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Osteology and phylogenetic relationships of *Furloichthys bonarellii* gen. and sp. nov. (Teleostei, Ichthyodectidae), a tropical fish from the Upper Cretaceous of central Italy

Ostéologie et relations phylogénétiques de *Furloichthys bonarellii* gen. et sp. nov. (Teleostei, Ichthyodectidae), un poisson tropical du Crétacé supérieur de l'Italie centrale

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Résumé: L'ostéologie de *Furloichthys bonarellii* gen. et sp. nov., un petit poisson ichthyodectidé du Cénomanien de la rivière Furlo (La Marche, Italie centrale), est étudiée en détails. Le nouveau genre diffère de tous les autres Ichthyodectidae connus par quelques caractères particuliers. L'ethmoïde latéral est réduit et largement séparé du mésethmoïde. L'ethmoïde latéro-basal (= ethmopalatin) est associé avec le mésethmoïde et non pas avec l'ethmoïde latéral. La courte mâchoire inférieure possède une symphyse étroite et le bord supérieur qui remonte de façon abrupte. La région coronoïde, formée à la fois par le dentaire et l'angulaire, est large, élevée et arrondie. Les infraorbitaires 1 et 3 se rejoignent en-dessous de l'infraorbitaire 2. Les hypuraux 3 à 5 sont fusionnés en une vaste plaque hypurale dorsale. *Furloichthys* possède également un autopalatin dont le processus articulaire est épaissi en forme de tête de marteau, 73 (45 + 28) vertèbres, des épineuraux et épipleuraux ossifiés, un épural libre, pas de neurépine bien marquée sur l'arc neural de la vertèbre préurale 1 et un hypural 1 à large tête articulaire. Dans la phylogénie des Ichthyodectidae, *Furloichthys* occupe une position intermédiaire entre *Cladocyclus*, *Chiromystus* et *Verraesichthys*, d'une part, et *Heckelichthys* et les genres plus spécialisés, d'autre part.

Mots clés: Teleostei, Ichthyodectidae, *Furloichthys bonarellii* gen. et sp. nov., ostéologie, relations, Crétacé supérieur marin, rivière Furlo, La Marche, Italie centrale.

Abstract: The osteology of *Furloichthys bonarellii* gen. and sp. nov., a small ichthyodectid fish from the marine Cenomanian of the Furlo river (The Marche, central Italy), is studied in details. The new genus differs from all the other known Ichthyodectidae by a few peculiar characters. The lateral ethmoid is reduced and largely separated from the mesethmoid. The latero-basal ethmoid (= ethmopalatine) is associated with the mesethmoid and not with the lateral ethmoid. The short lower jaw has a narrow symphysis and an upper margin that raises up abruptly. The coronoid region, formed by both the dentary and the angular, is broad, deep and rounded. The infraorbitals 1 and 3 meet together below infraorbital 2. The hypurals 3 to 5 are fused in a large dorsal hypural plate. *Furloichthys* also exhibits an autopalatine with an enlarged hammer-head like articular process, 73 (45 + 28) vertebrae, bony epineurals and epipleurals, one free epural, no well marked neural spine on the preural vertebra 1 and the hypural 1 with a broad articular head. Within the phylogeny of Ichthyodectidae, *Furloichthys* occupies an intermediate position between *Cladocyclus*, *Chiromystus* and *Verraesichthys*, on the one hand, and *Heckelichthys* plus the more specialized genera, on the other hand.

Key words: Teleostei, Ichthyodectidae, *Furloichthys bonarellii* gen. and sp. nov., osteology, relationships, marine Upper Cretaceous, Furlo river, the Marche, central Italy.

INTRODUCTION

The Bonarelli level is a marine Upper Cenomanian stratum of blackish or brownish bituminous clays present in the Apennines, in Umbria and in the Marche, central Italy (DESIO, 1973), with an estimated age of 91.5 My (ARTHUR & PREMOLI SILVA, 1982). It happens during the Cenomanian-Turonian Oceanic Anoxic Event (OAE) 2.

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Near the city of Fossombrone, in the Marche, the Bonarelli level is found in the "Cava della Contessa", a quarry located on the southern slopes of the Pietralata Mountain, just above the Defile of the Furlo river [Gola del Furlo] (Fig. 1; CAPASSO, 2007). The presence there of fossil fishes in the Bonarelli level was reported for the first time by CANUTI et al. (1966). A first list of these fishes was given by BIZZARINI & COCCIONI (1990) and was completed later by CAPASSO (2007). But no exhaustive study of these fossil fishes has been done until now.

The aim of our present paper is to describe the osteology and precise the relationships of a new ichthyodectid genus (Teleostei) discovered in the deposits of the Bonarelli level in the "Cava della Contessa".

Ichtyodectidae are a family of Mesozoic marine fishes that ranges in age from the Oxfordian (Upper Jurassic) to the Maastrichtian (Upper Cretaceous). They have an almost worldwide distribution. They are long-bodied fishes, with the dorsal and anal fins positioned at the same level, near the tail. Most of them have a protruded lower jaw, which led to their nickname of "bull-dog" fishes. Some species reach five or six meters in length. They were among the major predators within the fish communities of the Cretaceous seas.

Ichthyodectid fishes are numerous in the marine Cretaceous deposits of Italy, with at least five genera: *Saurodon* HAYS, 1830, *Capassoichthys* TAVERNE, 2015 and *Altamuraichthys* TAVERNE, 2016, all three from the Campanian-Maastrichtian of Nardò, Puglia, *Cladocyclus* AGASSIZ, 1841 in the Albian of Pietraroja, Campania and *Garganoichthys* TAVERNE, 2009 in the Santonian of Apricena, Puglia (TAVERNE, 1997, 2009, 2015, 2016; TAVERNE & BRONZI, 1999; SIGNORE *et al.*, 2006).

Fig. 1. Location map of Fossombrone (1), the Defile of Furlo River [Gola del Furlo] (2) and the Pietralata Mountain (3), The Marche, central Italy.

MATERIAL AND METHODS

The material hereafter studied belongs to the CAPASSO registered collection (CLC) in Chieti. The specimen 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 (CCL) in Chieti (Italy) 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 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).

ABBREVIATIONS USED IN THE TEXT-FIGURES

AN	=	angular
APAL	=	autopalatine
ASPH	=	autosphenotic
BR	=	branchial bone
BRSTG	=	branchiostegal ray
CHY	=	anterior ceratohyal
CBR	=	ceratobranchial
CLT	=	cleithrum
COR	=	hypocoracoid
DBHY	=	dermobasihyal
DN	=	dentary
EBR	=	epibranchial
EP	=	epural
EPI	=	epiotic (= epioccipital)
EPIN	=	epineural
EPIV	=	epipleural
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
HEM	=	haemal arch
HEMAP	=	haemapophysis (= parapophysis)
HEMEP	=	haemal spine
HY 1-6	=	hypurals 1 to 6
HYOM	=	hyomandibula
IC	=	intercalar
IORB 1-4	=	infraorbitals 1 to 4
LBETH	=	latero-basal ethmoid (= ethmopalatine)
LEP	=	lepidotrich (= fin ray)
LETH	=	lateral ethmoid
METH	=	mesethmoid
MX	=	maxilla
NEUR	=	neural arch
NEUREP	=	neural spine
N PU1	=	neural arch of preural vertebra 1
NP PU2	=	neural spine of preural vertebra 2
OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
PHY	=	parhypural
PMX	=	premaxilla
POP	=	preopercle
PT	=	posttemporal
PTE	=	pterotic
PU 1-4	=	preural vertebrae 1 to 4
QU	=	quadratic
RAD	=	pterygiophore (= radial)
RART	=	retroarticular
RI	=	rib
SMX 1, 2	=	supramaxillae 1 and 2
SN	=	supraneural (= predorsal)
SOC	=	supraoccipital

SOP	=	subopercle
ST	=	supratemporal (= extrascapular)
U 1, 2	=	ural vertebrae 1 and 2
UR 1-3	=	uroneurals 1 to 3
V	=	vertebra
VO	=	vomer
iorb. c.	=	infraorbital sensory canal
l.	=	left
m. c.	=	mandibular sensory canal
r.	=	rigth
sorb. c.	=	supraorbital sensory canal

SYSTEMATIC PALEONTOLOGY

Division Teleostei MÜLLER, 1846
Order Ichthyodectiformes BARDACK & SPRINKLE, 1969
Suborder Ichthyodectoidei ROMER, 1966
Family Ichthyodectidae CROOK, 1892

Furloichthys gen. nov.

Type-species: *Furloichthys bonarellii* gen. and sp. nov. (by monotypy)

Diagnosis

As for the species (monospecific genus).

Etymology

The generic name refers to the Furlo River. The Greek word *ichthys*, fish, is added.

Furloichthys bonarellii gen. and sp. nov.

Diagnosis

Small ichthyodectid fish. Well developed supraoccipital crest. Lateral ethmoid small and largely separated from the mesethmoid. Latero-basal ethmoid associated to the mesethmoid. Small tubular nasal. Autopalatine with an enlarged hammer-head like anterior process. Jaws bearing a few long spine-like teeth. Maxilla long, narrow, curved and without deepened anterior region. Two deep supramaxillae. Short lower jaw, with a narrow symphysis, an oral margin raising up abruptly and a deep, broad and rounded coronoid region. Articulation between the lower jaw and the quadrate located below the orbit anterior level. Retroarticular being part of the articular fossa for the quadrate. Third infraorbital strongly enlarged. First infraorbital reaching the third infraorbital below the second infraorbital. Preopercle with a broad ventral region. Pelvic fins inserted at the level of the posterior region of the abdominal cavity. Number of vertebrae: 73 (45 + 28). Ossified epineurals and epipleurals present. One free epural. No well marked spine on the neural arch of preural vertebra 1. Hypurals 1 and two fused proximally, forming a broad articular head. Hypurals 3 to 5 fused in a large dorsal hypural plate.

Etymology

The specific name is dedicated to Guido BONARELLI (1871-1951), the Italian geologist and palaeontologist who was the first to describe the geological stratum today known as the Bonarelli level.

Holotype

Specimen CLC I-163, a nearly complete specimen (the impair fins are partly missing) (Fig. 2). The last vertebrae are separated from the axial skeleton and located just above. Total length (without the caudal fin): 20 cm.

Formation and locality

Marine Cenomanian, Bonarelli level (OAE 2), quarry « Cava della Contessa », slopes of the Pietralata Mountain, above the Defile of the Furlo River, near Fossombrone, the Marche, central Italy (Fig. 1).

Fig. 2. *Furloichthys bonarellii* gen. and sp. nov. Holotype CLC I-163.

Morphometric data (Fig. 3)

The morphometric data are given in percentage (%) of the standard length (19.5 cm) of the holotype.

Length of the head …….. 23.4 %
Depth of the head (in the occipital region) …… 15.7 %
Maximum depth of the body ……. 15.0 %
Prepelvic length …….. 75.0 %

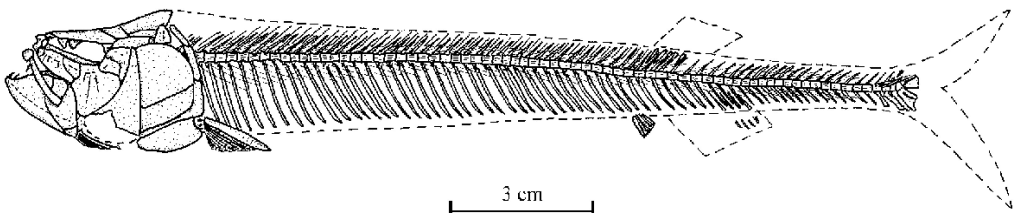

Fig. 3. *Furloichthys bonarellii* gen. and sp. nov. Reconstruction of holotype CLC I-163.

Osteology

The skull (Figs 4, 5)

The braincase is rather small compared to the size of the entire skull, as often in ichthyodectid fishes.

The small but massive mesethmoid is formed by the fused dermethmoid (= rostral) and the underlying endochondral supraethmoïd. The lateral ethmoid is a reduced bone, attached to the frontal but not reaching the parasphenoid. It is also largely separated from the mesethmoid. That is an unusual condition. The latero-basal ethmoid (= ethmopalatine) is sutured to the mesethmoid and has no contact with the lateral ethmoid, another unusual condition. The nasal is tubular and very short. A long, thin and toothless vomer is visible below the most anterior region of the parasphenoid. Anteriorly, below the mesethmoid, the vomer is slightly broadened. That is probably due to the presence of a fused hypoethmoid.

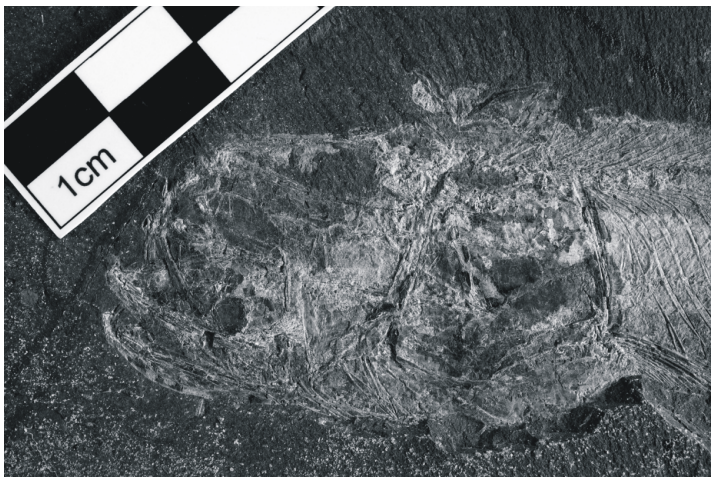

Fig. 4. *Furloichthys bonarellii* gen. and sp. nov. Head region of holotype CLC I-163.

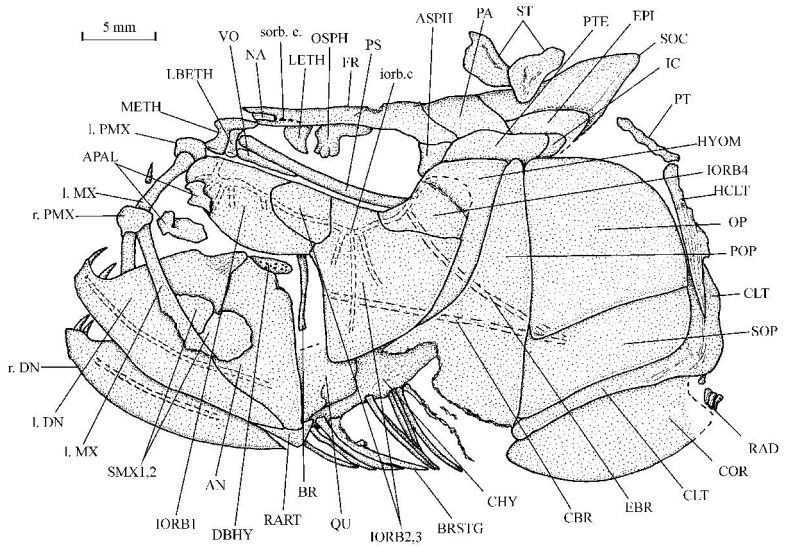

Fig. 5. *Furloichthys bonarellii* gen. and sp. nov. Skull and pectoral girdle of holotype CLC I-163.

The skull roof is formed by a rather short and narrow frontal, a wide parietal, a long pterotic, an epiotic (= epioccipital) and a supraoccipital that bears a large triangular median crest. The frontal profile from the mesethmoid to the posterior pointed corner of the supraoccipital crest is almost

rectilinear, without an angle between the parietal and the supraoccipital. The skull is medioparietal. The parietal is a large bone with a slightly pointed anterior extremity located on the mid-line of the skull and wedged between the two frontals. Such a shape exists in the ichthyodectid fishes having the two parietals fused in one median bone. That is very probably the case in *Furloichthys*. The parietal is not involved in the formation of the supraoccipital crest. The small autosphenotic is sutured with both the frontal and the pterotic. The two large plate-like supratemporals are preserved but displaced above the supraoccipital due to the fossilisation. Three small pores of the supraorbital sensory canal are present on the frontal, just behind the nasal. The otic sensory canal is not visible.

The trabecular portion of the parasphenoid is long, narrow and toothless. A small orbitosphenoid lies under the frontal, just behind the lateral ethmoid. No pleurosphenoid or basisphenoid is visible. The prootic, exoccipital, basioccipital and intercalary are hidden by the hyomandibula and the opercle.

Both autopalatines are preserved under the first infraorbital. They have an enlarged hammer-head anterior articular process. A small part of the quadrate is visible under the third infraorbital.

The small triangular plate-like premaxilla seems toothless. The maxilla is a long, narrow and curved bone. Its anterior region is not markedly deepened. A strong spine-like tooth is associated to the right maxilla. The two supramaxillae are incompletely preserved. They overlie the posterior extremity of the maxilla. They are short but rather deep in comparison to the maxilla narrowness.

The lower jaw is short. The articulation with the quadrate is located under the anterior margin of the orbit. The symphysis is rather narrow but the oral margin of the dentary raises up abruptly and the coronoid region, formed by both the dentary and the angular, is deep, broad and rounded. Two strong spine-like teeth are preserved on each dentary, near the symphysis. There is an autogenous retroarticular. The inner side of the mandible is not visible and the articular fossa for the quadrate is hidden. However, the articular head of the quadrate lies partly on the retroarticular. So, it is clear that this bone was a part of the articular fossa. The mandibular sensory canal is visible on both dentaries. The peculiar morphology of the mandible in *Furloichthys* is reminiscent of the strange mandibular shape of two closely allied Upper Cretaceous stomiiform fishes, *Pronotacanthus* WOODWARD, 1901 from Lebanon and *Protostomias* ARAMBOURG, 1943 from Morocco, Italy and Sicily (WOODWARD, 1901: pl. 15, fig. 1, 2; ARAMBOURG, 1954: figs 44, 45; TAVERNE, 1991: fig. 4).

The antorbital, supraorbital and dermosphenotic are not preserved. The first infraorbital (IORB 1) is a large bone. Its posterior extremity runs under the small second infraorbital (IORB 2) and reaches the third infraorbital (IORB 3) that is strongly enlarged. There is a large fourth infraorbital (IORB 4) but the presence of a fifth element in the series is uncertain. The posterior margin of IORB 3 and 4 meats the anterior border of the preopercle. The orbital sensory canal is well visible on the four infraorbitals. On IORB 1, the canal bears four ventral secondary tubules and its anterior extremity curves dorsally, forming the antorbital sensory commissure. No secondary tubules are present on IORB 2 but at least four long tubules are visible on IORB 3. The antorbital, supraorbital and dermosphenotic are not preserved.

The preopercle exhibits a long and broad dorsal branch and a shorter ventral branch Both the opercle and the subopercle are badly preserved but their contours are well visible. They are large bones. The interopercle is not preserved. There are about a dozen of thin branchiostegal rays.

The hyoid and branchial skeleton (Figs 4, 5)

The anterior part of the long, narrow and rod-like anterior ceratohyal and one branchial arch are visible. The ceratobranchial and the epibranchial are elongate but extremely thin. A small toothed dermobasihyal is also preserved just above the coronoid region of the mandible.

The girdles (Figs 2-5)

Only small fragments of the posttemporal are preserved. The hypercleithrum (= supracleithrum) is deep and narrow. The dorsal and ventral limbs of the cleithrum are well developed but rather thin. The hypocoracoid is a very wide plate-like bone that underlies the ventral branch of the cleithrum. The hypercoracoid (= scapula) is very small. No postcleithrum is visible. A few fragments of pectoral

pterygiophores are preserved. The pectoral fin is rather short and contains 11 rays. The first ray is broad, longer than the following rays and with a pointed distal extremity.

The pelvic bones are lost, due to the fossilisation. The ventral fins are very short. Each fin is composed of 8 rays. The ventral fin origin is located very far from the pectoral fin, at the end of the abdominal cavity, below the suture between the 44th and the 45th vertebrae.

The axial skeleton (Figs 2, 6)

The axial skeleton is broken in four places and the last caudal vertebrae are located separately above the preceding caudal elements. However, all the vertebrae are preserved. There are 73 vertebrae, 45 in the abdominal region and 28, including the two ural centra, in the caudal region. The abdominal vertebrae are longer than deep, with their lateral faces ornamented with thin horizontal ridges. The vertebrae are a little shorter in the caudal region and principally the last ones. All the neural and haemal elements are autogenous. The neural and haemal spines are thin, rather short and very obliquely oriented. In the abdominal region, the haemal arches are represented by small paired haemapophyses (= parapophyses). There are long epineurals and epipleurals all along the axial skeleton, except at the level of the last caudal vertebrae. Generally, Ichthyodectidae are devoid of ossified epipleurals (PATTERSON & JOHNSON, 1995: 12). However, some rare ichthyodectid fishes with long bony epipleurals are known (TAVERNE, 1997: fig. 3C, D, 2009: fig. 4). The first epineurals are fused to the neural arches. They are free in the caudal region. There are long and thin ribs but their exact number is unknown, some of them being missing in the region before the pelvic girdle. The last abdominal vertebrae that bear small ribs already exhibit short haemal spines. A few supraneurals are visible but, once again, most of them are missing, due to the fossilisation.

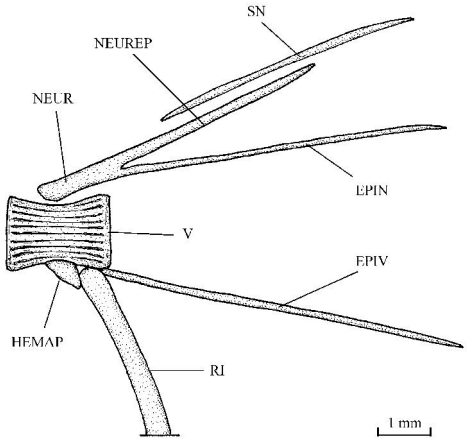

Fig. 6. *Furloichthys bonarellii* gen. and sp. nov. Eighth vertebra of holotype CLC I-163.

The dorsal and anal fins

The dorsal and anal fins are not preserved. However, fragments of five dorsal pterygiophores are visible at the level of the 46th to the 49th vertebrae, and fragments of four anal pterygiophores and of a few anal fin rays are present at the level of the 51st to the 53d vertebrae. So, it appears that the dorsal fin is located close to the caudal region and almost opposite to the anal fin.

The caudal skeleton (Figs 7, 8)

The first preural (PU1) and the two ural centra (U1, 2) are upturned and not fused together. The neural and haemal pieces involved in the caudal endoskeleton, including the hypurals (HY1-6), are autogenous. PU2 still bears a complete neural spine. The neural arch of PU1 is devoid of neural spine but bears a small dorsal point that could be the last remain of an extremely reduced spine. The

parhypural of PU1 and the haemal spines of PU2 and PU3 are broadened, the preceding haemal spines being much thinner. There is one free epural that is comma-shaped, with a broad dorsal region and an acuminate ventral extremity. The large HY1 and the smaller HY2 are fused by their broad articular heads but are simply sutured more distally. The articulate head of the ventral hypurals is not upturned. HY3 to 5 are fused together, forming a wide dorsal hypural plate. The narrow HY6 is not fused to this plate. Fragments of three long and thin uroneurals are preserved. They reach anteriorly the level of PU1. It is possible that more uroneurals were present in the living fish but lost during the fossilisation. Indeed, Ichthyodectidae often possess five or six uroneurals.

The caudal fin is not preserved but small fragments of caudal rays are visible.

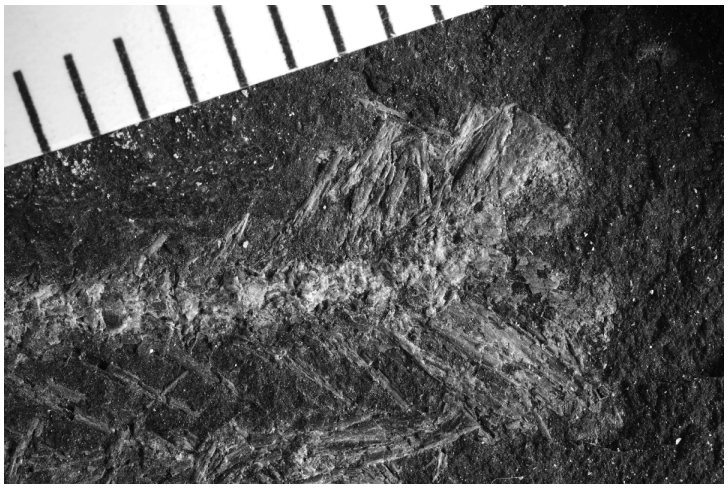

Fig. 7. *Furloichthys bonarellii* gen. and sp. nov. Caudal region of holotype CLC I-163.

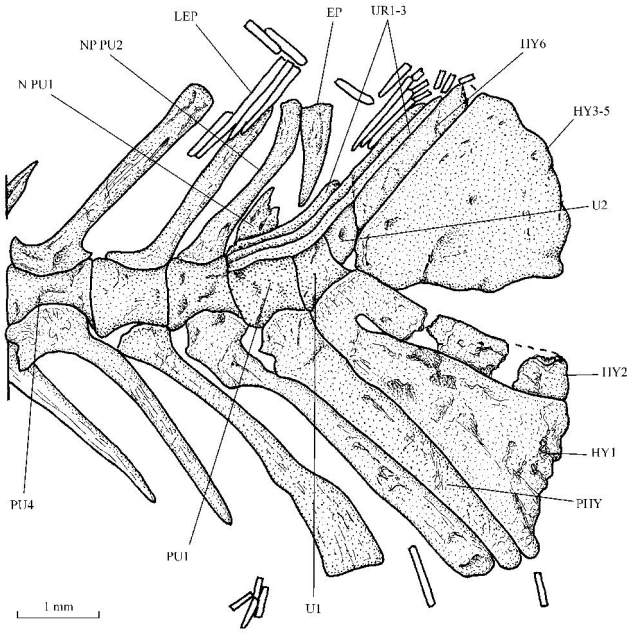

Fig. 8. *Furloichthys bonarellii* gen. and sp. nov. Caudal skeleton of holotype CLC I-163.

The squamation

Only small fragments of cycloid scales are present. It is not possible to precise the size and the ornamentation of the complete scales.

DISCUSSION

The relationships of *Furloichthys* within Teleostei

Furloichthys has a medioparietal skull, a maxilla that forms the greatest part of the oral margin of the upper jaw, two supramaxillae, a well developed orbitosphenoid, wide posterior infraorbitals, large supratemporals, an abdominal pelvic girdle, no traces of dorsal and anal spines, well developed intermuscular bones, the three last vertebrae (PU1, U1 and U2) not fused together, a neural arch on PU1, at least three uroneurals and cycloid scales. All these characters attest that the new Italian fossil fish is a primitive teleost.

Furloichthys also exhibits a latero-basal ethmoid, a prognathous lower jaw, probably a wide median parietal, a large supraoccipital crest, an elongate body, a dorsal fin located in the posterior region of the body and long uroneurals that partly cover the lateral faces of the last vertebrae. Within primitive teleosts, the combination of these characters only occurs in the family Ichthyodectidae.

Furloichthys and *Protostomias*

When commenting the present paper, a colleague paleoichthyologist mistakenly concluded that *Furloichthys bonarellii* was not an ichthyodectid but a synonym of *Protostomias maroccanus* ARAMBOURG, 1943, a well known fossil stomiiform fish from the Cenomanian of Morocco and the Cenomanian-Turonian of Italy and Sicily (ARAMBOURG, 1943, 1954; LEONARDI, 1966; SORBINI, 1976; TAVERNE, 1991; CAPASSO, 2007). The first author (L. T.) of the present paper did the same mistake when he saw for the first time sample CLC I-163 and before its study. He also thought that it was a specimen of *P. maroccanus*. Indeed, *F. bonarellii* and *P. maroccanus* share a more or less similar external morphology and the same peculiar shape of the lower jaw. But the two species differ by numerous skeletal characters. That is why we think interesting to briefly compare the two fishes to avoid future readers to do the same erroneous interpretation.

The osteological data on *P. maroccanus* hereafter mentioned come from ARAMBOURG (1954) and TAVERNE (1991).

(1) The skull is medioparietal in *F. bonarellii* and lateroparietal in *P. maroccanus*.

(2) A latero-basal etmoid (= ethmopalatine) is present in *F. bonarellii* but is absent in *P. maroccanus*.

(3) The orbitosphenoid is present and located just behind the lateral ethmoid in *F. bonarellii* The orbistosphenoid is absent in *P. maroccanus*.

(4) The supraoccipital of *F. bonarellii* bears a large median crest. The supraoccipital crest is extremely reduced in *P. maroccanus*.

(5) *F. bonarellii* has a very short premaxilla and a long maxilla. *P. maroccanus* exhibits an elongate premaxilla that forms the first half of the upper jaw oral margin.

(6) Two supramaxillae are present in *F. bonarellii*. The premaxillae are missing in *P. maroccanus*.

(7) *F. bonarellii* has a small infraorbital 2 and large infraorbitals 1 and 3. On the contrary, infraorbital 2 is greatly hypertrophied in *P. maroccanus* and much larger than infraorbitals 1 and 3.

(8) The last branchiostegal ray is a thin bone in *F. bonarellii*, while this last branchiostegal ray is greatly hypertrophied and almost as broad as the subopercle in *P. maroccanus*.

(9) The hypocoracoid of *F. bonarellii* is hypertrophied. That of *P. maroccanus* is of median size.

(10) The axial skeleton of *F. bonarellii* contains 73 vertebrae, of which 45 in the abdominal region and 28 in the caudal region. *P. maroccanus* has 81 vertebrae, of which 54 in the abdominal region and 27 in the caudal region.

(11) The epineurals are fused to the neural arches in *F. bonarellii*. They are not fused to the neural arches in *P. maroccanus*.

(12) The vertebrae PU1 and U1 are not fused together in *F. bonarellii*. These two vertebrae are fused in an elongate compound element in *P. maroccanus*.

(13) In *F. bonarellii* the vertebra PU1 bears a neural arch. Such a neural arch is missing on PU1 in *P. maroccanus*.

(14) The vertebra PU2 bears a complete neural spine in *F. bonarellii*. In *P. maroccanus* the neural spine on PU2 is reduced.

(15) *F. bonarellii* exhibits only one coma-shaped epural in the caudal skeleton. *P. maroccanus* has two rod-like epurals.
(16) Hypurals 1 and 2 are fused together by their articular heads in *F. bonarellii*. These two ventral hypurals are totally separated in *P. maroccanus*.
(17) Three thin uroneurals are present in *F. bonarellii* and they partially cover le lateral faces of vertebrae PU1, U1 and U2. Only 1 uroneural is present in *P. maroccanus* and is dorsally located in regard to the vertebral centra.

The preceding list of compared characters clearly proves that *F. bonarellii* is not a synonym of *P. maroccanus*. The two fossil fishes obviously are different.

The generic validity of *Furloichthys*

Furloichthys differs from all the known Ichthyodectidae by at least five characters that prove the generic validity of this new Italian fossil fish: (1) the lateral ethmoid is small, largely separated from the mesethmoid and devoid of contact with the parasphenoid, (2) the latero-basal ethmoid (= ethmopalatine) is associated to the mesethmoid and not to the lateral ethmoid, (3) the maxilla is curved and extremely narrow, (4) IORB 1 reaches IORB 3 below IORB 2, and (5) HY3 to 5 are fused in a large dorsal hypural plate. No other ichthyodectid fish shares these characters.

The systematic position of *Furloichthys* within Ichthyodectidae

The phylogeny of the Ichthyodectidae has been thoroughly studied during the last half-century by numerous specialists (BARDACK, 1965; TAVERNE, 1986, 2008, 2009, 2010; MAISEY, 1991; STEWART, 1999, TAVERNE & CHANET, 2000; ALVARADO-ORTEGA, 2004; BLANCO-PIÑÓN & ALVARADO-ORTEGA, 2007; ALVARADO-ORTEGA & BRITO, 2010; MKHITARYAN & AVERIANOV, 2011; CAVIN *et al.,* 2012; BERRELL *et al.*, 2014). We base our discussion hereafter on some of the characters used by these authors to define exactly the systematic position of *Furloichthys* within the family.

(1) *Thrissops* AGASSIZ, 1833, the most primitive ichthyodectid fish, *Unamichthys* ALVARADO-ORTEGA, 2004 et *Ogunichthys* ALVARADO-ORTEGA & BRITO, 2010 exhibit a pair of medially joined parietals (TAVERNE, 1977: 8; ALVARADO-ORTEGA, 2004: figs 3B, 4B; ALVARADO-ORTEGA & BRITO, 2010: 300; CAVIN *et al.*, 2012: 44). That is the plesiomorphic condition within Ichthyodectidae. The other genera of the family, share a new apomorphy. Their two parietals are fused in a median bone of which the pointed anterior extremity is wedged between the two frontals. That seems to be also the case in *Furloichthys*.

(2) The anterior part of the palatine of *Furloichthys* is deepened, forming a hammer head-like process for the articulation with the ethmoid region and with the maxilla. This character is shared by *Heckelichthys* TAVERNE, 2008 (TAVERNE, 1986: fig. 4) and the more evolved genera (STEWART, 1900: pl. 33, 42, fig. 4, pl. 53, 55; BARDACK, 1965: figs 9, 11, 16; TAVERNE, 2008: fig. 2; among others). In primitive genera, the anterior articular head of the palatine remains rather flat as, for instance, in *Cladocyclus* (PATTERSON & ROSEN, 1977: figs 2, 3) and in *Altamuraichthys* (TAVERNE, 2016: fig. 4) or is irregularly shaped (TAVERNE, 1977: figs 6, 8, 2008: fig. 9; ALVARADO-ORTEGA, 2004: fig. 3B; CAVIN *et al.*, 2012: figs 6, 11, 32).

(3) In *Furloichthys*, the maxilla is narrow all along its length. The anterior region of the bone is not markedly deepened. A rather similar situation occurs in the primitive genera of the family, such as *Thrissops* and a few others. They have all a broader maxilla than that of the new Italian ichthyodectid but the anterior portion of their maxilla is not particularly deepened (TAVERNE, 1977: figs 5, 7, 8, 2010: figs 5, 14, 19, 2016: fig. 4; PATTERSON & ROSEN, 1977: figs 1-3; ALVARADO-ORTEGA & BRITO, 2010: fig. 3A, B, C; CAVIN *et al.*, 2012: figs 4B, 5). In the more specialized genera of the family, such as *Saurocephalus* HARLAN, 1824, *Saurodon*, *Xiphactinus* LEIDY, 1870, *Ichthyodectes* COPE, 1870, *Prosaurodon* STEWART, 1999, *Vallecillichthys* BLANCO-PIÑÓN & ALVARADO-ORTEGA, 2007 and *Capassoichthys*, the anterior region of the maxilla is considerably deepened (STEWART, 1900: pl. 33, 36, fig. 3, pl. 37-40; LOOMIS, 1900: pl. 24, fig. 2, pl. 25, fig. 2; BARDACK, 1965: figs 9, 16; BARDACK & SPRINKLE, 1969: fig. 5; TAVERNE & BRONZI,

1999: fig. 3; STEWART, 1999: figs 3-6; BLANCO-PIÑÓN & ALVARADO-ORTEGA, 2007: fig. 3; CAVIN *et al.*, 2012: figs 30A, B, 31A, B; TAVERNE, 2015: fig. 4).

(4) The lower jaw of *Furloichthys* is short, with a narrow symphysis, a strongly ascending upper margin of the dentary and a deep and broad coronoid region involving both the dentary and the angular. This mandibular shape is close to that of two primitive members of the family, *Thrissops* and *Ogunichthys* (TAVERNE, 1977: figs 5-8; ALVARADO-ORTEGA & BRITO, 2010: figs 5A, D, 7D) and also to that of *Allothrissops* NYBELIN, 1964 and *Occithrissops* SCHAEFFER & PATTERSON, 1984, two ichthyodectiform fishes less specialized than the Ichthyodectidae (PATTERSON & ROSEN, 1977: fig. 9A; SCHAEFFER & PATTERSON, 1984: fig. 28A). However, the raising of the upper margin of the dentary and the development of the coronoid region in *Furloichthys* are still much more important than in the four preceding genera. In more advanced Ichthyodectidae, the lower jaw has a less ascending upper margin. The coronoid process is strongly reduced and only formed by the dentary (STEWART, 1900: pl. 34, 35, 37-40; LOOMIS, 1900: pl. 24, figs 3, 4, 6, pl. 25, fig. 3; BARDACK & SPRINKLE, 1969: fig. 6; PATTERSON & ROSEN, 1977: fig. 8C; TAVERNE & BRONZI, 1999: fig. 3; TAVERNE, 2010: fig. 14; 2015: fig. 5, 2016: fig. 4). The lower jaw of the evolved ichthyodectid fish *Garganoichthys* exhibits the primitive mandibular pattern (TAVERNE, 2009: fig. 2). That is probably a reversion.

(5) The retroarticular of *Furloichthys* is involved in the lower jaw articular facet for the quadrate. That is the plesiomorphic condition for the Ichthyodectidae (PATTERSON & ROSEN, 1977: 101; TAVERNE, 2010: fig. 15; among others). This primitive mandibular character still persists in *Cladocyclus* (PATTERSON & ROSEN, 1977: fig. 8 B, C). In more advanced ichthyodectid fishes, the retroarticular is excluded from the articular facet for the quadrate (BARDACK, 1965: fig. 10, 20 B; BARDACK & SPRINKLE, 1969: fig. 6; NELSON, 1973: fig. 3 A-C, 6 A; TAVERNE, 2009: fig. 2, 2015: fig. 6).

(6) The neural spine on PU 1 is very short or absent in the primitive ichthyodectid genera. That is the case in *Thrissops*, *Ogunichthys*, *Unamichthys*, *Eubiodectes* HAY, 1903, *Cladocyclus*, *Chiromystus* COPE, 1885, *Verraesichthys* TAVERNE, 2010 and *Altamuraichthys* (TAVERNE, 1977: figs 14, 15, 2010: figs 11, 22, 2016: figs 10, 13, 14; PATTERSON & ROSEN, 1977: figs 14, 19, 20; ALVARADO-ORTEGA, 2004: fig. 7B; ALVARADO-ORTEGA & BRITO, 2010: 303; CAVIN *et al.*, 2012: 21, fig. 17). The same feature occurs in *Furloichthys*. In the advanced ichthyodectid genera, PU1 and sometimes also U 1 bear a complete neural spine. Such a morphology is present in *Heckelichtys*, *Garganoichthys*, the Saurodontinae, the Ichthyodectinae and the Gillicinae, (LOOMIS, 1900, pl. 23, fig. 6; CAVENDER, 1966: fig. 1B; TAVERNE, 1986: fig. 5, 1997: figs 4, 5, 2009: fig. 5; WILSON & CHALIFA, 1989: fig. 4).

(7) In *Furloichthys*, there is one free epural. The primitive genera *Thrissops*, *Ogunichthys* and *Unamichthys* still possess 3 epurals (TAVERNE, 1977: figs 14, 15; PATTERSON & ROSEN, 1977: fig. 14; ALVARADO-ORTEGA, 2004: fig. 7B; ALVARADO-ORTEGA & BRITO, 2010: 303). *Eubiodectes* and *Altamuraichthys* exhibit only 2 free epurals (PATTERSON & ROSEN, 1977: fig. 20; CAVIN *et al.*, 2012: 21, fig. 17; TAVERNE, 2016: figs 10, 13). In *Cladocyclus*, *Chiromystus* COPE, 1885 and *Verraesichthys* TAVERNE, 2010, there is only one free epural (PATTERSON & ROSEN, 1977: fig. 19; TAVERNE, 2010: figs 11, 22, 2016: fig. 14) as in *Furloichthys*. In *Heckelichtys*, *Garganoichthys*, the Saurodontinae, the Ichthyodectinae and the Gillicinae, there is no free epural (LOOMIS, 1900, pl. 23, fig. 6; CAVENDER, 1966: fig. 1B; TAVERNE, 1986: fig. 5, 1997: figs 4, 5, 2009: fig. 5; WILSON & CHALIFA, 1989: fig. 4). The complete neural spine present on PU 1 in those advanced genera seems to be the result of the capture of the free epural by the last neural arch. There is thus a link between characters (6) and (7).

(8) HY1 has a broad and not upturned proximal region in *Furloichthys*. The same morphology is present in the primitive genera of the family, from *Thrissops* to *Heckelichthys* (TAVERNE, 1977: figs 14, 15, 1986: fig. 5, 2010, figs 12, 22, 2016: figs 10, 13, 14; PATTERSON & ROSEN, 1977: figs 13, 14, 19, 20; MAISEY, 1991: fig. p. 199 [in the middle]; ALVARADO-ORTEGA, 2004: fig. 7A, B). In *Garganoichthys* and in the Saurodontinae, the Ichthyodectinae and the Gillicinae, the articular head of HY1 is narrow, elongated and straightened (CAVENDER, 1966: figs 1, 3; ROSEN & PATTERSON, 1977: figs 15, 16; WILSON & CHALIFA, 1989: fig. 4; TAVERNE, 1997: figs 4, 5, 2009: fig. 5, 2010: fig. 23).

Characters (3), (4), (5) and (8) indicate that *Furloichthys* is a rather primitive ichthyodectid fish and characters (1) and (7) that it is more specialized than *Thrissops*, *Ogunichthys* and *Unamichthys*. For characters (5), (6), (7) and (8), *Furloichthys* is located among the genera less advanced than *Heckelichthys*, *Capassoichthys*, the Saurodontinae, the Ichthyodectinae and the Gillicinae but, for character (2), *Furloichthys* is connected to the group comprising *Heckelichthys* and the more evolved members of the family.

So, within the phylogeny of Ichthyodectidae, *Furloichthys* occupies an intermediate position between the plesiomorphic *Cladocyclus*, *Chiromystus*, *Verraesichthys* and the less advanced genera, on the one hand, and the apomorphic *Heckelichthys* plus the more specialized genera, on the other hand.

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