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The Pantodontidae (Teleostei, Osteoglossomorpha) from the marine Cenomanian (Upper Cretaceous) of Lebanon. 1°. *Pankowskipiscis haqelensis* gen. and sp. nov.

Les Pantodontidae (Teleostei, Osteoglossomorpha) du Cénomanien marin (Crétacé supérieur) du Liban. 1°. *Pankowskipiscis haquelensis* gen. et sp. nov.

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Résumé: L'ostéologie et la position systématique de *Pankowskipiscis haqelensis*, un poisson fossile du Cénomanien marin du Liban, sont étudiées en détails. Le crâne et le squelette caudal montrent que ce poisson appartient à l'ordre des Osteoglossiformes. Quelques caractères crâniens, tels que la présence d'un postfrontal, la bulle sacculo-lagénaire hypertrophiée et le pariétal formant le bord supérieur de la fosse temporale, rapportent plus particulièrement *P. haqelensis* à la famille des Pantodontidae.

Mots-clés: Osteoglossomorpha, Pantodontidae, *Pankowskipsicis haqelensis* gen. and sp. nov., ostéologie, phylogénie, Cénomanien marin, Liban.

Abstract: The osteology and the systematic position of *Pankowskipiscis haqelensi*, a fossil fish from the marine Cenomanian of Lebanon, are studied in details. The skull and the caudal skeleton indicate that this fish belongs to the order Osteoglossiformes. Some cranial characters, such as the presence of a postfrontal, the hypertrophied saccular-lagenar bulla and the parietal forming the upper margin of the temporal fossa, refer more particularly *P. haquelensis* to the family Pantodontidae.

Key words: Osteoglossomorpha, Pantodontidae, *Pankowskipiscis haqelensis* gen. and sp. nov., osteology, phylogeny, marine Cenomanian, Lebanon.

INTRODUCTION

The family Pantodontidae belongs to the superorder Osteoglossomorpha, a lineage of primitive teleosts known from the Jurassic-Cretaceous boundary to the present days. The family generally is ranged within the order Osteoglossiformes, the suborder Osteoglossoidei and is regarded as the sister-group of the Osteoglossidae (see for instance NELSON *et al.*, 2016). However, a genetic study of LAVOUÉ & SULLIVAN (2004) gives another phylogenetic result and places the Pantodontidae as the plesiomorphic sister-lineage of both the Osteoglossiformes and the Mormyriformes.

During a long time the family contained only one genus, *Pantodon* PETERS, 1876, and one species, *Pantodon buchholzi* PETERS, 1876, the butterfly-fish, a small recent species from the continental waters of Africa. But recently TAVERNE & CAPASSO (2012) described a fossil pantodontid fish from the marine Cenomanian of Lebanon, *Prognathoglossum kalassyi* TAVERNE & CAPASSO, 2012, a fish that was firstly considered as a Lophotidae (GAYET *et al.*, 2012: fig. p. 158 below).

A few other undescribed fossil marine pantodontid genera exist in the Cenomanian of Lebanon (pers. observ.). One of them is figured in GAYET *et al.* (2012: fig. p. 157) and presented as a Bregmacerotidae.

The present paper is the first one of a series devoted to the osteological and phylogenetic study of those Lebanese fossil pantodontid fishes.

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MATERIAL AND METHODS

The specimens hereafter examined belong to the paleontological collection of the Belgian Royal Institute of Natural Sciences (IRSNB). They were studied with a stereomicroscope Wild M5. The drawings were made by the author with a camera lucida.

List of abbreviations used in the text-figures

AN	=	angular
ANT	=	antorbital
APAL	=	autopalatine
ART	=	articular
ASPH	=	autosphenotic
BBR	=	basibranchial toothed plate
BRSTG	=	branchiostegal ray
CLT	=	cleithrum
COR	=	hypocoracoid (= coracoid)
DETH	=	dermethmoid (= rostral)
DN	=	dentary
ECPT	=	ectopterygoid
ENPT	=	entopterygoid
EP 1-2	=	epurals 1 and 2
EPI	=	epiotic (= epioccipital)
ETH	=	supraethmoid or hypoethmoid
EXO	=	exoccipital
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
HEMAP	=	haemapophysis (= parapophysis)
HEMEP	=	haemal spine
HY 1-5	=	hypurals 1 to 5
IC	=	intercalar
IORB 1-5	=	infraorbitals 1 to 5
LEP	=	lepidotrich (= fin ray)
LETH	=	lateral ethmoid
METH	=	mesethmoid
MPT	=	metapterygoid
MX	=	maxilla
NA	=	nasal
NEUREP	=	neural spine
N PU1	=	neural arch of preural vertebra 1
N U1	=	neural arch of ural vertebra 1
NP V1, V2	=	neural spines of vertebrae 1 and 2
OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
PELV	=	pelvic bone
PHY	=	parhypural
PMX	=	premaxilla
POFR	=	postfrontal
POP	=	preopercle
PRO	=	prootic
PS	=	parasphenoid
PSPH	=	pleurosphenoid
PT	=	posttemporal
PTE	=	pterotic
PU 1-4	=	preural vertebrae 1 to 4
QU	=	quadrate
RAD	=	pterygiophore (= radial)
RART	=	retroarticular
RI	=	rib

SCA	=	hypercoracoid (= scapula)
SN 1-3	=	supraneurals 1 to 3
SOP	=	subopercle
SY	=	symplectic
U 1, 2	=	ural vertebrae 1 and 2
UR	=	uroneural
V 2-3	=	vertebrae 2 and 3
VO	=	vomer
pop. c.	=	preopercular sensory canal
s. l. b.	=	saccular-lagenar bulla
t. f.	=	temporal fossa

SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii KLEIN, 1885
Series Neopterygii REGAN, 1923
Division Teleostei MÜLLER, 1846
Superorder Osteoglossomorpha GREENWOOD *et al.*, 1966
Order Osteoglossiformes BERG, 1937
Suborder Osteoglossoidei REGAN, 1909
Family Pantodontidae PETERS, 1876
Genus ***Pankowskipiscis*** gen. nov.

Type-species:

Pankowskipiscis haqelensis gen. and sp. nov. (by monotypy).

Diagnosis

As for the species (monospecific genus)

Etymology

The name of the new genus is chosen to honour the PANKOWSKI family (Rockville, Maryland, U.S.A.) who generously offered the specimen hereafter studied to the Royal Belgian Institute for Natural Sciences (IRSNB). The Latin word *piscis*, fish, is added to their surname.

Species ***Pankowskipiscis haqelensis*** gen. and sp. nov.

Diagnosis

Small pantodontid fish. Short snout. Frontal profile strongly aquiline. Dermethmoid (= rostral) autogenous and overhanging the mesethmoid. Small tubular nasals separated from each other by the frontals. Temporal fossa laterally located. Large parietal forming the dorsal margin of the lateral fossa. Postfrontal present. Lateral ethmoid, orbistosphenoid and pleurosphenoid hypertrophied, reaching the parasphenoid and forming a complete bony interorbital septum in the adult fish. Narrow parasphenoid bearing strong conical teeth all along its trabecular region. Rounded saccular-lagenar bulla. Jaws strongly toothed with large conical teeth. Maxilla with a broadened posterior region. No supramaxilla. Large articular. Autogenous retroarticular. Small tubular antorbital. Three small anterior and two large posterior infraorbitals. Preopercle with two branches. Opercle hypertrophied. Subopercle strongly reduced. Broad toothed dermobasibranchial. Posttemporal rod-like and horizontally oriented. Cleithrum with two well developed limbs. Broad hypocoracoid. Pelvic girdle abdominal. Axial skeleton containing 46 to 48 vertebrae (23 to 25 abdominal + 23 caudal). 22-23 pairs of ribs. Extremely long dorsal fin (66 rays). Anterior extremity of the dorsal fin entering in a deep notch of the cranial posterior border and reaching the level of the orbit. Short anal fin (11 rays, 11 pterygiophores). Preural centrum 1 (PU1) and ural centra 1 and 2 (U1, U2) not fused together. U1 and U2 strongly reduced. Preural centrum 2 (PU2) bearing the last complete neural spine. PU1 and U1 bearing a small spatulate neural arch but no neural spine. Five hypurals (HY1-5). HY1 and HY2 fused together in adult fish and fused to U1. HY3, 4, 5 autogenous. HY3 not broadened. 2 epurals. One urodermal. Forked caudal fin with 16 principal rays. Small cycloid scales, with horizontally oriented *circuli* and no reticulum.

Etymology

The specific name of the new fish refers to the village of Haqel (Lebanon) where the specimen hereafter studied was discovered.

Holotype

Sample IRSNB P 10269, the two sides of a complete specimen (Figs 1, 2). Total length: 99 mm. Standard length: 83 mm.

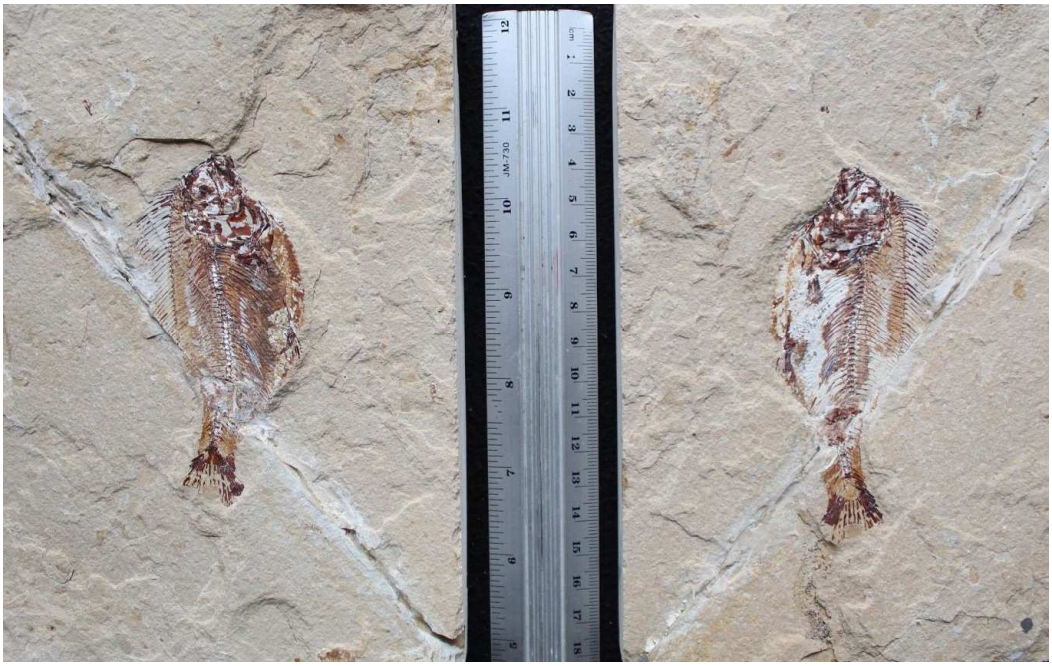

Figure 1: *Pankowskipiscis haqelensis* gen. and sp. nov. Holotype IRSNB P 10269 (side a [above], side b [below].

Figure 2: *Pankowskipiscis haqelensis* gen. and sp. nov. Holotype IRSNB P 10269 (side a). Total length: 99 mm.

Paratypes

Sample IRSNB P 10270, a juvenile specimen (Fig. 3). Total length: 41 mm. Standard length: 33 mm.

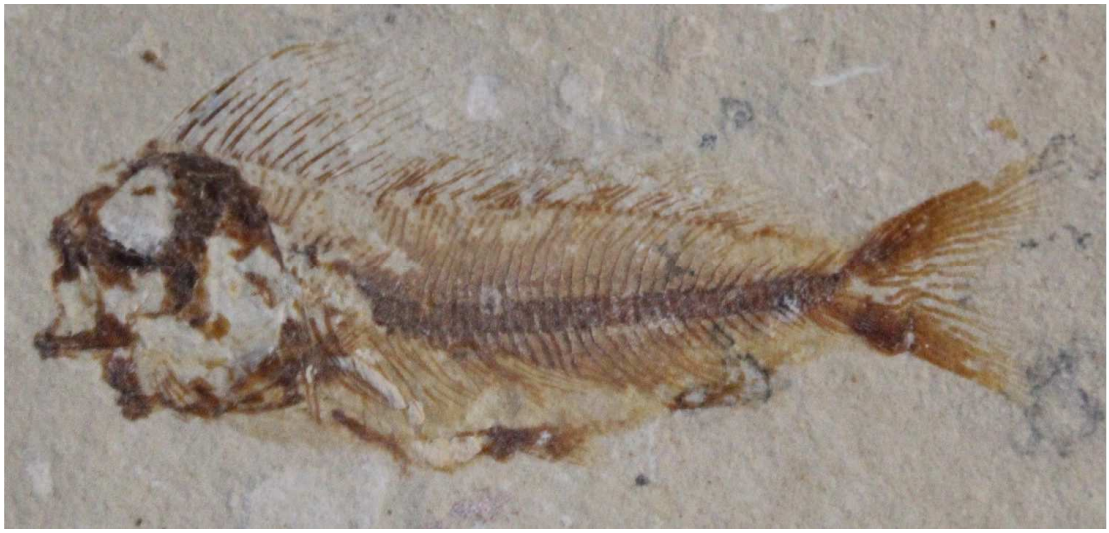

Figure 3: *Pankowskipiscis haqelensis* gen. and sp. nov. Paratype IRSNB P 10270 Total length: 41 mm.

Formation and locality

Marine Upper Cenomanian deposits of Haqel, Lebanon.

General morphology and morphometric data (Figs 1, 2)

Pankowskipictis haqelensis is a small and rather deep-bodied fish. The following morphometric data are given in percentage (%) of the standard length (83 mm) of the holotype.

Length of the head (opercle included) ……. 28.9 %
Depth of the head (in the occipital region) …….. 24.4 %
Maximum depth of the body ..... 45.8 %
Prepelvic length ……... 58.7 %
Basal length of the dorsal fin ……... 88.9 %
Preanal length …… .83,6 %
Basal length of the anal fin ……..... 14.7 %
Depth of the caudal peduncle …….. 13.3 %

Osteology

The skull (Figs 4-10)

The braincase and the jaws are rather small compared with the body size but the opercular series and the branchiostegal region are enlarged. The snout is short and the frontal profile strongly aquiline.

The mesethmoid is divided in two parts, a small plate-like dermethmoid (= rostral) located just before the frontal and a small but more massive endochondral bone, probably the supraethmoid or the hypoethmoid. The short and tubular nasal is located along the anterior extremity of the frontal. The small rod-like and toothless vomer is located under the anterior extremity of the parasphenoid. The lateral ethmoid is extremely enlarged in the holotype. It extends from the frontal dorsally to the parasphenoid ventrally. The lateral ethmoid is less developed in the juvenile sample.

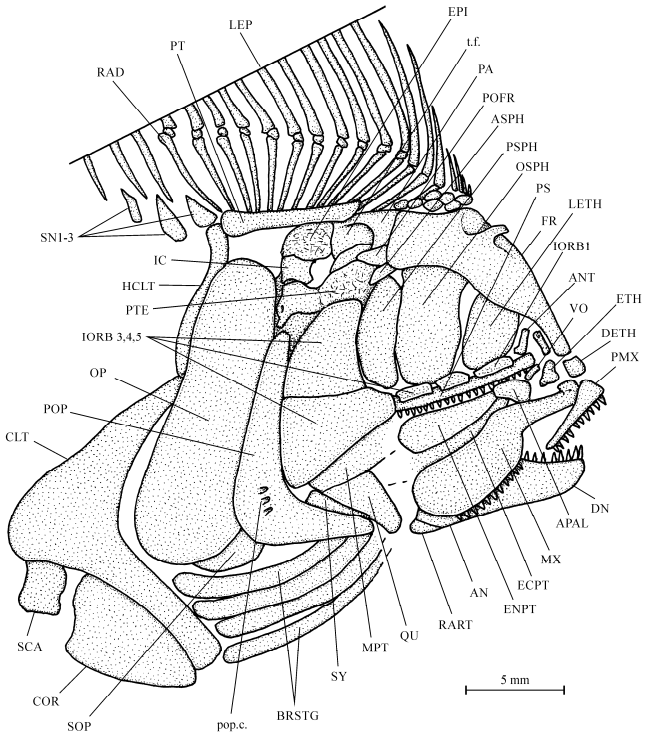

Figure 4: *Pankowskipiscis haqelensis* gen. and sp. nov. Reconstruction of the skull based on the two sides of the holotype, completed by paratype for a few details. The scale refers to holotype.

There is a deep notch in the middle of the skull roof posterior border that separates the right parietal and the posterior part of the right frontal from their left counterparts. This large notch allows the insertion of the first dorsal pterygiophores till the frontal, at the level of the orbit.

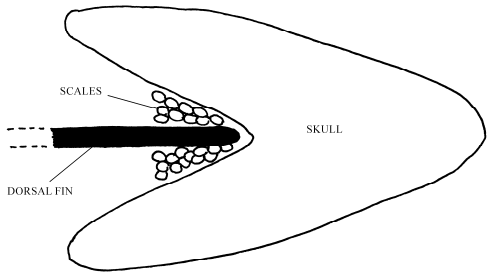

Figure 5: *Pankowskipiscis haqelensis* gen. and sp. nov. Schematic figure of the skull roof in dorsal view, showing the deep notch in the cranial rear and the penetration of the dorsal fin till the orbit level.

The elongate frontal forms the major part of the skull roof. The bone is curved, with a horizontal posterior region and an obliquely oriented anterior part. A narrow bony arch rises out from the middle of the frontal and overhangs a depressed region that probably contains an open supraorbital sensory canal, as in the recent *Pantodon* (TAVERNE, 1978: figs 31, 32). A small postfrontal is present just behind the frontal and is well visible on the right side of the holotype. The parietal is a large bone. A small autosphenotic is located below the postfrontal. The supraoccipital is not visible. The bone probably is pushed into the posterior notch of the skull roof.

The temporal (= posttemporal) fossa is well visible on the right side of the holotype. This fossa is located on the lateral wall of the skull and not on its rear as usual in teleosts. The fossa is bordered dorsally by the parietal and the epiotic (= epioccipital), anteriorly by the parietal and the postfrontal, ventrally by the pterotic and posteriorly by the intercalar and the epiotic. The supratemporal (= extrascapular, scalebone) is not preserved.

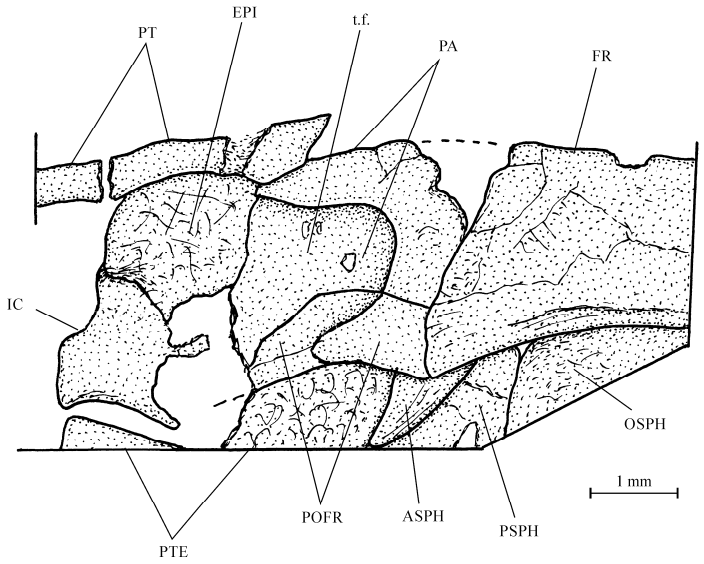

Figure 6: *Pankowskipiscis haqelensis* gen. and sp. nov. Holotype (side a). Part of the skull showing the region of the temporal fossa.

The orbitosphenoid is preserved on the left side of the specimen and the pleurosphenoid on the right side. They are both extremely large bones that extend from the frontal to the parasphenoid, forming so with the lateral ethmoid a complete bony interorbital septum. The orbitosphenoid and the pleurosphenoid are not yet ossified in the juvenile specimen. No basisphenoid is visible. The parasphenoid is a long and narrow bone. It bears strong conical teeth all along its trabecular region.

The exoccipital and the basioccipital are not preserved. The upper part of the opercle is lost on the left side of the holotype and the prootic is visible just above the broken border of the opercle. This prootic is swollen, forming a large rounded saccular-lagenar bulla.

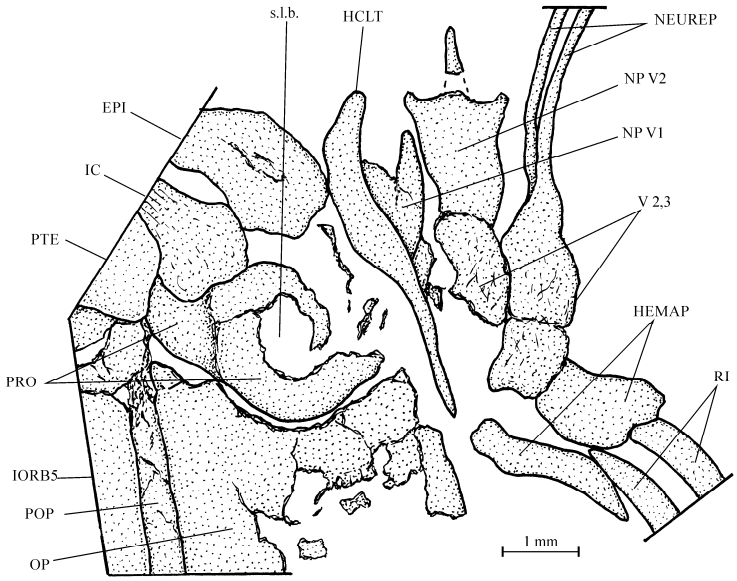

Figure 7: *Pankowskipiscis haqelensis* gen. and sp. nov. Holotype (side b). Part of the skull showing the region of the saccular-lagenar bulla.

A part of the metapterygoid, a fragment of the entopterygoid, the complete ectopterygoid, the autopalatine, the quadrate and the symplectic are visible on the right side of the specimen. The entopterygoid and the ectopterygoid are toothless. The autopalatine is a bulky bone. No dermopalatine is present. The quadrate is triangle-shaped. The symplectic is broad and rod-like.

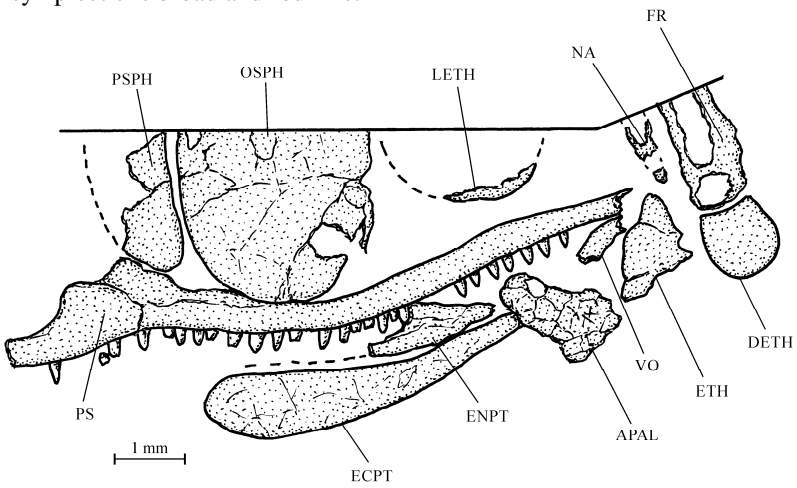

Figure 8: *Pankowskipiscis haqelensis* gen. and sp. nov. Holotype (side a). Part of the skull showing the region of the toothed parasphenoid.

Three narrow anterior infraorbitals are preserved just above the parasphenoid in the paratype. In both specimens, there are two large infraorbitals located just before the dorsal branch of the preopercle. The ventral element is the wider. The dorsal bone is smaller. A tubular antorbital is visible on the left side of the holotype. The dermosphenotic is not preserved. There is no supraorbital.

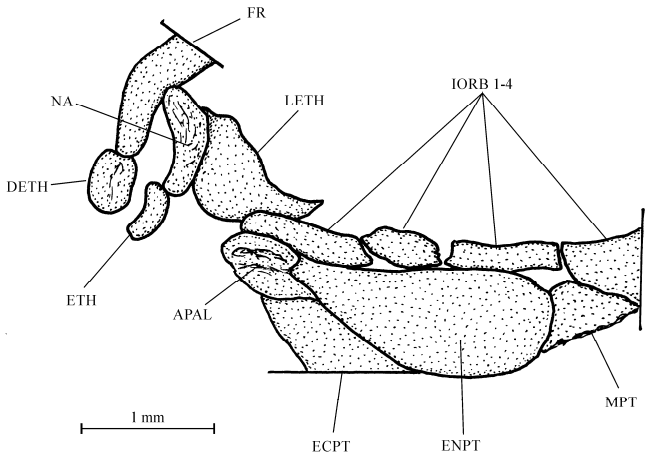

Figure 9: *Pankowskipiscis haqelensis* gen. and sp. nov. Paratype. Part of the skull showing the three small anterior infraorbitals.

The premaxilla, the maxilla and the dentary bear a row of strong conical teeth, still larger than those of the parasphenoid. The premaxilla is a long and narrow bone with a swollen anterior region. The maxilla is divided in two regions, a narrow anterior branch overhanging the premaxilla and an extremely broadened plate-like posterior region that covers the posterior part of the mandible. This enlarging is more important in the holotype than in the paratype. A few broken teeth are preserved on the maxilla of the adult specimen but the maxilla of the juvenile bears teeth all along its oral margin. No supramaxilla is present.

The preopercle is divided in two branches, the dorsal one being the longest. Three openings of the preopercular sensory canal are visible in the lower part of the dorsal branch. The opercle is not very broad but extremely high. Its height slightly exceeds the length of the vertical branch of the preopercle. Two fragments of a small subopercle are visible on the left side of the holotype. Four long and broad branchiostegal rays are present below the opercle and preopercle.

The hyomandibula and the hyoid bar are hidden by the posterior infraorbitals and the preopercle. Fragments of a large entirely toothed dermobasibranchial plate are visible on both sides of the holotype, between the maxilla and the quadrate.

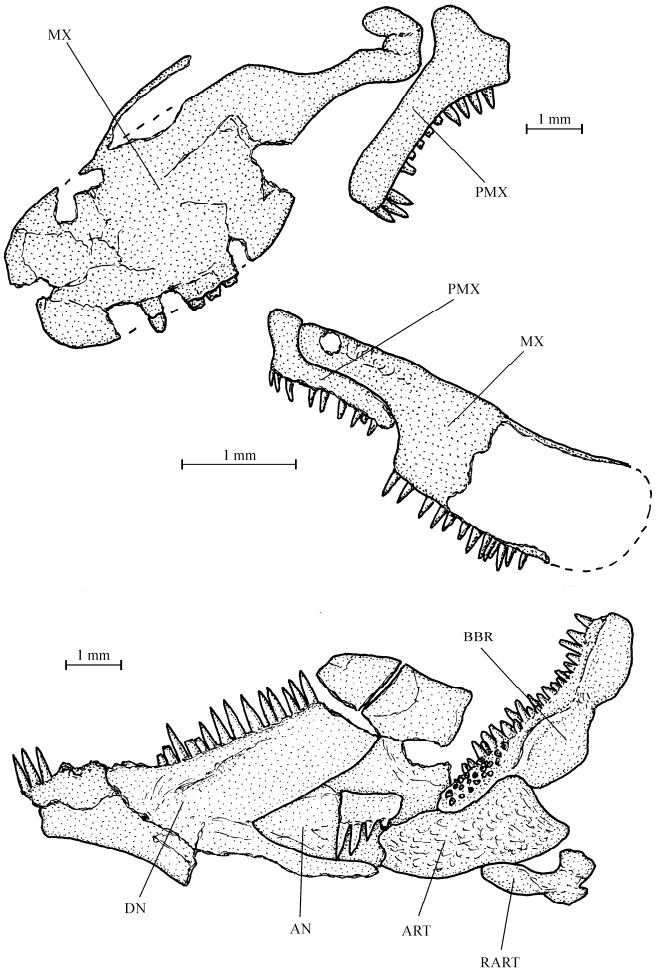

Figure 10: *Pankowskipiscis haqelensis* gen. and sp. nov. Above: upper jaw of the holotype, side a. In the middle: upper jaw of the paratype. Below: lower jaw of the holotype, side b.

The girdles (Figs 4, 11)

The posttemporal is a long, rod-like and horizontally oriented bone. Its anterior extremity rests on the epiotic and the parietal. The hypercleithrum (= supracleithrum) is narrow. Both the dorsal and the ventral branches of the cleithrum are well developed. The posterior ventral region of the bone is enlarged. The hypercoracoid (= scapula) and the hypocoracoid (= coracoid) are well visible below the ventral branch of the cleithrum. The hypocoracoid is broad and more or less triangle-shaped. The pectoral fin contains 10 rays. They are segmented and branched. The first one has an enlarged basis.

The pelvic girdle is located on the abdomen and the origin of the ventral fins is positioned at the level of the junction between the twenty-fifth and the twenty-sixth vertebrae in the holotype. The pelvic bone is elongated and rod-like. But its basal region is broadened and exhibits a short and acuminate posterior process. There are 10 segmented rays. The first one is shorter than the others and has a pointed extremity. The other rays are branched. One pterygiophore is present.

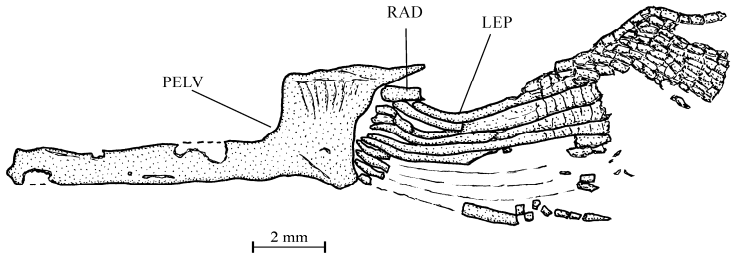

Figure 11: *Pankowskipiscis haqelensis* gen. and sp. nov. Pelvic girdle of the holotype, side b.

The axial skeleton (Figs 1-3)

The vertebral column is incompletely preserved on the holotype. However, all the neural spines are present, at least as fragments, allowing the exact count of the vertebrae. There are 46 centra, 23 abdominal and 23 caudal, including the two ural vertebrae. The first and the second neural spines are short and broadened. The following neural spines of the abdominal region are bifid. The neural spines of the caudal region are simple. The centra of the abdominal region bear well developed haemapophyses (= parapophyses) and those of the caudal region long haemal spines. The last haemapophyses are as long as the first haemal spines. In the paratype, the axial skeleton contains 48 vertebrae, 25 abdominal and 23 caudal, the two ural centra included. There are 22 (holotype) or 23 (paratype) pairs of ribs. Most of them are long and obliquely oriented. The last three pairs of ribs are short.

Three short triangle-shaped supraneurals are visible just behind the skull on the holotype, the first two on the right side and the third one on the left side.

There is a series of elongate epineurals all along the vertebral axis. The first ones are fused to the corresponding neural arches, while the posterior ones are autogenous. A series of autogenous epipleurals are present at the level of the last ribs and the first haemal spines. The posterior epipleurals have a bifid anterior extremity.

The dorsal and anal fins (Figs 1-4)

The dorsal fin is extremely elongated and begins above the skull, at the frontal and orbit level. In the holotype, the fin begins with 7 short spiny rays, the other rays being much longer, segmented and branched. The posterior part of the fin is missing on both sides of the holotype but a fragment of the last dorsal pterygiophore is preserved just above the neural spine of the fifth preural centrum. In the paratype, the dorsal fin contains 4 small spiny rays and 57 segmented and branched rays. But traces of 5 weakly ossified posterior rays also are visible. The total number for the dorsal fin is thus 66 (4 + 62) rays in the juvenile specimen. Only the upper tip of the rays are segmented and branched in both samples.

A great part of the anal fin is missing in the holotype. In the paratype, the fin contains 1 spiny ray, at least 10 segmented and branched rays and is supported by 11 pterygiophores. The first pterygiophore is extremely elongated and obliquely oriented in both specimens. The origin of the anal fin is located at the level of the junction of the thirty-fourth and the thirty-fifth vertebrae in the holotype.

The caudal skeleton and fin (Fig. 12)

The caudal skeleton is preserved in imprints and bones. By combining the elements visible on the two sides of the holotype, it is possible to reconstruct exactly the complete structure. The last neural spines are articulated on the vertebrae, contrarily to the last haemal arches that are fused to the corresponding centra. The second preural centrum (PU2) bears the last complete neural spine (NP PU2). The first preural (PU1) and the first ural centra (U1) only exhibit a spatulate neural arch. There is a small autogenous second ural centrum (U2). The rather narrow parhypural is fused to PU1. In the holotype, the two ventral hypurals (HY1, 2) are fused together, forming a broad plate, and to the strongly reduced U1. The juvenile paratype exhibits the same caudal morphology as the holotype, with a reduced U1 and a still more reduced autogenous U2, but HY1 and HY2 are not yet fused together and with U1. There is only one elongate uroneural (UR). Its broadened rounded ventral extremity partly covers the lateral faces of U2, U1 and PU1. Two short epurals are present between NP PU2 and UR. There are three autogenous dorsal hypurals (HY3, 4, 5). They are not especially enlarged. HY3 and HY 4 are articulated on U2. The imprint of the smaller HY5 is clearly visible on the right side of the holotype.

The caudal fin is forked. The fin is incomplete in the holotype. The caudal fin contains 4 upper, 3 lower procurrent rays and 16 principal rays in the paratype.

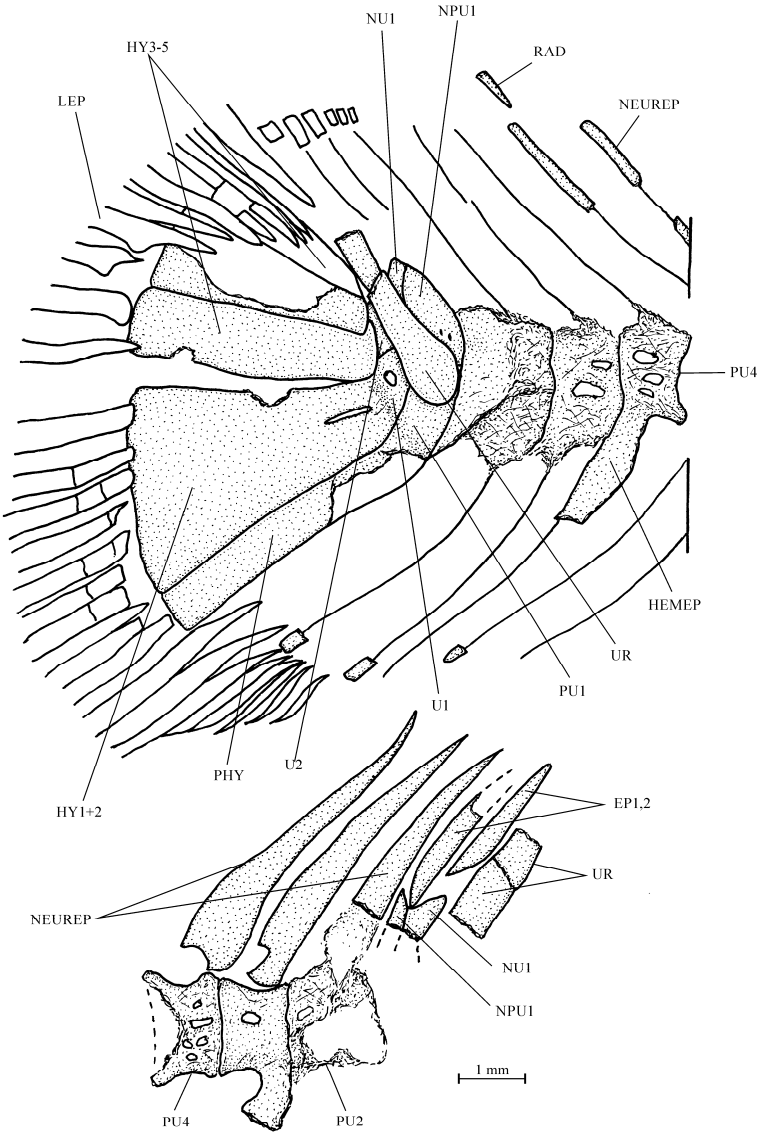

Figure 12: *Pankowskipiscis haqelensis* gen. and sp. nov. Caudal skeleton of the holotype, side a (above), side b (below).

Squamation

The scales are small, more or less rounded and not reticulated. A few horizontally oriented *circuli* are visible on some scales.

DISCUSSION

Pankowskipiscis within Teleostei

Pankowskipiscis has a maxilla forming the major part of the upper jaw border. An orbitosphenoid and an antorbital are present. The pelvic girdle is in abdominal position. The dorsal and anal fins are devoid of strong anterior spines. PU1, U1 and U2 are individualized and not fused in a terminal centrum. The scales are not ctenoid. These characters indicate that the new Lebanese fossil fish is a rather primitive teleost.

Pankowskipiscis also exhibits a series of mixed primitive and specialized features. The dermethmoid (= rostral) and the endochondral part of the mesethmoid are autogenous. The temporal fossa is laterally located. The parasphenoid is strongly toothed. There are only two large posterior infraorbitals. The supraorbital is absent. The jaws bear strong teeth. The supramaxilla is missing. The opercle is hypertrophied and the subopercle reduced. A large and broad toothed dermobasibranchial is present. Both PU1 and U1 bear short spatulate neural arches. There is only one uroneural. HY1 and 2 are fused and form a ventral hypural plate in the adult fish. There are only 16 principal rays in the caudal fin. Within the primitive teleosts, the addition of all those characters is only present in some members of the Osteoglossiformes.

Pankowskipiscis within Osteoglossiformes

The temporal fossa is bordered dorsally by the parietal in *Pankowskipiscis*. The parietal does not reach the temporal fossa in Osteoglossidae (TAVERNE, 1977: figs 43, 44, 72, 72, 1978: figs 3, 21; among others) and reaches the fossa in an extremely reduced area in Arapaimidae (TAVERNE, 1977: figs 104, 125; among others). The frontal of *Pankowskipiscis* bears a narrow bony arch over the largely open supraorbital sensory canal. A postfrontal is present. Such a bone is absent in the non-pantodontid Osteoglossiformes. The saccular-lagenar bulla is hypertrophied. A well developed orbitosphenoid is present and reaches ventrally the parasphenoid. The toothed basibranchial is broadened, while this bone is narrow in Osteoglossidae and Arapaimidae (TAVERNE, 1977: figs 56, 85, 109, 136). The scales are not reticulated, another difference with the Osteoglossidae an Arapaimidae. All those characters also are present in *Pantodon* (TAVERNE, 1978: figs 31-34) and most of them in *Prognathoglossum* (TAVERNE & CAPASSO, 2012: fig. 4). The placement of *Pankowskipiscis* in the family Pantodontidae is thus completely justified.

The skull and the caudal skeleton of *Pankowskipiscis* greatly differ from those of the recent *Pantodon* (TAVERNE, 1978: figs 30-34, 40, 41, 54) and of the Cenomanian *Prognathoglossum* (TAVERNE & CAPASSO, 2012: figs 3, 4, 12). *Pankowspiscis* clearly deserves its peculiar generic status within the family.

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