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New data on the osteology of *Sorbinichthys elusivo* (Teleostei, Clupeomorpha, Ellimmichthyiformes) from the marine Cenomanian (Upper Cretaceous) of Lebanon and on the phylogenetic relationships of the genus *Sorbinichthys*

Nouvelles données sur l'ostéologie de *Sorbinichthys elusivo* (Teleostei, Clupeomorpha, Ellimmichthyiformes) du Cénomanien marin (Crétacé supérieur) du Liban et sur les relations phylogénétiques du genre *Sorbinichthys*

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Résumé : L'ostéologie de *Sorbinichthys elusivo*, un poisson clupéomorphe du Cénomanien marin (Crétacé supérieur) du Liban, est réétudiée de façon approfondie. Des commentaires sont faits à propos de la position systématique de *Sorbinichthys* au sein de l'ordre des Ellimmichthyiformes. Ce genre occupe une position intermédiaire entre deux taxons primitifs, *Ornategumum* et les Scutatuspinosidae, d'une part, et les autres membres de l'ordre, d'autre part. *Sorbinichthys* parait proche de *Diplomystus*. Les deux genres présentent des épines sur le bord postérieur des écussons dorsaux, un caractères absent chez les autres Ellimmichthyiformes.

Mots-clés: Teleostei, Clupeomorpha, Ellimmichthyformes, *Sorbinichthys elusivo*, ostéologie, relations, Crétacé supérieur marin, Liban.

Abstract : The osteology of *Sorbinichthys elusivo*, a clupeomorph fish from the marine Cenomanian (Upper Cretaceous) of Lebanon, is re-studied in a detailed way. Comments are given on the systematic position of *Sorbinichthys* within the order Elmmichthyiformes. This genus occupies an intermediate position between two primitive taxa, *Ornategulum* and the Scutatuspinosidae, on the one hand, and the other members of the order, on the other hand. *Sorbinichthys* seems close to *Diplomystus*. The two genera exhibit spines on the posterior margin of their dorsal scutes, a character not present in the other Ellimmichthyiformes.

Key words: Teleostei, Clupeomorpha, Ellimmichthyiformes, *Sorbinichthys elusivo*, osteology, relationships, marine Upper Cretaceous, Lebanon.

INTRODUCTION

The genus *Sorbinichthys* BANNIKOV & BACCHIA, 2000, the species *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000 and the family Sorbinichthyidae were erected for a small teleost known at that time by three specimens from the marine Cenomanian (Upper Cretaceous) of Ein Nammoura, Lebanon (BANNIKOV & BACCHIA, 2000). The original scribers left this fossil fish incertae ordinis within the superorder Clupeomorpha. Later it was included in the primitive order Ellimichthyiformes (FOREY *et al.*, 2003).

A second species, *Sorbinichthys africanus* MURRAY & WILSON, 2011, was described a few years later from the marine Cenomanian-Turonian of Morocco and added to the genus (MURRAY & WILSON, 2011).

Until now, the skull of *Sorbinichthys* was poorly known (BANNIKOV & BACCHIA, 2000: fig. 4; MURRAY & WILSON, 2011: fig. 5). A more careful preparation of the holotype of *Sorbinichthys elusivo* allows today a much more detailed description of the skull of *Sorbinichthys* than those previously given.
The aim of the present paper is thus to re-describe the skeleton of *Sorbinichthys elusivo* and to re-discuss the phylogenetic position of the genus within Ellimmichthyiformes

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MATERIAL AND METHODS

The specimen hereafter described belongs to the CAPASSO paleontological collection (CLC) in Chieti (Italy). The material was studied with a stereomicroscope Leica Wild M 8. The figures were drawn by the first author (L. T.) and the photos made by M. Luciano LULLO, from the University of Chieti-Pescara. Aspersions with ethanol were used to improve some observations.

The CAPASSO collection is legally registered by a decree of the Ministero per I Beni e le Attività Culturali under the date of October 11th 1999, following the disposition of the Italian law 1089/39. The specimens of this collection were also subject to prescription in order of conservation and availability to the studies on the basis of the article 30 of the Italian law N° 42/2004. The Soprintendenza per I Beni Archeologici dell'Abruzzo-Chieti has authorized the two authors to study this collection by two letters bearing the dates of May 5th, 2011 (ref.: MBAC-SBA-ABR PROT 0004537 05/05/ 2011 Cl. 34.25.01/2.1) and July 30th, 2014 (ref.: MBAC-SBA-ABR PROT 0005618 31/07/2014 Cl. 34.25.01/2.1).

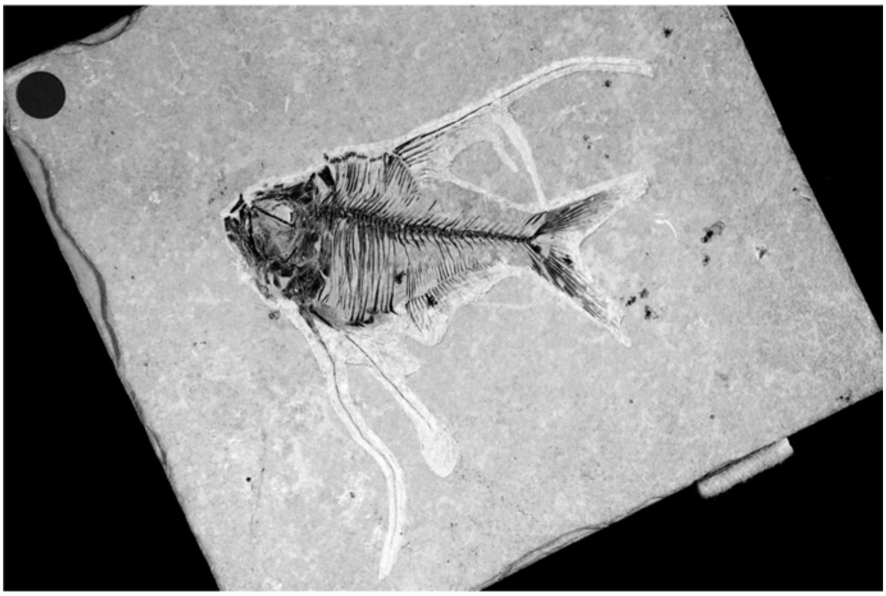

Figure 1: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Holotype CLC S-431a. Complete specimen with the elongate dorsal and pectoral rays. Total length: 72 mm.

Institutional abbreviations

AMNH = American Museum of Natural History
IRSNB = Royal Institute of Natural Sciences of Belgium
MZULB = Zoological Museum of the Free University of Brussels

List of abbreviations used in the text-figures

APAL = autopalatine
ASPH = autosphenotic
BO = basioccipital
BRSTG = branchiostegal ray
BSPH = basisphenoid
CLT = cleithrum
DN = dentary
DETH = dermethmoid (= rostral)
ECPT = ectopterygoid
ENPT = entopterygoid
EP1-3 = epurals 1 to 3
EPI = epiotic (= epioccipital)
ETH = endochondral part of the mesethmoid
FR = frontal

HCLT = hypercleithrum (= supracleithrum)
HEMEP = haemal spine
HYOM = hyomandibula
LEP = lepidotrichium (= ray)
LETH = lateral ethmoid
MPT = metapterygoid
MX = maxilla
NA = nasal
NEUREP = neural spine
N PU1 = neural arch of the first preural vertebra
NP PU1 = neural spine of the first preural vertebra
OP = opercle
OSPH = orbitosphenoid
PA = parietal
PELV = pelvic bone
PHY = parhypural
PMX = premaxilla
POP = preopercle
PS = parasphenoid
PSPH = pleurosphenoid (= pterosphenoid)
PT = posttemporal
PTE = pterotic
PU1-4 = preural vertebrae 1 to 4
QU = quadrate
RAD = pterygiophores (= radials)
RART = retroarticular
RI = rib
SCL = sclerotic bone
SCU = scutes (dorsal, ventral and caudal)
SCU pr. = ventral processes attached to the last dorsal scutes
SMX 1, 2 = supramaxilla (anterior, posterior)
SN 1-10 = supraneurals 1 to 10
SOC = supraoccipital
SOP = subopercle
SORB = supraorbital
ST = supratemporal (= extrascapular, scalebone)
SY = symplectic
U1, 2 = ural vertebrae 1 and 2
UR1-3 = uroneurals 1 to 3
V1-3 = first three vertebrae
VO = vomer
br. = broken
pr. f. = pre-epiotic fossa
t. f. = temporal (= posttemporal) fossa

SYSTEMATIC PALEONTOLOGY

Division Teleostei MÜLLER, 1846
Cohort Clupeocephale PATTERSON & ROSEN, 1977
Superorder Clupeomorpha GREENWOOD *et al.*, 1966
Order Ellimmichthyiformes GRANDE, 1982
Family Sorbinichthyidae BANNIKOV & BACCHIA, 2000
Genus *Sorbinichthys* BANNIKOV & BACCHIA, 2000

Emended diagnosis

Small ellimmichthyiform fish with a maximum total length of 15 cm. Frontal weakly ornamented. Parietal small. Skull medioparietal. Jaws toothed with minute teeth. Posttemporal large, boomerang-like, with a broad upper margin on the dorsal branch. Cleithrum “L”-shaped. Pectoral fin inserted low on the flank. Second pectoral ray and second dorsal ray elongated. Pelvic girdle reduced, with short ventral fins. Five or six hypurals. HY2 articulated to U1 and U2 and not fused to U1. An extremely enlarged “U”-shaped diastema between HY2 and HY3. Epurals reduced or absent. Anterior dorsal and ventral procurrent caudal rays elongated, needle-shaped and deeply inserted between the last neural and haemal spines. No caudal scutes. Dorsal ridge scutes series complete between the head and the dorsal fin. 25 to 30 dorsal scutes, with lateral wings and some of them with spines on the posterior margin. 12 to 14 ventral scutes, with 3 postpelvic.

Species *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000

Emended diagnosis

Sorbinichthys with an enlarged orbitosphenoid reaching anteriorly the lateral ethmoid and ventrally the parasphenoid. Supraoccipital small, with an acuminate and upwardly directed crest. A small preepiotic fossa located between the parietal, the epiotic and the supraoccipital. Basipterygoid process of the parasphenoid absent. Lower jaw articulated with the quadrate at the level of the middle of the orbit. Two supramaxillae present. Second pectoral ray and second dorsal ray extremely elongated. 17-18 abdominal vertebrae. 22-23 caudal vertebrae., including the two ural ones 10 supraneurals. 15-16 ribs. Dorsal fin with 14-15 rays and 13-14 pterygiophores. Anal fin with 28-31 rays and 26-29 pterygiophores. First uroneural extending anteriorly on PU2. 6 hypurals present. 3 extremely reduced epurals present. 25 dorsal scutes. 14 ventral scutes, 11 pre- and 3 postpelvic.

Holotype

Sample CLC 431a, b. Part (a) and acid prepared counterpart (b) of a complete specimen (Figs 1-3). Total length: 72 cm. Standard length: 61 mm.

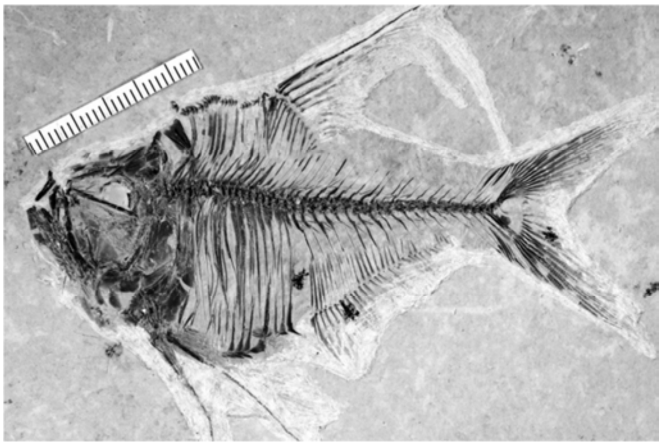

Figure 2: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Holotype CLC S-431a.

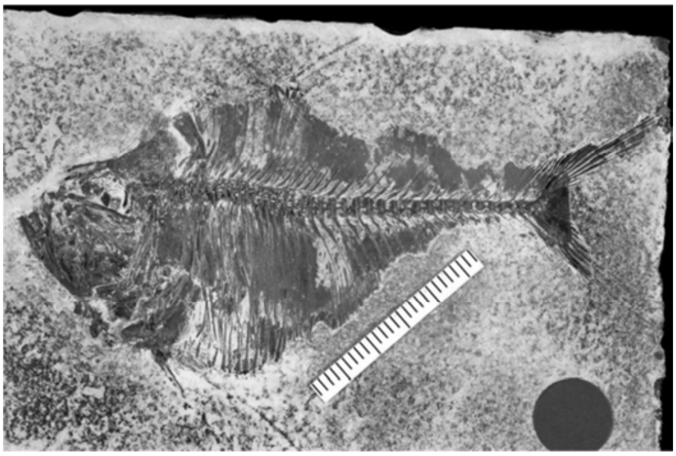

Figure 3: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Holotype CLC S-431b (acid prepared counterpart).

General morphology and morphometric data (Figs 1-3)

The body is moderately deep and laterally compressed. The dorsal profile rises from the head to the dorsal fin and then slopes down to the tail, forming a well marked angle at the origin of the dorsal fin. The following morphometric data are given in percentage (%) of the standard length (61 mm) of the holotype.

Length of the head (opercle included)	32.0 %
Depth of the head (in the occipital region)	39.4 %
Maximum depth of the body	58.1 %
Length of the second pectoral ray	84.8 %
Prepelvic length	52.7 %
Predorsal length	54.2 %
Basal length of the dorsal fin	16.7 %
Length of the second dorsal ray	85.6 %
Preanal length	61.2 %
Basal length of the anal fin	34.5 %
Depth of the caudal peduncle	13.3 %

Osteology

The skull (Figs 4-6)

The frontal profile is obliquely oriented and slightly concave, because of the shape of the supraoccipital.

The mesethmoid forms the anterior extremity of the braincase and is composed by two associated elements, a thin dermic bony layer, the dermethmoid (= rostral), forming the upper area (visible on side a) and a small ossified endochondral part (present on sides a, b). The lateral ethmoid is well developed. There is a short tubular nasal (visible on side a, displaced above the frontal).

The frontal forms the major part of the skull roof. The bone is narrow anteriorly but it broadens posteriorly. This posterior area of the frontal is ornamented with a few ridges and a series of thin minute denticles. The posterior margin of the frontal slightly overhangs the parietal in the mid-line of the skull roof. The parietal and the epiotic (= epioccipital) are small bones. The skull is medioparietal and not lateroparietal as written by BANNIKOV & BACCHIA (2000: 5). The large pterotic is deeper than broad. The small supraocciptal bears a well marked acuminate and upwardly directed crest. A large foramen for the glossopharyngeal (IX) and the vagus (X) nerves is opened in the lower area of the exoccipital. The basioccipital is massive and rounded.

A small pre-epiotic fossa is opened between the parietal, the epiotic and the supraoccipital. The temporal (= posttemporal) fossa is located on the rear of the braincase. Anteriorly, the fossa is bordered by the pterotic, the exoccipital and the epiotic, dorsally by the epiotic and the supraoccipital and ventrally by the exoccipital. A small supratemporal (= extrascapular, scalebone) covers the fossa.

The orbitosphenoid is a large bone. It reaches the lateral ethmoid anteriorly, the frontal dorsally and the parasphenoid ventrally. The pleurosphenoid is smaller and remains placed against the frontal. A well developed basisphenoid is present. The parasphenoid is long, narrow and toothless. The foramen for the internal carotid artery is visible. There is no basipterygoid process on the parasphenoid in *S. elusivo* but a basipterygoid process is present in *S. africanus* (MURRAY & WILSON, 2011: 5).

The autopalatine is a small bulky bone. There is no dermopalatine. The entopterygoid bears a few minute teeth near its upper margin. The posterior region of the bone overhangs the wide metapterygoid and reaches the anterior border of the preopercle. The ectopterygoid is toothless. The quadrate is triangular in shape, with a well marked articular condyle for the lower jaw and a well developed quadratic process

The antorbital, the infraorbital series and the dermosphenotic are not preserved. Only fragments of the bony sclerotic ring are present.

The oral border of the premaxilla, the maxilla and the dentary bears minute conical teeth. A small symphyseal ascending process is present on the prémaxilla. The maxilla is elongated, rather narrow and slightly arched. There are two well developed supramaxillae. The articulation between the lower jaw and the quadrate is located at the level of the middle of the orbit. A small retroarticular is present.

The dorsal branch of the preopercle is long and narrow. The ventral branch is much shorter but broader. The preopercular sensory canal is well marked. Four short secondary tubules are visible at the angle of the two branches. The opercle is a large bone deeper than broad. It bears numerous radiating ridges and a small notch in the middle of its upper margin. The subopercle is small, more or less triangular in shape and it exhibits a small anterior dorsal pointed process. The outer surface of the bone is ornamented by a few radiating ridges. The interopercle is not visible. At least five branchiostegal rays are present under the preopercle. The two last rays are broader than the preceding ones.

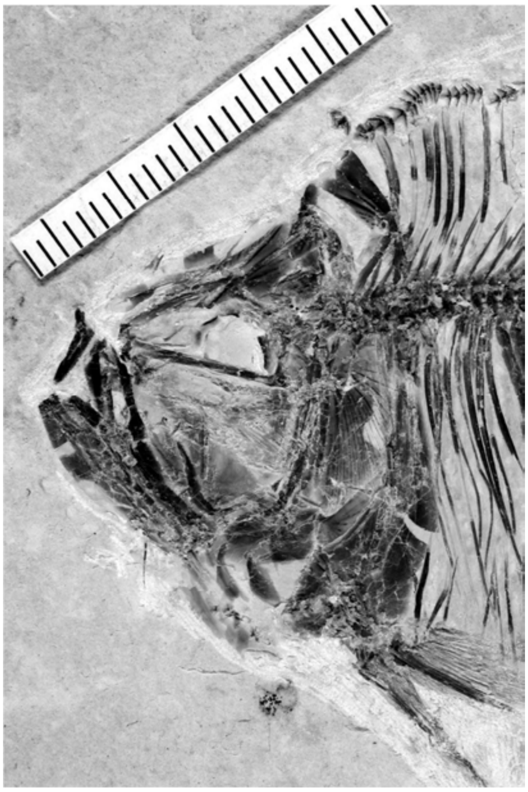

Figure 4: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Head region of holotype CLC S-431a.

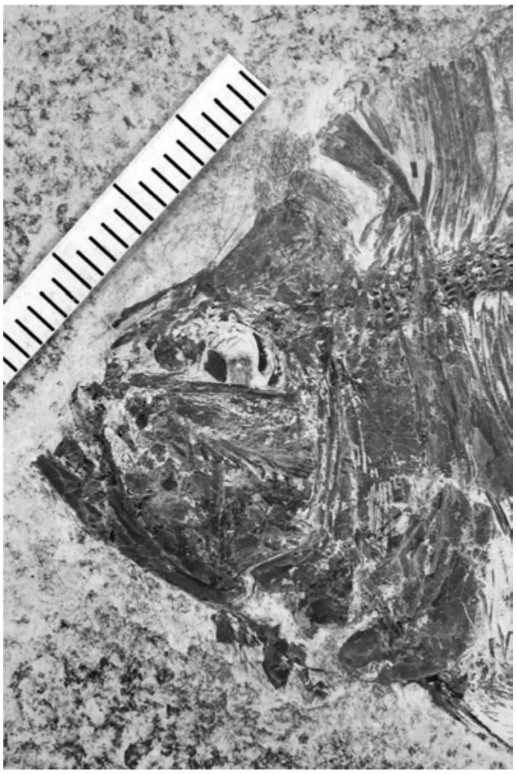

Figure 5: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Head region of holotype CLC S-431b.

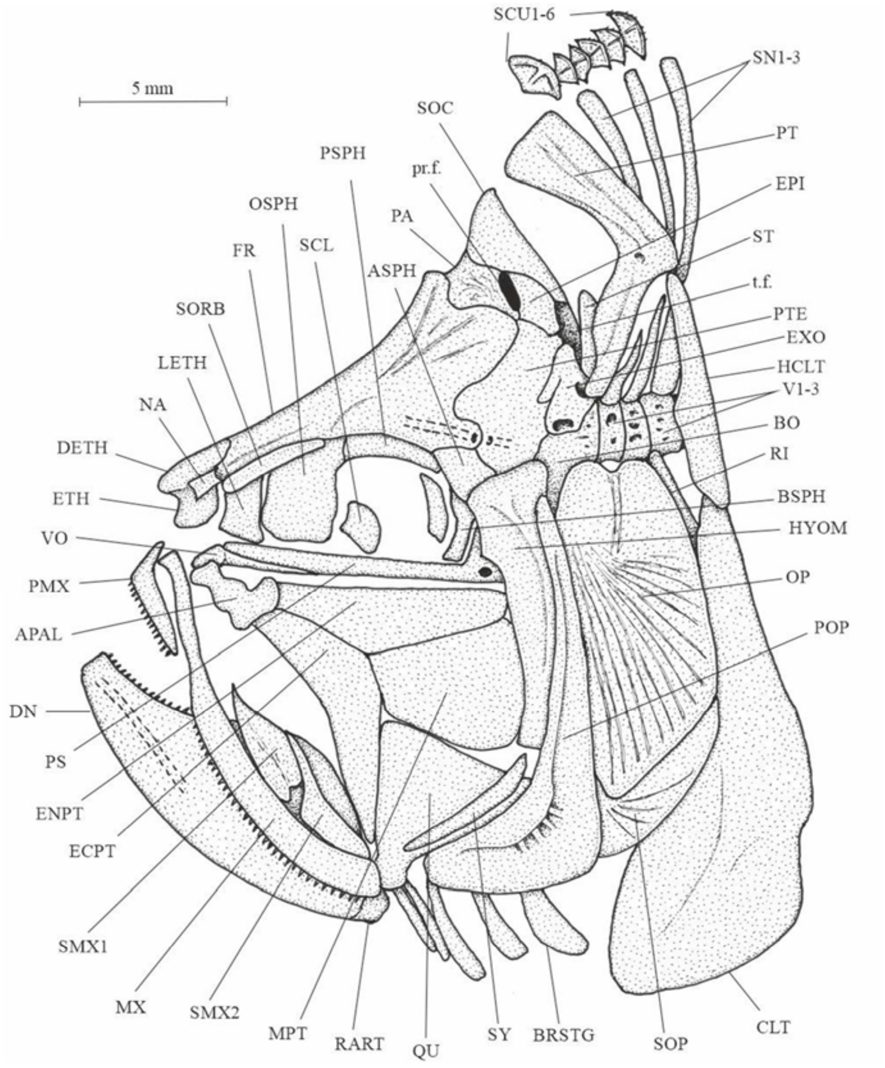

Figure 6: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Reconstruction of the skull and the pectoral girdle based on the two sides (a, b) of holotype CLC S-431.

The hyoid and branchial skeleton (Figs 4-6)

The hyomandibula is a small but deep bone, with a single articular head and a weakly developed anterior wing. The symplectic is wedged between the body of the quadrate and the quadratic process. The hyoid bar is not clearly visible in any specimen of *S. elusivo* and the presence of a beryciform foramen is thus uncertain. However, in *S. africanus*, the anterior ceratohyal is pierced by a small beryciform foramen (MURRAY & WILSON, 2011: fig. 5).

The girdles (Figs 4-6)

The posttemporal is a large boomerang-like bone. Its long dorsal branch has a broad upper margin. Its ventral branch is a little shorter than the dorsal one. The hypercleithrum (= supracleithrum) is narrow and rather short. The cleithrum is strongly developed, "L"-shaped, with a narrow dorsal branch and an enlarged and obliquely oriented ventral branch that hides the hypercoracoid (= scapula) and the hypocoracoid. There are three vertically elongated postcleithra, well visible on side b of the holotype. The pectoral fins are inserted low on the flank, near the ventral border of the body. The exact number of pectoral rays is uncertain but seems close to 12. The first ray is short, unsegmented and acuminate. The second ray is segmented, unbranched and extremely elongated. The other rays are shorter, segmented and branched.

The pelvic girdle is small. The pelvic bones are drop-like. The ventral fins are short. They are incomplete in the holotype. BANNIKOV & BACCHIA (2000: 9) mention about 7 rays.

The axial skeleton (Figs 1-3, 6)

The axial skeleton of the holotype contains 40 vertebrae, 18 abdominal and 22 caudal, including the two ural centra. BANNIKOV & BACCHIA (2000: 5) mention 39 to 41 vertebrae, with 17 to 18 abdominal. The abdominal centra bear three or four longitudinal crests on their lateral faces and they are a little shorter than the caudal centra that exhibit only one longitudinal crest on the lateral face. The first neural spines of the abdominal region are double. The other neural spines are medially fused. The last abdominal vertebrae bear small haemapophyses (= parapophyses) but the first ones are devoid of these haemal structures. The last haemapophysis is longer than the preceding ones. The haemal spines of the caudal region are well developed.

There are 10 supraneurals between the head and the dorsal fin. They are long, and narrow. They reach dorsally the level of the dorsal scutes and ventrally the neural spines. The tenth supraneural is a little shorter The lower region of all these bones is slightly inclined anteriorly.

The holotype has 16 pairs of ribs, the first one being inserted on the third vertebra. BANNIKOV & BACCHIA (2000: 7) mention 15 or 16 pairs of ribs. They are elongated, except the last one that is strongly reduced. The posterior ribs exhibit anterior wing-like extensions in the upper region. The first ribs are articulated in pits of the centra but the last ones are inserted on the haemapohyses.

There are epineurals all along the vertebral axis, except at the level of the last caudal centra. The first epineurals are fused to the corresponding neural arches. The others are free. The epipleurals are restricted to the caudal region but they do not extend till the last caudal vertebrae. Most of these intermuscular bones are forked. There are at least a few epicentrals.

The dorsal and anal fins (Figs 1-3)

The dorsal fin of the holotype contains 14 rays supported by 14 pterygiophores. The first ray is short, unsegmented and acuminate. The second ray is extremely elongated, segmented but not branched. The other rays are segmented and branched. The third to the sixth rays are also long. The first pterygiophore is divided in two long ventral branches.

The anal fin of the holotype contains 30 rays supported by 29 pterygiophores. The first two rays are short, unsegmented and acuminate. They are linked to the first pterygiophore. The third ray is segmented but not branched. The other rays are segmented and branched. The specimens of *S. elusive* described by BANNIKOV & BACCHIA (2000: figs 1a, b, 2, 3, 4) and those of *S. africanus* studied by MURRAY & WILSON (2011: figs 1, 2A, B,, 3) have a short third anal ray. However, ZARAGÜETA BAGILS (2004: fig. 1) figures a specimen of *S. elusivo* with a very elongated third anal ray.

BANNIKOV & BACCHIA (2000: 9) mention 14-15 rays and 13-14 pterygiophores for the dorsal fin and 28-31 rays and 26-29 pterygiophores for the anal fin in *S. elusivo*.

The caudal skeleton (Figs 7-9)

The last caudal vertebrae progressively decrease in size. The first preural vertebra (PU1), the first and the second ural vertebrae (U1, U2) are not fused together. U1 is not reduced. The last neural and haemal spines are narrow and fused to their corresponding centra. The haemal spines associated to the third and the second preural vertebrae (PU3, PU2) are elongated. PU2 bears the last complete neural spine. There is only a small neural arch (N PU1) on PU1. In *S. africanus*, there is a short thin neural spine on PU1 (MURRAY & WILSON, 2011: fig. 6). No neural arch is associated to U1. The long and narrow parhypural is fused to PU1. There are three short and extremely thin epurals (EP1, 2, 3). The epurals are missing in *S. africanus* (ibid., 2011: fig. 6). There are 6 hypurals (HY1 to 6). It is possible but not certain that *S. africanus* has only five hypurals (ibid., 2011: fig. 6). HY1 is markedly enlarged in its posterior area. HY2 is more narrow. HY3 is moderately broadened. HY3, 5 and 6 are short and narrow. The articular heads of HY1 and HY2 are well developed. HY1 is articulated with U1, while HY2 is articulated with both U1 and U2. HY3 is articulated with U2. HY4, 5 and 6 are located behind the last centrum. There is a extremely wide “U” shaped diastema between HY2 and HY3. There are three autogenous uroneurals (UR1, 2, 3). The anterior extremity of the long UR1 reaches PU2. UR2 begins just after U2 and its distal tip is located at little beyond the distal extremity of UR1. UR3 is short.

The caudal fin is forked and contains 19 principal rays, 9 upper and 8 lower procurrent rays. The most anterior procurrent rays each lobe are elongated, well separated the ones from the others and deeply imbricated between the last neural and haemal spines.

Figure 7: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Caudal region of holotype CLC S-431b.

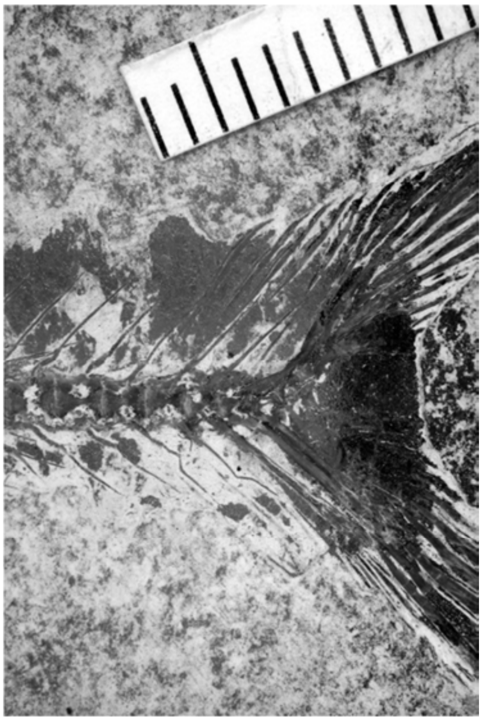

Figure 8: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Caudal region of holotype CLC S-431a.

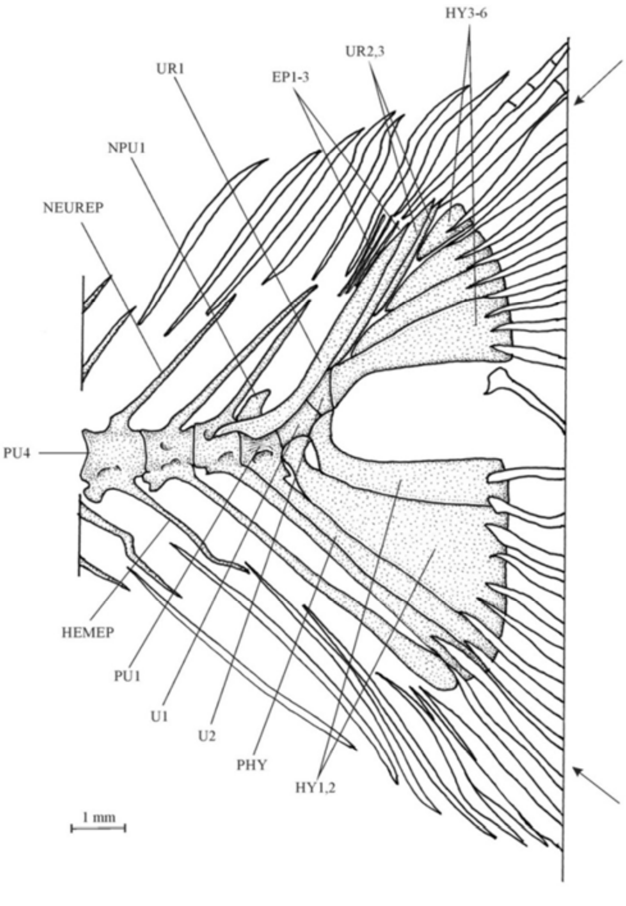

Figure 9: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Reconstruction of the caudal skeleton based on the two sides (a, b) of holotype CLC S-431. The arrows point on the most external principal caudal rays in both lobes.

The squamation (Figs 10-13)

The squamation is badly preserved. Traces of large cycloid scales are visible but not the lateral line.

There are 25 dorsal scutes. They are of different shape and size but most of them are subrhomboidal with small spines on their posterior margin. Long ventral processes are fused to the last scutes. These processes differ from the supraneurals. The last process is forked and its branches are entangled with the first dorsal pterygiophores. BANNIKOV & BACCHIA (2000) do not mention this character but MURRAY & WILSON (2011: 7) describe the same structure in *S. africanus*.

The ventral keel contains 14 scutes, 11 pre- and 3 postpelvic. They have long and narrow ascending wings and a strongly marked median posterior point at their basis.

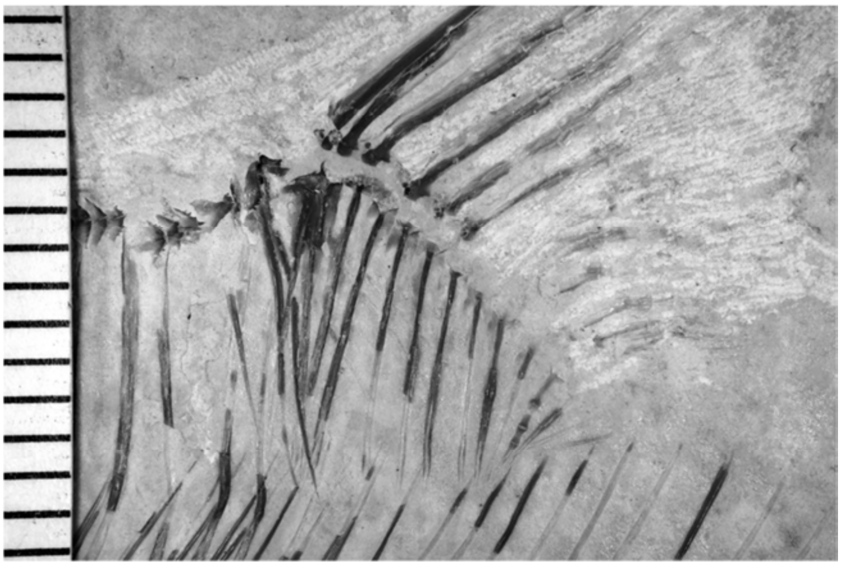

Figure 10: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Last dorsal scutes and first dorsal pterygiophores of holotype CLC S-431a.

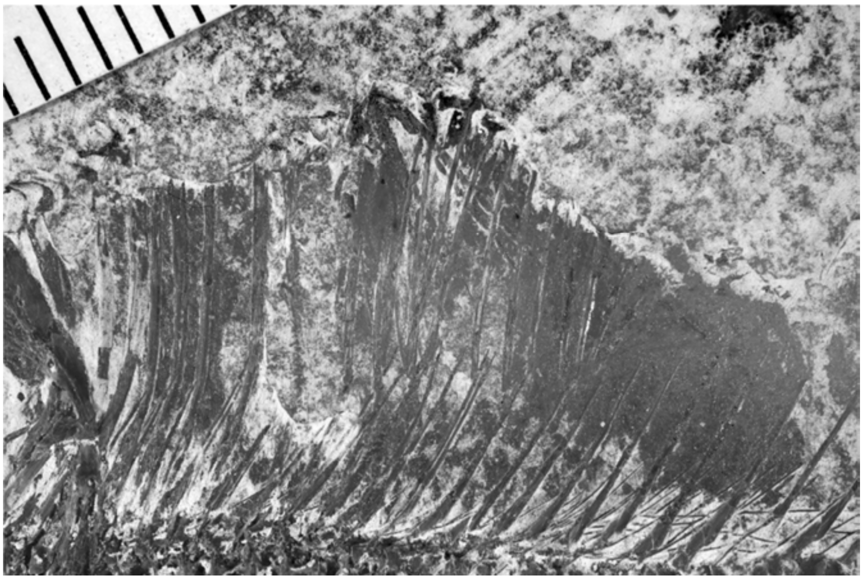

Figure 11: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Last dorsal scutes and first dorsal pterygiophores of holotype CLC S-431b.

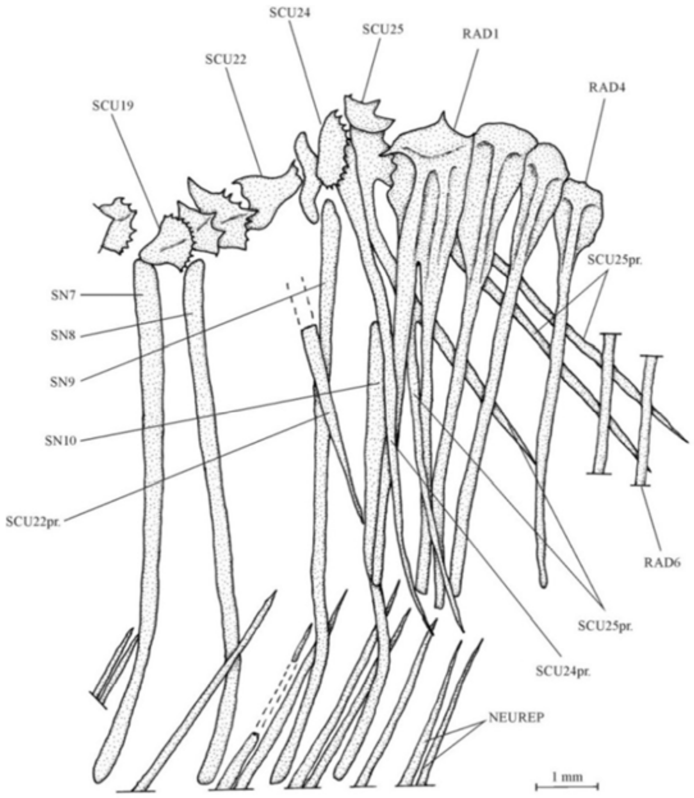

Figure 12: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Reconstruction of the last dorsal scutes and the first dorsal pterygiophores based on the two sides (a, b) of holotype CLC S-431.

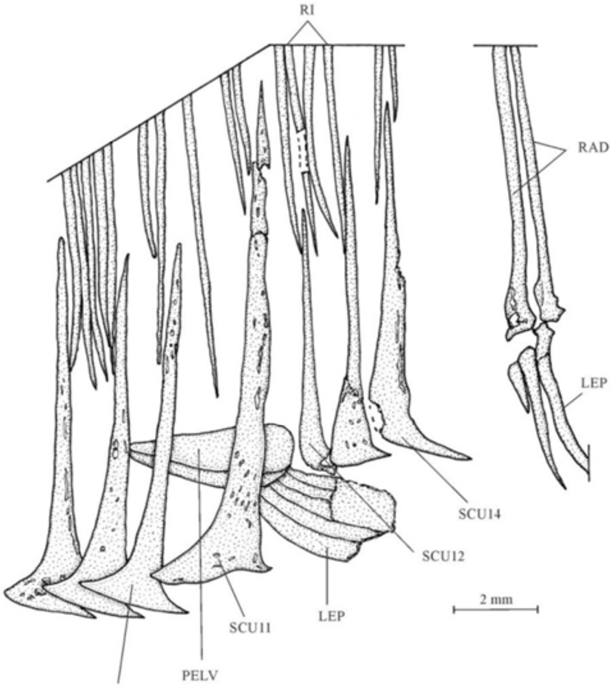

Figure 13: *Sorbinichthys elusivo* BANNIKOV & BACCHIA, 2000. Last ventral scutes and pelvic girdle of holotype CLC S-431a.

DISCUSSION

Sorbinichthys within Ckupeomorpha

The family Ellimmichthyidae and the order Ellimmichthyiformes were erected by GRANDE (1982) to contain two genera of primitive Clupeomorpha, *Diplomystus* COPE, 1877 and *Ellimmichthys* JORDAN & GILBERT, 1919, and were based on only one apomorphy, the dorsal scutes bearing lateral expanded wings. Later, many other genera were added to this order and the genus *Sorbinichthys* was one of them.

The skull of *Sorbinichthys* has preserved a series of primitive characters present in Ellimmichthyiformes but already lost in Clupeiformes. The skull is medioparietal. The temporal fossa is located on the rear of the braincase. The *recessus lateralis* is not yet present. A small beryciform foramen is present on the anterior ceratohyal. The caudal skeleton of *Sorbinichthys* is also rather primitive. UR1 is autogenous. U1 is well developed. HY1 contacts U1. Within Clupeomorpha, such a caudal morphology is only known in Ellimmichthyiformes and in Denticipitoidei (GREENWOOD, 1968: fig. 20) but differs from the more evolved caudal skeleton of Clupeoidei. *Sorbinichthys* also exhibits dorsal scutes that have expanded lateral wings, another feature characterizing Ellimmichthyformes. Undoubtedly, *Sorbinichthys* belongs to this last order and not to the Clupeiformes.

Sorbinichthys within Ellimmichthyiformes

The phylogeny within Ellimmichthyiformes was studied by numerous authors during the last four decades (GRANDE, 1982; TAVERNE, 1997; CHANG & MAISEY, 2003; ZARAGÜETA BAGILS, 2004; ALVARADO-ORTEGA *et al.*, 2008; MURRAY & WILSON, 2013; VERNYGORA *et al.*, 2016; VERNYGORA & MURRAY, 2016, 2021; MURRAY *et al.*, 2016; MARRAMA, & CARNEVALE, 2017; BOUKHALFA *et al.*, 2018; MARRAMA *et al.*, 2019).

It is clear that *Sorbinichthys* occupies a very peculiar place within Ellimmichthyiformes. Indeed the genus exhibits a series of apomorphic characters not present in any other member of the order, for instance its hypertrophied and boomerang-shaped posttemporal, the extreme atrophy or the disappearance of the three epurals, the wide "U"-shaped diastema between HY2 and HY3, HY2 not fused to U1, the size and the disposition of the procurrent caudal rays and its last dorsal scutes bearing long acuminate processes that overlap the first dorsal pterygiophores.

However, the systematic position proposed for *Sorbinichthys* in these phylogenetic hypotheses greatly varies from the one to the other. Some authors consider *Sorbinichthys* as the most primitive lineage within the order, while others place the genus in more advanced and variable positions. The problem deserves thus some new comments.

Most specialists consider the genus *Ornategulum* FOREY, 1973, a fossil fish from the marine Cenomanian of Lebanon, as the primitive sister-taxon of all the Clupeomorpha or, at least, the one of all the Ellimmichthyiformes. The body is elongated. The skull is rather primitive (FOREY, 1973, figs 1-5) but not especially representative of the clupeomorph cranial architecture. The posterior part of the frontal, the parietal and the pterotic are slightly ornamented. The two parietals meet on the mid-line. The supratemporal covers a pit located on the rear of the braincase and bordered by the pterotic laterally, the epiotic internally and the intercalary ventrally (ibid., 1973: fig. 2). FOREY considers this pit as a rudimentary pre-epiotic fossa (ibid., 1973: 1306). Nevertheless, this pit seems better correspond to a classical temporal (= posttemporal) fossa of a primitive teleost than to the tiny pre-epiotic fossa of a clupeomorph fish. The supraneurals are ranged in a parallel direction (pers. obs., not described by FOREY). There are neither dorsal nor ventral scutes (ibid., 1973, fig. 8). The caudal skeleton has the typical ellimmichthyiform morphology (Fig. 14; ibid. 1973, fig. 7) but is not really primitive for this order. Indeed, U1 is already strongly reduced and HY1 has a small articular head slightly disjoined from U1. However, the short NP PU1 frequently is divided in two parts, a possible indication that a neural arch on U1 is preserved and fused to NP PU1 (Fig. 14; ibid., 1973: fig. 7C). Some specimens have still seven hypurals (ibid., 1973: fig. 7A), while others have only six ones (Fig. 14). HY3 is moderately enlarged. UR1 bears a wing-like anterior expansion.

The family Scutatuspinosidae *sensu* VERNYGORA *et al.* (2016) contains three genera of primitive clupeomorph fishes with a torpedo-like body and supraneurals arranged in a parallel way, *Scutatuspinosus* DA SILVA SANTOS and SILVA CORRÉA, 1985 from the Hauterivian-Barremoian of Brazil, *Ranulfoichthys* ALVARADO-ORTEGA, 2014 from the Albian of Mexico and *Foreyclupea* VERNYGORA *et al.*, 2016 from the Albian of Canada. *Scutatuspinosus* exhibits well developed dorsal and ventral scutes; the ventral elements have weakly marked ascending wings (DE FIGUEIREDO & RIBEIRO, 2017: figs 1b, 11b, c). *Ranulfoichthys* has thickened scales in place of true scutes on the dorsal border between the head and the dorsal fin and a complete series of ventral scutes that also have very short ascending wings (ALVARADO-ORTEGA (2014: figs 2A, B, C, 6A, B, 11). *Foreyclupea* is known by only one incomplete specimen. The presence of dorsal scutes is uncertain, the dorsal margin between the skull and the dorsal fin being missing, but there is a complete series of ventral scutes that bear well developed ascending wings as in the more evolved Ellimmichthyiformes (VERNYGORA *et al.*, 2016: fig1A, B, 2). VERNYGORA *et al.* (2016: fig 4) and VERNYGORA & MURRAY (2021: fig. 8) consider the three fishes as the direct apomorphic group after *Ornategulum* within Ellimmichthyiformes. We completely agree with this phylogenetic interpretation.

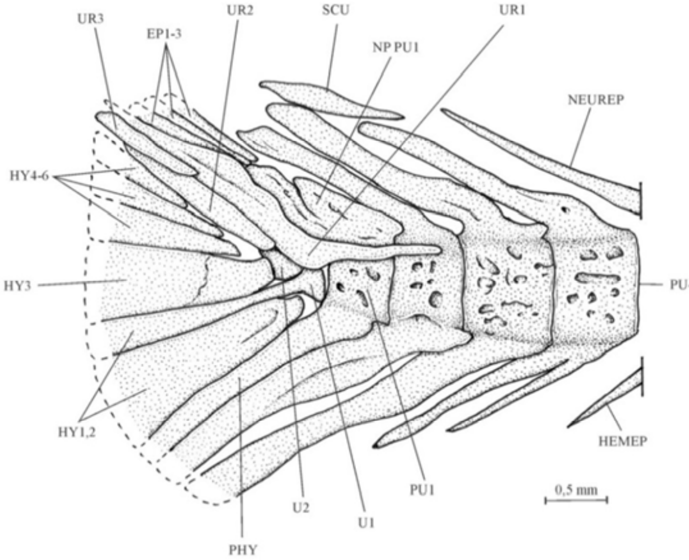

Figure 14: *Ornategulum sardinoides* (PICTET, 1850). Caudal skeleton of specimen IRSNB P 10296 (Cenomanian, Haqel, Lebanon). The specimen exhibits the unusual condition of having two haemal spines on PU4. The short NP PU1 has a double structure, a feature already observed by FOREY (1973: 1313, fig. 7C) in some specimens.

In *Sorbinichthys* and the other Ellimmichthyiformes, the body becomes deeper and is no more torpedo-like. When the skull is well preserved in fishes of this large group, a true preepiotic fossa is visible, generally located between the epiotic, the supraoccipital and the parietal, and the temporal (= posttemporal) fossa is still positioned on the rear of the braincase, between the pterotic, the epiotic and the exoccipital (Fig. 6; PATTERSON, 1967: fig. 7; FOREY *et al.*, 2003: figs 40, 41; FOREY, 2004: figs 3-6; among others).

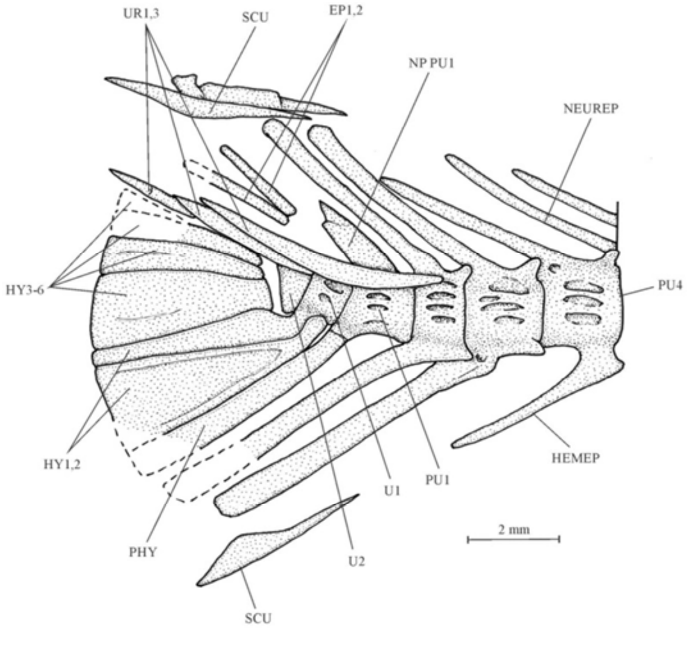

Figure 15: *Ellimma branneri* (JORDAN, 1910). Caudal skeleton of specimen AMNH 10048 (Aptian, Muribeca Formation, Sergipe Basin, Brazil).

Sorbinichthys and a few other genera, such as *Ellimma* JORDAN, 1913, have preserved the primitive condition of having HY3 moderately broadened as in *Ornategulum* (Fig. 15; CHANG & MAISEY, 2003: fig. 8A, B; CHANG & GRANDE, 1997: fig. 8A, B; FOREY *et al.*, 2003: fig. 44; ALVARADO-ORTEGA & OVALLES-DAMIAN (2008: fig. 5A, B; DE FIGUEIREDO, 2009: fig. 10). Most Ellimmichthyiformes, including *Armigatus* GRANDE, 1982 and *Diplomystus* COPE, 1877 (Figs 16, 17), shared the apomorphic character of having HY3 markedly enlarged.

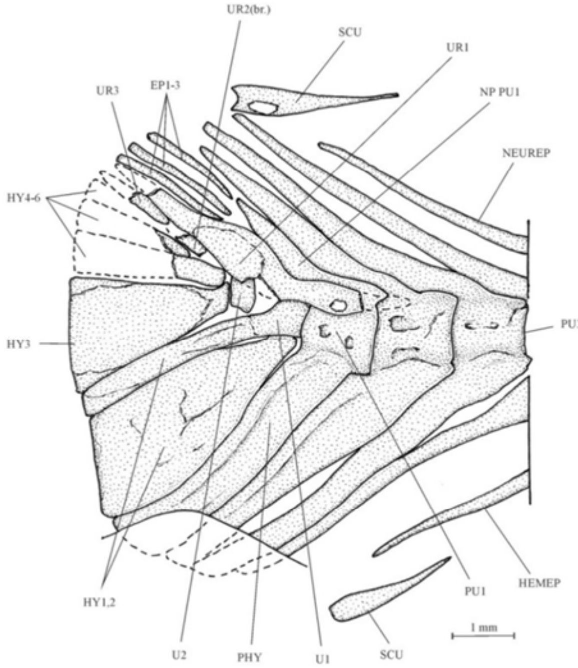

Figure 16: *Armigatus brevissimus* (DE BLAINVILLE, 1818). Caudal skeleton of specimen IRSNB P 10297 (Cenomanian, Haqel, Lebanon).

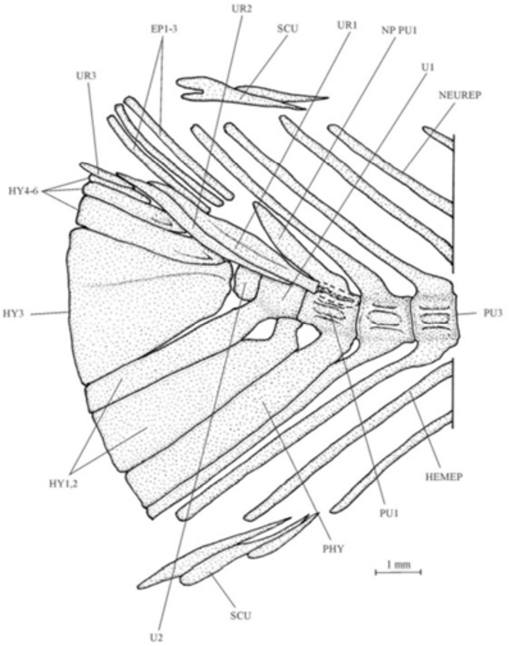

Figure 17: *Diplomystus dentatus* COPE, 1877. Caudal skeleton of specimen MZULB N° 4 (Eocene, Green River Shales, Wyoming, U.S.A.).

Sorbinichthys has a "L"-shaped cleithrum, the primitive condition found in *Ornategulum* (FOREY, 1973: fig. 6), *Ranulfoichthys* (ALVARADO-ORTEGA2014: fig. 4) and *Foreyclupea* (VERNYGORA *et al.*, 2016: figs 1B, 3B). The other Ellimmichthyiformes exhibit a "S"-shaped cleithrum, a more evolved morphology.

Ornategulum and the Scutatuspinosidae have the supraneural oriented in a parallel direction. On the contrary, most Ellimmichthyiformes exhibit a peculiar and specialized condition of their supraneurals. They are slightly curved, with a broadened upper region, and their ventral extremities point more or less in the same direction, giving a fan-like morphology to the supraneural series. (Fig. 18). In *Sorbinichthys*, The spraneural are elongated, narrow, more or less parallel, with their ventral region anteriorly curved and inserted between the neural spines, an intermediary condition.

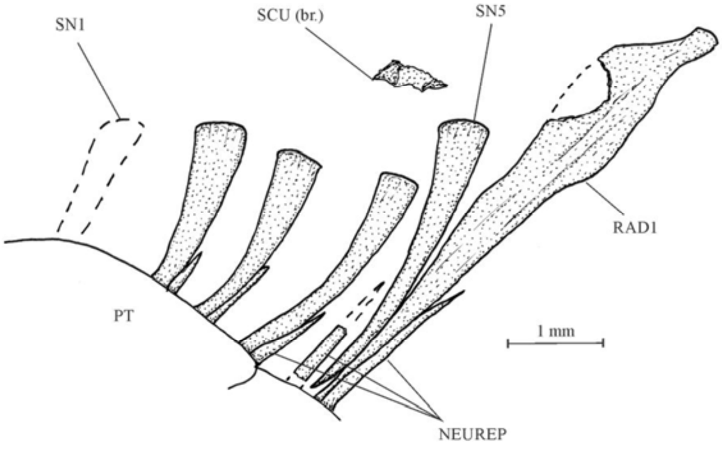

Figure 18: *Armigatus brevissimus* (DE BLAINVILLE, 1818). The fan-like morphology of the supraneurals of specimen IRSNB P 10298 (Cenomanian, Haqel, Lebanon).

Sorbinichthys has a weakly ornamented frontal and practically no ornamentation on the parietal. Generally, Ellimmichthyiformes exhibit a strongly ornamented frontal and parietal, a more advanced character.

These few features indicate that *Sorbinichthys* occupies in the phylogeny of Ellimmichthyiformes and intermediate position between the plesiomorphic lineages of *Ornategulum* and the Scutatuspinosidae, on the one hand, and the other members of the order, on the other hand. VERNYGORA & MURRAY (2021: fig. 8) have more or less the same opinion.

Sorbinichthys also seems to have a close relationship with *Diplomystus*. The two genera share a very peculiar character not present in other Ellimmichthyiformes. The posterior margin of the dorsal scutes bear well marked spines (Fig. 12; GRANDE, 1982: figs 9, 13).

MARRAMA & CARNEVALE (2017) re-study the skeleton of *Gasteroclupea branisai* SIGNEUX, 1964, a fossil clupeomorph fish from the Late Cretaceous and Paleocene of South America. This fish was ranged in the family Clupeidae and in a new subfamily, the Gasteroclupeinae, by SIGNEUX (1964). Later, it was considered by GRANDE (1985) as a member of the order Clupeiformes, the suborder Clupeoidei and the superfamily Pristigasteroidea. MARRAMA & CARNEVALE (2017) have a different opinion. They consider that *G. branisai* belongs to the order Ellimmichthyiformes and is the sister-genus of *Sorbinichthys*. They create the new suborder Sorbinichthyoidei for these two genera. We will give some comments on that supposed close relationships between the two fishes in a forthcoming paper.

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