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The Pantodontidae (Teleostei, Osteoglossomorpha) from the marine Cenomanian (Upper Cretaceous) of Lebanon. 2°. *Petersichthys libanicus* gen. and sp. nov.

Les Pantodontidae (Teleostei, Osteoglossomorpha) du Cénomanien marin (Crétacé supérieur) du Liban. 2°. *Petersichthys libanicus* gen. et sp. nov.

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Abstract: The osteology and the systematic position of *Petersichthys libanicus* gen. and sp. nov., a fossil fish from the marine Cenomanian of Lebanon, are studied in details. The skeletal characters clearly refer this fish to the order Osteoglossiformes. A few peculiar cranial features, such as the presence of a postfrontal and the parietal forming the upper margin of the temporal fossa, indicate that *P. libanicus* belongs to the family Pantodontidae. Within this family, the new genus is more closely allied with *Pankowskipiscis* than with *Pantodon* and *Prognathoglossum*.

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

Résumé: L'ostéologie et la position systématique de *Petersichthys libanicus* gen. et sp. nov., un poisson fossile du Cénomanien marin du Liban, sont étudiées en détails. Les caractères du squelette réfèrent clairement ce poisson à l'ordre des Osteoglossiformes. Certains traits crâniens, tels que la présence d'un postfrontal et le pariétal formant le bord supérieur de la fosse temporale, montrent que *P. libanicus* appartient à la famille des Pantodontidae. Au sein de cette famille, le nouveau genre est un plus proche parent de *Pankowskipiscis* que de *Pantodon* et *Prognathoglossum*.

Mots-clés: Osteoglossomorpha, Pantodontidae, *Petersichthys libanicus* gen. et sp. nov., ostéologie, phylogénie, Cénomanien marin, Liban.

INTRODUCTION

The family Pantodontidae was erected to contain a small osteoglossomorph fish from the continental waters of Africa, the genus *Pantodon* Peters, 1876 and its unique species *Pantodon buchholzi* Peters, 1876, also known as the African butterfly fish. During a long time, *Pantodon* was the only genus ranged in the family. But recently, two monospecific fossil fish genera from the marine Cenomanian of Lebanon were included in the Pantodontidae, *Prognathoglossum kalassyi* TAVERNE & CAPASSO, 2012, a fish that was firstly considered as a Lophotidae (GAYET *et al.*, 2012: fig. p. 158 below), and *Pankowskipiscis haqelensis* TAVERNE, 2022, a small species with an elongate dorsal fin beginning at the frontal level (TAVERNE & CAPASSO, 2012; TAVERNE, 2022).

The family Pantodontidae generally is ranged within the order Osteoglossiformes and the suborder Osteoglossoidei. Most authors regard the family as the sister-lineage of the Osteoglossidae (see for instance NELSON *et al.*, 2016). However, a recent genetic study gives another phylogenetic result and places the Pantodontidae as the plesiomorphic sister-group of both the Osteoglossiformes and the Mormyriformes (LAVOUÉ & SULLIVAN, 2004).

The present paper is the second one of a series devoted to the osteological and phylogenetic study of those Lebanese fossil pantodontid fishes. Its aim is to describe the skeleton of a third new pantodontid genus from the marine Cenomanian of Lebanon and to define its phylogenetic relationships.

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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

ANT	=	antorbital
ASPH	=	autosphenotic
BRSTG	=	branchiostegal ray
CHY p .	=	posterior ceratohyal
CLT	=	cleithrum
COR	=	hypocoracoid (= coracoid)
DETH	=	dermethmoid (= rostral)
DN (l., r.)	=	dentary (left, right)
EP 1-2	=	epurals 1 and 2
EPI	=	epiotic (= epioccipital)
EPIN	=	epineural
EPIPL	=	epipleural
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
HEMAP	=	haemapophysis (= parapophysis)
HEMEP	=	haemal spine
HY 1-2	=	hypurals 1 and 2
IC	=	intercalar
IORB 1-5	=	infraorbitals 1 to 5
LETH	=	lateral ethmoid
MPT	=	metapterygoid
MX	=	maxilla
NA	=	nasal
NEUREP	=	neural spine
N PU1	=	neural arch of preural vertebra 1
N U1a-b	=	neural arches of ural vertebra 1a and 1b
NP V1, 2, 3	=	neural spines of the first three vertebrae
OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
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)
RART	=	retroarticular
RI	=	rib
SCA	=	hypercoracoid (= scapula)
SY	=	symplectic
U 1a, 1b	=	the two components of ural vertebra 1
U 2 + HY3-X	=	ural vertebra 2 and the fused hypural 3 and “X”
UR	=	uroneural
V 21, 26	=	vertebrae (twenty-first, twenty-sixth)
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 ***Petersichthys*** gen. nov.

Type-species:

Petersichthys libanicus 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 German zoologist Wilhelm Carl Hartwich PETERS (1815-1883) who was the first describer of the genus *Pantodon*. The Greek word *ichthys*, fish, is added to his surname.

Species ***Petersichthys libanicus*** gen. and sp. nov.

Diagnosis

Small pantodontid fish, with a moderately deep body. Short snout. Frontal profile almost restilinear. Dermethmoid (= rostral) autogenous. Small tubular nasal lying along the frontal. Temporal fossa laterally located. Wide parietal forming the dorsal margin of the temporal fossa. Postfrontal present. Lateral ethmoid and orbistosphenoid reaching the parasphenoid and forming a complete bony interorbital septum. Parasphenoid narrow and bearing small conical teeth in the trabecular region. Jaws bearing conical teeth. Maxilla not broadened in the posterior region. No supramaxilla. Autogenous retroarticular. Small tubular antorbital. Three small anterior and two large posterior infraorbitals. Preopercle with two branches, the dorsal one elongate, the ventral one short and broad. Opercle hypertrophied. No subopercle. Three narrow branchiostegal rays. Posttemporal triangular and vertically oriented. Pelvic girdle abdominal. Axial skeleton containing 49 vertebrae (21 abdominal + 28 caudal). 18 pairs of ribs. Extremely long dorsal fin (62 rays). Dorsal fin entering in a deep notch of the posterior margin of the skull roof and reaching the level of the orbit. Frontal overhanging the parietal at the level of the posterior notch. Last vertebrae narrow. 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 small spatulate neural arches but no neural spine. U2 fused with a dorsal hypural plate. Two 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 Lebanon, the country where the specimen hereafter studied was discovered.

Holotype

Sample IRSNB P 10271, a complete specimen (Fig. 1). Total length: 67 mm. Standard length: 52 mm.

Formation and locality

Marine Upper Cenomanian deposits of Haqel, Lebanon.

General morphology and morphometric data (Fig. 1)

Figure 1: *Petersichthys libanicus* gen. and sp. nov. Holotype IRSNB P 10271. Total length: 67 mm.

General morphology and morphometric data (Fig. 1)

Petersichthys libanicus is a small fish with a moderately deep body. The following morphometric data are given in percentage (%) of the standard length (52 mm) of the holotype.

Length of the head (opercle included) …….	31.6 %
Depth of the head (in the occipital region) ……	28.8 %
Maximum depth of the body	37.2 %
Prepelvic length ……..	59.5 %
Basal length of the dorsal fin ……...	69.8 %
Preanal length …….	74.4 %
Basal length of the anal fin …….....	?
Depth of the caudal peduncle ……..	14.9 %

Osteology

The skull (Fig. 2)

The skull is imperfectly preserved and some bones are missing. The braincase and the jaws are rather small compared with the body size but the preopercle and the opercule are hypertrophied. The snout is short and the frontal profile more or less rectilinear.

The small autogenous plate-like dermethmoid (= rostral) is the only preserved element of the mesethmoid complex. There is no trace of the supraethmoid or the hypoethmoid. The short and tubular nasal is located along the anterior extremity of the frontal, just opposite to the antorbital. The vomer is not preserved. A small ventral fragment of the lateral ethmoid is visible just above the parasphenoid but the major part of the bone is lost.

There is a deep notch in the middle of the posterior border of the skull roof. The notch separates the right parietal and the posterior part of the right frontal from their left counterparts. At the level of the notch, the frontal occupies a higher position than the underlying parietal. This large notch allows the insertion of the dorsal fin till the frontal, at the level of the orbit.

The frontal forms the major part of the skull roof but a great part of the bone is missing. A rather large postfrontal is present at the posterior lateral corner of the frontal. The parietal is a large bone but its posterior region is missing. 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 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, anteriorly by the frontal and the postfrontal, ventrally by

the pterotic and posteriorly by the intercalar and the epiotic (= epioccipital). A large plate-like supratemporal (= extrascapular, scalebone) covers the fossa.

The orbitosphenoid is a wide bone that extends from the frontal to the parasphenoid. Only the upper part of the pleurosphenoid is preserved. It is probable that the lateral ethmoid, the orbitosphenoid and the pleurosphenoid formed a complete bony interorbital septum as in *Pankowskipiscis haquelensis* (TAVERNE, 2022: fig. 4). No basisphenoid is visible. The trabecular part of the parasphenoid is preserved as an imprint. The bone is narrow. Three small conical teeth are preserved just below the orbitosphenoid. The trabecular region of the parasphenoid probably bore a complete row of teeth. The prootic, the exoccipital and the basioccipital are not visible.

The autopalatine, the entopterygoid and the ectopterygoid are not preserved. The anterior margin of the metapterygoid, the articular head of the quadrate and an imprint of the symplectic are visible.

A short tubular antorbital is located near the nasal and overhangs the first infraorbital. The second infraorbital is missing. A trace of a long and narrow third infraorbital is present. Fragments of two larger infraorbitals, the fourth and the fifth ones, are located just before the dorsal branch of the preopercle. These two posterior infraorbitals are less wide than the ones of *Pankowskipiscis*. The dermosphenotic is not preserved. There is no supraorbital.

The premaxilla is located before the dermethmoid but the bone is incomplete and no tooth is visible. The maxilla is short and not especially broadened. Three conical teeth are preserved on the oral margin. No supramaxilla is present. Fragments of the two dentaries and a retroarticular are the only preserved regions of the lower jaw. Three conical teeth are present on the upper margin of the right dentary.

The large preopercle is divided in two branches, the dorsal one being the longest. The ventral branch is short but broad. The hypertrophied opercle is extremely high. Its height exceeds the length of the vertical branch of the preopercle. The lower border of the opercle reaches the pectoral girdle. No place is left for a subopercle. Three long and narrow branchiostegal rays are attached to a fragment of the posterior ceratohyal.

The hyomandibula and the elements of the branchial skeleton are not visible.

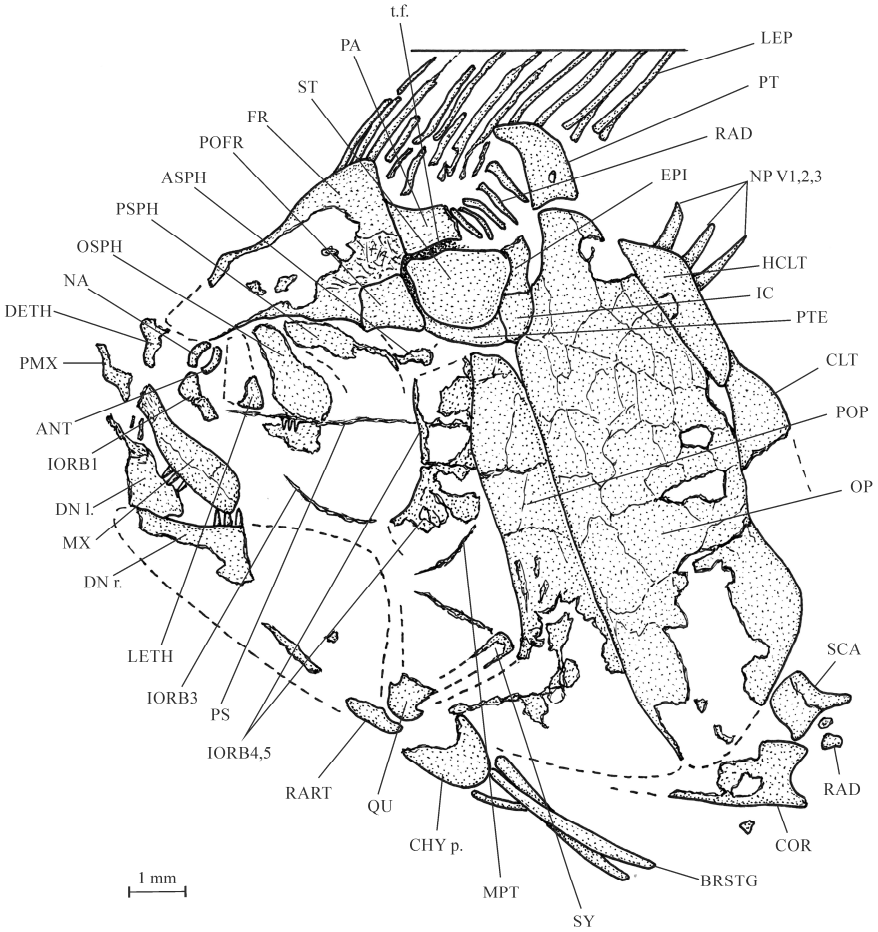

Figure 2: *Petersichthys libanicus* gen. and sp. nov. Skull and pectoral girdle of holotype IRSNB P 10271.

The girdles (Fig. 2)

The pectoral girdle is incomplete as only the most upper part of the cleithrum is present. The posttemporal is more or less triangular, with a hooked dorsal extremity, vertically oriented and located just above the opercle. The hypercleithrum (= supracleithrum) is long and narrow. The hypercoracoid (= scapula) and the hypocoracoid (= coracoid) are well visible below the opercle. The hypocoracoid seems broad but a part of the bone is lost. The pectoral fin contains 10 rays but the two last are preserved as weakly market imprints. The first ray has an enlarged basis and is segmented but not branched. The nine others are segmented and branched.

Only a small fragment of the pelvic bone is present. The ventral fin contains 10 rays and its origin is located at the level of the connection between the twenty-fourth and the twenty-fifth vertebrae.

The axial skeleton (Figs 1, 3)

There are 49 vertebrae, 21 abdominal and 28 caudal, including the ural centra. A median and horizontally oriented crest is visible on the best preserved vertebrae. The neural and haemal spines are long and narrow. The first neural spines are bifid. The vertebrae bear well developed haemapophyses in the abdominal region. The first three haemal spines are short, markedly broadened and with an acuminate lower extremity. The fourth haemal spine is a little longer. Its proximal region is narrow, while the distal part is enlarged. The following haemal spines are normal.

There are 18 pairs of elongate ribs. No supraneural is visible. Epineurals are present all along the vertebral axis. They are fused to the corresponding neural arches in the abdominal region. Those of the caudal region are autogenous and less ossified. Free epipleurals are present at the end of the abdominal region and in the caudal region. The last ones are weakly ossified.

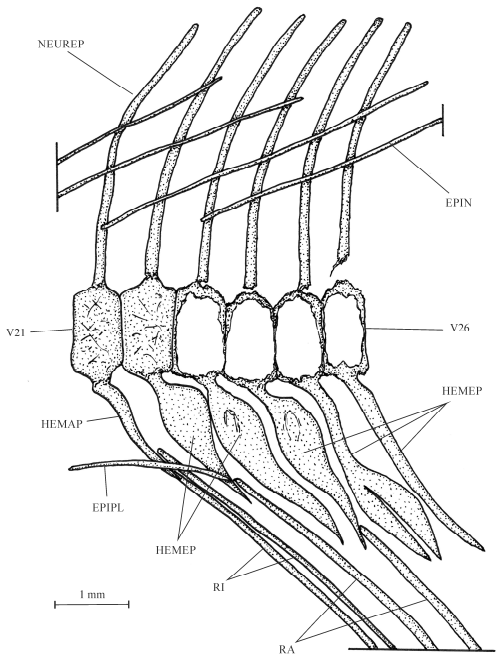

Figure 3: *Petersichthys libanicus* gen. and sp. nov. Last abdominal vertebra and first caudal vertebrae of holotype IRSNB P 10271.

The dorsal and anal fins (Fig. 1)

The dorsal fin is extremely elongated. Its origin is located above the skull, at the frontal and orbit level. The fin begins with 3 short spiny rays. The other 59 rays are much longer and segmented. The first one is pointed and they others are branched. The first pterygiophores located at the cranial level are not visible. At the body level each pterygiophore supports one ray.

Only a part of the anal fin is present. The fin is supported by 14 pterygiophores, some complete, others preserved as fragments. The first pterygiophores are long and obliquely oriented. The last 8 rays are preserved.

The first ones are lost. When complete, the anal fin probably contained about 15 rays. The anal fin origin is located at the level of the thirty-third vertebra.

The caudal skeleton and fin (Fig. 4)

The caudal skeleton is well preserved and almost complete. The last centra are deep but extremely narrow. The first ural vertebra is divided in two components, one anterior and one posterior centrum (U1a, U1b). Such a caudal morphology recalls the one of some Lycopteridae (TAVERNE, 1977: figs 37-39; among others), the most primitive family within Osteoglossomorpha. This division in two elements of the first ural vertebra in the holotype of *Petersichthys libanicus* probably is an individual abnormal variation. It is probable that the other specimens of the species had a unique first ural centrum as usual in most primitive teleosts. The last neural spines are fused to the vertebrae, contrarily to the last haemal arches that are articulated to the corresponding centra. The second preural centrum (PU2) bears the last neural spine (NP PU2) which is a little shorter than the preceding ones. The first preural vertebra (PU1) and each component of the first ural vertebra (U1a, U1b) only exhibit a spatulate neural arch. The second ural centrum (U2) is fused to an upper hypural plate (HY3 + X) which is incompletely preserved. The rather narrow parhypural is articulated and not fused to PU1. The two ventral hypurals (HY1, 2) are autogenous. HY1 is broader than HY2 and is articulated on U1a, while HY2 rests on U1b. There is only one elongate uroneural (UR). Its rounded ventral extremity partly covers the spatulate neural arch of U1a. The lower extremities of two short epurals are present behind NP PU2.

The caudal fin is forked and contains 6 upper, 7 lower procurrent rays and 16 principal rays.

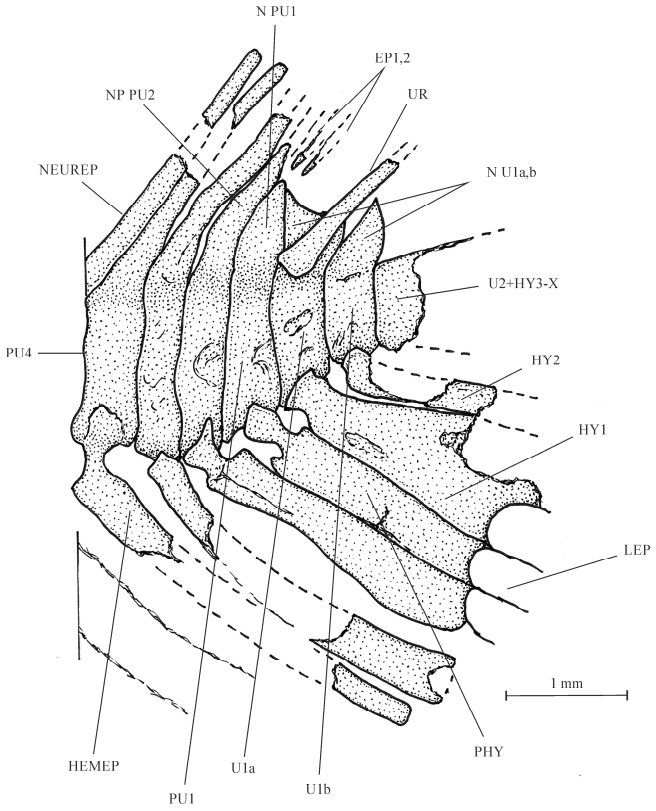

Figure 4: *Petersichthys libanicus* gen. and sp. nov. Caudal skeleton of holotype IRSNB P 10271.

Squamation

The squamation is badly preserved. The scales are small, rounded and cycloid. No reticulum is visible.

DISCUSSION

Petersichthys within Teleostei

Petersichthys is a rather primitive teleost. Indeed, the orbitosphenoid and the antorbital are present. The maxilla forms the major part of the upper jaw margin. The pelvic girdle is in abdominal position. The first neural spines are bifid. The first epineurals are fused to the neural arches. The dorsal and anal fins are devoid of strong anterior spines. PU1, U1 and U2 are not fused in a terminal vertebra. The scales are cycloid.

Petersichthys also exhibits a few peculiar characters. The dermethmoid (= rostral) is autogenous. The temporal fossa is wide and located on the lateral side of the skull and not on its rear. The parasphenoid is toothed. There are only two large posterior infraorbitals. The supraorbital is absent. The jaws bear conical teeth. The supramaxilla and the subopercle are missing. The preopercle and the opercle are hypertrophied. Both PU1 and U1 bear short spatulate neural arches. U2 is fused with a dorsal hypural plate. Only one uroneural is present. There are only 16 principal rays in the caudal fin. Within the primitive teleosts, the addition of all those features is only present in some members of the Osteoglossiformes.

Petersichthys within Osteoglossiformes

The dorsal margin of the temporal fossa is formed by the parietal in *Petersichthys* as in the Pantodontidae (TAVERNE, 1978: figs 31, 32, 34, 2022: figs 4, 6; TAVERNE & CAPASSO, 2012: fig. 4). The parietal is excluded from the temporal fossa in the Osteoglossidae (TAVERNE, 1977: figs 43, 44, 72, 72, 1978: figs 3, 21; among others) and contacts the fossa in only one point in Arapaimidae (TAVERNE, 1977: figs 104, 125; among others). A postfrontal is present as in the Pantodontidae. Such a bone is absent in all the other families of Osteoglossiformes. The scales are not reticulated, another difference with the Osteoglossidae and Arapaimidae. The placement of *Petersichthys* in the family Pantodontidae seems thus completely justified.

Petersichthys within Pantodontidae

Petersichthys shares some peculiar characters with *Pankowskipiscis*. In both genera, the dorsal fin enters in a deep notch of the posterior border of the skull roof and the origin of the fin is located above the frontal and the orbit, the braincase is rather small and the opercle is hypertrophied. But the two fishes differ by many other features. *Pankowskipiscis* has the frontal and the parietal located at the same level, a much broader maxilla, stronger teeth on the jaws, a small subopercle, wider posterior infraorbitals, larger branchiostegal rays, a rod-like and horizontally oriented posttemporal, broader preural vertebrae, a ventral hypural plate fused to a reduced U1, a small autogenous U2, a larger uroneural and three autogenous dorsal hypurals (TAVERNE, 2022: figs 4, 10, 12). *Petersichthys* and *Pankowskipiscis* undoubtedly represent two different genera. The skull and the caudal skeleton of *Petersichthys* also greatly differ from those of the recent *Pantodon* (TAVERNE, 1978: figs 30-34, 40, 41, 54; among others) and of the Cenomanian *Prognathoglossum* (TAVERNE & CAPASSO, 2012: figs 3, 4, 12).

Petersichthys clearly deserves its peculiar generic status within the family Pantodontidae.

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