SPANISH JOURNAL OF PALAEONTOLOGY

Characterization of coelacanth scales from the Early Cretaceous freshwater locality of Las Hoyas, upper Barremian (Cuenca, Spain)

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Martín-Abad, H., Newbrey, M.G., Woolfolk, F. & Blanco-Moreno, C. 2017. Characterization of coelacanth scales from the Early Cretaceous freshwater locality of Las Hoyas, upper Barremian (Cuenca, Spain). [Caracterización de escamas de celacanto en el yacimiento continental del Cretácico Inferior de Las Hoyas, Barremiense superior (Cuenca, España)]. *Spanish Journal of Palaeontology*, 32 (2), 331-342.

Manuscript received 9 December 2016
Manuscript accepted 22 May 2017

ABSTRACT

Coelacanths are rare, mostly marine fishes, but the species from the Lower Cretaceous Spanish locality of Las Hoyas (Barremian) is a freshwater form and we know almost nothing about it. The Las Hoyas specimens are very rare and relatively incomplete, but there are still many things we can learn from the isolated skeletons and scales. First, the coelacanth scales were distinguished from other superficially similar scales (i.e., other "amioid" scales). Coelacanth scales are distinguished by the presence of a smooth central surface, a particular pattern of arrangement of concentric growth cessation marks, and mainly a relatively short posterior field with thick elongated ridges. Only a few articulated coelacanth specimens have been recovered from Las Hoyas to date, and only 7.3% (n = 11) of the total isolated scales are coelacanth. The Las Hoyas coelacanth scales represent relatively large individuals. This suggests that a natural population of the coelacanth may have not inhabited permanently the freshwater pool represented

RESUMEN

Los celacantos son peces poco comunes, fundamentalmente habitantes de aguas marinas. Sin embargo, el celacanto del Cretácico Inferior (Barremiense) de Las Hoyas es una forma de agua dulce de la que no sabemos prácticamente nada. Los restos de celacanto son raros en Las Hoyas y relativamente incompletos, pero esto no implica que no podamos obtener una gran cantidad de información a partir de sus elementos esqueléticos y escamas. Las escamas de celacanto pueden diferenciarse de otras escamas de tipo "amioideo" encontradas en el yacimiento. Las escamas de celacanto se caracterizan por una superficie central lisa, un patrón particular de marcas de parada de crecimiento concéntricas, y especialmente un campo posterior relativamente corto con una serie de gruesas crestas alargadas. Hasta la fecha, tan solo unos pocos especímenes articulados de celacanto se han encontrado en Las Hoyas, y sólo un 7.3% (n = 11) de las escamas aisladas pueden asignarse a este taxón, todas ellas representando individuos

https://doi.org/10.7203/sjp.32.2.17047

by the excavated area of Las Hoyas because small juveniles should be the most common sizes.

Keywords: Isolated scales, scale anatomical characters, coelacanth palaeobiology, Latimeriidae.

relativamente grandes. Esto sugiere que posiblemente una población natural de celacantos no habitaba permanentemente el sistema representado por el área excavada de Las Hoyas, ya que en ese caso las formas juveniles deberían ser las más abundantes.

Palabras clave: Escamas aisladas, características anatómicas de escamas, paleobiología de celacantos, Latimeriidae.

1. INTRODUCTION

Las Hoyas is famous mostly for the exceptionally well-preserved remains of some important tetrapod fossils, including primitive birds, dinosaurs, a pterosaur and a mammal (Poyato-Ariza & Buscalioni, 2016). However, the vertebrate association of this locality is actually dominated by fishes. At least 18 different taxa of fishes have been identified at Las Hoyas, including condrichthyans and osteichthyans (Soler-Gijón *et al*., 2016; Poyato-Ariza & Martín-Abad, 2016). Osteichthyans are represented mostly by actinopterygian fishes (pycnodontiforms, ginglymodians, amiiforms, teleosts), but some remains belonging to a coelacanth have also been found.

The coelacanth is the least common osteichthyan at Las Hoyas (Poyato-Ariza & Martín-Abad, 2016), and so far only a few articulated specimens have been recovered. Despite the exceptional preservation that characterizes the fossil record of this locality (e.g., Gupta *et al*., 2008; Poyato-Ariza & Buscalioni, 2016), the coelacanth remains are usually not very well preserved. As a consequence, no detailed anatomical and taxonomical studies of Las Hoyas coelacanth have been conducted to date. The Las Hoyas coelacanth was initially referred to the species *Holophagus leridae* (Sanz *et al*., 1988; Poyato-Ariza & Wenz, 1995), due to its similarity with the coelacanth from the Spanish Fossil-Lagerstätte of El Montsec; however, it also exhibits a few distinct features, and thus is currently regarded as cf. "*Holophagus*" sp. (Poyato-Ariza, 2005a). Nonetheless, the genus *Holophagus* is now being restricted to the lower Lias (Forey, 1991), suggesting that the species from Las Hoyas would probably belong to a different genus (Poyato-Ariza & Martín-Abad, 2016).

The fossil fish collection of Las Hoyas includes numerous isolated scales. A large proportion of these isolated scales are of the "amioid"-type. The term "amioid" is somewhat misleading when referring to scales, since they are not only present in amioid fishes (Amiiformes), but in several other groups of non-amioid actinopterygians, (Arratia, 2015; Arratia & Schultze, 2007; Schultze, 1966, 1977), and even in coelacanths (Schultze, 1977).

Usually, isolated scales of coelacanths are easy to identify following the description by Forey (1998), mainly based on their strong ornamentation. However, in some taxa this ornamentation is not that conspicuous, giving the scales an appearance more similar to that of the "amioid" scales of some actinopterygians. Therefore, in the localities where different "amioid"-scale-bearing taxa co-occur, the isolated scales can sometimes be difficult to differentiate from each other; this is the particular case of Las Hoyas (Martín-Abad, 2016). One coelacanth and three amiiform taxa have been reported from this locality (Poyato-Ariza & Martín-Abad, 2016). The objective of the present paper is to provide a thorough description of the scales of the coelacanth from Las Hoyas to distinguish isolated scales of the distinct "amioid"-scale bearing taxa. For that purpose, the isolated scales found in the fossil collection of Las Hoyas will be compared to the known articulated specimens of coelacanths and other "amioid"-scales-bearing taxa from the locality (i.e., amiiformes), to develop a list of diagnostic characteristics. Previous work by Martín-Abad (2016) describes isolated amioid scales from Las Hoyas belonging to the three amiiform taxa. Finally, we discuss the palaeoecological implications of the presence of isolated coelacanth scales, and their preservation and size distribution, with regard to the freshwater palaeonvironment. To better understand the palaeoecology of fossil coelacanths, a brief summary of the biology of the extant coelacanths is included in the following section.

2. EXTANT COELACANTHS

There are two critically endangered, extant species, *Latimeria chalumnae* and *L. menadoensis*, which live in the western Indian Ocean near the Comoro Islands, and off the east coast of Africa. Coelacanths are marine species that normally live at depths greater than 100 m (Hissmann *et al*., 2006). *Latimeria menadoensis* inhabit warm water temperatures, 17.8-20.1°C, at a depth of 155 m (Fricke *et al*., 2000). Coelacanths exhibit low sexual reproduction and late maturation (Thornycroft & Booth, 2012). Heemstra & Greenwood (1992) reported that one female contained 26 fetuses. The pups are about 40 cm long at birth (Froese & Palomares, 2000). The largest specimens known to date

of *Latimeria chalumnae* and *L. menadoensis* are 183 cm (not 200 cm as reported in Fishbase) and 140 cm total length, respectively (Fishbase.org; Froese & Palomares, 2000; Fricke *et al*., 2000).

Coelacanths reside in the same area over many years and exhibit extraordinary breeding philopatry (Fricke *et al*., 2011). One study showed adult coelacanths inhabited many caves within their home range and immigrated to other caves outside of the census area over many years (Fricke *et al*., 2011). No juveniles were recorded in Fricke's study, and he concluded that juveniles live below the depth of adults (Fricke *et al*., 2011). Segregation of habitat may indicate the danger of cannibalism (Fricke *et al*., 2011). Coelacanths are known to be nocturnal, and they occupy caves during the day (Hissmann *et al*., 2006). The sightings of individuals in the canyons of Greater St Lucia Wetland Park in Africa reveal that the Sodwana coelacanths use canyons as homes for at least four years (Hissmann *et al*., 2006). Coelacanths of the Comoros are known to be loyal to several different caves throughout their lives (Hissmann *et al*., 2006).

3. MATERIAL AND METHODS

3.1. Geological setting and excavation procedures

The upper Barremian (Lower Cretaceous) fossil site of Las Hoyas forms part of the La Huérguina Formation, and is located near the city of Cuenca. It has been interpreted as a shallow pool within a larger regional subtropical freshwater wetland ecosystem (Buscalioni & Fregenal-Martínez, 2010; Fregenal-Martínez & Meléndez, 2016). No marine influence has been detected at the locality according to isotopic and rare earth analyses (Poyato-Ariza *et al*., 1998; Bailleul *et al*., 2011). The palaeoecosystem was regulated by a seasonal climate regime that would experience cyclical oscillations of the water level (Fregenal-Martínez & Meléndez, 2000). During the wet seasons, the water level rose, connecting Las Hoyas to larger water masses in the watershed; whereas during the dry seasons, the Las Hoyas pool would probably be temporarily disconnected and covered by microbial mats.

The early fieldwork campaigns at Las Hoyas were characterized by exploratory-sampling excavation, and consequently no precise information about the exact stratigraphy and provenance of the fossils within the locality was recorded. In more recent years, a more systematic layer-by-layer excavation in square sampling areas has been carried out (Buscalioni & Fregenal-Martínez, 2010; Buscalioni & Poyato-Ariza, 2016), which has allowed us to keep record of the exact provenance of the fossils. Yet many of the specimens that comprise the fossil collection do not come from these square sampling areas, but from the exploration of the debris dumps that were created during the opening of the squares. These debris dumps are searched every few years to minimize the number of disregarded fossils in the locality. As a result, part of the fossils that have been added to the collection since opening the sampling areas, in the last years, also lack exact stratigraphic information.

3.2. Material examined

Only one relatively complete and well-preserved coelacanth specimen has been found at Las Hoyas; the smallest specimens are better preserved but are usually not completely ossified. Other specimens include mostly caudal fins, the largest of which are preserved only as imprints, not preserving any bone. The available material does not show significant variability to suggest the presence of more than one species.

A total of 151 unidentified isolated fish scales (or groups of isolated scales found together, probably belonging to the same individual and thus counted as a single specimen here) from Las Hoyas were examined. For a complete list of the material examined, see the Appendix.

Only mechanical techniques were used for preparing the isolated scales; they were prepared mainly with insect display pins under the microscope. Scales were coated with ammonium chloride to highlight the relief of the different structures.

The antero-posterior length was recorded for each isolated coelacanth scale as well as for the scale of the best preserved articulated specimen, in mm. A histogram was used to graphically represent whether small individuals were present at Las Hoyas.

3.3. Institutional abbreviations

JM, Jura-Museum (Eichstätt, Germany). **MCCM-LH**, Museo de las Ciencias de Castilla-La Mancha, Las Hoyas collection (Cuenca, Spain). **NKMB**, Naturkunde-Museum Bamberg (Bamberg, Germany).

4. RESULTS

4.1. Anatomical description of the coelacanth scales from Las Hoyas

The scales of the coelacanth recovered at Las Hoyas (Fig. 1) are thin "amioid" scales, and lack a shiny layer of enamel tissue. They are ovoid in shape, with the posterior margin slightly more acuminated than the anterior margin, which

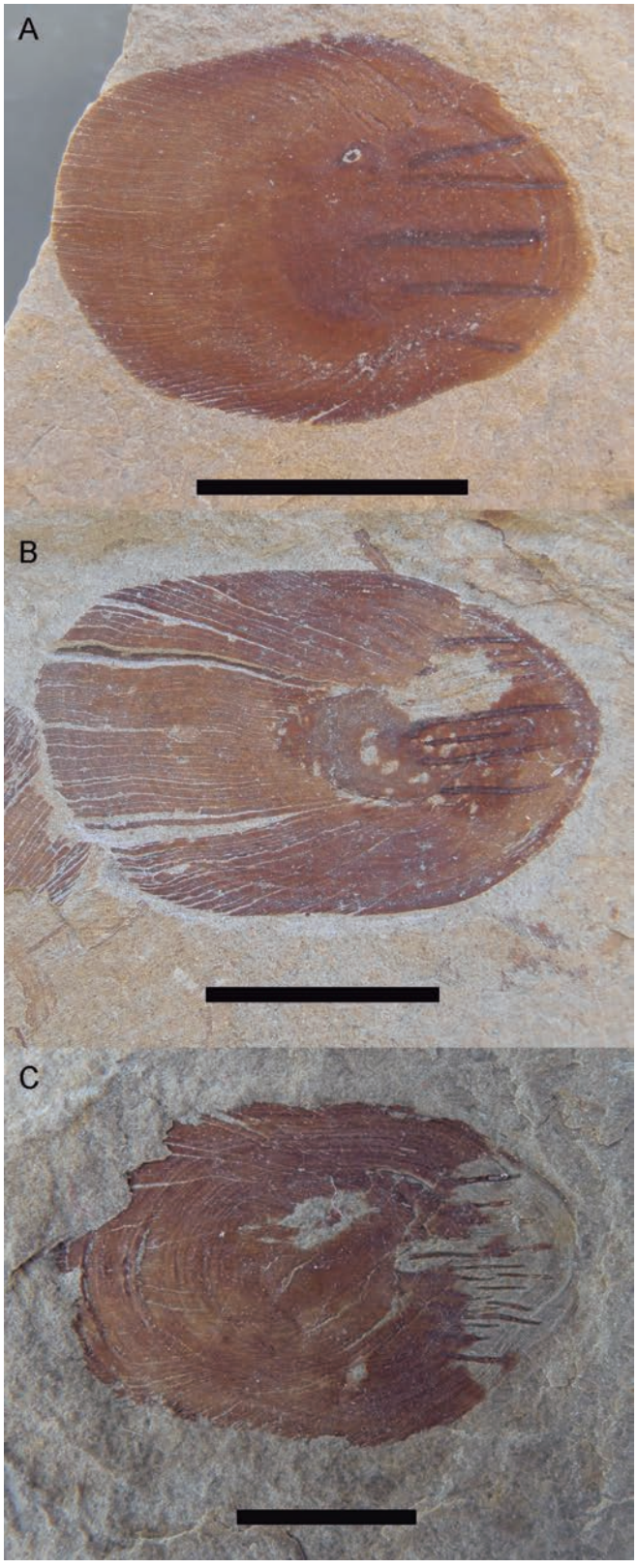

Figure 1. Isolated coelacanth scales recovered from Las Hoyas locality. **a)** Specimen MCCM-LH 37156. **b)** Specimen MCCM-LH 9406a/b. **c)** Specimen MCCM-LH 5276b. Anterior facing left. Scale bars = 5 mm.

is more rounded. The scales are approximately 1.5 times longer than they are deep.

The focus is not easy to identify, since the central part of the scale is smooth (lacks detail), and the ridges in this area are difficult to follow. This smoother area is relatively large, covering part of the anterior, lateral, and posterior fields, and based on the preservation on specimen MCCM-LH 28210a/b (Fig. 2) seems to present a different ossification. This smooth area is not a consequence of the scales being regenerated, since it is present in all the scales. The focus is best observed on the isolated scales

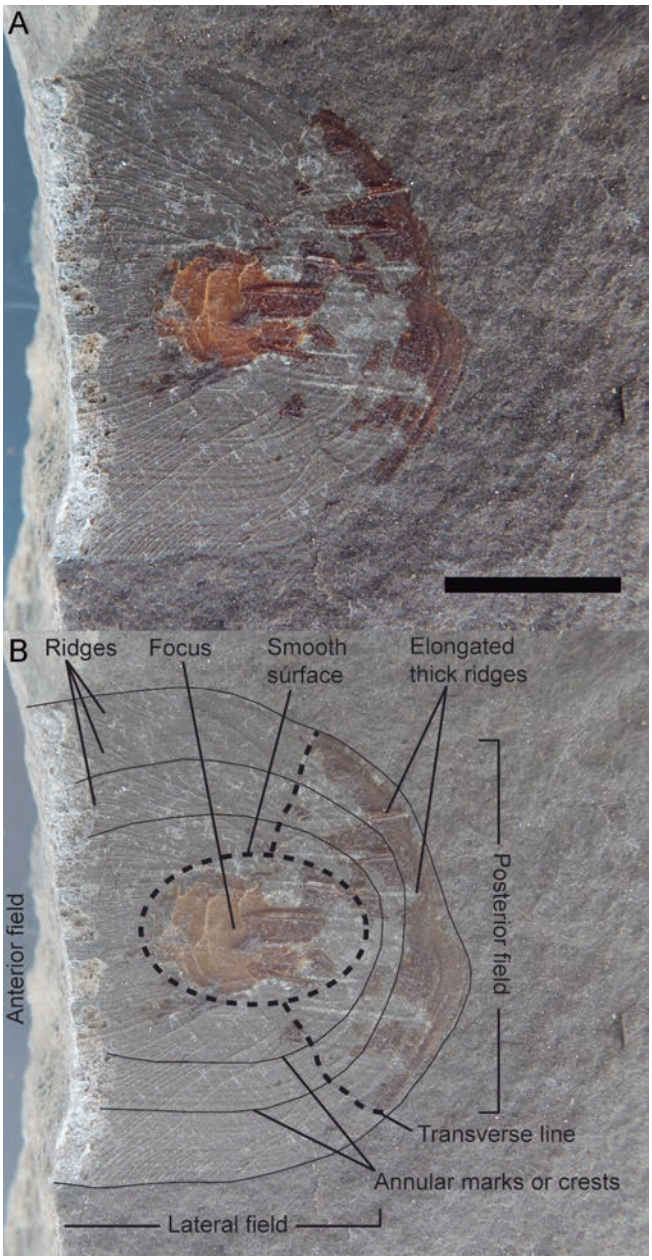

Figure 2. Incomplete isolated coelacanth scale recovered from Las Hoyas locality. **a)** Picture of specimen MCCM-LH 28210a/b. **b)** Anatomical characters drawn over picture on **(a)**. Anterior facing left. Scale bar = 5 mm.

MCCM-LH 840a/b and 5089a, which exhibit an imprint of the surface of the scale (the bony tissue of this area is either not preserved or preserved on the counterslab, MCCM-LH 5089b). The focus of MCCM-LH 415 is well defined, located closer to the posterior margin of the scale than to the anterior margin, and approximately at 1/3 of the longitudinal distance from the posterior margin.

The anterior, lateral and posterior fields are covered by very thin ridges radiating from the focus and the transverse line, running more or less parallel to each other. The ridges on the anterior field are straight, and extend to the anterior margin of the scale. The ridges on the lateral fields are curved, and sequentially shorten near the transverse line. The ridges on the posterior field are much shorter.

The boundaries between the anterior and the lateral fields are not clear, since anastomoses are difficult to identify between the ridges at the limit of these fields. In comparison, the boundaries of these fields are easier to identify in other "amioid" scales, where there are numerous anastomoses affecting the ridges between them (e.g., amiiform "amioid" scales at this same locality; see Martín-Abad, 2016). The transverse line, that is, the boundary between the lateral and posterior fields, is easier to identify, although it is not well defined. The transverse line is anteriorly convex, and extends from the postero-dorsal and postero-ventral edges of the scales to approximately the middle of the focal area. The transverse line is situated anterior to, or just crossing the anterior part of, the thick ridges on the posterior field (see below). A few anastomoses seem to be present on the transverse line, although they are difficult to identify.

The main ornamental features on these scales are a series of elongated, thick ridges (not to be confused with the thin ridges covering most of the surface of the scale described above), on the posterior or exposed field. These thick ridges are more or less parallel to each other, the medial ones being usually longer. On many of the specimens, these ridges are actually preserved as negative imprints (they were probably not preserved during the fossilization process), but small parts of them are preserved on some specimens. The ridges are always widely separated from each other, in contrast to being densely-packed and touching each other across the entire posterior field in other coelacanth taxa (see for example figures 1 and 2 in Yabumoto & Neuman, 2004). The number of these ridges is significantly and positively related to size of the scale ($Y = 1.526e^{1.524x}$; $n = 10$; $R^2 = 0.775$; 95% CI for $m = 0.740$ to 2.309) (Table 1, Fig. 3). Smaller scales show a single row of ridges, whereas larger scales can have two rows of ridges, at least on the medial part of the

Table 1. Measurements of antero-posterior length of the scales of the best preserved articulated specimen (MCCM-LH 007aR) and the identified coelacanth isolated scales from Las Hoyas.

MCCM-LH	007aR	415	840a/b	930	2328	5089a/b	5276a/b	9406a/b	17011	28210a/b	37156	37179
L (cm)	0.52	≈1.31	≥1.12	1.50	≥0.83	≥1.07	1.55	1.19	1.63	>1.27	0.97	>1.25
Ridges	5?	13+	?	11	?	4	17	9	19+	13	5	13?

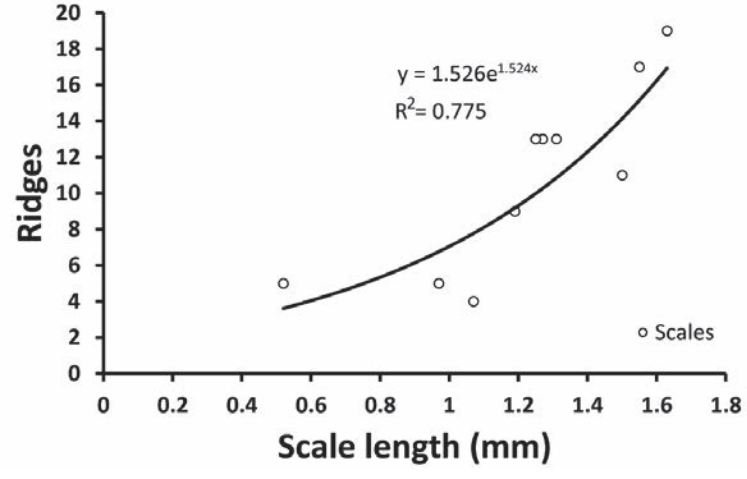

Figure 3. The significant relationship between scale length and the number of posterior ridges on scales of Las Hoyas coelacanths. The open circles represent isolated scales and one scale from a partial, articulated individual (MCCM-LH 007aR). The line indicates a significant exponential regression.

exposed field. Yabumoto & Neuman (2004) also suggested that the number of ridges probably increases with size in *Diplurus* and *Whiteia*. Forey (1998) also suggested that the ornamentation can vary among different species of *Diplurus*, as well as across the body of a single specimen, which seems to occur as well in *Macropoma* (Fig. 4). The high degree of articulation on specimen MCCM-LH 007aR prevents us from properly checking if the number of ridges varies also across its body, since the scales overlap each other, but most of the visible scales seem to present five elongated ridges.

Concentric marks, also termed crests, are usually very conspicuous on the surface of the scale, especially on the posterior and lateral fields. These concentric crests are usually interpreted as growth cessation marks, and are used in fisheries for calculating the chronological age of the fish. On the coelacanth scales studied here, there appear to be more concentric crests on larger scales. However, the usefulness of annual marks to age coelacanths is under debate (see Hureau & Ozouf, 1977; Fricke & Hissmann, 2000; Froese & Palomares, 2000).

4.2. Identification of isolated scales in Las Hoyas fossil collection

Only 11 out of the 151 unidentified isolated fish scales examined were confidently identified as coelacanth scales according to the description given above: MCCM-LH 415, 840a/b, 930, 2328, 5089a/b, 5276a/b, 9406a/b, 17011, 28210a/b, 37156, 37179. The remaining 140 isolated scales belong to either amiiforms or other yet unidentified taxa.

On the articulated specimens, the scales are best observable in specimen MCCM-LH 007aR. Specimen MCCM-LH 144P also presents identifiable impressions of the scales. Specimens MCCM-LH 9445a/b and 33227 have scales preserved, but they are still too small to show details. The scales of the remaining specimens are poorly preserved or not reliably identifiable. As it was observed on the articulated skeletons, the scales do not show anatomical differences that suggest the presence of more than one species.

The antero-posterior length of the scales was measured in the best-preserved articulated specimen (MCCM-LH 007aR), and measured or estimated in the isolated coelacanth scales (Table 1). In total, scales ranged in length from 0.52–1.63 cm and the mean was 1.2 cm. In a histogram of scale sizes, the size class of 1.01–1.25 cm are most commonly represented as the mean, median and mode (Fig. 5). Scales larger than the mean are more common than scales smaller than the mean.

5. DISCUSSION

5.1. Differentiation between isolated amiiform and coelacanthiform “amioid” type scales at Las Hoyas

As summarized by Schultze (1996), “amioid” scales are elasmoid (flexible, round) with longitudinally to radially arranged ridges or rods on the overlapped field, instead of

Figure 4. Scales of the coelacanth *Macropoma willemoesii* from the Upper Jurassic Solnhofen archipelago in Germany, showing the scale ornamentation. Specimen JM SOS 2207. Scale bar = 1 cm.

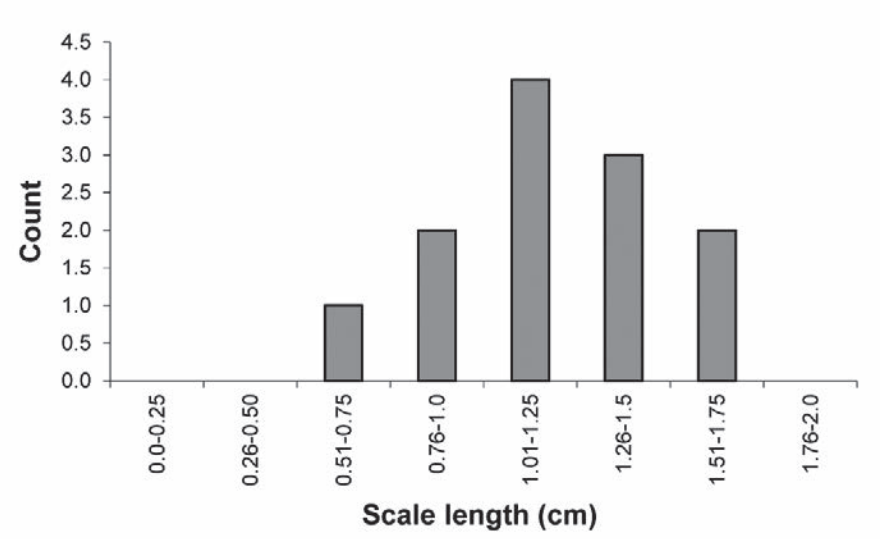

Figure 5. Size/frequency histogram of coelacanth scales from Las Hoyas. The histogram is comprised of isolated scales and one scale from a partial, articulated individual (MCCM-LH 007aR).

forming concentric circuli that run parallel to the margin of the scale. "Amioid" scales are also characterized by the lack of several structures usually present in the scales of other actinopterygian fishes, such as ctenii, radii, enamel tissue, vascular canals, thick bony base, or peg-and-socket articulation.

In short, the "amioid" scales of coelacanths are formed by a basal layer of cellular isopedine, which is laid down as a series of layers enclosing collagen fibers in different orientations; the surface layer consists of cellular bone, dentine and enamel or enameloid (Forey, 1998). The exposed part of the scale is pigmented and ornamented by a series of thick ridges of enamel (e.g., Smith *et al*., 1972; Yabumoto & Neuman, 2004). These thick ridges can be elongated, sharp, and usually not very numerous, such as in the coelacanth *Macropoma* (Woodward, 1909; Lambers, 1996); or they can be short and crowded, such as in *Garnbergia* (Martin & Wenz, 1984; Yabumoto & Neuman, 2004).

The presence of thick ridges is also a good indicator of coelacanth scales, especially when the ridges are numerous and crowded. However, when these ridges are less numerous and conspicuous, the overall appearance of the coelacanth scales can be very similar to that of other "amioid" scales, such as those of amiiform fishes. The detailed description provided above allows to distinguish the coelacanth "amioid" scales from the "amioid" scales belonging to the three taxa of amiiform fishes present at Las Hoyas.

In summary, the scales of the coelacanth species are characterized by the presence of a smooth central surface, a particular pattern of arrangement of concentric growth cessation marks, and mainly a relatively short posterior or exposed field with elongated thick ridges. This contrasts with the description provided by Martín-Abad (2016) for the three amiiform taxa. The first amiiform species presents scales that are rounded to quadrangular in shape, and are characterized by the presence of a thick rim around their posterior field; anastomoses are clearly visible on the crests. The second species presents scales that are ovoid in shape, with a posterior field occupying one third of the scale where the crests are hard to observe, and numerous anastomoses defining a clear transverse line. Finally, the scales of the third species are subrectangular in shape, with a greatly reduced posterior field that is very thinly ossified; all the thin ridges covering the surface of the scale appear to originate at the focus, and not at the transverse line.

5.2. Taxonomical identification

A detailed anatomical description of the coelacanth species from Las Hoyas has not been carried out up to date, due to the relatively bad preservation of the scarce material that has been found. The anatomical characteristics of the scales noted here from the study of isolated scales support the conclusion of Poyato-Ariza & Wenz (1995) and Poyato-Ariza & Martín-Abad (2016), who stated that the ornamentation of the scales is similar to that of "*Holophagus"* from El Montsec and other latimerids, such as the Late Jurassic *Macropoma* (Fig. 4), mainly by the presence of a low number of elongated ridges on the exposed field. Forey (1998), Holder *et al*. (1999), and Wendruff & Wilson (2012) suggested that morphological characteristics of coelacanth scales can be informative and might be the best characters available in investigating coelacanth systematics, an opinion shared also by Hadiaty & Rachmatika (2003). However, until the scales of more fossil coelacanth taxa are described in detail, scale ornamentation should be used with caution for taxonomic purposes; for instance, other latimerid taxa have been reported to show more numerous and smaller, denticle-like

tubercles, instead of elongated ridges (e.g., *Latimeria*, *Libys*, and *Undina*), and some non-latimerid coelacanths, such as *Rebellatrix*, present elongated ridges (Wendruff & Wilson, 2012).

5.3. Palaeoecology of Las Hoyas coelacanth

The largest specimens known to date of *Latimeria chalumnae* and *L. menadoensis* are 183 cm and 140 cm total length (TL) respectively (Brunton, 1995; Fishbase.org; Froese & Palomares, 2000; Fricke *et al*., 2000). Our hypothesis is that the Las Hoyas coelacanth did not reach such lengths. It is difficult to estimate the TL of the largest specimens found at this locality, based on the current available data, because they are only represented by incomplete caudal fins and, unfortunately, the caudal fin is not preserved in the most complete specimen. Specimen MCCM LH 007aR measures about 20 cm TL, and a large representative scale is 0.53 cm long. According to Hureau & Ozouf (1997), in *Latimeria chalumnae* a 0.53 cm scale would belong to a 30.5 (0.45 cm scale) to 42.5 (0.61 cm scale) cm TL specimen, suggesting that scales are much longer in proportion to the body length in the Las Hoyas coelacanth than in the extant species. The largest isolated coelacanth scale found at Las Hoyas measures 1.63 cm in length. Taking into account the highly asymptotic growth of scales, the different proportion between scale and body lengths between the two taxa, and the length data gathered by Hureau & Ozouf (1977), a 1.63 cm scale would probably belong to a 45-50 cm TL individual. In that sense, the largest partially articulated specimens (fragments of caudal fins) found so far at the locality could represent the longer individuals of the population (always considering the possible bias due to the small sample of isolated scales available or the inadequate knowledge of their chronological ages).

Most of the other fish taxa found at Las Hoyas are mainly represented by small specimens. In fact, it has been repeatedly stated that the adult individuals of most fish taxa of this locality show a very interesting phenomenon of size reduction, maybe related with environmental stress (Poyato-Ariza, 2005b; Buscalioni & Fregenal-Martínez, 2010). Examples of this phenomenon are the two chanid fishes, *Rubiesichthys gregalis* and *Gordichthys conquensis*, and the two "*Lepidotes*" species. The largest articulated specimens of these taxa found at Las Hoyas are only a few centimeters in TL, while other Cretaceous relatives of these groups can reach up to almost two meters long (Poyato-Ariza & Martín-Abad, 2016).

The study of the isolated scales recovered at the locality indicates the existence of large individuals of species that are only represented by small articulated skeletons. These isolated scales are often larger than the scales in the largest articulated specimens of each fish taxon. The coelacanth species is not an exception; all the isolated scales assigned here to the coelacanth species are notably longer than those in the most complete specimen, MCCM-LH 007aR (Table 1), and thus belonged to larger individuals. The largest of the Las Hoyas coelacanth scales are smaller than those of the largest scales listed in Hureau & Ozouf (1977) suggesting that no such large individuals are present.

The size of small articulated specimens at Las Hoyas suggests relatively small sizes as adults. The extant *Latimeria chalumnae* gives birth to 35-38 cm long juveniles (Smith & Heemstra, 1995). The small articulated specimens found at Las Hoyas (Fig. 6) demonstrate that juveniles of this taxon were much smaller when they were born than those of *L. chalumnae*. Specimen MCCM-LH 26491a/b is less than 7 cm TL, and the incomplete specimens MCCM-LH 9445a/b, 31268a/b and 33227 represent even smaller individuals. Thus, specimen MCCM-LH 007aR, which measures around 20 cm TL, was probably not a juvenile. If this is so, then all isolated scales represent adult individuals.

In summary, most of the coelacanth remains found at Las Hoyas, including both articulated specimens and isolated scales, represent large individuals; only four specimens represent small individuals. A preservational bias can be discarded due to the exceptional preservation that characterizes the locality; additionally, very small isolated scales of other fishes have been recovered. Moreover, the systematic layer-by-layer methodology of excavation, where even the debris dumps are searched every few years, also minimizes the possible collection bias. Also, small fish are commonly preserved at Las Hoyas (Poyato-Ariza & Martín-Abad, 2016). This suggests that, despite the small sample size, 21 individuals so far between isolated scales and articulated specimens, the association of coelacanth individuals does not seem to represent a natural population (i.e., survival requires that juveniles should be the most abundant forms). In other words, coelacanths may not have spent their complete life cycle at the small pool represented by the excavated area of Las Hoyas.

Many freshwater fishes develop habitat partitioning throughout their life, that is, adults inhabit an area separate from juveniles, usually more restricted and protected for spawning; juveniles would then live in this area until they reach sexual maturity. Habitat partitioning is especially common in wetlands, which are typically patchy, arranged according to blurred ecotones, and generate a wide variety of microhabitats and environmental mosaics (van der Valk, 2006; van der Valk & Warner, 2009), as has also been suggested to happen at Las Hoyas (Buscalioni *et al*., 2016). Fricke *et al.* (2011) reported that juveniles of *Latimeria chalumnae* were not recorded with adults, leading to the conclusion they inhabited deeper habitats.

Specimens of Las Hoyas coelacanths are rare at the locality. We suggest four non-mutually exclusive hypotheses to address their scarcity. One, the population

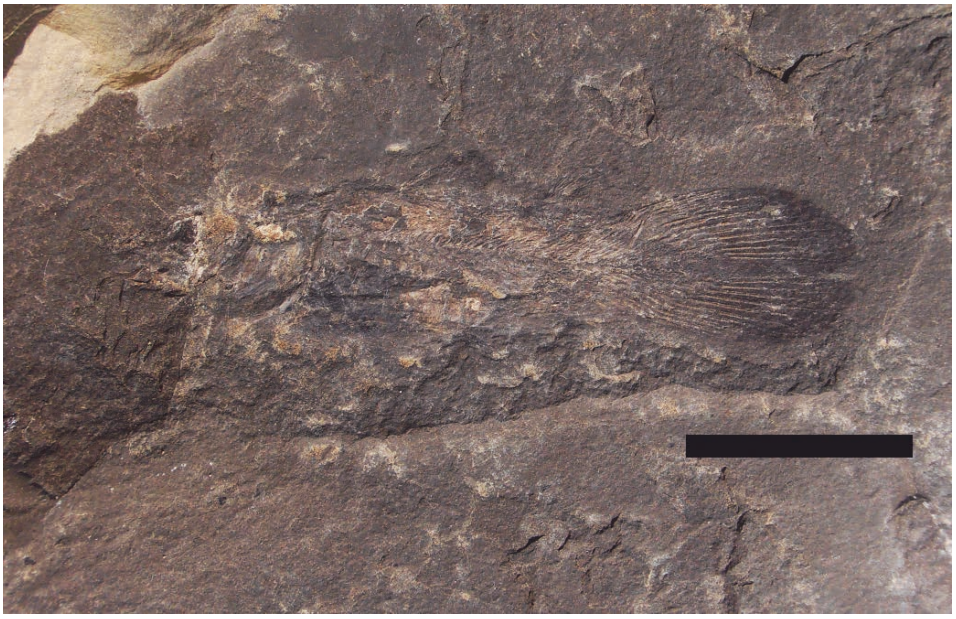

Figure 6. Small, almost complete and articulated specimen of the coelacanth from Las Hoyas locality. Specimen MCCM-LH 26491a. Scale bar = 2 cm.

of this coelacanth was small (i.e., there were far less individuals of coelacanth inhabiting the area than of any other fish). Although the social behaviour of *Latimeria chalumnae* is not well known, they apparently do not form large populations or fish banks, and only 13-14 individuals have been reported to shelter in the same cave at a time (Fricke *et al*., 1991; Fricke & Hissmann, 1994). Two, the coelacanth species only inhabited Las Hoyas for a (geologically) short period. Unfortunately, the current lack of precise stratigraphic information about the provenance of most isolated scales and articulated specimens does not permit a test of this hypothesis at this time. Three, the coelacanth did not live at all in the pond represented by the excavated area of Las Hoyas, but in a different, probably more stable and deeper water mass. If so, the scarce and badly preserved remains recovered might have been transported into the locality area during the wet seasons, when water levels were high and Las Hoyas was connected to other parts of the wetland ecosystem. Four, the coelacanth developed habitat partitioning, usually spending only part of its life cycle in this pond, thus accounting for the non-natural proportion between juvenile and adult individuals found so far at the locality.

6. CONCLUSIONS

This study morphologically distinguishes the scales of the Las Hoyas coelacanth from other types of "amioid" isolated scales recovered in this Early Cretaceous locality. The presence of a smooth central surface, a different pattern of arrangement of concentric growth cessation marks, and mainly a relatively short posterior or exposed field with elongated thick ridges differentiates the coelacanth scales from the "amioid" scales belonging to the three amiiform taxa that inhabited Las Hoyas. The description of coelacanth scales from Las Hoyas will prove useful for the identification of isolated scales found in other fossil localities in the future.

Coelacanth remains, including both articulated specimens and isolated scales, are rare at Las Hoyas. There are several factors that could contribute to their rare occurrence at Las Hoyas; it is even possible that they inhabited another nearby environment. In any case, most of them represent relatively large individuals, suggesting that a natural population (i.e., where juveniles are the most abundant individuals, and older forms are less common) did not inhabit the pool represented by the excavated area of Las Hoyas. Age and growth studies based on the analysis of growth cessation marks deposited on bones of fossil fishes have proven to be a useful tool for estimating palaeobiological parameters, including age of sexual maturity (Newbrey & Bozek, 2003). In this sense, future work on age and growth of Las Hoyas coelacanths will provide insight into the age distribution of these specimens, better define adult individuals, and finally clarify whether they developed habitat partitioning throughout their life.

ACKNOWLEDGEMENTS

We would like to thank Ángela Delgado Buscalioni, Francisco José Poyato Ariza (Universidad Autónoma de Madrid, Spain) and Marian Fregenal Martínez (Universidad Complutense de Madrid, Spain) for their discussions about

Las Hoyas palaeoecology. Reviews by Carlos Martínez Pérez and an anonymous reviewer helped improve the original manuscript. Funding for this project comes from a grant "Ayudas a la Investigación de la Sociedad Española de Paleontología, 2015-2016" provided to H.M.-A. This paper is a contribution to project CGL-2013-42643 P (MINECO, Spain).

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APPENDIX: MATERIAL EXAMINED

Articulated coelacanth material from Las Hoyas. MCCM-LH 007aR, 144P, 6137, 9077a/b, 9445a/b, 26491a/b, 26492a, 31268a/b, 32754a/b, 33227.

Isolated scales examined from Las Hoyas (n = 151). MCCM-LH 410, 415, 840a/b, 845, 930, 1031, 1075, 1566, 1602, 1612, 2049, 2158a/b, 2188, 2328, 2332, 2408a/b, 2410a/b, 2964, 2995, 3200, 3208, 3749, 5069, 5089a/b, 5276a/b, 5284, 5414a/b, 6080, 6172, 6209a/b, 6210+6211, 6369a/b, 6371a/b, 6372, 7053a/b, 7056a/b, 7060a/b, 7073a/b, 7074a/b, 7079a/b, 7139a/b, 7244a/b, 8090, 9406a/b, 9192, 9193, 9194, 9342a/b, 9621a/b, 9622a/b, 11178 a/b, 13506, 14094 a, 16010 a, 16334 a/b, 16630, 16724, 17011, 17080 a/b, 17197 a/b, 18017 a/b, 18050 a/b, 20051, 20072, 20136 a/b, 20534, 20619, 22084a/b, 22147a/b, 22213a/b, 22403a/b, 22404a/b, 22532a/b, 23928a/b, 26361a/b, 26530, 26924, 27038, 28210a/b, 28764a/b, 29137a, 29345, 29589, 29720a/b, 30106, 30348, 30419a/b, 30962a/b, 30976, 31052a/b, 31106a/b, 31367a/b, 31368a/b, 31372a/b, 31373a/b, 31374a/b, 31375a/b, 31381a/b, 31390a/b, 31424, 31427, 32032, 32056a/b, 32057, 32058, 32068a/b, 32077a/b, 32095a/b, 32123a, 32195a, 32236, 32242a/b, 32311a/b, 32313, 32314, 32362a/b, 32407a/b, 33368, 33373, 33381a/b, 33500b, 33540b, 37150a/b, 37151, 37152, 37153, 37154, 37155, 37156, 37157a/b, 37158a/b, 37159a/b, 37160a/b, 37161a/b, 37162, 37166, 37167, 37168, 37169, 37170, 37171, 37172, 37173, 37174, 37175, 37176, 37177, 37178, 37179, 910167, 928006a/b.

Comparative material. Coelacanthiformes indet., NKMB P-2008-watt-7 (isolated scale), P-2008-watt-591 (isolated scale): Wattendorf, Upper Jurassic, Germany. *Macropoma willemoesii*, JM SOS 2207 (disarticulated bones and scales): Solnhofen Archipelago, Upper Jurassic, Germany.