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An Eudromaeosaurian Theropod from Lo Hueco (Upper Cretaceous. Central Spain)

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Abstract: The Lo Hueco fossil site (Cuenca, Spain) is one of the most relevant localities for the study of Late Cretaceous continental vertebrate faunas from Europe. The fossil record of theropod dinosaurs from this locality is represented by scarce isolated postcranial materials that were preliminarily attributed to abelisaurids and to a possible giant bird, in addition to a large assemblage of isolated teeth that were related to different maniraptoran clades. Here, we describe an isolated partial left tibia articulated with the proximal tarsals and discuss their taxonomic affinities. A review of the European fossil record of Late Cretaceous theropods was performed to analyze possible changes in the faunistic composition during this period. The specimen from Lo Hueco exhibits some characters that have been interpreted as apomorphies for maniraptoran coelurosaurs and a combination of features compatible with deinonychosaurians. Within this clade, the specimen is more favorably comparable with velociraptorine dromaeosaurids and is tentatively interpreted as a member of this group. This specimen is one of the few non-dental specimens of dromaeosaurids described thus far from the Upper Cretaceous of the Iberian Peninsula and contributes to a better understanding of the composition and evolutionary history of the European theropod fauna during the last stages of the Mesozoic.

Keywords: Dinosauria; Maniraptora; Deinonychosauria; Campanian-Maastrichtian; Cuenca



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1. Introduction

The European Upper Cretaceous deposits have yielded an abundant record of dinosaurs and other continental vertebrates with a great number of sites discovered in the last decades (e.g., [1–8]). In this context, particularly relevant are the sedimentary units of the Ibero-Armorican domain, mainly distributed in the Lusitanian (Portugal), Iberian (central Spain), Pyrenees (north-eastern Spain and southern France), and Provence (south-eastern France) basins, together with correlative sequences from Transylvanian landmasses, mainly in the Hațeg and Rusca Montană basins of Romania and scatter assemblages from equivalent successions of the Netherlands, Belgium, southern Germany, Slovenia, Bulgaria, Ukraine, and European Russia (e.g., [1,2,9–18]). Unfortunately, the record of theropod dinosaurs in these levels is relatively scarce and mostly composed of fragmentary materials, challenging our interpretation about the evolutionary history of these faunas during the latest part of the Mesozoic in the European archipelago.

Here, an isolated partial tibia articulated with fused proximal tarsals of a small-sized theropod dinosaur collected in the paleontological locality of Lo Hueco (Cuenca Province, central Spain) is described, and their taxonomic affinities are discussed. In recent years, Lo Hueco has become one of the most relevant European fossil sites for the study of late Campanian-Maastrichtian continental vertebrate faunas. Abundant vertebrate fossils have been described from this locality, allowing the identification of a diverse fauna, including

several groups of dinosaurs, abundant materials of crocodyliforms, squamates, turtles and fishes (e.g., [19–24]). Theropod materials are relatively scarce in Lo Hueco and consist mainly of teeth and sparser, mostly isolated postcranial elements. The description and taxonomic interpretation of most of these specimens are in progress, but the analysis of a collection of isolated elements, essentially teeth, allowed a preliminary evaluation of the diversity of the theropod fauna from this locality. This fauna includes at least a medium-sized form with abelisauroid affinities and different paravian clades that comprises Velociraptorinae, Dromaeosaurinae, *Richardoestesia*, and *Paronychodon* as well as a possible giant bird [19,21,22,25,26]. This is the largest assemblage of Late Cretaceous theropods currently known in the Iberian fossil record and is very significant to better understand the evolutionary history of this group of dinosaurs during the final stages of the Mesozoic.

The specimen described shows several maniraptoran synapomorphies and a combination of features that is compatible with velociraptorine dromaeosaurids, representing the first non-dental material attributed to this clade of carnivorous dinosaurs in the Iberian Peninsula. A review of the European fossil record of Late Cretaceous theropods shows similarities but also differences on the faunal composition of the Iberian Peninsula and other equivalent European landmasses, particularly from France, Hungary and Romania. The identification of the specimen from Lo Hueco as a member of Velociraptorinae is in line with previous finds that suggested the presence of the maniraptoran lineage with Asiatic and possibly North American affinities in the Upper Cretaceous fossil record of Europe [27,28]. However, comparisons with other postcranial materials attributed to velociraptorine dromaeosaurids known in equivalent European levels, particularly with *Balaur bondoc* from the Maastrichtian of Romania, show that this specimen lacks some features, such as the completely fused tibiotarsus, that have been interpreted as modifications related to the island-dwelling effect [27,28]. Another difference of the faunal composition of theropod dinosaurs between the Ibero-Armorica and the Hațeg Island is the absence in the later of a large-sized form, which has also been interpreted as a consequence of stress paleoenvironmental conditions [29].

Traditionally, the Eudromaeosauridae was interpreted as containing two clades: Velociraptorinae and Dromaeosaurinae. Both include taxa with Asian and North American distributions (e.g., [30,31]), which were used as arguments supporting the existence of faunal interchange between Asia and North America during the Upper Cretaceous (e.g., [30,32,33]). Some recent analyses [34] recovered a Eudromaeosauria clade composed of three groups: Velociraptorinae (composed exclusively by taxa with Asian distribution), Dromaeosaurinae (composed of Late Cretaceous taxa from both Asia and North America), and Saurornitholestinae (composed exclusively by taxa with North American distribution). This geographic distribution indicates a diversification of eudromaeosaurians during the Late Cretaceous that was interpreted as being related with biogeographic variation [34]. In the last years, the identification in the European Upper Cretaceous of some deeply-nested theropods closely related to taxa from both Asia and North America, including velociraptorines and troodontids (e.g., [17,27,28]) together with early-branching forms with Gondwanan affinities, such as abelisauroids (e.g., [10,12]), highlight the implication of faunal interchange between Europe and other landmasses on the evolutionary history of the dinosaur faunas during the Upper Cretaceous. The fossil record of Lo Hueco has one of the most abundant and diverse assemblage of theropod dinosaurs from the European Campanian-Maastrichtian and thus is very significant to a better understanding of the composition and evolutionary history of these Late Cretaceous faunas.

1.1. The Fossil Record of Late Cretaceous Theropod Dinosaurs in European Landmasses

Here, we present a review of the fossil record of theropod dinosaurs from the Upper Cretaceous of Europe, mainly focusing on the Campanian and Maastrichtian. This review allows us to compare the theropod assemblages, establishing possible similarities and differences on the faunal composition from different European landmasses (Table 1). Some of the most significant occurrences from the Cenomanian to the early Campanian time

interval were also analysed to discuss the possible existence of changes on the theropod assemblages from the Iberian Peninsula and other correlative European paleogeographic areas during the Late Cretaceous.

Table 1. Distribution of the theropod dinosaur groups in the most significant Late Cretaceous European landmasses, spanning the Cenomanian to the late Maastrichtian. Question mark means uncertain identification.

Taxa	Cenomanian		Turonian to Early Santonian	Santonian to Early Campanian		Middle Campanian to Late Maastrichtian		
	Spain	France	Austria	France	Hungary	Spain	France	Romania
Abelisauroida indet.	[8]				[11]	[35]	[36]	
Tarascosaurus				[10]		? [10]		
Arcovenator						? [18,37]	[12]	
Tetanurae indet.			[38]		[11]			
Carcharodontosauridae indet.		[39,40]						
Coelurosauria indet.						[14]		
Elopteryx							? [41]	[42]
Bradycneme								[43]
"Heptasteornis"								[43]
Maniraptora indet.			[38]					
Ornithomimosauria indet.						? [44]		
Paraves indet.					[11]	[18]		[45]
Pneumatoraptor					[11]			
Dromaeosauridae indet.		[39,40]		[46]	[47]	[14,18]		[48]
Variraptor							[49]	
Pyroraptor							[50]	
Dromaeosaurinae indet.						[22]		
Velociraptorinae indet.						[22]	? [49]	[51]
Balaur								[27]
Troodontidae indet.		[39,40]						? [51]
Tamarro						[17]		
Paronychodon			[52]			[14,22]	[46]	? [51]
Richardoestes						[14,22]		

1.1.1. Campanian to Lower Maastrichtian

The European fossil record of Campanian dinosaurs is mostly represented in the region of Scania (southern Sweden), in the Villeveyrac Basin of Hérault (southern France), in the Winzendorf-Muthmannsdorf municipality of Niederösterreich (eastern Austria), and in the locality of Sebeş in the southwestern Transylvania, central Romania (e.g., [5]). One of the most significant fossil records of Campanian continental vertebrates come from coal-bearing beds of Austria. These levels have yielded an abundant and diverse assemblage of continental vertebrates, including different groups of dinosaurs [5]. However, the record of theropods is scarce and is only represented by two fragmentary teeth described as "*Megalosaurus pannoniensis*" [53], which has been compared to specimens from the Hungarian Iharkút locality and are referred to as early-branching tetanurans [5,11]. From the lower Maastrichtian deposits of the Volgograd region, in Russia, some isolated materials attributed to theropod dinosaurs have been described, including an isolated tooth interpreted as belonging to a dromaeosaurid, together with a braincase fragment (more recently attributed to an indeterminate ankylosaur [5]) and a metacarpal that were interpreted as belonging to a possible early-branching theropod [54].

In southern France, several dinosaur-bearing Campanian localities are known, mainly in Bouches-du-Rhône, Var and Hérault. These levels have yielded a diverse dinosaur

fauna that comprises ankylosaurs, ornithopods, sauropods, non-avian theropods, and birds (e.g., [5,55–57]). The fossil record of non-avian theropod dinosaurs is represented by several cranial and postcranial materials mostly assigned to abelisaurids (e.g., [5]). This group of theropods was first reported in France and was based on an almost complete maxilla collected from upper Campanian levels near the village of Pourcieux (Var), in the eastern part of the Aix-en-Provence Basin [36]. Later, the description of *Tarascosaurus salluvicus* [10] was based on a partial femur and some vertebrae from the lower Campanian of Le Beausset (Var) and was the second reference to abelisaurids in the Upper Cretaceous of France. More recently, several cranial and postcranial remains, including a well-preserved braincase of another abelisaurid taxon, *Arcovenator escotae* [12], was described from upper Campanian (possibly extending to the lower Maastrichtian [58]) deposits of the Jas-Neuf Sud locality (Var), in the Aix-en-Provence Basin. This taxon is considered to be more closely related to majungasaurine abelisaurids from India and Madagascar than to South American brachyrostran forms, highlighting the role of Europe in faunal dispersal during the early late Cretaceous [12]. Other specimens assigned to abelisaurids have been reported in different localities of late Campanian and early Maastrichtian age, including a tibia from La Boucharde (Aix-en-Provence Basin, Bouches-du-Rhône) [1] and several specimens (including abundant isolated teeth), that may represent different taxa, from the Cruzy area (Hérault) [5,59].

Apart from the abundant materials assigned to abelisaurids, the record of theropods from France includes incomplete postcranial materials and some isolated teeth from different upper Campanian and lower Maastrichtian localities, mostly attributed to different paravian theropods (e.g., [5,10,41,46,59,60]). A relatively abundant assemblage of small-sized isolated teeth from different localities in southern France has been described and includes specimens interpreted as belonging to juvenile deinonychosaurs (later referred to as Theropoda indet.), to indeterminate dromaeosaurids (some of them have been compared with velociraptorines) and to cf. *Panonychodon* sp. [10,46,60,61]. The postcranial materials were mainly tentatively related to different dromaeosaurids, including *Pyroraptor olympius* [50] and *Variraptor mechinorum* [49]. *P. olympius* was described based on a set of appendicular elements, and some vertebrae and associated teeth collected from the locality of La Boucharde (Bouches-du-Rhône). *V. mechinorum* was established based on an articulated posterior dorsal vertebra and sacrum, associated with a humerus and two vertebrae discovered in different localities from the Var department [49,50]. The validity and possible synonymy of these taxa have been largely debated (e.g., [1,61,62]). Based on the uncertain taxonomic identification of the holotype and the problematic association of the referred materials, some authors suggested that *V. mechinorum* is a *nomen dubium* [1,50]. Following the description of additional material referable to *Variraptor* from the upper Campanian-lower Maastrichtian deposits near Cruzy (Hérault) and Fox-Amphoux (Var), including an ilium that was suggested to belong to the same individual of the holotype, Chanthasit and Buffetaut [61] concluded that the two species, *P. olympius* and *V. mechinorum* may be valid. However, due to the lack of significant common elements, it is also conceivable that they represent the same taxon [5]. Other materials attributed to dromaeosaurid theropods were described from the localities of Fox-Amphoux (Var) and Roques-Hautes (Bouches-du-Rhône) [41]. These materials include a femur, a cervico-dorsal vertebra, a caudo-sacral vertebra, and several fragments of dorsal ribs that were tentatively related to the Transylvanian genus *Elopteryx* [41].

Finally, a significant record of fossil birds has also been reported in different upper Campanian and lower Maastrichtian localities of France. The presence of a giant bird in the Late Cretaceous of France was first reported by Buffetaut et al. [63], based on an incomplete synsacrum from Fox-Amphoux (Var). Later, Buffetaut and Le Loeuff [64] described a synsacrum and fragments of the pelvis, from Campagne-sur-Aude (Aude), associated with an incomplete femur from Villespassans (Hérault), based on which they established the taxon of early-branching ornithurine birds, *Gargantuavis philoinos*. More recently, some isolated materials of further Upper Cretaceous localities in the Var and

Hérault departments [13,65], but also from other European correlative levels, including the upper Campanian fossil-site of Laño, in Spain [66] have been attributed to *G. philoinos*. Furthermore, a well-preserved pelvis from Maastrichtian levels of the Hațeg Basin, in Romania was assigned to this taxon [67] but interpreted as belonging to a different gargantuaviid by Buffetaut and Angst [68]. Other fossil birds from the Upper Cretaceous of France include a humerus collected in the Massecaps locality, close to the village of Cruzy, and described as the holotype of *Martinavis cruziensis*, which is a taxon closely related to some euenantiornithine forms known in correlative levels of Argentina and North America [69]. Other French records of early Maastrichtian enantiornithine birds include a coracoid and a fragmentary femur collected close to the village of Cruzy (Hérault) [70] and a tibiotarsus described in the locality of Bastide-Neuve (Var) [71].

An abundant and diverse fossil record of continental vertebrates has been described in different Campanian-Maastrichtian localities from Spain, particularly in the Basque-Cantabrian and Iberian basins, in the north and center-east regions respectively (e.g., [18,22,37,44,72,73]). The paleontological locality of Chera, in Valencia (middle-upper Campanian), yielded a relatively abundant and diverse assemblage of vertebrates (e.g., [18,73–75]). However, theropod dinosaurs are represented by scarce isolated teeth that were interpreted as belonging to Theropoda indet., Neoceratosauria indet. (more recently referred to as cf. *Arcovenator*), Paraves indet. and Dromaeosauridae indet. [18,74]. Some small-sized tooth crowns from this locality were first tentatively attributed to cf. *Pyroraptor* [74], but they were more recently reinterpreted as belonging to an indeterminate dromaeosaurid [18]. Another Spanish paleontological locality, Armuña, in Segovia (upper Campanian) also provided abundant remains of different vertebrate groups, including a collection of materials attributed to theropod dinosaurs that are represented by some pedal phalanges, including two unguals, assigned to Theropoda indet. and six tooth crowns tentatively attributed to cf. *Arcovenator* ([37] and references therein). Among the most significant fossil records of late Campanian vertebrates currently known in Spain is that from the Laño fossil-site, in the Condado de Treviño (Basque-Cantabrian Basin). This locality has yielded an abundant and diverse assemblage of small-sized continental vertebrates, together with a diverse assemblage of dinosaurs (e.g., [6,14,18,76–79]). The fossil record from Laño has one of the most diversified associations of theropod dinosaurs currently known from the late Campanian of Europe, which are represented by some vertebrae, appendicular elements and a large collection of isolated teeth [6,14,18,44]. The isolated teeth are mostly represented by small-sized crowns that have been assigned to different coelurosaurian clades, including Paraves indet., Dromaeosauridae indet., cf. *Richardoestes* sp. and cf. *Paronychodon* sp. [6,14,18,44,77]. Torices et al. [14] interpreted some isolated tooth crowns from Laño as belonging to cf. *Pyroraptor olympius*, but more recent works note some differences between the Spanish specimens and the paratype teeth of this species, suggesting their identification as Dromaeosauridae indet. [18]. In addition, scanner mid- to large-sized crowns from Laño first assigned to ?Abelisauridae and to Theropoda indet. [14,76,77] were more recently referred to as *Arcovenator* [18]. A caudal vertebra and a pair of femora collected in this locality were also interpreted as belonging to a mid- to large-sized Abelisauroida that has been compared with the materials of *Tarascosaurus* from the Campanian of Beausset (Var) [10,76,80]. The postcranial material of theropod dinosaurs from Laño also includes a tibiotarsus with bird-like features and an isolated sacrum that was first interpreted as belonging to a pterosaur, however, was more recently assigned to *Gargantuavis* [6,66,81]. Finally, an isolated pedal ungual from Laño was tentatively assigned to Ornithomimosauria, but the specimen has not been described or figured [18,44].

Other Iberian fossil records from equivalent ages are known in the Lusitanian Basin of the central-west of Portugal, where scarce dinosaur remains were described in different localities of the regions of Aveiro, Viso, and Taveiro [9,82–86]. Sauvage [82] and Lapparent and Zbyszewski [83] described some isolated teeth and three manual ungual phalanges from the locality of Viso and assigned them as *Megalosaurus* sp. and as *Megalosaurus* cf.

pannoniensis, respectively. From the same region came four small caudal vertebrae that were first interpreted as belonging to a possible bird or to a long-tailed pterosaur [9,82,83]. The ungual phalanges and some of the caudal vertebrae from Viso were later reinterpreted as belonging to small maniraptoran coelurosaurs [85,86]. Later, the description of the fossil record of correlative levels in Taveiro, near Coimbra and Aveiro, allowed the identification of a relatively diverse fauna of theropods mostly composed of different groups of small-sized coelurosaurians, including materials tentatively attributed to troodontids and dromaeosaurids, together with some large-sized tooth crowns that were assigned as aff. Megalosauridae [9,84,87,88]. In the locality of Taveiro, some isolated teeth were also described, establishing the putative dromaeosaurid taxon *Euronychodon portucalensis* [88], which is currently regarded as junior synonym of *Paronychodon lacustris* [14,89,90]. In addition, some of the specimens from Taveiro first attributed to cf. Coeluridae [88] also show a combination of features compatible with *Paronychodon* [18]. Other teeth show similarities to those of cf. *Richardoestesia* and to other dromaeosaurid morphotypes described in the Ibero-Armorican Late Cretaceous record [18]. The identification of most of these materials is problematic, due to the fragmentary nature of the specimens, or the need to be updated, so the composition of the Late Cretaceous theropod fauna of the Lusitanian Basin is difficult to ascertain at the moment.

Upper Campanian-lower Maastrichtian deposits of the Pyrenees and Iberian basins, in central-west and northern Spain have also yielded a significant record of dinosaurs and other continental vertebrates. From the province of Lleida, some isolated theropod teeth were described and assigned to different morphotypes related to Theropoda indet., Coelurosauria indet., *Richardoestesia* sp. and *Pyroraptor olympius* [14]. Isasmendi et al. [18] argued that it is not possible to assign the tooth morphotype from Montrebei to *P. olympius*, suggesting it may belong to an indeterminate dromaeosaurid. The paleontological locality of Poyos in Guadalajara has yielded a significant fossil record of dinosaurs, including abundant remains of a large-sized abelisauroid theropod [35,91] that is currently in study. However, the most significant European fossil site with continental vertebrates known at the moment from this time interval is Lo Hueco in the Cuenca Province of central Spain. Abundant vertebrate fossils have been described from this locality, allowing the identification of a diverse fauna, including several groups of dinosaurs, but also abundant materials of crocodyliforms, squamates, turtles and fishes (e.g., [19–24]). Theropod materials from Lo Hueco mainly consisting of teeth and sparser, mostly isolated postcranial elements (including the tibia and proximal tarsals described below). Most of these specimens are under study, but the analysis of a collection of isolated teeth allowed the identification of several morphotypes related to different clades, including an indeterminate large or medium-sized theropod, and diverse paravians, comprised of some tooth crowns attributed to Velociraptorinae, Dromaeosaurinae, *Richardoestesia* and *Paronychodon* [19,21,22,25,26]. Postcranial materials of theropod dinosaurs are relatively abundant in Lo Hueco and most are possibly assigned to different members of Dromaeosauridae, but their diversity is not yet established [25]. At the moment, besides the specimen described, this record also includes an isolated metatarsal assigned to a medium or large-sized non-coelurosaurian neotheropod [92] and some cervical vertebrae tentatively related to a giant Ornithomorphid bird [25].

1.1.2. Late Maastrichtian

For the late Maastrichtian, one of the most significant European records of dinosaurs come from the Pyrenees region of southern France and the northeastern region of Spain. Apart from these regions, scarce dinosaur-bearing localities have been reported in the region of Bavaria of southern Germany, Slovenia, Bulgaria and the Crimea Peninsula [93–97]. Theropod materials from these regions are represented by a few isolated teeth, and some are assigned to indeterminate dromaeosaurids and to a troodontid-like morphotype, from the region of Kozina, in Slovenia [95], and a left humerus found in the Vratsa district of Bulgaria that has been interpreted as a possible ornithomimosaur [93]. An interesting upper

Maastrichtian ichnological dinosaur record was described in the Roztocze area of south-eastern Poland. This record includes several theropod footprints attributed to at least four ichnotaxa: *Irenesauripus* sp., which is characterized by medium-sized tridactyl footprints of uncertain affinities; *Velociraptorichnus* sp., which corresponds to small-sized didactyl footprints that have been interpreted as belonging to an indeterminate dromaeosaurid; *Macropodosaurus* sp., an ichnotaxon of functionally tetradactyl footprints traditionally related to therizinosauroids; and *Saurexallopus* sp., an ichnotaxon usually interpreted as belonging to oviraptorosaurs ([5,98,99] and references herein). In France, several dinosaur-bearing localities from this time interval are known, representing an abundant and diverse fauna, including a significant assemblage of theropods that are generally represented by isolated teeth, and mostly assigned to indeterminate dromaeosaurids, to the *Richardoestesia* morphotype and to "*Euronychodon*" sp. (e.g., [5,39,100]). In addition, some isolated limb elements belonging to medium-sized theropods have been described in the locality of Vitrolles-La-Plaine (Provence region) and these materials were interpreted as belonging to neoceratosaurs related to *Tarascosaurus* [39]. The French upper Maastrichtian record also includes a putative enantiornithine scapula that is the only avian specimen thus far reported in these levels [5].

The Spanish fossil record of late Maastrichtian dinosaurs came from the South Pyrenees Basin, in the Spanish north-eastern region, mainly in Huesca, Lleida and Barcelona provinces (e.g., [3,7,14,17,40,101–113]). The upper Maastrichtian levels of the Huesca province, in Aragón, has yielded an important collection of dinosaurs, and particularly of hadrosaurid ornithopods (e.g., [102–106]), but the record of theropods is scarce, represented by a few isolated tooth crowns, eggshells, and some postcranial fragments [14,101,109,112,113]. The isolated teeth mostly correspond to small-sized morphotypes that have been tentatively assigned to different coelurosaurian clades, including Dromaeosauridae indet., possible velociraptorines and dromaeosaurines, *Paronychodon* sp. and *Richardoestesia* [14,101,112]. Some medium to large-sized tooth crowns tentatively related to neoceratosaurs and more recently interpreted as probably belonging to Abelisauridae indet. were also reported [14,18]. Postcranial materials of theropods are very scarce in these levels and are represented by a pedal ungual II and the proximal part of an ulna attributed to indeterminate dromaeosaurids, together with a cervical vertebra of a large ornithuromorph bird [109,114]. The fossil record of theropods from this region also includes a diverse assemblage of eggshells that represent two different morphotypes attributable to the oogenus *Pseudogeckoolithus*, which have recently been referred to as maniraptoran theropods [113,115]. The only non-avian theropod taxa thus far described from the upper Maastrichtian fossil record of Spain is *Tamarro insperatus*, established based on a partial right metatarsal II collected in the Lleida province of Catalonia [17]. This taxon is interpreted as a jinfengopterygine troodontid and represents the first member of this clade reported from Europe and the only non-dental specimen attributable to troodontids known in the European Late Cretaceous [17]. Finally, some upper Maastrichtian localities in the Barcelona province are known with scarce dinosaur materials, including a fragment interpreted as belonging to a possible limb bone of an indeterminate theropod and a tooth attributed to a velociraptorine dromaeosaurid [18,111,116].

The Maastrichtian deposits in the Hațeg, Rusca Montană and Transylvania basins of northern Romania have yielded an abundant and diverse fauna of vertebrates (e.g., [5,51]). The fossil record of theropods is scarce in these levels but constitutes a relatively diverse assemblage mostly represented by isolated teeth and several postcranial materials, including few partial articulated skeletons (e.g., [27]). Among the earliest fossil vertebrates described from the Hațeg Basin are two incomplete femora (and a possible distal tibiotarsus) based on which Andrews [42] established the taxon *Elopteryx nopcsai*, first related to the Pelecaniformes clade of birds [117,118]. Later, other materials were assigned to this taxon, including two partial tibiotarsi that were subsequently interpreted as representing different species: "*Bradycneme draculae*" and "*Heptasteornis andrewsi*" [43]. In addition, several isolated femoral fragments at the collections of the Natural History Museum of London are

labelled as belonging to *Elopteryx*, but more recently some authors noted significant size and morphological differences among them, suggesting that more than a theropod taxon may be present [28]. The avian affinities of all these materials have been largely debated with many authors suggesting that they may belong to small non-avian theropods ([5,51] and references herein). Later, other remains from the Hațeg Basin were also attributed to *E. nopcsai*, but their affinities were much disputed [119]. These materials have been assigned to different theropod groups, including indeterminate maniraptoran tetanurans [51], dromaeosaurids [41], troodontids (e.g., [120]), ornithomimids [121] and more recently to alvarezsaurids [119,122]. A distal femur first attributed to *E. nopcsai* [42] was considered after as probably belonging to a small abelisaurid [51] and latter reinterpreted as the distal end of a large metatarsal of a possible hadrosaur [119].

The fossil record of theropods from the Maastrichtian levels of Romania also includes abundant isolated teeth, representing a diverse assemblage that includes an indeterminate medium-sized taxon, velociraptorine dromaeosaurids, troodontids, *Richardoestesia* and *Paronychodon* [51,123–131]. Other isolated cranial and postcranial materials have also been reported from these levels, including an articulated frontal and parietals identified as belonging to an indeterminate dromaeosaurid taxon tentatively related to *Saurornitholestes* [48] and a sacrum described as belonging to Paraves indet. [45]. The most complete theropod specimen currently known from the Maastrichtian record of Romania is *Balaur bondoc*, which is also one of the most complete non-avian theropod dinosaurs thus far described in the Late Cretaceous of Europe. This taxon is represented by an articulated partial postcranial skeleton that includes dorsal, sacral and caudal vertebrae, and much of the pectoral and pelvic girdles and limbs, and was discovered near the town of Sebeș, in the Transylvanian Basin [27]. It was first interpreted as a dromaeosaurid with close affinities with the Asian-North American clade of velociraptorine dromaeosaurids but showing extreme morphological specializations that have been interpreted as likely related to the island effect [27,28]. However, this specimen has subsequently been tentatively interpreted as belonging to an early branching avialan [132–134]. Isolated appendicular elements collected in equivalent sedimentary levels of the Hațeg Basin, previously considered to represent an oviraptorosaur, have been also related to *Balaur* and possibly represent a different species [5,28].

The European fossil record of Maastrichtian theropods also includes a proximal femur from the Maastricht Tuff in the Netherlands, first assigned as “*Megalosaurus bredai*” and later described as the holotype of *Betasuchus bredai* [5,135]. This taxon was long interpreted as representing an ornithomimosaur [135,136], but more recently it has been regarded as an early-branching theropod possibly related to Ceratosauria [137,138]. Apart from this specimen, the type of area of the Maastrichtian Stage (southeast Netherlands and northeast Belgium) has yielded some isolated materials attributed to different avian theropod taxa tentatively related to enantiornithines and ornithurines [139,140].

2. Geographical and Geological Context

The paleontological locality of Lo Hueco is located near the village of Fuentes, in the Cuenca Province of central-eastern Spain. The sedimentary sequence in the area of the fossil site was described in detail in [19,22]. It is mostly composed of alternating grey and red marly mudstones with some intercalations of sandy sandstone structures and sulphated (anhydrites or gypsums) bodies. These levels belong to the upper part of the Margas, Arcillas y Yesos de Villalba de la Sierra Formation (from hereon, Villalba de la Sierra Formation) ([19] and references herein). The age of the Villalba de la Sierra Formation spans the lower Campanian to the middle Eocene, but the stratigraphic succession in the area of Lo Hueco has been interpreted as corresponding to the upper Campanian-lower Maastrichtian time interval ([22] and references herein). This succession is interpreted as corresponding to deposits of a muddy coastal plain with edaphic intervals [19].

3. Materials and Methods

The specimen herein described consists of an isolated partial left tibia articulated with the proximal tarsals (HUE-02696) collected in Upper Cretaceous deposits of the Lo Hueco fossil site. Detailed descriptions, measurements, photographs, and schematic drawings of the specimen are presented. We followed the systematic nomenclature proposed by [141] and the phylogenetic interpretations detailed by [31] for Deinonychosauria and their in-groups Troodontidae and Dromaeosauridae (including Unenlagiinae, Microraptorinae, Dromaeosaurinae, and Velociraptorinae).

4. Discussion and Results

4.1. Systematic Paleontology

Dinosauria Owen, 1842 [142]
 Theropoda Marsh, 1881 [143]
 Coelurosauria von Huene, 1914 [144]
 Maniraptora (Gauthier, 1986 [145]) *sensu* Sereno, 1998 [141]
 Deinonychosauria (Colbert and Russell, 1969 [146]) *sensu* Sereno, 1998 [141]
 Dromaeosauridae (Matthew and Brown, 1922 [147]) *sensu* Sereno, 1998 [141]
 Eudromaeosauria Longrich and Currie, 2009 [30]
 Velociraptorinae indet. (Barsbold, 1983 [148]) *sensu* Currie, 1995 [149]

4.1.1. Description

The tibia HUE-02696 is relatively robust with almost parallel medial and lateral margins along most of the preserved length, except the distal end where the diaphysis shows a slight mediolateral expansion (Figure 1). In the anterior and lateral views, the tibia is slightly curved with shallow concave margins. The diaphysis has a somewhat D-shaped section at mid-length, with the long axis oriented mediolaterally, and the anterior margin almost flat and the posterior margin slightly convex. In the anterior view, the diaphysis has a longitudinal crest extending along the anteromedial margin for most of the diaphysis' length. This crest may be a preservation artifact due to a collapse of the central part of the diaphysis. However, in the lateral margin of this crest there is a flat surface that extends dorsoventrally, which is interpreted as the area for the contact with the fibula. The tibia is broken proximally around the level of the most dorsal end of the fibular crest. Although the proximal part is unknown, it preserves a fragment of the distal expansion of the cnemial crest that extends onto the anterior surface of the diaphysis. The fibular crest is incomplete distally due to the existence of a fracture in the middle section of the tibial diaphysis, but it is otherwise well-preserved. This is a low crest that extends in the lateral surface of the diaphysis, close to the proximal end of the tibia, and has a somewhat anterolateral orientation. The most proximal end of the fibular crest is placed approximately at the level of the ventral margin of the cnemial crest. The posterolateral surface of the tibia, adjacent to the fibular crest, has a shallow longitudinal concavity that is delimited by a low ridge. This structure is interpreted as the surface for articulation with the proximal part of the fibula.

In the posterior view, the tibia's diaphysis is mostly flat with a triangular distal expansion. The distal end has a small articular surface extending on the posterior surface of the tibia. A small distal crest projects longitudinally in the posteromedial margin of the tibia and another smaller crest is present adjacent to the posterolateral surface. A flexor groove is absent in the posterior surface of the distal end of the tibia, where only a shallow and broad concavity that is delimited by the previously described crests is present. In the medial view, the tibia is slightly convex transversely, almost straight longitudinally and with a slight proximal expansion and a distal end that projects somewhat anteriorly. Distally, the medial surface of the tibia has an oval rough area adjacent to the dorsal margin of the calcaneum. In the lateral view, the tibia's diaphysis is also mostly straight, but has a triangular proximal part that is formed by the ventral expansions of the cnemial crest in the anterior surface and the medial condyle in the posteromedial margin. The proximal part of the tibia is divided approximately at mid-length by the fibular crest forming shallow

concavities adjacent to it. The distal end is also slightly expanded anteroposteriorly, but much less than the proximal part. The calcaneum has a slightly concave lateral margin and an oval outline, longer anteroposteriorly than high dorsoventrally. A flat surface in the distolateral margin of the tibia is interpreted as the area for the articulation with the distal end of the fibula. This surface extends to the dorsal margin of the calcaneum, connecting with a small anterodorsal expansion, suggesting that the fibula would have articulated with this element and twisted proximally to articulate in the posterior surface of the fibular crest.

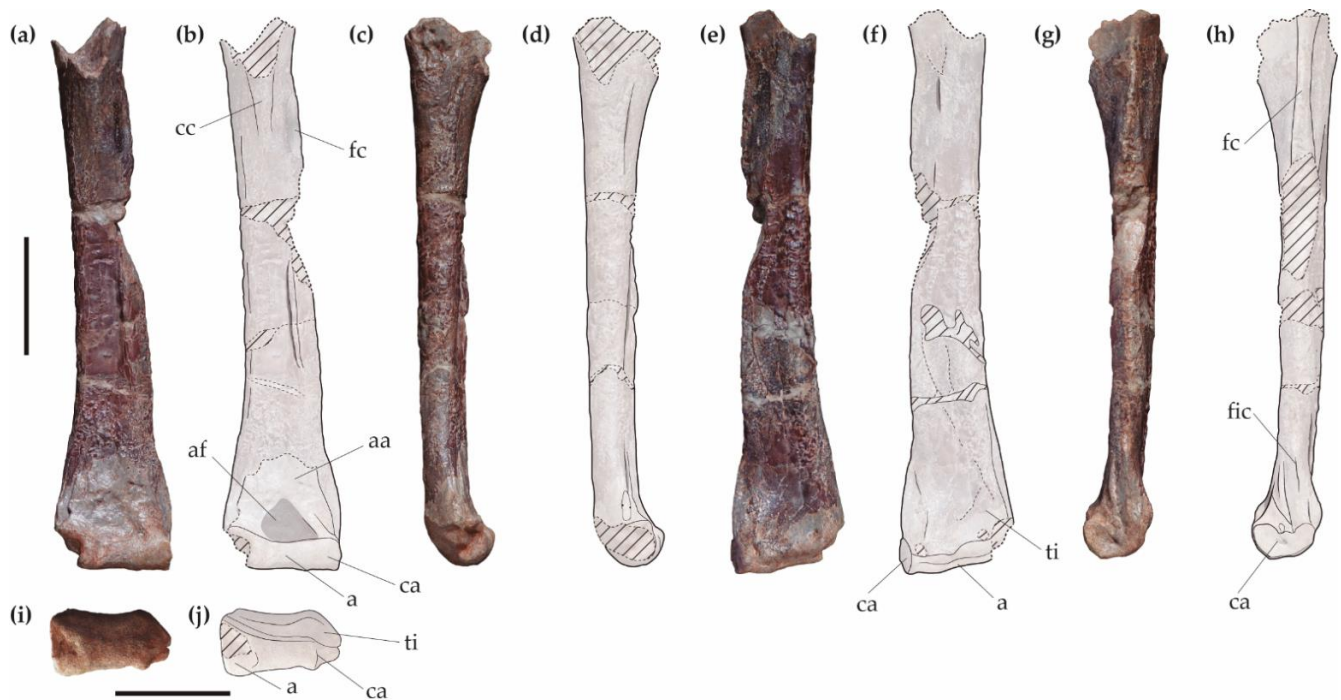


Figure 1. Articulated tibia and astragalus-calcaneum complex (HUE-02696) from Lo Hueco and interpretative line drawing in (a,b) anterior; (c,d) medial; (e,f) posterior; (g,h) lateral; and (i,j) distal views. Abbreviations: a, astragalus; aa, ascending process of the astragalus; af, anterior fossa; ca, calcaneum; cc, cnemial crest; fc, fibular crest; fic, contact for the fibula; ti, tibia. Scale bar = 5 cm.

The proximal tarsals are completely fused together, and they are also firmly articulated with the tibia. The calcaneum is continuous with the astragalus, and only distinguished by a slightly more expanded anterior margin. Despite the suture of the tarsals with the tibia still visible, they are fused in several points. The ascending process of the astragalus is a thin lamina that covers almost completely the anterior width of the distal surface of the tibia. The preserved part of the process has a sub-quadrangular shape, slightly wider than tall and with almost vertical margins. It is broken dorsally so the height of the process is not possible to be determined. As preserved, the ascending process is 34 mm in length, which is almost five times the dorsoventral height of the astragalar body that is 7 mm. A flat surface, which is delimited by a slightly oblique and low crest extending in the medial part of the distal anterior surface of the tibia, is interpreted as the limit of the area for the articulation with the ascending process, indicating that the process would have a length of at least 39 mm. The ascending process is separated from the condylar portion of the astragalus by a shallow depression that is better marked near the medial end and is delimited by a faintly longitudinal crest. The condyles of the astragalus are poorly developed with the astragalar distal margin being almost straight and the anterior one only slightly concave at mid-length, without any discernible intercondylar groove. However, the distal end of the astragalus-calcaneum complex is somewhat eroded, particularly the ventral part of the condyle of the astragalus, which would have extended more ventrally as is typical in

other coelurosaurian theropods (e.g., [31]). Nonetheless, an extensor groove seems to be genuinely absent or very shallow in this specimen. In the ventral view, the calcaneum projects much more extensively in the posterior surface of the tibia than the astragalus.

4.1.2. Comparison

Despite being incomplete and somewhat distorted, this partial tibia and proximal tarsals have some features that allow discussion of their taxonomic assignment. This specimen shows some features that have been considered as apomorphies for Coelurosauria, including: (1) the almost inexistent facet for reception of the ascending process of the astragalus in the anterodistal end of the tibia (present in some alvarezsaurids [150] as well as in some non-coelurosaurian theropods such as *Afromimus tenerensis* [151]); (2) the ascending process of the astragalus arising from the entire breadth of the astragalar body (not present in *Coelurus fragilis* [152]; some compsognathids [153,154]; alvarezsaurids [155,156]; and therizinosauroids [157]); and (3) the length of the ascending process more than twice the height of the astragalar body [62,158]. In HUE-02696, the ascending process of the astragalus is separated from the condylar portion of the astragalus by a shallow but well-defined fossa, which is considered a derived feature shared by all maniraptoran coelurosaurs [31]. In addition, a calcaneum and astragalus that are fused to each other but not to the tibia, as present in the specimen from Lo Hueco, have been recovered in some analyses as a synapomorphy of the Paraves clade [31]. However, an unfused calcaneum and astragalus is a feature present in some dromaeosaurids, such as the velociraptorines *Deinonychus antirrhopus* (recovered as a dromaeosaurine by [34]) and *Bambiraptor feinbergorum* (considered as a Saurornitholestinae by [34]), the dromaeosaurines *Utahraptor ostrommaysorum* and *Achillobator giganticus*, the microraptorian *Sinornithosaurus millenii* (this taxon is codified as having unfused astragalus and calcaneum by [31], but it has fused proximal tarsals according to [159]), or the unenlagiines *Unenlagia comahuensis* and *Austroraptor cabazi* (e.g., [31,159]). On the other hand, a calcaneum and astragalus completely fused to each other and to the tibia to form a tibiotarsus is characteristic of most alvarezsaurids and avialians but uncommon among non-avian paravian coelurosaurs (e.g., [160–163]). This feature is present in the velociraptorine *Linheraptor exquisitus* (considered as a junior synonym of *Tsaagan mangas* by [31]), the microraptorines *Graciliraptor lujiatunensis* and *Microraptor zhaoianus*, the toodontids *Troodon formosus* and *Mei long*, as well as in the Paraves incertae sedis *Balaurs bondoc* (e.g., [27,28,31,164–167]).

The tibia of the specimen from Lo Hueco has a quite robust appearance that resembles the proportions of some early-branching coelurosaurians (e.g., *Anikosaurius darwini*) or some dromaeosaurine dromaeosaurids (e.g., *Achillobator giganticus* and *Utahraptor ostrommaysorum*) as well as a tibia attributed to the putative dromaeosaurid *Dakotaraptor steini*, rather than the gracile and elongate limb bones of most maniraptorans, including alvarezsaurids, ornithomimosaurians, therizinosauroids and deinonychosaurs (see Table 2). However, the diaphysis of the tibia of HUE-02696 is somewhat collapsed anteroposteriorly and the proximal end is absent, so it is not possible to ascertain if this feature is due to distortion or represents the actual morphology.

Table 2. Measurements of the tibia (HUE-02696), in millimeters, from Lo Hueco and other coelurosaurian theropods. L = length; W (mL) = mediolateral width of the diaphysis at mid-length; W (ap) = anteroposterior width of the diaphysis at mid-length; W (mL)/L = ratio between the mediolateral width of the diaphysis and the length; Wd (mL) = distal mediolateral width; Wd (ap) = distal anteroposterior width; Wd (mL)/L = ratio between the mediolateral distal width and the length. * Indicates incomplete element; ^(a) indicates estimated measurement; ⁽¹⁾ indicates measurements taken from published images.

Specimen	L	W (mL)	W (ap)	W (mL)/L	Wd (mL)	Wd (ap)	Wd (mL)/L
HUE-02696	244 * 260 ^(a)	31.7	18	0.12	54	29	0.21

Table 2. Cont.

Specimen	L	W (ml)	W (ap)	W (ml)/L	Wd (ml)	Wd (ap)	Wd (ml)/L
<i>Mahakala omnogovae</i> (IGM 100/1033) [168,169]	110	-	-	-	-	-	-
<i>Dakotaraptor steini</i> (PBMNH.P.10.113.T) [170]	673	68.4 ⁽¹⁾	-	0.10	-	-	-
<i>Unenlagia comahuesis</i> (MCF PVPH 78) [171]	418 *	-	-	-	63 *	-	0.15
<i>Buitreraptor gonzalezorum</i> (MPCA 238 and MPCA 245) [159,172]	>149	12.2 ⁽¹⁾	8.5 ⁽¹⁾	0.08	-	-	-
<i>Austroraptor cabazai</i> (MML-195) [172]	565	-	-	-	140	-	0.25
<i>Rahonavis ostromi</i> (UA 8656) [162,173]	118	5	5	0.04	10	4	0.08
<i>Graciliraptor lujiatunensis</i> (IVPP V 13474) [28,168]	115	-	-	-	-	-	-
<i>Utahraptor ostromaysi</i> (CEU 184v.260) [173,174]	505	76.5 ⁽¹⁾	47.7 ⁽¹⁾	0.15	145	-	0.29
<i>Deinonychus antirrhopus</i> (AMNH 3015) [28,173,175,176]	312	-	18	-	63.3 *	-	0.20
<i>Deinonychus antirrhopus</i> (MCZ 4371) [28,175]	368	-	28.5	-	73	-	0.20
<i>Saurornitholestes langstoni</i> (MOR 660) [28,169]	301	-	-	-	-	-	-
<i>Bambiraptor feinbergorum</i> (FIP 001) [30,31,177]	168	-	-	-	-	-	-
<i>Balaur bondoc</i> (EME PV.313) [27,28]	153	11	12	0.07	25	-	0.16
<i>Velociraptor mongoliensis</i> (IGM 100/986) [178]	255	20 ⁽¹⁾	17.8 ⁽¹⁾	0.07	38.7	20	0.15
<i>Achillobator giganticus</i> (MNUFR 15) [31,179]	490	60.4 ⁽¹⁾	39.4 ⁽¹⁾	0.12	113	22.4	0.23
<i>Linheraptor exquisitus</i> (IVPP V16923) [166]	255	-	-	-	-	-	-

The diaphysis is slightly bowed medially in the anterior view as occurs in *Coelurus fragilis* [152], *Velociraptor mongoliensis* [178] and several other coelurosaurians, but it is almost straight in *Dakotaraptor steini* [170], *Mononykus olecranus* [155] and *Buitreraptor gonzalezorum* [159,180]. Despite being almost completely absent, the preserved fragment of the cnemial crest indicates a position in the proximal end of the anterior surface. In this feature, HUE-02696 is similar to *Mahakala omnogovae*, *Buitreraptor gonzalezorum*, *Velociraptor mongoliensis* and most other theropods, but differs from *Balaur bondoc*, in which the distal end of the cnemial crest twists medially such that it terminates along the anteromedial edge of the tibial diaphysis [28]. This specimen shares with *Mahakala omnogovae*, some microraptorians, such as *Graciliraptor lujiatunensis* and *Microraptor zhaoianus*, the unenlagiins *Buitreraptor gonzalezorum* and *Rahonavis ostromi* (recovered as an early-branching bird in some works (e.g., [181]), but see [182,183] for a different interpretation), as well as the velociraptorines *Velociraptor mongoliensis* and *Deinonychus antirrhopus*, the presence of a short and low fibular crest on the lateral surface of the proximal section of the diaphysis of the tibia [168,170]. However, in *Buitreraptor gonzalezorum*, the fibular crest is more proximally placed, almost reaching the proximal margin of the tibia [159]. On the contrary, in some early-branching coelurosaurians, including *Coelurus fragilis* and in *Dakotaraptor steini*, the fibular crest is comparatively higher and longer [152,170].

The distal end of the astragalus and calcaneum with condyles is separated by a shallow, almost indefinite sulcus and is a feature shared with most dromaeosaurids, except *Buitreraptor gonzalezorum*, which has distinct condyles separated by a prominent extensor groove on the anterior surface as also occurs in most troodontids, some alvarezsaurids and early-branching avialans [28,31]. On the other hand, the calcaneum is continuous with the anterior surface of the astragalus, which is similar to the morphology of *Mahakala omnogovae*, *Velociraptor mongoliensis* and most other dromaeosaurids, but contrasts with *Deinonychus antirrhopus*, which has a more prominent calcaneum [168,178]. A flat surface in the distolateral margin of the tibia that extends to the dorsal margin of the calcaneum similar to that present in HUE-02696 is described in *Velociraptor mongoliensis* and is interpreted as the area of articulation with the distal end of the fibula [178]. If this interpretation is correct, the fibula would articulate with the calcaneum, as is typical for most non-avian theropods with rare exceptions, such as the dromaeosaurids *Mahakala omnogovae* and *Rahonavis ostromi* [31,162,168]. In addition, the fibula should have twisted proximally to articulate in the posterior surface of the fibular crest, which is a configuration that seems to also be present in *Velociraptor mongoliensis* [178]. The proximal margin of the ascending process of the astragalus is much incomplete in the specimen from Lo Hueco, but it seems to have somewhat inclined lateral and medial margins as occurs in most maniraptorans (e.g., [178]). However, in some dromaeosaurids, the medial margin of the

ascending process of the astragalus is inclined, but the lateral one is straight and coincident with the edge of the tibia along all the height, as occurs in *Mahakala omogovae* [168] and *Dakotaraptor steini* [170], or both margins are straight and mostly parallel as in *Buitreraptor gonzalezorum* [159]. In this feature, HUE-02696 is more similar to *Velociraptor mongoliensis* or *Deinonychus antirrhopus* (see Figure 2).

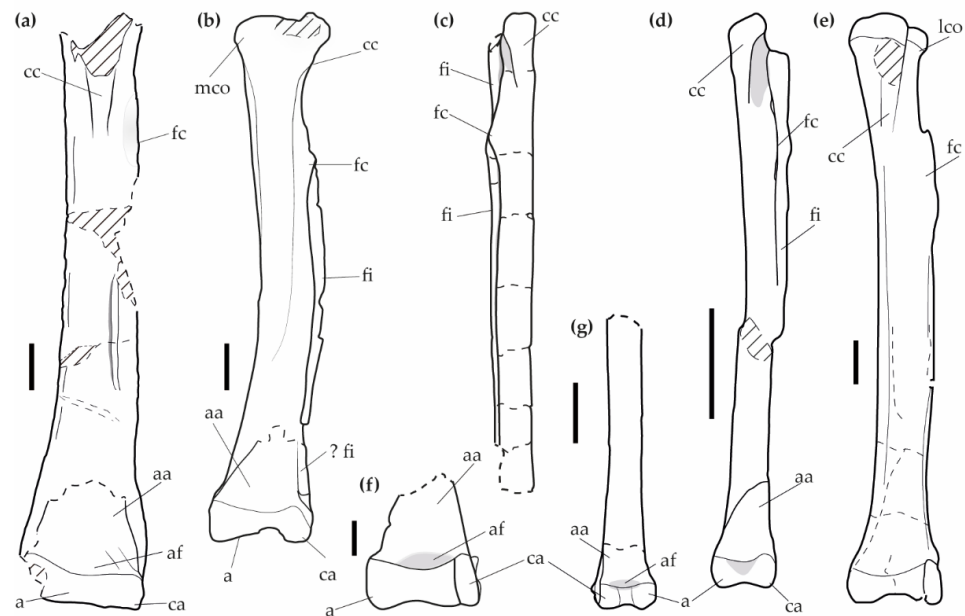


Figure 2. Line-drawing of the tibia and astragalus-calcaneum complex of different coelurosaurian theropods in anterior view: (a) HUE-02696; (b) left tibia and articulated proximal tarsals of *Velociraptor mongoliensis* (IGM 100/986) [178]; (c) proximal part of the right tibia and fibula of *Buitreraptor gonzalezorum* (MPCA 245) [159]; (d) left tibiotarsus of *Mahakala omogovae* (IGM 100/1033) [168]; (e) left tibia of *Dakotaraptor steini* (PBMNH.P.10.113.T) [170]; (f) left astragalus-calcaneum complex of *Deinonychus antirrhopus* (YPM 5226); (g) distal part of the right tibia articulated with the proximal tarsals of *Buitreraptor gonzalezorum* (MPCA 238) [159]. Abbreviations: a, astragalus; aa, ascending process of the astragalus; af, anterior fossa; ca, calcaneum; cc, cnemial crest; fc, fibular crest; fi, fibula; lco, lateral condyle; mco, medial condyle; ti, tibia. Question mark means uncertain interpretation. Scale bar (a–d) and (f–g) = 2 cm; (e) = 5 cm.

The combination of features present in this tibia and proximal tarsals from Lo Hueco are compatible with the identification of this specimen as a member of the dromaeosaurid clade. Within this group, HUE-02696 has a quite robust appearance that is strikingly distinct from the gracile morphology characteristic of unenlagiine and microraptorine dromaeosaurids. On the other hand, a fused astragalus and calcaneum as present in the specimen from Lo Hueco is a feature shared with some velociraptorines (except *Deinonychus antirrhopus*), in which the proximal tarsals are also sometimes fused with the tibia, as in *Tsaagan mangas*, whereas most dromaeosaurines have an unfused astragalus and calcaneum. Based on this combination of features, the specimen from Lo Hueco is assigned as a dromaeosaurid theropod and is tentatively interpreted as a member of the Velociraptorinae clade.

5. Discussion and Conclusions

The fossil record of theropod dinosaurs from the European Upper Cretaceous is fragmentary and mostly composed of isolated materials with uncertain taxonomic identification, which prevents our understanding on the evolutionary history of these faunas. This record includes only seven (or eight if *Variraptor mechinorum* and *Pyroraptor olympius* are different species) currently valid theropod taxa, besides some isolated teeth at-

tributed to *Richardoestesia* and *Paronychodon*. Most of these taxa, other than the abelisauroids *Arcovenator escotae* and *Tarascosaurus salluvicus*, have been interpreted as members of the Deinonychosauria clade. However, their phylogenetic affinities are not well established. Within this clade, the exceptions are *Balaur boldoc*, which was first interpreted as a velociraptorine but more recently has been tentatively related to Avialae and the recently described troodontid *Tamarro insperatus*. The Upper Cretaceous deposits of Spain have yielded the most diverse assemblage of theropods currently known in Europe (Figure 3). This record spans from the Cenomanian to the uppermost Maastrichtian and includes at least one large to medium-sized form related to abelisauroids and abundant materials attributed to different deinonychosaurians. An abundant record of abelisauroids is also known in correlative levels of France with at least two described taxa to which some specimens from Spain have been related. In addition, some appendicular elements and a few isolated teeth from the Santonian to early Campanian of Hungary have been also attributed to this clade. On the contrary, a large-sized predator has not been described from the Late Cretaceous record of Romania, which has been interpreted as related to island environmental constraints.

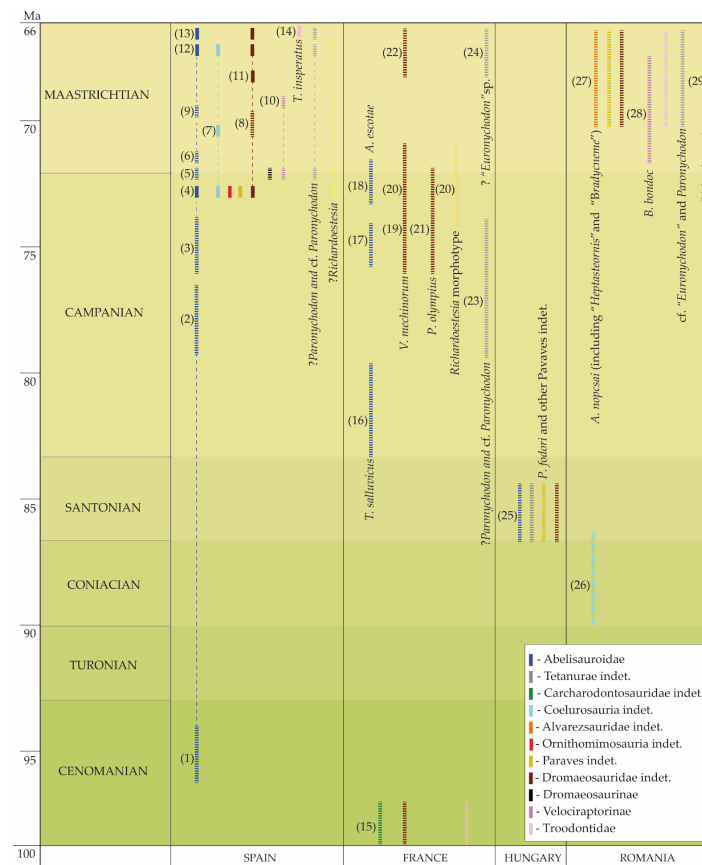


Figure 3. Temporal and geographical distribution of theropod dinosaur occurrences in the most significant European Late Cretaceous landmasses. Numbers in parenthesis indicate fossil sites: (1) Algora [8]; (2) Chera (e.g., [18,74]); (3) Armuña [37]; (4) Laño (e.g., [14,18]); (5) Lo Hueco [21,22]; (6) Poyos [35,91]; (7) Vicari 4 [14]; (8) Figuerola 2 [14]; (9) Montrebei [14]; (10) Peguera 1 [116]; (11) Fontllonga 6 [14]; (12) Blasi 1 and 2 [14]; (13) Serraduya del Pon/Beraruy and Moli del Baró [58]; (14) Sant Romá d'Abella [17]; (15) Charentes [184,185]; (16) Le Beausset [10]; (17) Pourcieux [36]; (18) Pourrières-Jas-Neuf [12]; (19) La Bastide Neuve [49]; (20) Cruzy and Vitrolles-La-Plaine [58,61]; (21) Trets-La Boucharde [47]; (22) Cassagnau [100]; (23) La Neuve [46]; (24) Marsoulas [5]; (25) Iharkút [4,5,186]; (26) Borod [5]; (27) Scoba, Sinpetru, Valioana, and Oarda de Jos (e.g., [42,117,119,126]); (28) Sebeş [27]; (29) Totesti [124]. The continuous line indicates precise occurrence, thin dashed line indicates uncertain temporal position and spaced dashed line indicates hypothetical occurrence (no data).

The fossil record of Late Cretaceous theropods from Spain is relatively abundant and diverse but is generally represented by fragmentary materials with uncertain taxonomic interpretations. At the moment, this record includes at least a medium to large-sized abelisauroid with a temporal distribution that extends from the middle-late Cenomanian to the late Maastrichtian (Figure 3). This record also includes a diverse assemblage of deeper nested theropods that are mostly identified based on isolated teeth attributed to dromaeosaurids, dromaeosaurines, velociraptorines, troodontids, *Richardoestesia* and *Paronychodon*. The tibia and proximal tarsals described are one of the few postcranial materials of theropod dinosaurs thus far described from the paleontological locality of Lo Hueco. This specimen has a combination of features compatible with velociraptorine deinonychosaurs, including the absence of a facet for the ascending process of the astragalus in the distal end of the tibia, the high and wide ascending process of the astragalus covering almost the entire mediolateral length of the distal tibia and extending more than twice the height of the astragalar body, the presence of a well-defined fossa at the base of the ascending process of the astragalus that separates the process from the condylar portion and the fusion of the calcaneum and astragalus. Based on this combination of features, HUE-02696 is interpreted as a eudromaeosaurid, tentatively related to Velociraptorinae. Materials attributed to velociraptorines have been described in several late Campanian and Maastrichtian localities of different European landmasses, mostly in Spain, Romania, and possibly in France. However, most of these materials are very fragmentary making it difficult to ascertain the phylogenetic affinities of the different European occurrences and their paleobiogeographic history. Most of the deinonychosaurian theropod groups identified in the European Late Cretaceous, including velociraptorines and troodontids, show a broad temporal range, extending from the upper Campanian up to the upper Maastrichtian. This distribution apparently indicates that the European theropod assemblages did not suffer significant changes of their composition during the last stages of the Late Cretaceous, which is in line with what has been found in previous works (e.g., [14,15,18,58]).

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