C. R. Palevol 16 (2017) 257–265

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Anatomical differentiation of isolated scales of amiiform fishes (Amiiformes, Actinopterygii) from the Early Cretaceous of Las Hoyas (Cuenca, Spain)

Différenciation anatomique d'écailles isolées de poissons ammiformes (Amiiformes, Actinoptérygiens) du Crétacé inférieur de Las Hoyas (Cuenca, Espagne)

Hugo Martín-Abad [a,b,c,*]

[a] *Unidad de Paleontología, Departamento de Biología, Universidad Autónoma de Madrid, Calle Darwin 2, 28049 Madrid, Spain*
[b] *JURASSICA Museum, route de Fontenais 21, CH-2900 Porrentruy, Switzerland*
[c] *Department of Geosciences, University of Fribourg, chemin du Musée 6, CH-1700 Fribourg, Switzerland*

ARTICLE INFO

Article history:
Received 21 January 2016
Accepted after revision 23 August 2016
Available online 4 October 2016

Handled by Philippe Janvier

Keywords:
Scale anatomy
Isolated scales
Amiiformes
Amia calva
Early Cretaceous
Las Hoyas
El Montsec

ABSTRACT

The scales of amiiform fishes are more different from each other than previously stated. The anatomy of the scales of the three amiiform taxa from the Early Cretaceous (Barremian) of Las Hoyas (Cuenca, Spain) is described in detail. The differences between them has allowed the segregation of isolated scales form the fossil record of this site into the three taxa, providing relatively large population samples that can be studied from a palaeobiological and palaeoecological point of view.

Mots clés :
Anatomie des écailles
Écailles isolées
Amiiformes
Amia calva
Crétacé inférieur
Las Hoyas
El Montsec

RÉSUMÉ

Les écailles des poissons amiiformes sont plus différentes les unes des autres que ce qu'on avait précédemment affirmé. L'anatomie des écailles des trois taxons d'amiiformes du Crétacé inférieur (Barrémien) de Las Hoyas (Cuenca, Espagne) est décrite en détail. Les différences observées permettent la répartition des écailles isolées de cette localité entre ces trois taxons, ce qui permet de disposer d'un échantillonnage assez large, autorisant des études paléobiologiques et paléoécologiques.

* Unidad de Paleontología, Departamento de Biología, Universidad Autónoma de Madrid, Calle Darwin 2, 28049 Madrid, Spain.
E-mail address: hugo.martin@uam.es

http://dx.doi.org/10.1016/j.crpv.2016.08.006
1631-0683/

1. Introduction

The scales of amiiform fishes have been the subject of many studies, mostly in the classical literature. The anatomy, histological origin and development, and ossification process of the scales of the only extant species of this order, *Amia calva*, have been studied in detail by numerous authors, including Mackintosh (1878), Cockerell (1911), Degener (1924), Lagler (1947), Jollie (1984), and especially Kerr (1952). More recently, their histological microstructure and mineralization have been described by Meunier (1981). Grande and Bemis (1998) describe and illustrate the ontogenetic development and individual size and shape variation of *A. calva* scales. Cooper and Schafer (1954), Cartier and Magnin (1967) and Schiavone (1982) studied the age and growth of *A. calva* by means of identifying growth cessation marks on their scales.

Schultze (1996) summarizes and discusses the phylogenetic distribution of different scale anatomies in actinopterygian fishes, establishing different types of scales. The "amioid" type of scales is described as elasmoid (flexible, round) with longitudinally to radially arranged ridges or rods on the overlapped field, instead of forming circuli parallel to the anterior margin of the scale. "Amioid" scales also lack several structures present in the scales of other actinopterygian fishes, such as ctenii, radii, enamel tissue, vascular canals, thick bony base, or peg-and-socket articulation. The term "amioid" scale should be used with caution [hence the usage of quotation marks here, following Grande and Bemis' (1998) recommendation], since this type of scales is present in amiids but also in caturids, ionoscopids, and other non-amioid actinopterygians (e.g., Arratia, 2015; Arratia and Schultze, 2007; Schultze, 1966, 1977). According to Schultze (1977), it is even present in sarcopterygians. On the contrary, it is not present, or at least is not the only type of scale present, in sinamiids, which are part of Amioidea (Grande and Bemis, 1998; Schultze, 1996).

Studies on fossil amiiform scales are much less common. Schultze (1966) compares the morphology and histology of several actinopterygians, including the amiiforms *Caturus* and *Urocles* (*Solnhofenamia*). Meunier and Poplin (1995) studied the histological microstructure and mineralization of the scales of *Amia robusta* from the Palaeocene of Cernay (France), and showed that it is practically the same than that of the scales of *A. calva*. Micklich (2012) studied the palaeobiology and the age and growth characteristics of *Cyclurus kehreri*, a representative of the subfamily Amiinae from the Eocene of Messel (Germany), in comparison with its extant relative in part by examining marks preserved on its scales.

On the basis of a comparison between the scales of numerous actinopterygian groups, Schultze (1996) suggests that a convergence occurred in the development of the scales of Amiidae and Caturidae (more particularly the genus *Caturus*), which are more similar to each other than to any other of the groups he studied, including Sinamiidae. However, the actual anatomical differences between the scales of the different taxa bearing "amioid"-type scales have never been addressed. For instance, in their monographic study on amiid fishes, Grande and Bemis (1998) describe the scales of every amiid species as being very similar or even undistinguishable from those of *A. calva*. Up to date, the only significant anatomical difference detected is a more ovoid to subrectangular contour in amiid scales in comparison to a more rounded contour in caturid scales (Grande and Bemis, 1998; Schultze, 1966, 1996).

The objective of the present paper is to provide a detailed description of the anatomy of the scales of the three different amiiform taxa from Las Hoyas fossil site (Spain), which will allow a taxonomical segregation of the isolated scales found at this locality. It is expected that these descriptions will serve as a starting point for the description of the scales of many more amiiform taxa. The final aim of this project is to offer a way of taxonomically identifying isolated scales, which can be found in fossil localities with a good quality of preservation, including Konservat-Lagerstätten, which can then provide important palaebiological and palaeoecological information.

2. Material and methods

For the present study, the scales of amiiform fishes from the Early Cretaceous (Barremian) fossiliferous laminated limestones of Las Hoyas (Cuenca, east-central Spain) are utilized. Fossils are usually preserved complete and articulated in this site (e.g., Martín-Abad and Poyato-Ariza, 2016); however, fish scales, due to their nature (i.e., scales drop naturally throughout fish life, and do not need from taphonomic events to detach from the bodies; for a discussion on this topic concerning both extant and fossil fish scales, see Micklich, 2012), are often found isolated. Amiiform fishes are relatively rare at Las Hoyas (Poyato-Ariza, 2005). Only approximately 300 out of over 5000 fish specimens correspond to amiiforms; in addition, a large proportion of these specimens are isolated scales, thus accounting for an important part of the information available to study the palaeobiology of these fishes.

Las Hoyas' amiiforms belong to three different taxa, all of which are represented in the site by complete or almost complete specimens (Fig. 1), which also preserve their scales articulated, thus allowing the comparison with isolated scales. These three taxa have traditionally been related to the three amiiform species described in the other Spanish Early Cretaceous Konservat-Lagerstätte, El Montsec: *Caturus tarraconensis*, *Amiopsis woodwardi*, and *Vidalamia catalunica* (see Wenz, 1968, 1971, 1988, 1995; Wenz and Poyato-Ariza, 1994, 1995). Although there are clearly some resemblances between the species of the two sites, a detailed analysis of both ichthyofaunas has revealed that both associations are more different from each other than previously thought (Poyato-Ariza and Martín-Abad, 2016). A full review and description of the amiiform taxa from Las Hoyas will be published elsewhere; in summary, a detailed anatomical study of these fishes makes clear that one of the species does not fall within the superfamily Amioidea (i.e., it is probably more closely related to *Caturus* and other taxa of the superfamily Caturoidea, or represents a new primitive lineage of amiiforms), while the other two are certainly members of the family Amiidae (Martín-Abad, 2015; Poyato-Ariza and Martín-Abad, 2016). In hold of new formal names for these three species, and for the sake of consistency, here the designations

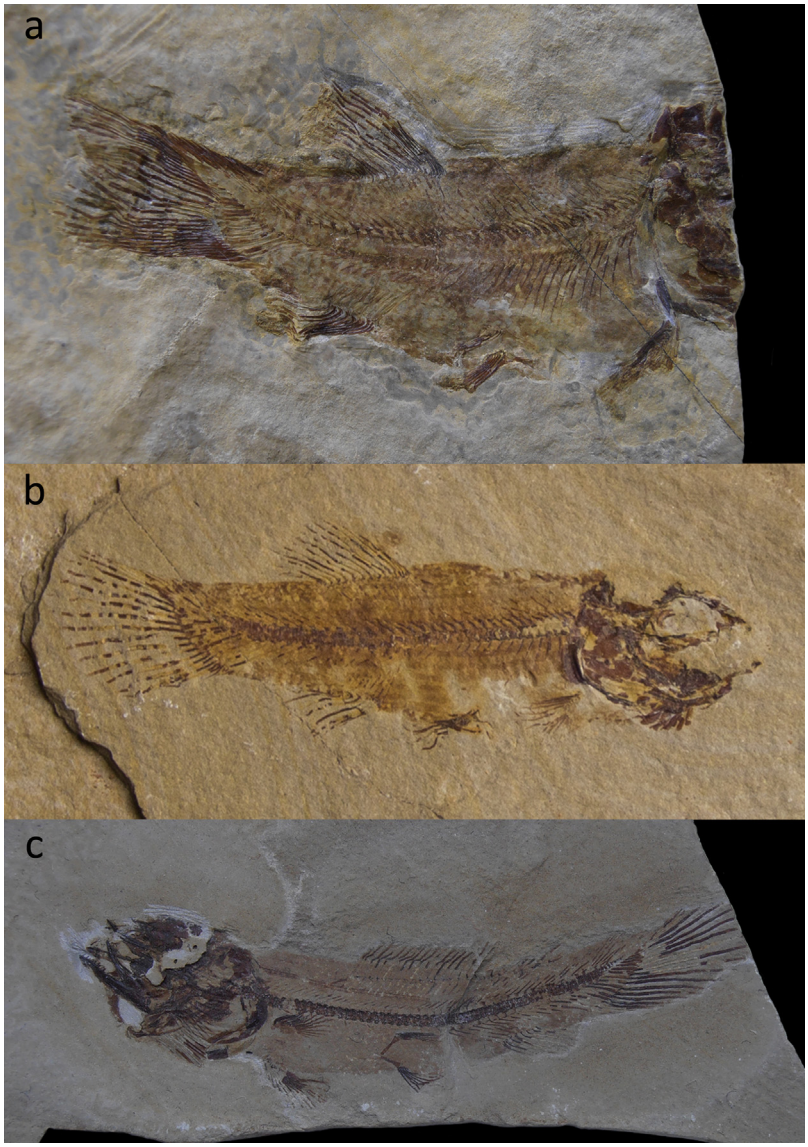


Fig. 1. Amiiform taxa from Las Hoyas: **a:** "*Caturus*"-like taxon, specimen MCCM LH 26022a; **b:** New taxon #1, specimen MCCM LH 11286; **c:** New taxon #2, specimen MCCM LH 28604. Scale bars equal 1 cm.
Fig. 1. Taxa de poissons amiiformes de Las Hoyas : **a :** *Caturus-like taxon*, spécimen MCCM LH 26022a ; **b :** *New taxon #1*, spécimen MCCM LH 11286 ; **c :** *New taxon #2*, spécimen MCCM LH 28604. Barres d'échelle = 1 cm.

provided by Martín-Abad (2015) will be used: "*Caturus*"-like taxon (to refer to the species previously related to *Caturus* from El Montsec, even though it clearly does not belong to that genus), New taxon #1 (to refer to the species previously related to *Amiopsis*), and New taxon #2 (to refer to the species previously related to *Vidalamia*).

2.1. Institutional abbreviations

IEI: Institut d'Estudis Ilerdencs, Lérida, Spain; **MCCM**: Museo de las Ciencias de Castilla-La Mancha, Cuenca, Spain (**LH**: Las Hoyas Collection); **MGB**: Museu de Geologia de Barcelona, Barcelona, Spain (**MSE**: El Montsec Collection); **MNHN**: Muséum national d'histoire naturelle (Institut de paléontologie), Paris, France; **UAM**: Universidad Autónoma de Madrid (**P-UAM-P**: Fish collection of the Unidad de Paleontología), Madrid, Spain; **UMMZ**: University of Michigan, Museum of Zoology, Ann Arbor, USA.

2.2. Material examined

"*Caturus*"-like taxon ($n = 44$): MCCM LH 520, 1176a, 2217a, 6139, 6369a, 7056a, 7060b, 7244a, 9192, 9622a, 15075b, 15300, 16215a, 16241b, 20136a, 20485a, 22382a, 23928b, 26022b, 26975b, 28160a, 30621, 31052a/b, 32032, 32056a, 32057, 32058, 32068b, 32077b, 32195a, 32242a/b,

32314, 37166, 37167, 37168, 37169, 37170, 37171, 37173, 37174, 37175, 37176, 37177, 37178. Barremian of Las Hoyas (Spain).

New taxon #1 ($n = 111$): MCCM LH 23, 65b, 76b, 85 R, 151 Pa, 162 P, 213b, 234, 374 Rb, 461, 868, 1082a, 1275, 2147a, 2186, 2318b, 2319, 2401a, 5099a, 6070a, 6371a, 7079a, 7095b, 7139b, 7452, 9113b, 9159a, 9226a, 9474a, 9576b, 9621b, 9645, 11172a, 11286, 11359b, 13127a, 13360a/b, 13398b, 13657b, 15196a, 15305a, 15470a, 15583a, 15783b, 15827b, 16040b, 16257a, 17139a, 17274b, 18038, 20008b, 20192b, 20226b, 20241a, 20263a, 20312, 20620b, 22115a, 22385b, 22600a, 23062b, 23322a, 23354a, 23455a, 23544b, 23561a, 23823a, 26457b, 27038, 28235, 28258b, 28299, 28419, 28639, 29500a, 29606a, 29866, 30731a, 30740a, 30766a, 30862, 30878b, 30933, 30941b, 31108a/b, 31280a/b, 32022a, 32059, 32236, 32244a/b, 32313, 32354b, 33381b, 33500b, 33540b, 35300a/b, 36104, 37152, 37153, 37154, 37155, 37156, 37157a/b, 37158a/b, 37159a/b, 37160a/b, 37161a/b, 37162, 37163, 37164a/b, 37165a/b. Barremian of Las Hoyas (Spain).

New taxon #2 ($n = 29$): MCCM LH 221b, 2131, 2149, 4143, 5389a, 6866, 7074a, 9224a, 9648a/b, 13020, 15835b, 16201a, 17431, 18017b, 20602, 22084b, 22403a, 26485b, 26530, 26772a, 26924, 28604, 29292b, 31367b, 32023a, 32407a/b, 32777, 37150a/b, 37151. Barremian of Las Hoyas (Spain).

Caturus tarraconensis ($n = 20$): IEI 800a, 958, 1269, 1270, 2045, 3356, G 207, G 616, G 624. MGB 513, 515, 551, V 9633. MNHN MSE 219, 321, 434, 555, 576, 826, 872. Berriasian–Valanginian of El Montsec (Spain).

Amiopsis woodwardi ($n = 8$): IEI 580, 5145, G 34, G 290, G 348. MGB V 9642. MNHN MSE 451, 844. Berriasian–Valanginian of El Montsec (Spain).

Vidalamia catalunica ($n = 8$): IEI 1313, 1351, 2865. MGB 567, 568. MNHN MSE 320, 504, 848. Berriasian–Valanginian of El Montsec (Spain).

A. calva ($n = 3$): P-UAM-P 022. UMMZ 190918-S, 205286-S. Extant species (North America).

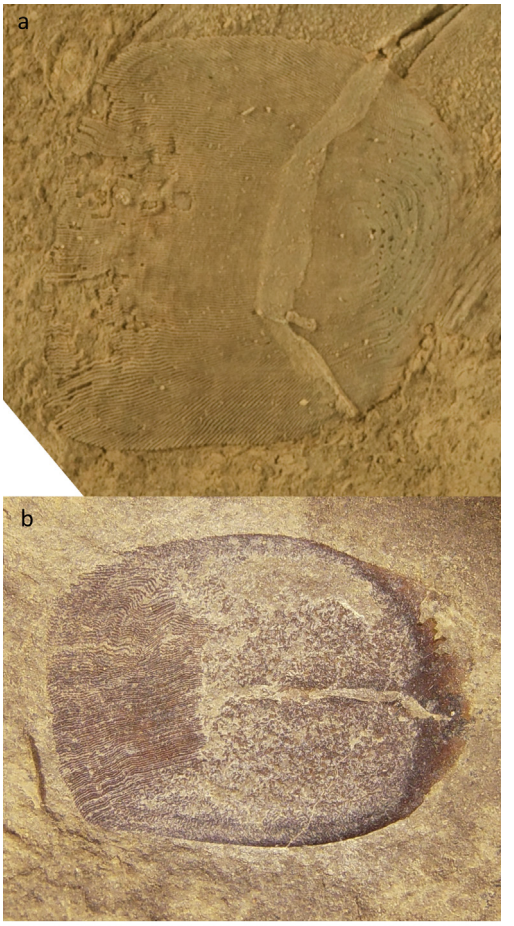
2.3. Terminology used for scale description

Terminology for scales description has been extensively discussed in the classic literature (e.g., Baudelot, 1873; Cockerell, 1911; Geinitz, 1868; Lagler, 1947; Schultze, 1966). Terminology used here follows Daniels (1996, figs. 7 and 8).

3. Description of anatomical features of the amiiform scales from Las Hoyas

3.1. Caturus-like taxon scales

The shape of the scales of "*Caturus*"-like taxon is roughly the same across the fish body, being rounded to slightly quadrangular. As far as can be seen in the few articulated specimens found to date, the scales are slightly smaller at the end of the caudal peduncle as well as in the anterior-most ventral region of the body, between both pectoral fins, but this needs to be confirmed with new, more complete and better preserved specimens.



1. Anastomoses between the anterior and lateral fields
2. Transverse line, almost striaght and with anastomoses
3. Crests
4. Focus
5. Thicker rim around the posterior field
6. Posterior field with ornamentation

The scales of "*Caturus*"-like taxon (Fig. 2) have a well-defined focus, or centre of ossification, which is an oval-shaped structure from where the ridges extend towards the margins of the scale. The focus is located at one-third to one-fourth of the length of the scale from the posterior margin; in other words, the posterior field occupies one-third to one-fourth of the length of the scale. The focus is transected by the transverse line, which is almost straight, and separates the posterior field from the anterior and lateral fields.

The ridges run mostly parallel to each other from the focus towards the margins of the scale; when approaching the focus, some of them converge with each other. The ridges are straighter when they contact the middle of the focus, and more curved when they contact the lateral and postero-lateral edges of it. There are approximately the same proportions of ridges ending at the anterior field than at any of the two lateral fields. All ridges present the same thickness.

Crests (which usually correspond to growth cessation marks) are relatively conspicuous in the anterior and lateral fields; in relatively large scales, the first and second crests (the closest to the focus) are less easily identifiable than the rest. Crests are more separated from each other on the anterior field, and become closer on the lateral fields. The longitudinal distance from one crest to the consecutive one gets much smaller the further away they are from the focus in the anterior field. In other words, crests are more crowded near the anterior margin of the scale, especially in old individuals. Anastomoses, that is, points where two or more ridges converge and fuse to each other to become one only ridge with the same thickness than the previous ones, are easily distinguishable. Anastomoses occur especially at the corner of the crests, where the anterior and lateral fields converge, and extend posteriorly a small distance along the crests in the lateral fields. Anastomoses are also conspicuous in the transverse line, where they seem to concentrate in several points. The first point is very close to the focus. The following points coincide with the posterior end of the crests where they reach the transverse line. The last crest, which roughly coincides with the age at death of any given individual, usually does not present anastomoses where it reaches the transverse line. Anastomoses can occur spread across the surface of the scale, not necessarily associated with any particular structure.

The posterior field, which comprises the surface of the scale posterior to the transverse line, does not present ridges. Semicircular crests are very conspicuous in the posterior field; they appear in higher number than that of crests in the anterior and lateral fields, and thus not all of them can be interpreted as growth cessation marks. Apart from these marks, the posterior field is characterized by an ornamentation pattern consisting in numerous small-sized, round foramina, the largest ones being located closer to the focus, where they seem to be more concentrated. The posterior field is surrounded by a rim that seems to be slightly more thickly ossified, giving the posterior margin of the scale a darker colour; this rim is especially visible in the inner view of the scale.

In medial view, the scales present a thicker surface, which covers the posterior field and the posterior part of the anterior and lateral fields of the scale. This surface has an ornamentation formed by small, tube-like tubercles. The scales of the lateral line bear a small ossified tube running longitudinally throughout the central axis of the scale (Fig. 2B).

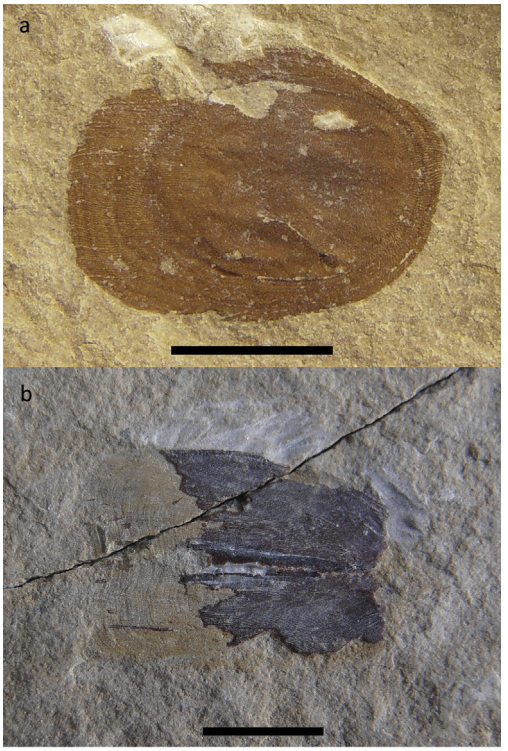
3.2. New taxon #1 scales

The shape of the scales is approximately constant throughout the body of New taxon #1, basically ovoid in contour and longer than deep, except for those scales covering the caudal fin rays, which are shorter and more circular.

The scales of New taxon #1 (Fig. 3) have a well-defined focus, located at one third of the length of the scale in the posterior part (although it is more posteriorly located in very young individuals). The transverse line runs from the focus to the posteroventral and posterodorsal corners of the scale. The transverse line is well-defined by numerous anastomoses forming a zigzag-like pattern. The posterior field occupies, thus, one third of the length of the scale. The ridges in this field run fairly straight from the focus and the anastomoses of the transverse line towards the posterior edge of the scale. The ridges in the lateral fields are curved in their origin in the focus and anastomoses, but are mostly straight and run towards the antero-dorsal and antero-ventral margin of the scale, parallel to each other. The ridges in the anterior field, all of them originating from the focus, run mostly straight from the focus to the anterior edge of the scale. The ridges of the lateral and anterior fields appear to be slightly narrower on their origin and become wider distally. This is more apparent in the ridges closer to the longitudinal axis of the scale. Crests are hardly observable in the anterior field, but are more conspicuous in the lateral fields, and even more in the posterior field. Anastomoses, usually associated to the crests in the lateral and anterior fields, are very hard to distinguish. The scales of the lateral line bear a small ossified tube running longitudinally throughout the central axis of the scale (Fig. 3B). In medial view, the scales present a thicker surface located closer to the posterior than to the anterior edge of the scale. This surface extends almost half of the length of the scale, and has an ornamentation formed by small, tube-like tubercles.

Fig. 2. Scales of "*Caturus*"-like taxon from the Barremian of Las Hoyas (Cuenca, Spain). **a:** Disarticulated scale from specimen MCCM LH 520a/b; the vertical structure in the middle of the scale is an artifact of an overlapping scale; **b:** specimen MCCM LH 29589, lateral line scale in medial view showing thin tube-like ossification for passage of the lateral line sensory canal, inner ornamented surface, and thick rim around the posterior field; **c:** schematic drawing showing the most important characteristics of the scales of this taxon. All three scales, anterior facing left. Scale bars equal 2 mm.

Fig. 2. Écailles d'un *Caturus-like taxon* du Barrémien de Las Hoyas (Cuenca, Espagne). **a :** Écaille désarticulée du spécimen MCCM LH 520a/b ; la structure verticale dans le milieu de l'écaille est un artefact dû à une autre écaille chevauchante ; **b :** spécimen MCCM LH 29589, écaille de la ligne latérale en vue médiale montrant une ossification mince en forme de tube pour le passage du canal sensoriel de la ligne latérale, la surface intérieure ornée, et le bord épais autour du champ postérieur ; **c :** dessin schématique montrant les caractéristiques les plus importantes des écailles de ce taxon. Pour les trois écailles, la partie antérieure se trouve vers la gauche. Barres d'échelle = 2 mm.



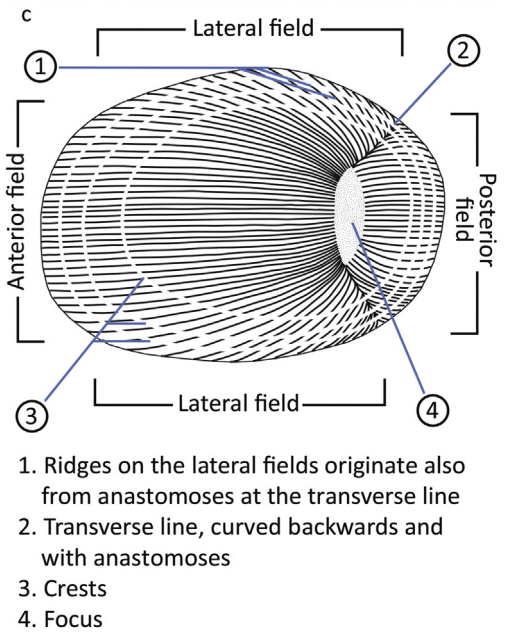


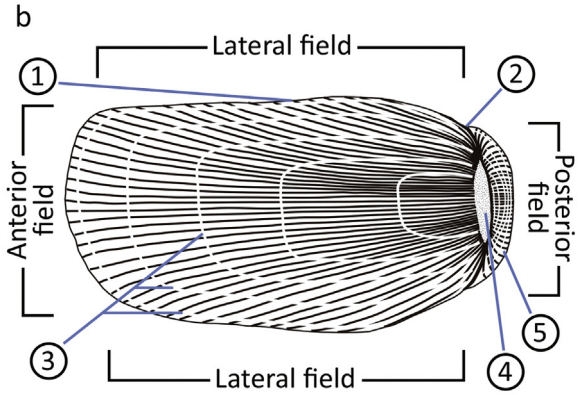
Fig. 3. Scales of New taxon #1 from the Barremian of Las Hoyas (Cuenca, Spain). **a:** Disarticulated scale from specimen MCCM LH 27038; **b:** specimen MCCM LH 37152, lateral line scale showing thin tube-like ossification for passage of the lateral line sensory canal; **c:** schematic drawing showing the most important characteristics of the scales of this taxon. All three scales, anterior facing left. Scale bars equal 3 mm.

Fig. 3. Écailles du *New taxon #1* du Barrémien de Las Hoyas (Cuenca, Espagne). **a :** Écaille désarticulée du spécimen MCCM LH 27038 ; **b :** spécimen MCCM LH 37152, écaille de la ligne latérale, montrant une ossification mince en forme de tube pour le passage du canal sensoriel de la ligne latérale ; **c :** dessin schématique montrant les caractéristiques les plus importantes des écailles de ce taxon. Pour les trois écailles, la partie antérieure se trouve vers la gauche. Barres d'échelle = 3 mm.

3.3. New taxon #2 scales

The shape of the scales, elongated-ovoid in contour, remains approximately constant throughout the body of the fish, being the posteriormost ones comparatively shorter.

The scales of New taxon #2 (Fig. 4) have a well-defined focus, located very close to the posterior edge of the scale. Consequently, the posterior field is very small, notably smaller than that in the scales of New taxon #1. This posterior field is extremely thin, and it is usually not even preserved or is very hard to observe. The transverse line is well-defined and runs, thus, very close to the posterior



1. Ridges on the lateral fields are slightly curved outwards distally
2. Transverse line, curved forward
3. Crests
4. Focus, located very close to the posterior margin of the scale
5. The posterior field is small and very thinly ossified

Fig. 4. Scales of New taxon #2 from the Barremian of Las Hoyas (Cuenca, Spain). **a:** Specimen MCCM LH 26924, isolated scale: **b:** schematic drawing showing the most important characteristics of the scales of this taxon. Both, anterior facing left. Scale bars equal 5 mm.

Fig. 4. Écailles du *New taxon #2* du Barrémien de Las Hoyas (Cuenca, Espagne). **a :** Spécimen MCCM LH 26924, écaille isolée ; **b :** dessin schématique montrant les caractéristiques les plus importantes des écailles de ce taxon. Pour les deux écailles, la partie antérieure se situe vers la gauche. Barres d'échelle = 5 mm.

edge of the scale, from the focus to the posteroventral and posterodorsal borders of the scale. These borders, due to the ellipsoidal rather than quadrangular contour of the scale, are located anterior to the focus; as a consequence, the transverse line is curved. All ridges start from the focus, some of them, the most lateral ones, being much curved at their origin. The ridges in the lateral fields tend to end at the antero-dorsal and antero-ventral corners of the scale, and are slightly curved outwards, instead of inwards as is more usual in the scales of other amiids. In the anterior field, the ridges run straighter, nearly parallel to each other, although they zigzag at the crests, ending at the anterior margin of the scale. In the posterior field, the short ridges run fairly straight from the focus towards the posterior edge of the scale. Crests are clearly distinguishable in all the fields, but especially in the anterior field. Anastomoses are very hard to identify in the scales of New taxon #2. When they are observable, they are located at the corners of the crests in the junction of the lateral and the anterior fields of the scale. In medial view, the scales present a thicker surface located closer to the posterior than to the anterior edge of the scale, very similar to that present in the scales of New taxon #1, but proportionally smaller; it also presents an ornamentation formed by small tubular tubercles. The scales of the lateral line bear a small ossified tube running longitudinally throughout the central axis of the scale.

4. Results and discussion

Up to now, no detailed description has been published that allows for a precise taxonomical segregation of isolated amiiform scales. Here, a number of anatomical characteristics of the scales of the three amiiform taxa of Las Hoyas' fossil record are discussed based on the study of the scales from articulated specimens; the main differences are summarized below:

"*Caturus*"-like taxon scales are rounded to quadrangular in shape. They are characterized by the presence of a thick rim around the posterior field. The posterior field and the focus are ornamented with small round foramina. In the posterior field, the crests are very notorious but ridges are hardly visible. Anastomoses are clearly visible on crests.

New taxon #1 scales are ovoid in shape. The posterior field occupies one third of the length of the scale (less in smaller specimens). The transverse line is easily observable, with numerous anastomoses. Many of the ridges running through the lateral fields originate in these anastomoses, instead of in the focus. Crests are hardly visible on the anterior field.

New taxon #2 scales are subrectangular in shape, more rounded in the posterior edge. The focus is located very close to the posterior edge of the scale, conforming to a greatly reduced posterior field. This posterior field is very thinly ossified. All ridges apparently originate in the focus. Crests are clearly visible, especially in the anterior field.

The detailed study of the anatomy of these scales has allowed for the identification of a total of 44 individuals of "*Caturus*"-like taxon, 111 of New taxon #1 and 29 of New taxon #2, including both articulated individuals and isolated scales.

Being able to taxonomically differentiate isolated scales is also important from a palaeobiological and palaeoecological point of view. It allows us to know at which stratigraphic levels a given species was present, even if

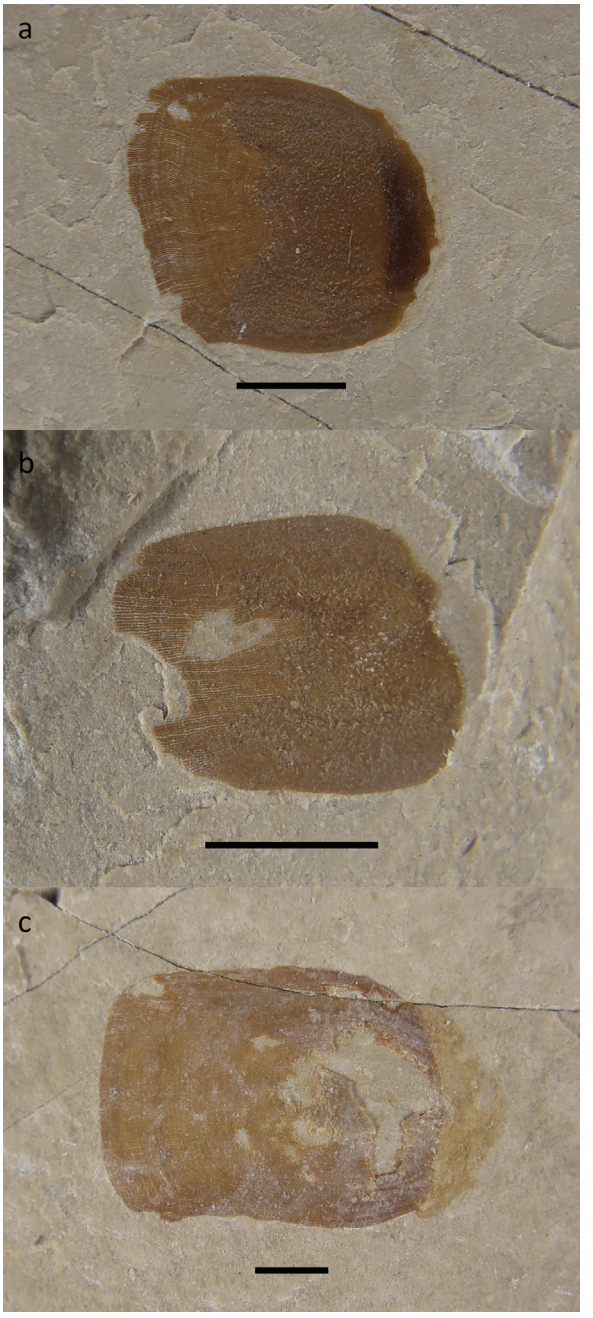


Fig. 5. Isolated scales of the three amiiform taxa from the Berriasian–Valanginian of El Montsec (Lérida, Spain). **a:** *Caturus tarraconensis* MNHN MSE 826a/b; **b:** *Amiopsis woodwardi* MNHN MSE 844a/b; **c:** *Vidalamia catalunica* MNHN MSE 848a/b. All three scales, anterior facing left. Scale bars equal 3 mm.

Fig. 5. Écailles isolées des trois espèces d'amiiformes du Berriasien–Valanginien d'El Montsec (Lérida, Espagne). **a :** *Caturus tarraconensis* MNHN MSE 826a/b ; **b :** *Amiopsis woodwardi* MNHN MSE 844a/b ; **c :** *Vidalamia catalunica* MNHN MSE 848a/b. Pour les trois écailles, la partie antérieure se trouve vers la gauche. Barres d'échelle = 3 mm.

no complete or articulated material has been found. In addition, it provides information about the type of facies in which they are found; for instance, in the particular case of Las Hoyas, the strong seasonality interpreted for the Western European Barremian localities (Haywood et al., 2004) resulted in two easily distinguishable types of facies, wet and dry, whose floral and faunal associations, and thus whose palaeoecology, were completely different (Buscalioni and Fregenal-Martínez, 2010). Likewise, it allows us to interpret whether distinct taxa cohabited in time and space, or if they inhabited different parts of the ecosystem or at different registered episodes. In a broader sense, it allows us to interpret how the association of a locality evolved in time. Moreover, it provides useful palaeobiological information as well, for example on the fish population structure and dynamics (e.g., Newbrey and Bozek, 2003; Newbrey et al., 2008).

Interestingly enough, the scales of Las Hoyas' amiiforms are very similar to those of the three taxa from El Montsec, to which they have been traditionally related. "*Caturus*"-like taxon scales clearly resemble those of *Caturus tarraconensis* (Fig. 5a) mainly in its ovoid, almost rounded contour and the presence of a thick posterior field. The scales of New taxon #1 and *Amiopsis woodwardi* (Fig. 5b) are similar in their ovoid (not rounded) contour and a relatively extended posterior field occupying about one third of the length of the scale. Finally, the scales of New taxon #2 and *Vidalamia catalunica* (Fig. 5c) are similar in their subrectangular contour (especially in the anterior field) and the very posterior position of the focus, which defines a very thin and small posterior field. These similarities suggest that, even if they do not represent the same species, each of the taxa from Las Hoyas is probably close to one of the taxa from El Montsec from a systematic point of view. In turn, this suggests a possible usage of scales for phylogenetical purposes; however, in the current state of knowledge, little can be said about this.

5. Conclusion

The "amioid"-type of scales is present in several groups of osteichthyan fishes, including all known representatives of the order Amiiformes, with the possible exception of the Asiatic sinamiids, which have been reported to present both "amioid" and non-"amioid" scales (e.g., Grande and Bemis, 1998). However, as presented here, the scales of amiiform fishes are much more different from each other than previously interpreted. A series of anatomical characteristics have been detected that have allowed differentiating the scales of the three taxa of amiiform fishes present in the Spanish Cretaceous locality of Las Hoyas, including the shape of the contour, position and definition of the focus of ossification, extension of the posterior field, presence of a thicker rim around the posterior field, presence of ornamentation on the posterior field, presence of conspicuous anastomoses in the crests and/or between the anterior and lateral fields or the transverse line, straightness of the transverse line, conspicuousness of crests on the anterior, lateral and/or posterior fields, presence of an ornamented surface on the inner view.

On the basis of these characteristics, and by comparing isolated scales and scales from articulated specimens, population samples of 44, 111 and 29 individuals have been gathered for the three amiiform taxa from Las Hoyas ("*Caturus*"-like taxon, New taxon #1, and New taxon #2, respectively). In this sense, taxonomically identifiable isolated scales have greatly increased the number of known individuals of these three species, since the number of articulated specimens is relatively low. In terms of the palaeobiology and palaeoecology of these fishes, larger population samples open the door to analyses of population dynamics and of the evolution of both the fish association and each particular species throughout the period of time recorded in the locality.

The final aim of this new line of investigation is to provide a key for the identification of scales of amiiform fishes based on a series of anatomical characteristics, including the ones already highlighted in the present paper. For this purpose, a description of the anatomy of scales from a large number of amiiform taxa will need to be carried out, including a high diversity of both amioids and caturoids. This set of characteristics might prove especially useful in microvertebrate sites where no complete specimens are found with articulated scales, as suggested by Arratia (2015), allowing for a taxonomical identification based on isolated scales.

Acknowledgements

Francisco José Poyato-Ariza (Universidad Autónoma de Madrid, Spain) and Michael G. Newbrey (Columbus State University, Georgia, US, and formerly Royal Tyrrell Museum of Paleontology, Alberta, Canada) are acknowledged for the thorough discussions on amiiform fishes. Ángela Delgado Buscalioni for her inputs on Las Hoyas' palaeoecosystem and the scientific direction of Las Hoyas Research Project. Jesús Madero Jarabo (Museo de las Ciencias de Castilla-La Mancha, Cuenca, Spain) for the loaning of the material. Thoughtful reviews by two anonymous reviewers and the editorial staff significantly improved the manuscript. Fig. 5 published with the permission of the Muséum national d'histoire naturelle (Paris, France). Funding for this project comes from a FPU grant provided to H. M.-A. (AP2007-00894, MICINN, Spain). Two travel grants to visit the Royal Tyrrell Museum of Paleontology were provided to H. M.-A. by Universidad Autónoma de Madrid. This paper is a contribution to projects CGL-2009-11838 (MICINN, Spain) and CGL-2013-42643 P (MINECO, Spain).

References

Arratia, G., 2015. Complexities of Early Teleostei and the evolution of particular morphological structures through time. Copeia 103 (4), 999–1025.

Arratia, G., Schultze, H.-P., 2007. *Eurycormus–Eurypoma*, two Jurassic actinopterygian genera with mixed identity. Foss. Rec. 10 (1), 17–37.

Baudelot, J.É.J., 1873. Recherches sur la structure et le développement des écailles des poissons osseux. Arch. Zool. Exp. Gen. 2, 87–224.

Buscalioni, A.D., Fregenal-Martínez, M.A., 2010. A holistic approach to the palaeoecology of Las Hoyas Konservat-Lagerstätte (La Huérguina Formation, Lower Cretaceous, Iberian Ranges, Spain). J. Iber. Geol. 36 (2), 297–326.

Cartier, D., Magnin, E., 1967. La croissance en longueur et en poids des *Amia calva* L. de la région de Montréal. Can. J. Zool. 45 (5), 797–804.

Cockerell, T.D.A., 1911. The scales of freshwater fishes. Biol. Bull. US 20, 367–376.
Cooper, G.P., Schafer, R.N., 1954. Studies on the population of legal-size fish in Whitemore Lake, Washtenaw and Livingstone Counties, Michigan. T. N. Am. Wildl. Nat. Res. 19, 239–258.
Daniels, R.A., 1996. Guide to the identification of scales of inland fishes of northeastern North America. New York State Mus. Bull. 488.
Degener, L.M., 1924. The development of the dentary bone and teeth of Amia calva. J. Morphol. 39, 113–155.
Geinitz, H.B., 1868. Die fossilen Fischschuppen aus dem Plänerkalke in Strehlen. Denk-schr. d. Gesellsch. f. Nat. u. Heilk. in Dresden 2, 1–18.
Grande, L., Bemis, W.E., 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of Natural History. J. Vert. Paleontol. Memoir 4 suppl. to vol. 18 (1), i–x (1–690).
Haywood, A.M., Valdes, P.J., Markwick, P.J., 2004. Cretaceous (Wealden) climates: a modelling perspective. Cretaceous Res. 25, 303–311.
Jollie, M., 1984. Development of the head and pectoral skeleton of *Amia* with a note on the scales. Gegenbaurs Morphol. Jahrb. Leipzig 130, 315–351.
Kerr, T., 1952. The scales of primitive living actinopterygians. Proc. Zool. Soc. Lon. 122, 55–78.
Lagler, K.F., 1947. Lepidological studies 1. Scale characters of the families of Great Lake Fishes. Trans. Am. Microsc. Soc. 66, 149–171.
Mackintosh, H.W., 1878. Note on the microscopic structure of the scale of *Amia calva*. Sci. Proc. R. Dublin Soc. New Series 1, 93–95.
Martín-Abad, H., (Unpublished PhD) 2015. Palaeobiology of the Amiiform Fishes from the Early Cretaceous of Las Hoyas: an Integrative Multidisciplinary Approach. Universidad Autónoma de Madrid, Madrid (397 p.).
Martín-Abad, H., Poyato-Ariza, F.J., 2016. Biostratinomic factors involved in fish preservation. In: Poyato-Ariza, F.J., Buscalioni, A.D. (Eds.), Las Hoyas: a Cretaceous wetland. A multidisciplinary synthesis after 25 years of research on an exceptional fossil Lagerstätte from Spain. Verlag Dr. Friedrich Pfeil, Munich, Germany, pp. 202–210.
Meunier, F.J., 1981. "Twisted plywood" structure and mineralization in the scales of a primitive living fish, *Amia calva*. Tissue Cell 13, 165–171.
Meunier, F., Poplin, C., 1995. Paleohistological study of the scales of *Amia robusta* Priem, 1901, Amiidae from the Thanetian (Paleocene) of Cernay (France). Geobios M.S. 19, 39–43.
Micklich, N., 2012. Peculiarities of the Messel fish fauna and their palaeoecological implications: a case study. Palaeobiodivers. Palaeoenviron. 92, 585–629.
Newbrey, M.G., Bozek, M.A., 2003. Age, growth, and mortality of *Joffrichthys triangulpterus* (Teleostei: Osteoglossidae) from the Paleocene Sentinel Butte Formation, North Dakota, USA. J. Vert. Paleontol. 23 (3), 494–500.
Newbrey, M.G., Wilson, M.V.H., Ashworth, A.C., 2008. Climate change and evolution of growth in Late Cretaceous to Recent North American Esociformes. In: Arratia, G., Schultze, H.-P., Wilson, M.V.H. (Eds.), Mesozoic Fishes 4-Systematics, Homology, and Nomenclature. Verlag Dr. Friedrich Pfeil, Munich, Germany, pp. 311–350.
Poyato-Ariza, F.J., 2005. Palaeoecology of the fishes from the Early Cretaceous lake of Las Hoyas, Cuenca, Spain, with a hypothesis of sexual dimorphism for the Chanidae *Rubiesichthys*. Bull. Kitakyushu Mus. Nat. Hist. Hum. Hist., Ser. A 3, 153–168.
Poyato-Ariza, F.J., Martín-Abad, H., 2016. Osteichthyans. In: Poyato-Ariza, F.J., Buscalioni, A.D. (Eds.), Las Hoyas: a Cretaceous wetland. A multidisciplinary synthesis after 25 years of research on an exceptional fossil Lagerstätte from Spain. Verlag Dr. Friedrich Pfeil, Munich, Germany, pp. 114–132.
Schiavone, A., 1982. Age and growth of bowfin in Butterfield Lake, New York. New York Fish Game J. 29 (1), 107.
Schultze, H.-P., 1966. Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von Ganoid- zu Rundschuppen). Neues Jahrb. Geol. P.-A. 126, 232–314.
Schultze, H.-P., 1977. Ausgangsform und Etwicklung der rhombischen Schuppen der Osteichthyes (Pisces). Paläontol. Z. 51 (3/4), 152–168.
Schultze, H.-P., 1996. The scales of Mesozoic actinopterygians. In: Arratia, G., Viohl, G. (Eds.), Mesozoic Fishes: Systematics and Paleoecology. Verlag Dr. Friedrich Pfeil, Munich, Germany, pp. 83–93.
Wenz, S., 1968. Note préliminaire sur la faune ichthyologique du Jurassique supérieur du Montsech (Espagne). Bull. Soc. geol. France 7 (X), 116–119.
Wenz, S., 1971. Anatomie et position systématique de *Vidalamia*, poisson holostéen du Jurassique supérieur du Montsech (Province de Lérida, Espagne). Ann. Paléontol. (Vert.) 56, 42–62.
Wenz, S., 1988. Les Amiidés (Pisces, Halecomorphi) du Crétacé inférieur du Montsec (province de Lérida, Espagne) : *Amiopsis woodwardi* (Sauvage, 1903). Quaderns Institut d'Estudis Ilerdencs 1, 1–50.
Wenz, S., 1995. Les Amiidés du Crétacé inférieur du Montsec (Province de Lleida, Espagne) : *Urocles sauvagei* (Vidal, 1915) synonyme de *Vidalamia catalunica* (Sauvage, 1903). Treb. Mus. Geol. Barc. 4, 5–13.
Wenz, S., Poyato-Ariza, F.J., 1994. Les Actinoptérygiens juvéniles du Crétacé inférieur du Montsec et de Las Hoyas (Espagne). Geobios M.S. 16, 203–212.
Wenz, S., Poyato-Ariza, F.J., 1995. Fishes. In: Martínez-Delclòs, X. (Ed.), Montsec and Montral-Alcover, two Konservat-Lagerstätten. Catalonia, Spain. In: II International Symposium Litographic Limestones, Institut d'Estudis Ilerdencs, Lérida, Spain, pp. 47–53.