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The Pantodontidae (Teleostei, Osteoglossomorpha) from the marine Cenomanian (Upper Cretaceous) of Lebanon. 4°. *Capassopiscis pankowskii* gen. and sp. nov.

Les Pantodontidae (Teleostei, Osteoglossomorpha) du Cénomanien marin (Crétacé supérieur) du Liban. 4°. *Capassopiscis pankowskii* gen. and sp. nov.

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Résumé: L'ostéologie et la position systématique de *Capassopiscis pankowskii*, un poisson fossile du Cénomanien marin du Liban, sont étudiées en détails. Les caractères du crâne, ceux du squelette caudal et la morphologie générale rapportent ce poisson à l'ordre des Osteoglossiformes et plus particulièrement à la famille des Pantodontidae. *Capassopiscis* possède les dermobasihyal et dermobasibranchial qui ne sont pas encore soudés l'un à l'autre, un petit centre ural 2 autogène et trois hypuraux dorsaux autogènes. Chez les autres poissons pantodontidés, le dermobasihyal et le dermobasibranchial sont fusionnés en un unique élément et la plupart d'entre eux ont le centre ural 2 soudé à une plaque hypurale dorsale. *Capassopiscis* est le genre le plus primitif décrit à ce jour au sein des Pantodontidae.

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

Abstract: The osteology and the systematic position of *Capassopiscis pankowskii*, a fossil fish from the marine Cenomanian of Lebanon, are studied in details. The characters of the skull, the general morphology and some features of the caudal skeleton clearly refer this fish to the order Osteoglossiformes and more particulary to the family Pantodontidae. *Capassopiscis* has the dermobasihyal and the dermobasibranchial not yet fused together, a small autogenous ural centrum 2 and three autogenous dorsal hypurals. The other pantodontid fishes exhibit the dermobasihyal and the dermobasibranchial fused together and most of them have the ural centrum 2 fused to a dorsal hypural plate. *Capassopiscis* is the most primitive genus described until now within Pantodontidae.

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

INTRODUCTION

The present paper describes the skeleton of a fifth new pantodontid fish from the marine Cenomanian (Upper Cretaceous) of Lebanon and determines precisely its systematic position within the family.

The family Pantodontidae belongs to the Osteoglossomorpha, a superorder of primitive teleosts that appears at the Jurassic-Cretaceous boundary and persists till the present days. Most authors range the family within the order Osteoglossiformes and the suborder Osteoglossoidei (NELSON *et al.*, 2016; among others). A recent genetic study gives another phylogenetic result that places the Pantodontidae as the plesiomorphic sister-group of both the Osteoglossiformes and the Mormyriformes (LAVOUÉ & SULLIVAN, 2004)

Today the family contained five monospecific genera, the recent *Pantodon buchholzi* PETERS, 1876 from the continental waters of Africa and four fossil fishes from the marine Cenomanian of Lebanon, *Prognathoglossum kalassyi* TAVERNE & CAPASSO, 2012, *Pankowskipiscis haqelensis* TAVERNE, 2021a, *Petersichthys libanicus* TAVERNE, 2021b and *Palaeopantodon vandersypeni* TAVERNE, 2021c (TAVERNE & CAPASSO, 2012; TAVERNE, 2021a, b, c). Some of these Lebanese fossil pantodonti fishes were previously figured and considered as members of the Bregmacerotidae and the Lophotidae (GAYET *et al.*, 2012:fig. p. 157, fig. p. 158 below).

The present paper is thus the fifth one of a series devoted to the osteological and phylogenetic study of those fossil Pantodontidae.

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MATERIAL AND METHODS

The specimen hereafter examined belongs to the paleontological collection of the Belgian Royal Institute of Natural Sciences (IRSNB). It was 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
BR	=	branchial bone
BRSTG	=	branchiostegal ray
CLT	=	cleithrum
COR	=	hypocoracoid (= coracoid)
DBBR	=	dermobasibranchial
DBHY	=	dermobasihyal
DETH	=	dermethmoid (= rostral)
DN	=	dentary
ECPT	=	ectopterygoid
ENPT	=	entopterygoid
EP	=	epural
EPI	=	epiotic (= epioccipital)
ETH	=	supraethmoid or hypoethmoid
EXO	=	exoccipital
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
HEMEP	=	haemal spine
HY 1-5	=	hypurals 1 to 5
IC	=	intercalar
IORB	=	posterior infraorbitals
LEP	=	lepidotrich (= fin ray)
LETH	=	lateral ethmoid
MPT	=	metapterygoid
MX	=	maxilla
NA	=	nasal
NEUREP	=	neural spine
N PU1-U1	=	neural arch of preural 1 and ural 1 vertebrae
NP PU2	=	neural spine of preural vertebra 2
NP V1, 2	=	neural spines of vertebrae 1 and 2
OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
PELV	=	pelvic bone
PHY	=	parhypural
PMX	=	premaxilla
POFR	=	postfrontal
POP	=	preopercle
PS	=	parasphenoid
PSPH	=	pleurosphenoid
PT	=	posttemporal
PTE	=	pterotic
PU 1-4	=	preural vertebrae 1 to 4
QU	=	quadrate
RAD	=	pterygiophore (= radial)
SCA	=	hypercoracoid (= scapula)
SN	=	supraneural
SOP	=	subopercle
ST	=	supratemporal (= scalebone)

SY	=	symplectic
U 1, 2	=	ural vertebrae 1 and 2
UR	=	uroneural
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 ***Capassopiscis*** gen. nov.

Type-species:

Capassopiscis pankowskii gen. and sp. nov. (by monotypy).

Diagnosis :

As for the species (monospecific genus)

Etymology :

The name of the new genus is dedicated to my friend and colleague, Prof. Dr. Luigi CAPASSO from the University G. D'Annunzio of Chieti-Pescara. The Latin word *piscis*, fish, is added to his surname.

Species *Capass**opiscis pankowskii*** gen. and sp. nov.

Diagnosis :

Small deep-bodied pantodontid fish. Snout very short. Frontal profile rectilinear and obliquely oriented. Dermethmoid (= rostral) autogenous, associated with the endochondral ethmoid. Nasal tubular. Temporal fossa laterally located. Parietal forming the dorsal margin of the temporal fossa. Postfrontal present. Lateral ethmoid, orbistosphenoid and pleurosphenoid reaching the parasphenoid and forming a complete bony interorbital septum. No basisphenoid. Parasphenoid narrow and toothed. Autopaline, ectopterygoid and entopterygoid toothless. Jaws extremely short. Premaxilla forming the major part of the upper jaw oral margin. Maxilla short, broad and edentulous. No supramaxilla. Lower jaw triangular. Dentary toothed. Small tubular antorbital. Two wide and deepest than broad posterior infraorbitals. Large triangular dermosphenotic. Preopercle with two branches, the dorsal one elongate, the ventral one short. Opercle hypertrophied. Subopercle reduced . Dermobasihyal and dermobasibranchial not fused together. Posttemporal small and vertically oriented. Pelvic girdle in abdominal position. Axial skeleton containing 48 vertebrae (25 abdominal + 23 caudal). Elongate dorsal fin beginning behind the head and containing 64 rays and 58 pterygiophores. First dorsal pterygiophore with a hooked dorsal anterior process supporting the first 6 short and spiny dorsal rays. Anal fin with 18 pterygiophores. Preural centrum 1 (PU1) and ural centra 1 and 2 (U1, U2) not fused together. Preural centrum 2 (PU2) bearing the last complete neural spine. PU1 and U1 bearing fused spatulate neural arches. U2 small and autogenous. At least one epural. One large uroneural reaching U1. Caudal fin forked, with 16 principal rays. Scales small, cycloid and not reticulated.

Etymology :

The specific name of the new fish is chosen to honour once again the PANKOWSKI family (Rockville, Maryland, U.S.A.) who generously offered the specimen hereafter studied to the Royal Belgian Institute for Natural Sciences (IRSNB).

Holotype :

Sample IRSNB P 10.272, a complete specimen (Fig. 1). Total length: 72 mm. Standard length: 60 mm.

Formation and locality :

Marine Upper Cenomanian deposits of Haqel, Lebanon.

General morphology and morphometric data (Fig. 1) :

Figure 1: *Capassopiscis pankowskii* gen. and sp. nov. Holotype IRSNB P 10.272. Total length: 72 mm.

Capassopiscis pankowskii is a small and rather deep-bodied fish. The following morphometric data are given in percentage (%) of the standard length (60 mm) of the holotype.

Length of the head (opercle included) …….. 27.5 %
Depth of the head (in the occipital region) …….. 36.2 %
Maximum depth of the body ..... 48.3 %
Prepelvic length ……... 58.9 %
Basal length of the dorsal fin ……... 78.3 %
Preanal length …….. 79.7 %
Basal length of the anal fin ……..... 15.9 %
Depth of the caudal peduncle …….. 17.4 %

Osteology

The skull (Fig. 2)

As in the other fossil pantodontid fishes, the braincase and the jaws are small compared with the body size but the opercle is hypertrophied. The frontal profile is almost rectilinear and obliquely oriented. The snout is very short

The mesethmoid is divided in two elements, a small plate-like dermethmoid (= rostral) located just before the frontal and a small underlying endochondral bone, probably the supraethmoid or the hypoethmoid. The nasal is tubular and located along the anterior extremity of the frontal. The lateral ethmoid is a large bone extending from the frontal dorsally to the parasphenoid ventrally. The vomer is not preserved.

The frontal forms the greatest part of the skull roof. There is a large postfrontal located along the posterior region of the frontal lateral margin. The parietal is a small bone that reaches the median region of the braincase roof (medioparietal skull). The autosphenotic is completely hidden by the dermosphenotic. The epiotic (= epioccipital) is a rather large and arched bone. The supraoccipital is not visible. The bone probably was small and covered by the epiotic in lateral view.

The temporal (= posttemporal) fossa is wide and located on the lateral wall of the braincase, not on its rear as in most teleosts. The fossa is bordered dorsally by the parietal and the epiotic, anteriorly by the frontal and the

postfrontal, ventrally by the pterotic and posteriorly by the epiotic and the small intercalar. A large supratemporal (= extrascapular, scalebone) covers almost entirely the fossa.

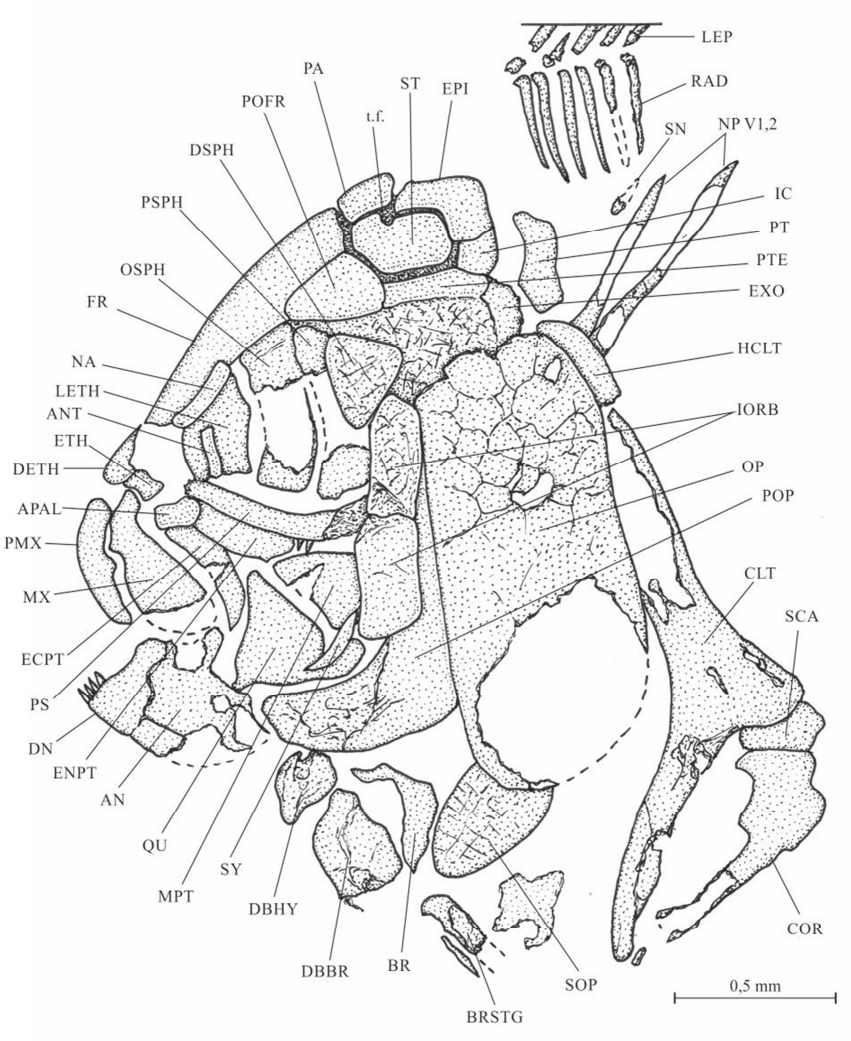

Figure 2: *Capassopiscis pankowskii* gen. and sp. nov. Skull and pectoral girdle of holotype IRSNB P 10.272.

Both the orbitosphenoid and the pleurosphenoid are extremely large bones that extend from the frontal to the parasphenoid. They form with the lateral ethmoid a complete bony interorbital septum. No basisphenoid is present. The parasphenoid is a long and narrow bone. No basipterygoid process is visible. Two small conical teeth are preserved in its trabecular region, just behind the entopterygoid.

The exoccipital is preserved behind the pterotic. The prootic and the basioccipital are not visible, being covered by the upper part of the opercle.

The autopalatine, the entopterygoid, the ectopterygoid, the metapterygoid, the quadrate and the symplectic are well visible. The autopalatine is a small bulky bone. No dermopalatine is present The entopterygoid and the ectopterygoid are toothless..The quadrate is triangle-shaped. The symplectic is coma-like.

A short tubular antorbital is lying on the lateral ethmoid. The ventral infraorbitals are not preserved and only the two posterior infraorbitals are present. They are wide bones, deepest than broad. The large dermosphenotic is triangular in shape. There is no supraorbital.

The jaws are extremely short. No teeth are preserved on the premaxilla and the maxilla. The premaxilla is elongated and forms the major part of the upper oral margin. The maxilla is divided in two regions, a small narrow anterior branch and a broadened plate-like posterior part. No supramaxilla is present. The lower jaw is almost triangle-shaped. Four small conical teeth are preserved on the oral margin of the dentary. A part of a wide angular is visible. The articular and the retroarticular are not preserved.

The preopercle is divided in two branches, a long and narrow dorsal one and a short but broad ventral one. The enlarged opercle is broad and extremely high. Its height slightly exceeds the length of the vertical branch of

the preopercle. The small subopercle is visible under the opercle. A fragment of a branchiostegal ray is present below the preopercle.

The hyomandibula and the hyoid bar are not visible, being hidden by the infraorbitals and the preopercle. The dermobasihyal and the dermobasibranchial are short but broad bones. They are not fused together. They are preserved from their ventral side. So, it is not possible to see if these two bones were toothed or not. A branchial bone irregularly shaped, probably an epibranchial, is also visible just above the dermobasibranchial.

The girdles (Figs 2,3)

The posttemporal is a small bone located behind the epiotic and the intercalary. The hypercleithrum (= supracleithrum) is short and narrow. Both the dorsal and the ventral branches of the cleithrum are long but rather narrow. The hypercoracoid (= scapula) is small. The hypocoracoid (= coracoid) is long, with a slightly enlarged posterior region and a rather narrow anterior branch. The pectoral fin is incompletely preserved and contains 9 or 10 rays. Some of these rays are segmented but it is not possible to see if they were also branched, their tips being lost.

The pelvic girdle is located on the abdomen and the origin of the ventral fins is positioned at the level of the twenty-second vertebra. The pelvic bone is elongated and rod-like. Its basal region is slightly enlarged and exhibits a short and acuminate posterior process. The ventral fin exhibits 1 short initial spiny ray and 8 long rays. The posterior region of these rays is not preserved and it is not possible to know if they were segmented and branched or not. One pterygiophore (= radial) is present.

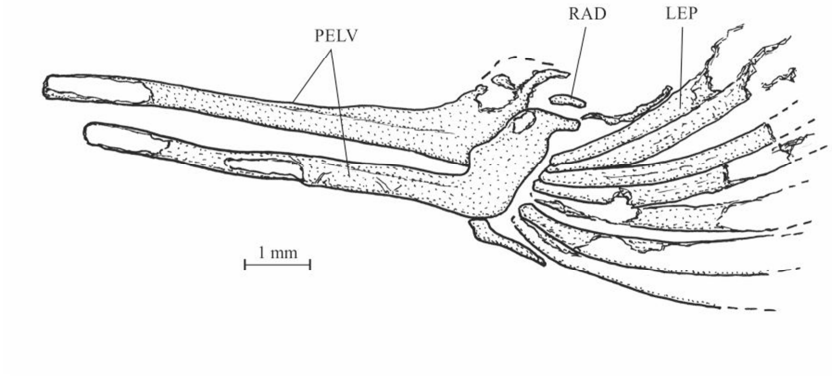

Figure 3 : *Capassopiscis pankowskii* gen. and sp. nov. Pelvic girdle of holotype IRSNB P 10.272.

The axial skeleton (Fig. 1)

The vertebral axis contains 48 centra, 25 abdominal and 23 caudal, including the two ural vertebrae. On the best preserved centra a small crest is visible at mid-height of the lateral side. The neural and the haemal spines are elongated. The centra of the abdominal region bear well developed haemapophyses (= parapophyses). The last haemapophyses are almost as long as the first haemal spines. There are 23 pairs of ribs. Most of them are extremely long and obliquely oriented. The last pairs of ribs are shortened. A small fragment of one supraneural is visible just before the first neural spine.

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 posterior part of the abdominal region and all along the caudal region. The last epineurals and epipleurals are poorly ossified and less marked than the preceding ones.

The dorsal and anal fins (Figs 1, 4)

The dorsal fin is extremely elongated. Its origin is located behind the head and not above the head as in some other pantodontid fishes. The fin begins with 6 short spiny rays, the following 58 rays being much longer, segmented and branched at their tips. The total number of rays for the entire dorsal fin is thus 64 (6 + 58). There are 58 pterygiophores. The first pterygiophore exhibits an anterior dorsal hooked process that sustains the first six spiny rays.

The anal fin is supported by 18 long pterygiophores. The rays are badly preserved and only as imprints. It seems that there are about 18 segmented and branched rays. The origin of the anal fin is located at the level of the thirty-fourth vertebra.

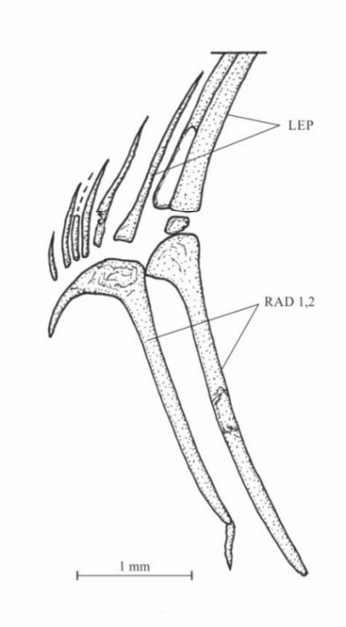

Figure 4 : *Capassopiscis pankowskii* gen. and sp. nov. Two first dorsal perygiophores and the corresponding dorsal rays of holotype IRSNB P 10.272.

The caudal skeleton and fin (Fig. 5)

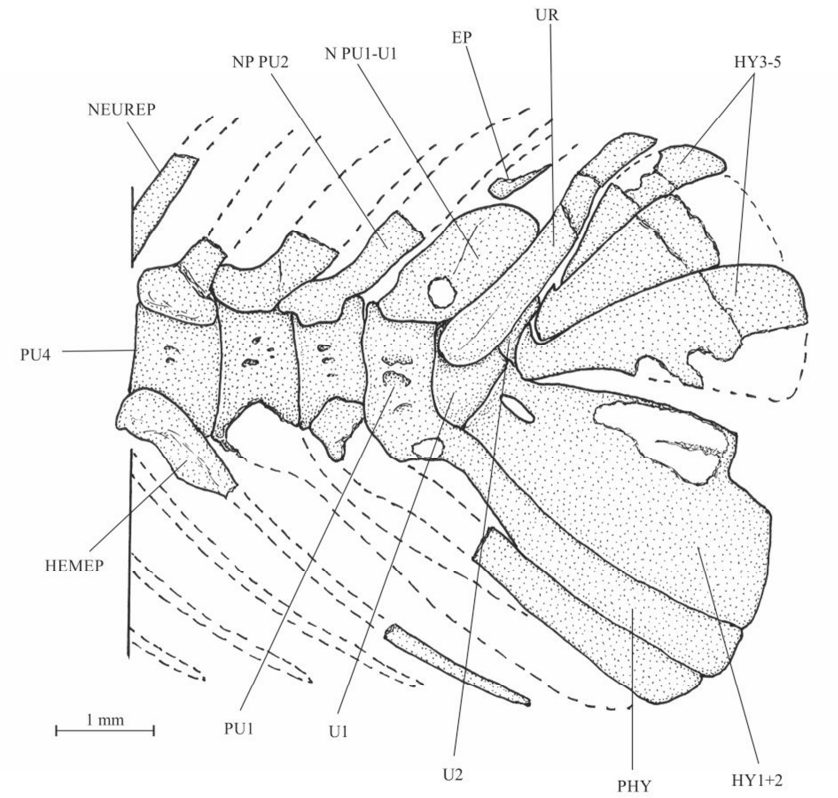

Figure 5: *Capassopiscis pankowskii* gen. and sp. nov. Caudal skeleton of holotype IRSNB P 10.272.

The caudal skeleton is rather well preserved. The last neural and haemal spines are articulated on the vertebrae. The second preural centrum (PU2) bears the last complete neural spine (NP PU2). The first preural (PU1) and the first ural centra (U1) exhibit only spatulate neural arches (N PU1-U1) that are fused together. There is a small autogenous second ural centrum (U2). The rather narrow parhypural is fused to PU1. The two ventral hypurals (HY1, HY2) are fused together, forming a broad plate that is articulated on the reduced U1. There is a small foramen located near the articular head of the plate. The HY2 component of the plate is shorter than the HY1 element. There is only one elongate uroneural (UR). Its broadened rounded ventral extremity partly covers the lateral faces of U1 and U2. A small fragment of one epural is visible above N PU1-U1. There are three autogenous dorsal hypurals (HY3, HY4, HY5). HY3 is slightly enlarged. HY3 and HY 4 are articulated on U2. HY 5 is located posteriorly to U2.

The caudal fin is forked. The fin contains 10 upper procurrent rays and 16 principal rays. The number of lower procurrent rays is unknown.

Squamation

The scales are small, cycloid, more or less rounded and not reticulated.

DISCUSSION

Capassopiscis within Teleostei

Capassopiscis exhibits a series of characters that clearly place this fish within the order Osteoglossiformes and more particularly within the family Pantodontidae. The temporal fossa is laterally located and the parietal forms a major part of its upper border. A postfrontal is present. The dermethmoid (= rostral) and the endochondral part of the mesethmoid are associated but autogenous. The orbitosphenoid and the pleurosphenoid are ossified. The basisphenoid is missing. The lower jaw and the parasphenoid bear conical teeth. The supramaxilla is lost. There are only two large posterior infraorbitals. The supraorbital is absent. The opercle is hypertrophied and the subopercle reduced. The dermobasihyal and the dermobasibanchial are large bones. PU1, U1 and U2 are individualized. PU1 and U1 bear short spatulate neural arches that fuse together. There is only one uroneural and five hypurals. HY1 and HY2 are fused and form a ventral hypural plate articulated with U1. There are only 16 principal rays in the caudal fin. The scales are small, cycloid and not reticulated.

Capassopiscis within Pantodontidae

Capassopiscis pankowskii and *Pankowskipiscis haqelensis* exhibit the more primitive caudal pattern within the family. Both fishes still have an autogenous U2 not fused to the dorsal hypurals that are also autogenous (Fig. 5; TAVERNE, 2021a: fig. 12). The recent *Pantodon buchholzi* and the fossil *Prognathoglossum kalassyi*, *Petersichthys libanicus* and *Palaeopantodon vandersypeni* share a more evolved caudal morphology, with U2 fused to a dorsal hypural plate (GREENWOOD, 1966: figs 7, 8; TAVERNE, 1978: fig. 54, 2021b: fig. 4, 2021c: fig. 4; HILTON, 2003: fig. 38C; TAVERNE & CAPASSO, 2012: figs 11, 12).

Capassopiscis pankowskii has the dermobasihyal and the dermobasibranchial separated the one from the other, a primitive condition (Fig. 2). *Pantodon buchholzi, Prognathoglossum kalassyi*, *Pankowskipiscis haqelensis* and *Palaeopantodon vandersypeni* exhibit the evolved condition of having these two hyoideo-branchial bones fused together (NELSON, 1968: fig. 8; TAVERNE, 1978: fig. 43, 2021a: fig. 10, 2021c: fig. 3; HILTON, 2003: fig. 30D; TAVERNE & CAPASSO, 2012: figs 2, 3). The situation is unknown in *Petersichthys libanicus*, these two bones being not preserved.

Pantodon buchholzi has an extremely hypertrophied hypocoracoid that bears a very long and very narrow posterior ventral process (GREENWOOD & THOMSON, 1960: num. figs; TAVERNE, 1978: fig. 44). The enlargement of the hypocoracoid is already marked in *Pankowskipiscis haquelensis* and *Prognathoglossum kalassyi* (TAVERNE, 2021a: fig. 4; TAVERNE & CAPASSO, 2012: fig. 6). In *Petersichtys libanicus* and *Palaeopantodon vandersypeni*, the hypocoracoid is incompletely preserved and its size remains unknown (TAVERNE, 2021b: fig. 2, 2021c: fig. 3) but the posterior process of the bone begins to lengthen in this last species. In *Capassopiscis pankowskii*, the hypocorcoracoid is not yet enlarged and there is no trace of a posterior process, once again a primitive condition.

On the basis of these three characters, *Capassopiscis* appears to be the most primitive genus within the family Pantodontidae.

The general morphology, the skull and the caudal skeleton of *Capassopiscis pankowskii* notably differ from their equivalents in the other Pantodontidae. The new fossil fish deserves thus its peculiar generic and specific status.

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