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UNRAVELLING ORNITHOPOD DIVERSITY IN THE LATE JURASSIC COASTAL ECOSYSTEMS OF EASTERN IBERIA (SPAIN)

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Abstract: Ornithopod osteological fossils from the Upper Jurassic of Europe are relatively scarce and often fragmentary compared to those of other dinosaurian groups. Recent discoveries, particularly from the Iberian Peninsula, have increased our understanding of the diversity of these dinosaurs, although much remains poorly understood. This study reports new ornithopod fossils from several sites in the provinces of Valencia and Teruel (Spain). Geologically, all the sites are located within the South Iberian Basin in the Villar del Arzobispo Formation (upper Kimmeridgian–Tithonian). These fossils represent almost half of the ornithopod discoveries in the region. Their systematic study reveals, for the first time, the presence of dryosaurids and small-sized ankylopollexians, while further confirming the presence of large-sized ankylopollexians. These findings significantly increase the known diversity of ornithopods in the Late Jurassic of eastern Iberia. Notably, small-sized ankylopollexians may have been among the potential trackmakers of the enigmatic small quadrupedal ornithopod tracks reported from this region. The coexistence of at least three distinct iguanodontian taxa suggests niche partitioning and a high level of ecological complexity within the herbivorous dinosaurian communities of the coastal ecosystems in eastern Iberia during the Late Jurassic, a pattern likely widespread across the Iberian landmass during this epoch.

Introduction

Ornithopods represent one of the most diverse and geographically widespread clades of herbivorous dinosaurs (e.g., Horner et al. 2004; Norman 2004; Norman et al. 2004; McDonald 2012; Poole 2022). Nevertheless, their osteological fossil record from the Upper Jurassic of Europe remains sparse and highly fragmentary (e.g., Buffetaut & Cacheleux 1997; Ruiz-Omeñaca et al. 2012; Escaso 2014; Vullo et al. 2014; Rotatori et al. 2020; Sánchez-Fenollosa et al. 2021a), in contrast to the relatively well-documented ornithopod faunas from the Morrison Formation (Gilmore 1909; Galton 1981; Carpenter & Wilson 2008; Carpenter & Galton 2018). Their fragmentary nature has hindered a comprehensive understanding of their diversity, evolutionary history, biology, and ecology.

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In recent years, considerable efforts have been made to address this gap, particularly in the Iberian Peninsula (Escaso 2014; Escaso et al. 2014; Rotatori et al. 2020, 2023, 2025; Sánchez-Fenollosa et al. 2022a, 2023a). Indeed, much of our current understanding of Upper Jurassic European ornithopods is derived from the Iberian fossil record. Three new species have been described from the Lusitanian Basin in Portugal: the dryomorphan *Hesperonyx martinhotomasorum* Rotatori, Ferrari, Sequero, Camilo, Mateus, and Moreno-Azanza, 2023 (Rotatori et al. 2023), the dryosaurid *Eousdryosaurus nanohallucis* Escaso, Ortega, Dantas, Malafaia, Silva, and Gasulla, 2014 (Escaso et al. 2014), and the early-diverging ankylopollexian *Draconyx loureiroi* Mateus and Antunes, 2001 (Mateus & Antunes 2001; Rotatori et al. 2022). Additionally, Rotatori et al. (2025) described other postcranial fossils (specimen SHN. JSS.015) referred to an indeterminate ankylopollexian, which potentially represents a new species. In eastern Spain, a new taxon of an early-diverging ankylopollexian, *Oblitosaurus bunnueli* Sánchez-Fenollosa, Verdú, and Cobos, 2023, has been described (Sánchez-Fenollosa et al. 2023a). Also noteworthy is the description of a postcranial skeleton tentatively classified as aff. *Camptosaurus* sp. Marsh, 1885 (Sánchez-Fenollosa et al. 2022a). Additional, albeit more fragmentary, ornithopod remains have been reported from various localities across the Iberian Peninsula (Pereda-Suberbiola et al. 2009; Malafaia et al. 2010; Ruiz-Omeñaca et al. 2012; Escaso 2014; Rotatori et al. 2020, 2025).

The osteological fossil record of ornithopods from the Upper Jurassic of the eastern Iberian Peninsula has traditionally been considered scarce and low in diversity. Previous studies in the Villar del Arzobispo Formation only documented large-sized ankylopollexians (Sánchez-Fenollosa et al. 2022a, 2023a). However, a notably morphological disparity has been reported among the ornithopod-attributed tracks (e.g., Santisteban et al. 2003; Castanera et al. 2013; Alcalá et al. 2014; Cobos et al. 2015). According to the current evidence, these ornithopods inhabited the Late Jurassic coastal ecosystems of eastern Iberia alongside other dinosaurs (e.g., Royo-Torres et al. 2006, 2009; Gascó et al. 2012; Sánchez-Fenollosa et al. 2025), crocodyliforms (Gamonal et al. 2018; Sánchez-Fenollosa et al. 2021b), testudinatans (Pérez-García et al. 2015), lissamphibians (Marquina-Blasco et al. 2018), and osteichthyans (e.g., Royo-Torres et al. 2006; Suñer & Martín 2009; Sánchez-Fenollosa & Cobos 2025). Plant communities were dominated by mosses, ferns, bennettitaleans, and conifers (Santos et al. 2018; López-Fernández et al. 2021).

In the present study, we describe several ornithopod specimens recovered from the provinces of Valencia and Teruel (Spain). The objectives of this work are to: (1) provide an osteological description of these fossils, (2) assess their taxonomic affinities, (3) review the ornithopod osteological record from the Villar del Arzobispo Formation, and (4) discuss the implications of the new findings for understanding ornithopod diversity and ecology in the Late Jurassic coastal ecosystems of eastern Iberia.

Institutional abbreviations: AR-1, fossils from the Mina Santa María (Ariño, Teruel, Spain) housed at MAP; MAP, Museo Aragonés de Paleontología, Teruel, Spain (fossils accessioned prior to 2011 were catalogued under CPT, Museo Fundación Conjunto Paleontológico de Teruel-Dinópolis); MPA, Museo Paleontológico de Alpuente, Alpuente, Spain; MTM, Magyar Természettudományi Múzeum, Budapest, Hungary; NHMUK, Natural History Museum, London, UK; SHN, Sociedade de Història Natural, Torres Vedras, Portugal; YPM, Yale Peabody Museum, New Heaven, USA.

Geographical and geological context

The fossils studied here came from four fossil sites in the eastern Iberian Peninsula (Fig. 1). The Cambrillas and By Pass sites are situated within the municipality of Alpuente (province of Valencia, Valencian Community, Spain). The RD-61 site lies within the municipality of Riodeva and the VS-1 site within the municipality of Veguillas de la Sierra (both in the province of Teruel, Aragon, Spain).

Geologically, all the sites are located within the South-Iberian Basin (Fig. 1). The South-Iberian Basin presents a NW-SE orientation and is part of the Mesozoic Iberian Extensional System (e.g., Campos-Soto et al. 2021). This basin was developed in eastern Iberia during the late Oxfordian–middle Albian and inverted during the Cenozoic Alpine Orogeny (Mas et al. 2004; Campos-Soto et al. 2021).

All the fossils examined in this study came from the Villar del Arzobispo Formation. This unit is formed by sandstone and clay beds with intercalations of limestone and marls (Mas et al. 1984). The Villar del Arzobispo Formation, dated to the Kimmeridgian–Tithonian stage or, locally, Kimmeridgian–early Berriasian? in the Las Zabacheras-Galve

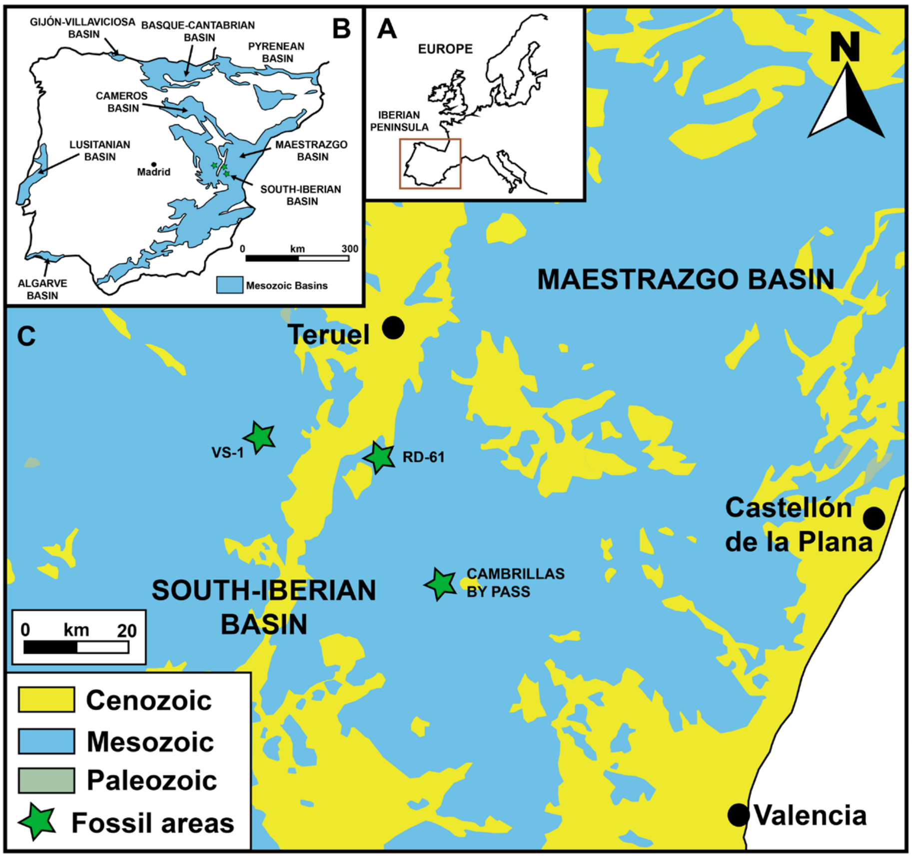


Fig. 1 - General geological cartography and location of the fossil areas (Alpuente [Cambrillas and By Pass], Riodeva [RD-61], and Veguillas de la Sierra [VS-1]) examined in this study (eastern Iberian Peninsula, Spain). Cartography modified from Campos-Soto et al. (2019).

area (sensu Campos-Soto et al. 2017, 2019), overlies the oncolitic limestone of the Higueruelas Formation (Kimmeridgian sensu Campos-Soto et al. 2016; Pacios et al. 2018).

The Villar Arzobispo Formation has been recognized in both the South-Iberian and Maestrazgo basins and it comprises two informal units (sensu Campos-Soto et al. 2019): (1) an essentially carbonate lower part (CLP, upper Kimmeridgian) interpreted as deposited in a shallow marine carbonate platform (2) and an essentially siliciclastic upper part (SUP, upper Kimmeridgian–Tithonian) interpreted as deposited in a coastal and alluvial plain. Other authors have interpreted through sequence stratigraphy that the Villar del Arzobispo Formation in the South-Iberian Basin was deposited in a wave-dominated delta (Santisteban & Santos-Cubedo 2008). Both interpretations are consistent with a coastal fluvial system discharging into a shallow marine platform.

Most of the vertebrate fossils (including those studied herein) were recovered from the SUP (Campos-Soto et al. 2017, 2019). This siliciclastic succession encompasses a diverse array of palaeoenvironments, including very shallow marine platforms, tidal flats, beaches, distributary channels, estuaries, wetlands, floodplains, and fluvial channels (ephemeral and perennial) (Santisteban & Santos-Cubedo 2008; Campos-Soto et al. 2017, 2019, 2021). According to Campos-Soto et al. (2021), deposition occurred under a seasonal palaeoclimate controlled by monsoonal-type precipitation.

Material and methods

The fossils studied comprise a pedal ungual phalanx (MPA-1015) from the Cambrillas site (Alpuente, Valencia); a left dentary tooth (MPA D-0277), an anterior caudal vertebra (MPA-1177), and a posterior caudal vertebra (MPA D-0204) from the By Pass site (Alpuente, Valencia); an anterior caudal vertebra (MAP-9099) from the RD-61 site (Riodeva, Teruel); and an anterior caudal vertebra (MAP-9101) from the VS-1 site (Veguillas de la Sierra, Teruel).

MPA-1015 was recovered ex situ as an isolated find at the Cambrillas site in 2018.

MPA D-0277, MPA-1177, and MPA D-0204

were recovered in situ from the By Pass site and are considered to most likely belong to the same specimen. This site was excavated in 2008 and yielded a diverse vertebrate assemblage, including theropods, sauropods, stegosaurs, crocodylomorphs, testudinatans, and osteichthyans (Suñer & Martín 2009). Notably, MPA-1177 was collected in 2024.

MAP-9099 was found in situ at the RD-61 site in 2024.

Finally, MAP-9101 was recovered ex situ from a crop field in 2024. In the same area, a caudal vertebra of *Turiasaurus riodevensis* Royo-Torres, Cobos, and Alcalá, 2006 (Royo-Torres et al. 2008) and numerous indeterminate bone fragments have also been collected.

Fossils from the municipality of Alpuente (MPA-1015, MPA D-0277, MPA-1177, and MPA D-0204) are housed in the Museo Paleontológico de Alpuente (Alpuente, province of Valencia, Spain). Fossils from Riodeva and Veguillas de la Sierra (MAP-9099 and MAP-9101) are housed in the Museo Aragonés de Paleontología (Teruel, province of Teruel, Spain).

All the elements were measured with a calliper (see Tab. 1).

The degree of neurocentral suture closure was assessed following the definitions provided by Brochu (1996).

A systematic study was conducted through comparative anatomy, considering both the morphometric data and qualitative anatomical features of each element. The fossil material was mainly compared with other Late Jurassic and Early Cretaceous ornithopods described in the literature.

We considered the Late Jurassic '*Nanosaurus*-like' ornithischians as early-diverging neornithischians, following most phylogenetic analyses (e.g., Boyd 2015; Han et al. 2018; Andrzejewski et al. 2019; Bell et al. 2019; Fonseca et al. 2024; Maidment & Barrett 2025), rather than as early-diverging ornithopods (e.g., Dieudonné et al. 2021; Bertozzo et al. 2025). Moreover, it is important to note that the taxonomy of those minute-sized neornithischians from the Morrison Formation is problematic (e.g., Carpenter & Galton 2018; Barrett & Maidment 2025) due to the fragmentary and poorly preserved nature of their type specimens, which also affects their phylogenetic affinities. This systematic uncertainty further supports excluding them from Ornithopoda in the present study.

Systematic palaeontology

DINOSAURIA Owen, 1842 (sensu Langer et al. 2020)
ORNITHISCHIA Seeley, 1888 (sensu Madzia et al. 2021)
ORNITHOPODA Marsh, 1881 (sensu Madzia et al. 2021)

Gen. et sp. indet.

Referred material: A pedal ungual phalanx (MPA-1015) (Fig. 2).

Locality and horizon: Cambrillas site (Alpuente, Valencia, Spain), eastern Iberian Range, South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic (upper Kimmeridgian-Tithonian) (Fig. 1).

Description. MPA-1015 is a pedal ungual phalanx, tentatively attributed to digit III (Fig. 2). It does not appear to have suffered taphonomical breakage or distortion. The ungual exhibits a symmetrical appearance in dorsal and plantar views. The specimen is elongated proximodistally, slightly expanding mediolaterally. It is slightly arched dorsoplantarly culminating in a pointed tip (Fig. 2). The proximal articular facet is concave and sub-circular in outline (Fig. 2B). Distinct neurovascular grooves extend longitudinally along both the lateral and medial surfaces (Fig. 2C, D). Medial and lateral flaps are not well-developed in this ungual.

ORNITHOPODA Marsh, 1881 (sensu Madzia et al. 2021)
IGUANODONTIA Baur, 1891 (sensu Madzia et al. 2021)
DRYOMORPHA Sereno, 1986 (sensu Madzia et al. 2021)
DRYOSAURIDAE Milner and Norman, 1984 (sensu Madzia et al. 2021)

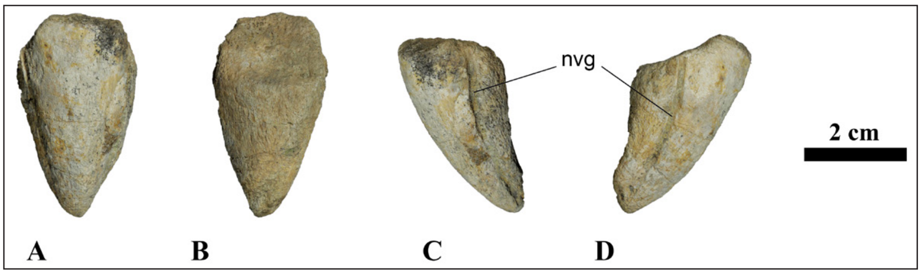
Gen. et sp. indet.

Referred material: An anterior caudal vertebra (MAP-9099) (Fig. 3).

Locality and horizon: RD-61 site (Riodeva, Teruel, Spain), eastern Iberian Range, South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic (upper Kimmeridgian-Tithonian) (Fig. 1).

Description. MAP-9099 is an almost complete and taphonomically undistorted anterior caudal vertebra (Fig. 3). It likely corresponds to a posi-

Fig. 2 - Ornithopod pedal ungual phalanx (MPA-1015) from the Cambrillas fossil site (Alpuente, Valencia, Spain). MPA-1015 in dorsal (A), plantar (B), ?lateral (C), and ?medial (D) views. Abbreviations: nvg, neurovascular groove.



tion ranging from the 4th to the 8th. The centrum is longer anteroposteriorly than tall dorsoventrally and wide mediolaterally (Tab. 1), and slightly amphicoelous (Fig. 3A, C). The articular facets are equidimensional (Tab. 1) and sub-hexagonal in shape (Fig. 3A, C). The lateral surfaces are gently concave anteroposteriorly and several nutrient foramina are present (Fig. 3B). Ventrally, it exhibits a longitudinal groove and chevron facets (Fig. 3E). The neural arch is fused to the centrum, and the neurocentral suture is fully closed (Fig. 3B, F). The neural canal is subcircular in shape (Fig. 3A, C). Transverse processes arise at the base of the neural arch (Fig. 3A-D). The right transverse process is almost completely preserved, dorsoventrally compressed, and posteriorly oriented (Fig. 3A-E). Prezygapophyses are broken but postzygapophyses are well preserved. They face lateroventrally and slightly overhang the posterior articular facet of the centrum (Fig. 3B, C). The articular facets are flat and elliptical in outline (Fig. 3B). The neural spine is broken at the base (Fig. 3A-D).

DRYOMORPHA Sereno, 1986 (sensu Madzia et al. 2021)
ANKYLOPOLLEXIA Sereno, 1986 (sensu Sánchez-Fenollosa et al. 2023a)

Gen. et sp. indet.

Referred material: A left dentary tooth (MPA D-0277), an anterior caudal vertebra (MPA-1177), and a posterior caudal vertebra (MPA D-0204) from the By Pass fossil site (Fig. 4).

An anterior caudal vertebra (MAP-9101) from the VS-1 fossil site (Fig. 5).

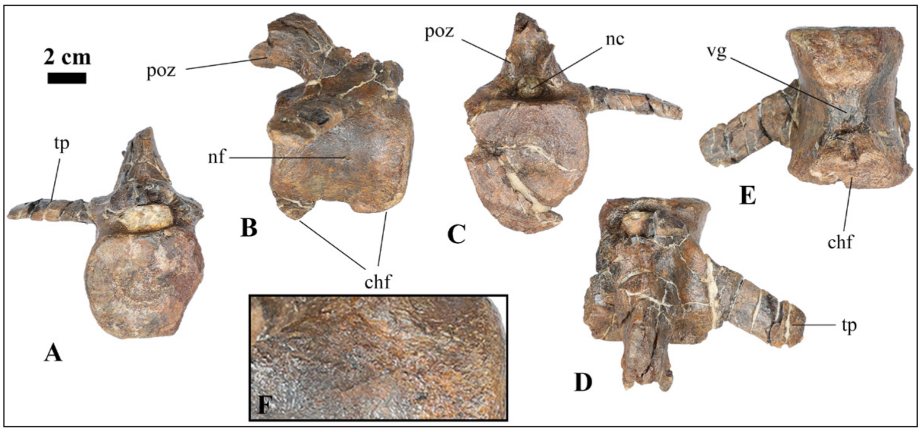
Locality and horizon: By Pass site (Alpuente, Valencia, Spain), eastern Iberian Range, South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic (upper Kimmeridgian-Tithonian) (Fig. 1).

VS-1 site (Veguillas de la Sierra, Teruel, Spain), eastern Iberian Range, South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic (upper Kimmeridgian-Tithonian) (Fig. 1).

Description

By Pass specimen (Fig. 4). MPA D-0277 is a left dentary tooth (Fig. 4A-D). It is well-preserved and taphonomically undistorted. The tooth is strongly arched towards the labial side (Fig. 4C). The crown is shield-shaped and the enamel is restricted to the lingual surface (Fig. 4A-D). Lingually, a prominent primary ridge extends basiapically and it is located towards the centre of the crown, slightly distal at most. Two basiapical and less prominent secondary ridges are located each of one near to the distal and the mesial carinae (Fig. 4A, D). The non-enamelled labial surface of the crown lacks ridges (Fig. 4B). Both carinae exhibit several tongue-shaped denticles that extend from the apex to the upper half of

Fig. 3 - Dryosaurid anterior caudal vertebra (MAP-9099) from the RD-61 fossil site (Riodeva, Teruel, Spain). MAP-9099 in anterior (A), right lateral (B), posterior (C), dorsal (D), and ventral (E) views. Detailed image of the neurocentral suture from the right lateral (F). Abbreviations: chf, chevron facet; nc, neural canal; nf, nutrient foramen; poz, postzygapophysis; tp, transverse process; vg, ventral groove.



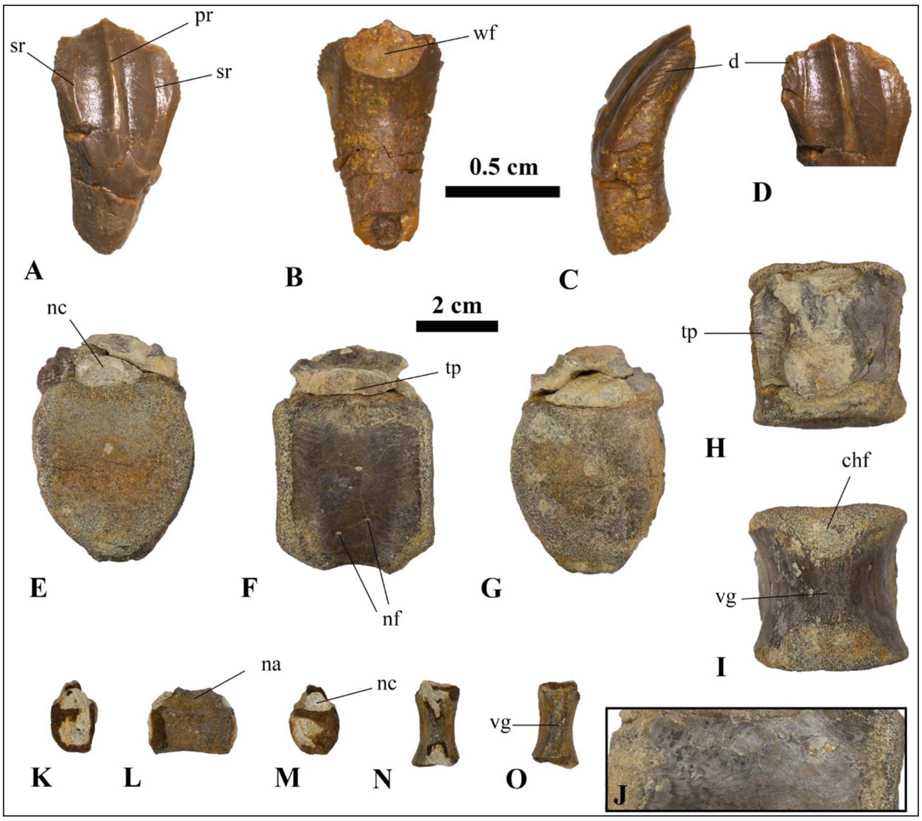


Fig. 4 - Ankylopollexian fossils from the By Pass fossil site (Alpuente, Valencia, Spain). Left dentary tooth (MPA D-0277) in lingual (A, D), labial (B), and mesial (C) views. Anterior caudal vertebra (MPA-1177) in anterior (E), left lateral (F), posterior (G), dorsal (H), and ventral (I) views. Detailed image of the neurocentral suture from the right lateral (J). Posterior caudal vertebra (MPA D-0204) in anterior (J), left lateral (K), posterior (L), dorsal (M), and ventral (N) views. Abbreviations: chf, chevron facet; d, denticles; na, neural arch; nc, neural canal; nf, nutrient foramen; pr, primary ridge; sr, secondary ridge; tp, transverse process; vg, ventral groove; wf, wear facet.

the crown (Fig. 4A, C, D). A well-developed oblique wear facet is located apically, primarily on the labial surface (Fig. 4B). There is no cingulum separating the crown and root on the lingual surface (Fig. 4A-D). There are both mesial and distal depressions to accommodate growing contiguous teeth (Fig. 4A, C). The root is incomplete, with a circular cross-section (Fig. 4A-D).

MPA-1177 (Fig. 4E-J) and MPA D-0204 (Fig. 4K-O) consist of small anterior and posterior caudal vertebrae, respectively. MPA-1177 likely corresponds to a position ranging from the 5th to the 10th, whereas MPA D-0204 is interpreted as corresponding to approximately the 25th. They are taphonomically undistorted but their neural arches are incomplete (Fig. 4E-O). MPA-1177 has an equidimensional centrum (Tab. 1), whereas the centrum of MPA D-0204 is notably longer anteroposteriorly than tall dorsoventrally and wide lateromedially (Tab. 1). The articular facets of both vertebrae are roughly equidimensional, and sub-hexagonal to sub-circular in shape (Fig. 4E, G, K, M). The lateral surfaces of both vertebrae are gently concave anteroposteriorly, with MPA-1177 exhibiting several nutrient foramina (Fig. 4F). From this view, they appear to exhibit no noticeable slope between both articular facets (Fig. 4F, L). Ventrally, both vertebrae show a longitudinal groove (Fig. 4I, O), though only MPA-1177 has facets for the articulation of the chevrons (Fig. 4I). The neural arches of both vertebrae are fused to the centra, and their neurocentral sutures are fully closed (Fig. 4F, J, L). The neural canals are sub-circular in shape (Fig. 4E, G, K, M). Transverse processes are present at the base of the neural arch in MPA-1177 (Fig. 4F).

VS-1 specimen (Fig. 5). MAP-9101 is a large anterior caudal vertebra (Fig. 5) and likely corresponds to a position ranging from the 1th to the 3th. It shows no taphonomic distortion and only the ventral-most part of the neural arch is preserved (Fig. 5A-D). The centrum is anteroposteriorly compressed (Tab. 1) and slightly amphicoelous (Fig. 5A, C). The articular facets are taller dorsoventrally than wide lateromedially (Tab. 1), and sub-circular in shape (Fig. 5A, C). Laterally, the surfaces are gently concave anteroposteriorly and have several nutrient foramina (Fig. 5B). From this view, the vertebra appears to be a bit sloped (Fig. 5B), suggesting that the tail was slightly downward from the sacrum. There is a wide longitudinal groove in the ventral surface, and it also has large chevron facets (Fig. 5E). The neural arch is fused to the centrum with the sinuous neurocentral suture partially closed (Fig. 5B, F). The neural canal is sub-circular in shape (Fig. 5A, C). The bases of the transverse

CAMBRILLAS (ALPUENTE, VALENCIA) – ORNITHOPODA INDET.					
	L	Wp(ml)	Wp(dp)		
Pedal ungual phalanx (MPA-1015)	40.6	21.4	19.5		
RD-61 (RIODEVA, TERUEL) – DRYOSAURIDAE INDET.					
	CL	AAFH	AAFW	PAFH	PAFW
Anterior caudal vertebra (MAP-9099)	73.4	57.5	59.6	61.1	61.2
BY PASS (ALPUENTE, VALENCIA) – ANKYLOPOLLEXIA INDET.					
	H(ba)	W(md)			
Left dentary tooth (MPA D-0277)	10.3	5.7			
	CL	AAFH	AAFW	PAFH	PAFW
Anterior caudal vertebra (MPA-1177)	38.3	37.3	39.8	33.8	38.1
Posterior caudal vertebra (MPA D-0204)	21.4	10.5	10.5	10.7	11.5
VS-1 (VEGUILLAS DE LA SIERRA, TERUEL) – ANKYLOPOLLEXIA INDET.					
Anterior caudal vertebra (MAP-9101)	71.3	77.4	71.5	77.1	72.6

Tab. 1 - Measurements (in mm) of the ornithopod fossils described in this study. Abbreviations: AAFH, anterior articular facet height; AAFW, anterior articular facet width; CL, centrum length; H(ba), height measured basioapically; L, length; PAFH, posterior articular facet height; PAFW, posterior articular facet width; W(md), width measured mesiodistally; Wp(dp), proximal width measured dorsoplantarly; Wp(ml),

processes are preserved on both sides of the neural arch (Fig. 5A-D).

Discussion

Comparisons

Cambrillas specimen (Fig. 2). The pedal ungual phalanx MPA-1015 (likely from digit III) differs considerably from the strongly curved, elongated, and lateromedially compressed pedal ungual phalanges found in theropods (Madsen 1976; Chiappe & Göhlich 2010; Rauhut et al. 2012; Evers & Wings 2020). However, it closely resembles the less lateromedially compressed and pointed pedal ungual phalanges of several Late Jurassic ornithopods, particularly early-diverging ankylopollexians (Carpenter & Galton 2018; Rotatori et al. 2022). Notably, contemporaneous early-diverging neornithischians and dryosaurids appear to have more elongated, slender, and pointed pedal unguals (Galton 1981; Escaso et al. 2014; Carpenter & Galton 2018; Maidment & Barrett 2025). MPA-1015 also differs from the more dorsoplantarly compressed ungual of the Late Jurassic dryomorphan *H. martinhotomasorum* (Rotatori et al. 2023). Additionally, it differs from the flattened and blunt-ended unguals of Early Cretaceous styracosternans (Norman 1980; McDonald et al. 2010; Xu et al. 2018; Bonsor et al. 2023; Lockwood et al. 2024), but resembles that of the Late Cretaceous early-diverging ornithopod *Thescelosaurus neglectus* Gilmore, 1913 (Gilmore 1913).

Accordingly, MPA-1015 is conservatively referred to as Ornithopoda indet., although its morphology and comparisons with other Late Jurassic ornithopods suggests a possible affinity with Ankylopollexia.

RD-61 specimen (Fig. 3). The anterior caudal vertebra MAP-9099 (likely corresponding to the 4th–8th) exhibits hexagonal articular facets, a feature typical of Iguanodontia (Norman 2004), in contrast to the more rounded articular facets of early-diverging neornithischians and early-diverging ornithopods, such as the contemporaneous '*Nanosaurus agilis*' Marsh, 1877 (YPM VP 1882, Carpenter & Galton 2018), *Enigmacursor mollyborthwickae* Maidment and Barrett, 2025 (Maidment & Barrett 2025), and *Yandusaurus hongheensis* He, 1979 (He & Cai 1984) and the Early Cretaceous *Hypsilophodon foxii* Huxley, 1869 (Galton 1974) and *Gideonmantellia amosanjuanae* Ruiz-Omeñaca, Canudo, Cuenca-Bescós, Cruzado-Caballero, Gasca, and Moreno-Azanza, 2012 (Ruiz-Omeñaca et al. 2012).

It has an elongated centrum (Tab. 1) similar to those in contemporaneous dryosaurids such as *Dryosaurus altus* Marsh, 1878 (Shepherd et al. 1977; Galton 1981), *Dysalotosaurus lettowvorbecki* Virchow, 1919 (Janensch 1955), and *E. nanohallucis* (Escaso et al. 2014), as well as the Early Cretaceous dryosaurid *Valdosaurus canaliculatus* Galton, 1975 (Barrett 2016). This contrasts with the anteroposteriorly compressed (length/height and length/width ≤ 1.0) anterior caudal centra of contemporaneous early-diverging ankylopollexians such as *C. dispar* Marsh, 1879 (Gilmore 1909), *C.* (= *Uteodon* McDonald, 2011) *aphanoecetes* Carpenter and Wilson, 2008 (Carpenter & Wilson 2008), *C.* (= *Cumnoria* Seeley, 1888) *prestwichii* Hulke, 1880 (Galton & Powell 1980; Maidment et al. 2022), and *D. loureiroi* (Rotatori et al. 2022).

Consequently, although MAP-9099 is an isolated remain and its referral is mainly based on a plesiomorphic character, it exhibits a unique combination of features that makes it more similar to dryosaurids than to any other contemporaneous ornithopod, and it is therefore tentatively referred to as Dryosauridae indet.

By Pass specimen (Fig. 4). The dentary tooth MPA D-0277 (Fig. 4A-D; 6B) shares several cha-

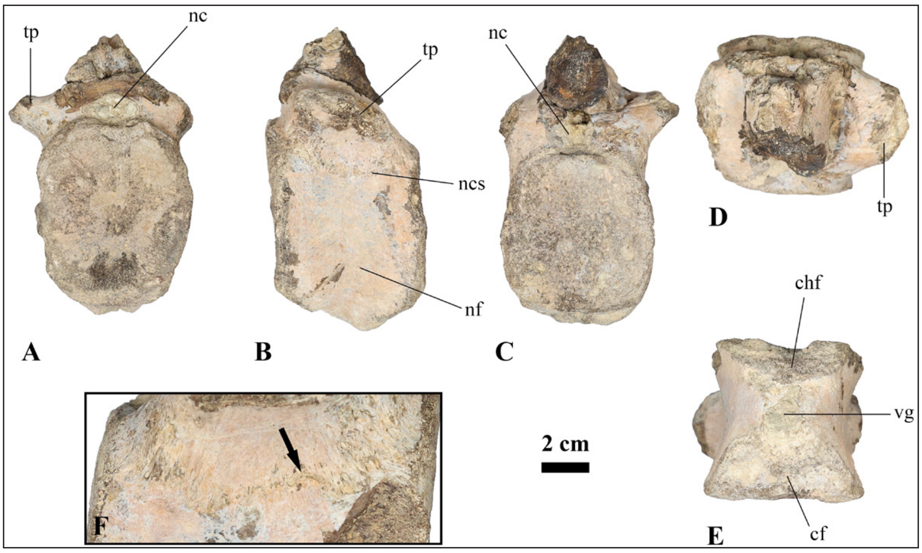


Fig. 5 - Ankylopollexian anterior caudal vertebra (MAP-9101) from the VS-1 fossil site (Veguillas de la Sierra, Teruel, Spain). MAP-9101 in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. Detailed image of the neurocentral suture from the right lateral (F). Abbreviations: chf, chevron facet; nc, neural canal; ncs, neurocentral suture (also indicated by an arrow); nf, nutrient foramen; tp, transverse process; vg, ventral groove.

racters with contemporaneous dryomorphan ornithopods (Gilmore 1909; Galton 1983, 2007, 2009; Maidment et al. 2022; Forster et al. 2023; Sánchez-Fenollosa et al. 2023a): (1) a shield-shaped crown, (2) no cingulum, (3) reduced ornamentation ridges in both number and length, and (4) a strong oblique wear facet in the apical region. These features contrast with the dentary teeth of early-diverging neornithischians, early-diverging ornithopods, and other iguanodontians, such as the contemporaneous '*Phyllodon henkeli*' Thulborn, 1973 (Thulborn 1973; Rauhut 2001), '*N. agilis*' (Galton 2007; Carpenter & Galton 2018), and *Minimocursor phunoiensis* Manitkoon, Deesri, Khalloufi, Nonsrirach, Suteethorn, Chanthasit, Boonla, and Buffetaut, 2023 (Manitkoon et al. 2023), the Early Cretaceous *Hy. foxii* (Fig. 6A; Galton 1974, 2009), *Jeholosaurus shangyuanensis* Xu, Wang, and You, 2000 (Bertozzo et al. 2025), *Convolosaurus marri* Andrzejewski, Winkler, and Jacobs, 2019 (Andrzejewski et al. 2019), and *Tenontosaurus tilletti* Ostrom, 1970 (Thomas 2015), and the Late Cretaceous *Talenkauen santacrucensis* Novas, Cambiaso, and Ambrossio, 2004 (Rozadilla et al. 2019) and *Mochlodon vorosi* Ösi, Prondvai, Butler, and Weishampel, 2012 (Fig. 6B).

The enamelled lingual surface of MPA D-0277 exhibits a subcentral (or slightly distal) primary ridge with a mesial and distal secondary ridge (Fig. 4A, D; 6B), similar to that in the contemporaneous early-diverging ankylopollexian *C. aphanoecetes* (Carpenter & Wilson 2008; Carpenter & Galton 2018). This condition contrasts with the subcentral primary ridge associated with multiple secondary and accessory ridges of dryosaurids, such as *Dr. altus* (Galton 1983, 2007; Carpenter & Galton 2018), *Dr. elderae* Carpenter and Galton, 2018 (Carpenter & Galton 2018), *Dy. lettowvorbecki* (Galton 1983, Carpenter & Galton 2018), and *Iyuku raathi* Forster, de Klerk, Poole, Chinsamy-Turan, Roberts, and Ross, 2023 (Forster et al. 2023). Additionally, it also differs from the distally offset primary ridge associated with a parallel and mesial secondary ridge(s), observed in the Late Jurassic early-diverging ankylopollexians *C. dispar* (Gilmore 1909; Galton 2007; Carpenter & Galton 2018), *C. prestwichii* (Galton & Powell 1980; Maidment et al. 2022), and *O. bunnueli* (Fig. 6D), as well as with Early Cretaceous styracosternans (Fig. 6E, F; Norman 1980, 1986; McDonald et al. 2010; Boyd & Pagnac 2015; Gasulla et al. 2015; Lockwood et al. 2021, 2024; Bonsor et al. 2023).

The anterior caudal vertebra MPA-1177 (likely corresponding to the 5th–10th) exhibits an anteroposteriorly compressed centrum (Tab. 1; Fig. 4E-I) similar to those of contemporaneous early-diverging ankylopollexians (Gilmore 1909; Carpenter & Wilson 2008; Carpenter & Galton 2018; Maidment et al. 2022; Rotatori et al. 2022). This condition contrast with the elongated (length/height and length/width > 1.0) anterior caudal centra of dryosaurids (Fig. 3; Janensch 1955; Shepherd et al. 1977; Galton 1981; Escaso et al. 2014).

Considering the limited number of elements and based on apomorphic characters of the dentary tooth and the anterior caudal vertebra, the By Pass specimen is tentatively referred to as Ankylopollexia indet. These fossils (also the posterior caudal vertebra MPA D-0204) are considered to likely belong to a single specimen because they were recovered from

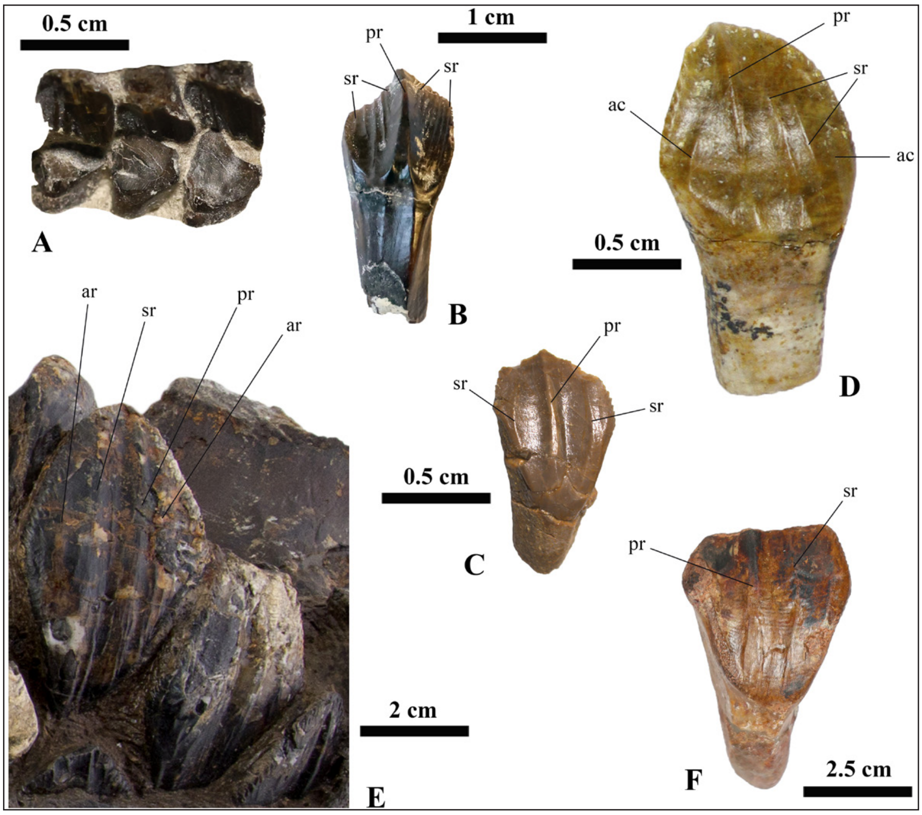


Fig. 6 - Teeth comparison of ornithopods from the Late Jurassic to Early Cretaceous. A, left maxillary and dentary teeth of *Hypsilophodon foxii* Huxley, 1869 (NHMUK PV R197, holotype) in labial view. B, left dentary tooth of *Mochlodon vorosi* Ősi, Prondvai, Butler, and Weishampel, 2012 (MTM V 2012.18.1) in lingual view. C, left dentary tooth of Ankylopollexia indet. (MPA D-0277, By Pass specimen) in lingual view. D, left dentary tooth of *Oblitosaurus bunnueli* Sánchez-Fenollosa, Verdú, and Cobos, 2023 (CPT-1440, holotype) in lingual view. E, right dentary teeth of *Proa valdearinnoensis* McDonald, Espílez, Mampel, Kirkland, and Alcalá, 2012 (AR-1-2013/19, holotype) in lingual view. F, left dentary tooth of *Iguanodon galvensis* Verdú, Royo-Torres, Cobos, and Alcalá, 2015 (MAP-8141, SC-8 specimen) in lingual view. Abbreviations: ar, accessory ridge; pr, primary ridge; sr, secondary ridge.

the same layer at the site and exhibit consistent size and morphological features.

VS-1 specimen (Fig. 5). The anterior caudal vertebra MAP-9101 (likely corresponding to the 1th–3th) also exhibits an anteroposteriorly compressed centrum (length/height and length/width ≤ 1.0) indicating a clear affinity with contemporaneous ankylopollexians (Gilmore 1909; Carpenter & Wilson 2008; Carpenter & Galton 2018; Maidment et al. 2022; Rotatori et al. 2022). This contrasts with the elongated anterior caudal centra observed in dryosaurids (Fig. 3; Janensch 1955; Shepherd et al. 1977; Galton 1981; Escaso et al. 2014), as well as in contemporaneous early-diverging neornithischians (Carpenter & Galton 2018; Manitkoon et al. 2023; Maidment & Barrett 2025; Yang et al. 2025).

Given this feature and the isolated nature of the specimen, MAP-9101 is tentatively referred to as Ankylopollexia indet.

The osteological ornithopod record from the Villar del Arzobispo Formation: an update

The Villar del Arzobispo Formation is a transitional lithostratigraphic unit located in the eastern Iberian Peninsula, known for its diverse dinosaurian fossil record. However, ornithopod fossils are underrepresented and typically fragmentary when compared to other dinosaurian groups such as sauropods and stegosaurs (e.g., Sanz et al. 1987; Casanovas-Cladellas et al. 1999; Royo-Torres et al. 2006, 2009, 2021; Cobos et al. 2010; Pérez-Pueyo et al. 2019; Sánchez-Fenollosa et al. 2022b, 2025; Sánchez-Fenollosa & Cobos 2025; Suñer et al. 2022).

The earliest reports of ornithopods from the Villar del Arzobispo Formation date back to the early 2000s (Royo-Torres et al. 2006; Pereda-Suberbiola et al. 2009; Suñer & Martín 2009). The first formal description of ornithopod fossils occurred in 2009, and these consisted of a cervical centrum and two caudal centra from the historical site of Cerrito del Olmo (Tab. 2). However, this material was too fragmentary to know their taxonomic affinity with certainty, and it was referred to as Ornithopoda indet. (Pereda-Suberbiola et al. 2009).

Although several conference communications on ornithopods from this lithostratigraphic unit were presented (Gascó et al. 2013; Sánchez-Fenollosa et al. 2019, 2021c), it was not until more than a decade later that a second specimen was formally described (Sánchez-Fenollosa et al. 2022a). The Fuentecillas specimen, an early-diverging ankylopollexian, was tentatively assigned to aff. *Camptosaurus* sp. based on the presence of amphicoelous caudal

SITE	PREVIOUS SYSTEMATICS	CURRENT SYSTEMATICS	MATERIAL	MUNICIPALITY	REFERENCES
By Pass	-	Ankylopollexia indet.	A dentary tooth and two caudal vertebrae	Alpuente (Valencia)	This paper
Cambrillas	-	Ornithopoda indet.	A pedal ungual phalanx	Alpuente (Valencia)	This paper
Cerrito del Olmo	Ornithopoda indet.	Ornithopoda indet.	A cervical centrum and two caudal centra	Alpuente (Valencia)	Pereda-Suberbiola et al. (2009)
Fuentecillas	aff. *Camptosaurus* sp.	Ankylopollexia indet.	A cervical centrum, a dorsal centrum, a dorsosacral centrum, four sacral centra, a caudosacral centrum, five caudal centra, and a partial left humerus	Alpuente (Valencia)	Sánchez-Fenollosa et al. (2022a); this paper
La Presa	Ornithopoda indet.	Ornithopoda indet.	Undescribed	Alpuente (Valencia)	Sánchez-Fenollosa and Suñer (2025)
RD-10 (Barrihonda-El Humero)	*Oblitosaurus bunnueli*	*Oblitosaurus bunnueli*	A dentary tooth, a right ungual pollex of the manus, and an almost complete left hindlimb	Riodeva (Teruel)	Sánchez-Fenollosa et al. (2023a)
RD-34 (Están de Colón)	Ornithopoda indet.	Ornithopoda indet.	Undescribed	Riodeva (Teruel)	Sánchez-Fenollosa and Cobos (2025)
RD-61	-	Dryosauridae indet.	A caudal vertebra	Riodeva (Teruel)	This paper
VS-1	-	Ankylopollexia indet.	A caudal vertebra	Veguillas de la Sierra (Teruel)	This paper

Tab. 2 - Osteological ornithopod record from the Villar del Arzobispo Formation, Upper Jurassic (upper Kimmeridgian–Tithonian), eastern Iberian Peninsula (Spain).

vertebrae (Sánchez-Fenollosa et al. 2022a). However, *D. loureiroi* also exhibits this type of articular facets, as suggested by personal observations and a recent redescription (Rotatori et al. 2022; pers. obs.). Therefore, the assignment to aff. *Camptosaurus* sp. based in this argument is no longer supported. As a result, the Fuentecillas specimen is reclassified here to as Ankylopollexia indet.

In 2023, a new ornithopod genus and species, *O. bunnueli*, was described for the first time from the Villar del Arzobispo Formation (Sánchez-Fenollosa et al. 2023a). This discovery marked a significant addition to the dinosaurian record of the region and to the evolutionary history of ankylopollexians. *O. bunnueli* is the largest ornithopod identified in the European Upper Jurassic and is closely related to the Portuguese *D. loureiroi* (Sánchez-Fenollosa et al. 2023a). Furthermore, it contributed to identifying a potential trackmaker for large ornithopod tracks (25-35 cm in length) found in contemporaneous sediments of the Iberian Peninsula (Sánchez-Fenollosa et al. 2023a, 2023b).

Recently, an ornithopod-dominated assemblage has been reported from this lithostratigraphic unit (Sánchez-Fenollosa & Suñer 2025). The preliminary study has suggested that the ornithopod fossils likely belong to a single specimen (Sánchez-Fenollosa & Suñer 2025), which is currently undescribed and awaiting full preparation. In addition, some ornithopod remains have also been reported at the Están de Colón (RD-34) site (Sánchez-Fenollosa & Cobos 2025).

Therefore, although these are isolated remains, the findings described in this work represent almost half of the known ornithopod discoveries from this region (Tab. 2), and their study has significant implications for the palaeobiodiversity and palaeoecology of the Villar del Arzobispo Formation (see below).

Implications for the diversity and ecology of Late Jurassic ornithopods from eastern Iberia

Prior to this study, the recorded diversity of ornithopods in eastern Iberia was very low (Tab. 2). Previous research had only identified large-sized ankylopollexians, such as the Fuentecillas specimen (Sánchez-Fenollosa et al. 2022a) and *O. bunnueli* (Sánchez-Fenollosa et al. 2023a).

The discovery of MAP-9099 (Fig. 3) represents the first evidence of dryosaurids in eastern Iberia. This group of iguanodontian ornithopods had previously been reported in a few regions of Europe in Upper Jurassic lithostratigraphic units. They are relatively well-represented in western Iberia, where *E. nanohallucis* was identified (Escaso et al. 2014), along with fragmentary cranial and postcranial material (Malafaia et al. 2010; Escaso 2014; Rotatori et al. 2020). In northwestern France, an isolated femur was referred to as *Dryosaurus* sp. Marsh, 1894 by Buffetaut and Cacheleux (1997). Dryosaurids are highly abundant in contemporaneous geological formations from other regions, such as North America and central Africa. In North America, they are well-represented in the Morrison Formation (Kimmeridgian-Tithonian sensu Trujillo & Kowallis 2015), with numerous specimens of *Dryosaurus* spp. (Shepherd et al. 1977; Galton 1981, 1983; Carpenter & Galton 2018). Similarly, in central Africa, dryosaurids are relatively common in the Middle Dinosaur Member of the Tendaguru Formation (upper Kimmeridgian sensu Bussert et al. 2009), where numerous specimens of *Dy. lettowvorbecki* representing different ontogenetic stages were recovered (Janensch 1955; Galton 1981; Hübner 2018; Hübner & Rauhut 2010; Hübner et al. 2021). This ornithopod group is also present in at least the Middle Jurassic of Europe (Ruiz-Omeñaca et al. 2007) and the Lower Cretaceous of Europe and Africa (Galton & Taquet 1982; Ruiz-Omeñaca et al. 2007; Galton 2009; Barrett et al. 2011; Barrett 2016; Forster et al. 2023).

MAP-9099 (Tab. 1; Fig. 3) is large (CL equal to 73.4 mm) compared to other dryosaurid species (e.g., CL ranges from 20 to 60 mm) (Janensch 1955; Galton 1981; Escaso et al. 2014; Barrett 2016). Taking as a reference the CL of anterior caudal vertebrae of some dryosaurids and their body lengths (adults ranges from 4–4.5 m) (Galton 1981; Barrett 2016), it is estimated that this specimen likely reached a length of around 5–5.5 m. This considerable size is consistent with the broader pattern of gigantism observed among several dinosaurian clades in eastern Iberia during the Late Jurassic, including giant turiasaurian sauropods (Royo-Torres et al. 2006, 2021), massive dacentrurine stegosaurs (Cobos et al. 2010; Sánchez-Fenollosa et al. 2022b, 2025), large ankylopollexian ornithopods (Sánchez-Fenollosa et al. 2023a), enormous tetanuran theropods (Gascó et al. 2012; Cobos et al. 2014), among others.

Fossils from the By Pass site (Fig. 4) belong to a small-sized ankylopollexian, representing the first record of this type of ornithopod in the region. Until now, ankylopollexians from eastern Iberia were only known from large-sized forms (Sánchez-Fenollosa et al. 2022a, 2023a). The presence of small-sized ankylopollexians accords with previous findings in Portugal, where taxa such as the early-diverging ankylopollexian *D. loureiroi* (4–5 m in length sensu Rotatori et al. 2022) and the dryomorphan of uncertain affinities *H. martinhotomasorum* (3–4 m in length sensu Rotatori et al. 2023) were reported. In England, the early-diverging ankylopollexian *C. prestwichii* is represented by a single and almost complete specimen (Galton & Powell 1980; Maidment et al. 2022). This reached 3.5 m in length (Galton & Powell 1980), although it is clearly an osteologically immature specimen.

MAP-9101 (Fig. 5) is an anterior caudal vertebra belonging to a large-sized ornithopod. In fact, it is one of the largest ornithopod caudal vertebrae reported from the Upper Jurassic worldwide, at least within the current scope of our knowledge. This finding aligns with the recently described *O. bunnueli* (Sánchez-Fenollosa et al. 2023a), which has been estimated to have reached 6-7 m in length, further supporting the presence of large-sized ankylopollexians in the coastal ecosystems of eastern Iberia during the Late Jurassic.

The dryosaurid vertebra MAP-9099 (Tab. 1; Fig. 3) and the ankylopollexian vertebra MPA-1177 (Tab. 1; Fig. 4E-J) are notably smaller than the ankylopollexian vertebra MAP-9101 (Tab. 1; Fig. 5). However, whereas the neurocentral sutures in MAP-9099 (Fig. 3B, F) and MPA-1177 (Fig. 4F, J) are fully closed, the neurocentral suture in MAP-9101 (Fig. 5B, F) remains partially closed. Although assessing ontogenetic maturity using only the closure degree of neurocentral sutures may be problematic (Griffin et al. 2021), this suggests that despite its significantly larger size, MAP-9101 was likely less skeletally mature compared to both MAP-9099 and MPA-1177. Hence, the size disparity between small- and large-sized ankylopollexians would have been even greater once both achieved skeletal maturity. This observation also supports the hypothesis that both small- and large-sized ankylopollexians coexisted in eastern Iberia during the Late Jurassic.

This great diversity of ornithopods agrees with the disparity of ornithopod tracks previously discovered in the region: minute- to small-sized *Anomoepus*-like Hitchcock, 1848 tracks, small- to medium-sized *Dinehichnus*-like Lockley, dos Santos, Meyer, and Hunt, 1998 tracks, and medium- to large-sized *Iguanodontipus*-like Sarjeant, Delair, and Lockley, 1998 tracks (Santisteban et al. 2003; Castanera et al. 2013, 2020; Alcalá et al. 2014; Cobos et al. 2015; Guarido et al. 2024; pers. obs.). The discovery of small-sized ankylopollexians in eastern Iberia suggests that, in addition to juveniles of large-sized ankylopollexians, they may have been the trackmakers of the small quadrupedal ornithopod tracks

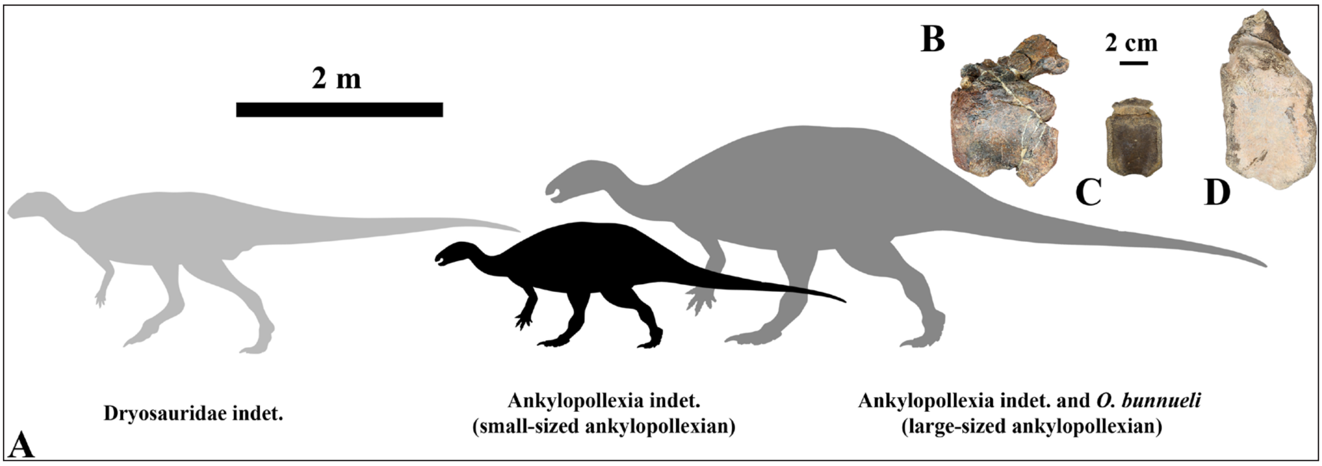


Fig. 7 - Ornithopod fauna in the coastal ecosystems of eastern Iberia during the Late Jurassic (A). Comparison of the anterior caudal vertebrae (MAP-9099, MPA-1177, and MAP-9101 in left lateral view) examined in this study (B-D). Silhouettes were obtained from PhyloPic.

(Castanera et al. 2013; Alcalá et al. 2014) found in this region. This correlation between the osteological and ichnological evidence further supports the presence of a diverse ornithopod fauna in eastern Iberia during the Late Jurassic (Fig. 7), reflecting a wide range of body sizes, ecological roles, and locomotor adaptations.

The coexistence of at least three different iguanodontian taxa (Fig. 7) – medium-sized dryosaurids (MAP-9099), small-sized ankylopollexians (By Pass specimen), and large-sized ankylopollexians (MAP-9101, Fuentecillas specimen, and *O. bunnueli*) – likely reflects resource, spatial and temporal niche partitioning in the coastal ecosystems of eastern Iberia during the Late Jurassic. These different ecological strategies would have allowed these ornithopods, in addition to other herbivorous dinosaurs such as stegosaurs and sauropods, to reduce interspecific competition. This palaeobiodiversity underscores the complexity of the Late Jurassic herbivorous dinosaurian communities in eastern Iberia.

Interestingly, the coexistence of at least three iguanodontians has also been reported in the Late Jurassic of western Iberia and they are phylogenetically closely related to those from eastern Iberia (Escaso et al. 2014; Rotatori et al. 2020, 2023, 2025). This suggests that such ecological complexity may have been widespread across the Iberian landmass during this epoch, likely favoured by the presence of similar climatic conditions and fluvial and coastal palaeoenvironments (Myers et al. 2012; Mateus et al. 2017; Campos-Soto et al. 2021). This iguanodontian diversity and potential niche partitioning could also be expected in palaeogeographically proximate regions of Europe with similar settings, or even in some areas of the more arid and continental (Turner & Peterson 2004; Myers et al. 2014) Morrison Formation of North America. Indeed, the combined faunal, geological, and geotectonical evidence supports a land connection between North America and Iberia during the late Kimmeridgian–early Tithonian (e.g., Pérez-Moreno et al. 1999; Escaso et al. 2007; Brikiatis 2016).

Tooth wear rates and microwear analyses suggest that Late Jurassic iguanodontians such as the dryosaurids *Dr. altus* and *Dy. lettowvorbecki* and the early-diverging ankylopollexian *C. dispar*, were selective feeders consuming nutrient-rich plant parts like fleshy leaves, buds, and fruiting bodies (Ösi et al. 2024). Likewise, high $\delta^{44/40}$Ca values recorded in tooth enamel of *Camptosaurus* sp. (National Dinosaur Monument, Morrison Formation) is consistent with this interpretation, confirming a preference for leaves and buds, which are enriched in ^{44}Ca compared to roots and stems (Norris et al. 2025). Iberian Late Jurassic iguanodontians likely had similar browsing and frugivory behaviours.

Conclusions

Several new ornithopod fossils from eastern Spain (provinces of Valencia and Teruel) have been described in this study. These fossils were found at various fossil sites within the South-Iberian Basin, concretely in the Villar del Arzobispo Formation (Upper Jurassic, upper Kimmeridgian–Tithonian).

The specimens described here represent almost half of the ornithopod discoveries made in this region to date.

The fossils consist of: (1) a pedal ungual phalanx (MPA-1015) (Cambrillas site, Alpuente) assigned to Ornithopoda indet., (2) an anterior caudal vertebra (MAP-9099) (RD-61 site, Riodeva) assigned to Dryosauridae indet., (3) a dentary tooth (MPA D-0277), an anterior caudal vertebra (MPA-1177), and a posterior caudal vertebra (MPA D-0204) (By Pass site, Alpuente), and (4) an anterior caudal vertebra (MAP-9101) (VS-1 site, Veguillas de la Sierra) assigned to Ankylopollexia indet.

MAP-9099 represents the first evidence of dryosaurids in eastern Iberia. Moreover, the fossils from the By Pass site belong to a small-sized ankylopollexian, representing the first record of this type of ornithopod and potentially identifying a trackmaker for some enigmatic small quadrupedal ornithopod tracks found in the region. Finally, MAP-9101 is attributed to a large-sized ankylopollexian, further supporting the presence of these ornithopods, such as *O. bunnueli*.

The coexistence of at least three different iguanodontian taxa likely reflects niche partitioning (resource, spatial, and temporal) and suggests a high level of ecological complexity within the herbivorous dinosaurian communities of the coastal ecosystems in eastern Iberia during the Late Jurassic. This ecological complexity was likely widespread across the Iberian landmass in this epoch, favoured by the presence of similar climatic conditions and palaeoenvironments.

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Data availability. The authors confirm that the data supporting the results and conclusions of this study are available within the article. The fossils studied here are deposited in two public museums (Museo Paleontológico de Alpuente and Museo Aragonés de Paleontología).

Conflict of interest. The authors declare no conflicts of interest.

Author contributions. Conceptualization: S.S.-F., M.S., and A.C; Resources: S.S.-F., F.J.V., M.S., and A.C.; Investigation: S.S.-F., F.J.V., M.S., and A.C.; Data Curation: S.S.-F., F.J.V., M.S., and A.C.; Methodology: S.S.-F., F.J.V., M.S., and A.C.; Formal Analysis: S.S.-F. and F.J.V.; Validation: S.S.-F., F.J.V., M.S., and A.C.; Writing – Original Draft: S.S.-F.; Writing – Review & Editing: S.S.-F., F.J.V., M.S., and A.C.; Visualization: S.S.-F.; Supervision: F.J.V., M.S., and A.C.; Project Administration: M.S. and A.C. Funding acquisition: A.C.

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