

The biota of the Upper Cretaceous site of Lo Hueco (Cuenca, Spain)

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Abstract

The Late Cretaceous (Campanian-Maastrichtian) fossil site of Lo Hueco was recently discovered close to the village of Fuentes (Cuenca, Spain) during the cutting of a little hill for installation of the railway of the Madrid-Levante high-speed train. To date, it has yielded a rich collection of well-preserved Cretaceous macrofossils, including plants, invertebrates, and vertebrates. The recovered fossil assemblage is mainly composed of plants, molluscs (bivalves and gastropods), actinopterygians and teleostean fishes, amphibians, panpleurodiran (bothremydids) and pancryptodiran turtles, squamate lizards, eusuchian crocodyliforms, rhabdodontid ornithopods, theropods (mainly dromaeosaurids), and titanosaur sauropods. This assemblage was deposited in a near-coastal muddy floodplain crossed by distributary sandy channels, exposed intermittently to brackish or marine and freshwater flooding as well as to partial or total desiccation events.

The Konzentrat-Lagerstatt of Lo Hueco constitutes a singular accumulation of fossils representing individuals of some particular lineages of continental tetrapods, especially titanosaurs, eusuchians and bothremiid turtles. In the case of the titanosaurs, the site has yielded multiple partial skeletons in anatomical connection or with a low dispersion of their skeletal elements. A combination of new taxa, new records of taxa previously known in the Iberian Peninsula, and relatively common taxa in the European record compose the Lo Hueco biota. The particular conditions of the fossil site of Lo Hueco and the preliminary results indicate that the analysis of the geological context, the floral and faunal content, and the taphonomical features of the site provide elements that will be especially useful for reassess the evolutionary history of some lineages of European Late Cretaceous reptiles.

Keywords: fossil vertebrates, biodiversity, Campanian-Maastrichtian, Cretaceous, Cuenca, Spain

Resumen

El yacimiento paleontológico de Lo Hueco fue descubierto recientemente en niveles del Cretácico Superior (Campaniense-Maastrichtiense) cerca de la localidad de Fuentes (Cuenca, España) durante el desmonte de una pequeña colina para la instalación de las vías del acceso ferroviario de alta velocidad Madrid-Levante. Hasta la fecha, el yacimiento ha proporcionado una abundante colección de microfósiles cretácicos en buen estado de preservación que incluye plantas, invertebrados y vertebrados. El conjunto de animales representados se compone principalmente de moluscos (bivalvos y gasterópodos), peces actinoptergios y teleósteos, anfibios, tortugas panpleurodiras (botremiididos) y pancryptodiras, lagartos, crocodylomorfos eusuquios, ornitópodos rhabdodóntidos, terópodos (principalmente dromeosáuridos) y saurópodos titanosáurios. Este conjunto se acumuló en un ambiente sedimentario correspondiente a una llanura de inundación fangosa cercana a la costa atravesada por canales distribuidores, expuesta de forma intermitente a condiciones salobres, marinas o dulceacuicolas, así como a eventos parciales o totales de desecación.

El Konzentrat-Lagerstatt de Lo Hueco constituye una acumulación singular de fósiles que representan individuos de algunos linajes de tetrapodos continentales, particularmente titanosáurios, eusuquios y bothremiididos. En el caso de los titanosáurios, el yacimiento ha proporcionado varios esqueletos parciales en conexión anatómica o con baja dispersión de sus elementos. La biota de Lo Hueco está compuesta por una combinación de nuevos taxones, nuevas citas para la Península Ibérica y taxones relativamente comunes en el ámbito europeo. Estas condiciones particulares, los resultados preliminares indican que el análisis del contexto geológico, el contenido de flora y fauna y las características tafonómicas del yacimiento son especialmente útiles para reevaluar la historia evolutiva de algunos linajes de reptiles del Cretácico Superior europeo.

Palabras clave: vertebrados fósiles, biodiversidad, Campaniense-Maastrichtiense, Cretácico, Cuenca, España

1. Introduction

The Upper Cretaceous (Campanian-Maastrichtian) marly mudstone fossil site of Lo Hueco is located near the village of Fuentes, Cuenca Province, Spain (Fig. 1). It was discovered in 2007 during the cutting of a little hill for installation of the Madrid-Levante train railway. The paleontological intervention in Lo Hueco was not a preventive or routine excavation. There was no previous evidence of the presence of a fossil bed there, so the discovery occurred after the onset of the activity of civil works. When the paleontological activity began, the fossil beds had already been partially affected by the earthworks and the presence of a huge amount of macrofossils in the site was evident. Under these conditions, both paleontological excavation and civil work planning significantly conditioned each other.

The evaluation phase started in July 2007, confirming the existence of a rich fossil site and characterizing the fossil beds and their size as comprising approximately ten hectares. At least two of these hectares were included in the area affected by the civil work. The first phase consisted in a single excavation campaign affecting near 100,000 cubic meters of sediments. This excavation involved the combination of various techniques: paleontological monitoring of the mechanical removal of levels, topographical and stratigraphic control of the extraction of fossils, systematic sampling of excavation grids and systematic collection of sediment samples for the analysis of the microfossils (Fig. 2). As a result, more than 10,000 fossil remains and 25 tons of rocks were

collected. This constitutes one of the largest collections of vertebrate remains from the Upper Cretaceous of Europe. Currently, the collection of Lo Hueco is housed in a 1,000 m² facility provided by the Museo de las Ciencias de Castilla-La Mancha in Cuenca, where a preparation laboratory has been established. The management of such a large and complex collection substantially makes the research activity of some taxonomic groups difficult, with particular requirements of conservation and preparation. Recently, the systematic preparation of this material has been intensified, particularly the one corresponding to the sauropod remains.

We consider that the study and interpretation of this fossil site will represent a relevant contribution to the knowledge of the southwestern European Upper Campanian-Lower Maastrichtian record. The present paper outlines the still very preliminary results obtained to date by the multidisciplinary group working on the analysis of the Lo Hueco collection.

2. Geological context

The fossil site of Lo Hueco is located in the southwestern branch of the Iberian Ranges, on the Arcas-Fuentes Syncline. It includes an interval in the “Garumn” facies, which is the informal term for the marls, clays and gypsums, mainly reddish, deposited in shallow marine, coastal or continental environments of south-western Europe during the last part of the Cretaceous and the early Paleogene (Leymerie, 1862). These beds belong to the upper part of the “Margas, Arcillas y Yesos de Villalba de la Sierra” Formation (Vilas *et al.*,

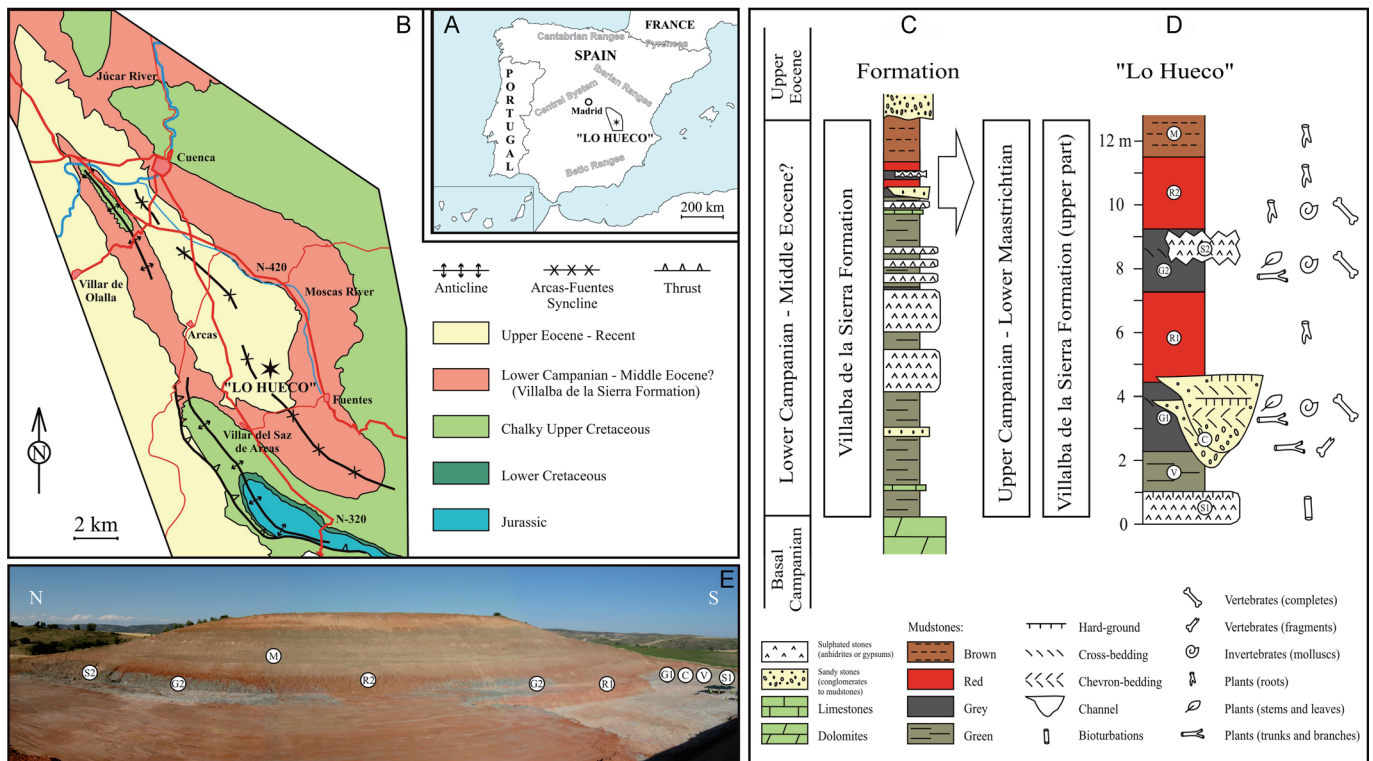


Fig. 1.- Geographic and geologic setting of the palaeontological site of Lo Hueco. A: General geographic location. B: Detailed geological situation inside the Arcas-Fuentes Syncline. C-D: Sections of the Villalba de la Sierra Formation (schematic, 1C), and of the site (detailed, 1D). E: Lateral view of the eastern talus of the outcrop during the excavation phase, with the identified lithosomes.

1982) (Fig. 1). A stratigraphic succession of green (V), grey (G1), red (R1), grey (G2), red (R2) and brown (M) beds of marly mudstones, separated by gradual boundaries, is identified in Lo Hueco. A sharp boundary partially modified the succession by a first sulphatic interval (S1) that cuts Bed V and by a second sulphatic interval (S2) that distorts at least part of Level G2. In addition, an erosive surface modified it by a sandy channel structure (C) that interrupts Levels V, G1 and R1 (Barroso-Barcenilla *et al.*, 2009a, 2010; Carenas *et al.*, 2011; Cambra-Moo *et al.*, 2012) (Fig. 1).

Four of these stratigraphic lithosomes have yielded the main part of the fossils from Lo Hueco: Structure C, Levels G1 and G2, and the lower part of Level R2. Lithosome C, interpreted as the deposits of a distributary sandy channel, is composed of sandy conglomerates and breccias, with a relatively high proportion of clasts (mainly pebbles of silica and phosphatic bone fragments, but also soft clasts of clays and carbonates) and a low proportion of matrix and cement (<20%), sandstones, and sandy mudstones. It exhibits numerous erosive surfaces and tractive deposits and has in its sandy mudstone fraction relevant proportions of quartz (30-25%), calcite (20-15%), feldspar (10-5%), and clay minerals (55-40%) (Barroso-Barcenilla *et al.*, 2009a, 2010; González-Acebrón *et al.*, 2010).

Bed G1 corresponds to the proximal part of a flooded muddy plain, close to the distributary channels. Bed G2 and the lower part of Bed R2, are respectively interpreted as the distal

part of a flooded muddy plain (distant from the distributary channels) and the partially or totally dried part of a muddy plain. All of them are composed of marly mudstones, with a relatively high proportion of clay minerals (>85%), moderate proportion of gypsums (<15%), and low proportion (10-5%) of calcium carbonates (calcite). These beds show mainly planar or parallel bedding and locally wavy and massive bedding, and some thin sandy interbeds with cross-bedding (especially in the upper part of Beds G1 and G2). Their clay minerals include illite (65-30%), kaolinite (50-20%), smectite (25-0%), and chlorite (2.5-0%) (Barroso-Barcenilla *et al.*, 2009b, 2010; Coruña *et al.*, 2011). All the stratigraphic lithosomes of this site contain a significant quantity of gypsum, but this mineral is especially abundant in the S1 and S2 intervals (Barroso-Barcenilla *et al.*, 2009a, 2010; Carenas *et al.*, 2011; González-Acebrón *et al.*, 2014).

3. Taphonomy

Concerning the fossil assemblage of Lo Hueco, several modes of preservation can be described (Fig. 3). Plants, mainly represented by fragments of wood, herbaceous stems and leaves, and roots, appear mostly as carbonified fossils (Fernández-López, 2000). Specifically, woody plants (tree trunks and some branches) usually maintain their original volume in part, with the interior partially or totally infilled or replaced by gypsum. Other plant specimens show resinous material in

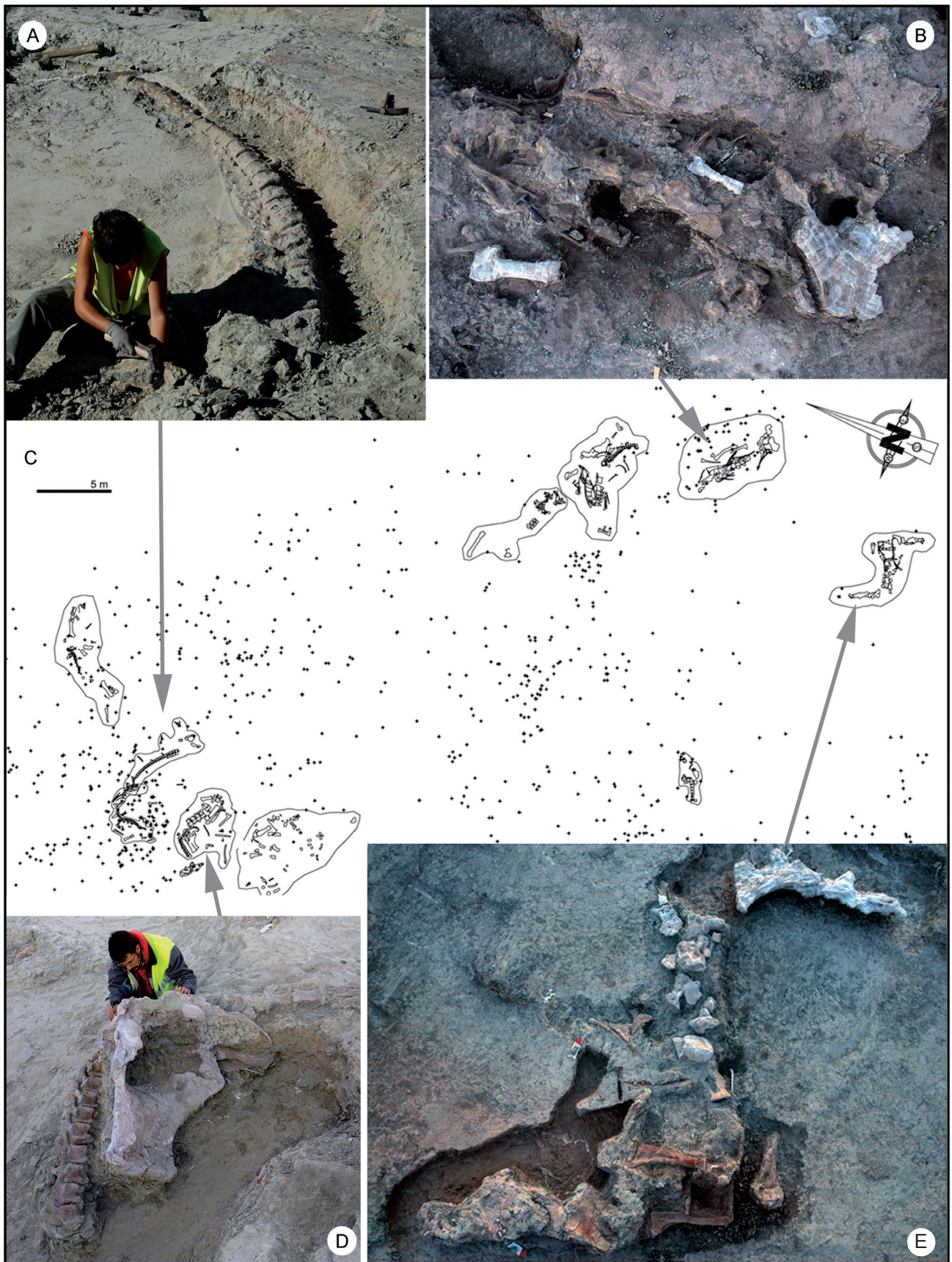


Fig. 2.- General cartography of one of the excavation areas (G1) at Lo Hueco and photographs of the extraction process of some specimens. A: Titanosauria indet. (HUE-02309), series of proximal caudal vertebrae. B: Titanosauria indet. (HUE-00984), series of dorsal vertebrae. C: Map of the extracted samples in the southern sector of the level G1 at Lo Hueco. D: Titanosauria indet. (HUE-02957), series of proximal caudal and posterior dorsal vertebrae and pelvic girdle. E: Titanosauria indet. (HUE-00267), series of cervical vertebrae and appendicular elements.

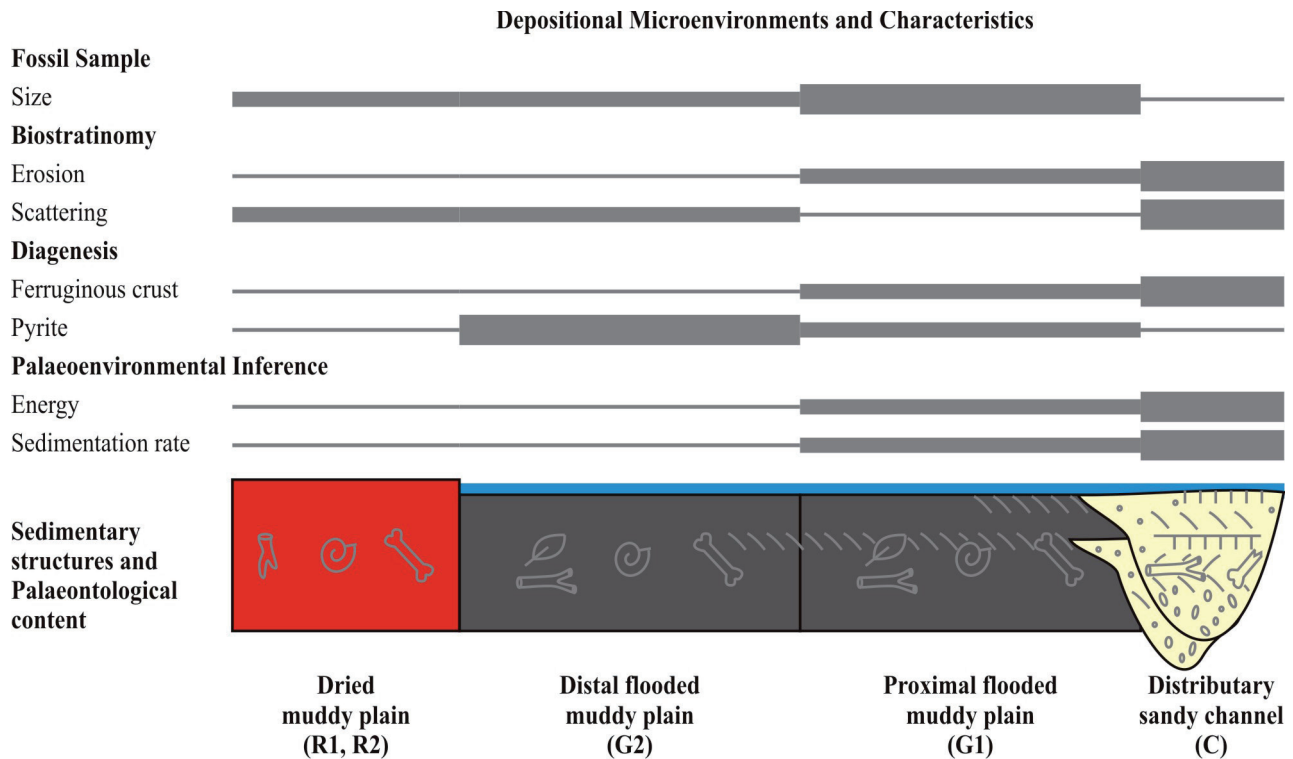


Fig. 3.- Taphonomic interpretation of the depositional microenvironments of Lo Hueco. The taphonomic alterations are measured in terms of: “Fossil sample size” (centimetric to decimetric), “Biostratinomy” that represents the early taphonomic alterations (Erosion: from no signs to largely abraded or fragmented remains; and Scattering: that represent the level of disarticulation and dispersion, from almost complete exemplars to isolated macroremains), “Diagenesis” (ferruginous crusts, and pyrite), and “Palaeoenvironmental inference” (energy, and sedimentation rate). The thickness of the horizontal bars represents the relative degree of the measured parameter. The symbols of the sedimentary structures and palaeontological content correspond to those of Fig. 1.

the lumen of their well-preserved tracheids and parenchyma cells (Cambra-Moo *et al.*, 2013). Invertebrates appear preserved as internal moulds of marly mudstones (bivalves) or gypsum (gastropods). Vertebrates, which constitute the largest part of the fossil assemblage, are represented by hard parts such as bones, teeth, plates, osteoderms and scales that mainly retain the original structure finely preserved in their interior with moderate diagenetic modifications. All of the vertebrate remains were restricted to Lithosome C, Beds G1 and G2, and the lower part of Bed R2, which has permitted us to define them, on the basis of their geological and taphonomic description, as taphofacies or bonebeds (*sensu* Rogers *et al.*, 2007; Cambra-Moo *et al.*, 2012). On the one hand, taking into account the biostratinomic description, it can be highlighted that Taphofacies C generally contains highly altered macrofossils (of centimetric size, fragmented and with signs of mechanical erosion processes, such as abrasion, see Fig. 3) that appear always disarticulated, scattered, and randomly distributed (Barroso-Barcenilla *et al.*, 2009a; Cambra-Moo *et al.*, 2009, 2012). On the other hand, the taphofacies G1, G2 and R2 have larger (of decimetric size, see Fig. 2) and slight or no eroded macrofossils. Specifically, Taphofacies G1 preserves an important number of totally or partially articulated specimens, mainly sauropod dinosaurs (the largest macroremains), with a low degree of scattering and a mainly parallel and perpendicular orientation to Taphofacies C. Taphofacies

G2 and R2, by contrast, contain macrofossils that are rarely articulated and randomly scattered (Barroso-Barcenilla *et al.*, 2009a; Cambra-Moo *et al.*, 2009, 2012).

Regarding diagenetic modifications, most macrofossils (especially bones) macroscopically have, from inside to outside: a first infilling of gypsum (in inner cavities), a ferruginous crust (outer surfaces, usually thicker in the fossils from Taphofacies C and G1 than in those from Taphofacies G2 and R2), and a second growth of gypsum crystals (covering outer surfaces and eventually crossing the ferruginous crust and first gypsum infilling). Some fossils, frequently from the darkest deposits of Taphofacies G1 and, mostly, G2 present microcrystalline pyrite formed inside their intimal structure (Barroso-Barcenilla *et al.*, 2009a; Cambra-Moo *et al.*, 2009, 2012).

4. Fossil record

The Lo Hueco site has yielded fossil remains representing both micro and macro plants and animals. The macroscopic invertebrate remains are relatively scarce and generally represented by gastropods and bivalves. The uniqueness of the site lies in the richness and abundance of vertebrate fossils (Ortega *et al.*, 2008). The main recognized groups are fishes, turtles, squamates, crocodylians, and non-avian dinosaurs. Among these, turtles, crocodiles and dinosaurs (orni-

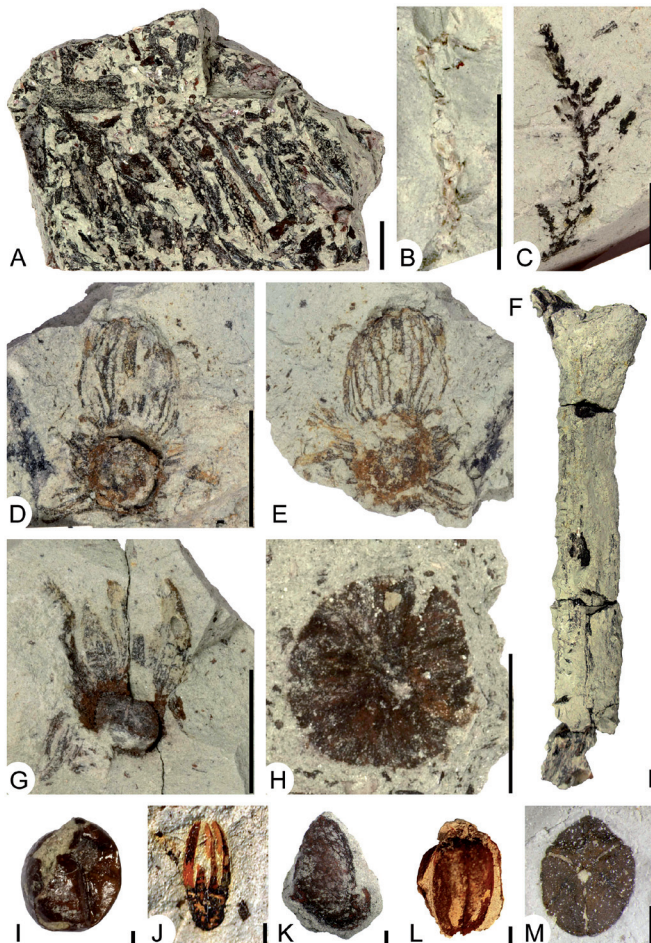


Fig. 4.- Vegetal remains from Lo Hueco. A: Slab of rock showing various plant fragments including numerous brown-coloured cuticles (HUE-06989). B: Unbranched, brachyphyllous conifer stem showing spirally-arranged, appressed leaves with free part equal or shorter in length than the leaf cushion (HUE-07484). C: Second-order branched, pagiophyllous, conifer stem showing several branches and spirally-arranged leaves with free part longer than the leaf cushion (HUE-08617). D-E: Probable freshwater, aquatic, free-floating *Limnobiophyllum* sp. showing a stocky stem with a unique orbicular leaf, campylodromous primary veins, longitudinal elongated meshes of higher order veins, and simple adventitious roots (HUE-08091). F: Carbonized stem showing a branching at the top (HUE-07719). G: Laterally-compressed *Limnobiophyllum* sp. showing a stocky stem with 5 (or more) rather lanceolate leaves, with faint campylodromous primary veins and a few adventitious roots (HUE-07484). H: Inflorescence-like specimen showing numerous units (flowers?) radiating from the centre (HUE-08618). I-M: Several types of seeds preserved as cuticles or iron oxides (HUE-05554, 07393, 07530, 08110, and 07594, respectively). Scale bar equals 10 mm in A-H and 1 mm in I-M.

thopods, theropods, and sauropods) are the best represented. The most abundant record of dinosaurs in Lo Hueco consists of thousands of titanosaur specimens that can be attributed to, at least, two distinct taxa. Albeit they are less abundant, the diversity of theropods is the greatest among the dinosaurs represented at Lo Hueco. Moreover, some groups mentioned in previous papers (e.g. Ortega et al., 2008), such as amphibians, some squamates, or possible remains of pterosaurs, are

so poorly represented that it is not possible, at present, to provide further information.

4.1. Palynomorphs

The preliminary analysis of the spore/pollen content revealed a relatively rich palynoflora, mainly integrated by terrestrial palynomorphs (Peyrot et al., 2013). The palynological assemblage is characterized by the dominant angiosperms, and subordinate spores and gymnosperms. The angiosperm component accounted for about 80 % of the pollinic sum and was represented by more than 20 taxa, including the common Upper Cretaceous monocolpates (*Arecipites*, *Liliacidites*, and *Monocolpopollenites*). Tricolpate and triporate pollen grains (including *Normapollens* representatives) were common but rarely reached dominance. Monoporate pollen grains related to modern representatives of Sparganiaceae, Restionaceae, and Thyphaceae were, however, well represented. The gymnosperms were mainly integrated *Inaperturopollenites* and bisaccate pollen grains related to Cupressaceae-Taxodiaceae and Pinaceae, respectively. Cryptogams included *Leptolepidites*, *Deltoidospora*, and *Polypodiaceoisporites*. The coenobial green algae *Pediastrum* spp. were consistently recorded in the samples. As a whole, the palynofloras suggest the presence of a tropical near-coast palaeovegetation integrated by swamp or local wetland vegetation with subordinate arboreal component (i.e. Fagales, gymnosperms). The palynofloras of the site revealed different micro-environments probably related to water availability within a near-coast environment. The presence of a high number of pollen grains related to Typhaceae, distinguishes the assemblages of Lo Hueco from other Late Cretaceous European palynofloras (Walbec, Maastricht, Campo, Tercis) (Peyrot et al., 2013).

4.2. Meso and mega plant remains

Fossil plants from Lo Hueco consist of millimetric (meso-) to pluricentric (mega-) remains. They are preserved as impressions and compressions, and include charred debris and cuticles (Fig. 4). Several specimens show yellow to orange iron oxide deposits on their surfaces and inside the structures. Some others have infillings of gypsum or are contained inside gypsum.

Spirally-arranged leaved conifers include shoots of *Brachyphyllum* type, with the length of free part of appressed leaf equal or shorter than the leaf cushion, and of *Pagiophyllum* type with the free part longer than the leaf cushion.

Large leaf laminae suggest that several types of angiosperms are present (Fig. 4). Among these are specimens that closely resemble the freshwater free-floating fossil *Limnobiophyllum* (Stockey et al., 1997). The extremely short, stocky stem, the single-developed, sessile, entire-margined, orbicular leaf, the campylodromous venation with 10 or 11 primary veins, the longitudinal elongated meshes of higher order veins, and the numerous simple adventitious roots of

the specimen HUE-08091 (Fig. 4D, E) are features that definitively fall within the range of the genus diagnosis emended by Stockey *et al.* (1997). The specimen HUE-07484 (Fig. 4) is laterally compressed, and shows five leaves with fainter venation pattern. Due to the resemblance with living plants such as the freshwater *Spirodela* Schleiden, Kvaček (1995) and Stockey *et al.* (1997) placed *Limnobiophyllum* in Lemnaceae within Arales. However, considering the most recent phylogeny, *Limnobiophyllum* must be now included in Lemnoideae of Araceae and within Alismatales. Some specimens correspond to angiosperm reproductive organs. A globular inflorescence shows numerous units (flowers?) radiating from the centre (Fig. 4H). There are several types of seeds (Fig. 4I-M). Cuticles were extracted using maceration of bulk sediments in a dilute solution of hydrogen peroxide, washed and sieved under tap water, and prepared and examined under light microscope and scanning electron microscope (SEM). Stumps, roots, logs, and branches are also present and those preserved as charcoals were studied under SEM.

4.3. Molluscs

The Lo Hueco taphonomic conditions for the fossilization of carbonated remains justify the low number of collected specimens, biasing the real abundance and diversity of these invertebrates in the palaeoenvironment.

Molluscs are mainly preserved as internal casts of marly mudstones without hinge details (bivalves), or of gypsum (most of gastropods), and have been kept in open nomenclature until additional discovery of more complete specimens. Bivalves are recorded as freshwater unionids assigned to Margaritiferidae (?*Margaritifera*) and Unionidae (?*Anodonta*), and as heterodontids from Corbiculidae (?*Corbicula*) and Pisidiidae (?*Pisidium*). Gastropods are known after at least two species of possible Melanopsidae (?*Faunus*) (Callapez *et al.*, 2011, 2013). Due to poor preservation, these taxonomic identifications are tentatively based on the overall shape and details of external ornamentation visible in the composite moulds. Both bivalve and gastropod taxa are widely known from the Upper Cretaceous and Cenozoic freshwater environments. The occurrence of Melanopsidae can also be related to some influence of moderately brackish conditions. All bivalves have been found disarticulated, a fact that can be related to energetic episodes in the aquatic depositional environment. Therefore, although their presence at the site is rare, these aquatic molluscs provide additional data that improve our knowledge about the reconstruction of the original Cretaceous palaeoenvironment and its ecosystem.

4.4. Fishes

Fossil fishes from Lo Hueco have been collected from screenwashing and picking of fossil micro-remains. Most of the specimens consist of isolated fish remains (Fig. 5), and mainly correspond to ganoid scales and teeth (Torices *et al.*,

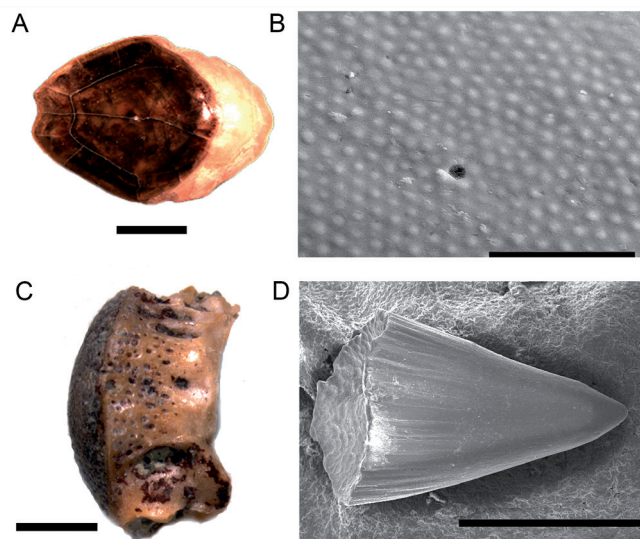


Fig. 5.- Fish remains from Lo Hueco. A: Lepisosteid dorsal ganoid scale (HUE-09000). B: Microornamentation of the ganoid surface of a lepisosteid scale (HUE-09017) under SEM observation. C: Lepisosteid opisthocoelic cervical vertebrae (HUE-09024). D: Apical fragment of lepisosteid plicidentine tooth under SEM observation. Scale bar equals 1 mm in A, C-D and 50 µm in B.

2010a, 2011; Serrano *et al.*, 2012). Most of the scales present the general morphology of those of the lepisosteids (Actinopterygii, Lepisosteidae): rhomboidal contour and cross section composed of two layers, an upper ganoid layer and a basal bony one. Lepisosteids are a very abundant freshwater neopterygian group from the Upper Cretaceous and Cenozoic continental deposits worldwide (Wiley, 1976; Grande, 2010). However, nowadays they are restricted to the Eastern portion of North America and Central America.

The technique used for studying ganoid scales follows the methodology proposed by Gayet and Meunier (1986), who analyzed and compared the differences in the ornamental pattern among the different groups of actinopterygian fishes with ganoid scales. The scale ornamentation consists of micrometric ganoid tubercles spread over the scale surface. According to these authors, the size of these tubercles and the distance between them are constant not only within each lineage, but also within each genus (Gayet and Meunier, 1986; Gayet *et al.*, 2002).

The analysis of the scale micro-ornamentation under SEM observation (Fig. 5) assigns the scales from Lo Hueco to *Atractosteus*, in contrast to previous works that assigned them to *Lepisosteus* (Serrano *et al.*, 2012). The presence of *Atractosteus* in the Iberian Peninsula was also documented in the Upper Campanian-basal Maastrichtian of Laño (Condado de Treviño, Burgos), based on an isolated supracleithrum (Cavin, 1999).

Other lepisosteid remains recovered are teeth with plicidentine, skull bones, and opisthocoelic vertebrae. These vertebrae are unique to this lineage within Actinopterygii (Wiley, 1976; Grande, 2010). Less abundant are teeth assigned to other actinopterygian fishes: Pycnodontoidea, Amiidae,

and Albulidae (Torices *et al.*, 2010a, 2011). Numerous amphicoelic vertebrae have also been collected, which can be only considered for the time as corresponding to unidentified Actinopterygii members.

4.5. Turtles

The first identified and described articulated remains of Bothremydidae in the Spanish record came from Lo Hueco (Pérez-García *et al.*, 2009a). The abundant material recovered (Fig. 6A-D) is providing relevant information to increase the knowledge of this clade of Pleurodira. A high percentage of the turtle specimens identified corresponds to Bothremydidae. Prior to the study of this material, *Polysternon* was regarded as the unique representative of Bothremydidae whose presence was confirmed in the Spanish record (Lapparent de Broin and Murelaga, 1999). Some articulated specimens of Lo Hueco show that other bothremydid taxa also inhabited the Iberian Peninsula in the Late Cretaceous. In addition, some plates recognized from other localities are similar to those of the bothremydids of Lo Hueco (Pérez-García *et al.*, 2010). In this sense, “*Elochelys*” *convenarum*, a taxon so far only recognized by its holotype, a relatively complete shell from the Maastrichtian of Haute-Garonne (France) (Laurent *et al.*, 2002a), is identified in Lo Hueco. The information on the morphological variability of the European bothremydids is so far very limited. The comparison between the material

known of *Elochelys perfecta* and the specimens identified as “*Elochelys*” *convenarum* open the discussion of the validity of the two species of the genus, allowing the possibility to expand the known range of intraspecific variation in both species. However, given the criteria used for the identification of other members of Bothremydidae, the combination of characters that distinguish these two species justifies their assignment to two distinct genera. The species present in Lo Hueco was assigned to the new genus *Iberoccitanemys* (Pérez-García *et al.*, 2012a).

A second member of Foxemydina within Bothremydidae is present in Lo Hueco (Fig. 6). The current state of knowledge allows its identification as an indeterminate taxon belonging to the clade of *Polysternon* and *Foxemys*. This identification is the first evidence that robustly demonstrates the sympatric coexistence of two different members of Bothremydidae in a Late Cretaceous ecosystem of Europe (Pérez-García *et al.*, 2013). The identification of a member of Bothremydidae naturally leads to the assignment of the other specimens found in the same locality to the same taxon. However, the recognition of two taxa in the same site shows that the revision of many of the previous identifications is necessary. In fact, many of them should be reassigned to Bothremydidae indet. or to Foxemydina indet.

Besides members of Bothremydidae, a second clade of turtles, whose record is very rare, is identified in the site of Lo Hueco. It is attributed to an indeterminate representative

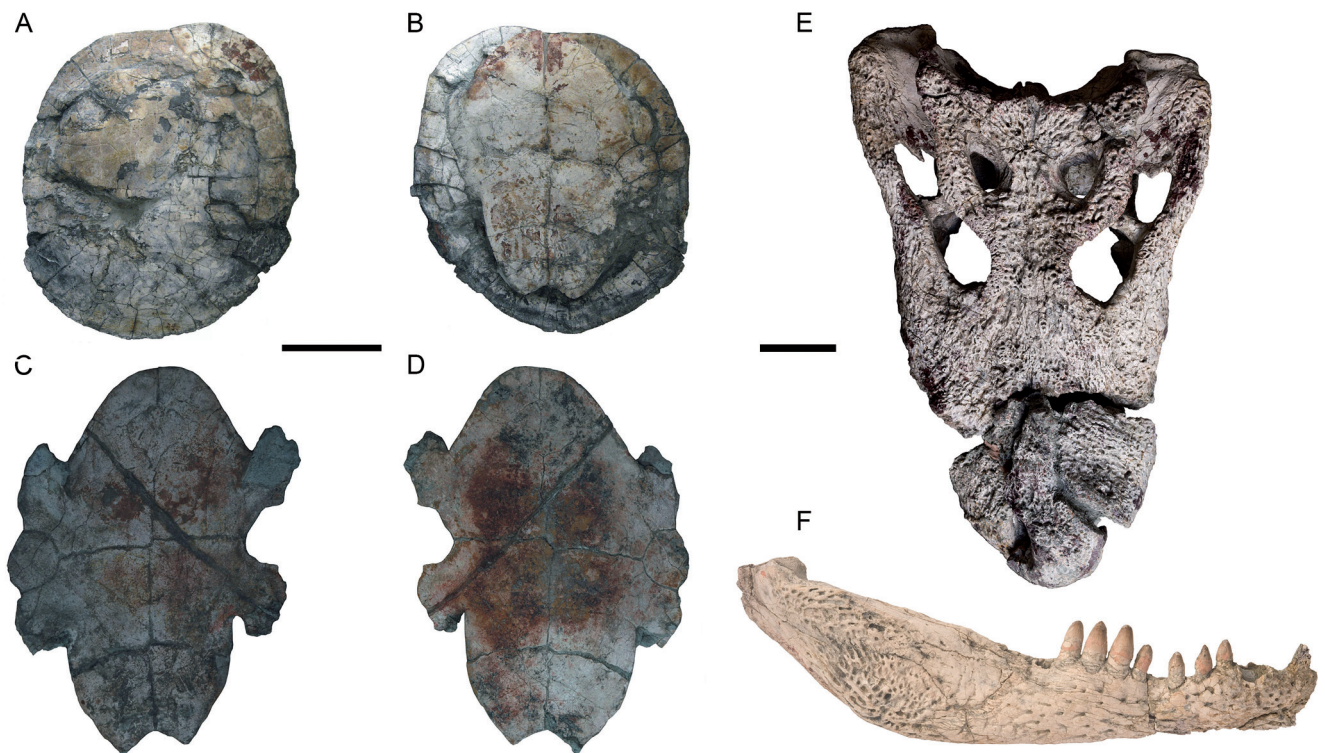


Fig. 6.- Testudines and crocodyliform remains from Lo Hueco. A-B: Dorsal (A) and ventral (B) views of a shell of the bothremydid turtle *Iberoccitanemys convenarum* (HUE-04913). C-D: Dorsal (C) and ventral (D) views of a plastron of a bothremydid *Foxemydina* indet. (HUE-01220). E: Dorsal view of the skull of a non-crocodylian Eusuchia (HUE-02920). F: Labial view of the mandible of a non-crocodylian Eusuchia (HUE-05161). Scale bar equals 50 mm.

of Pan-Cryptodira (Pérez-García *et al.*, 2009b). It is a large turtle, with a carapace at least one metre in length. Despite the abundance of members of Solemydidae (stem Testudines) and Dortokidae (stem Pleurodira) in the southwestern European Late Cretaceous record (Lapparent de Broin and Murelaga, 1999; Pérez-García *et al.*, 2012b), none of them has been collected in Lo Hueco.

4.6. Squamates

Squamate remains are relatively rare at Lo Hueco, but the specimens are recognized as highly diverse when compared to the available record from the Late Cretaceous of Europe. Some Spanish sites have yielded squamate remains that mostly do not have a precise identification. For example, some remains of lacertilians and madtsoiid snakes at Laño (Rage, 1999), Anguidae and Lacertoidea at Arén (López-Martínez *et al.*, 2001; Blain *et al.*, 2010), and some unidentified cranial fragments and isolated vertebrae in Chera, Valencia (Company, 2004) have been reported. Some unidentified forms (including varanoids) have also been described in Aveiro, Viso, and Taveiro, Portugal (Antunes and de Broin, 1988). In southern France, several squamates have been reported in Champ-Garimond (Iguanidae indet., Lacertilia indet.), Casagnau (Varanoidea indet.), and Cruzy (Varanoidea indet. and Lacertilia indet.) (Buffetaut *et al.*, 1996, 1999; Sigé *et al.*, 1997; Garcia *et al.*, 1999, 2000; Laurent *et al.*, 2002b).

At Lo Hueco, a set of cranial elements that were preliminary assigned to Lacertoidea (a mandibular fragment and an isolated tooth) and Iguania (several maxillary and mandibular remains with some tricuspid teeth) (Narváez and Ortega, 2010; Torices *et al.*, 2010a) have been recognized.

Various vertebrae, probably belonging to a new genus of Varanoidea, have also been collected. Their anatomical and microanatomical features reveal that these vertebrae probably belong to a non-marine “pythonomorph-lizard” (Houssaye *et al.*, 2013).

Most of the micro and macro remains, currently under study, correspond to taxa hitherto unpublished for the Iberian record. Therefore, the diversity of the Upper Cretaceous Iberian squamate fauna is clearly higher than recognized presently.

4.7. Crocodyliforms

Crocodyliformes are one of the most abundant and better-preserved vertebrate groups represented at Lo Hueco. Abundant isolated and articulated cranial and postcranial bones have been found (Fig. 6E-F). Presently, a set of ten skulls has been collected and identified, in a preliminary analysis, as belonging to at least two different taxa of non-Crocodylia eusuchians.

The first is a medium-sized crocodyliform with a relatively wide and round rostrum (Fig. 6E-F). It has characteristic large teeth, separated by narrow interalveolar spaces. Although

this taxon has a close relationship with *Allodaposuchus*, it shows remarkable differences that suggest that it is a new genus (Narváez and Ortega, 2012; Narváez *et al.*, 2013). The second crocodyliform is also a medium-sized animal that has a more elongate snout and a slender rostrum. It also exhibits features that suggest a close relationship with the Iberian *Allodaposuchus*, but, again, it has characters that distinguish it from the known representatives of this genus and from the other crocodile represented at the site.

Members of two groups probably compose the European record of non-crocodylian eusuchians. The first is Hylaeochampsidae, a monophyletic group represented by small forms as *Hylaeochampsia*, from the Barremian of the Isle of Wight (Clark and Norell, 1992); *Pietraroiasuchus*, from the Albian of Italy (Buscalioni *et al.*, 2011); *Iharkutosuchus*, from the Santonian of Hungary (Ősi *et al.*, 2007); and *Acynodon* from the Campanian-Maastrichtian of Spain, France and Italy (Buscalioni *et al.*, 1997, 1999; Martin, 2007; Delfino *et al.*, 2008). Specimens from Romania, France and Spain compose a second non-crocodylian eusuchian group (Buscalioni *et al.*, 2001; Puértolas-Pascual *et al.*, 2014) generally assigned to *Allodaposuchus*.

Other taxa from the Upper Cretaceous of Europe, such as the supposed alligatoroids *Massaliasuchus* and *Musturbalsuchus*, from France and Spain (Buscalioni *et al.*, 1997, 1999; Martin and Buffetaut, 2008) or the putative Spanish crocodyloid *Arenysuchus* from Spain (Puértolas *et al.*, 2011), are probably also close to these basal groups (Narváez and Ortega, 2011). Most recent phylogenetic analyses (Buscalioni *et al.*, 2011; Puértolas-Pascual *et al.*, 2014) place *Allodaposuchus* as the sister clade of Hylaeochampsidae.

The preliminary study of Lo Hueco taxa indicates that they are related to forms close to *Allodaposuchus* and phylogenetically situated at the base of Eusuchia. This supports the hypothesis of the existence of a group of basal non-crocodylian eusuchians formed exclusively by European taxa, and shows a complex distribution of these forms in the Upper Cretaceous European Archipelago (Narváez *et al.*, 2013).

4.8. Ornithischian dinosaurs

Although some preliminary works indicated the possible presence of ankylosaur remains (Ortega *et al.*, 2008), the presence of thyreophorans is not certain at Lo Hueco. Consequently, the ornithischians at Lo Hueco are presently restricted to the basal iguanodontian Rhabdodontidae. This group of ornithopod dinosaurs is considered as both endemic from the Late Cretaceous of Europe (Weishampel *et al.*, 2003; Ősi *et al.*, 2012) and having a more complicated evolutionary history given the controversial systematic position of the Australian genus *Muttaborrasaurus* (McDonald, 2012). The clade includes three genera, each containing two species, ranging from the Santonian to the Maastrichtian. In southern France and the Iberian Peninsula, only *Rhabdodon* is recognized, whereas in Austria, Hungary and Romania two genera

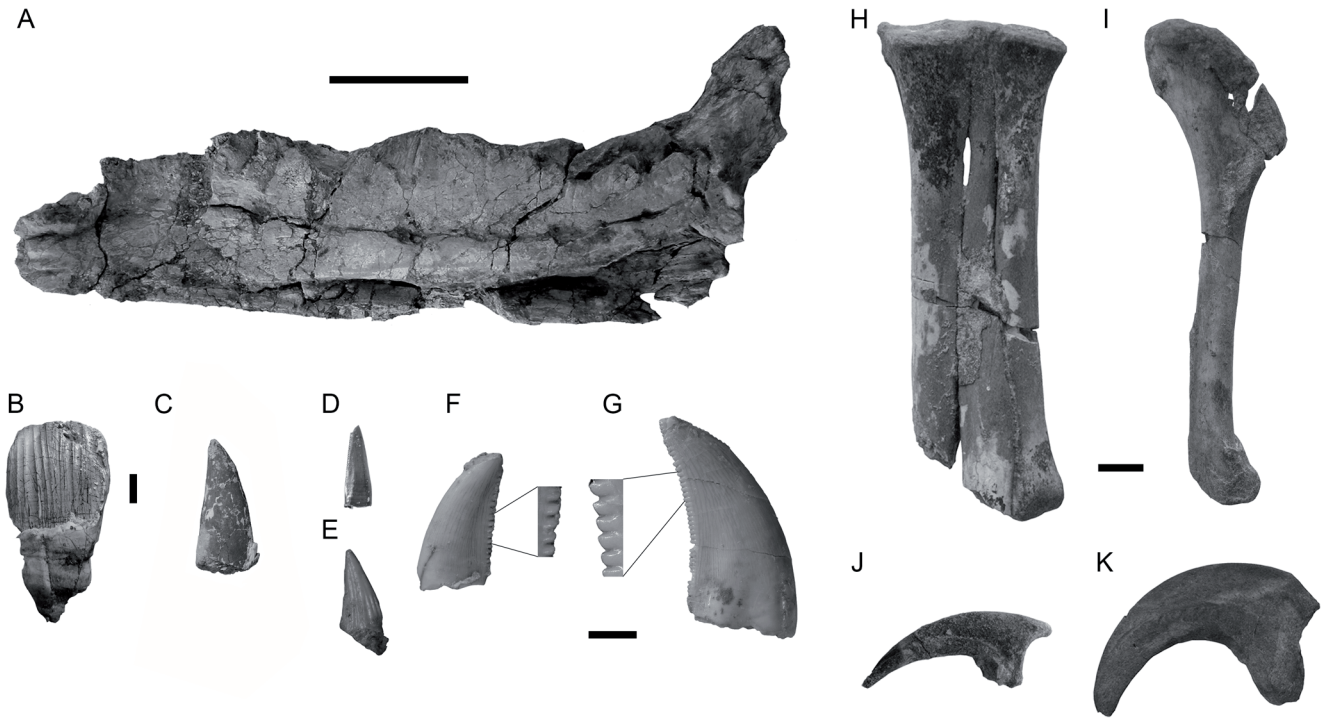


Fig. 7.- Cranial and postcranial ornithomorph and theropod remains from Lo Hueco A: Right dentary of the ornithomorph *Rhabdodon* sp. (HUE-05310) in lingual view. B: Maxillary tooth of the ornithomorph *Rhabdodon* sp. (HUE-04479) in labial view. C: Tooth of Theropoda indet. (HUE-10054). D: Tooth of cf. *Richardoestesia* (HUE-10050). E: Tooth of cf. *Paronychodon* (HUE-10053). F: Tooth of Dromaeosaurinae indet. (HUE-10052). G: Tooth of Velociraptorinae indet. (HUE-10051). H: Theropod metatarsals in anterior view (HUE-08445). I: Left theropod humerus in medial view (HUE-08477). J-K: Theropod ungual phalanx (HUE-08466 and HUE-02991). Scale bar equals 50 mm in A, 3mm in B-G, and 100 mm in H-K. (HUE-08466 y HUE-02991).

(*Mochlodon* and *Zalmoxes*) have been described (Ösi et al., 2012).

The rhabdodontid remains of Lo Hueco include cranial and postcranial bones (Fig. 7A-B). The cranial remains consist of isolated dentary and maxillary teeth and a right dentary (Escaso et al., 2009). Both maxillary and dentary teeth are similar to those of rhabdodontids in having a well-developed and central primary ridge. Moreover, the isolated maxillary teeth bear parallel ridges as in other rhabdodontids. The general morphology of the dentary is similar to that of other rhabdodontids and it shares with *Rhabdodon* and *Zalmoxes* a rostroventrally-inclined symphysis. A recent work on the rhabdodontid postcranial remains of Lo Hueco described two femora and an ischium of three different individuals (Escaso et al., 2012). This work concluded that the femora are robust as in *Rhabdodon* individuals, differing from *Mochlodon* and *Zalmoxes*, in which the femora are more lightly constructed (Ösi et al., 2012). The morphology of the ischium is similar to that of *Zalmoxes* (Weishampel et al., 2003) and *Rhabdodon* (Pincemaille-Quillévéré, 2002).

In conclusion, the rhabdodontids of Lo Hueco show a character combination that is not conclusive, but that is congruent with the described morphological variation of *Rhabdodon*. Thus, it is preferred provisionally to refer these ornithomorphs to *Rhabdodon* sp.

4.9. Theropod dinosaurs

The theropod remains mainly consist of teeth and scarcer postcranial material (Fig. 7C-K). The diversity at the site is constituted by a medium-size primitive form, whose characters are congruent with abelisaurid ceratosaurians previously described from the Iberocretaceous Upper Cretaceous (Astibia et al., 1990; Le Loeuff, 1992; Tortosa et al., 2014), and remains of maniraptoran theropods representing various members of Paraves, whose analysis is still in progress. Presently, theropod diversity at Lo Hueco has been established on the basis on teeth whose analysis identifies five morphotypes. Two of the morphotypes present a very similar morphological blade-like shape with similar height, FABL (fore-aft basal length), and width. In both, posterior denticles density is 2.5-6 denticles per millimetre (measured in the middle of the carina) and the anterior denticle density is 3-6 denticles per millimetre. These characters are comparable quantitatively and qualitatively with those described in dromaeosaurid teeth. However, a morphotype presents posterior and anterior square denticles, while the other presents denticles that are slightly pointed towards the top of the tooth. Based on these differences, the first is attributed to Dromaeosaurinae (Fig. 7F) whereas the second is attributed to Velociraptorinae (Fig. 7G) (Torices et al., 2012).



Fig. 8.- Cranial and postcranial titanosaurian remains from Lo Hueco. A-B: Tooth (HUE-01212) in labial (A) and lingual (B) views. C-D: Tooth (HUE-02687) in distal (C) and labial (D) views. E-F: Skull (HUE-08741) referred to *Ampelosaurus* sp. (*sensu* Knoll et al., 2013) in dorsal (E) and ventral (F) views. G: Anterior cervical vertebra (HUE-03128) in left view. H: Anterior caudal vertebra (HUE-03101) in left view. I: Middle caudal vertebra (HUE-03028) in left view. J: Right ischium (HUE-03134/16) in lateral view. K: Left humerus (HUE-01549) in anterior view. L-M: Two right femurs (HUE-03108 and HUE-01319) in posterior view. N: Right fibula (HUE-03087) in lateral view. O: Right tibia (HUE-03082) in posterior view. P-R: Osteoderm (HUE-00561) in dorsal (P), ventral (Q), and lateral (R) views. S-T: Osteoderm (HUE-01330) in dorsal (S) and lateral (T) views. Scale bar equals 50 mm in A-F, and 100 mm in the remaining figures. Abbreviations: cc, cnemial crest; dc, deltopectoral crest; lb, lateral bulges; ts, trochanter shelf.

A small tooth represents the third morphotype (Fig. 7D). The general morphology of the tooth resembles an isosceles triangle and its denticles are small. Morphological and morphometric characters are similar to those of the teeth attributed to *Richardoestesia*, and so, are identified as cf. *Richardoestesia* (Torices et al., 2010b, 2012).

The fourth morphotype is represented by a small tooth with longitudinal ridges along the labial and lingual flanks (Fig. 7E). These longitudinal ridges are similar to those of the teeth of *Paronychodon* from the Upper Cretaceous of North America (Torices et al., 2012).

The fifth morphotype belongs to a larger, medium-size theropod (Fig. 7C). Unfortunately, it is badly preserved and the enamel has disappeared. Its general morphology is blade-like, laterally-compressed and it is possible to observe the trace of denticles that have been eroded. For this reason it can only be identified as Theropoda indet. (Torices et al., 2012).

The abundance of theropod teeth (nearly one hundred and fifty recovered teeth) makes the record of Lo Hueco one of the richest in Europe. The composition of this carnivorous fauna is similar to others described for the same age in the Iberian Peninsula and Europe with the presence of different taxa of dromeosaurids, a large theropod, and taxa similar to the North Americans *Richardoestesia* and *Paronychodon* (Torices et al., in press).

4.10. Sauropod dinosaurs

The presently known diversity of titanosaurian sauropods from the Upper Cretaceous of Europe is so far composed of five genera. However, new evidence indicates that it was probably higher. There are two valid genera described in southern France: *Ampelosaurus atacis* (Le Loeuff, 1995) and *Atsinganosaurus velauciensis* (Garcia et al., 2010). Two additional titanosaurs are known from Transylvania (now central Romania): *Magyarosaurus dacus* (Huene, 1932) and *Paludititan nalatzensis* (Csiki et al., 2010). In northern Spain, the Upper Cretaceous site of Laño yielded material referred to the only Iberian titanosaur described to date: *Lirainosaurus astibiae* (Sanz et al., 1999).

So far, Lo Hueco has yielded more than 10,000 fossils of which nearly half corresponds to titanosaurian remains (Fig. 2). There are more than twenty sets representing partial skeletons of several individuals. These partial skeletons frequently preserve parts of the series of caudal vertebrae that can be articulated with elements of the pelvic girdle, appendicular remains, and even with part of the dorsal vertebrae series. The analysis of the distribution of the isolated remains in the fossil site will establish the relationship between them and several of the partial skeletons, providing a relatively complete sampling of some of the represented taxa. For the moment, preliminary comparisons indicate the presence of at least two titanosaur morphotypes based on two types of cranial morphologies, appendicular bones, and teeth.

Despite the wealth of sauropod bones collected from Lo Hueco, only few cranial specimens have been retrieved. Among them, are two types of braincases. One (Fig. 8E-F) presents some similarities with the braincase of *Ampelosaurus atacis* from the Upper Campanian-Lower Maastrichtian of France. However, there are also many differences that suggest its consideration as *Ampelosaurus* sp. (Knoll et al., 2013a). The other is a short and deep skull in overall morphology. It also presents a flat occiput that is a phylogenetically restricted character within titanosaurs. This same condition is found in both *Ampelosaurus* and *Jainosaurus septentrionalis*, the latter from the Maastrichtian of India. Nevertheless, this second morphotype presents a dorsoventrally elliptical foramen magnum that differentiates it from *Ampelosaurus*. It appears close to the “*Jainosaurus* morph” braincase and a phylogenetic proximity with *Jainosaurus* is likely (Knoll et al., 2013b).

The analysis of the sauropod tooth morphology at Lo Hueco (Fig. 8A-B) also identifies two morphotypes that can be correlated to those of other European titanosaurs (Díez Díaz et al., 2013). The first (Fig. 8A) has the same morphology as the robust spatulated teeth found in Fox-Amphoux-Métisson, southern France (Díez Díaz et al., 2012a) and Masecaps (Díez Díaz et al., 2013). The second morphotype (Fig. 8B) is similar to the gracile spatulated teeth of *Atsinganosaurus* (Díez Díaz et al., 2014). The microwear patterns on the apical wear facets of both morphotypes of teeth support the hypothesis of a non-selective diet on soft stems, such as herbaceous plants. However, the microwear differences also suggest niche partition for both species (Díez Díaz et al., 2014).

Titanosaurian osteoderms are commonly found at Lo Hueco (Fig. 8P-T). All these osteoderms are variations of the described bulb and root morphotype (Csiki, 1999; D’Emic et al. 2009). They are large osteoderms with an amygdaloid outline, one or more visceral keels and two well differentiated regions: a round end (the bulb), and a more elongated and irregularly ornamented region (the root). These osteoderms display a high variability ranging from rounded osteoderms, whose roots are a just little bit longer than the bulb (Fig. 8P, Q, T), to elongated osteoderms, whose roots are up to five times longer than the bulb (Fig. 8R-S). One titanosaurian individual (specimen HUE-EC-3) was found associated with two osteoderms: one very elongated and a rounded one. This supports the idea that the variability of osteoderms found at Lo Hueco represents intra-individual variability (Vidal et al., 2014).

The study of the axial and appendicular remains (Fig. 8G-O) is in a preliminary stage, but it also confirms the presence of two types of titanosaurs (Ortega et al., 2008). Although based on partial results, the phylogenetic assignment of Lo Hueco titanosaurs and their relationships with the other titanosaur described in Europe is not well understood yet. At present there are not shared morphologies between Lo Hueco morphotypes and *Lirainosaurus astibiae*. However, some Lo Hueco cranial remains and tooth morphologies can be recog-

nized in sites from southern France supporting the hypothesis of a broader distribution of some titanosaurs throughout the Ibero-Armorican Realm.

The presence of two titanosaurian taxa in Lo Hueco that can be distinguished from the well-known species *Lirainosaurus astibiae* corroborates the rise of the sauropod diversity from the Late Cretaceous of the Iberian Peninsula, as suggested by some previous studies on the biota of Lo Hueco (Díez Díaz *et al.*, 2012b).

The simultaneous presence of two titanosaurian taxa is relatively common in others Upper Campanian-Lower Maastrichtian sites, such as Bellevue, Velaux, Massecaps or Fox-Amphoux-Métisson in southern France, which produces a high level of uncertainty in the attribution of isolated remains that appear together in these sites.

5. Stable isotope analyses

Stable isotope analyses ($\delta^{18}\text{O}_{\text{PO}_4}$, $\delta^{13}\text{C}$, and $\delta^{18}\text{O}_{\text{CO}_3}$) carried out on the Lo Hueco multi-taxa terrestrial vertebrate assemblage have provided valuable information about climatic and environmental conditions that existed in Iberia during the Late Campanian-Early Maastrichtian (Late Cretaceous). $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ and temperature values estimated from dinosaurs, crocodyli-forms, turtles and lepisosteids (mean $\delta^{18}\text{O}_{\text{H}_2\text{O}} = -3.0 \pm 1.2\text{‰}$; mean temperature = $22.0 \pm 4.4^\circ\text{C}$) are in good agreement with subtropical $\delta^{18}\text{O}$ precipitation values observed today and with temperatures estimated in other studies for the Lo Hueco latitude ($\sim 31^\circ\text{N}$) during the Late Campanian-Early Maastrichtian (Amiot *et al.*, 2004; Sellwood and Valdes, 2006; Domingo *et al.*, 2013). Seasonal thermal variability was estimated as the difference between temperature of the warmest months (TWMs), yielded by crocodyli-forms and turtles, whose biapatite mineralizes during the warm season, and mean annual temperature (MAT), supplied by theropods that record ingested water throughout the year. Lo Hueco $\Delta\text{TWMs-MAT}$ results (ranging from $2.2 \pm 0.1^\circ\text{C}$ to $7.4 \pm 0.2^\circ\text{C}$) do not indicate a significant greater seasonal thermal variability when compared to seasonal studies of Cretaceous Tethyan rudists (Steuber *et al.*, 2005) and modern subtropical conditions.

From a paleoecological standpoint, $\delta^{13}\text{C}$ values of the Lo Hueco sauropods ($-10.5 \pm 0.8\text{‰}$) point to consumption of pure C_3 vegetation, a fact supported by bulk organic matter $\delta^{13}\text{C}$ values ($-25.1 \pm 1.4\text{‰}$) from Lo Hueco sediments. The estimated fractionation value between sauropod enamel and diet ($\Delta^{13}\text{C}_{\text{enamel-diet}}$) is $\sim 15\text{‰}$, lower than other fractionation values calculated for sauropods ($\sim 16\text{‰}$; Tütken *et al.*, 2011) and ornithischians ($\sim 18\text{‰}$; Fricke and Pearson, 2008; Fricke *et al.*, 2008), and probably points to differences in metabolic and/or physiological processes or different utilization of plant organic compounds and/or plant parts. Although the Lo Hueco crocodyli-form material remains under study and no paleoecological remarks have been attained yet from a morphological perspective, isotopic results indicate that these crocodyli-forms may have incorporated food items from brackish

waters as indicated by their $\delta^{13}\text{C}$ values, whereas they avoided ingesting saline water and preferentially consumed freshwater, as suggested by their $\delta^{18}\text{O}_{\text{CO}_3}$ values when compared with isotopic values of modern crocodyli-forms inhabiting subtropical regions. Finally, the Lo Hueco turtles record the lowest $\delta^{13}\text{C}$ and $\delta^{18}\text{O}_{\text{CO}_3}$ values of the vertebrate assemblage likely indicating a diet based on a mixture of aquatic and terrestrial C_3 vegetation and/or invertebrates and ingestion of water with an inland source, a fact that agrees well with their taxonomic designation (Bothremydidae).

6. Prospective

Scientific interest in Lo Hueco Konzentrat-Lagerstatt lies in the large number of fossils found and the excellent conditions of preservation of the specimens. The site contains an unusual abundance of individuals of continental tetrapods, particularly titanosaur sauropods, crocodiles, and turtles. Moreover, in the case of titanosaurs, the site yielded multiple partial skeletons in articulation or with a low dispersion of its elements. Given these factors, the Konzentrat-Lagerstatt of Lo Hueco (Cambra-Moo *et al.*, 2013) is unique not only for the Spanish record but also for the entire Upper Campanian-Lower Maastrichtian record of Europe.

The biota identified at Lo Hueco presents a particular association of species, including the presence of new taxa and new records for the Iberian Peninsula of relatively common taxa in the European realm. In addition, this diversity reflects the absence of taxa frequently encountered in the Iberocretaceous Upper Cretaceous (even in the Campanian-Maastrichtian record), constituting a bias that may depend on ecological factors.

The taphonomic analysis together with the geological context and the flora and fauna provide an approach to ecological and paleoenvironmental reconstruction of the Lo Hueco wetland ecosystem with some singularities. Noticeable among them is the presence of unusual patterns of preservation such as the first remains of fossilized wood in gypsum for the Upper Cretaceous (Cambra-Moo *et al.*, 2013), or the recognition of the oldest evidence of wetland vegetation under stressful conditions showing characteristics of a modern community of plants (Peyrot *et al.*, 2013).

The conditions of preservation of the fossil remains of Lo Hueco contain other uniquenesses of which at least two are especially relevant to Late Cretaceous faunas. The discovery of large terrestrial tetrapods with skeletons in articulation or high association with good histological preservation of individuals at various stages of growth will provide for the possibility of ontogenetic studies in some lineages of reptiles.

The combination of information from skeletal sets, abundance of remains for some taxa, and the possible ontogenetic series analysis facilitate the evaluation of the sources of both intra and interspecific variability of some taxa. This reassessment of the evolutionary history of some lineages of reptiles from the Late Cretaceous of Europe, especially titanosaurian

sauropods, eusuchian crocodyliforms, and pleurodiran bothremydid turtles will appear in future studies.

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