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# The Pantodontidae (Teleostei, Osteoglossomorpha) from the marine Cenomanian (Upper Cretaceous) of Lebanon. 6°. *Cretapantodon polli* gen. and sp. nov.

## Les Pantodontidae (Teleostei, Osteoglossomorpha) du Cénomanien marin (Crétacé supérieur) du Liban. 6°. *Cretapantodon polli* gen. et sp. nov.

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**Abstract:** The osteology and the systematic position of *Cretapantodon polli* 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 *C. polli* belongs to the family Pantodontidae.

**Keywords**: Osteoglossomorpha, Pantodontidae, *Cretapantodon polli* gen. and sp. nov., osteology, phylogeny, marine Cenomanian, Lebanon.

**Résumé:** L'ostéologie et la position systématique de *Cretapantodon polli* 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 *C. polli* appartient à la famille des Pantodontidae.

**Mots-clés** : Osteoglossomorpha, Pantodontidae, *Cretapantodon polli* gen. et sp. nov., ostéologie, phylogénie, Cénomanien, Liban.

## INTRODUCTION

Until recently the family Pantodontidae only contains *Pantodon buchholzi* PETERS, 1876, a small freshwater osteoglossomorph fish from Africa. Today, five monospecific fossil fish genera from the marine Cenomanian of Lebanon are added to this family, *Prognathoglossum kalassyi* TAVERNE & CAPASSO, 2012, a fish that was firstly considered as a Lophotidae (GAYET *et al.*, 2012: fig. p. 158 below), *Pankowskipiscis haqelensis* TAVERNE, 2021a, *Petersichthys libanicus* TAVERNE, 2021b, *Palaeopantodon vandersypeni* TAVERNE, 2021c and *Capassopiscis pankowskii* TAVERNE, 2022 (TAVERNE & CAPASSO, 2012; TAVERNE, 2021a, b, c, 2022).

The family Pantodontidae generally is included within the order Osteoglossiformes, the suborder Osteoglossoidei and considered as the sister-lineage of the Osteoglossidae (see for instance NELSON *et al.*, 2016). However, the recent genetic study of LAVOUÉ & SULLIVAN (2004) leads to a different conclusion and places the Pantodontidae as the plesiomorphic sister-group of both the Osteoglossiformes and the Mormyriformes.

The present paper is the sixth one of a series devoted to the osteological and phylogenetic study of those Lebanese fossil pantodontid fishes. It describes the skeleton of a sixth new pantodontid genus from the marine Cenomanian of Lebanon and defines its phylogenetic relationships.

## 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.

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**List of abbreviations used in the text-figures**

| | | |
|---|---|---|
| AN | = | angular |
| ANT | = | antorbital |
| BRSTG | = | branchiostegal ray |
| CHY a. | = | anterior ceratohyal |
| CLT | = | cleithrum |
| COR | = | hypocoracoid (= coracoid) |
| DETH | = | dermethmoid (= rostral) |
| DN | = | dentary |
| DSPH | = | dermosphenotic |
| ENPT | = | entopterygoid |
| EP 1-2 | = | epurals 1 and 2 |
| EPI | = | epiotic (= epioccipital) |
| FR | = | frontal |
| HCLT | = | hypercleithrum (= supracleithrum) |
| HEMEP | = | haemal spine |
| HHY | = | hypohyal |
| HY 1-5 | = | hypurals 1 to 5 |
| HYOM | = | hyomandibula |
| IC | = | intercalar |
| IORB 3-4 | = | infraorbitals 3 and 4 |
| LEP | = | fin rays |
| LETH | = | lateral ethmoid |
| MPT | = | metapterygoid |
| MX (r., l.) | = | maxilla (right, left) |
| NA | = | nasal |
| NEUREP | = | neural spine |
| NP PU2 | = | neural spine of preural vertebra 2 |
| N PU1 | = | neural arch of preural vertebra 1 |
| N U1 | = | neural arch of ural vertebra 1 |
| OP | = | opercle |
| OSPH | = | orbitosphenoid |
| PA | = | parietal |
| PHY | = | parhypural |
| PMX (r., l.) | = | premaxilla (right, left) |
| POFR | = | postfrontal |
| POP | = | preopercle |
| PS | = | parasphenoid |
| PSPH | = | pleurosphenoid |
| PT | = | posttemporal |
| PTE | = | pterotic |
| PU 1-5 | = | preural vertebrae 1 to 5 |
| QU | = | quadrate |
| RAD | = | pterygiophore (= radial) |
| SCA | = | hypercoracoid (= scapula) |
| SOP | = | subopercle |
| ST | = | supratemporal (extrascapular, scalebone) |
| SY | = | symplectic |
| U 1-2 | = | ural vertebrae 1 and 2 |
| UR | = | uroneural |
| fr. | = | fragment |
| 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 ***Cretapantodon*** gen. nov.

**Type-species**:

*Cretapantodon polli* gen. and sp. nov. (by monotypy).

**Diagnosis**

As for the species (monospecific genus)

**Etymology**

The name of the new genus unites the word Cretaceous and the generic name of the Recent *Pantodon*. Species ***Cretapantodon polli*** gen. and sp. nov.

**Diagnosis**

Small pantodontid fish, with a moderately deep body. Short snout. Frontal profile restilinear. Dermethmoid (= rostral) autogenous. Small tubular nasal lying along the frontal. Wide parietal. Postfrontal present. Temporal fossa laterally located and surrounded by the frontal, the parietal, the pterotic, the intercalary and the postfrontal.. Lateral ethmoid, orbistosphenoid and pleurosphenoid reaching the parasphenoid and forming a complete bony interorbital septum. No basisphenoid. Parasphenoid moderately broad and entirely covered by small conical teeth in the trabecular region. Jaws bearing strong conical teeth. Maxilla not broadened in the posterior region. No supramaxilla. Small tubular antorbital. Two large posterior infraorbitals. A wide triangular dermosphenotic. No supraorbital. Preopercle with two branches, the dorsal one elongate, the ventral one short and broad. Opercle hypertrophied and extremely deep. Small subopercle. A series of thin branchiostegal rays. Hypocoracoid with a pointed process at its posterior ventral corner. Pelvic girdle abdominal. Axial skeleton containing 48 vertebrae (26 abdominal + 22 caudal). 21 pairs of ribs. The first four haemal spines broadened. Extremely long dorsal fin (53 rays). Dorsal fin entering in a deep notch of the posterior margin of the skull roof and reaching the level of the orbit. Anal fin with 11 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 bearing a small spatulate neural arch. U1 bearing an extremely reduced neural arch. U2 fused with a dorsal hypural plate. The two ventral hypurals fused. Two epurals. One urodermal. Forked caudal fin with 16 principal rays. Small cycloid scales, deeper than long, with weakly marked granulations and no reticulum.

**Etymology**

The specific name of the new fish is given in honour of the late Prof. Dr. Max POLL (1908-1991), an eminent specialist of the African fish fauna who was also my Mentor during my own formation in ichthyology sixty years ago.

**Holotype**

Sample IRSNB P 10391, a complete specimen (Fig. 1). Total length: 94 mm. Standard length: 77 mm.

**Formation and locality**

Marine Upper Cenomanian deposits of Haqel, Lebanon.

**General morphology and morphometric data** (Fig. 1)

*Cretapantodon polli* is a small fish with a moderately deep body. The following morphometric data are given in percentage (%) of the standard length (77 mm) of the holotype.

| | |
|---|---|
| Length of the head (opercle included) | 27.5 % |
| Depth of the head (in the occipital region) | 37.5 % |
| Maximum depth of the body | 46.2 % |
| Prepelvic length | 58.1 % |
| Basal length of the dorsal fin | 78.1 % |
| Preanal length | 77.5 % |
| Basal length of the anal fin | 12.5 % |
| Depth of the caudal peduncle | 15.6 % |


**Figure 1.-** *Cretapantodon polli* gen. and sp. nov. Holotype IRSNB P 10391 Total length: 94 mm. This specimen was erroneously presented as the holotype of *Capassopiscis pankowskii* in TAVERNE (2022a: fig. 1). The true holotype of *Capassopiscis pankowskii* is shown in TAVERNE (2022b: fig. 1).

## Osteology

***The skull*** (Fig. 2)

The skull is well preserved and is deeper than long. The snout is short and obliquely oriented. The frontal profile is 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 endochondral components of the mesethmoid. They probably were cartilaginous and so not preserved. The short and tubular nasal is located along the anterior extremity of the frontal, just before the antorbital. The lateral ethmoid is visible just behind the antorbital and its posterior border meets the anterior margin of the orbitosphenoid. The vomer is not preserved.

There is a deep notch in the middle of the posterior border of the skull roof. This notch separates the right parietal and the posterior part of the right frontal from their left counterparts and 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. A small rod-like postfrontal is present at the posterior lateral corner of the frontal. The parietal is a large bone. The autosphenotic is completely hidden by the dermosphenotic. 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, ventrally by the postfrontal and the pterotic and posteriorly by the intercalar and the pterotic. The epiotic (= epioccipital) does not border the fossa. The fossa is covered by a large plate-like supratemporal (= extrascapular, scalebone).

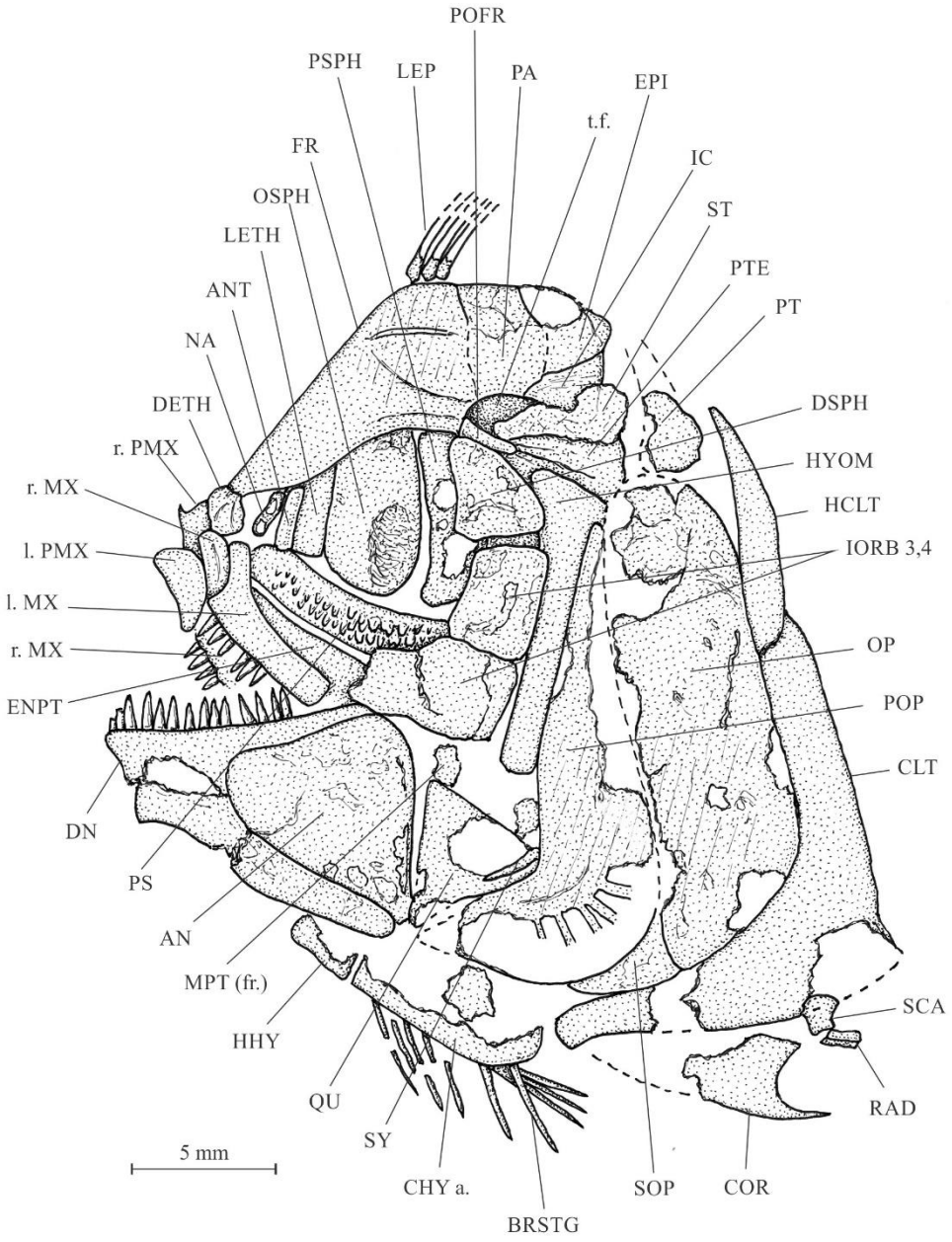


**Figure 2.-** *Cretapantodon polli* gen. and sp. nov. Skull and pectoral girdle of holotype IRSNB P 10391.

The orbitosphenoid and the pleurosphenoid are wide bones that extend from the frontal to the parasphenoid. The lateral ethmoid, the orbitosphenoid and the pleurosphenoid formed a complete bony interorbital septum. No basisphenoid is visible. Only the trabecular region of the parasphenoid is preserved. The bone is rather broad and it bears numerous teeth all along its length. The prootic, the exoccipital and the basioccipital are not visible.

The autopalatine and the ectopterygoid are not preserved. A small portion of the entopterygoid is visible just above the maxilla. Two very small fragments of the metapterygoid are present just above the dorsal margin of the quadrate. The quadrate is triangular in shape. The bone bears a quadratic process. A short and narrow symplectic is visible between the quadrate and its process.

A short tubular antorbital is located on the lateral ethmoid and just behind the nasal. The anterior infraorbitals are missing. Two large posterior infraorbitals, probably the third and he fourth ones, are located just before the ventral branch of the hyomandibula. The wide dermosphenotic is .triangle-shaped. There is no supraorbital.

The two premaxilla are preserved. They are devoid of ascending process. No teeth are visible but that is perhaps an artefact due to the fossilization. The maxilla is short, moderately broad and devoid of posterior widening. Large conical teeth are preserved all along the oral margin. No supramaxilla is present. The lower jaw

is short and rather deep at the coronoid level. The dentary bears the same teeth as the maxilla. A large angular is visible but not the articular and the retroarticular.

The large preopercle is divided in two branches, the dorsal one being the longest. The ventral branch is very short but broad. The preopercular sensory canal with five secondary tubules is visible in the lower portion of the bone. The hypertrophied opercle is extremely high but not very broad. Its height exceeds the length of the vertical branch of the preopercle. The lower border of the opercle reaches the pectoral girdle level. The reduced subopercle is located before the opercle and below the preopercle. Fragments of seven short and thin branchiostegal rays are attached to the anterior ceratohyal. The hypohyal and the anterior ceratohyal are partly preserved but not the posterior ceratohyal.

The hyomandibula exhibits a narrow condylar head and a long ventral branch. The posterior forked extremity of the narrow urohyal is visible behind the branchiostegal rays.

***The girdles*** (Fig. 2)

The pectoral girdle is rather complete but only the basal part of the posttemporal and the posterior part of the hypocoracoid (= coracoid) are present. The hypercleithrum (= supracleithrum) is long and narrow. The hypercoracoid (= scapula) is strongly reduced. The hypocoracoid bears a thin acuminate process located at its ventral posterior corner. The pectoral fin is badly preserved. There are about 13 rays but their distal extremities are lost.

The pelvic girdle is in abdominal position. The pelvic bones are elongated. Each ventral fin contains 6 segmented and branched rays. The origin of the ventral fins is located at the level of the twenty-second vertebra.

***The axial skeleton*** (Fig. 1 & 3)

There are 48 vertebrae, 26 abdominal and 22 caudal, including the ural centra. The first three vertebrae are hidden by the opercle and the hypercleithrum but their neural spines are well visible. A median and horizontally oriented crest is visible on the best preserved vertebrae. This crest separates two small holes. Most neural and haemal arches are fused to their centra. The neural and haemal spines are long and narrow. The first neural spines are bifid. The abdominal vertebrae bear well developed haemapophyses. The first four haemal spines are short, markedly broadened and with an acuminate lower extremity. Such a specialized situation also exists in *Petersichthys libanicus* (TAVERNE, 2021b: fig. 3). The following haemal spines are normal.

There are 21 pairs of elongate ribs. No supraneural is visible. Epineurals are present all along the vertebral axis. They are fused to the corresponding neural arches till the thirteenth vertebra. The other epineurals 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.

***The dorsal and anal fins*** (Fig. 1)

The dorsal fin is extremely elongated. Its origin is located at the frontal and orbit level, in the posterior notch of the skull roof. The fin contains 53 rays. The first three are short and pointed. The others are longer, segmented and branched at their distal tip. Only 48 pterygiophores are visible. The first pterygiophores located at the cranial level are not visible. At the body level each pterygiophore supports one ray.

The anal fin is short. The fin is supported by 11 pterygiophores. The first pterygiophore bears the first three rays. Each other pterygiophore support one ray. The last rays are not preserved. But the total number of rays must be 13. The first ray is short, spiny and unsegmented. The second ray is longer, segmented and pointed. All the other rays are segmented and branched at their distal tip. The anal fin origin is located at the level of the thirty-third vertebra.

***The caudal skeleton and fin*** (Fig. 3)

The caudal skeleton is well preserved and almost complete. The last centra are deeper than long. The last neural arches are fused to the vertebrae, contrarily to the last haemal arches and the parhypural (PHY) that are articulated to the corresponding centra. The second preural centrum (PU2) bears the last neural spine (NP PU2). The first preural vertebra (PU1) only exhibits a short spatulate neural arch (N PU1). The first ural centrum (U1) bears a reduced neural arch (N U1). There are two epurals (EP1, 2), one uroneural (UR) and five hypurals (HY1-5). HY1 and 2 are fused, forming a ventral hypural plate that is articulated on U1. HY3 and HY4 are joined, forming a dorsal hypural plate that is fused to the second ural centrum (U2). The suture between HY3 and HY4 is still visible. HY5 is autogenous.

The caudal fin is forked and contains 17 upper, 15 lower procurrent rays and 16 principal rays.

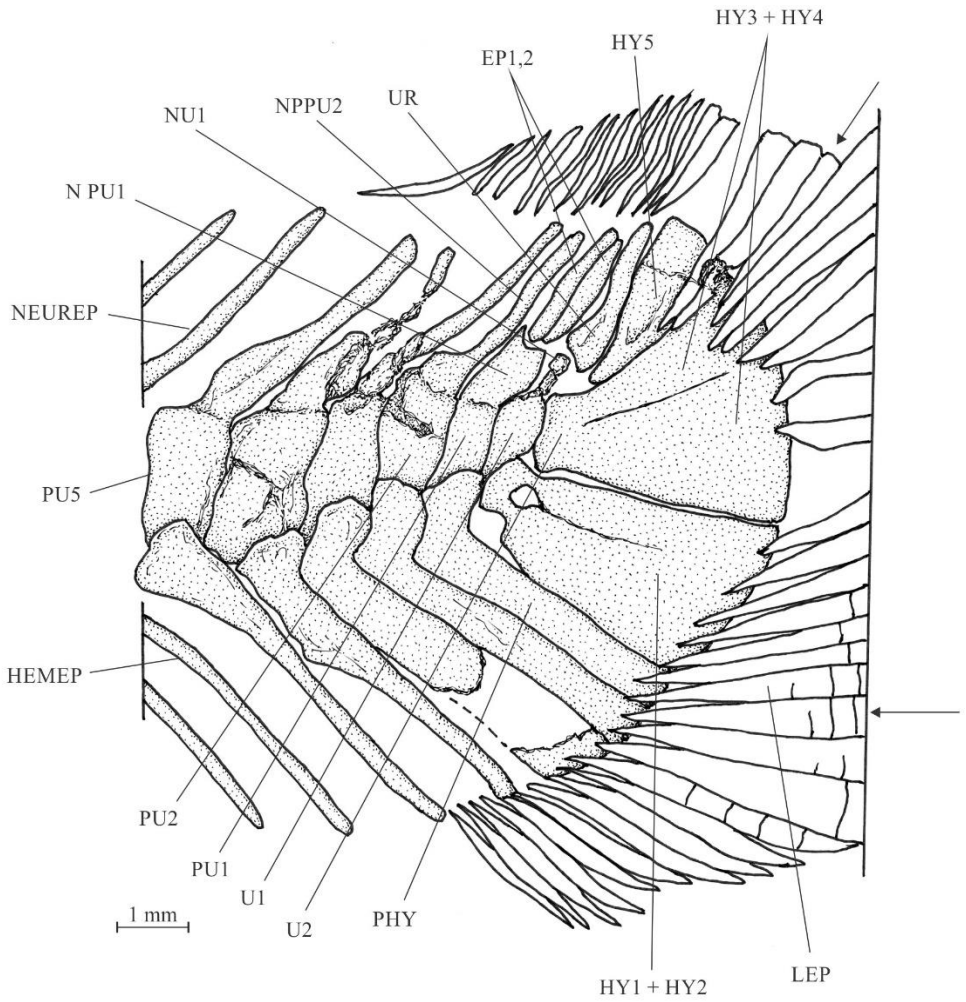


**Figure 3.-** *Petersichthys libanicus* gen. and sp. nov. Caudal skeleton of holotype IRSNB P 10391.

***Squamation***

The scales are small, ovoid, deeper than long, with some weakly marked granulations. No reticulum is visible.

## DISCUSSION

***Cretapantodon* within Teleostei**

As the other fossil Lebanese Pantodontidae, *Cretapantodon* exhibits a series of characters attesting a systematic position within the Osteoglossiformes. 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. The basisphenoid is missing. There are only two large posterior infraorbitals. The supraorbital is absent. The jaws bear strong conical teeth. The supramaxilla is missing. The preopercle and the opercle are hypertrophied. Both PU1 and U1 bear short 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.

***Cretapantodon* within Osteoglossiformes**

The temporal fossa of *Cretapantodon* is dorsally bordered by the parietal and ventrally by the postfrontal as in Pantodontidae (TAVERNE, 1978: figs 31, 32, 34, 2021a: figs 4, 6, 2021b: fig. 2, 2021c: fig. 3, 2022: fig. 2; 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 only in Pantodontidae but is missing in all the other families of Osteoglossiformes. The scales are not reticulated, another difference with Osteoglossidae and Arapaimidae. The placement of *Cretapantodon* in the family Pantodontidae seems thus completely justified.

### *Cretapantodon* within Pantodontidae

*Cretapantodon* shares a very peculiar apomorphy with two other fossil pantodontid fishes, *Pankowskipiscis* and *Petersichthys*. In the three genera, the dorsal fin enters in a deep notch of the posterior margin of the skull roof and the origin of the fin is located above the frontal and the orbit, (Fig. 2; TAVERNE, 2021a: fig. 4, 2021b: fig. 2). The three fishes seem thus closely related.

*Cretapantodon* and *Petersichthys* share another apomorphy, the broadening of the first haemal spines (TAVERNE, 2021b: fig. 3), a character not present in *Pankowskipiscis*.

The hypocoracoid of the Recent *Pantodon* presents a highly specialized feature, an extremely long and acuminate process at its ventral posterior corner (TAVERNE, 1978: fig. 44). Such a process also exists in *Palaeopantodon*, the closest relative of the modern *Pantodon*, but is much more shorter (TAVERNE, 2021c: fig.3). *Cretapantodon* exhibits the same short process on the hypocoracoid (Fig. 2). A still more reduced process is present in *Petersichthys* (TAVERNE, 2021b: fig. 2). Such a process is absent in *Prognathoglossum*, *Pankowskipiscis* and *Capassopiscis*, the three other fossil Pantodontidae (TAVERNE & CAPASSO, 2012: fig. 6; TAVERNE, 2021a: fig. 4, 2022: fig. 2).

*Pantodon* and *Palaeopantodon* have the pelvic girdle in thoracic position, a specialized character (TAVERNE, 1978: fig. 29, 2021c: figs 1, 3). All the other fossil Pantodontidae have the pelvic girdle in abdominal position, a plesiomorphic condition (TAVERNE & CAPASSO, 2012: fig. 1; TAVERNE, 2021a: fig. 2, 2021b: fig. 1, 2022b: fig. 1).

On these osteological bases, the systematic position of *Cretapantodon* within the phylogeny of the family appears to lie between the plesiomorphic *Petersichthys*, at the one hand, and the apomorphic *Palaeopantodon* and *Pantodon*, on the other hand.


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