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Comments on the phylogenetic relationships of *Pholidorhynchodon malzannii* and *Eurycormus speciosus* (Teleostei, “Pholidophoriformes”), two Mesozoic tropical fishes

Commentaires sur les relations phylogénétiques de *Pholidorhynchodon malzannii* et d’*Eurycormus speciosus* (Teleostei, “Pholidophoriformes”), deux poissons tropicaux du Mésozoïque

Louis TAVERNE [*] & Luigi CAPASSO [**]

Résumé : Les relations phylogénétiques de *Pholidorhynchodon malzannii* et d’*Eurycormus speciosus*, deux téléostéens mésozoïques du groupe des « Pholidophoriformes », sont commentées sur la base des données ostéologiques disponibles. En conclusion, l’appartenance de *Pholidorhynchodon* aux Pholidophoridae *sensu stricto* est contestée et le genre est rapporté à la famille des Ankylophoridae. Il est également montré qu’*Eurycormus* est plus évolué que *Catervariolus* et non pas moins évolué, comme certains le pensent. Des arguments anatomiques sont avancés qui militent pour le placement d’*Eurycormus* dans la famille des Ankylophoridae.

Mots-clés: Teleostei, “Pholidophoriformes”, *Pholidorhynchodon malzannii*, *Eurycormus speciosus*, ostéologie, relations, Mésozoïque.

Abstract : The phylogenetic relationships of *Pholidorhynchodon malzannii* and *Eurycormus speciosus*, two Mesozoic teleosts of the “Pholidophoriformes” lineage, are commented on the basis of the available osteological data. To conclude, the belonging of *Pholidorhynchodon* to the Pholidophoridae *sensu stricto* is contested and the genus is ranged within the family Ankylophoridae. It is also shown that *Eurycormus* is more evolved than *Catervariolus* and not less evolved, as thought by some. Anatomical arguments are developed that militate for the inclusion of *Eurycormus* in the family Ankylophoridae.

Key words: Teleostei, “Pholidophoriformes”, *Pholidorhynchodon malzannii*, *Eurycormus speciosus*, osteology, relationships, Mesozoic.

INTRODUCTION

The Mesozoic primitive Teleostei with ganoid scales and a peg-and-socket articulation are extremely numerous and have a worldwide distribution. In the past, they were traditionally ranged in the “Pholidophoriformes”, an order that is now considered as highly heterogenous (PATTERSON, 1973; ARRATIA, 2000, 2013, 2015; TAVERNE, 2011a, b, c, 2014a, b, 2015). The break-up of this polyphyletic and artificial order in monophyletic lineages is now begun. ARRATIA (2013) restricted the Pholidophoriformes to the unique family Pholidophoridae *sensu stricto*. TAVERNE (2011c, 2014a, b, 2015) erected three new orders, the Ligulelliformes, Catervarioliformes and Ankylophoriformes, respectively for the Ligulellidae, Catervariolidae and Ankylophoridae, three families formerly ranged within “Pholidophoriformes”.

It is why, in our present paper, we write “Pholidophoriformes” when referring to all the families and genera ever included in this polyphyletic order and Pholidophoriformes when we consider only the Pholidophoridae *sensu stricto*.

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The aim of the present paper is to comment on the phylogenetic relationships of two "pholidophoriform" teleosts, *Pholidorhynchodon malzannii* ZAMBELLI, 1980 and *Eurycormus speciosus* WAGNER, 1863. Indeed, their systematic position is problematic. For this purpose, we use hereafter not only the data provided on these two fishes by the scientific literature (PATTERSON, 1973, ZAMBELLI, 1980, ARRATIA, 1999, 2013, 2015, GRANDE & BEMIS, 1999 and ARRATIA & SCHULTZE, 2007) but also our own observations on one well preserved specimen of each concerned species.

MATERIAL AND METHODS

The specimens of *Pholidorhynchodon malzannii* and of *Eurycormus speciosus* used in our present study belong to the CAPASSO paleontological collection (CLC) in Chieti (Abruzzo, Italy). Both samples are complete and fossilized with the skull roof exposed in dorsal view. The specimen of *Ph. malzannii* (CLC I-438, total length: 50 mm) was collected in the "Cava Ratta", a quarry close to the village of Gazzaniga, near Cene (Lombardy, Italy), and was donated to Mario CAPASSO (Luigi CAPASSO's father) in the autumn 1967 (Fig. 1). The specimen of *E. speciosus* (CLC S-1234, total length: 187 mm) comes from the marine Tithonian strata of the Solnhofen Limestone (Bavaria, Germany) (Fig. 6).

The material was studied with a Leica Wild M8 stereomicroscope. The drawings of the figures were made by the first author (L. T.) and the photos by M. Luciano LULLO, from the University of Chieti-Pescara. .

The CAPASSO paleontological collection is legally registered and was declared part of the Italian cultural heritage 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 of cultural heritage protection N° 1089/1939. 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 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).

List of the abbreviations used in the text-figures

ANT = antorbital
ASPH = autosphenotic
DETH = dermethmoid (= rostral)
DPTE = dermopterotic
EPI = epiotic (= epioccipital)
FR = frontal
HYOM = hyomandibula
IORB 2 = infraorbital 2
LDETH = lateral dermethmoid
MX = maxilla
NA = nasal
PA = parietal
PMX = premaxilla
POP = preopercle
PORB = postorbital (= suborbital)
PRO = prootic
PS = parasphenoid
SMX 1, 2 = supramaxillae 1 and 2
SOC = supraoccipital
SORB 1, 2 = supraorbitals 1 and 2

ST = supratemporal (= extrascapular)
b. pr. = basipterygoid process of parasphenoid
br. = broken
ext. c. = extrascapular sensory commissure
l. = left
ol. f. = olfactive foramen
ot. c. = otic (postorbital) sensory canal
pa. c. = parietal sensory commissure
pop. c. = preopercular sensory canal
ps. t. = teeth on the parasphenoid
sorb. c. = supraorbital sensory canal
r. = right
ro. c. = rostral sensory commissure
t. f. = temporal (posttemporal) fossa

THE SYSTEMATIC RELATIONSHIPS OF *PHOLIDORHYNCHODON MALZANNII*

Foreword

ARRATIA (2013) has included eight genera from the Carnian and Norian (Late Triassic) of northern Italy and Austria in the family Pholidophoridae *sensu stricto*, *Pholidophorus* AGASSIZ, 1832, *Parapholidophorus* ZAMBELLI, 1975, *Pholidophoretes* GRIFFITH, 1977, *Pholidoctenus* ZAMBELLI, 1977, *Pholidorhynchodon* ZAMBELLI, 1980, *Zambellichthys* ARRATIA, 2013, *Annaichthys* ARRATIA, 2013 and *Knerichthys* ARRATIA, 2013. Recently, two other new genera were added to this family, *Malingichthys* TINTORI *et al.*, 2015 from the Ladinian (Middle Triassic) of southern China and *Ceneichthys* TAVERNE & CAPASSO, 2015 from the Norian of northern Italy (TINTORI *et al.*, 2015; TAVERNE & CAPASSO, 2015).

Pholidorhynchodon is a monospecific genus. Its unique species, *Pholidorhynchodon malzannii*, is only known in the Norian (Zorzino Formation) of Cene, Lombardy, northern Italy. The fish lived in the warm marine waters that covered the region at that time (TINTORI, 1991). *Pholidorhynchodon* was firstly studied by ZAMBELLI (1980). A much more detailed description was done recently by ARRATIA (2013). TAVERNE (2011a) considered this species as a probable member of the Ankylophoridae, while ARRATIA (2013) ranged this fish in the Pholidophoridae *sensu stricto*. There is thus a doubt concerning the familial status of this species. The analysis of a few cranial features can bring some light to solve the problem.

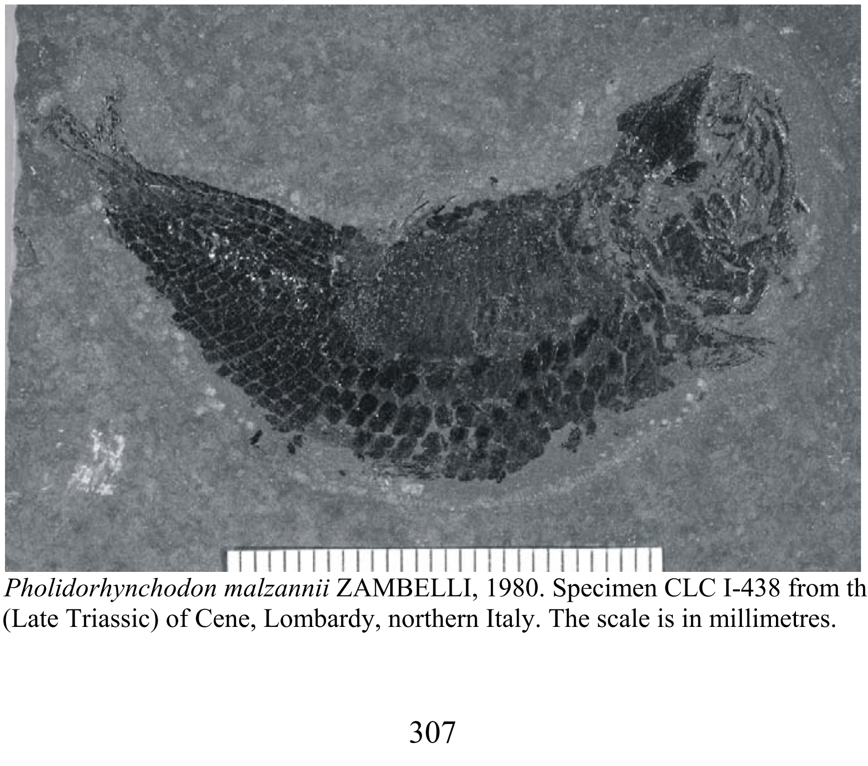

Figure 1. *Pholidorhynchodon malzannii* ZAMBELLI, 1980. Specimen CLC I-438 from the Norian (Late Triassic) of Cene, Lombardy, northern Italy. The scale is in millimetres.

Comments on some osteological characters (Figs 1-5)

(1) Among the nine characters defining the Pholidophoridae in the phylogeny proposed by Arratia (2013, node C1), the first mentioned (character [1(1)]) concerned the bones of the skull roof that are fused in a single plate. She considers this feature as an important autapomorphy of the family. However, the situation is not so simple. There is only a tendency to have the bones of the skull roof more or less fused together in Pholidophoridae. Generally, the members of the family exhibit a suture between the two frontals, with the parietal and the dermopterotic frequently fused with the frontal (ARRATIA, 2013: numerous fig.). But there are pholidophorid specimens with the parietal and the dermopterotic well separated and also separated from the frontal (TINTORI *et al.*, 2015: figs 4A, B, 7C) or with all the skull roof bones well individualized (TAVERNE & CAPASSO, 2015: fig. 5). Moreover, this partial or total fusion of the bones of the skull roof is not the apanage of the Pholidophoridae only. Other lineages previously reported to the "Pholidophoriformes" possess exactly the same tendency, for instance Ligulellidae and Pleuropholidae (TAVERNE & CAPASSO, 2015: fig. 10) or members of the genus *"Pholidophorus" sensu lato* (BIESE, 1927: figs 11, 20). A partial or total fusion between the skull roof bones also appears in many primitive neopterygian lineages, such as for instance the Perleidiformes (BÜRGIN, 1992: figs 94A, B, C, 108, 125-127), the Peltopleuriformes (ibid., 1992: figs 154D, 155A, 182A, B185), the Aspidorhynchiformes (BARTHOLOMAI, 2004: fig. 7A; BRITO & EBERT, 2009: fig. 5B; BOGAN *et al.*, 2011: fig. 3) and some others.

In *Pholidorhynchodon*, four possible morphologies of the skull roof exist. The bones may be completely separated into individual elements, separated only at the frontal level, partially separated by incomplete sutures or entirely fused in one plate (ARRATIA, 2013: 61-63, figs 46, 47A, B, 49A, B). Sample CLC I-438 of *Pholidorhynchodon malzannii* exhibits the unfused pattern, with all the skull roof bones simply sutured together (Figs 2, 3).

(2) Members of the family Pholidophoridae are devoid of ossified supraoccipital (ARRATIA, 2013, character [13(0)]). But it seems that the endocranium remains for a great part unossified in Pholidophoridae. Indeed, neither ARRATIA (2013) nor TINTORI *et al.* (2015) or TAVERNE & CAPASSO (2015) mention an endocranial bone in the numerous specimens described, with the only exception of one specimen of *Zambellichthys* that exhibits an ethmoid bone and an autosphenotic (ARRATIA, 2013: fig. 29). If the adult endocranium of Pholidophoridae remains essentially cartilaginous, it is not surprising that a bony supraoccipital is missing.

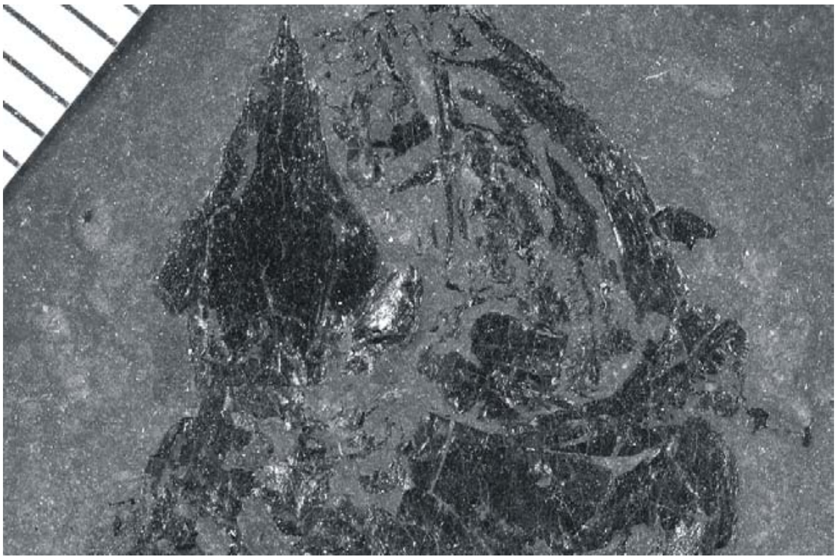

Figure 2. *Pholidorhynchodon malzannii* ZAMBELLI, 1980. Head region of specimen CLC I-438. The scale is in millimetres.

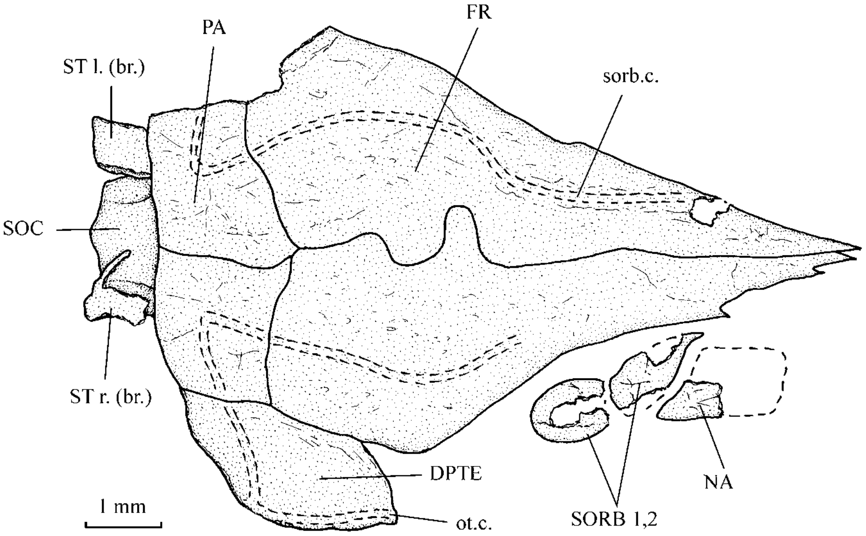

Figure 3. *Pholidorhynchodon malzannii* ZAMBELLI, 1980. Skull roof of specimen CLC I-438.

In many "pholidophoriform" teleosts, the region of the braincase just posterior to the parietals is covered by the supratemporals and the posttemporals and the possible presence of a supraoccipital is not observable. However, some fossil fishes attributed in the past to the "Pholidophoriformes" have an ossified supraoccipital. That is the case for instance of *"Pholidophorus" limbata* AGASSIZ, 1844, *Dorsetichthys bechei* (AGASSIZ, 1844), *Siemensichthys macrocephalus* (AGASSIZ, 1844), *"Pholidophorus" germanicus* QUENSTEDT, 1858, the Callovian *"Pholidophorus"* sp., *Ichthyokentema purbeckensis* (DAVIES, 1887), *Catervariolus hornemani* DE SAINT-SEINE, 1955, *Songanella callida* DE SAINT-SEINE & CASIER, 1962 and still a few others (GRIFFITH & PATTERSON, 1963: figs 1, 2, 4 ; PATTERSON, 1975: figs 44, 55, 70, 82, 145, 151; ARRATIA, 2000: fig. 5; TAVERNE, 2011b: figs 9, 10, 2014a: figs 5, 6).

In specimen CLC I-438 of *Pholidorhynchodon malzannii*, the skull roof is exposed in dorsal view. The two supratemporals are broken and a well developed bony supraoccipital is clearly visible between them, forming a large protuberance just posterior to the parietals (Fig. 3).

(3) The two premaxillae meet at the symphysis in Pholidophoridae and a toothed free lateral dermethmoid is never mentioned (ARRATIA, 2013: numerous fig.; TAVERNE & CAPASSO, 2015: fig. 5). In *Pholidorhynchodon*, a pair of toothed lateral dermethmoïds is located at the symphysis and the toothed premaxillae are more laterally positioned (Fig. 4; ZAMBELLI, 1980: figs 1, 2; ARRATIA, 2013: figs 49A, B, 52A) as in Catervariolidae (TAVERNE, 2011b: figs 8-12, 17, 19, 2014a: figs 4-7, 2015: fig. 2), in Ichthyokentemidae (PATTERSON, 1975: fig. 126; GRIFFITH, 1977: fig. 26) and at least in some ankylophorid genera (PATTERSON, 1975: figs 82, 121, 124, 125, 145; ARRATIA, 1999: fig. 6C, 2000: fig. 15A; TAVERNE, 2011a: figs 4, 5, 2014b: figs 4, 6). In the ankylophorid genera *Ankylophorus* GAUDANT, 1978 and *Lehmanophorus* GAUDANT, 1978, the premaxilla seems to be also located posterior to the upper jaw symphysis (GAUDANT, 1978: pl. 1, fig. 2, pl. 2, fig. 1).

(4) The nasal forms a part of the orbital margin in Pholidophoridae (ARRATIA, 2013, character [23(1)]). In a specimen of *Pholidorhynchodon* with a complete antorbital preserved, the dorsal branch of this bone separates the nasal from the orbit (ARRATIA, 2013: fig.47A). A nasal separated from the orbit by the antorbital is known in Catervariolidae (TAVERNE, 2011b: figs 8, 13A, B, C, D, 15, 2014a: figs 4, 5, 2015: fig. 2) and in Ichthyokentemidae (GRIFFITH & PATTERSON, 1963: fig. 6; GRIFFITH, 1977: fig. 26). In the best preserved specimens of Ankylophoridae, the nasal is separated from the orbital margin by the antorbital or by the first supraorbital or by both bones (GAUDANT, 1978: pl. 1, fig. 2, pl. 2, fig. 1; TAVERNE, 2011a: fig. 4, 2014b: figs 4, 6).

(5) The parasphenoid is toothless in Pholidophoridae (ARRATIA, 2013: 15), whereas this bone bears a small patch of minute teeth just in front of the basipterygoid process in *Pholidorhynchodon* (Fig. 5). A partially toothed parasphenoid is present in some

"phololidophoriform" fishes (GRIFFITH & PATTERSON, 1963: figs 2, 3; PATTERSON, 1975: fig. 62; TAVERNE, 2011b: figs 10, 11, 18, 2014a: figs 6, 9).

(6) A crest separates the dental and spenial regions on the outer face of the dentary in Pholidophoridae (ARRATIA, 2013, character [70(1)]). Such a crest exists in *Pholidorhynchodon* (ZAMBELLI , 1980: fig. 5B; ARRATIA, 2013: 68) but is also present in some Ankylophoridae (GAUDANT, 1979: 104, 106, 111; TAVERNE, 2011a: 137, fig.8) and in a few other "pholidophoriform" fishes not belonging to the Pholidophoridae (NYBELIN, 1966: pl. 7, fig. 2, pl. 12, fig. 2, pl. 13, fig. 15, fig. 5).

(7) A toothed autogenous coronoid is present in *Pholidorhynchodon* (ARRATIA, 2013: fig. 47C). Such a bone is unknown in Pholidophoridae. Two or three coronoids are associated to the dentary in Catervariolidae (TAVERNE, 2011b: fig. 28A, B) and one coronoid is present in Ichthyokentemidae (GRIFFITH & PATTERSON, 1963: fig. 9).

(8) The bony quadratic process is missing or is very feebly developed in Pholidophoridae (ARRATIA, 2013, character [78(0)]) but is present in many other "pholidophoriform" fishes (GRIFFITH & PATTERSON, 1963: fig. 10; GAUDANT, 1978: pl. 1, fig. 2, pl. 2, fig. 1, pl. 3, fig. 2; ARRATIA, 2000: figs 8, 14, 15D; TAVERNE, 2011a: figs 6, 9, 2011b: figs 21, 24, 2014a: fig. 10; among others). The quadrate of *Pholidorhynchodon* is incompletely known. It is impossible to say if a bony quadratic process was present or not (ARRATIA, 2013: 69, fig. 52B). Unfortunately, the quadrate is not preserved in the specimen CLC I-438 of *Pholidorhynchodon malzannii*.

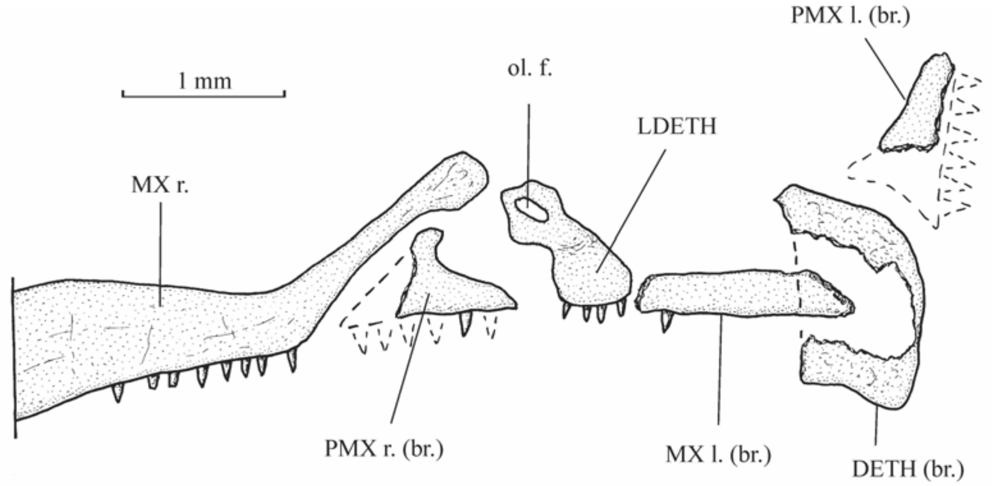

Figure 4. *Pholidorhynchodon malzannii* ZAMBELLI, 1980. Snout area of specimen CLC I-438. The maxillary and the rostral rostral regions, disjoined on this sample by the fossilisation, are brought near again on the figure.

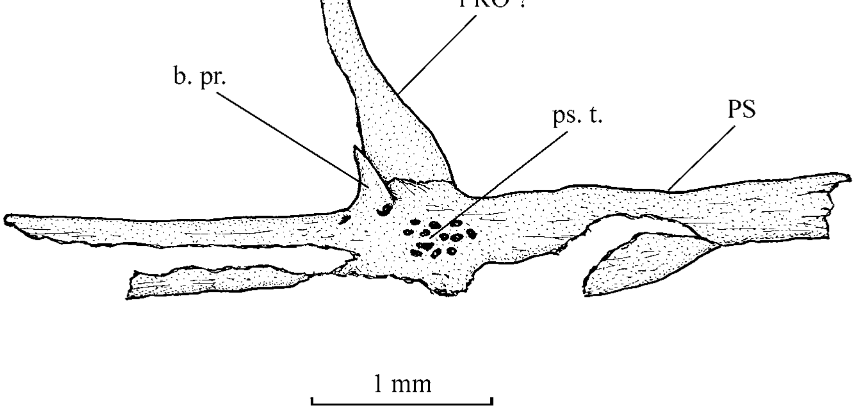

Figure 5. *Pholidorhynchodon malzannii* ZAMBELLI, 1980. Parashenoid of specimen CLC I-438 in ventral view.

CONCLUSIONS

The characters discussed in points (1), (6) and (8) seem not pertinent to decide if *Pholidorhynchodon* belongs or not to the Pholidophoridae *sensu stricto*. For the characters mentioned in points (2), (3), (4), (5) and (7), the Italian genus completely differs from the other members of the family. Such an amount of important differences with the other Pholidophoridae makes it uneasy to consider *Pholidorhynchodon* as a member of this family. On the contrary, the characters evocated in points (2), (3), (4) and (5) that are present in *Pholidorhynchodon* agree with the placement of this genus in the Ankylophoridae *sensu* Taverne (2011a).

THE SYSTEMATIC RELATIONSHIPS OF *EURYCORMUS SPECIOSUS*

Foreword

Eurycormus speciosus is the type- and only valid species of the genus *Eurycormus* WAGNER, 1863, a fossil fish that lived in the tropical lagoon of Solnhofen, Bavaria, Germany, during the Tithonian (Late Jurassic) (BARTHEL *et al.*, 1990; among others). The two English Late Jurassic species *Eurycormus egertoni* (AGASSIZ, 1843) and *Eurycormus grandis* WOODWARD, 1889 are now reported to the genus *Eurypoma* HUXLEY, 1866, an amiiform fish (ARRATIA & SCHULTZE, 2007).

The "pholidophorid" nature of *Eurycormus* was firstly recognized by PATTERSON (1973). Later, ARRATIA (2000) included *Eurycormus* in her *Siemensichthys*-group, with two other "pholidophorid" genera, *Ankylophorus* and *Siemensichthys* ARRATIA, 2000. More recently, ARRATIA (2013, 2015) maintained the *Siemensichthys*-group but with a different composition than previously. She included the "pholidophorid" *Lehmanophorus* in the lineage but excluded *Eurycormus* from the group. She placed this fish (her Node D) in her phylogenetic tree just above the Pholidophoridae *sensu stricto* (her Node C1) and at a more plesiomorphic level than *Catervariolus* DE SAINT-SEINE, 1955 (her Node E) and than the *Siemensichthys*-group (her Node F1). In her hypothesis, Pholidophoridae are the more primitive group of the fishes ranged in the "Pholidophoriformes". On the other hand, in the phylogeny proposed by TAVERNE (2011a, 2014b), Catervariolidae are considered as the more primitive branch within "Pholidophoriformes", while *Eurycormus* is positioned as the less specialized member of Ankylophoridae, a family that he placed as the immediate apomorphic sister-lineage of Catervariolidae. TAVERNE (2015: 251-255) largely explained why he disagreed with ARRATIA (2013, 2015) concerning the systematic placement of Catervariolidae. TAVERNE (2011a, 2014b, 2015) point of view is confirmed in a recent phylogenetical analysis provided by XU & ZHAO in a still unpublished paper concerning a primitive ganoid teleost from the Middle Triassic of China (pers. com., February 2016).

But before the discussion on the systematic position of *Eurycormus*, it is necessary to briefly remind the story of the Ankylophoridae. The family was erected by GAUDANT (1978) to contain two genera of the Late Jurassic of France, *Ankylophorus* and *Lehmanophorus*. The *Siemensichthys*-group, as now understand by ARRATIA (2013, 2015), includes these two genera and *Siemensichthys*. However, she does not use the name Ankylophoridae for the group. In the meantime, TAVERNE (2011a, 2014b) considerably enlarged the Ankylophoridae, incorporating in this family not only the *Siemensichthys*-group but also *Eurycormus* and some other genera. The placement of a few poorly known species in the Ankylophoridae *sensu* TAVERNE (2011a) must be confirmed or rejected after new anatomical investigations.

So, concerning the relationships of *Eurycormus*, two hypotheses are in presence and the problem deserves some comments. In the phylogeny proposed by ARRATIA (2013), all the characters of her Node E separate *Catervariolus* from *Eurycormus* and indicate that this last genus occupies a more plesiomorphic position than *Catervariolus*. Thus, we shall examine hereafter those characters in the first eight points of the following chapter and also a few other characters.

Comments on some osteological characters (Figs 6-8)

(1) *Catervariolus* exhibits an ossified supraoccipital (TAVERNE, 2011b: fig. 9-11, 19). That is an advanced feature (ARRATIA, 2013, character [13(1)]. *Eurycomus* is quoted by ARRATIA (2013, character [13(0)]) as devoid of bony supraoccipital. The few samples of *Eurycormus* described in the scientific literature are fossilized in lateral view, with the occipital region not preserved (PATTERSON, 1973: fig. 14) or covered by the supratemporal (GRANDE & BEMIS, 1998: fig. 421C). So, until now, it was not possible to know if a supraoccipital was present or not in this fish. The specimen CLC S-1234 of *Eurycormus speciosus* is fossilized with the skull roof in dorsal view. A small but well developed bony supraoccipital is clearly visible between the two epiotics and behind the parietals and the supratemporals (Figs 7, 8). Thus, *Eurycormus* does possess an ossified supraoccipital, as *Catervariolus*.

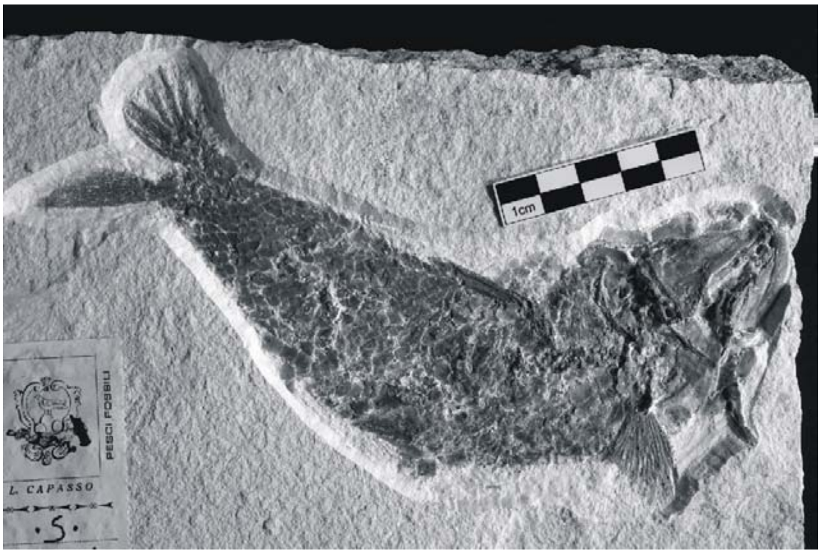

Figure 6. *Eurycormus speciosus* WAGNER, 1863. Specimen CLC S-1234 from the Tithonian (Late Jurassic) of Solnhofen, Bavaria, Germany. The scale is in centimetres.

Figure 7. *Eurycormus speciosus* WAGNER, 1863. Head region of specimen CLC S-1234. The scale is in centimetres.

(2) The braincase of *Eurycormus* is considered by ARRATIA (2013) as devoid of sutures between the cartilage bones in adult specimens, a primitive feature (ARRATIA, 2013, character [18(0)]). Such sutures are well visible in *Catervariolus* (TAVERNE, 2011b: figs 10, 11, 18-20;

ARRATIA, 2013, character [18(1)]). However, only the lateral ethmoid and the autosphenotic are known in *Eurycormus* but not the other parts of the endocranium (Fig. 8; PATTERSON, 1973: fig. 14; GRAND & BEMIS, 1998: fig. 421C; ARRATIA, 1999: fig. 6C). So, the absence of sutures between the cartilage bones of the skull in *Eurycormus* is only a conjecture and not an incontestable reality.

(3) ARRATIA (2013, character [56(0)]) quotes the maxilla of *Catervariolus* as extending behind the orbit and thus longer than that of *Eurycormus* (ibid., 2013, character [56(1)]). In fact, the maxillae of both fishes have the same length and reach the posterior border of the orbit (Fig. 8; PATTERSON, 1973: fig. 14; GRANDE & BEMIS, 1998: fig. 421C)

(4) The symplectic is medial to the posterior margin of the quadrate in *Catervariolus* (TAVERNE, 2011b: figs 21, 24; ARRATIA, 2013, character [80(1)]) but is considered as posterior to the posterior margin of the quadrate in *Eurycormus* (ibid., 2013, character [80(0)]). However, the symplectic of *Eurycormus* was never described and is unknown until now.

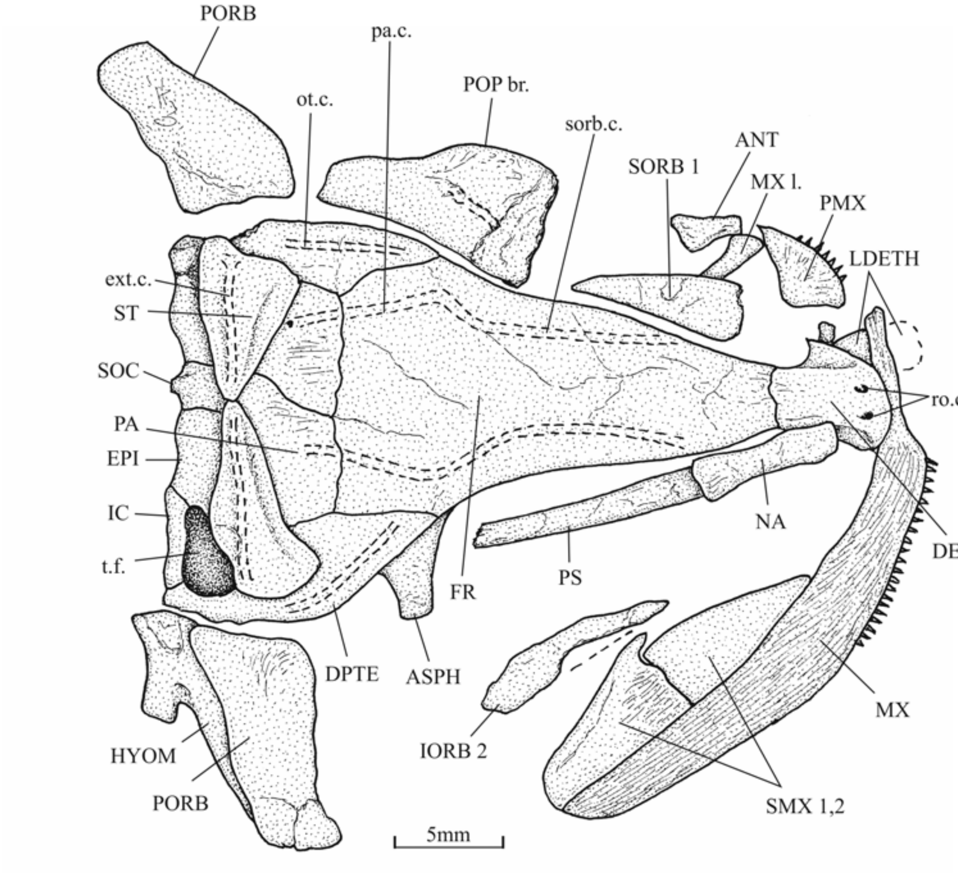

Figure 8. *Eurycormus speciosus* WAGNER, 1863. Skull of specimen CLC S-1234.
In this sample the two frontals are fused in one unique bone.

(5) The vertebrae of the caudal region of *Catervariolus* are said composed of a chordacentrum and a surrounding autocentrum by ARRATIA (2013, character [96(1)]), whereas those of *Eurycormus* are more primitive and only formed by a chordacentrum (ibid., 2013, character [96(0)]). TAVERNE (2015: 253) has explained why the presence of autocentra is doubtful in *Catervariolus*.

(6) Epipleurals are mentioned as present in *Catervariolus* by ARRATIA (2013, character [103(1)]) and absent in *Eurycormus* (ibid., 2013, character [103(0)]). In fact, *Catervariolus* is completely devoid of epipleurals (TAVERNE, 2011b: 202) as *Eurycormus*. In this case, the character attributed to *Catervariolus* by ARRATIA (2013) is misquoted.

(7) ARRATIA (2013) ranged *Catervariolus* in a group of fishes having four pectoral radials (ibid., 2013, character [110(1)]), while *Eurycormus* is considered as more primitive and not having four pectoral radials (ibid., 2013, character [110(0)]). However, the exact number of pectoral radials is unknown in *Catervariolus* (TAVERNE, 2011b: 198) and in *Eurycormus*. Moreover, the "four pectoral

radials" pattern already exists in fossil fishes less advanced than *Catervariolus* and *Eurycormus*, such as the Pachycormidae (JESSEN, 1972: pl. 25, fig. 1; MAINWARING, 1978: fig. 29).

(8) For ARRATIA (2013), only the ural neural arches are modified into uroneurals in *Catervariolus* (ibid., 2013, character [131(1)]). In *Eurycormus*, the situation is more primitive and additional components are added to the uroneural series (ibid., 2013, character [131(0)]). In fact, the situation is identical in the two fishes, the first preural neural arch being included in the uroneural series in *Catervariolus* (TAVERNE, 2011B: figs 50-52) as in *Eurycormus* (PATTERSON, 1973: fig. 15; ARRATIA & LAMBERS, 1996: fig. 14A; ARRATIA, 1999: fig. 15).

(9) *Eurycormus* exhibits two large supramaxillae articulated on the upper margin of the maxilla (Fig. 8; PATTERSON, 1973: fig. 14; GRAND & BEMIS, 1998: fig. 421C; ARRATIA, 1999: fig. 6C), an advanced character, while *Catervariolus* has only one small supramaxilla above the maxilla (TAVERNE, 2011b: figs 8, 35), a primitive condition.

(10) Two supraorbitals are present in *Eurycormus* (PATTERSON, 1973: fig. 14; GRAND & BEMIS, 1998: fig. 421C). That is an evolved character. *Catervariolus* has three supraorbitals (TAVERNE, 2011b: figs 8, 9, 13A, B, C, D, 16A), a more plesiomorphic feature.

(11) The posterior infraorbitals of *Eurycormus* are followed by only one large and two small postorbitals (= suborbitals) (PATTERSON, 1973: fig. 14; GRAND & BEMIS, 1998: fig. 421C), whereas *Catervariolus* preserves the primitive condition of having three large and two reduced postorbitals (TAVERNE, 2011b: fig. 8).

(12) *Eurycormus* has a broad preopercle, with a well developed ventral branch (PATTERSON, 1973: fig. 14; GRAND & BEMIS, 1998: fig. 421C), an apomorphic character. A primitive crescent-like preopercle is present in *Catervariolus* (TAVERNE, 2011b: fig. 8).

(13) In *Catervariolus*, the articulation between the segments of the fin rays is straight (ibid., 2011b: fig. 48, 49, 57), a primitive condition. Some segments of the fin rays exhibit an evolved sigmoid articulation in *Eurycormus* (ARRATIA, 2008: figs 7A, 20).

CONCLUSIONS

The characters studied in points (1) to (8) concerned the Node E of the phylogenetic hypothesis proposed by ARRATIA (2013). All those characters clearly appear irrelevant to prove that *Catervariolus* would be in any way more specialized than *Eurycormus*. On the other hand, for the characters discussed in points (9) to (13), *Eurycormus* is obviously more evolved than *Catervariolus*. So, as a conclusion, we consider that *Eurycormus* occupies a more apomorphic level in the phylogenetic tree of "Pholidophoriformes" than *Catervariolus* (*contra* ARRATIA, 2013).

As for the inclusion of *Eurycormus* in Ankylophoridae by TAVERNE (2011a), that systematic position essentially rests on the presence of lateral dermethmoids with a well developed nasal process that are located at the symphysis between the two premaxillae, on its large preopercle with well developed dorsal and ventral branches, on its elongate lower jaw with a more or less rectilinear upper margin and on the long toothed region of its dentary (Figs 6, 8; PATTERSON, 1973: fig. 14; GRAND & BEMIS, 1998: fig. 421C; ARRATIA, 1999: fig. 6C).

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