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The ecology of the Lower Cretaceous coelacanths from Las Hoyas Konservat-Lagerstätte (Cuenca, Spain): A new insight after the integration of palaeontological and sedimentological data

Ecología de los celacantos del Cretácico Inferior del Konservat-Lagerstätte de Las Hoyas (Cuenca, España): Una nueva perspectiva tras la integración de datos paleontológicos y sedimentológicos

Hugo MARTÍN-ABAD & Marian FREGENAL-MARTÍNEZ

Abstract: Coelacanths are very rare in the upper Barremian fossil site of Las Hoyas (Cuenca, Spain). However, being one of the few predatory ichthyophagous fishes preserved at the locality, understanding their ecology is fundamental to continue advancing in our comprehension of the dynamics of this palaeowetland. A previous study based on the size distribution of the coelacanth specimens suggests that a natural population of this species did not inhabit the excavated area of Las Hoyas, perhaps due to them practicing habitat partitioning. Here we analyze the sedimentological characteristics of the laminae where these fossils were preserved. In the light of the extensive previous knowledge on the stratigraphy, depositional environments and evolution of Las Hoyas, we conclude that coelacanth fossils are preserved in "wet" facies associations, indicating that they were not present in this part of the wetland permanently, but during periods of overall flooding of the system and high connectivity among the different environments composing the regional-scale wetland.

Resumen: Los celacantos son fósiles poco comunes en el yacimiento del Barremiense superior de Las Hoyas (Cuenca, España). Sin embargo, dado que se trata de una de las pocas especies de peces predadores ictiófagos preservados en esta localidad, conocer su ecología es fundamental para seguir avanzando en la comprensión de la dinámica de este paleohumedal. Un estudio previo basado en la distribución de tamaños de los restos de celacantos sugiere que una población natural de esta especie no habitó el área excavada de Las Hoyas, posiblemente debido a que practicaran partición del hábitat. Aquí se analizan las características sedimentológicas de las láminas donde estos fósiles se preservaron. A la luz del extenso conocimiento previo de la estratigrafía, ambiente deposicional y evolución de Las Hoyas, se concluye que los fósiles de celacanto están preservados en asociaciones de facies "húmedas", lo que indica que no estaban presentes en esta parte del humedal de forma permanente, sino durante periodos de inundación del sistema y alta conectividad entre los distintos ambientes que componían este humedal de escala regional.

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Corresponding author:
Hugo Martín-Abad
hugo.martin@uam.es

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INTRODUCTION

The well-known upper Barremian (Lower Cretaceous) fossil locality of Las Hoyas (Iberian Ranges, Cuenca), once interpreted as a lake (*e.g.*, Sanz *et al.*, 1988), is currently understood as part of a regional-scale subtropical wetland under a strongly seasonal climate (Fregenal-Martínez & Buscalioni, 2009; Buscalioni & Fregenal-Martínez, 2010; Fregenal-Martínez & Meléndez, 2016). This new interpretation is the result of extensive sedimentological, stratigraphical, taphonomical and palaeobiological work developed since 1984, when the locality was first found. As befits a wetland, Las Hoyas palaeoecosystem was composed of a multitude of different micro-habitats (flooded plains, ponds, small lakes, channels, sloughs) that changed over time, altogether drawing the picture of a dynamic ecosystem rather than the stationary portrait of a moment of life's past that is usually associated to fossil sites.

This dynamic ecosystem approach is most strongly supported by the presence of significant seasonally influenced differences in the biological diversity recorded at the locality: the wet seasons record a higher diversity but a lower abundance of fossils, whereas the dry seasons are characterized by a lower

diversity but a much higher abundance of fossils that show a better preservation (Buscalioni & Fregenal-Martínez, 2010). While these differences might partially be consequence of a more intense growth of microbial mats that inhibited the decomposition of organisms during the dry seasons (Iniesto *et al*., 2015, 2016), recent studies on coprolites (Barrios-de Pedro *et al*., 2018) and the fern *Cladophlebis* (Blanco-Moreno & Buscalioni, 2021) have shown that these differences do not correspond solely to a taphonomic bias.

Moreover the fossil record of the locality documents as well larger-scale changes through time in the distribution of the species (Martín-Abad *et al*., 2019), entailing that the variations in Las Hoyas' diversity are not only due to seasonality. For instance, an analysis of the record of ferns in the locality (Blanco-Moreno *et al*., 2018) suggests that they would have defined different associations both horizontally (in space) and vertically (in time). Likewise, a preliminary analysis of the record of the tetrapods recovered from the locality (Martín-Abad *et al*., 2017a), as well as the study of their foot tracks (Moratalla *et al*., 2017), have shown that their distribution is not homogeneous throughout the fossiliferous layers of the site.

The distribution of fishes, however, has not yet been analyzed to that extent, mostly due to the somehow overwhelmingly large sample that the locality has yielded, which surpasses 5.000 specimens. With at least 20 different species and morphotypes identified so far at the site (Poyato-Ariza & Martín-Abad, 2016a), fishes were the most diverse and abundant group of vertebrates at Las Hoyas palaeowetland, where they occupied a variety of ecological niches (Poyato-Ariza & Martín-Abad, 2013, 2016b). Together with the insects, fishes constitute one of the hubs of the trophic network of the ecosystem (Buscalioni *et al*., 2016), that is, they participated in a large proportion of the trophic interrelationships among the totality of the species that inhabited the wetland. Therefore, fishes are the group whose study can contribute the most to our understanding of the dynamics of this palaeowetland, since a small change on the ichthyocommunity can strongly affect the whole network.

Among these fishes, amiiforms and coelacanths play an especially important role in the trophic network, because they are the only fish species that can play the role of ichthyofagous predators in the locality (although their diet includes other preys as well; Poyato-Ariza, 2005), and thus interrelate with basically all other fishes. For that particular reason, they are a good starting point to explore the dynamics of the ichthyofauna at Las Hoyas. A preliminary study of the size distribution of the three amiiforms fishes from the locality (Martín-Abad, 2015) suggests that the three of them practiced habitat partitioning, where the juvenile individuals and the adults do not share the same part of the ecosystem. This behavior is also observable in the only extant species of the order Amiiformes, *Amia calva*, which inhabits freshwater ecosystems of the Eastern Coast of North America; adults of this species usually live in deeper waters, coming into shallows during the breeding season, preferring to spawn in protected, calm shallow areas of lakes or in the very slow moving backwaters of rivers (*e.g*., Becker, 1983; Cross & Collins, 1995), and it is very rare to observe juveniles in the pools where the adults live (Koch *et al*., 2009). Habitat partitioning is common in recent wetlands, where the mosaic of blurred ecotones generates a variety of microhabitats (van der Valk, 2006; van der Valk & Warner, 2009), including both deeper and shallower, more calm waters.

A similar study was carried out focusing on the coelacanth remains at Las Hoyas (Martín-Abad *et al*., 2017b), even though coelacanths are very rare at this site. This study shows that most of the coelacanth remains would represent relatively large-sized individuals, thus suggesting that a natural population may have not inhabited permanently the part of the wetland recorded at the excavated area of Las Hoyas, because small individuals should be the most common sizes. Small individuals are exclusively represented by articulated specimens, whereas large individuals are mostly represented by isolated scales. Altogether, these data led to four non-mutually exclusive hypotheses to explain their population dynamics: 1) the coelacanth population was much smaller than that of other fishes at the locality; 2) this species only inhabited Las Hoyas for a (geologically) short period (*i.e*., coelacanth remains would only be recorded in some particular layers); 3) the coelacanth did not live at all at the excavated area of Las Hoyas, but in a different part of the wetland, and the remains would have been transported into the locality; 4) the coelacanth practiced habitat partitioning.

The objective of the present study is to further explore the hypotheses proposed by Martín-Abad *et al*. (2017b) by analyzing and interpreting the sedimentological characteristics of the fossiliferous layers where the coelacanth remains have been preserved, in terms of environments and environmental evolution.

GEOLOGICAL FRAMEWORK

Las Hoyas fossil site is located in the Serranía de Cuenca, 30 km far east of the city of Cuenca, and belongs to the upper Barremian La Huérguina Fm (Fregenal-Martínez *et al*., 2017). The Serranía is part of the southwestern area of the Iberian Range, a NW-SE trending chain of mountains located in the central-eastern half of Spain (Fig. 1A) that resulted from the tectonic inversion of a Mesozoic intraplate rift system known as Iberian Basin, which underwent an initial Late Permian–Early Triassic rifting phase and a second major rifting cycle during the Late Jurassic–Early Cretaceous (Salas & Casas, 1993; Salas *et al*., 2001; Liesa *et al*., 2019) that divided it into several palaeogeographic domains (Soria *et al*., 2000; Liesa *et al*., 2019). The NW-SE trending Alto Tajo-Montes Universales (**ATMU**) and the NE-SW trending Landete-Teruel (**LT**) fault systems controlled

the palaeogeographical evolution of the southwestern area of the Iberian Basin, and divided it into three palaeogeographical domains, Cuenca, Albarracín and Valencia domains (Aurell *et al.*, 2019) (Fig. 1B), in turn divided into many basins of graben and half-graben type.

Cuenca Domain experienced two episodes of rifting during the late Jurassic–early Cretaceous rifting cycle, late Barremian and Aptian in age respectively (Fregenal-Martínez *et al.*, 2017; Aurell *et al.*, 2019): The late Barremian successions are composed of two laterally related continental units, the mixed

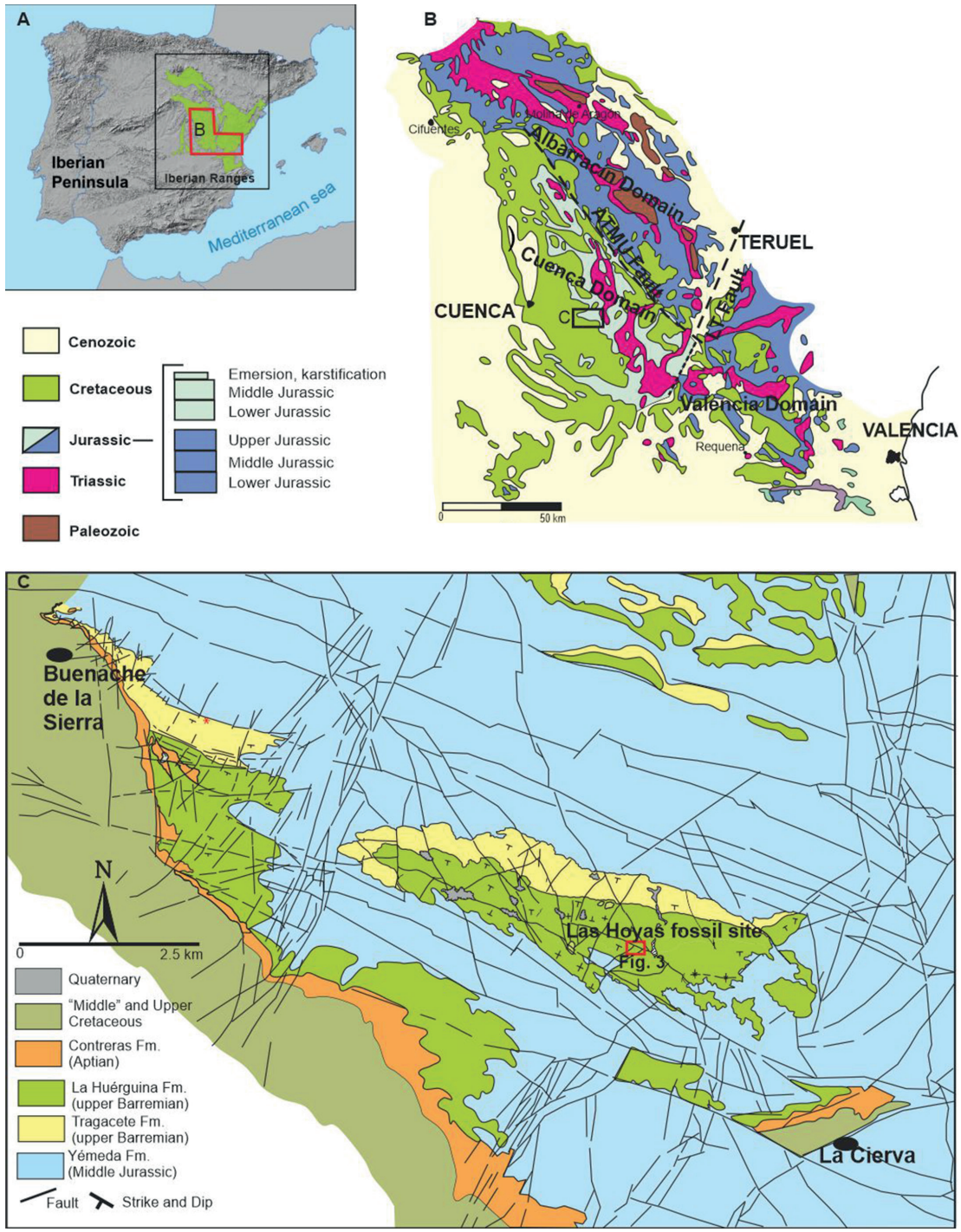

Figure 1. A, Location of the Iberian Ranges in the Iberian Peninsula; **B,** Geological map of the southwestern Iberian Ranges, where the location of the main palaeogeographical domains for the Late Jurassic–Early Cretaceous rift system (Cuenca, Albarracín and Valencia) have been depicted. Those palaeogeographical domains were defined by the presence and activity of the Alto Tajo-Montes Universales (**ATMU**) and the Landete-Teruel (**LT**) fault systems; **C,** Geological map of the area where Las Hoyas syncline is located. The general regional stratigraphic pattern of the Jurassic–Lower Cretaceous in the Serranía de Cuenca is well represented and complete in this area. The position of Las Hoyas fossil site has also been pointed, the square correspond with the map of the excavated area presented in Figure 3.

carbonate-siliciclastic Tragacete Fm and the carbonate La Huérguina Fm (Fregenal-Martínez *et al*., 2017). La Huérguina Fm overlies and expands over the Tragacete Fm with gradual or abrupt contact from the south-central areas to the edges of the Cuenca Domain. Thickness of these units is very variable (10–170 m for Tragacete Fm, and 10–100 m for La Huérguina Fm) due to the compartmentalization of the Cuenca sedimentary Domain into many small normal fault-related subbasins defined by a main set of extensional faults broadly directed N110 with steep and relatively long (more than 20 km) transfer faults NE-SW to N-S directed (Fregenal-Martínez *et al*., 2014a, 2017; Elez *et al*., 2015).

The Tragacete Fm is mostly composed of fine-grained sediments, red clays silts and marls, with pervasive palustrine features and well-developed paleosols. Interfingered with clays there are lens-shaped bodies of siliciclastic, carbonatic and mixed composition.

La Huérguina Fm consists of limestones with abundant charophytes and ostracods, oncolitic conglomerates, oncolitic and stromatolitic limestones as well as bioclastic and intraclastic calcarenites. Marls and silty to marly limestones rich in plants remains are also present. Palustrine facies and features are common.

The paleontological content of Tragacete and La Huérguina formations includes cyanophycean algae, charophytes, ostracods, bivalves, gastropods, pollen, vegetal remains, fish and skeletal remains of tetrapods. In the Tragacete Fm the presence of localities extremely rich in both, macro- and microskeletal remains of vertebrates or "bone beds" (Buscalioni *et al*., 2008) is remarkable. In La Huérguina Fm it is noteworthy the presence of Konservat-Lagerstätten type (Seilacher *et al*., 1985) localities, being the most outstanding Las Hoyas fossil site (Poyato-Ariza & Buscalioni, 2016).

Late Barremian sedimentation occurred in continental and fully freshwater aquatic and terrestrial environments without marine influence (De Vicente & Martín Closas, 2013; Fregenal-Martínez & Meléndez, 2016; Fregenal-Martínez *et al*., 2017). The Tragacete and La Huérgina formations correspond to two environmental belts of a freshwater regional system of wetlands: drained areas with higher terrigenous input, and poorly drained areas with minor terrigenous input and dominant lacustrine conditions, respectively. Sedimentation occurred in a mosaic of alluvial, fluviolacustrine, palustrine and lacustrine environments, composed of ponds, small lakes, channels, waterlogged soils, marshy and swampy inundated plains, and soils in hummocks of vegetation, among others. All that resulted in a complex depositional architecture (Fregenal-Martínez *et al*., 2017; Aurell *et al*., 2019).

As a whole the sediments of Tragacete and La Huérguina formations reflect deposition in a landscape of large inland subtropical and tropical wetlands, poorly drained and strongly controlled by seasonal climate (Meléndez, 1983; Gómez-Fernández, 1988; Gierlowski-Kordesch & Janofske, 1989; Gierlowski-Kordesch *et al*., 1991; Fregenal-Martínez, 1994, 1998; Fregenal-Martínez & Meléndez, 2000, 2016; Buscalioni *et al*., 2008, 2016; Buscalioni & Fregenal-Martínez, 2010; De Vicente & Martín Closas, 2013; Fregenal-Martínez *et al*., 2014b, 2017; Muñoz-García *et al*., 2015; Aurell *et al*., 2019).

LAS HOYAS *KONSERVAT-LAGERSTTÄTE*: DEPOSITIONAL AND ENVIRONMENTAL FRAMEWORK

Las Hoyas fossil site is part of the record of La Huérguina Fm at a small (45 km^2), elongated half-graben basin, 7 km long (strike section) and 2 km wide (dip section), known as Las Hoyas Basin. It is nowadays represented by a syncline made up of deposits of Tragacete and La Huérguina formations overlying the marine Jurassic limestones of the Yémeda Fm (Fig. 1C).

Las Hoyas fossil site is located at the central part of Las Hoyas Basin (Fig. 1C) and it is part of a sedimentary sequence composed by three facies association, each passing gradually into the next, and which from bottom to top correspond to (Fig. 2A, 2B): (1) laminated limestones that contain the exceptionally well-preserved floral and faunal record of Las Hoyas Konservat-Lagerstätte; (2) irregular slabby and thin-bedded limestones; (3) cross-bedded and massive limestones. The vertical and lateral arrangement of these three facies association reveal patterns which are, by far, more complex than simple gradual transitions, although this is the general tendency. When depositional architecture is described in three dimensions, the distribution of facies (at the scale of each association and in the transitions between them) resembles a complex mosaic-like pattern (Fig. 2C).

The laminated limestones are composed almost entirely of calcium carbonate, with only a small fraction of clays and organic matter. At macroscopic scale, lamination consists of a millimeter-scale alternation of wavy dark and light laminae (Fig. 3A). Despite the homogeneous appearance of the laminated facies at field scale, two basic, alternating facies associations have been petrographically distinguished, plus several transitional facies in between: (1) The first association of microfacies is made up of massive or positively graded millimetric laminae deposited by underflow currents and decantation of allochthonous detrital very fine carbonate particles and vegetal debris. These levels alternate with wavy laminae of dense micrite and microsparite, which in turn correspond to calcification of thin microbial mats. This microfacies association was deposited under a persistent, shallow lamina of water during seasonal flooding and longer-term wet periods whose high water levels favored more lacustrine conditions (Buscalioni & Fregenal-Martínez, 2010; Fregenal-Martínez & Meléndez, 2016) (Fig. 3). (2) The second association of microfacies reflects the autochthonous production of carbonate linked to the growth of benthic microbial mats during periods of low water level conditions. Fossilized microbial mats show

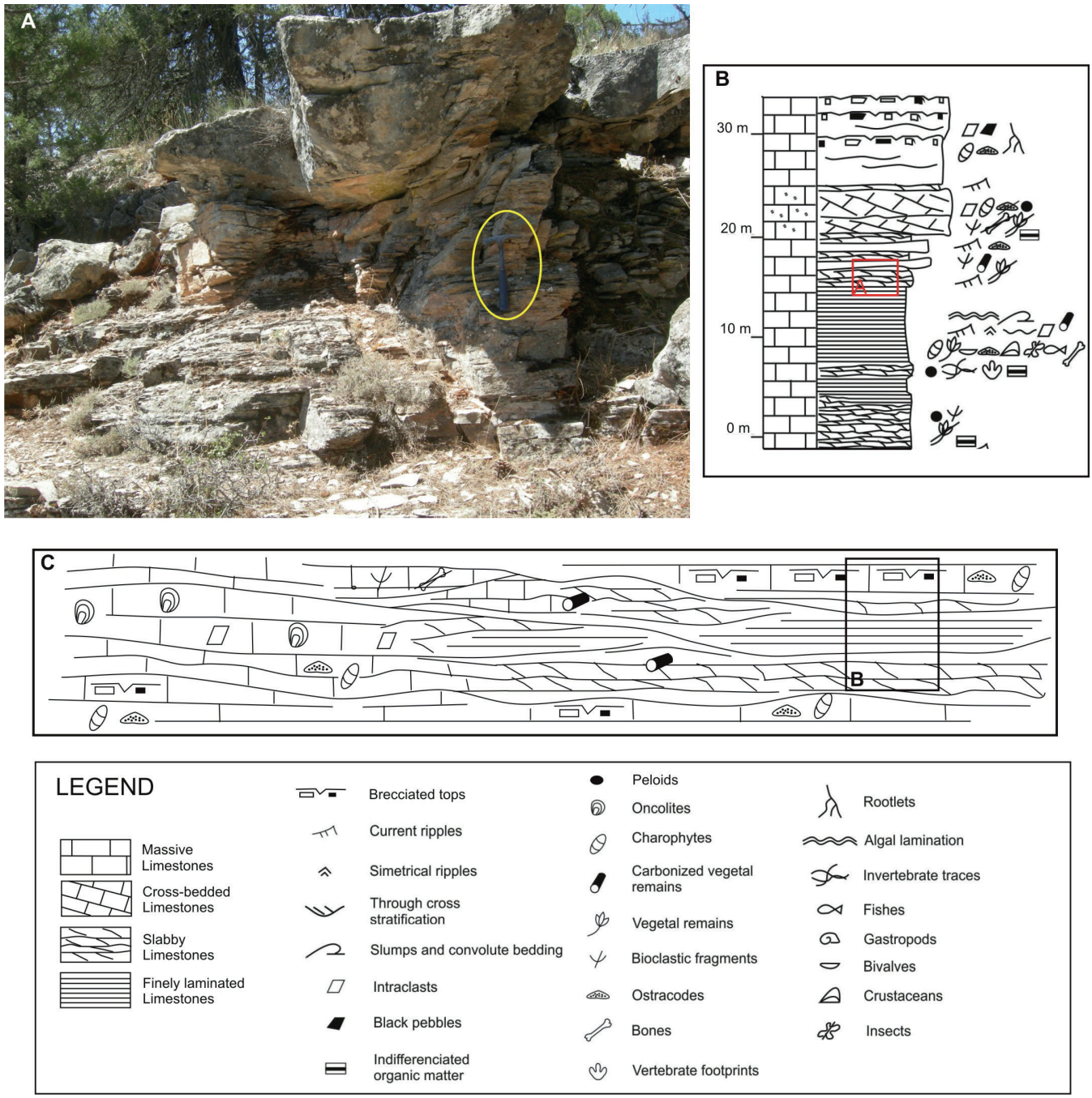

Figure 2. A, Outcrop view of the sequence of facies associations that resulted from the evolution of the depositional system where Las Hoyas fossil site was preserved in the basal term of the sequence composed of finely laminated limestones, and followed by irregular slabby and thin-bedded limestones, and topped by cross-bedded and massive limestones; **B,** Log of the sequence of facies associations; **C,** Out of scale sketch of the complex depositional architecture that the vertical and lateral actual arrangement of these three facies association show. Modified from Fregenal-Martínez *et al*. (2014a).

the typical features of laminations of stromatolites (Riding, 2000, 2011). They consist of wavy, irregular laminae of micrite, miscrosparite, sparite, or peloidal micrite, which, in general, lack porosity, show a very homogeneous fabric, and are densely packed (Fig. 3C). They enclose small pockets and thin discontinuous laminae of detrital trapped grains, or alternate with laminae of very fine detrital carbonate sediments with debris of plants and other organic remains that were transported during occasional floods. Some tops of calcified microbial mats show desiccation cracks, and flakes of the desiccated mats are incorporated as clasts into the detrital laminae. At macroscopic scale, microbially induced sedimentary structures (**MISS**) and mat related structures (**MRS**) (Noffke *et al*., 2001, 2006; Noffke, 2009), such as wrinkle marks, multidirectional chaotic ripple marks, erosional remnants and pockets and polygonal desiccation cracks are quite common.

Those microfacies represent sedimentation during drier periods with very low water levels (Buscalioni & Fregenal-Martínez, 2010; Fregenal-Martínez & Meléndez, 2016).

The stratigraphic arrangement of all these microfacies follows a cyclic vertical pattern, where the first microfacies association passes gradually into the second. That cyclical patterns occurs at several scales, form milimetric alternations of laminae produced by decantation of allochthonous material and microbial mats, to 20- to 50-cm-thick, laterally persistent sequences composed of hundreds of milimetric lamine with a well-distributed dominance of one of the two microfacies associations and a prominent overall stratigraphic tendency (Fig. 3C). The alternation of both associations supports strong water level oscillations associated to the alternation of wet and dry periods (Buscalioni & Fregenal-Martínez, 2010; Fregenal-Martínez & Meléndez, 2016).

The fossiliferous laminated limestones accumulated in a shallow marginal lacustrine environment, pools with frequent, seasonal water-level oscillation, and filled with layered microbial mats. Those pools were integrated into a larger wetland complex. In Las Hoyas fossil site, at least two different pools coexisted laterally and evolved in time by laterally shifting their position (Fregenal-Martínez & Meléndez, 2016).

The pools filled with microbial mats were located at the marginal areas and terminal reaches of an environmental belt, where the dominant processes

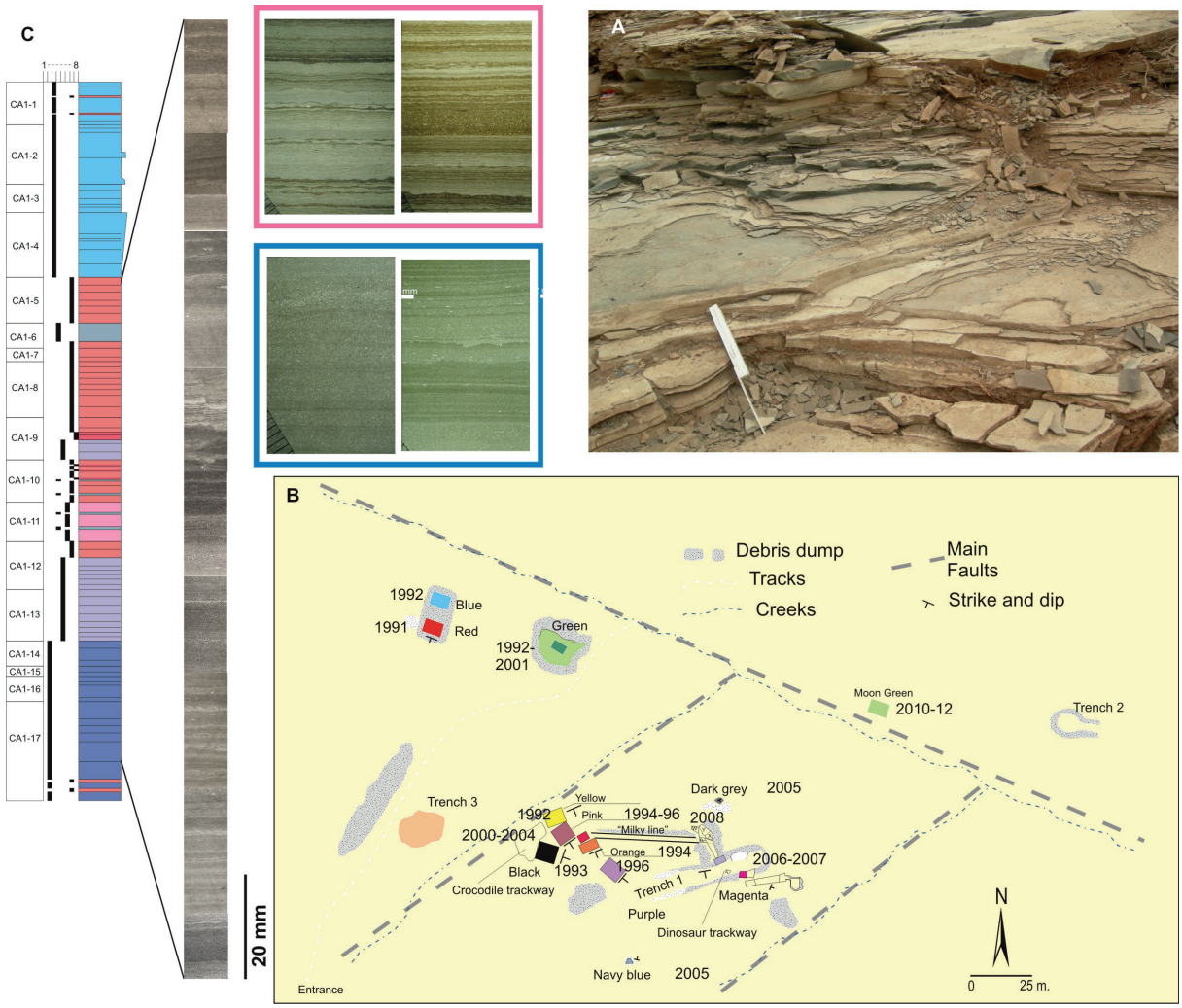

Figure 3. A, Field view of laminated fossiliferous limestones in Las Hoyas fossil site; **B,** Map of the excavation area of Las Hoyas (after Fregenal-Martínez & Meléndez, 2016). See figure 1C for location within Las Hoyas syncline; **C,** To show the typical cyclical arrangement of "wet" and "dry" microfacies association of Las Hoyas, the reconstructed stratigraphic succession of laminated facies of Trench 1 of Las Hoyas fossil site is shown. This succession was obtained from thin sections, after a continuous layer by layer sampling (each interval labeled in the log at left correspond to one thin section, note that scale is in mm). Up to eight different microfacies have been recognized numbered from 1 to 8 in the log at left and also represented by colors that range from deep blue to deep pink. The succession displays cyclical alternation of facies deposited during periods of wet (blue and bluish colored intervals) and dry (pink and pinkish colored intervals) environmental conditions. Two examples of each type of facies under the petrographic microscope are also shown. Modified from Fregenal-Martínez and Meléndez (2016).

were the slow unconfined drainage of vegetal remains and bioclastic calcarenites (Fregenal-Martínez & Meléndez, 2016). Sedimentation in the unconfined drainage belt is represented by regular slabby, thin bedded and cross-bedded limestones. Irregular slabby and thin bedded limestones were produced by processes of slow traction and sedimentation by flows of carbonate skeletal remains and vegetal debris, and by processes of accumulation and decantation of massive and peloidal carbonate mud, whereas cross-bedded limestones correspond to calcarenitic subaquatic dunes formed by unidirectional currents, that migrated during seasonal flooding and remained inactive during dry seasons and periods of low water, allowing development of small patches of microbial mats in the small throughs on top of the bars. In turn, cross-bedded limestones are associated and intercalated with massive charophyte limestones, which correspond to sedimentation in quiet lacustrine environments with abundant charophyte meadows, evolving upwards into palustrine environments. Cross-bedded and massive charophyte limestones are distributed following a mosaic-like pattern. Therefore, this association as a whole might correspond to sedimentation in areas where quiet lacustrine conditions alternate with periods of unconfined flowing and drainage of accumulated sediments, probably during seasonal flooding (Fregenal-Martínez & Meléndez, 2016).

As a whole the emerging picture of the depositional system of Las Hoyas is composed of pools filled with microbial mats integrated in a shallow unconfined drainage belt that redistributed the carbonate sediments produced in the unconfined drainage belt itself, and in quiet and open lacustrine areas dominated by development of charophyte meadows. All the environmental belts of this depositional system underwent seasonal oscillations of water level: they were inundated during wet seasons, thus promoting more quiet and lacustrine environmental conditions, and slowly drained when the flood peak fell down, thus favoring the development of deposits produced by flow and transport processes. In different ways, processes of traction of sediments, and production and accumulation of carbonate under more lacustrine conditions alternate in all of them, thus supporting the prominent role of seasonal subtropical climate on sedimentary dynamics (Fregenal-Martínez & Meléndez, 2016).

MATERIAL AND METHODS

Las Hoyas coelacanth material

The coelacanth from Las Hoyas was originally assigned to the species *Holophagus leridae* because of the overall similarities of the ichthyofauna from this locality to that from El Montsec in Lérida (Sanz *et al*., 1988). However, that genus is currently restricted to the lower Lias (Forey, 1991, 1998), and Las Hoyas fossils certainly show some differential characteristics; therefore, this material is currently listed as cf. "*Holophagus*" sp. (Poyato-Ariza & Martín-Abad, 2016a) pending a detailed anatomical and taxonomical reevaluation.

Coelacanth remains are rare at Las Hoyas; up to date, only a total of 25 fossils can be assigned to this species (the 21 specimens referred in Martín-Abad *et al*., 2017b, plus four newly identified remains): 12 complete or partially articulated specimens, consisting mostly on juvenile specimens and caudal fins of large-sized individuals, and 13 isolated scales belonging to relatively large-sized individuals (Fig. 4). A preliminary observation of the articulated material (Poyato-Ariza & Wenz, 1995; Poyato-Ariza & Martín-Abad, 2016a) as well as the detailed anatomical study of the scales (Martín-Abad *et al*., 2017b) does not show differences that could suggest the presence of more than one species. Las Hoyas' fossil collection is housed at Museo de Paleontología de Castilla-La Mancha in Cuenca (**MUPA**).

Articulated specimens. MUPA-LH 007aR, 144P, 4143, 6137, 9077a/b, 9445a/b, 20400, 26491a/b, 26492a/b, 31268a/b, 32754a/b, 33227.

Isolated scales. MUPA-LH LH 415, 840a/b, 930, 2328, 2916a/b, 5089a/b, 5276a/b, 9406a/b, 13679, 17011, 28210a/b, 37156, 37179.

The Las Hoyas coelacanth scales are of the amioid type, but the isolated scales can reliably be distinguished from other amioid scales present at the locality (*i.e.*, scales of the three amiiform fishes; Martín-Abad, 2016) by the presence of a smooth central surface, a particular pattern of arrangement of putative concentric growth cessation marks, and mainly a relatively short posterior field with thick elongated ridges (Martín-Abad *et al*., 2017b).

Stratigraphic data

Excavations at Las Hoyas are carried out in sampling areas, or "squares", approximately 30 m^2 in size. These sampling areas are usually given the name of a colour (*e.g.*, "green square"), but some particular areas receive more specific names (*e.g.*, "trench 1"; Fig. 3). The squares occupy different positions within the stratigraphical column of the locality, and usually the fossils that are collected have very precise stratigraphical information associated to them. However, that is not the case for all specimens; the fossils recovered in the first field campaigns often do not have this information because the excavations in those first years were not as systematic, consisting on exploratory samplings. Additionally, fossils that are found re-searching the debris dumps do not have this information either. Given that a large proportion of the coelacanth fossils were recovered in the first excavation campaigns, there is stratigraphical data available only for 8 out of the 25 total specimens:

Green square: MUPA-LH 4143, 6137, 9406a/b, 9445a/b.
Trench 1: MUPA-LH 9077a/b, 13679.
Chikuto square: MUPA-LH 31268a/b.
Magenta square: MUPA-LH 33227.

Sedimentological analysis

In order to analyze the sedimentological characteristics of the layers where the coelacanth fossils are preserved, thin sections were prepared from the rocks without damaging the fossils. Thin sections were prepared from 17 out of the 25 samples; the remaining eight samples were not sectioned because the rocks were too thin to produce informative sections, and the integrity of the fossils could be compromised.

Thin sections. MUPA-LH 144P, 840a/b, 2328, 5089a/b, 5276a/b, 9077b, 9406, 9445a/b, 13679, 17011, 20400, 26491a/b, 28210, 31268a/b, 32754, 37156, 37179.
The thin sections obtained from the fossils lacking precise stratigraphical information were compared to thin sections available from different sampling squares of the locality, with the objective of identifying whether their sedimentological characteristics would match those of a particular type of facies.

Thin sections were prepared at the lab facilities of the Stratigraphy Section of the Department of Geodynamics, Stratigraphy and Palaeontology of the Universidad Complutense de Madrid.
The sedimentological analysis is supported by the extensive previous knowledge on the stratigraphy, depositional environments and evolution of Las Hoyas and its palaeogeographical framework at several scales. The mere sedimentological analysis of the samples would not be understandable without the proper information and previous interpretations on the context.

RESULTS

Seventeen thin sections have been analyzed in order to determine if both articulated specimens and isolated scales show a preferential association with the microfacies association described in Las Hoyas fossiliferous laminated limestones (Fregenal-Martínez & Meléndez, 2016), that have been also thoroughly described above.
Seven samples correspond to articulated specimens and ten to isolated scales. Fifteen out of the seventeen samples analyzed clearly match any of the varieties

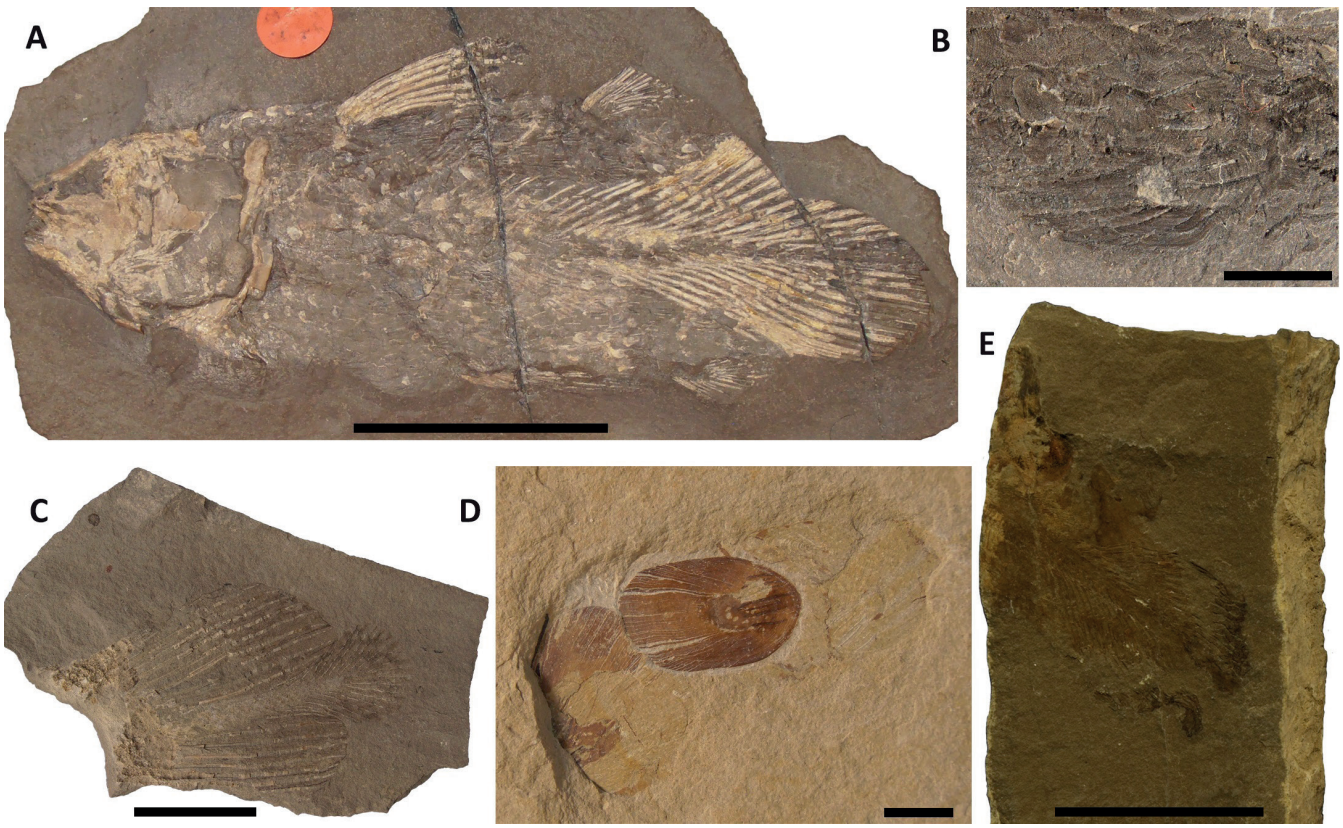

Figure 4. Coelacanth fossils from Las Hoyas. **A,** MUPA-LH 007a, articulated medium to large-sized individual; scale bar = 5 cm; **B,** Close-up of the scales of the specimen in A; scale bar = 5 mm; **C,** MUPA-LH 32754a/b, articulated caudal fin where the middle lobe is preserved; scale bar = 2 cm; **D,** MUPA-LH 9406a/b, isolated scales; scale bar = 5 mm; **E,** MUPA-LH 31268a/b, incomplete articulated small-sized individual; scale bar = 2 cm.

of microfacies that compose the "wet" microfacies association, and the two remaining (LH 13679 and LH 20400) show a strong synsedimentary deformation, and are composed by slumpized laminae of microfacies typical of the "dry" microfacies associations.

In turn, all of the analyzed samples of the "wet" association can be separated into two different types of "wet" microfacies: (A) Massive or graded millimeter laminae of allochthonous detrital carbonate particles (peloids, bioclast fragments, vegetal remains) of relatively "coarse" silty grain size; (B) Millimeter laminae of massive micrite and very fine grained clay-sized detrital carbonate particles with intercalated thin wavy laminae of microsparite (calcified microbial mats).

Both types are related with sedimentation under a permanent shallow lamina of water during periods of overall flooding of the systems and high connectivity among the different environments, thus allowing the incoming of allochthonous sediments into the pool of Las Hoyas. However, type A would better represent sedimentation of allochthonous particles by means of underflows and overflows drained during flooding surges, while type B would represent processes of decantation of very fine grained suspended material and regrowth of microbial mats during flooding maximum peaks, when the high water level inhibited effective drainage.

Although the size of the whole analyzed sample is quite small and it is difficult to define a tendency, isolated scales tend to appear in microfacies A (7 out of 9 samples) whereas articulated fish ten to associate with microfacies B (4 out of 6 samples) (Tab. 1; Fig. 5).

Therefore, articulated specimens seems to have been preserved coinciding with maximum water level and maximum connectivity of environments with dominant environmental lacustrine conditions all over the depositional system. Isolated scales are also associated to high water levels but can be either part of allochthonous sediments incoming the pool, or just remains settled from the water column.

The "wet" microfacies association appear all along the entire successions of Las Hoyas laminated limestones, but it is dominant and outstanding in the lower part of the succession, at the red, blue, green and moon green squares (Fig. 3B). It is noteworthy that most microfacies recorded in green square correspond to the types A and B herein described. Hence it is likely that most of the sample analyzed come from this part of the site or laterally equivalent areas.

DISCUSION

The preliminary study of the coelacanth remains (Martín-Abad *et al*., 2017b) suggested that a natural population did not permanently inhabit the part of the wetland represented by Las Hoyas fossil site. The size distribution of the coelacanth fossils indicates that most of them would represent relatively large-sized individuals (in comparison to the majority of fishes at Las Hoyas). Normally, in a natural population juveniles would be expected to represent the most common class. In the extant coelacanth *Latimeria chalumnae*, however, a recent study (Mahé *et al*., 2021) has confirmed that the sexual maturation time, the gestation time and the longevity are very long, and thus juveniles do not necessarily represent the most common class in their populations. However, this distribution has also been suggested to be due to habitat partitioning, since no juvenile has ever been spotted in the caves where the adults live (Fricke *et al*., 2011). As for the other extant species, *Latimeria menadoensis*, juveniles have been recently observed

Table 1. Type of fossil, stratigraphic position, microfacies and microfacies association of the sectioned specimens.

Sample	Fossil	Stratigraphic position	Microfacies association	Microfacies
LH 144 P	Articulated fish	Unknown	"Wet"	B
LH 840 a/b	Isolated scale	Unknown	"Wet"	B
LH 2328	Isolated scale	Unknown	"Wet"	A
LH 5089 a/b	Isolated scale	Unknown	"Wet"	A
LH 5276 a/b	Isolated scale	Unknown	"Wet"	B
LH 9077 b	Articulated fish	Trench 1	"Wet"	B
LH 9406	Isolated scale	Green Square	"Wet"	A
LH 9445 a/b	Articulated fish	Green Square	"Wet"	A
LH 13679	Isolated scale	Trench 1	"Dry" highly deformed	
LH 17011	Isolated scale	Unknown	"Wet"	A
LH 20400	Articulated fish	Unknown	"Dry" highly deformed	
LH 26491 a/b	Articulated fish	Unknown	"Wet"	B
LH 28210	Isolated scale	Unknown	"Wet"	A
LH 31268 a/b	Articulated fish	Chikuto Square	"Wet"	B
LH 32754	Articulated fish	Unknown	"Wet"	A
LH 37156	Isolated scale	Unknown	"Wet"	A
LH 37179	Isolated scale	Unknown	"Wet"	A

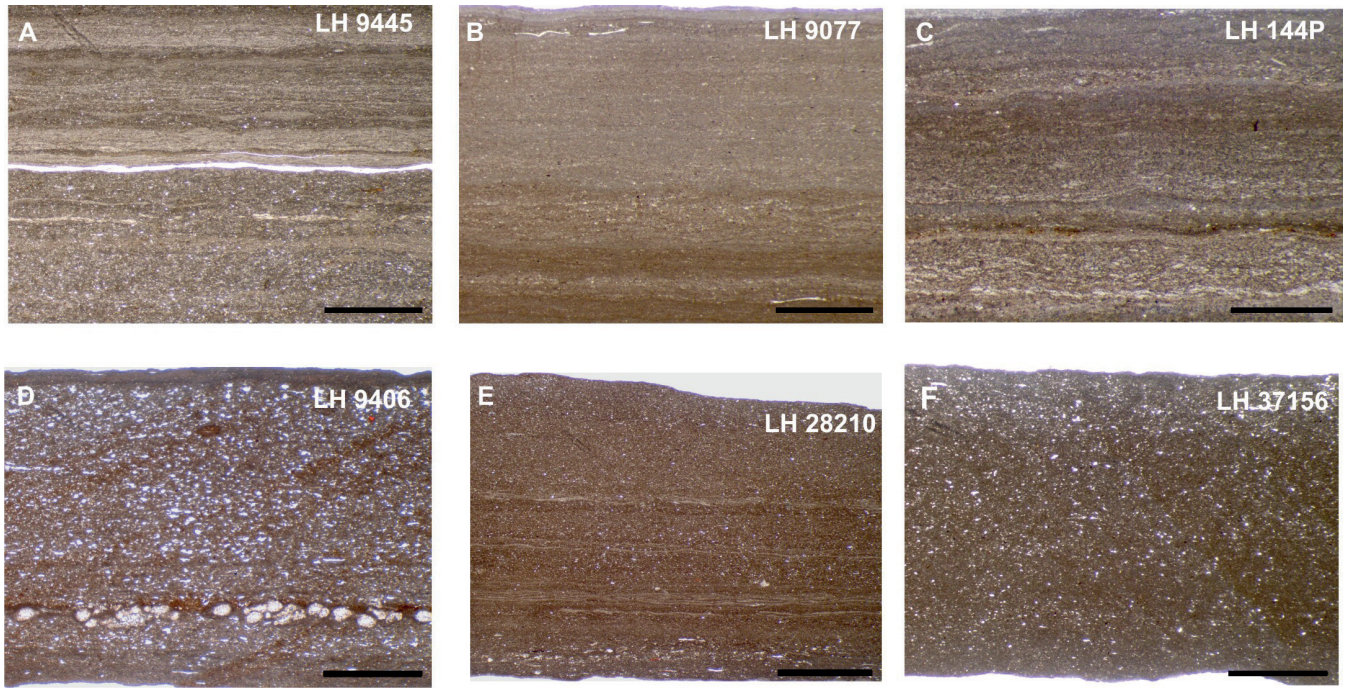

Figure 5. Examples of different types of microfacies all of them belonging to the "wet" microfacies association where the articulated skeletal remains and isolated scales studied in this work were preserved. **A–C,** Correspond to articulated remains, and are composed by type-B microfacies; and **D–F,** To isolated scales in type-A microfacies, being the grain size coarser in D and F than in E; scale bar = 5 mm.

swimming at the range of depth where adults were previously observed (Iwata *et al*., 2019), so it seems to follow a different strategy. Nonetheless, given the vast ecological difference between the extant species (*L. chalumnae* is a marine, deep-water dweller reaching up to 1.83 m in length (Hissmann *et al*., 2006)) and the species from Las Hoyas (most likely a relatively small-sized fish), it cannot be assumed that the fossil species would behave in the same way as any of the extant species. In fact, habitat partitioning is a common practice for freshwater fishes, and particularly in wetlands, where adults usually live in deeper, more stable waters and move to shallower, more protected waters for spawning; juveniles would remain in these protected areas until their age of sexual maturity, when they join the adults. In a fossil locality, such kind of practices would be expected to be evidenced by non-natural size distributions of the remains, similar to the distribution of coelacanth remains found at Las Hoyas. In any case, there are numerous problems when it comes to interpret this kind of behavior in fossil coelacanths, because we know little about their age and growth biology. The growth rate, life span, and age of sexual maturity of *Latimeria chalumnae* have been a controversial topic for decades (Hureau & Ozouf, 1977; Froese & Palomares, 2000). Just very recently new protocols for estimating the chronological ages of coelacanths from lines of arrested growth deposited on their biomineralized structures, including scales, have been developed (Woolfolk *et al*., 2018; Newbrey *et al*., 2020; Mahé *et al*., 2021), which suggest that their growth and sexual maturity are even slower than previously believed. These studies are even more challenging for fossil coelacanths; in the particular case of the species from Las Hoyas, its isolated scales show marks that could correspond to lines of arrested growth; however, the difficulty of interpreting these marks implies the convenience of contrasting the data they provide with lines of arrested growth preserved on other skeletal structures (Woolfolk *et al*., 2018; Newbrey *et al*., 2020). Moreover, as stated above, the extant species might not even make the best comparative organism in this particular case, not only in terms of ecological differences, but also because the phylogenetic affinities of the fossil species are still unknown. Recent advances in the coelacanth phylogeny (Cavin *et al*., 2019; Toriño *et al*., 2021) suggest that only two families were present in the Cretaceous, the latimeriids and the mawsoniids. While the predominance of brackish and freshwater forms in Mawsoniidae might suggest that Las Hoyas' species could belong to this family, more material needs to be prepared and studied to confidently assign this taxon to one or the other family, thus establishing a more precise phylogenetic framework to interpret the palaeobiological adaptations of this species.

The results of the sedimentological analysis of the limestones containing coelacanth remains do not help to clarify whether the species at Las Hoyas practiced habitat partitioning, since all fossils appear to have been produced in similar depositional conditions, corresponding to the wet microfacies associations. There is no apparent difference between the small and

the large specimens, they both appear associated to wet facies. A possible evidence of habitat partitioning would be the smaller individuals appearing associated to dryer facies and the adults to wetter facies; in that case, it could be interpreted that the juveniles would inhabit shallower areas of the wetland that could get isolated from deeper, more stable waters (*i.e.*, wetter facies) where the adults, mostly represented by isolated scales, would live. However, that does not seem to be the case. It could be argued that the isolated scales, which are easily transported, could have come from a further area; and in fact they tend to be associated to the A type microfacies, while articulated fishes tend to appear associated to the B type microfacies. However, the sample is too small to draw conclusions, and moreover there does not seem to be a pattern of differential preservation that suggests different biostratinomic processes (*i.e.*, there are both isolated scales and articulated remains well preserved and badly preserved), and a more detailed taphonomical analyses of the remains would be required to accept that hypothesis.

Nonetheless, in that sense it is interesting to note that half of the remains whose stratigraphic provenance is known come from the green square, and the facies preserving all the remains can also be related to green square-type of facies. As a matter of fact, the green square is a very particular one in the locality, presenting a very characteristic biotic association which includes relatively large-sized bivalves and most importantly the only evidence of large, articulated remains of the fern *Weichselia reticulata*, which are interpreted to have been transported from a further away part of the ecosystem in a time when the water column was deeper and the different parts of the wetland could have been connected.

Altogether, the evidences suggest that, independently of the coelacanths practicing habitat partitioning or not, they were much rarer than most of the other fishes that inhabited the wetland, and their presence in the ecosystem seems to have been restricted in time, being associated to particularly water-rich conditions that are registered in the sedimentological record of the locality as wet facies.

CONCLUSIONS

Concerning the four non-mutually exclusive hypotheses that Martín-Abad *et al.* (2017b) proposed regarding the ecology of the coelacanth species at Las Hoyas, the joint study of the size distribution, the stratigraphical provenance and the sedimentological characteristics of the fossils allows us to conclude that: 1) with a total of 25 identified remains, the coelacanth is much less common than most other fishes collected at the locality; 2) the coelacanths were not permanently present in this part of the wetland, being associated exclusively to wet facies; 3) at least some of the coelacanth fossils have been recovered from layers whose association is interpreted as the result of a transportation event, and that could even be the case for most of them; 4) although the size (*i.e.*, age) distribution of the remains suggest that the coelacanth practiced habitat partitioning, the results presented here do neither corroborate nor deny it. Further research with these fossils, such as a detailed taphonomical analysis of the preservation and the study of the age and growth biology of the species, are necessary to better comprehend the ecology of this unique freshwater coelacanth from Las Hoyas.

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Author details. **Hugo Martín-Abad**[1] & **Marian Fregenal-Martínez**[2]. [1]Departamento de Biología, Facultad de Ciencias, Universidad Autónoma de Madrid. C/ Darwin, 2, Campus de Cantoblanco, 28049 Madrid; [2]Departamento de Estratigrafía, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid. C/ José Antonio Novais 2, 28040 Madrid. hugo.martin@uam.es, mariana@geo.ucm.es

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