

# A new Clupavidae (Teleostei, Ostariophysii) from the Cenomanian of Daoura (Morocco)

*Un nouveau Clupavidae (Teleostei, Ostariophysii) du Cénomanién de Daoura (Maroc)*

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**Abstract** — *Lusitanichthys africanus* n. sp. from Daoura, an Upper Cenomanian locality situated about 100 km south of Erfoud (southeastern Morocco), is described. *L. africanus* is very similar to *L. characiformis*. *Lusitanichthys* shows modifications of the first vertebral elements indicating the presence of a primitive Weberian apparatus. *Clupavus maroccanus* and *Lusitanichthys* belong to the clupavids. Anatomical characters of *L. africanus* from the Weberian apparatus and the caudal skeleton allow us to include it in Otophysi without sure indications of ordinal affinities. (© 1999 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS.)

**Teleostei / Ostariophysii / Clupavidae / new taxon / Cenomanian / Morocco**

**Résumé** — *Lusitanichthys africanus* n. sp. du Cénomanién supérieur de Daoura, une localité située à une centaine de kilomètres au sud d'Erfoud (Sud-Est du Maroc), est décrit. *L. africanus* est très proche de *L. characiformis*. *Lusitanichthys* présente des modifications des premiers éléments vertébraux, indiquant la présence d'un appareil de Weber primitif. *Clupavus maroccanus* et *Lusitanichthys* appartiennent à la famille des clupavides. Les caractères de l'appareil de Weber et du squelette caudal de *Lusitanichthys* permettent de l'inclure dans les Otophysi, sans précision sur ses affinités avec un ordre particulier. (© 1999 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS.)

**Teleostei / Ostariophysii / Clupavidae / taxon nouveau / Cénomanién / Maroc**

## Version abrégée p. 693

### 1. Introduction

A locality situated about 100 km south of Erfoud (Morocco), on the escarpment of the Kem Kem plateau near the Oued Daoura, has yielded fossils of small fishes. The ichthyofauna now comprises five different forms and is similar to the fish assemblage of Jebel Tselfat, Morocco (Cavin and Dutheil, in press). Comparison of these fish assemblages with Tethysian faunas and analysis of the

succession of Moroccan fish faunas of the early Late Cretaceous give an Upper Cenomanian age for the Jebel Tselfat and Daoura localities (Cavin and Dutheil, in press). The faunal list comprises an indeterminate pycnodont, two Clupeomorphs, a Clupavid characterized below and a *Rhynchodercetis*.

The fishes are small (33 mm or less of standard length) and preserved as negatives on fine sandstone slabs. Bone material is rarely preserved and anatomical structures are

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**Note communicated by Yves Coppens.**

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barely distinguishable on the original specimens. The descriptions and illustrations are based on black silicone positive casts. The specimens are kept in the Natural History Museum in Boulogne-sur-Mer, France (BHN).

The systematic affinities of clupavids have been the subject of debate, and they are now generally regarded as primitive Otophysi (Patterson, 1993). Clupeomorpha and Ostariophysi are now grouped in a monophyletic group on morphological and molecular evidence. This taxon is named either Otocephala (Johnson and Patterson, 1996) or Ostarioclupeomorpha (Arratia, 1997), the former having priority over the latter.

## 2. Systematic palaeontology

Subclass Teleostei  
Cohort Clupeocephala  
Subcohort Otocephala  
Superorder Ostariophysi  
Series Otophysi

Order *incertae sedis*  
Family Clupavidae

Genus *Lusitanichthys* Gayet, 1981

*Lusitanichthys africanus* n. sp.

*Holotype*: BHN 2P40, complete specimen, Daoura, Morocco (figure 1).

*Additional material*: BHN 2P41 — BHN 2P43.

*Locus typicus*: Daoura, southeastern Morocco.

*Age*: probably Upper Cenomanian.

*Derivatio nominis*: first discovery of a species of this genus in Africa.

*Diagnosis*: *Lusitanichthys* that differs from *L. characiformis* by the long and thin anterior process of the posterior supramaxilla, and by the thin neural spines on the preural vertebrae 3 and 2; pectoral fin with 18 rays; 39 to 41 vertebrae (with ural centra).

## 3. Description

The available specimens are small (between 20 and 33 mm in standard length) and the body is elongated (the maximum depth is about 20 % of the standard length). Because no incomplete ossification of bones is visible on the skeletons, we suspect that the specimens are adults of small size and not juvenile forms.

**Cranial bones** (figure 2A). The bones are unornamented. The frontals are large, slightly broad anteriorly and their lateral margins are curved above the orbit. There is a notch on the posterior extremity of the medial border of each frontal forming the anterior margin of a fontanelle as in *L. characiformis* (Gayet, 1981; 1985a). This fenestra differs from those observed in *C. maroccanus* in which it is mainly formed by notches in parietals (Taverne, 1995). The parietals are poorly preserved; they are small and apparently close the fontanelle posteriorly. I am uncertain whether there is a contact between both parietals. The posterior part of the skull roof is poorly preserved.

The lateral ethmoids form well-developed ventrolateral wings extending below the level of the parasphenoid. A triangular bone is visible posterior to the lateral ethmoid of the specimen BHN 2P40 similar to the rhinosphenoid described in *L. characiformis* (Gayet, 1981; 1985a). The parasphenoid is visible as a rectilinear rod of bone below the orbit. The other bones of the braincase are not visible except a portion of the orbitosphenoid and pleurosphenoid in the posterior part of the orbit of the holotype.

The orbital bones are poorly preserved in all specimens.

**Upper jaw** (figure 2B). The upper jaw is similar to those of other clupavids, except the dorsoposterior part of the posterior supramaxilla, which is more developed than that of *C. maroccanus* and its anterior process which is longer and thinner than that of *L. characiformis*. No teeth are visible on the bones of the upper jaw.

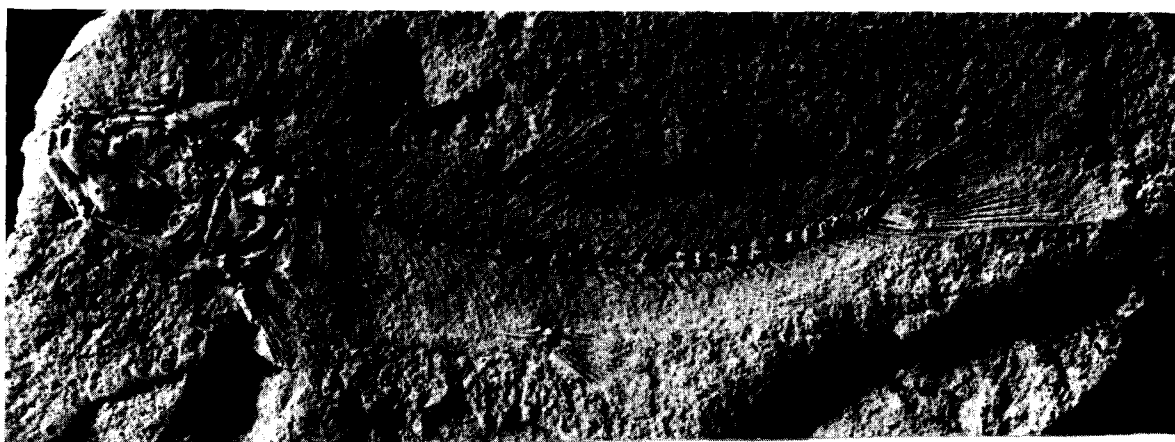
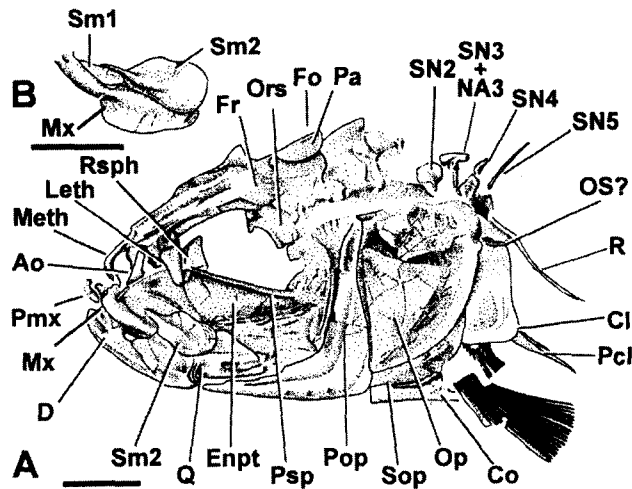


Figure 1. *Lusitanichthys africanus* n. sp. Holotype (BHN 2P40). Silicone cast. Scale bar: 10 mm.

Figure 1

*Lusitanichthys africanus* n. sp. Holotype (BHN 2P40). Empreinte en silicone. Barre d'échelle : 10 mm.



**Figure 2.** *Lusitanichthys africanus* n. sp. A. Holotype (BHN 2P40). Head. Scale bar: 2 mm. B. Upper jaw (BHN 2P41). Scale bar: 2 mm. Abbreviations: Ao, antorbital; Cl, cleithrum; Co, coracoid; D, dentary; Enpt, entopterygoid; Fo, fontanelle; Fr, frontal; Leth, lateral ethmoid; Meth, mesethmoid; Mx, maxilla; NA, neural arch; Op, opercle; Ors, orbitosphenoid; Os, os suspensorium; Pa, parietal; Pcl, postcleithrum; Pmx, premaxilla; Pop, preopercle; Psp, parasphenoid; Q, quadrate; R, rib; Rsph, rhinosphenoid; Sm, supramaxilla; SN, supraneural; Sop, subopercle.

*Lusitanichthys africanus* n. sp. A. Holotype (BHN 2P40). Tête. Barre d'échelle : 2 mm. B. mâchoire supérieure (BHN 2P41). Barre d'échelle : 2 mm. Abréviations : Ao, antorbitaire ; Cl, cleithrum ; Co, coracoïde ; D, dentaire ; Enpt, entoptérygoïde ; Fo, fontanelle ; Fr, frontal ; Leth, ethmoïde latéral ; Meth, mésethmoïde ; Mx, maxillaire ; NA, arc neural ; Op, opercule ; Ors, orbitosphénoïde ; Os, os suspensorium ; Pa, pariétal ; Pcl, postcleithrum ; Pmx, prémaxillaire ; Pop, préopercule ; Psp, parasphénoïde ; Q, carré ; R, côte ; Rsph, rhinosphénoïde ; Sm, supramaxillaire ; SN, supraneural ; Sop, sous-opercule.

**Lower jaw** (figure 2A). The lower jaw is deep and short, and the mandibular symphysis is shallow. Laterally it consists of a dentary, a large angulo-articular and a small retroarticular at the posteroventral corner of the jaw. No teeth are visible on the oral margin.

**Suspensorium.** The narrow hyomandibula has an anteroventrally sloping articular facet for the neurocranium as in *C. maroccanus* and *L. characiformis*. The other bones of the suspensorium are poorly preserved.

**Opercular bones** (figure 2A). The opercular bones are close in shape to those of *C. maroccanus* and *L. characiformis*.

**Vertebrae and intermuscular bones.** There are 23 to 25 abdominal vertebrae and 16 caudal vertebrae (including 2 preural and 2 ural centra). The total number of vertebrae varies therefore between 39 and 41. The anteriormost vertebrae are modified and reminiscent of those observed in *L. characiformis* (Gayet, 1981, 1985a). The first centrum and its possible associated element were not observed because of the type of preservation of the specimens. The following centra are not visible either, but their neural elements can be seen on the specimens BHN 2P40 (figure 2A), -41 and -43. There is a proportionally large

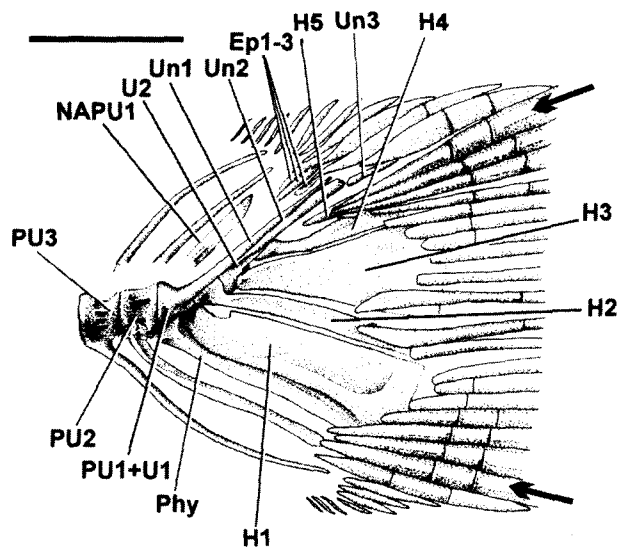
dorsal element, subrectangular in shape and with a ventral process. This bone agrees well the second supraneural described for *L. characiformis*. A hammer-shaped bone, situated posteriorly to the second supraneural, is observed on several specimens: the dorso-anterior extremity is enlarged and lies close to the second supraneural and the ventral process is elongated, with a thin proximal extremity applied again to the next neural arch, probably coming into contact with its corresponding centrum. This bone looks like the structure corresponding to the fusion of the third neural arch, neural spine and supraneural described in *L. characiformis*. The next neural arch is enlarged with a lateral depression, and dorsally extended by a spiny neural spine. Ventrally a subhorizontal posteriorly spiny extremity of bone is visible backward to the pectoral girdle on the specimens BHN 2P40. It probably corresponds to the distal head of the fourth rib (the 'os suspensorium' of *L. characiformis*). The subsequent vertebrae are unmodified.

The neural spines are unfused for the first 21 abdominal vertebrae at least. Eight free supraneurals are present between the fifth vertebra and the first pterygiophore. Epineurals are present until the 27th vertebra. Epipleurals are apparently present in association with the last nine abdominal vertebrae and with the first three caudal vertebrae.

**Dorsal and anal fins** (figure 1). The dorsal fin begins at the level of the 12th vertebra and ends at the 20th. There are 12 dorsal pterygiophores supporting 14 rays. The first pterygiophore is enlarged and triangular in shape. There are four simple precurrent rays.

The anal fin begins at the level of the 28th vertebrae and ends at the 32nd and there are almost 12 rays.

**Caudal skeleton and fin** (figure 3). The caudal skeleton is very similar to that of *L. characiformis*. The neural spines of the preural vertebrae (PU3-PU2) are thin, without a bony plate on their proximal anterior half as in *L. characiformis* (Gayet, 1981), and the neural spine on PU2 is not reduced. There are two ural centra; the first one bears a well-developed spatulate neural spine and is regarded as the fusion of the first preural and first ural centra. The parhypural is applied against but not fused with the centrum and shows no hypurapophysis. There are five hypurals. The first one is broad and is applied against the compound centrum. On the holotype, a notch is present on the antero-dorsal edge of the first hypural. The second one is relatively narrow and fused with the compound centrum. Three uroneurals are visible: the first one is elongate and proximally fused with the lateral face of the first compound ural centrum. There are apparently three epurals. No scute is visible. There are 11 simple dorsal precurrent rays, the last two are segmented, 10 dorsal principal rays, 9 ventral principal rays and 8 simple ventral precurrent rays, the last one is segmented. The lowest ray of the upper lobe and the uppermost ray of the lower lobe exhibit spatulate proximal extremities resting respectively on the third and second hypurals.



**Figure 3.** *Lusitanichthys africanus* n. sp. Holotype (BHN 2P40). Caudal skeleton. Scale bar, 1 mm. Arrows mark the outermost principal fin-rays. Abbreviations: Ep, epural; H, hypural; NAPU, neural arch of a preural vertebra; Phy, parhypural; PU, preural centrum; U, ural centrum; Un, uroneural.

*Lusitanichthys africanus* n. sp. Holotype (BHN 2P40). Squelette caudal. Barre d'échelle : 1 mm. Les flèches marquent les rayons principaux externes. Abréviations : Ep, épural ; H, hypural ; NAPU, arc neural d'une vertèbre préurale ; Phy, parhypural ; PU, centrum préural ; U, centrum ural ; Un, uroneural.

**Paired girdles and fins** (figures 1 and 2). The structure of the pectoral girdle is similar to that of *L. characiformis*. There are 18 pectoral rays.

The pelvic bone extends from the level of the 16th to 20th centra. It is a triangular bone with a slightly convex mesial margin. There are almost 10 pelvic rays.

**Squamation.** The scales are poorly preserved. They are very thin and of cycloid type.

#### 4. Systematic affinities

*L. africanus* agrees with the short diagnosis proposed by Gayet (1981) for the genus *Lusitanichthys*: vertebral elements of the first centra are notably modified, the first hypural articulates autogenously with the first ural centrum and there are three epurals (the latter character is uncertain for *L. africanus*). Gayet then added (1985a) that some specimens of *L. characiformis* possess an hypural 1 separated from the compound centrum by hiatus. Both characters are also observed on *C. maroccanus* (Gayet, 1981; Taverne, 1995).

The Salminopsidae which are regarded as primitive Characiformes by Gayet (1985a, b, 1986a) differ from *L. africanus* by the presence of teeth and by the structure of the Weberian apparatus.

##### *Clupavidae*

Gayet (1981) placed *L. characiformis* in the family Clupavidae because it shares resemblances in the Weberian apparatus and caudal skeleton with *C. maroccanus*. The

family Clupavidae was created by Bertin and Arambourg (1958) and was regarded first as Clupeoidei (Taverne, 1977), then, following the discovery of a Weberian apparatus, as an Ostariophysi close to Characoidei (Gayet, 1981, 1985a). Taverne (1995) pointed out differences between *Lusitanichthys* and *Clupavus*. He regarded *Clupavus* as the sister group of Characiformes+Siluriformes because of one apomorphy shared by *Clupavus* and Characiformes: an enlarged modified supraneural is tilted anteriorly and articulates with the posterior margin of the cranium (character [62] of Fink and Fink, 1981).

My own observation of the specimen of *C. maroccanus* showing the best preserved Weberian apparatus (T 142D, Muséum national d'Histoire naturelle, Paris) differs from those of Taverne (1995, figure 3). The anteriormost dorsal elements of the first vertebrae are crushed and I was unable to recognize the scaphium, the intercalarium and/or third neural arch and the large supraneural articulating with the posterior margin of the cranium. Consequently, I considered that the character [62] of Fink and Fink (1981) is unclear in *C. maroccanus* and does not allow one to place this species as the sister group of Characiformes+Siluriformes. This specimen clearly shows modifications of the elements associated with the first vertebrae, in particular the presence of an os suspensorium, but I regard the shape and the organization of these elements as still unclear.

I observed a trace of a subrectangular bone behind the lateral ethmoid on several specimens of *C. maroccanus* (DTS 245D, DTS 249, DTS 113) that could be interpreted as a rhinosphenoid.

Other differences between *L. characiformis* and *C. maroccanus* pointed out by Taverne (1995) are unreliable because the specimens available are too poorly preserved.

In conclusion the certain differences observed between *Clupavus* and *Lusitanichthys* (shape of the mesethmoid, number of epurals) do not justify placing these genera in different families.

##### *Clupavidae and Ostariophysi*

A recent study reviewed 127 Ostariophysan characters (Fink and Fink, 1996). Few of them are visible on the specimens of *L. africanus*. The characters (Fink and Fink's numbers (1981, 1996) in brackets) are discussed independently but not integrated into a cladistic analysis because too much information is missing. *L. africanus* possesses two supramaxillae in contrast to most Ostariophysi [41]. Two supramaxillae are present in *L. characiformis* and one is present in *Chanoides macropoma* that is regarded as the sister group of Otophysi (Patterson, 1984; Fink and Fink, 1996). *L. africanus* lacks jaw teeth [42] as do Gonorrhynchiformes, Cypriniformes and *Chanoides macropoma*. This feature is homoplastic for Ostariophysi and characterizes gonorrhynchiforms and crown-group otophysans (Fink and Fink, 1996). The new species shows two synapomorphies of Otophysi in the Weberian apparatus. One is the ventral expansion of anteriormost one or two supraneurals forming a synchondral joint with neural

arches 3–4 [60]. This state is present for supraneural 2 but modified for supraneural 3, which is probably fused with its neural spine and arch. The other synapomorphy in the Weberian apparatus is the probable presence of an os suspensorium [88]. The character [110] of Fink and Fink (1981), “in Otophysi, the caudal support skeleton has a compound terminal centrum consisting [...] of the first preural centrum, the two ural centra, and the anterior pair of uroneurals” corresponds to three different characters: [110<sup>i</sup>] fusion of PU1 and U1, [110<sup>ii</sup>] fusion of U1 and U2, [110<sup>iii</sup>] fusion of U1 and the first pair of uroneurals. *L. africanus* shows two of them ([110<sup>i</sup>] and [110<sup>iii</sup>]) and another synapomorphy of the caudal support of Otophysi: the hypural 2 is fused with the compound centrum [114]. *L. africanus* lacks an Otophysan synapomorphy: presence of two or fewer epurals [115].

The modifications observed in the anterior vertebrae 2 to 4 ([60], [88?]) and the characters of the caudal support ([110<sup>i</sup>], [110<sup>iii</sup>], [114]) clearly show Otophysan affinities even though a precise phylogenetic reconstruction may not be possible.

#### *Clupavidae and Characiformes*

Gayet (1981) situated *L. characiformis* as the sister-group of Characidae because it shares some apomorphies with the latter. Severe disagreements about Gayet's interpretation of several characters of *L. characiformis* and other fossil Ostariophysi were raised by different authors in an exchange of papers (Fink et al. 1984; Patterson, 1984, Gayet, 1985a, 1986a, b; Fink and Fink, 1996). For *L. characiformis* and its systematic affinities the discussion turned to characters [2], [4], [7], [9], [12], [15], [25], [37], [39], [41], [44], [61], [62], [66], [69], [71], [73], [75], [79], [81], [85], [88], [111], [113].

I have not seen the specimens of *L. characiformis* and here only the questionable characters visible on the specimens of *L. africanus* are mentioned.

The presence of a rhinosphenoid is the single character found in *L. africanus* indicating affinities with the Characidae (Gayet, 1985a). But *L. africanus* does not possess other synapomorphies of Characiformes ([61], [112]) and Characiformes ([71], [113]). Consequently the characters

do not support the placement of *L. africanus* and other clupavids as the sister group to characids. Homology between the rhinosphenoid of characids and the “rhinosphenoid” of clupavids is questionable. The phylogenetic relationships of the clupavids among Ostariophysi may not be elucidated before a general agreement on the numerous discussed characters of *L. characiformis* and *C. maroccanus* is obtained: this is not the topic of this paper.

## 5. Conclusion

At the present time, little palaeontological and sedimentological evidence is available to reconstruct the paleoenvironmental conditions for the deposits of the locality. The composition of the fish assemblage is close to that of the marine locality of Jebel Tselfat. *Lusitanichthys* is known outside Africa in marine Cenomanian deposits of Portugal. This evidence and the very fine sandstone of the matrix probably indicate a shallow marine depositional environment.

Cavin and Dutheil (in press) showed that southeastern Moroccan fish faunas from the early Late Cretaceous are related to South American fish assemblages until the Lower Turonian. Central-Tethysian influences seem to be limited to a short period of time during the beginning of the transgressive phase of the Upper Cenomanian.

Today the Ostariophysi make up almost 75 % of the freshwater fishes of the world. The oldest record of a possible Ostariophysi is from the Upper Tithonian of Bavaria, Germany, with *Tischlingerichthys viohli* (Arratia, 1997). Then several Anatophysi, the sister group of Otophysi, are known in Lower Cretaceous marine deposits of various localities in the world. The clupavids may represent the first radiation of a primitive clade of Otophysi at the base of the Upper Cretaceous in marine environments. This radiation is now restricted to the Cenomanian of the Central Tethys. The fact that it is difficult to observe details of the structure of the first vertebrae and of the caudal skeleton on these small fishes may possibly explain why so few clupavids are now recognized.

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## Version abrégée

De nombreux spécimens de poissons de petite taille ont été découverts dans une localité située à environ 100 km au sud d'Erfoud (Maroc) dans la falaise constituant le soubassement des Kem Kem, près de l'oued Daoura. La faune comprend actuellement 5 taxons différents (un pycnodonte, deux clupéomorphes, un Clupavidae décrit ci-dessous et un *Rhynchoder cetis*), tous proches taxonomiquement des formes découvertes dans la localité du Jebel Tselfat (Cavin et Dutheil, sous presse). Ces deux localités sont datées du Cénomanien supérieur, sur la base de l'étude de l'évolution des ichtyofaunes marocaines au début du Crétacé supérieur (Cavin et Dutheil, sous presse). Les

spécimens sont préservés en négatif, dans une gangue de grès très fin et laminé. Ils sont déposés au musée d'Histoire naturelle de Boulogne-sur-Mer (BHN). Les descriptions et illustrations sont fondées sur des empreintes en silicone des originaux.

La systématique des Clupavidae a été très discutée (Gayet, 1981, 1985a, 1986a, b ; Fink et al. 1984 ; Patterson, 1984 ; Fink et Fink, 1996). Ils sont actuellement généralement considérés comme des Otophysi primitifs (Patterson, 1993). Les Clupeomorpha et les Ostariophysi ont été récemment regroupés dans un taxon monophylétique, sur la base de caractères morpho-

logiques et moléculaires, nommé successivement Otocephala (Johnson et Patterson, 1996) puis Ostarioclupeomorpha (Arratia, 1997), le premier terme ayant la priorité sur le second.

*Lusitanichthys africanus* n. sp. (figure 1) se distingue de *L. characiformis*, du Cénomaniens du Portugal (Gayet, 1981), par le processus antérieur du supramaxillaire postérieur long et fin et par des épines neurales des vertèbres préurales 3 et 2 fines : 18 rayons à la nageoire pectorale, 39 à 41 vertèbres (avec les centra uraux).

Le crâne (figure 2) est proche de ceux de *Lusitanichthys characiformis* et de *Clupavus maroccanus* du Cénomaniens de Jebel Tselfat (Taverne, 1977). Une fontanelle postérieure, formée principalement par les frontaux, et un rhinosphénoïde sont présents. Un éventuel contact entre les pariétaux n'a pas été observé. Les ethmoïdes latéraux sont très développés et dépassent ventralement le parasphénoïde. Les mâchoires sont apparemment édentées et deux supramaxillaires sont présents, le postérieur possédant un processus antérieur long et fin (figure 2B). La mandibule est très élevée et sa symphyse basse. Il y a de 23 à 25 vertèbres abdominales et 16 caudales. Les éléments vertébraux associés aux premières vertèbres abdominales sont modifiés : le second supraneural est bien développé, sub-rectangulaire avec un processus ventral, et le troisième a une extrémité distale en forme de marteau. Le squelette caudal (figure 3) montre des épines neurales des vertèbres préurales 3 et 2 fines, contrairement à celles de *L. characiformis*, qui présentent antérieurement une plaque osseuse sur leur moitié proximale (Gayet, 1981). Le premier centrum ural correspond à la fusion des centra ural 1 et préural 1. Ce centrum composé porte une épine neurale spatulée et est fusionné à la première paire d'uroneuraux. Le premier hypural est en contact, mais non fusionné, avec le centrum, alors que le second hypural est, quant à lui, fusionné. Un second centrum ural libre est présent.

*L. africanus* possède les caractères qui définissent le genre *Lusitanichthys* (Gayet, 1981, 1985a) : les éléments vertébraux des premiers centra sont nettement modifiés, le premier hypural est soit libre, soit en contact avec le premier centrum ural ; trois épuraux sont présents. Ce genre est inclus dans la famille des Clupavidae. Les différences signalées par Taverne (1995) pour distinguer au niveau familial *Lusitanichthys* de *Clupavus maroccanus* n'ont pas été reconnues sur les spécimens de *C. maroccanus* observés (MNHN, Paris) ou ne sont pas suffisantes pour rejeter le regroupement de ces deux genres au sein des Clupavidae. En particulier, le caractère permettant à Taverne de placer *C. maroccanus* en groupe frère des Characiformes + Siluriformes (un grand supraneural antérieur

incliné antérieurement et articulé au bord postérieur du crâne, caractère [62] de Fink et Fink, 1981) n'a pas été observé, alors que des empreintes de traces osseuses pouvant correspondre à un rhinosphénoïde sont présentes sur plusieurs spécimens (DTS 245D, DTS 249, DTS 113, MNHN, Paris).

Les Clupavidae sont considérés comme des Otophysi *incertae sedis*. Les caractères concernés par cette attribution systématique, signalés suivant la numérotation de la révision des Ostariophysi de Fink et Fink (1996), sont des modifications des premières vertèbres constituant un appareil de Weber simple ([60] une expansion ventrale du premier ou des deux supra-neuraux antérieurs formant un joint synchondral avec les arcs neuraux ; [88 ?] la présence probable d'un os suspensorium) et des caractères du squelette caudal. Une des synapomorphies des Otophysi définie par Fink et Fink (1981, 1996), [110] la présence d'un centrum terminal correspondant à la fusion du centrum préural 1, de deux centra uraux et de la paire antérieure d'uroneuraux, représente en réalité trois synapomorphies différentes : [110'] fusion des centra préural 1 et ural 1, [110''] fusion des centra uraux 1 et 2, [110'''] fusion de la paire antérieure d'uroneuraux avec le centrum ural 1. *L. africanus* possède deux de ces synapomorphies ([110'] et [110''']) et son hypural 2 est fusionné au centrum terminal [114]. *L. africanus* possède une synapomorphie des Characidae, la présence d'un rhinosphénoïde (Gayet, 1985a). Cependant, *L. africanus* ne possède pas certaines des synapomorphies de Characiformes ([61], [112]) et de Characiformes ([71], [113]). Le placement de *L. africanus* et des autres clupavides en groupe frère des characidés n'est donc pas justifié. L'homologie entre le rhinosphénoïde des characidés et le « rhinosphénoïde » des clupavides est mise en doute.

Actuellement, peu d'informations sont disponibles sur l'environnement de dépôt de la localité type de *L. africanus*. Les similitudes taxonomiques entre cette faune et celle du Jebel Tselfat (Cavin et Dutheil, sous-pressé), la présence du genre *Lusitanichthys* connu par ailleurs dans le Cénomaniens marin du Portugal et le grès très fin constituant la gangue des fossiles indiquent que le milieu de dépôt était probablement un environnement marin de faible profondeur. Les faunes de poissons du début du Crétacé supérieur du Sud-Est marocain présentent des affinités avec les ichtyofaunes sud-américaines, jusqu'au Turonien inférieur au moins, avec une phase montrant des influences centre-téthysiennes au début de la transgression du Cénomaniens supérieur (Cavin et Dutheil, sous-pressé).

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