in this study were recovered from microvertebrate-bearing levels in the lower part of the Praia Azul Member (Lourinhã Formation), within the Consolação Sub-basin. The Lourinhã Fm, dated to the upper Kimmeridgian–lower Tithonian, represents fluvio-deltaic environments interbedded with shallow marine incursions. Within this formation, the Praia Azul Member records alternating marine-influenced and continental deposits, reflecting three major transgressive episodes (e.g., Taylor et al., 2014; and references therein). The crocodylomorph fossils were recovered from sediments deposited between the first and second transgressive episodes. The fossil-bearing horizons consist predominantly of grey marls and silts, interpreted as low-energy floodplain or shallow lagoonal settings. Despite coming from different localities (Zimbral, Porto das Barcas, Peralta Sul), all specimens share a comparable stratigraphic context within the lower Praia Azul Member, dating to the late Kimmeridgian–early Tithonian transition (Late Jurassic).

Anatomical description

The specimen ML2631 consists of a skull table (3.6 cm in length) with an associated braincase, recovered from a nodule at the microvertebrate site of Zimbral (Lourinhã). Although the specimen was micro-CT scanned, the presence of dense mineral veins (likely indicating the nodule is a septarian concretion) caused significant imaging artefacts, which obscured some regions of the skull and complicated segmentation. Despite these limitations, we were able to digitally reconstruct most of the skull as well as several internal structures, including the brain cavity, inner ear, and cranial nerve pathways. The specimen exhibits several morphological features that support its referral to Atoposauridae indet. (Pochat-Cottilloux et al., 2024). Notably, the quadrate, squamosal, and otoccipital do not meet to enclose the cranioquadrate passage. A shallow sulcus or fossa is present at the suture between the parietal and squamosal. Although this feature is strongly developed in some notosuchians (*Notosuchus*) and paralligatorids (*Wannchampsus*), in ML2631 it is more subtle and restricted to the anterior part of the

suture, resembling the condition observed in some atoposaurids such as *Theriosuchus pusillus* and *Varanosuchus*. A low sagittal crest is also present along the dorsal surface of the parietal and frontal. The lateral margin of the squamosal shows a discontinuous groove for the ear valve musculature, a pattern also seen in atoposaurids such as *Aprosuchus* and *Varanosuchus*, as well as in paralligatorids like *Paralligator* and *Shamosuchus*. Although typical atoposaurids possess a squamosal prong with a depression along its posterolateral margin, this feature could not be confidently assessed in ML2631, as the corresponding region was partially affected by erosion.

The specimen ML2322 is a partial skeleton recovered from the site Peralta Sul. The preserved material includes a fairly complete skull (estimated total skull length: 6.3 cm; skull table: 2 cm), lower jaws, osteoderms, cervical, dorsal and caudal vertebrae, a coracoid, part of the ilium, and most of the forelimb and hindlimb bones. Thanks to the micro-CT scan, some endocranial cavities could also be segmented. Most of the features observed in ML2631 are also present in ML2322. In addition, ML2322 displays several traits typically found in atoposaurids. These include a broad oreinirostral rostrum and teeth with the characteristic atoposaurid morphology: the crowns are slightly compressed labiolingually, and the lingual surface is ornamented with centrally oriented apical ridges and fan-shaped lateral ridges extending toward the carinae. Unlike ML2631, the right squamosal in ML2322 is well preserved and clearly exhibits a squamosal prong with a depression along its posterolateral margin, forming a distinct step. As in atoposaurids, the dorsal osteoderms are arranged in two parallel rows and bear an anterior process or peg located anterolaterally. Compared to the condition in goniopholidids, this peg is less developed, and the lateral margin of the osteoderm is less ventrally inclined.

Specimen ML2688 was recovered in Porto das Barcas locality, notably found in association with a nearly complete skeleton of a juvenile ornithopod dinosaur. It consists of a partial postcranial skeleton preserved in articulation, including sixteen vertebrae (pre-sacral, sacral, and caudal), the right ilium, an almost complete right hindlimb, and over 100 osteoderms. The osteoderms show the distinctive arrangement pattern observed in atoposaurids: two paramedian rows of rectangular, lateromedially oriented osteoderms in the sacral region, and four rows of anteroposteriorly aligned square osteoderms in the caudal region. These features, together with the small overall body size (estimated at ~1.5 m based on femur dimensions) and general neosuchian morphology, suggest affinities with Atoposauridae. However, due to the absence of cranial material and the relatively large size of the individual (considerably exceeding the typical body length of atoposaurids, which usually do not surpass 0.5 m) its precise taxonomic assignment and comparison with the other two specimens remain tentative.

Ontogenetic considerations

Specimens ML2631 and ML2322 likely belong to the same taxon, as they present similar morphology and originate from laterally equivalent levels within the same facies. However, a comparison of their skull table lengths (3.6 cm in ML2631 and 2.0 cm in ML2322) shows that ML2631 is 1.8 times longer. Consequently, the morphological differences observed between the two specimens may be explained by ontogenetic variation. These differences include, for example, a more pronounced sagittal ridge on the dorsal surface of the skull table and more developed tuberosities on the basioccipital, supraoccipital, and quadrate in ML2631. In contrast, ML2322 shows a lower degree of cranial suture fusion, the absence of a sulcus at the squamosal–parietal suture, the presence of a squamosal lobe with a depressed posterolateral margin, and a more juvenile brain morphology. Regarding the postcranial skeletons of ML2322 and ML2688, the

latter is considerably larger, with a femur length of 10.5 cm compared to 4.2 cm in ML2322 (that is, 2.5 times longer). Despite the shared osteoderm morphology between the two, the greater robustness of the long bones in ML2688 could also reflect ontogenetic differences rather than taxonomic disparity. Finding additional overlapping material and new specimens could help resolve these uncertainties.

Conclussions

The newly described atoposaurid specimens from the Upper Jurassic of the Lourinhã Formation significantly expand our knowledge of the diversity, morphology, and ontogenetic variation within this clade in the Iberian Peninsula. The comparative analysis of three well-preserved individuals from stratigraphically equivalent levels suggests the presence of at least one dwarf atoposaurid taxon, possibly represented by different growth stages. Although one of the specimens (ML2688) is unusually large for the group (an estimate of 1.5 m in total length), its anatomical features and osteoderm arrangement are consistent with atoposaurid morphology, highlighting the need for further investigation.

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Skin impressions associated with dinosaur tracks from the Upper Jurassic of Veguillas de la Sierra (Villar del Arzobispo Fm., Teruel)

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Keywords: Kimmeridgian–Tithonian, South-Iberian Basin, ichnites, Ornithopoda, Iguanodontipodidae.

Introduction

Dinosaur skin impressions associated with tracks are rare in the Iberian Peninsula, being only found in a few tracksites. These records include impressions attributed to sauropods (e.g. García Ramos *et al.*, 2000), stegosaurs (e.g. Guillaume *et al.*, 2022), theropods (e.g. Pascual-Arribas & Hernández-Medrano, 2011), and ornithopods (e.g. Cobos *et al.*, 2016; García-Cobeña *et al.*, 2024).

The Iberian Basin (north and eastern region of the Iberian Peninsula) stands out for its Upper Jurassic–Lower Cretaceous continental to transitional sedimentary record, which favored the preservation of both osteological and ichnological dinosaur fossils.

In particular, the South-Iberian Basin (provinces of Teruel and Valencia, Spain) contains a high number of dinosaur fossil sites from the Upper Jurassic (Kimmeridgian–Tithonian) Villar del Arzobispo Formation (Campos-Soto *et al.*, 2019), mainly osteological fossils of several taxa, including huge sauropods, stegosaurs, ornithopods and theropods (see Sánchez-Fenollosa *et al.*, 2024 and references therein). Among the ichnological record fewer tracksites have been reported. However, tracks attributed to several groups have been described, those attributed to theropods and ornithopods being the most abundant (e.g.: Santisteban *et al.*, 2003).

In this work, an *ex-situ* block containing skin impressions associated with dinosaur ichnites is described and analyzed in order to understand the relationship between the scale impressions and the tracks. The block was found in a field located in levels from the Villar del Arzobispo Formation in the municipality of Veguillas de la Sierra (southwestern province of Teruel).

Results

MAP-8444 is a sandstone block that exhibits two tridactyl tracks associated with skin impressions. These tracks (VS2-1R-1 and VS2-1R-2) are tridactyl. The block contains four areas with skin impressions, two of them associated with the ichnite VS2-1R-2 and two isolated (VS2-1R-3 and VS2-1R-4).

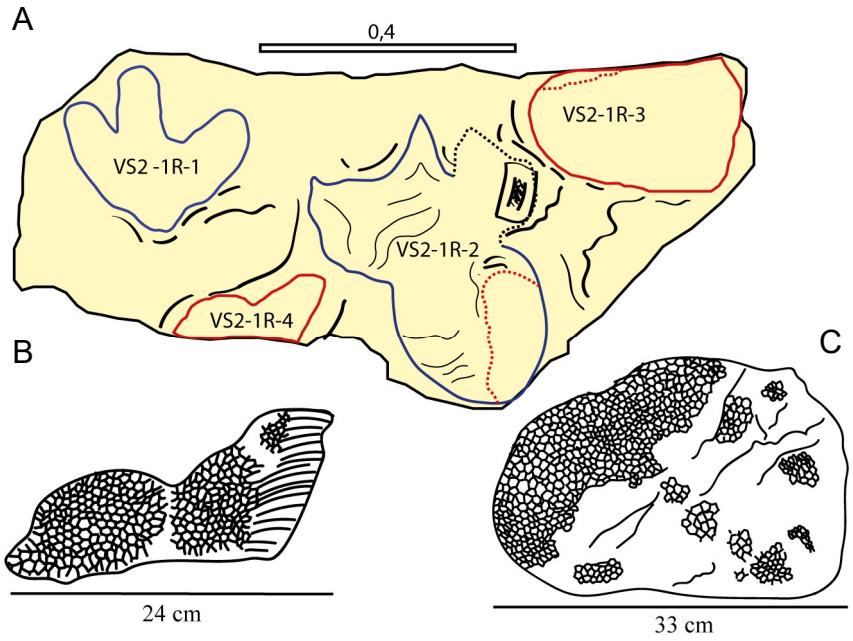

Figure 1. A) Inferred outlines of the tracks (in blue) and skin impression areas (in red) at the block from Veguillas de la Sierra (Teruel). B, C) Detailed drawings of the skin impressions VS2-1R-4 (B) and VS2-1R-3 (C).

The tracks are medium-sized (FL ~ 25 cm) and display different morphologies. VS2-1R-2 is a deep cast of a tridactyl track characterized by having acuminated digits and a large metatarsal impression with associated skin impressions. VS2-1R-1 is also a tridactyl track, but shallower, and exhibits wide digits with rounded distal ends, without associated skin impressions. Both tracks have similar morphometric data (e.g.: low mesaxony, similar length/width ratio), despite the observed differences that are possibly a consequence of deformation processes linked to the state of the substrate.

The skin impressions are characterized by impressions of small scales (4-7 mm diameter) of hexagonal to pentagonal contours, tuberculated and sometimes bounded by movement longitudinal striae. Of the four areas of skin impressions distinguished in the block, two are directly associated with the metatarsal impression and the other two (VS2-1R-3 and VS2-1R-4) are separated from the ichnites, with no direct association.

Discussion

The well-defined tracks (VS2-1R-1 and VS2-1R-2) are natural casts exhibiting a tridactyl morphology. The identification of tridactyl ornithopod and theropod tracks from the Upper Jurassic is complex due to their similarity (e.g.: Castanera *et al.*, 2013). However, VS2-1R-1 shows features (e.g.: subsymmetrical pes tracks that are as wide as or wider than long; digit pads longer than wide; notches in the proximal part of the digit II and IV) that allow its classification within the ichnofamily Iguanodontipodidae (Díaz-Martínez *et al.*, 2015).

Several hypotheses are proposed to explain the distribution and preservation of tracks associated with concrete areas that preserve skin impressions. Firstly, some specimens of the ornithischian ichnotaxa *Anomoepus* and *Moyenisauropus* are associated to some concrete areas with skin impressions, which are explained as consequence of a resting behavior of their trackmakers (Ellenberger, 1974; Lallensack *et al.*, 2022). It consists of a resting posture in which the trackmaker lies part of its body on the ground, leaving a distribution of skin impressions close to their pes and manus tracks. This kind of behavior may explain the subparallel position of the pes tracks, the large metatarsal

impression in VS2-1R-2 and the distribution of some of the skin impressions, and the similarity among the preserved scales. Nonetheless, it is hard to explain the different preservation of the two tracks (despite the similar morphometric data) and the rather far location of the VS2-1R-3.

Alternatively, due to the observed differences in the preservation across the block, another hypothesis involves multiple track-making events. Instead of attributing all the tracks to a single trackmaker, a second hypothesis include two tridactyl trackmakers passing through the area at different times, in the same direction, but under varying substrate conditions. This hypothesis would suggest a resting posture just by the tridactyl individual who left track VS2-1R-2 and the associated skin impressions, and an ornithopod passed later, leaving only a single footprint (VS2-1R-1). A third hypothesis proposes that a tridactyl trackmaker firstly produced a resting trace, including track VS2-1R-2 and a parallel footprint currently not well identified in the block, and that a second individual stepped later producing VS2-1R-1.

Skin impressions pose an additional challenge since scale patterns and morphologies within major dinosaur groups are highly variable and may appear similar or identical depending on the body region to which they belong (Hendricks *et al.*, 2022). Therefore, a global compilation of skin impressions from the Upper Jurassic–Lower Cretaceous interval has been conducted to compare them with those found on block MAP-8444, aiding in the identification of the trackmaker. Thus, the scales are very similar to those of ornithopods (e.g. Bell, 2012; Guillaume *et al.*, 2022). Further work is needed to properly understand which of the three hypotheses is most robust, but the ornithopod affinities of both the tracks (at least VS2-1R-1) and the skin impressions are noteworthy.

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Datos preliminares del fémur de un ornitisquio indeterminado del Santoniense (Cretácico Superior) de Argentina

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Palabras claves: postcraneal, Formación Bajo de la Carpa, Cuenca Neuquina.

Introducción

El registro fósil de dinosaurios del Cretácico de Sudamérica destaca por la abundancia de dinosaurios del clado Saurischia (saurópodos y terópodos), siendo los restos pertenecientes a Ornithischia escasos en comparación (Cruzado-Caballero *et al*., 2018). Dentro del registro fósil de Ornithischia en Sudamérica encontramos representantes de ornitópodos y tireóforos (Alarcón-Muñoz *et al*., 2023; Riguetti *et al*., 2022).

Relativo a los ornitópodos, este es el clado más abundante tanto en especies descritas como en restos indeterminados destacando los restos de los clados Elasmaria y Hadrosauridae. La mayor parte del registro se localiza en Argentina, con la excepción de un ornitópodo indeterminado del Turoniense-Santoniense procedente de Uruguay, el elasmario *Tietasaura derbyiana* con una edad de Valanginiense-Hauteriviense de Brasil (el registro más antiguo) y el hadrosauroideo no-hadrosáurido *Gonkoken nanoi* (Cruzado-Caballero *et al*., 2018; Alarcón-Muñoz *et al*., 2023; Bandeira *et al*., 2024). Con respecto a Thyreophora, durante el Cretácico sudamericano están presentes los anquilosaurios con varias especies descritas de Chile y Argentina y los estegosaurios con un taxón indeterminado solo en Argentina (Soto-Acuña et al., 2021; Pereda-Subierbiola et al., 2013).

En el presente trabajo presentamos los resultados preliminares del estudio de un fémur derecho (MAU-PV-CO-684; Figura 1) de un ornitisquio de pequeño tamaño depositado en el Museo Argentino Urquiza y Parque de Dinosaurios Rinconsaurus de Rincón de los Sauces (Provincia de Neuquén, Argentina).

Contexto geográfico y geológico

MAU-PV-CO-684 procede del área fosilífera Cerro Overo-La Invernada ubicada al norte de la Cuenca Neuquina. El material fue encontrado en sedimentos de la Formación Bajo de la Carpa (Santoniense, Cretácico).

Descripción

MAU-PV-CO-684 es un fémur derecho (Figura 1) con una longitud total preservada entre los dos fragmentos de 86,2 mm (fragmento proximal) y 46,7 mm

(fragmento distal). Pertenecería probablemente a un individuo adulto, ya que las epífisis se muestras fusionadas, a pesar de la ligera erosión que muestran los extremos proximal, en la cabeza femoral y trocánter menor, y distal, en el cóndilo lateral. Además, se observa la depresión donde inserta el *M. caudofemoralis longus*. El fragmento proximal conserva la cabeza femoral, el trocánter mayor, el trocánter menor y el cuarto trocánter, mientras que el fragmento distal preserva los cóndilos medial y lateral. En vista medial, el fragmento proximal muestra una curvatura en la diáfisis anteroposteriormente. La cabeza femoral es de pequeño tamaño y en vista proximal tiene una forma subcuadrangular. Ésta se encuentra separada del trocánter mayor por una pequeña hendidura. El trocánter menor está fusionado al trocánter mayor. Con respecto al cuarto trocánter este tiene forma de triángulo escaleno y no es colgante.

En el fragmento distal en vista distal, los extremos de los cóndilos son divergentes. El surco extensor es estrecho en sentido lateromedial y presenta una ligera hendidura que le confiere una forma en "U", mientras que el surco flexor es relativamente amplio y superficial, adoptando una morfología en "V".

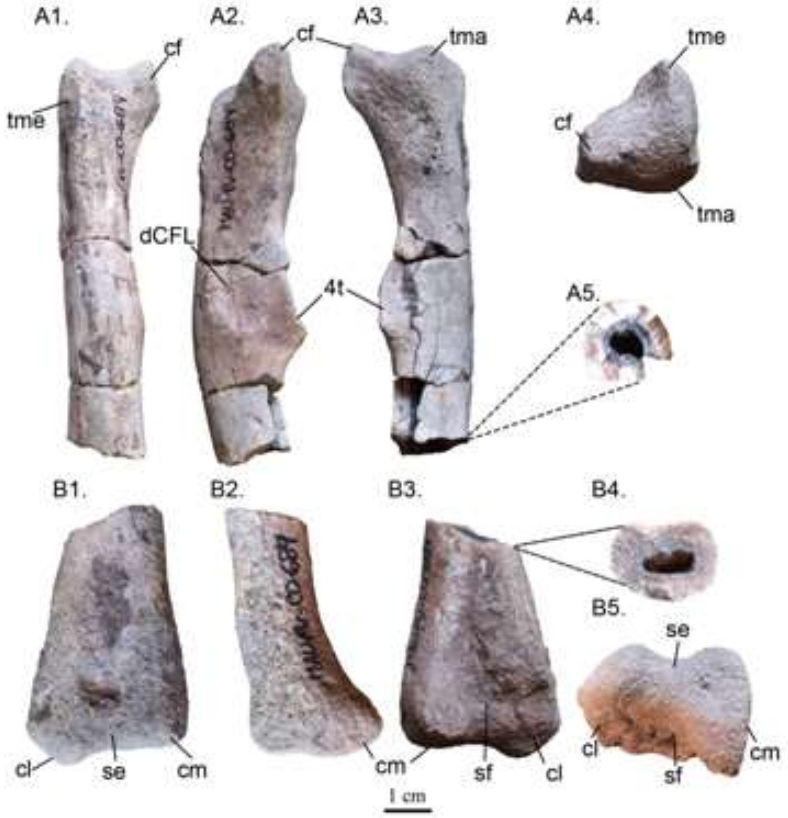

Fig. 1. Fémur derecho MAU-PV-CO-684. A1-5 Fragmento proximal en vistas anterior (1), medial (2), posterior (3), proximal (4) y transversal (5). B1-5 Fragmento distal en vistas anterior (1), medial (2), posterior (3), proximal (4) y transversal (5). Abreviaciones: cf, cabeza femoral; cl, cóndilo lateral; cm, cóndilo medial; d. CFL, depresión del *M. caudofemoralis longus*; se, surco extensor; sf, surco flexor; tma, trocánter mayor; tme, trocánter menor; 4t, cuarto trocánter. Escala: 1 cm.

Comparación

MAU-PV-CO-684 fue comparado con todos los grupos de ornitísquios presentes durante el Cretácico en Sudamérica. Se distingue principalmente de los tireóforos por ser más grácil, tener una marcada constricción entre la cabeza femoral y el trocánter mayor, una diáfisis curvada anteroposteriomente y los cóndilos distales menos desarrollados

(Weishampel et al., 2004). Estas características lo diferencian de los tireóforos y acercan MAU-PV-CO-684 a los ornitópodos de pequeño tamaño, como pueden ser *Notohypsilophodon comodorensis, Anabisetia saldiviai* y *Gasparinisaura cincosaltensis*, entre otros. Sin embargo, MAU-PV-CO-684 muestra ciertas diferencias tanto en el extremo proximal como en el distal. Así, podemos ver que en vista proximal el lateral del trocánter menor no es tan estrecho como en otros taxa. Además, la cabeza femoral está ligeramente por encima del trocánter mayor, al contrario de otros taxa argentinos. Con respecto al cuarto trocánter éste difiere de los elasmarios al no ser colgante, asemejándose más a los observados en iguanodóntidos. Por último, el extremo distal en vista distal difiere de otros ornitópodos en cuanto al desarrollo del surco extensor, siendo más similar a ornitópodos tempranamente divergentes.

Conclusiones

MAU-PV-CO-684 muestra ciertos caracteres morfológicos compatibles con el clado Ornithopoda, tales como el arqueamiento anteroposterior de la diáfisis, la separación entre la cabeza femoral y el trocánter mayor, entre otros. Además, el pequeño tamaño nos indicaría que podría ser un ornitópodo bípedo comparable con *Gasparinisaura cincosaltensis*, *Notohypsilophodon comodorensis* o *Anabisetia saldiviai.* A la espera de hallazgo de nuevos materiales en la zona de procedencia, MAU-PV-CO-684 se asigna provisionalmente como Ornithopoda indet.

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New basal ornithopod dinosaur remains from the Barremian-Aptian site of Viajete (Burgos, northern Spain)

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Keywords: Viajete, Lower Cretaceous, Castrillo de la Reina, ornithopod, *Hypsilophodon*.

Ornithopoda are a clade of ornithischian dinosaurs that represent one of the most successful groups within the superorder Dinosauria, especially during the Cretaceous period. Since the term Ornithopoda was first coined, the definition of the group and its taxonomic structure have been altered numerous times over the years, especially for those smaller members that are also considered to be the most basal, whose phylogenetic position is still subject to intense debate today (Boyd, 2015; Dieudonné et al., 2016; Poole, 2022; Fonseca et al., 2024). This phylogenetic confusion mainly affects families such as Hypsilophodontidae, Dryosauridae, Rhabdodontidae and Thescelosauridae (Madzia et al., (2021).

The Iberian record of these basal ornithopods is relatively rich and diverse, being the most complete in Europe in the case of hypsilophondontids (Ruiz-Omeñaca, 2001). In the Lower Cretaceosus from the western sector of the Cameros Basin, in the environment of the locality of Salas de los Infantes (Burgos) numerous associations of fossil remains of small ornithopods have recovered, some of which have been studied over the years (Torcida Fernández-Baldor et al., 2005; Dieudonné et al., 2016, 2020, 2023). Among the most outstanding sites for providing this type of remains are the sites of Los Peñucos-La Ballesta (Pinilla de los Moros Formation, upper Hauterivian-lower Barremian), La Solana, Río Gete, Las Rozas, El Peñascal, Arroyo Cistierna, La Tejera and Viajete (Castrillo de la Reina Formation, upper Barremien-lower Aptian) (Martín-Closas and Alonso Millán, 1998).

In the year 1995, two sets of bones with a clear dinosaur morphology were discovered in the Viajete site, including several fragments attributable to different parts of the premaxilla and dentary, fragments of scapulae and ilium, several vertebral centra and neural arches from different zones of the vertebral column, and fragments corresponding to most of the bones from the forelimbs and hind limbs. Several individuals have been identified and assigned to the same taxon. After a preliminary study, these remains have been attributed to basal ornithopods, but they have yet to be described and properly classified.

In this work, the first detailed study and description of these remains is carried out, and their possible affinities with the genus *Hypsilophodon* and other genera and clades of basal ornithopods are analyzed, in order to establish the kinship relationships of these skeletal remains.

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How might a limping dinosaur move? Understanding the limits of the locomotion of an ornithopod from the Arcillas de Morella Formation (Castellón, Spain)

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Keywords: Styracosterna, Lower Cretaceous, Arcilla de Morella Formation, Pathology, Myology

Locomotion in non-avian dinosaurs is one of the most captivating aspects of the modern paleobiology of vertebrates. Despite the obvious constraints, the validation of biomechanical studies using fossils can be developed by a variety of methods: building of musculoskeletal models, analyzing fossilized footprints, comparing them with extant taxa, and studying the osseous elements (Falkingham, 2025). Among non-avian dinosaurs, a significant research on the reconstruction of inferred locomotion in styracosternan ornithopods has been conducted in recent years (Maidment et al., 2014; Barret & Maidment, 2017; Dempsey et al., 2025).

Additionally, these dinosaurs are also known to have had a high number of palaeopathologies among the Mesozoic terrestrial vertebrates. (Rothschild & Martin, 2006; Witzmann et al., 2008; Tanke & Rothschild, 2014; Ramírez-Velasco et al., 2017) Nevertheless, it is extremely rare to find pathologies or anomalous anatomical conditions affecting the mechanical processes of normal gait in any group of non-avian dinosaurs,considering the nature of the fossil record.

Non-hadrosauroid styracosternan ornithopods are one of the best represented dinosaurs in the Lower Cretaceous European terrestrial vertebrate fossil record. In this context, the Arcillas de Morella Formation, in northeastern Spain, has provided a large amount of evidence for more than a decade (Gasulla, 2015). Among these, a nearly complete adult specimen from the Mas de la Parreta Quarry (CMP-5), characterized by several pathologies in its axial bones, exhibits an osteological anomaly in its left ilium. This anomaly consists of a markedly different morphology and proportions compared to its right counterpart. This results ina noticeable asymmetry of the pelvic girdle that affects the suprailiac crest and iliac plate muscle origins, mainly *M. iliofemoralis, M. Iliotibialis* and possibly *M. Iliofibularis* (Norman, 1986; Dilkes, 1999; Dilkes et al., 2012). Additionally, the morphology of the acetabulum would also be affected by this asymmetry.

To analyze how this anomalous condition would affect the dinosaur, both 3D models of the pelvic girdle and the hindlimbs were created. Consequently, we have used photogrammetry to reconstruct the pelvis, right fibula and the first caudal vertebra of this individual. Additionally, photogrammetry was also implemented to finalize the reconstruction of the hindlimbs by utilizing bone elements from other individuals from the same fossiliferous area. These were scaled according to the proportions of the studied individual. Finally, the virtual skeleton was assembled using Blender software, establishing the areas of muscle origins and insertions.

Therefore, the musculature reconstruction of this styracosternan provides a detailed examination of an unusual pelvic condition observed in a non-avian dinosaur. Regarding its lifestyle, this condition likely caused the styracosternan ornithopod to limp.

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New evidence of dacentrurine stegosaurs from the Late Jurassic of eastern Iberia (Alpuente, Valencia)

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Keywords: Thyreophora, Stegosauria, Dacentrurinae, Villar del Arzobispo Formation, Los Serranos region, systematics.

Introduction

Dacentrurinae is a clade of neostegosaurs that includes several species (Sánchez-Fenollosa & Cobos, 2025): *Alcovasaurus longispinus* (Late Jurassic, North America), *Kentrosaurus aethiopicus* (Late Jurassic, Africa), *Adratiklit boulahfa* (Middle Jurassic, Africa), *Thyreosaurus atlasicus* (Middle Jurassic, Africa), and *Dacentrurus armatus* (Late Jurassic, Europe).

The European Late Jurassic stegosaurian fossil record is relatively abundant and is mainly composed of specimens referred to as *Dacentrurus armatus* or indeterminate dacentrurines (e.g., Galton, 1985; Mateus et al., 2009; Cobos et al., 2010; Company et al., 2010; Sánchez-Fenollosa et al., 2022, 2025). *D. armatus* is known since the end of the 19th century (Owen, 1875). Mateus et al. (2009) described a second dacentrurine species, '*Miragaia longicollum*', and diagnosed it on the basis of anatomical elements unknown in the holotype of *D. armatus* (Galton, 1985). Later, some authors challenged its validity (Cobos et al., 2010; Cobos & Gascó, 2013; Escaso, 2014), but others supported it (Costa & Mateus, 2019). However, a recent systematic assessment (Sánchez-Fenollosa et al., 2025) found that: (1) defining two contemporaneous taxa based on non-overlapping elements introduces significant taxonomic uncertainty; (2) European Late Jurassic dacentrurines exhibit high morphological homogeneity; (3) '*M. longicollum*' should be regarded as a junior synonym of *D. armatus*; and (4) currently there is no solid evidence for more than one dacentrurine species.

Here, we present a preliminary study of some stegosaurian fossils recovered from the By Pass fossil site (Alpuente, Valencia).

Geographical and geological context

The By Pass fossil site is situated within the municipality of Alpuente (province of Valencia, Spain). Geologically, it is located within the South-Iberian Basin in beds of the Villar del Arzobispo Formation (upper Kimmeridgian–Tithonian *sensu* Campos-Soto et al., 2019).

Results and discussion

The By Pass fossil site was discovered during the heritage monitoring of the construction of a road near the town of Alpuente (Suñer & Martin, 2009). This site yielded numerous fossils corresponding to stegosaurs, ornithopods, theropods, sauropods, crocodylomorphs, testudinatans, and osteichthyans (Suñer & Martin, 2009; Sánchez-Fenollosa et al., in this volume). Recent fossil preparation work has enabled the systematic study of some of these remains.

The stegosaurian remains examined here comprise an anterior dorsal vertebra, a posterior dorsal vertebra, a mid-caudal vertebra with its chevron, and a left terminal caudal dermal spine.

The dorsal vertebrae exhibit centra wider than long, resembling those of the dacentrurines *Adratiklit boulahfa* (Maidment et al., 2020), *Thyreosaurus atlasicus* (Zafaty et al., 2024), and *Dacentrurus armatus* (e.g., Galton, 1985; Mateus et al., 2009; Costa & Mateus, 2019; Sánchez-Fenollosa et al., 2025). The mid-caudal vertebra exhibits a centrum wider than long and heart-shaped, similar to those observed in the dacentrurines *Kentrosaurus aethiopicus* (Hennig, 1925) and *D. armatus* (Galton, 1985; Costa & Mateus, 2019; Sánchez-Fenollosa et al., 2022, 2025). The stocky terminal caudal dermal spine is presumably long, comparable to those of the dacentrurines *Alcovasaurus. longispinus* (Galton & Carpenter, 2016) and *K. aethiopicus* (Galton, 1982). This feature, along with the presence of a large base and/or a shaft with a rhomboidal cross-section, is also observed in several dacentrurine specimens from the European Late Jurassic (e.g., Company et al., 2010; Escaso, 2014; Galton, 2016; Costa & Mateus, 2019).

Given the presence of dacentrurine synapomorphies, the absence of autapomorphies, and the preliminary nature of the study, these fossils are referred to as Dacentrurinae indet.

The future preparation and research of this stegosaurian material from the By Pass site will provide further insights into the systematics and diversity of this group of stegosaurs.

A comprehensive approach that includes the entire Late Jurassic stegosaurian record, including this specimen, is essential for establishing robust and consistent species delimitations.

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New data on the ornithopods (Ornithischia, Ornithopoda) from eastern Iberia (Late Jurassic, Spain): Preliminary insights into their diversity

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Introduction

Ornithopods were among the most diverse and geographically widespread dinosaurs. Nevertheless, their osteological fossil record from the Upper Jurassic of Europe is particularly scarce and fragmentary (e.g., Sánchez-Fenollosa et al. 2021 and references therein), so their diversity remains partially obscured. In recent years, considerable efforts have been made to reverse this situation, concretely in the Iberian Peninsula (e.g., Escaso et al. 2014; Sánchez-Fenollosa et al. 2022, 2023; Rotatori et al. 2023, 2025).

Here, we present a preliminary study of some ornithopod fossils recovered from the provinces of Valencia and Teruel (Spain).

Geographical and geological context

All the sites are in the eastern Iberian Peninsula. The By Pass fossil site is situated within the municipality of Alpuente (province of Valencia, Valencian Community, Spain), while the RD-61 fossil site lies within the municipality of Riodeva (province of Teruel, Aragón, Spain).

Geologically, both sites are located within the South-Iberian Basin in beds of the Villar del Arzobispo Formation (upper Kimmeridgian–Tithonian *sensu* Campos-Soto et al. 2019).

Results and discussion

The fossils studied here comprise a left dentary tooth, an anterior caudal vertebra, and a posterior caudal vertebra from the By Pass site (Alpuente, Valencia), and an anterior caudal vertebra from the RD-61 site (Riodeva, Teruel).

A preliminary systematic study of these fossils suggests the presence of previously unrecorded ornithopods in the region, potentially increasing the known diversity of the group in this area.

Previous research had only identified medium- to large-sized ankylopollexians, such as the Fuentecillas specimen (Sánchez-Fenollosa et al. 2022) and *Oblitosaurus bunnueli* (Sánchez-Fenollosa et al. 2023). The likely coexistence of several ornithopod taxa may reflect niche partitioning.

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Aragonés de Fomento. Part of the studied material was found during the palaeontological works carried out in the construction of the CV-345 road (named ‘By Pass’) and financed by the Diputació de València.

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New data on the paleodiversity of spinosaurids (Dinosauria: Theropoda) in the Lower Cretaceous of the Maestrazgo Basin (Eastern Spain)

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Keywords: Spinosauridae, diversity, isolated teeth, heterodonty

The fossil record of Iberian Lower Cretaceous spinosaurids is relatively abundant, although most of the remains correspond to isolated teeth. Despite this, five different genera have been described from the Iberian Peninsula (*Camarillasaurus*, *Iberospinus*, *Protathlitis*, *Vallibonavenatrix* and *Riojavenatrix*), and there are more than twice as many spinosaurid tooth morphotypes. This raises discussions not only about spinosaurid diversity but also about the possibility of heterodonty within the group. In recent years, new techniques have been applied to improve taxonomy for isolated theropod teeth. These include multivariate statistical analysis, and more traditional methodologies (such as cladistic analyses) to which new morphological characters are incorporated (e.g. ornamentation and patterns present in different structures of the enamel). We propose a study of a collection of 28 isolated spinosaurid teeth from various upper Barremian sites of the Arcillas de Morella Formation (Morella, Spain) in the Maestrazgo Basin. Analyses based on multivariate statistics and geometric morphometry have been conducted on this material complementing the systematic analyses performed using traditional methodologies. The results obtained allow for the discrimination of three morphotypes of teeth: one interpreted as lateral teeth of Baryonychinae indet., another interpreted as a mesial tooth of Baryonychinae indet. (which has a rounder base than lateral ones), and a third interpreted as lateral teeth of Spinosaurinae indet. (due to its more circular base and lack of preserved denticles). These results confirm the synchrony and sympatry of the two lineages of Spinosauridae in the Barremian of the Maestrazgo Basin, but more information and material are needed to clarify whether the detected disparity is due to taxonomic diversity or intraspecific causes (such as heterodonty processes). Nevertheless, additional studies and more material are required to characterize their dental morphological disparity.

Large dinosaur footprint casts from the Lower Cretaceous of Salas de los Infantes (Burgos, Spain).

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Keywords: Cameros basin, tracks, *Caririchnium*, Sauropoda, cast

New dinosaur footprint discoveries from the Pinilla de los Moros Fm. are reported (Upper Hauterivian– Aptian) in the western sector of the Cameros Basin (Salas de los Infantes, Burgos, Spain). This formation is constituted by red clays, sandstones, and conglomerate beds interpreted as a fluvial system, characterized by well-developed floodplains and channel belts (from more interconnected to isolated) (Platt, 1989; Clemente y Pérez Arlucea, 1993).

Up to now, one ichnological site had been documented in the Pinilla de los Moros Fm near Salas de los Infantes: Costalomo (Torcida et al., 2006; Huerta et al., 2012), along with isolated, undescribed natural casts of dinosaur footprints. Several new outcrops have been identified in the surroundings of Salas de los Infantes during field surveys conducted by the Colectivo Arqueológico y Paleontológico de Salas (C.A.S.). These footprints have a large size. This contribution describes three of these casts, currently housed in the Salas de los Infantes Dinosaur Museum.

From the Caminos Anchos III site comes CASIII,1 a tridactyl track measuring 51 cm in length and width, and 50 cm in depth. The digit impressions are short and blunt, with digit III being the most anteriorly projected. Digits II and IV are nearly parallel to digit III and exhibit a posterior notch extending toward a broad, rounded heel region. Parallel striations are preserved on the internal wall of the track fill, interpreted as drag traces left by the animal's foot skin as it moved through the muddy substrate. At the same stratigraphic level, a dermal spine from an indeterminate ankylosaur was also recovered.

At the Tenadas de Camarma-Castrovido (TCC) site, two isolated tracks have been documented. Specimen MDS-TCC,1 is a cast of a large track measuring 85 cm in length, 74 cm in width and 36 cm in depth. The track preserves impressions of five laterally rotated digits (I–V). Digit I is short, anteriorly oriented, slightly rotated laterally, and terminates in a sharp point. Digit II also ends in a pointed tip, is longer than digit I, and aligned along the anteroposterior axis of the track. Digits III and IV are relatively long and wide; digit II distal end is broken, while digit IV terminates bluntly. Digit V is very short, barely projecting, with a rounded contour and situated laterally. Parallel striations are observed on the internal wall of the track fill, attributed to skin impressions made during foot movement in mud. The same site has also yielded fragments of bennettitaleans and *Tempskya*-type ferns.

Specimen MDS-TCC,2 is a tridactyl track measuring 64 cm in length, 63 cm in width and 15 cm in depth. The track has short, broad digit impressions and rounded outlines. Digit III is longer than digits II and IV. The track has a broad, rounded posterior

margin. Longitudinal parallel striations and slight lateral displacement of the digits indicate foot movement through muddy substrate.

Although the preservation of the tracks is not optimal, it allows for discussion on ichnotaxonomy and the potential trackmakers. The morphology of the tracks from Caminos Anchos III and MDS-TCC,2 is consistent with the ichnogenus *Caririchnium*, which is well-represented in Early Cretaceous tracksites across the Iberian Peninsula and attributed to large indeterminate styracosternan ornithopods, also cf. *Iguanodon* sp. (Díaz-Martínez et al., 2015; Castanera et al., 2022; García Cobeña et al., 2023). In contrast, the morphology of track MDS-TCC,1 is characteristic of a sauropod pes. It preserves at least two claw impressions (digits I and II), while digit III is broken distally, and digits IV and V lack preserved claw marks.

This study expands our knowledge of dinosaur faunal diversity during the Upper Hauterivian–Lower Barremian interval of the Early Cretaceous in the western Cameros Basin, documenting for the first time in this interval the presence of large-bodied sauropods.

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Preliminary insights into Late Cretaceous dinosaur jaw biomechanics by means of dental microwear from south-western Europe

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Keywords: Maastrichtian, Europe, microwear, biomechanics, dinosaur

Understanding how dinosaurs fed could offer us insights into their behavior, diet, and ecological constraints. In the last 20 years, several works have contributed to the understanding of dinosaur feeding biomechanics by means of several methods like 3D modelling and biomechanical analyses (Rybczynski et al., 2008; Weishampel and Norman, 1989).

Among these studies, only microwear analysis has provided direct evidence to support the aforementioned models and hypothesis for dinosaur feeding biomechanics (Williams et al., 2009). Such evidence is derived from the orientation distribution of scratches, elongated microwear features present on a dental wear facet. Their orientation correlates with food-to-tooth and tooth-to-tooth contact, thus allowing us to infer relative the motion of the jaws against each other during feeding (Mallon & Anderson, 2014; Whitlock, 2011; Williams et al., 2009; Wyenberg-Henzler et al., 2022).

Although these studies have provided evidence for the feeding mechanisms of all the main groups of dinosaurs (Fiorillo, 1998; Mallon & Anderson, 2014; Torices et al., 2018; Wiersma and Sander, 2017), most of the known microwear studies in dinosaurs have been applied to North American taxa. Therefore, the study of dinosaur microwear is scarce in Europe (Ősi et al., 2022) and jaw biomechanics have never been studied.

Thus, as part of a larger effort to further characterise the microwear patterns from European dinosaur groups and their paleobiological implications (Vázquez et al., in press), we used a directional analysis of the scratches present in those patterns to infer the jaw biomechanics during feeding of these animals. We have also compared our results with the known feeding biomechanics based on North American taxa. Despite their morphological similarity, the European insular faunas may have presented substantial biomechanical or etological differences with mainland species, or completely new adaptations to environments with limited resources.

The present study analyses teeth from dinosaurs native to the Ibero-Armorican Domain (a south-western Europe region that once was the largest island of the Late Cretaceous European Archipelago). Representatives from the phytophagous groups have been sampled from several localities (Blanco et al., 2015; Company et al., 2009; Díez Díaz et al., 2012 a, 2012 b, 2013, 2014, 2018; Fondevilla et al., 2018; Gaete, 2021; López-Martínez et al., 1999; Prieto-Márquez et al., 2013; Vázquez et al., 2024) like titanosaurians (Els Nerets, Fox-Amphoux-Métisson, Laño, Lo Hueco), nodosaurids (Biscarri, Fontllonga-6), and hadrosauroids (Basturs Poble, L'Espinau, Tricouté-3).

We have then measured the mean length and orientation of the scratches present in the microwear pattern of each sampled tooth with ImageJ/Fiji (v. 2.14.0).

Considering that most of the samples were found isolated and that their position on the toothrow may prove ambiguous, measurements were taken considering the apex as 0º (instead of the mesial side like in Mallon & Anderson, 2014; Wyenberg-Henzler et al., 2022) and angles ranged from 0-180º.

These directions were then mirrored and plotted as rosewind diagrams in R Studio (v. 4.5.0) and analysed using the CircMLE package (Fitak & Johnsen, 2017) after Wyenberg-Henzler et al. (2022) to determine which "classes" or groupings of scratches emerged from the microwear patterns.

As part of a recent microwear analysis of Ibero-Armorican phytophagous dinosaur groups (Vázquez et al., In press), we also obtained the orientation of the scratches for each microwear pattern on the studied teeth.

Ibero-Armorican titanosaurians show a complexity in their microwear orientations previously unaccounted for in sauropods. Even though there are examples of mostly unimodal distributions (Lo Hueco and Laño morphotypes), the motion does not appear to be purely orthal as previously hypothesised, but rather oblique. The only cases when an orthal movement of the jaws is inferred from apicobasal scratches (Els Nerets, Fox-Amphoux-Métisson), it is not the main component of jaw movements, which is characterised by a bimodal pattern of highly dispersed oblique apicobasal directions and mesiodistal features, implying a propalinal component to their jaw biomechanics.

The hadrosauroid microwear from Ibero-Armorica, like the one from L'Espinau locality, shows a greater resemblance to previously known jaw biomechanics of continental forms, with a bimodal (or trimodal) distribution of oblique scratches as the power stroke and mesiodistal orientations indicative of propalinality. The latter fore-aft movement is more used in our sample than in mainland species. to the point that, contrary to other hadrosauroids, *Canardia garonnensis* shows a unimodal distribution of scratches that suggests a purely orthal power stroke with slight propalinality during mastication.

Ibero-Armorican nodosaurids, especially the Biscarri samples, show a mainly unimodal distribution of scratches, and coincide with previous interpretations (Mallon & Anderson, 2014) of an oblique orthal main motion of the jaw with some propalinal movement. However, this propalinal component is more heavily dominant in the microwear from Fontllonga-6, suggesting a lower angle of occlusion or an extremely different tooth alignment for the indeterminate species.

In conclusion, the study of Ibero-Armorican dinosaur microwear supports previous hypothesis regarding the basic jaw motions of the main groups of phytophagous dinosaurs, which are shared by both mainland and insular representatives (Fiorillo, 1998; Mallon & Anderson, 2014; Ősi et al., 2022). It has also provided support for previously hypothesised more complex jaw motions for nodosaurids (Mallon & Anderson, 2014; Ősi et al., 2022). Similarly, we have observed that titanosaurian feeding mechanisms were not as simplistic as previously thought (Fiorillo, 1998; Whitlock, 2011).

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An overview of the evolution of Spinosauridae and a new phylogenetic analysis

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Introduction

In recent years, the diversity of spinosaurid theropods has increased drastically, especially in the European domain. Some of these taxa were previously interpreted to belong to other spinosaurid genera (e.g. *Iberospinus* (Mateus & Estraviz-López, 2022), originally described as *Baryonyx* (Mateus et al., 2011)) while others were originally described as non-spinosaurid theropods (e.g. *Camarillasaurus* (Samathi et al., 2021) originally described as a ceratosaur (Sánchez-Hernández & Benton, 2012)). In addition, the diagnostic nature of taxa that were considered either *nomina dubia* or junior synonyms of previously named taxa is subject of discussion (Evers et al., 2015; Smyth et al., 2020). This increase in diversity has brought some instability to the phylogenetic relationships of Spinosauridae. We present a comprehensive new phylogenetic analysis to evaluate the relationships of the clade and explore their evolutionary history.

Previous phylogenetic analyses of Spinosauridae

Previous efforts to explore the phylogenetic relationships of Spinosauridae derive from three main datasets: Carrano et al. (2012), Cau (2018) and Sereno et al. (1998). These had originally different scopes, which were to explore the diversity of Megalosauroidea (Sereno et al., 1998), to explore the diversity of non-coelurosaurid tetanurans (Carrano et al., 2012), and to explore the evolution of the avian body plan (Cau, 2018). Despite this, the majority of analyses retrieved consistently a pair of sister clades with similar composition: Baryonychinae and Spinosaurinae, albeit some taxa like *Vallibonavenatrix* or *Ichthyovenator* jump between clades. Some analyses however do not retrieve either of those clades (Evers et al., 2015) or only retrieve Spinosaurinae (Smyth et al., 2020).

New Phylogenetic Analysis

Our dataset is based on Sereno et al. (1998) and subsequent modifications in Sereno et al. (2022). It includes 159 morphological characters (39 new) with cranial and postcranial characters almost evenly distributed (51% and 49% of the dataset respectively) and 22 terminal species or specimens (6 outgroup, 16 ingroup). All characters were regarded as independent and unordered. A first traditional search of 1000 Wagner trees with 10 tree bisection reconnection (TBR) replicates per tree with equally weighed characters yielded 42 minimum length trees. Three fragmentary ingroup taxa are identified as wildcard by the interPCR (iterative Positional Congruence Reduced) subroutine in TNT. *A posteriori* pruning of these taxa yielded a fully resolved strict consensus which retrieves Spinosaurinae and Baryonychinae with the Iberian taxa *Camarillasaurus* and *Riojavenatrix* outside this dichotomy as the earliest diverging representatives of Spinosauridae.

Finally, a tip dated Bayesian analysis was performed to include both morphological and temporal data and to further evaluate positions of wildcard taxa. The analysis ran for a total of 20 million generations, which reached convergence relatively early, with sampling occurring every 1,000 generations. The first 20% of sampled trees were discarded to eliminate the initial burn-in phase of the analysis prior to reaching convergence. The resulting tree has a very similar topology to the pruned consensus tree, with the only major differences of retrieving *Riojavenatrix* as a Baryonychine spinosaurid and *Protathlitis* as the sister taxon of *Iberospinus*. In this tree, *Camarillasaurus* is the only spinosaurid outside the Baryonychinae + Spinosauridae dichotomy.

The evolutionary history of Spinosauridae

The evolutionary history that emerges from combining the information of previous phylogenetic analyses with our new approach can be summarized in three distinct stages of spinosaurid evolution:

1) A first phase accounting for approximately half of spinosaurid evolution, is known thus far only from isolated teeth in Upper Jurassic or Lower Cretaceous rocks. Here the array of shared features of all later spinosaurids arose. These trophic, structural and sociosexual adaptations have masked major differences in skull and dental form that arose between the two main clades Baryonychinae and Spinosaurinae during this poorly documented phase, such as a dentary with a high number of reduced yet tightly packed teeth and a extremely long symphysis in the former and fewer but more spaced teeth of disparate sizes and a dentary symphysis limited to the ramus underlying the premaxillary rosette in the latter.

2) In the Lower Cretaceous, spinosaurids diversified in habitats bordering the Tethys Sea, where they were the largest and most common predators in Gondwana and Laurasia. In the north continent, most representatives were baryonychines while in the less sampled south there is no clear dominance of each group. Coexistence in the same formation of Baryonychinae and Spinosaurinae only occurs in the Arcillas de Morella Fm (*Protathlitis* and *Vallibonavenatrix*).

3) A final phase began before the close of the Albian, with the extinction of Baryonychinae and the presence of Spinosaurinae limited to northern South America and Africa. By the early to middle Cenomanian, spinosaurines reached maximum body size, taking their fish-eating adaptations further and ceding most inland predation to equal-sized carcharodontosaurids.

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New insights into Allodaposuchidae vertebrae anatomy: taxonomic assignment of Lo Hueco morphotypes

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Allodaposuchidae is an eusuchian clade endemic to the Late Cretaceous of Europe (Narváez et al., 2015), which has become a keystone in our knowledge of early eusuchian evolution in recent decades. The first allodaposuchid species to be described, *Allodaposuchus precedens* Nopcsa, 1928, was based on fossil remains from the Maastrichtian of Romania. Since then, several new species have been described at various Campanian-Maastrichtian fossil sites in Spain and France. Most of the described allodaposuchids lack or only preserve scarce postcranial remains (Blanco et al, 2014). Consequently, the abundant postcranial fossil remains of allodaposuchids from the Lo Hueco fossil site (Cuenca, Spain) are of particular importance in addressing the anatomy of these basal eusuchians. At the Lo Hueco site, two allodaposuchids have been described: *Lohuecosuchus megadontos* (Narváez et al., 2015) and *Agaresuchus fontisensis* (Narváez et al., 2016). These two sympatric and synchronic species were first described using the cranial remains that were available at the time. In contrast, the postcranial anatomy of these species was only preliminarily explored in a number of studies (de Celis et al., 2018; Villanueva et al., 2024).

Despite the recognition of two different postcranial morphotypes (appendicular and axial) among the remains of Lo Hueco, these could not be confidently assigned to either of the two allodaposuchid species from this site (de Celis et al., 2018; Villanueva et al., 2025). In parallel, there has been a surge of interest in the postcranial skeleton of crocodylomorphs in general, and eusuchians in particular (e.g. Molnar et al., 2015, Stein et al., 2017; Iijima and Kubo, 2019; Scavezzoni and Fischer, 2023), with different aspects like their morphology, functional biology, and disparity being explored. Numerous studies have emphasized a previously underestimated disparity and locomotor complexity (e.g., Chamero et al., 2013 Iijima et al., 2019), with significant evolutionary implications. In this context, the importance of a deeper study of allodaposuchid postcranial anatomy is highlighted.

Following the association between a series of postcranial remains and the holotype of *Agaresuchus fontisensis*, along with previous work on morphotype identification, one of the vertebral morphotypes from Lo Hueco can now be confidently assigned to one of the two recognized allodaposuchid species. Consequently, the second morphotype can be reasonably attributed to the other species. This study formally establishes the taxonomic identity of the axial eusuchian morphotypes previously recognized at Lo Hueco, with the one formerly presented as "robust" being *L. megadontos* and the one presented as "slender" being *A. fontisensis.* In addition, the morphology of the vertebral elements

belonging to both species is described and compared. As a consequence of these results, the axial record of the Lo Hueco allodaposuchids becomes a valuable dataset for future studies regarding the macroevolutionary transformations of the postcranial skeleton in early eusuchians.

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