

# Amiiforms from the Iberian Peninsula: historic review and research prospects

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## Abstract

The fossil record of amiiform fishes from the Iberian Peninsula is known from 12 different sites. It extends along the three periods of the Mesozoic era, being much more abundant during the Early Cretaceous. The majority of these sites has yielded isolated remains, mostly teeth; complete and articulated specimens are known from three Konservat-Lagerstätten only: Montral-Alcover, El Montsec, and Las Hoyas. Generic and specific level assessments are possible in these three localities only.

The historical taxonomical problems of the cited amiiform taxa are commented. Special mention deserves the case of the genus *Urocles* (= *Megalurus*), traditionally cited from El Montsec and Las Hoyas. This genus is invalid since 1998, but its taxonomic history goes back to the 1830's.

The amiiform fishes from Las Hoyas have traditionally been assigned to the same taxa as those coming from El Montsec, but they have not been studied in detail yet, so their taxonomical assessment is in need of confirmation. These specimens, characterized by a great quality of preservation and an abundant record, may provide significant information concerning the ontogenetic development of the fishes of this order.

## Introduction

**The amiiform fishes:** Amiiformes HAY (1929) is an order of neopterygian fishes with an only extant species of the type genus, *Amia calva*; their peak of diversity occurred during the Mesozoic. Since there are very few living non-teleosts neopterygians, this order is considered to be as a very relevant group from a systematic and paleobiogeographic point of view, especially when dealing with its phylogenetic relationships with the Teleostei. In the last thirty years diverse hypotheses about the relationship between amiiforms and teleosts have been offered, in an attempt to solve the debate on whether they are sister-groups or not. GRANDE & BEMIS (1998) provided a cladistic analysis resolving a clade containing both teleosts and amiiforms as sister-groups; this clade has traditionally been called Halecostomi. They redescribed the order Amiiformes, which they diagnosed by the following three evolutionary novelties: phylogenetic reduction in the number of ossified ural neural arches to two or less (character secondarily lost within Caturidae); phylogenetic loss of the opisthotic bone (character apparently convergent with lepisosteids and more derived teleosts); and phylogenetic loss of the pterotic bone.

GRANDE & BEMIS (1998) also divided the amiiforms into two superfamilies, Amioidea and Caturioidea, each of which is in turn divided into two families, respectively: Amiidae and Sinamiidae, and Caturidae and Liodesmidae.

Although it is considered as a principally Mesozoic order, Amiiformes present a relatively long chronostratigraphical record, which extends at least from the Jurassic, or even the Triassic, if the identifications made by BELTAN (1972, 1984) and LIU et al. (2002) are correct, to the Recent *Amia calva*, that inhabits freshwaters systems of the eastern North America. The amiiform fossil record also presents a wide-ranged geographical distribution that could be considered almost cosmopolite; however, the vast majority of the known fossil material has been discovered in sites from the North Hemisphere, probably as a result of bias in paleontological field work. This is partly evidenced by their distribution reaching very high latitudes (ESTES & HUTCHINSON 1980, LEHMAN 1951).



**Fig. 1.** Chronostratigraphic distribution of the Iberian sites that have yielded remains of amiiform fishes. The assessment of the material from Montral-Alcover to the order Amiiformes is doubtful.

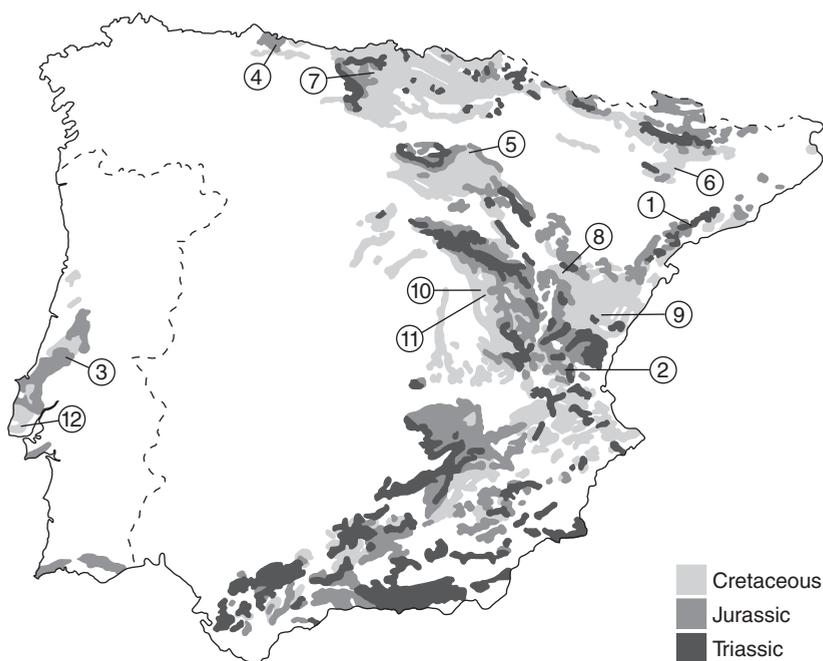
**Table 1.**

Distribution of the taxonomic assessments of the amiiform fishes cited from Mesozoic localities of the Iberian Peninsula.

	Montral-Alcover	Sot de Chera & Loriguilla	Guimarota	Tereñes & Lastres	Cuenca de Cameros	El Montsec	Vega de Pas I	Galve	Alcaine	Buenache de la Sierra	Las Hoyas	Cacém-Alcântara
Amiiformes indet.				●	●		●	●				
Caturidae indet.		●	●									
<i>Caturus</i> sp.	?								●	●	●	
<i>Caturus tarraconensis</i>						●						
Amiidae indet.			●	●					●	●		●
Amiopsinae indet.										●		
<i>Amiopsis woodwardi</i>						●					●	
<i>Vidalamia catalunica</i>						●					●	

**The Spanish record:** A number of nominal genera have been described within the Amiiformes, mainly in the family Amiidae. The present paper is included in a revision project on the amiiforms from Las Hoyas fossil site (Cuenca, Spain), currently in progress. In this sense, the main objective of the present paper is to offer the most relevant references on amiiform fishes from the Iberian Peninsula, in order to provide a biogeographical and chronostratigraphical framework for the amiiforms of Las Hoyas. Some of these references appear in the few compilations of the Spanish material published in the second half of the past century, which are faunal lists mainly focused on the Cretaceous period (BATALLER 1960, POYATO-ARIZA & WENZ 1990, POYATO-ARIZA et al. 1999). Those concerning only amiids that were published before 1998 were already included in GRANDE & BEMIS (1998); the posterior references to this family in the Iberian Peninsula are compiled in the present paper for the first time, together with all available references to the other families of this order.

Chronostratigraphically, the Iberian record of amiiform fishes extends from the Oxfordian-Kimmeridgian (Late Jurassic) to the middle-to-late Cenomanian (Upper Cretaceous), being thus exclusively Mesozoic (Fig. 1). The first appearance of the order could be traced back to the late Ladinian (Middle Triassic) according to BELTAN (1972, 1984) and VÍA-BOADA et al. (1977), but other authors (CARTANYÀ



**Fig. 2.**

Mesozoic Iberian sites that have yielded remains of amiiform fishes. Numeration of localities corresponds to that from Figure 1.

1995, 1999) considered their assessment doubtful and in need of a revision. Geographically, the sites that have yielded remains of amiiform fishes are mainly concentrated in the northern and oriental regions of Spain and in the occidental coast of Portugal. To date, no insular outcrops have been reported from Spain or Portugal. Figure 2 shows the Iberian localities from Triassic, Jurassic, and Cretaceous beds.

In general terms, the Iberian record could be divided into two sets. On one hand there are several sites whose remains appear to be more or less isolated and disarticulated, thereby creating problems with taxonomy. This set includes remains that have been reported as Actinopterygii indet., Neopterygii indet., Halecostomi indet., Halecomorphi indet., or Holostei indet., but they will not be considered in the present paper, since their assessment to the order Amiiiformes would require a detailed revision that lies outside of the scope of the present work. On the other hand, there are a few Konservat-Lagerstätten which present an extensive and excellently-preserved fish record that usually allows a much more precise taxonomic assignment. Among these last ones, there are two localities that are especially relevant: El Montsec and Las Hoyas.

In some cases, the material was originally described under names that have been changed in the course of history. In other cases, the remains do not really belong to the amiiform taxa they were initially assigned to or the corresponding taxa are not included in the Amiiiformes anymore. Each particular case will be presented and discussed in detail below, following a systematic order (Table 1), with special reference to the genus *Urocles* (= *Megalurus*), of which the taxonomic history is quite complex.

**Vernacular suffixes and institutional abbreviations:** The vernacular suffixes are used in this paper following GRANDE & BEMIS (1999).

Institutional abbreviations used here are as follow: **MCCM**, Museo de las Ciencias de Castilla-La Mancha, Cuenca, Spain (**LH**, Las Hoyas Collection; **MSE**, El Montsec Collection); **MMGB**, Museo Municipal de Geología de Barcelona, Barcelona, Spain; **MNHN**, Muséum National d'Histoire Naturelle (Institut de Paléontologie), Paris, France.

## The amiiform record from the Iberian Peninsula

**Taxa no longer assigned to the Amiiformes:** Two different genera have been traditionally included within the Amiiformes, but subsequently were transferred to other orders. These are *Eoeugnathus* (i.e. BELTAN 1984, CARTANYÀ 1995) and *Ophiopsis* (i.e. CARTANYÀ 1999).

**Amiiformes indet.:** In many localities the remains of amiiform fishes have been cited, of which the quality and/or integrity of preservation only allows an identification as lower rank Amiiformes.

The oldest record of Amiiformes indet. comes from a series of cliffs of the so-called Coast of the Dinosaurs (province of Asturias, northern Spain), where different Jurassic formations appear. In two of these formations, Tereñes and Lastres (Kimmeridgian), amiiform remains have been found, so far as isolated bones only (RUIZ-OMENACA et al. 2006).

Following a chronostratigraphical sequence, Amiiformes indet. are found in the Cameros Basin (La Rioja, northern Spain). The Lower Cretaceous of this basin is divided into different units in the northwestern region of the Iberian Range. Amiiform remains were found in the following localities: the Oncala Group (Tithonian-Berriasian), the Urbión Group (Berriasian-Aptian), and the Enciso Group (Aptian), and they consist of isolated elements currently under study (BERMÚDEZ-ROCHAS & POYATO-ARIZA 2007).

Isolated teeth of Amiiformes indet. have been found in the site known as Vega de Pas I (BERMÚDEZ-ROCHAS & POYATO-ARIZA 2007, BERMÚDEZ-ROCHAS et al. 2007, MORATALLA et al. 2007). This outcrop is placed on the beds of the Pas river, near the locality of Vega de Pas (Cantabria, central northern coast of Spain), and it has been assigned to the Viviparus layers of the Vega de Pas formation, Hauterivian-Barremian in age, located in the occidental-most region of the Basque-Cantabrian Basin (BERMÚDEZ-ROCHAS et al. 2007).

Finally, remains that were determined as Amiiformes indet. have also been cited from Galve. Galve is a locality with several different sites, just like El Montsec. It is situated in the Galve Subbasin, which is part of the Lower Cretaceous Maestrazgo Basin of the central Iberian Range. Several faunistic lists of the vertebrate record from this locality have been published but the most recent is by RUIZ-OMENACA et al. (2004). Remains of Amiiformes indet. are also known from two different formations of this subbasin: El Castellar, upper Hauterivian-lower Barremian in age, and Camarillas, lower Barremian in age. These remains had previously been cited as Amiidae indet. by DÍEZ et al. (1995), CANUDO et al. (1996a,b), and ESTES & SANCHÍZ (1982) for the El Castellar Formation, and by ESTES & SANCHÍZ (1982), and CUENCA-BESCÓS et al. (1994) for the Camarillas formation. In both cases, the material consists mainly of isolated teeth, although some vertebrae and toothed palatal bones have also been found and assigned to this family.

### Family Caturidae

**Caturidae indet.:** All the remains assigned to the superfamily Caturoidea have been included in the family Caturidae. Some specimens are very well preserved (see *Caturus* below), but some others do not allow a taxonomic determination more precise than Caturidae indet.

The central area of the Iberian Ranges spreads out between the cities of Barcelona, Zaragoza and Valencia. The upper Jurassic of this area has been divided into different units, two of which correspond to the formations known as Sot de Chera and Loriguilla, taking their names from close villages. These two adjacent units have been dated as Oxfordian-Kimmeridgian and Kimmeridgian, respectively. Numerous amiiform remains have been found from these two units in the province of Valencia. Specifically, these remains are teeth that have been classified as caturids on the basis of their lanceolated morphology, characterized by an arrow-shaped apex and lateral sharp edges (KRIWET 1998).

The other site where Caturidae indet. remains have been cited is Guimarota. It is an outcrop located inside a coal mine, placed near the locality of Leiria, in central Portugal. The coal veins where the fossil remains have been found were dated as lower Kimmeridgian, according to its associations of ostracods and charophytes (KRIWET 1998, 2005). The Caturidae indet. remains consist of some isolated teeth (KRIWET 2000).

***Caturus* sp.:** *Caturus* is probably one of the most abundant genera in Mesozoic fish associations. It includes several species, but only one has been assessed at specific level in the Iberian fossil record (see below under *Caturus tarraconensis*); most of the remains of this genus have been cited as *Caturus* sp.

The earliest record of *Caturus* sp. corresponds to the already commented doubtful assessments made by BELTAN (1972, 1984) and VÍA-BOADA et al. (1977) for the specimens coming from the laminated dolo-

mites of Montral-Alcover. This upper Ladinian (Middle Triassic; CALVET & TUCKER 1995, QUESADA & AGUERA-GONZÁLEZ 2005) outcrop is placed between the localities of Mont-Ral and Alcover (Tarragona, northeastern Spain), in the so-called Montañas de Prades, which are part of the Cordillera Costero-Catalana. The fishes of this outcrop usually appear as impressions without any remains of organic tissues, but are mostly represented by complete, articulated organisms (CARTANYÀ 1995). BELTAN (1984) includes this genus in the family Amiidae. CARTANYÀ (1995, 1999) includes it in the family Caturidae, although he clearly stresses the need of a complete re-examination of the specimens to clarify their taxonomic assignment.

Following the chronostratigraphical order, the next site where *Caturus* sp. remains have been cited is Alcaine, located in the province of Teruel. This outcrop is considered as lower Barremian in age (POYATO-ARIZA et al. 1999). Only a personal communication makes allusion to the appearance of this genus in this site (POYATO-ARIZA et al. 1999).

A third vertebrate assemblage where *Caturus* sp. has been noted is from the Buenache de la Sierra site. It is located in the Buenache de la Sierra Subbasin, which is part of the Serranía de Cuenca (Southwestern Iberian Ranges), some 18 Km east of the city of Cuenca. It is relatively close to the Las Hoyas fossil site. As a matter of fact, the depositional layers that fill the so-called Cubeta de Las Hoyas, dated as lower Barremian, belong to the same formation (La Huérguina Formation) than those filling the Buenache de la Sierra Subbasin. However, only two of the depositional sequences outcropping at Las Hoyas, the oldest ones, outcrop at Buenache de la Sierra as well; they are known as Rambla de las Cruces I and II (BUSCALIONI et al. 2008). Most of the record of this outcrop consists on microfossils, including some teeth whose morphotype has been attributed to the genus *Caturus* (BUSCALIONI et al. 2008).

The youngest record of *Caturus* sp. is that of Las Hoyas fossil site. This very famous Konservat-Lagerstätte is placed in the municipal term of La Cierva, province of Cuenca, eastern central Spain. It is constituted by lithographic limestones that were deposited filling the Cubeta de Las Hoyas, which is part of the Great Iberian Basin, located in the Serranía de Cuenca (Southwestern Iberian Ranges), belonging to the La Huérguina formation (FREGENAL-MARTÍNEZ & MELÉNDEZ 1995a). This outcrop is considered upper Barremian in age (DIÉGUEZ et al. 1995), and its limestones have yielded a great diversity of ichthyological remains (e. g., POYATO-ARIZA & WENZ 1995, POYATO-ARIZA 2005a, ESCASO et al. 2005), which are characterized by its extremely good preservation, and are often complete, although incomplete or disarticulated specimens occur as well. The amiiform fishes from this site are currently under study, so their taxonomical assignment is preliminary. The genus *Caturus* is probably the least abundant of them, although it is known from both juvenile and adult specimens (WENZ & POYATO-ARIZA 1994). Specific assessment of the *Caturus* from Las Hoyas will hopefully be available after the ongoing revision.

***Caturus tarraconensis*:** The good preservation of the fossils from the El Montsec outcrop has allowed an assignment of the respective materials to species *Caturus tarraconensis* (Fig. 3A), which is an endemic species of this outcrop. The Lagerstätte of El Montsec, located in the nearby Spanish province of Lérida, is part of the southern unity of the Pyrenees Chain. The depositional layers that constitute the fossil-yielding sites of El Montsec belong to the upper Berriasian-lower Valanginian sequence, which is divided into two different lithostratigraphic unities: La Serra del Montsec and La Pedrera de Rúbies (FREGENAL-MARTÍNEZ & MELÉNDEZ, 1995b). These sites have yielded a very diverse faunal assemblage, especially concerning fish fossils, which have been described in numerous publications and summarized by WENZ & POYATO-ARIZA (1995). Although being rare, *Caturus tarraconensis* is known to reach even 180 cm in length (WENZ & POYATO-ARIZA 1995). The currently available information does not suggest a close relationship between *Caturus tarraconensis* and the *Caturus* sp. from Las Hoyas, even though their faunal assemblages are quite similar (SANZ et al. 1988, WENZ & POYATO-ARIZA 1995).

## Family Amiidae

**Amiidae indet.:** All remains assigned to the superfamily Amioidea have been included in the family Amiidae. According to GRANDE & BEMIS (1998), this family is comprised of four different subfamilies (plus some taxa of indeterminate subfamily); at least two of them have been identified in the Portuguese and Spanish sites. However, the preservation of some amiid remains do not permit assignment at even a subfamily-level.

The coal mine of Guimarota has yielded other amiiform remains beside the caturid teeth discussed above; an incomplete but partially articulated specimen shows different elements of the skull, scales and a vertebral centrum. It was preliminarily assigned to the caturids (KRIWET 2000), but a subsequent analysis determined it to be more likely an Amiidae indet. (KRIWET 2005).

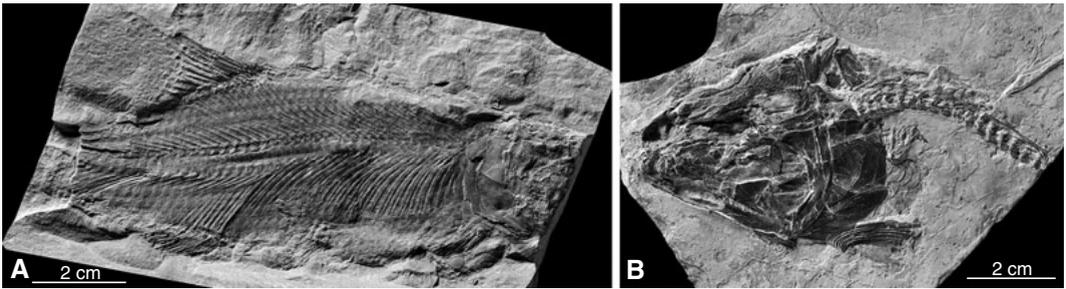


Fig. 3.

A, *Caturus tarraconensis*; specimen MNHN MSE 30a. B, *Amiopsis woodwardi*; specimen MNHN MSE 29. (Photographs C. LEMZAOUDA).

Some remains from the Lastres Formation, different from the Amiiformes indet. materials commented above, were also assigned as Amiidae indet. (RUIZ-OMENACA et al. 2006).

According to POYATO-ARIZA et al. (1999), Amiidae indet. remains have been found in Alcaine, where the genus *Caturus* has been cited as well (see above).

The outcrop of Buenache de la Sierra (see *Caturus* sp. above), also yields remains of teeth of a second amiiform morphotype classified as Amiidae indet. although, they probably belong to the subfamily Amiopsinae, along with the remains of other fossils previously classified in the Amiopsinae (BUSCALIONI et al. 2008), as will be explained in the following section.

Finally, remains of Amiidae indet. have been cited in sediments of several Portuguese localities between Cacém and Alcântara, to the west from Lisboa, dated as middle Cenomanian (Upper Cretaceous). This material consists of some partial frontal bones, scales, palatal bones and partial dentaries. Originally, these remains were assigned to the species *Paleamia cenomaniensis* by JONET (1981), with its corresponding holotype and paratypes. GRANDE & BEMIS (1998) considered these remains as Amiidae *nomen dubium*, on the basis of the doubtful application of the diagnosis made by JONET (1981) and on the fact that there is no evidence that all specimens belong to the same taxon, as they were found in diverse localities of different temporal horizons. According to GRANDE & BEMIS (1998), only the scales of the paratype series could be classified as Amiidae indet., and the rest are of difficult determination.

**Amiopsinae indet.:** As discussed above, the outcrop of Buenache de la Sierra has yielded a diverse record of amiiform fishes. Beside the morphotypes (based on teeth) assigned to *Caturus* sp. and Amiidae indet., some vertebral centra have also been found. They correspond to the description given by GRANDE & BEMIS (1998) for the subfamily Amiopsinae (BUSCALIONI et al. 2008), and thus have been classified as Amiopsinae indet.. They may or may not belong to the same taxon as the Amiidae indet. teeth mentioned above, but, at present, do not allow for a more precise assignment.

***Amiopsis woodwardi*:** Only the specimens from the Konservat-Lagerstätten of El Montsec and Las Hoyas are complete enough to allow a specific assessment. One of these species is *Caturus tarraconensis* (see above). A second species, *Amiopsis woodwardi* (Fig. 3B), is endemic to these two fossil sites.

This species is rare in El Montsec, but complete adult and juvenile specimens have been reported, of which adults reach up to 20 cm in length (WENZ 1988, WENZ & POYATO-ARIZA 1994, 1995). The taxonomic history of *Amiopsis woodwardi* at El Montsec is quite complicated, and it was previously assigned to the invalid genus *Urocles*. The controversy around this genus involves the other amiid species described from this outcrop, *Vidalamia catalunica* (see below), and will be explained in detail in the next section of this paper.

*Amiopsis woodwardi* is not very common in the Las Hoyas fossil site. The adult specimens, which can reach up to 20 cm in length (POYATO-ARIZA & WENZ 1995), are less abundant than the juvenile ones. These specimens seem to correspond to the description by GRANDE & BEMIS (1998) for the genus *Amiopsis* which, on the other hand, is not very well supported. The assignment to *Amiopsis woodwardi* has traditionally been made on the basis of the global similarities of the fish assemblages of El Montsec and Las Hoyas (SANZ et al. 1988, POYATO-ARIZA & WENZ 1995), and is in need of revision (MARTÍN-ABAD & POYATO-ARIZA work in progress).

***Vidalamia catalunica*:** The subfamily Vidalamiinae is also present in the Iberian fossil record. As *Amiopsis woodwardi*, *Vidalamia catalunica* has only been identified in El Montsec and Las Hoyas. *Vidalamia* and its type and only species are endemic to these two sites.

*Vidalamia catalunica* is easily distinguishable from the other amiid species from El Montsec, *Amiopsis woodwardi*, mainly by its longer dorsal fin. It is known from very few specimens in this locality. They can reach up to 50 cm in estimated total length (WENZ 1971, WENZ & POYATO-ARIZA 1995). Its taxonomic history also includes assignment to the invalid genus *Urocles*, as in the case of *Amiopsis woodwardi* (see following section).

*Vidalamia catalunica* is also very rare at Las Hoyas, being one of the largest fishes of this fauna (POYATO-ARIZA 2005b). As for *Amiopsis woodwardi*, the specimens of *Vidalamia* from Las Hoyas have been traditionally described under the same specific name as those of El Montsec due to the global similarities of the two fish faunas, so that further review is needed to confirm whether they are the same species or not.

### Taxonomic history of *Urocles* and *Megalurus*

Nowadays, the genus *Urocles* (= *Megalurus*) is no longer valid; but until just a few years ago, it was considered as a relatively diverse and abundant one, with species in different fossil fish assemblages. Due to its historic relevance and its numerous citations, especially in the European record, including the Iberian Peninsula, it seems relevant to summarize the meandrous taxonomic history of this genus.

**First citation:** Georg Graf zu MÜNSTER, around 1830, cited the genus *Megalurus* for the first time in a series of unpublished manuscripts, where four new species were included in this genus, all from the Solnhofen area (Bavaria, southern Germany). Unfortunately, these manuscripts are not accessible today, and the respective information comes from Louis AGASSIZ (LANGE 1968).

**“Ganoid” or teleost?:** AGASSIZ (1833-1843, Tome I: 68) was the very first to attempt a comprehensive taxonomic arrangement of fossil fishes in several orders. He formally described the genus *Megalurus* on the basis of its more outstanding feature, its caudal region, and included it in his “Ordre des Ganoidés” (AGASSIZ 1833-1843, tome II, pt. 2: 145). A few years later, MÜLLER (1845) revisited part of AGASSIZ’s arrangement. He mainly differentiated between two great groups: the Ganoidei and the Teleostei, assigning *Megalurus* to the former.

*Megalurus* does present what at the time were considered typical features of the “ganoid” fishes, such as a strong terminal bending of the vertebral column and an unequal development of the dorsal and the ventral caudal lobes. However, it also shows a number of features that may somehow relate it to teleostean fishes, such as a well-developed supraoccipital or the absence of fringing fulcra in the fins. As a consequence, the taxonomic assignment of *Urocles* (= *Megalurus*) has experienced multiple changes since AGASSIZ’s and MÜLLER’s classifications, mainly about its inclusion in one of these two great groups, depending on which set of features was particularly emphasized in the arrangements proposed by subsequent authors. Thus, some of the most important ichthyologists of the nineteenth century, like EGERTON (1858a,b) or QUENSTEDT (1885), thought it to be, more or less questionably, a member of the “ganoid fishes”, whereas others, like VETTER (1881), assigned it to the teleostean fishes, while some others did not maintain a constant opinion about it, like WAGNER (1861, 1863).

**Modern assignment:** LÜTKEN (1869), who shared VETTER’s opinion, placed *Megalurus* close to AGASSIZ’s Halecoidei, a group within the Teleostei. He was also the first who became aware of the similarities between *Megalurus* and the extant *Amia calva*. Some twenty years later, ZITTEL (1887-1890) provided extended data to support this similarity; furthermore, he put *Megalurus* and *Amia*, together with *Amiopsis*, into the Halecomorphi COPE, 1872, a family considered within the “ganoid fishes” at that time, mostly on the basis of the internal structure of their scales. Subsequent authors did agree, so *Megalurus* was no longer considered a teleost. Later on, *Megalurus* was considered as an actinopterygian within the family Amiidae BONAPARTE, 1838 by WOODWARD (1895, 1902), which was included either within the “Ganoidei” (KRAMBERGER-GORJANOVIC 1895, SAUVAGE 1903, VIDAL 1915) or the “Holostei” (REMANE 1936, RAYNER 1941, ROMER 1947, SAINT-SEINE 1949).

**Priority and synonymy:** The generic name *Synergus* was proposed by GISTEL (1848) as a substitute for *Megalurus*, since the latter was already used for a genus of birds described by HORSFIELD (1821). How-

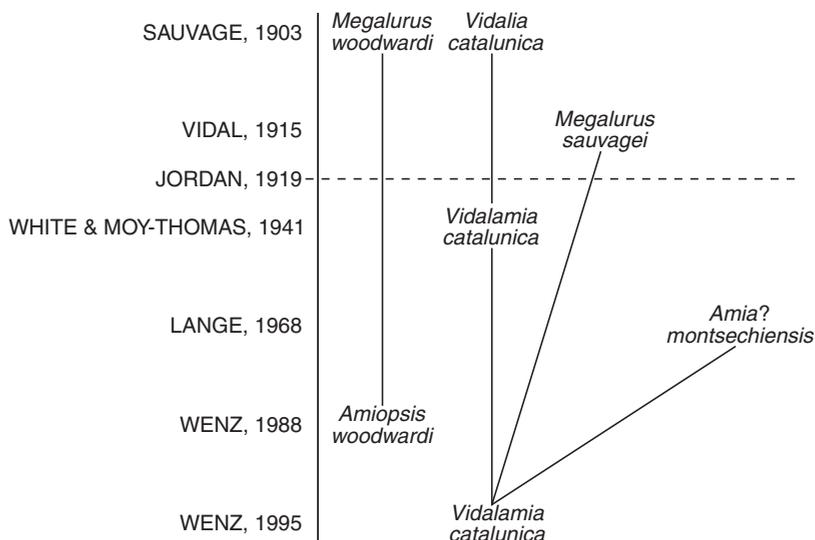
ever, this change seems to have passed unnoticed, since most of the authors of the time continued to use the invalid name *Megalurus*. Nearly a century later, JORDAN (1919) proposed the new name *Urocles* due to the synonymy of *Synergus* with a genus of hymenopteran insects described by HARTIG (1840). Unfortunately, JORDAN (1919) did not explain the etymological origin of the new generic name *Urocles*. Based on the etymology provided by BORROR (1971), we suggest that the first part of the name is adapted from the Greek “ουρα” (“ura”), “tail”. As for the second part of the name, it might come: either from “κλεις” (“kleis”), “to close”, in reference to its posteriorly rounded, non-forked caudal fin; or from “κλεος” (“kleos”), “glory”, meaning that the tail is the most significant part of the animal.

**Modern-times revisions:** The first modern extensive revision of the genus *Urocles* was done by LANGE (1968). Until this monograph, up to 15 different species had been described within *Urocles* (= *Megalurus*), out of only about thirty specimens that had been found all over the world. He examined numerous new specimens, reaching a total of 104, and concluded that only 10 of the previously defined species could be considered valid, plus a new one that he described in that paper.

The last chapter of the taxonomic history of the genus *Urocles* was written 30 years later by GRANDE & BEMIS (1998). They realized that most of the species accepted by LANGE (1968) and by previous authors were actually falling into synonymy with each other and with other species belonging to different genera of the order Amiiformes. The type species of the genus, *Urocles lepidotus* (= *Megalurus lepidotus* AGASSIZ, 1833) was not an exception, fitting into the diagnosis of the genus *Amiopsis* KNER 1863; *Urocles* had then to be considered as a junior synonym of *Amiopsis*, thus becoming an invalid generic name.

### The Spanish species of *Urocles* (= *Megalurus*)

As stated above, remains ascribed to the genus *Urocles* have been cited mainly from European fossil sites (Germany, France, England, and Spain), although some specimens have also been mentioned in outcrops of Brazil and Equatorial Guinea. Chronostratigraphically, *Urocles* has been cited from the Kimmeridgian-Tithonian (Upper Jurassic) of Solnhofen (Germany) to the Barremian of Las Hoyas. In this section, the taxonomic history of the species described within the genus *Urocles* in the Iberian record will be commented on in detail (Fig. 4). It is not the aim of this paper to mention all the publications that make any reference to the genus *Urocles*, but to review only those that involved a change in the synonymy or any other taxonomical aspect of each species.



**Fig. 4.** Schematical synopsis showing the nomenclatural changes undergone by the species of *Urocles* (= *Megalurus*) originally described in Spain.

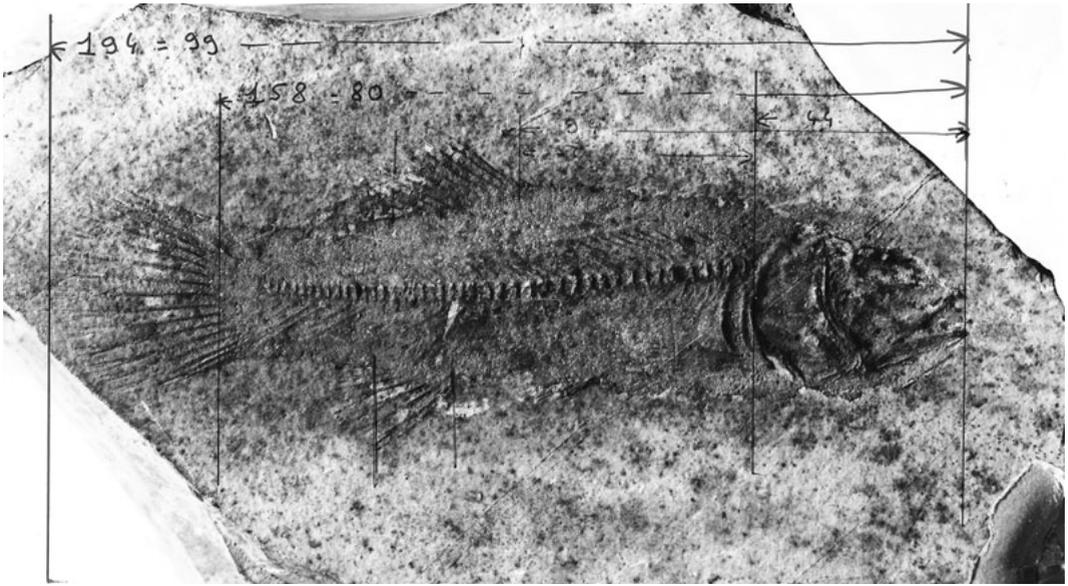


Fig. 5. "*Urocles* sp.", specimen MMGB 533, from El Montsec with hand-made measurements of Sylvie WENZ. (Courtesy of S. WENZ).

SAUVAGE (1903) described the first species of *Megalurus* coming from the Early Cretaceous lithographic limestones of El Montsec as *Megalurus woodwardi*. VIDAL (1915) described a second species of *Megalurus* from the fossil site La Pedrera, *Megalurus sauvagei*. LANGE (1968) described *Amia? montsechiensis* as a new amiid species coming also from El Montsec, and placed it phylogenetically very close to *Urocles*.

The fish fauna from El Montsec was completely revised by WENZ (1968, 1971, 1988; Fig. 5). She realized that *Urocles woodwardi* fits better into the genus *Amiopsis*, and renamed it as *Amiopsis woodwardi* (WENZ 1988). WENZ & POYATO-ARIZA (1994) and WENZ (1995) suggested a synonymy between the second nominal species, *Urocles sauvagei* and another species from the same outcrop, *Vidalia catalunica* SAUVAGE, 1903. WHITE & MOY-THOMAS (1941) had previously changed the name of this species to *Vidalamia catalunica*, due to the synonymy of *Vidalia* with a genus of dipterous insects. Unfortunately, they did not explain why they chose this name. Thus, *Megalurus sauvagei* and *Vidalia catalunica* are one and the same species, *Vidalamia catalunica* (SAUVAGE, 1903), a taxon in which WENZ (1995) also included *Amia? montsechiensis*.

SANZ et al. (1988) also mentioned *Urocles woodwardi* in the fossil record of Las Hoyas fossil site. WENZ (1988) and POYATO-ARIZA & WENZ (1995) stated that the material assigned to this species actually belongs to the genus *Amiopsis*. Nowadays, *Amiopsis woodwardi* and *Vidalamia catalunica* are the only amiid taxa cited from Las Hoyas (SANZ et al. 1988, POYATO-ARIZA & WENZ 1995). GRANDE & BEMIS (1998) agreed, maintaining the validity of both species, which they include within their subfamilies Amiopsinae and Vidalamiinae respectively.

### Concluding remarks

Up to now, the fossil record of amiiform fishes from the Iberian Peninsula is derived from twelve different fossil sites (some of them constituted by several outcrops); ten of them are included in the Spanish national territory, and the other two from the Portuguese territory. No insular references of amiiform material have been made for any of the two countries. Only one doubtful reference refers to material of the Triassic (Middle Triassic, specifically); three references refer to material of the Late Jurassic; and the other eight references refer to material of the Cretaceous (seven from the Early Cretaceous and one from the Late Cretaceous).



Fig. 6.

A, One of the smallest specimens found at Las Hoyas ascribed to the genus *Amiopsis*; MCCR LH 085 R. Scale bar = 1 cm. B, Isolated tooth of an amiiform fish found at Buenache de la Sierra. Scale bar = 1 mm.

In spite of the relatively abundant record of amiiform fishes, complete and articulated specimens are only known from three outcrops in the Iberian Peninsula, the Konservat-Lagerstätten of Montral-Alcover, El Montsec, and Las Hoyas. The rest of the fossil sites have yielded no more than fragmentary elements and very incomplete semiarticulated specimens, such as the one found in the Portuguese coal mine of Guimarota. The isolated amiiform remains usually consist mostly, or even exclusively, of teeth (Fig. 6B). Teeth are the hardest elements, most favorable not to be destroyed during fossilization, thus very probably reflecting a significant taphonomic bias. This taphonomic bias implies that these fish associations cannot be considered to be a reliable representation of the whole original communities. Reliable interpretations of composition of the complete original communities should only be described from the three Lagerstätten, where taphonomic factors or agents of protection must have occurred, thus favoring the preservation of a more representative fossil association.

The differential taphonomic processes, and their consequent biases, are the cause of the variable degree of taxonomic precision available when trying to identify the amiiform remains of the Iberian Peninsula. This happens mostly because of the lack of generic or specific characters in the teeth that can be assigned to the amiiforms. As a consequence, 12 out of the 21 valid amiiform citations do not reach down to the generic level (they correspond either to order, family or subfamily indet.); four are generic (all *Caturus*); and only five taxa have been specifically identified: three from El Montsec and two from Las Hoyas.

Among the most promising remains in need of revision are those from Las Hoyas, characterized by their completeness and exceptional preservation. Three different amiiform taxa have been cited from this locality: *Caturus* sp., *Amiopsis woodwardi*, and *Vidalamia catalunica*. Their specific assessment was done by comparison with the taxa from El Montsec, mainly on the basis of the global similarities between the fish assemblages of the two sites and the characters preliminary noted at the moment. However, the remains of Las Hoyas have not been studied in detail so far, and their taxonomic assessment is in need of confirmation.

Beside its taxonomic significance, the amiiform fossil record from Las Hoyas may prove to be very informative involving the ontogenetic development of these taxa, since both juvenile and adults have been unearthed, including some of the smallest amiiform specimens ever recovered worldwide (Fig. 6A). As shown by GRANDE & BEMIS (1998), a detailed account of the ontogenetic development, whenever possible, is a key factor to accomplish a precise systematic and taxonomic classification, mostly because it helps to determine the intra- and inter-specific variation of the different systematic characters, due either to individual variation or to growth. This will hopefully be part of the ongoing project of revision of the Amiiformes from Las Hoyas.

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