

## Mesozoic clupeomorphs of North Africa: diversity and phylogeny

Bouziane Khalloufi<sup>1,\*</sup>, Didier B. Dutheil<sup>2</sup>, Paulo M. Brito<sup>3</sup>, Théo Mora<sup>1</sup> and René Zaragüeta Bagils<sup>1</sup>

<sup>1</sup>Laboratoire Informatique et Systématique UMR 7205, Université Pierre et Marie Curie,  
Muséum national d'Histoire naturelle, Paris, France  
<sup>2</sup>11 bis, rue Jorge Semprún, F-75012 Paris, France

<sup>3</sup>Departamento de Zoologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil

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**Abstract** - Clupeomorpha, nowadays represented among others by herrings, anchovies and sprats, possess a fossil record extended back at least to early Cretaceous. Until Eocene, they were mainly represented by Ellimmichthyiformes, an extinct clade of double and triple armored forms encountered in marine and continental environments. In North Africa, four Late Cretaceous localities have yielded clupeomorph remains, representing at least nine species. Their phylogenetic positions are discussed but remain unclear, mainly owing to the definition of the characters, which include several homoplastic and plesiomorphic features.

**Keywords:** Clupeomorpha, Cretaceous, North Africa

### 1. Introduction

Clupeomorpha, nowadays represented among others by herrings, anchovies and sprats, possess a fossil record extended back at least to early Cretaceous. Until Eocene, they were mainly represented by Ellimmichthyiformes, an extinct clade of double and triple armored forms encountered in marine and continental environments. In North Africa, four Cretaceous localities have yielded clupeomorph remains (Khalloufi *et al.*, 2017). In Morocco, a form has been identified in the Jbel Tselfat (Arambourg, 1954), five species are present in the Akrabou Formation (Murray and Wilson, 2011, 2013; Vernygora and Murray, 2015; pers. obs.), and two unpublished taxa have been signaled in the Kem Kem beds, in the Jbel Oum Tkout locality (Dutheil, 1999). In Tunisia, a species was described by Gaudant and Gaudant (1971). Apart from four recently described species from the Akrabou Formation, all these taxa are new or poorly known. These last forms are reviewed herein and their phylogenetic relationships are discussed.

### 2. Materials

The studied specimens are housed in the palaeontological collections of the Muséum national d'Histoire naturelle, Paris (France), the Muséum d'Histoire Naturelle de Marseille (France) and the Muséum d'Histoire Naturelle de Marrakech (Morocco).

### 3. Localities and taxa

#### 3.1 Jbel Tselfat, Cenomanian-Turonian boundary, Morocco

This deposit belongs to a thrust sheet located in northern Morocco, close to the cities of Meknes and Sidi Kacem. The Cretaceous fossiliferous levels are formed by black shales associated with the Anoxic Oceanic Event 2, an episode of massive deposition of organic matter dated at the Cenomanian-Turonian boundary. Two sites are known, Aïn el Kerma, showing a dark matrix, and Sigda, with a more brownish facies. The palaeoenvironment is reconstructed as deep marine, and a comparable fauna is known from Italy (Leonardi, 1966; Sorbini, 1976). In his review of the ichthyofauna of the Jbel Tselfat, Arambourg (1954) attributed two small incomplete specimens to "*Diplomystus*" (= *Armigatus*) *brevissimus*.

#### 3.1.1 Ellimmichthyiformes incertae sedis

**Description.** Both specimens are restricted to the anterior part of the body. The skull is higher than long. The parietals are in contact with each other and ornamented by deep grooves. The opercle is unornamented and very narrow. No teeth are observed on the jaws, but the preservation is limited. The hyoid arch is partly visible and shows hypohyals which are higher than long. The cleithrum is narrow and slightly S-shaped, with a fin of about twelve rays. The post-temporal possesses a crenulated posterior margin. The pelvic fin is formed by about eight rays.

The axial skeleton comprises 15 abdominal verte-

\*Author for correspondence: khalloufi@mnhn.fr

brae, each one bearing a thin pair of ribs. The caudal series is incomplete. The dorsal fin starts at the level of the 10th vertebra and is composed of at least by 15 rays. At the anterior insertion point of the fin, the dorsal profile shows a fairly marked angle. The anal fin begins from the 20th vertebra and shows at least 20 rays. Two series of scutes are present. The ventral one is formed by scutes with high lateral wings and a small median spiny keel posteriorly oriented. A dorsal series is cited by Arambourg (1954) on one specimen but the scutes are actually restricted to small fragments; this area was probably damaged since the original description. The caudal skeleton is unknown.

**Discussion.** The poor and incomplete preservation of the skeletons precludes a detailed anatomical description and the precise affinities of these specimens remain unclear. The presence of ventral scutes supports their inclusion among Clupeomorpha. The morphology of the skull, notably the presence of two supramaxillae and the shape of the maxilla, corroborates with this position. The presence of two well developed series of scutes corresponds to Ellimmichthyiformes. The post-temporal with a crenulated posterior margin and the shape of the hypohyals, higher than long, are considered as features of the genus *Armigatus*, following Forey *et al.* (2003). On the contrary, the posteriormost ribs supported by parapophyses of increasing length are encountered in Paraclupeidae and Sorbinichthyidae, but are uncommon in *Armigatus* or *Diplomystus* (an exception being *A. oligodentatus*). Other features of paraclupeids or sorbinichthyids are however not observed in the two specimens. This species is tentatively considered as an ellimmichthyiform *incertae sedis*, pending its inclusion in a phylogenetic analysis.

### 3.2 Agoult, Akrabou Formation, late Cenomanian-early Turonian, Morocco

This recently discovered locality, also known under the name of Gara Sbaa and misnamed Daoura by (Cavin and Dutheil, 1999), is formed by limestone slabs overhanging the continental Kem Kem beds, southeastern Morocco. The palaeoenvironment is reconstructed as marine littoral. Four species are currently known, the sorbinichthyid *Sorbinichthys africanus* Murray and Wilson, 2011, the paraclupeids *Thorectichthys rhadinus* and *Thorectichthys marocensis* both described by (Murray and Wilson, 2013), and the armigatid *Armigatus oligodentatus* Vernygora and Murray, 2015. A fifth unpublished species is represented by a single specimen, herein referred to the genus *Rhombichthys*.

#### 3.2.1 *Rhombichthys* sp.

**Description.** The diamond-shaped body of ca. 70mm in standard length is almost twice higher than long (the standard length represents 51% of the total depth). The axial skeleton comprises 33-34 vertebrae, with abdominal centra anteroposteriorly constricted. The last abdominal vertebrae possess elongated parapophyses which support small ribs. The posterior predorsal scutes have elongated lateral wings, and the last scute is claw-shaped. The ventral scute series is formed by about 35 scutes with very elongated lateral wings. The scutes located posteriorly to

the apex of the ventral profile possess a strong posteriorly oriented spine.

**Discussion.** The diamond-shaped body, the peculiar ventral scute series and the claw-shaped posteriormost dorsal scute permit to refer this specimen to the genus *Rhombichthys*. From this preliminary description, no significant differences are observed in comparison to the Palestinian form *R. intocabilis* Khalloufi *et al.*, 2010.

### 3.3 Jbel Oum Tkout (OT1), Kem Kem beds, Cenomanian, Morocco

This small clayey lens, located in the beginning of the unit II of the Kem Kem beds, is dated as Cenomanian (Dutheil, 1999). The presence of a faunal assemblage including unionids, odonats, ephemeropters and polypterids strongly suggests a freshwater palaeoenvironment. At least two species of clupeomorphs are present.

#### 3.3.1 *Triplomystus* sp.

**Description.** At least five specimens are known. This deep-bodied fish, with a total depth representing ca. 50% of the standard length, shows a marked angle at the insertion of the dorsal fin. The skull roof possesses ornamented parietals and a well developed supraoccipital crest. All bones associated to the jaws are toothless. The opercle is large and ornamented by strong radial ridges.

The axial skeleton is formed by 27 to 29-30 vertebrae including 14 abdominal and 2 ural centra. Each abdominal centrum supports a pair of ribs directly inserted in deep pits on the lateral surfaces. The three last ribs, decreasing in size, are supported by elongated parapophyses. Epineurals and epipleurals are restricted to the last abdominal and the first caudal vertebrae.

The predorsal scute series is formed by nine scutes of increasing size. The last ones possess ovoid lateral wings and a prominent anvil-shaped median keel. The ventral series of scutes is formed by elements with reduced lateral wings and a median spiny keel. The post-dorsal series is formed by eight or nine large scutes with a postero-dorsally oriented spine. Scutes show no ornamentation.

In the caudal skeleton, the first ural centrum bears a large first hypural and a fused stick-shaped second hypural. Three other hypurals are supported by the second ural centrum. The hypural diastema is small. Three epurals fill the space between the first and the second preural centrum neural arches and spines. In some specimens, soft tissues are preserved, like mineralized muscles or the spinal cord.

**Discussion.** The presence of a post-dorsal series of scutes is considered as a synapomorphy of Triplomystini (Murray and Wilson, 2013). Inside this tribe, two genera are known: the deep-bodied *Triplomystus* and the more elongated *Scutatoclupea* (see Forey *et al.*, 2003; Alvarado-Ortega and Ovalles-Damián, 2008; Bannikov, 2015). The species from OT1 differs from the latter by its high body, the lesser number of vertebrae, the ornamented opercle and the shape and the weak number of scutes of each series. It mainly differs from *Triplomystus* by the morphology of its predorsal scutes, (unornamented, with an anvil shaped process and with more reduced lateral wings), the moderate extension of the ventral scute lateral

wings, and by the greater size of its ribs. These last differences are weak and a simple emendation of the genus *Triplozystus* is proposed to include this new species.

### 3.3.2 Clupeomorpha incertae sedis

**Description.** Ten specimens with a body slightly elongated to deep are tentatively referred to this new species. The skull is characterized by a well developed supraoccipital crest, toothless jaws and an unornamented opercle. The axial skeleton is formed by 14-15 abdominal and 16 caudal vertebrae. The dorsal fin possesses 11 rays and the anal fin 14 rays. Two series of scutes are present. The dorsal series is formed by a dozen of small unornamented scutes, subequal in size, and extended from the skull to the dorsal fin. They are mainly formed by a small posteriorly oriented spine, with very reduced lateral wings. The ventral series is also formed by spiny scutes with small lateral wings.

The caudal skeleton comprises six hypurals, the second and the third ones delimitating a small distal diastema. A caudal scute is present anteriorly to the rays. Three epurals are present but they do not contact the second preural centrum neural spine.

**Discussion.** Among ellimmichthyiforms, predorsal scutes of subequal size are only present in *Armigatus*, *Diplomystus* and sorbinichthyids. In the genus *Armigatus*, the predorsal series is incomplete and in sorbinichthyids, scutes are deeper than long, two features not encountered in this species. This species also differs from *Diplomystus* in several aspects, like the morphology of the ventral scutes, the insertion of the last ribs and the position of the epurals. A comparison with non-ellimmichthyiform double armored clupeomorphs is needed to discuss more generally of its phylogenetic relationships. This species is considered as a *Clupeomorpha incertae sedis*.

## 3.4 Gabès, Upper Cretaceous, Tunisia

*"Diplomystus" solignaci* was described by Gaudant and Gaudant (1971) from a unique specimen preserved in a limestone slab. The exact collect locality remains unknown but Gaudant and Gaudant (1971) thought to identify it in the surroundings of the Djebel Halouga, close to the city of Gabès, and they proposed a "Senonian" age. The specimen is briefly redescribed here, emphasizing the differences or the additional features in comparison to the original description.

### 3.4.1 Paraclupeidae incertae sedis

The specimen, of 105mm in standard length, is subcomplet. Some features of the skull are well observed, like the presence of endopterygoid teeth (but the parasphenoid is toothless) and tooth alveoli in the premaxilla and the dentary. The anterior ceratohyal is well seen without determining whether it is incomplete or devoid of beryciform foramen. The opercle is striated by radial ridges, the subopercle is unornamented. The cleithrum is S-shaped.

About 24-26 abdominal and 15 caudal vertebrae are present (including the two ural centra). Ribs are directly inserted into the centra, except for the last eight ones, supported by parapophyses of increasing length. Epineurals and epipleurals are restricted to the last abdominal and the first caudal vertebrae. No epicentrals are seen.

The dorsal series of scutes leaves a gap posteriorly to the skull roof, but this gap is possibly simply caused by a preservation bias. The posteriormost predorsal scutes show lateral wings increasing in size. These scutes are apparently unornamented. The ventral series is formed by about 50 scutes, extended from the isthmus to the anus. The lateral wings of these scutes are elongated and in contact with the adjacent ones in almost all their length.

The caudal skeleton shows five to six hypurals. The first one possesses a proximal upward process, the second one is stick-shaped and fused to the first ural centrum. The third hypural contacts the second one, leaving no hypural diastema, at least in their proximal part. Three curved epurals are in contact with the neural spine of the second preural centrum.

**Discussion.** This species was removed from the genus *Diplomystus* by Grande (1982) on the basis of the plesiomorphic combination of features used by Gaudant and Gaudant (1971). As highlighted by Alvarado-Ortega *et al.* (2008), Murray and Wilson (2013), Vernygora and Murray (2015), and Marramá and Carnevale (2016), the presence of the posteriormost dorsal scutes more developed in size and the postpelvic abdominal scutes with a strong ventral spine correspond more to a paraclupeid. Other features support this position, like the marked angle at the insertion of the dorsal fin or the insertion of the last ribs, which are uncommon in *Armigatus* and *Diplomystus* (however, *D. birdi* shows the former feature). A close relationship with the genera *Rhombichthys* and *Ellimmichthys* was proposed (for example by Murray and Wilson, 2013; Marramá and Carnevale, 2016) but this position is mainly supported by plesiomorphic states (e.g., the number of epurals or the absence of caudal scute, or homoplastic characters (e.g., subrectangular scutes) in posterior part of predorsal series). This species is considered as a paraclupeid *incertae sedis*.

## 4. Conclusions and Perspectives

At least nine species of clupeomorphs were present in North Africa during Late Cretaceous, in a large variety of palaeoenvironments. A series of recent phylogenetic analyses (e.g., Zaragüeta Bagils, 2004; Alvarado-Ortega *et al.*, 2008; Murray and Wilson, 2013; Vernygora and Murray, 2015; Marramá and Carnevale, 2016) allow a better understanding of the intrarelationships of fossil clupeomorphs, especially ellimmichthyiforms. A cladistic analysis including eight North African Cretaceous species was conducted herein. If the results permit to retrieve in part some of the main clades previously defined, like the paraclupeids or the sorbinichthyids, the lack of consensual relationships highlights the necessity of a deep redefinition of the characters, as hypotheses of homology. Morphological phylogenetics should be based, as far as possible, on highly informative and precisely described character-states. They would be the backbone supporting phylogenetic relationships

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