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A new insight into the Protobramidae (Teleostei, Tselfatiiformes), a fossil fish family from the marine Cenomanian (Upper Cretaceous) of Lebanon

Un nouveau regard sur les Protobramidae (Teleostei, Tselfatiiformes), une famille de poissons fossiles du Cénomanien marin (Crétacé supérieur) du Liban

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Résumé: L'étude de nouveaux spécimens d'*Abisaadichthys* et d'*Eusebichthys*, deux genres appartenant aux Protobramidae (Tselfatiiformes), une famille de téléostéens du Cénomanien marin (Crétacé supérieur) du Liban, a fait mieux connaître le squelette de ces poissons. La découverte d'une ceinture pelvienne en position thoracique chez *Eusebichthys* a permis une meilleure compréhension de la phylogénie au sein de la famille.

Mots-clés: Teleostei, Tselfatiiformes, Protobramidae, *Abisaadichthys libanicus*, *Eusebichthys byblosi*, ostéologie, relations, Cénomanien marin, Liban.

Abstract: The study of new specimens of *Abisaadichthys* and *Eusebichthys*, two genera belonging to the Protobramidae (Tselfatiiformes), a teleost family from the marine Cenomanian (Upper Cretaceous) of Lebanon, gives a better knowledge of the skeleton of these fishes. The discovery of a pelvic girdle in thoracic position in *Eusebichthys* allows a better understanding of the phylogeny within the family.

Key words: Teleostei, Tselfatiiformes, Protobramidae, *Abisaadichthys libanicus*, *Eusebichthys byblosi*, osteology, relationships, marine Cenomanian, Lebanon.

INTRODUCTION

Protobramidae is one of the three families, with the Eoplethodidae and the Plethodidae (= Bananogmiidae, Tselfatiidae), that constitute the order Tselfatiiformes (= Bananogmiiformes), a fossil teleost lineage known from the Albian (Lower Cretaceous) to the Campanian (Upper Cretaceous) in Europe, North, Central and South America, North Africa, the Near and the Far East (TAVERNE & GAYET, 2004, 2005; CAVIN & FOREY, 2008; TAVERNE & LISTON, 2017).

Protobramids are small fishes. The largest ones do not exceed 20 cm in total length. They are endemic in the marine Cenomanian (Upper Cretaceous) of Lebanon. No other occurrence is known. Today, the family contains three genera, *Protobrama* WOODWARD, 1942, *Eusebichthys* TAVERNE & GAYET, 2004 and *Abisaadichthys* TAVERNE & GAYET, 2004, distributed in four species, *Protobrama avus* WOODWARD, 1942, *Protobrama woodwardi* TAVERNE & GAYET, 2004, *Eusebichthys byblosi* TAVERNE & GAYET, 2004 and *Abisaadichthys libanicus* TAVERNE & GAYET, 2004. However, a fourth unnamed genus exists (GAYET *et al.*, 2012: 118, fig. above left). It has the same general morphology of *P. avus* but differs from *Protobrama* by the presence of a pelvic girdle, an anatomical structure lost in this last genus. Unfortunately, the unique specimen of that fourth genus belongs to a private collection and is not available for a scientific study.

The original description of *Abisaadichthys libanicus* is based on the holotype only (University of Lyon, FSL-573086) and that of *Eusebichthys byblosi* on two specimens, the holotype (Muséum National d'Histoire Naturelle de Paris, MNHN – HAK 306) and one paratype (Museum of the ABI SAAD family at Jbail (= Byblos), Lebanon, ABSA – 1).

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Unfortunately, the skull is crushed and badly preserved in the three specimens used for the original description. So, the cranial reconstructions proposed by TAVERNE & GAYET (2004: figs 17, 23) are by far not perfect.

The CAPASSO registered collection in Chiety (Italy) contains samples of these two species with a well better preserved skull. The aim of the present paper is thus to re-describe the skeleton of *A. libanicus* and *E. byblosi* in a more accurate and detailed way than previously and to discuss the bearing of these new data on the phylogeny of the family. The present study also allows a morphometric comparison of our new material with the specimens previously described (TAVERNE & GAYET, 2004).

MATERIAL AND METHODS

The specimens studied in the present paper belong to the CAPASSO collection (CLC) in Chieti (The Abruzzi, Italy). They were examined 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 and razing light 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).

List of abbreviations used in the text-figures

AN	=	angular
ANT	=	antorbital
ART	=	articular
ASPH	=	autosphenotic
BRSTG	=	branchiostegal ray
BSPH	=	basisphenoid
CLT	=	cleithrum
COR	=	hypocoracoid (= coracoid *sensu stricto*)
ENPT	=	entopterygoid
EP1, 2	=	epurals 1 and 2
EPI	=	epiotic (= epioccipital)
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
HEM	=	haemal arch
HEMEP	=	haemal spine
HY 1, 3	=	hypurals 1 and 3
HYOM	=	hyomandibula
IOP	=	interopercle
IORB 1-7	=	infraorbitals 1 to 7
LEP	=	lepidotrich (= fin ray)
LEP p.	=	lepidotrich of the pectoral fins
LEP v.	=	lepidotrich of the ventral fins
LETH	=	lateral ethmoid
METH	=	mesethmoid
MX	=	maxilla
NA	=	nasal
NEUR	=	neural arch
NEUREP	=	neural spine
NP PU1	=	neural spine of preural vertebra 1
OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
PELV	=	pelvic bone
PHY	=	parhypural
POP	=	preopercle
PRO	=	prootic
PS	=	parasphenoid
PSPH	=	pleurosphenoid

PT	=	posttemporal
PTE	=	pterotic
PU 1-5	=	preural vertebrae 1 to 5
QU	=	quadrate
RART	=	retroarticular
SC	=	scales
SCL	=	sclerotic bone
SOC	=	supraoccipital
SOP	=	subopercle
ST	=	supratemporal (= extrascapular)
SY	=	symplectic
U 1, 2	=	ural vertebrae 1 and 2
UR 1-3	=	uroneurals 1 to 3
f. IV	=	foramen for the pathetic nerve (IV)
fr.	=	fragment
f. t.	=	temporal (= posttemporal) fossa
iorb. c.	=	infraorbital sensory canal
l.	=	left
r.	=	rigth

SYSTEMATIC PALEONTOLOGY

Division Teleostei MÜLLER, 1846
Cohort Clupeocephala PATTERSON & ROSEN, 1977
Order Tselfatiiformes NELSON, 1994
Family Protobramidae LE DANOIS & LE DANOIS, 1964
Genus ***Abisaadichthys*** TAVERNE & GAYET, 2004
Species ***Abisaadichthys libanicus*** TAVERNE & GAYET, 2004

Studied specimen

Sample CLC S-290. A complete specimen (Fig. 1) from the marine Upper Cenomanian of Haqel, Lebanon. Total length: 148 mm. Standard length: 115 mm.

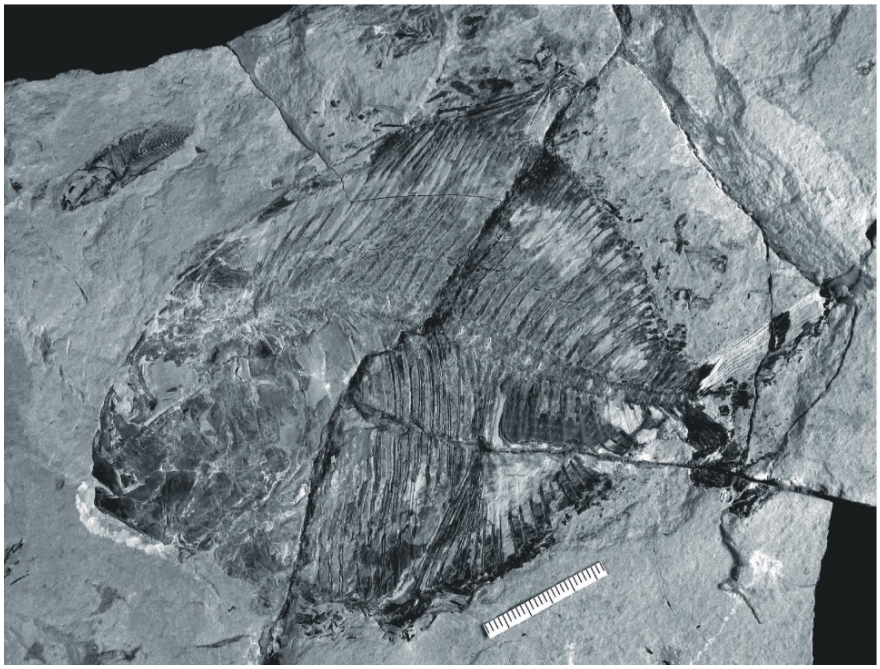

Fig. 1. *Abisaadichthys libanicus* TAVERNE & GAYET, 2004. Specimen CLC S-290.

General morphology and morphometric data (Fig. 1)

With a total length of 148 mm, specimen CLC S-290 is much larger than the holotype of the species that has only 70 mm in total length. The new specimen is also much deeper than the holotype. The following list compares the morphometric data of sample CLC S-290 and of the holotype (cf. TAVERNE & GAYET, 2004: 301). These data are given in percentage (%) of the standard length of sample CLC S-290 (115 mm) and of the holotype (55 mm).

	CLC S-290	Holotype
Head length (opercle included)	38.2 %	38.4 %
Head depth (occipital level)	50.9 %	43.4 %%
Maximum body depth (just before the dorsal fin)	86.0 %	60.4 %
Predorsal length	55.4 %	55.7 %
Preanal length	51.0 %	55.8 %

Osteology

The skull (Figs 2, 3)

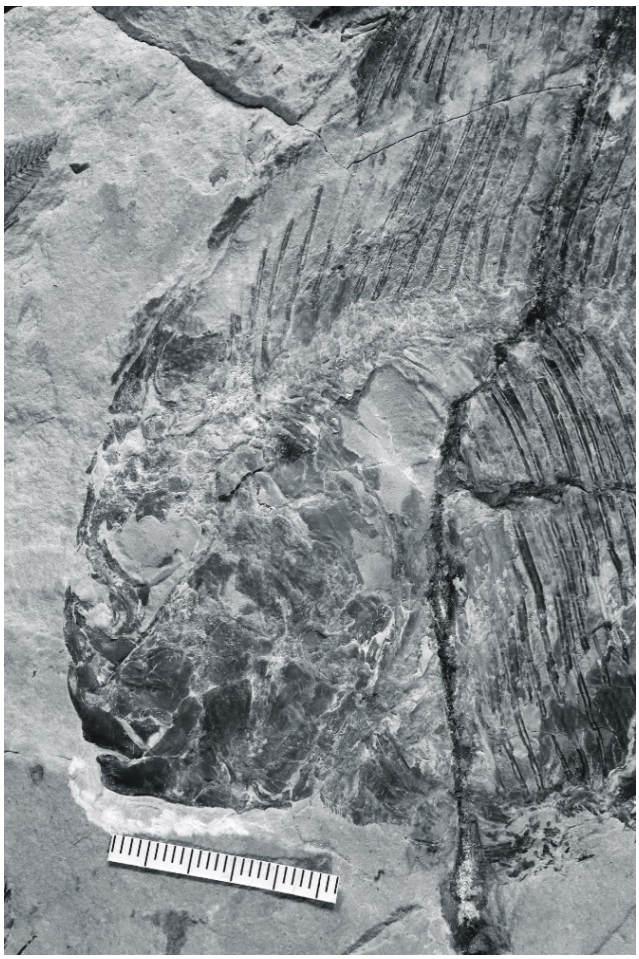

Fig. 2. *Abisaadichthys libanicus* TAVERNE & GAYET, 2004. Head region of specimen CLC S-290.

The snout is very short and almost aquiline in CLC S-290. The mesethmoid is a long, narrow, vertically oriented and feebly arched bone. Its ventral extremity is slightly broadened, forming a small plate. There is a narrow wing-like extension along the middle region of the posterior margin of the bone. The nasal is short and tubular. A large lateral ethmoid is present. It has no contact with the mesethmoid. The vomer is not visible.

The skull roof is triangular in shape. The frontal has a narrow anterior region and a broader posterior one but is not so short than the bone figured in TAVERNE & GAYET (2004: fig. 23). In CLC S-290, the most anterior part of the frontal does not join the mesethmoid but is ventrally bent due to a taphonomic distortion. The parietal is well developed and the skull is medioparietal. The pterotic is a deep and long bone. A small autosphenotic is also visible. The epiotic (= epioccipital) is partly hidden by the supratemporal (= extrascapular). The supraoccipital bears an enormous posterior acuminate median crest.

There is a small ovoid temporal (= posttemporal) fossa laterally located on the skull and not on the rear of the braincase. The fossa is surrounded by the parietal dorsally, by the epiotic posteriorly and by the pterotic and the frontal ventrally. The supratemporal is small, more or less rounded and located just behind the fossa. TAVERNE & GAYET (2004: fig. 23) do not figure a contact between the frontal and the fossa and show a rod-like supratemporal.

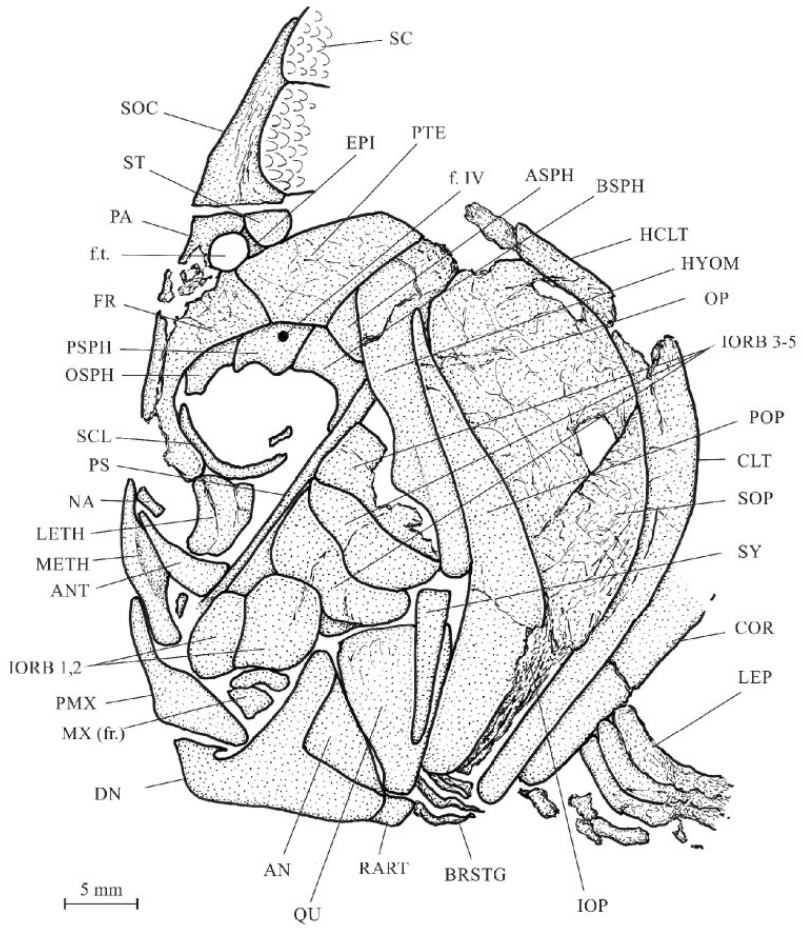

Fig. 3. *Abisaadichthys libanicus* TAVERNE & GAYET, 2004. Skull and pectoral girdle of specimen CLC S-290.

The orbitosphenoid, the pleurosphenoid and the basisphenoid are present. The orbitosphenoid is strongly reduced. The pleurosphenoid bears a foramen for the pathetic nerve (IV). The trabecular region of the parasphenoid is straight, toothless and obliquely oriented. There is no basipterygoid process. The prootic, the exoccipital, the intercalary and the basioccipital are hidden by the hyomandibula and the opercle.

The quadrate is triangular in shape, deep but rather narrow, with a strongly developed articular condyle and a long quadratic bony process parallel to the body of the bone. The other pieces of the quadratic arch are not visible on sample CLC S-290, except a small region of the entopterygoid and a very small part of the metapterygoid that appears under the infraorbitals. In the holotype, the palatine and the entopterygoid are covered by small dental alveoli (TAVERNE & GAYET, 2004: 302).

The jaws are toothless in CLC S-290 but a few small conical teeth are visible on the premaxilla and the dentary of the holotype (ibid., 2004: fig. 23). The premaxilla is a large and long bone that bears an elongate, narrow symphyseal ascending process. The premaxilla of the holotype was described as devoid of ascending process. This apparent absence is thus not real but due to an artefact of fossilisation. The narrow maxilla is incomplete on the holotype and only a small anterior part of the bone is visible on CLC S-290. The lower jaw is short but extremely deep in the coronoid region. The coronoid apex is formed by the dentary only, without a participation of the angular. A well marked "leptolepid" notch is present in the oral margin of the dentary. The articular is not known. There is a small autogenous retroarticular in which the condyle of the quadrate is fitted.

Only a few fragments of some large infraorbitals are present in the holotype. In sample CLC S-290, the antorbital and the first five infraorbitals are visible. The antorbital is a deep triangular bone that extends along the mesethmoid. The five visible infraorbitals are hypertrophied. They are positioned below the parasphenoid. The posterior infraorbitals are not preserved. The total number of the infraorbitals was thus much higher than the five ones usually present in teleosts. No supraorbital is visible. There is a sclerotic bony ring.

The preopercle has well developed dorsal and ventral branches, the dorsal one being longer but narrower than ventral. A small part of the interopercle is visible under the preopercle in CLC S-290. The opercle is a wide and more or less ovoid bone. The subopercle is much smaller. Fragments of a few branchiostegal rays are present below the preopercle.

The hyomandibula is elongated but rather narrow. Its articular head is not divided. A long symplectic is present between the body of the quadrate and its quadratic bony process in CLC S-290.

The girdles (Fig. 3)

Specimen CLC S-290 does not bring new information about the girdles in *Abisaadichthys libanicus*. In the holotype the pelvic girdle has a thoracic position and the ventral fins are extremely long (TAVERNE & GAYET, 2004: fig. 24). The pelvic girdle is not visible in CLC S-290.

The axial skeleton (Fig. 1)

The shape and the size of the vertebrae is studied and figured in a detailed way in the holotype (ibid., 2004: fig. 25). The vertebrae of sample CLC S-290 are completely similar in shape and size than those of the holotype. However, the vertebral count slightly differs. The holotype has 40 (16 + 24) vertebrae, while CLC S-290 exhibits only 37 (18 + 19) centra. The holotype has twelve pairs of ribs and CLC S-290 fifteen pairs.

The dorsal and anal fins (Fig. 1)

In CLC S-290, the rays of the dorsal and the anal fins are incompletely preserved but it is possible to count the pterygiophores (= axonosts). CLC S-290 has 45 pterygiophores in the dorsal fin and 25 pterygiophores in the anal fin. The holotype has respectively 42 and 24 pterygiophores in these two fins.

The caudal skeleton and fin (Figs 4, 5)

The caudal skeleton is less complete in CLC S-290 than in the holotype but the characters are similar. The preural vertebra 1 (PU1) and the ural vertebrae 1 and 2 (U1, 2) are individualized but smaller than the preceding vertebrae. PU1 bears a complete neural spine. There are 3 uroneurals, the first one being broadened and the two following rod-like. Specimen CLC S-290 also exhibits 2 short epurals located just above the neural spine of the preural vertebra 2. No epural is visible on the holotype.

There are 19 principal rays in the caudal fin of the holotype. The fin is partly missing in CLC S-290 but the hypurostegy is more pronounced than in the holotype.

The squamation

The scales are better preserved in CLC S-290 than in the holotype. They are rounded but extremely small.

Genus ***Eusebichthys*** TAVERNE & GAYET, 2004
Species ***Eusebichthys byblosi*** TAVERNE & GAYET, 2004

Studied specimens

Sample CLC S-460. A complete specimen (Fig. 6) from the marine Upper Cenomanian of Haqel, Lebanon. Total length: 200 mm. Standard length: 150 mm.

Sample CLC S-463a, b. Part and counterpart of a complete specimen (Figs 7, 8) from the marine Upper Cenomanian of Haqel, Lebanon. Total length: 155 mm. Standard length: 119 mm.

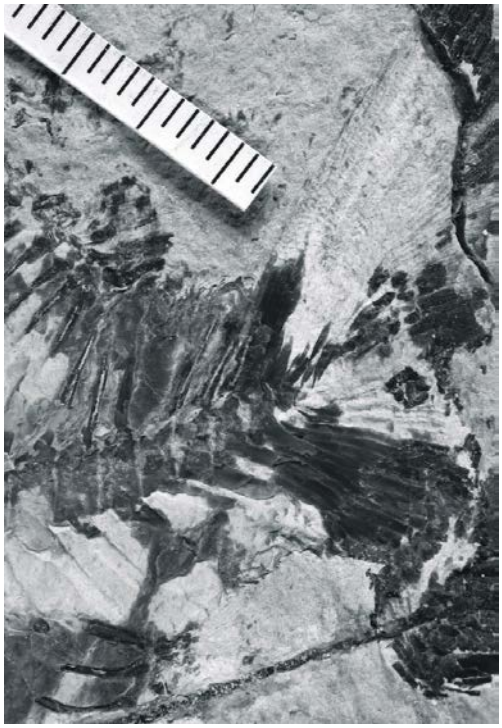

Fig. 4. *Abisaadichthys libanicus* TAVERNE & GAYET, 2004. Tail region of specimen CLC S-290.

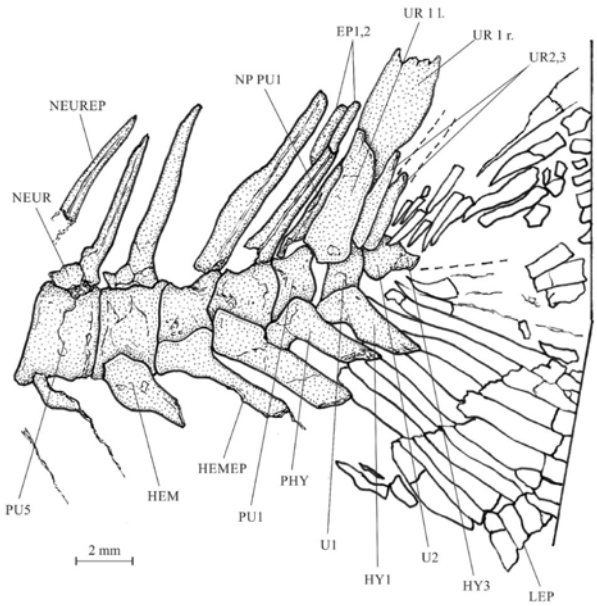

Fig. 5. *Abisaadichthys libanicus* TAVERNE & GAYET, 2004. Caudal skeleton of specimen CLC S-290.

Fig. 6. *Eusebichthys byblosi* TAVERNE & GAYET, 2004. Specimen CLC S-460.

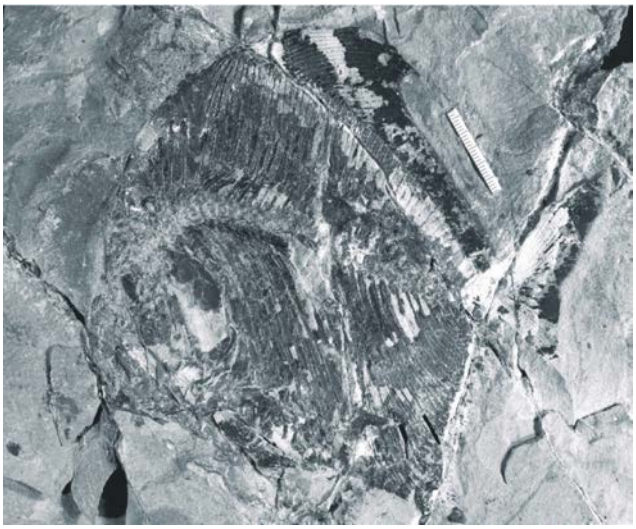

Fig. 7. *Eusebichthys byblosi* TAVERNE & GAYET, 2004. Specimen CLC S-463a.

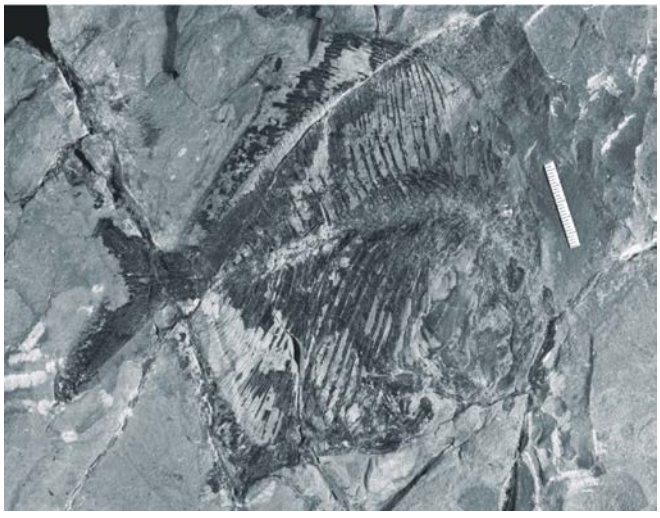

Fig. 8. *Eusebichthys byblosi* TAVERNE & GAYET, 2004. Specimen CLC S-463b.

Osteology

The skull (Figs 9, 10)

The mesethmoid is a small lozenge-shaped bone that bears a small lateral process on each side. Posteriorly, the mesethmoid reaches the frontal. Two rod-like nasals laterally surround the mesethmoid. The narrow lateral ethmoid is suspended to the frontal and has no contact with the mesethmoid. Ventrally, the lateral ethmoid reaches the level of the parasphenoid. The vomer is not visible.

Fig. 9. *Eusebichthys byblosi* TAVERNE & GAYET, 2004. Head region of specimen CLC S-460.

The frontal is long and broad all along its length. The parietal is a large bone and the skull is medioparietal. The supraoccipital bears a very elongate crest that largely outpaces the rear of the braincase and on which the upper margin of the enlarged posttemporal is pressed. The autosphenotic, the pterotic and the epiotic (= epioccipital) are also present along the lateral side of the skull roof behind the level of the orbit.

A wide rounded temporal (= posttemporal) fossa is clearly visible on sample CLC S-460. This fossa is located on the lateral side of the braincase and not on its rear as usually in teleosts. The dorsal margin of the fossa is formed by the parietal and the posterior and the ventral margins by the extremely narrow epiotic. Parts of the frontal and of the pterotic are lost due to the fossilization. But the imprint of the suture between the two bones is clearly visible on the substratum and allows seeing that the frontal forms the anterior margin of the fossa. The pterotic reaches the fossa in one point only, just before the ventral region of the epiotic. A small triangular supratemporal (= extrascapular, scale bone) is visible behind the epiotic.

The orbitosphenoid, the pleurosphenoid and the basisphenoid are well preserved on sample CLC S-460. They are rather small bones that do not form an interorbital bony septum. Only small fragments of the parasphenoid are visible on specimen CLC S-460 but the trabecular part of the bone is complete on the holotype and the paratype, showing that the parasphenoid is toothless and devoid of basipterygoid process.

The anterior border of the prootic is visible on CLC S-460, just before the hyomandibula, but the exoccipital, the intercalar and the basioccipital are hidden by the opercle and the hyomandibula.

The palatine is not preserved in any available specimen. Sample CLC S-460 exhibits parts of the entopterygoid with tiny rounded teeth and minute dental alveoli. The metapterygoid is a large bone, as seen on the holotype. No bony process is visible on the triangle-shaped quadrate.

The jaws are toothless. The premaxilla has a long oral branch that forms almost the first half of the upper jaw. The bone bears an elongate symphyseal ascending process that reaches the mesethmoid. The maxilla

is long and narrow. There is no supramaxilla. The lower jaw is triangular in shape, with a narrow symphysis and a deeper coronoid region. Sample CLC S-460 exhibits the inner side of the mandible, showing a massive autogenous articular. A well marked "leptolepid" notch is clearly visible in the upper margin of the dentary in this specimen. There is a small autogenous retroarticular.

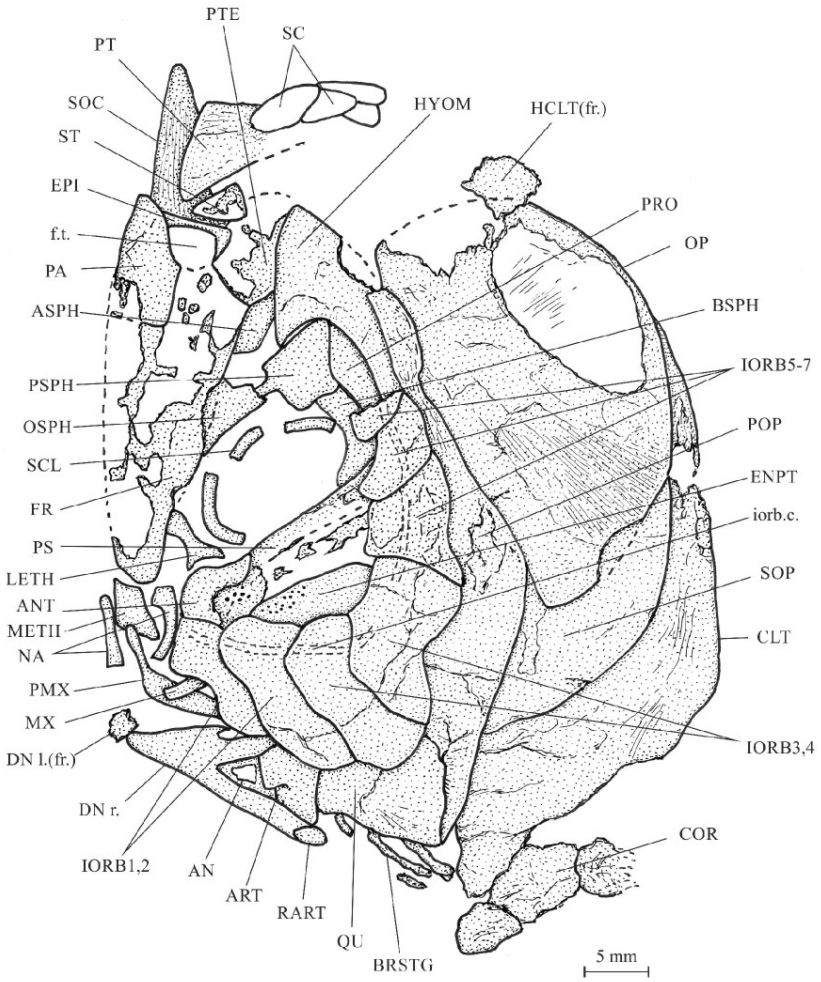

Fig. 10. *Eusebichthys byblosi* TAVERNE & GAYET, 2004. Skull and pectoral girdle of specimen CLC S-460.

The antorbital, six infraorbitals and a small part of a seventh one are preserved on sample CLC S-460. The small antorbital is located just above the first infraorbital and is sutured to it. The infraorbitals 1 to 4 exhibit a deep ventral expansion that partly covers the upper jaw and a small region of the preopercle. The sixth infraorbital is positioned at the level of the parasphenoid and the seventh a little more dorsally. The series is not complete and the uppermost posterior infraorbitals are missing. When complete the infraorbital series probably contains at least eight or nine elements and not five as the normal count in teleosts. The dermosphenotic is not preserved in any specimen. No supraorbital is visible. There is a sclerotic bony ring.

The opercle, subopercle and preopercle are crushed on CLC S-460 and S-463a, b. But these three bones are well preserved on the holotype and the paratype. The preopercle has a long but narrow dorsal branch and a shorter but much broader ventral branch. The opercle is a wide bone, with a straight anterior border and a rounded posterior margin. The subopercle is much smaller. The interopercle is never visible. There are at least nine branchiostegal rays.

The holotype exhibits a perfectly preserved hyomandibula. The bone is deep, rather narrow, with a unique articular condyle for the skull and a knob-like opercular process.

The girdles (Figs 9-12)

The pectoral girdle is well described and figured in TAVERNE & GAYET (2004: 299, fig. 17).

The two pectoral fins are largely disjoined on sample CLC S-460. Two pelvic bones and fragments of two ventral fins are preserved and well visible in the space between the pectoral fins and just above. The ventral fin begins with a long pointed ray and there are at least eight other ray. Until now, ***Eusebichthys byblosi*** was thought to be devoid of pelvic girdle as in ***Protobrama***.

Fig. 11. *Eusebichthys byblosi* TAVERNE & GAYET, 2004. Pectoral and pelvic region of specimen CLC S-460.

The postcranial skeleton

The exact number of vertebrae and of rays and pterygiophores of the dorsal and anal fins is not known in samples CLC S-460 and S-463a, b. The caudal endoskeleton and fin is not preserved in these specimens. However, the vertebral axis, the caudal skeleton and the impaired fins are described in a detailed way in TAVERNE & GAYET (2004). We refer the readers to that paper for the information concerning these parts of the skeleton.

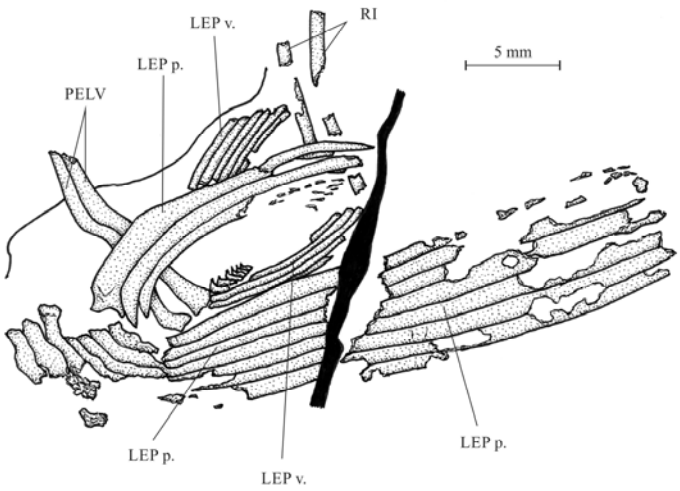

Fig. 12. *Eusebichthys byblosi* TAVERNE & GAYET, 2004. Pectoral fins, pelvic bones and ventral fins of specimen CLC S-460.

DISCUSSION

A part of the dorsal region is lost in the holotype of *Eusebichthys byblosi*. So the maximum depth of the body was measured on the paratype, with a value of about 60 % of the standard length (TAVERNE & GAYET, 2004: 296). GAYET *et al.* (2012: 118, 119) show the photos of three other specimens, with a body depth of respectively 61 %, 78 % and 87 % of the standard length. Such important differences in the trunk height lead GAYET *et al.* (2012) to think that the specimens with a body depth of 78 % and 87 % represent one or two new species of *Eusebichthys*. The CAPASSO collection contains two other samples of the genus, one with a trunk height of 72 % and the other with 104 % of the standard length. However, all these specimens have approximately the same cranial osteology and the same counts for the vertebrae, the ribs, the pectoral, dorsal, anal and caudal fin pterygiophores or rays. In those conditions, it seems preferable to consider that these body depth differences are due to individual, sexual, nutritional or seasonal variations rather than to the presence of several sympatric species in the genus.

It is to be noted that a marked difference in the body depth also occurs between the two known specimens of *Abisaadichthys libanicus*. This character seems thus present in both genera.

The present study of the new specimens brings a well better and more complete understanding of the skull in *Abisaadichthys* and *Eusebichthys* than previously. From now on, the snout region, the temporal fossa, the jaws and the infraorbital series are known in details.

We have seen that the frontal is one of the bones bordering the temporal fossa in *Abisaadichthys* and *Eusebichthys*. In *Protobrama*, the frontal is excluded from the margin of the fossa (TAVERNE & GAYET, 2004: figs 4, 11).

The presence of a "leptolepid" notch in the oral margin of the dentary of *Abisaadichthys* and *Eusebichthys* is another discovery.

We have also seen that the important multiplication of the infraorbitals present in *Protobrama* already occurs in *Abisaadichthys* and *Eusebichthys*. This feature is thus a general character of the family. However, the infraorbitals are large bones in *Abisaadichthys* and *Eusebichthys*, while they are reduced to numerous small square-like bones in *Protobrama* (ibid., 2004: figs 4, 11).

Nevertheless, the principal discovery done during our study is the unexpected presence of a thoracic located pelvic girdle with small ventral fins in *Eusebichthys*.

Abisaadichthys, the most primitive genus of the family Protobramidae, still exhibits a well developed pelvic girdle in thoracic position and with long ventral fins (ibid., 2004: figs 22, 24). On the other hand, the loss of the pelvic girdle and of the ventral fins is one of the major apomorphies of *Protobrama*, the most evolved genus of the lineage (ibid., 2004: figs 3, 11). Previously, *Eusebichthys* was also described as devoid of pelvic girdle (ibid., 2004: 299) and the loss of that girdle was thus considered as a character acquired during the evolutionary transition from *Abisaadichthys* to *Eusebichthys* (ibid., 2004: fig. 28, character 31). So, the presence within the family of a fourth still unnamed genus (GAYET *et al.*, 2012: 118, fig. above left) states a real problem. Indeed, this fourth genus still preserves a well developed pelvic girdle but also shares with *Protobrama* a series of advanced characters not present in *Eusebichthys*, *i. e.*, the general body shape, the lengthening of the ventral branch of the cleithrum, the pectoral fins inserted high on the flanks and the extremely oblique orientation of the first anal pterygiophores. The present discovery of a pelvic girdle in *Eusebichthys* solves the problem. Now, we know that the loss of the pelvic girdle does not occur during the passage from *Abisaadichthys* to *Eusebichthys* but during the one from the unnamed fourth genus to *Protobrama*.

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