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# The Pantodontidae (Teleostei, Osteoglossomorpha) from the marine Cenomanian (Upper Cretaceous) of Lebanon. 3°. *Palaeopantodon vandersypeni* gen. and sp. nov.

## Les Pantodontidae (Teleostei, Osteoglossomorpha) du Cénomanien marin (Crétacé supérieur) du Liban. 3°. *Palaeopantodon vandersypeni* gen. et sp. nov.

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**Résumé:** L'ostéologie et la position systématique de *Palaeopantodon vandersypeni* gen. and 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 et plus particulièrement à la famille des Pantodontidae. Au sein de cette famille, le nouveau genre partage avec l'actuel *Pantodon* quatre importantes apomorphies, l'élargissement du nasal, la position avancée de la ceinture pelvienne, l'allongement des nageoires ventrales et le développement de neurépines complètes sur les vertèbres préurale 1 et urale 1. Les trois autres genres fossiles de Pantodontidae, *Prognathoglossum*, *Pankowskipiscis* et *Petersichthys* ont un petit nasal tubulaire, la ceinture pelvienne en position abdominale, les nageoires ventrales courtes, la dernière neurépine complète sur la vertèbre préurale 2, un arc neural en forme de spatule sur les vertèbres préurale 1 et urale 1 et un ou deux épuraux.

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

**Abstract:** The osteology and the systematic position of *Palaeopantodon vandersypeni* 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 and more particularly to the family Pantodontidae. Within this family, the new genus shares five important apomorphies with the recent *Pantodon*, the broadening of the nasal, the advanced position of the pelvic girdle, the lengthening of the ventral fins, the development of complete neural spines on the preural vertebra 1 and on the ural vertebra 1 and the lost of the epurals. The three other fossil pantodontid genera, *Prognathoglossum*, *Pankowskipiscis* and *Petersichthys*, have a small tubular nasal, the pelvic girdle in abdominal position, short ventral fins, the last complete neural spine on the preural vertebra 2, spatulate neural arches on the preural vertebra 1 and on the ural vertebra 1 and one or two epurals.

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

## INTRODUCTION

The family Pantodontidae belongs to the Osteoglossomorpha, a superorder of primitive teleosts known from the terminal Jurassic to the present times. Most authors range the family within the order Osteoglossiformes and the suborder Osteoglossoidei and regard the lineage as the sister-group of the Osteoglossidae (NELSON *et al.*, 2016). However, a recent genetic study places the Pantodontidae as the plesiomorphic sister-lineage of both the Osteoglossiformes and the Mormyriformes (LAVOUÉ & SULLIVAN, 2004). During more than a century the family contained only one genus, *Pantodon* PETERS, 1876, and one species, *Pantodon buchholzi* PETERS, 1876, the butterfly-fish, a small modern species from the continental waters of Africa. Recently, three fossil pantodontid genera, *Prognathoglossum* TAVERNE & CAPASSO, 2012, *Pankowskipiscis* TAVERNE, 2021 and *Petersichthys* TAVERNE, 2022, were described from the marine Cenomanian of Lebanon (TAVERNE & CAPASSO, 2012; TAVERNE, 2021, 2022).

The present paper is the third one of a series devoted to the study of the osteology and phylogeny of those numerous Lebanese fossil pantodontid fishes. Its aim is to describe the skeleton of a fourth new pantodontid genus from the marine Cenomanian of Lebanon and to define its phylogenetic relationships. A specimen of this species was figured in GAYET *et al.*, 2012: fig. p. 157) and considered as a Bregmacerotidae.

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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 and the photos by Mr. Adriano VANDERSYPEN from the IRSNB.

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

| | | |
|---|---|---|
| AN | = | angular |
| ANT | = | antorbital |
| APAL | = | autopalatine |
| ASPH | = | autosphenotic |
| CLT | = | cleithrum |
| COR | = | hypocoracoid (= coracoid) |
| DBHY-BBR | = | dermobasihyal-basibranchial |
| DETH | = | dermethmoid (= rostral) |
| DN | = | dentary |
| ECPT | = | ectopterygoid |
| ENPT | = | entopterygoid |
| EPI | = | epiotic (= epioccipital) |
| EXO | = | exoccipital |
| FR | = | frontal |
| HCLT | = | hypercleithrum (= supracleithrum) |
| HEMEP | = | haemal spine |
| HY 1-5 | = | hypurals 1 to 5 |
| HYOM | = | hyomandibula |
| IC | = | intercalar |
| IORB 1-3 | = | infraorbitals 1 to 3 |
| LEP | = | lepidotrichia (= rays) |
| LETH | = | lateral ethmoid |
| MPT | = | metapterygoid |
| MX | = | maxilla |
| NA | = | nasal |
| NEUREP | = | neural spine |
| NP PU1, 2 | = | neural spine of preural vertebrae 1 and 2 |
| NP U1 | = | neural spine of ural vertebra 1 |
| N U1 | = | neural arch of ural vertebra 1 |
| OP | = | opercle |
| OSPH | = | orbitosphenoid |
| PA | = | parietal |
| PECT | = | pectoral fin |
| PEL | = | 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 |
| SCA | = | hypercoracoid (= scapula) |
| SOC | = | supraoccipital |
| SOP | = | subopercle |
| U 1 | = | ural vertebra 1 |
| U 2 + HY3-X | = | ural vertebra 2 and the fused hypural 3 and “X” |

| | | |
|---|---|---|
| UR | = | uroneural |
| V1-4 | = | first four vertebrae |
| VENT | = | ventral fin |
| VO | = | vomer |
| m. c. | = | mandibular sensory canal |
| sorb. c. | = | supraorbital sensory canal |
| 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 ***Palaeopantodon*** gen. nov.

Type-species:

*Palaeopantodon vandersypeni* gen. and sp. nov. (by monotypy).

**Diagnosis**

As for the species (monospecific genus)

**Etymology**

The name of the new genus begins with the Greek prefix *palaios*, ancient, and refers to the recent genus *Pantodon*.

Species ***Palaeopantodon vandersypeni*** gen. and sp. nov.

**Diagnosis**

Small deep-bodied pantodontid fish. Snout very short. Frontal profile arched. Dermethmoid (= rostral) autogenous. Nasal long and broad. Frontal slightly overhanging the parietal. Temporal fossa laterally located. Large 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. Parasphenoid narrow and toothless. Autopaline, ectopterygoid and entopterygoid wide and toothless. Jaws obliquely oriented. Premaxilla bearing conical teeth. Maxilla long, narrow and edentulous. No supramaxilla. Autogenous retroarticular. Small tubular antorbital. First infraorbital large. Second and third infraorbitals tubular. Preopercle with two branches, the dorsal one elongate, the ventral one short. Opercle hypertrophied. Subopercle reduced . Dermobasihyal and dermobasibranchial fused together, forming a long and broad toothed plate. Posttemporal small. Pelvic girdle in jugular position. Ventral fins extremely elongated. Axial skeleton containing 38 vertebrae (16 abdominal + 22 caudal). Extremely long dorsal fin beginning just behind the head. Preural centrum 1 (PU1) and ural centra 1 and 2 (U1, U2) not fused together. PU1 and U1 bearing complete neural spines. U2 fused with a dorsal hypural plate. No epural. One small narrow urodermal. Forked caudal fin, with 8 principal rays in the dorsal lobe. .

**Etymology**

The specific name of the new fish is chosen to honour Mr. Adriano VANDERSYPEN of the IRSNB and to thank him for the precious help he gave me during the last years for my scientific works.

**Holotype**

Sample IRSNB P 8279, a complete juvenile specimen (Fig. 1). Total length: 21 mm. Standard length: 17 mm.

**Formation and locality**

Marine Upper Cenomanian deposits of Haqel, Lebanon.

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

*Palaeopantodon vandersypeni* is a small fish with a deep body. The following morphometric data are given in percentage (%) of the standard length (17 mm) of the holotype.

Length of the head (opercle included) …….. 31.8 %
Depth of the head (in the occipital region) …….. 43.7 %
Maximum depth of the body ..... 55.9 %
Prepelvic length …….. 25.3 %
Length of the ventral fins …… 51.2 %
Basal length of the dorsal fin ……... 87.0 %
Preanal length ……. 78.8 %
Basal length of the anal fin ……..... 17.6 %
Depth of the caudal peduncle …….. 15.9 %

**Figure 1:** *Palaeopantodon vandersypeni* gen. and sp. nov. Holotype IRSNB P 8279. The scale is in mm.

**Osteology**

***The skull*** (Figs 2, 3)

The skull is more ossified than the body, the specimen being a juvenile one. The snout is very short, prognathous, with obliquely oriented jaws. The frontal profile is angular, with an arched frontal.

The small autogenous plate-like dermethmoid (= rostral) is the only preserved element of the mesethmoid complex. No trace of the supraethmoid or the hypoethmoid is present. The nasal is enlarged and located along the dermethmoid and the anterior extremity of the frontal. The vomer is short, narrow and edentulous. The lateral ethmoid is badly preserved. It is a wide bone located behind the nasal and just above the parasphenoid.

The frontal forms the major part of the skull roof but the anterior region of the bone is lost. The posterior part of a broad and opened supraorbital sensory canal is visible on the posterior region of the frontal. There is no contact with an otic sensory canal. A fragment of the postfrontal is preserved at the posterior lateral corner of the frontal. The parietal is an elongate but rather narrow bone. The posterior margin of the frontal slightly overhangs

the parietal. A small fragment of the autosphenotic is located below the postfrontal. The supraoccipital is positioned behind the epiotic (= epioccipital). The intercalar and the exoccipital are also present. The pterotic is divided in two elements, a thin dermal component (dermopterotic) and a larger endochondral component (endopterotic). It is highly probable that these two elements were completely fused in adult specimens.

The wide temporal (= posttemporal) fossa is entirely located on the lateral wall of the skull. The fossa is bordered dorsally by the parietal, anteriorly by the parietal, the frontal, the postfrontal and the dermopterotic, ventrally by the dermopterotic and posteriorly by the epiotic. The supratemporal (= extrascapular, scalebone) is not preserved.

The orbitosphenoid and the pleurosphenoid are large bones that extend from the frontal to the parasphenoid. The lateral ethmoid, the orbitosphenoid and the pleurosphenoid form a complete bony interorbital septum. No basisphenoid is visible. The parasphenoid is narrow and toothless. The bone bears a pair of very short basipterygoid processes. The anterior region of the prootic is visible. The basioccipital is hidden by the opercle.

The autopalatine, the entopterygoid and the ectopterygoid are wide and toothless bones. The metaperygoid and the quadrate also are preserved but not the symplectic.

A short tubular antorbital is located just above the nasal and below the frontal. The first infraorbital is a large bone. The second and the third infraorbitals are tubular. No trace of the posterior infraorbitals and of the dermosphenotic is preserved. There is no supraorbital.

The jaws are obliquely oriented. Fragments of the two premaxillae are visible. One conical tooth is associated to each of them. The maxilla is long, narrow and toothless. No supramaxilla is present. Parts of the dentary, of the angular and a reduced autogenous retroarticular are the only preserved regions of the lower jaw. The oral border of the lower jaw is hidden by the maxilla and a large branchial bone. It is thus not possible to know if the dentary bore teeth or not.

The preopercle is divided in two branches. The dorsal one is narrow but extremely elongated. The ventral branch is shorter but also broader. The hypertrophied opercle is extremely high. Its height exceeds the length of the vertical branch of the preopercle. A small subopercle is present below the opercle. The branchiostegal rays are not visible.

The ventral branch of the hyomandibula lies along the preopercle. The dermobasihyal and the dermobasibranchial are fused together. They form a long and broad plate that bears numerous small dental alveoli, the corresponding thin teeth being lost during the fossilisation.

**Figure 2:** *Palaeopantodon vandersypeni* gen. and sp. nov. Head region of holotype IRSNB P 8279.

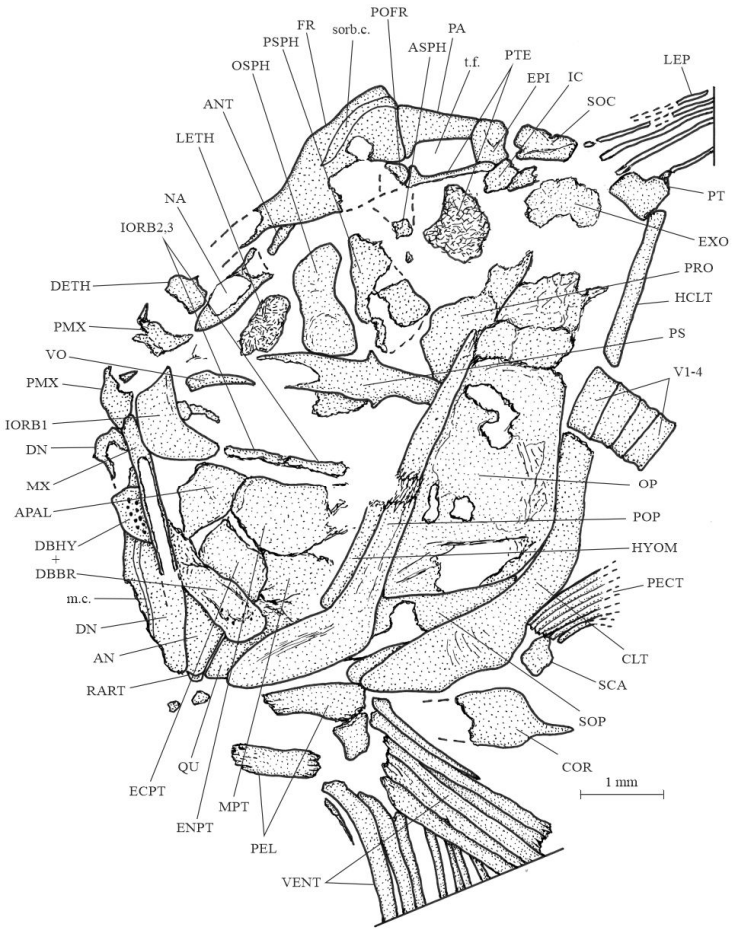


**Figure 3:** *Palaeopantodon vandersypeni* gen. and sp. nov. Skull, pectoral and pelvic girdles of holotype IRSNB P 8279.

***The girdles*** (Fig. 3)

The posttemporal is a small plate-like bone located just above the long rod-like hypercleithrum (= supracleithrum). The cleithrum is arched and rather narrow. A small hypercoracoid (= scapula) and a fragment of a larger hypocoracoid (= coracoid) are also visible. The posterior border of the hypocoracoid bears a short acuminate posterior process. The pectoral fin contains 7 short and weakly marked rays.

The pelvic girdle occupies a jugular position, under the skull and before the pectoral fin. The pelvic bones are short but broad. Each ventral fin begins with a short spiny ray and contains 9 extremely elongate rays that reach the anal fin. The rays are segmented at their distal extremities but not branched. The first long ray is a little stronger than the following ones.

***The axial skeleton*** (Figs 1, 3)

The axial skeleton is weakly ossified. There are 38 vertebrae, 16 abdominal and 22 caudal, including the two ural centra. The vertebrae are deeper than long, except a few ones in the caudal region. The neural and haemal spines are long and narrow. The neural spines are rectilinear and the haemal spines arched. The vertebrae bear small haemapophyses in the abdominal region. The ribs seem not yet developed. No supraneural and no ossified epineurals and epipleurals are visible.

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

The dorsal fin begins just after the supraoccipital and extends all along the dorsal margin of the body. The exact number of rays and pterygiophores is not determinable. At the body level each pterygiophore supports one ray.

The anal fin contains 12 rather long rays. They are segmented at their distal extremities. Only weakly marked traces of pterygiophores are visible. The anal fin origin is located at the level of the twenty-sixth vertebra.

***The caudal skeleton and fin*** (Fig. 4)

The caudal skeleton is rather well preserved and almost complete. Till the preural vertebra 3, the centra are a little longer than deep. The last vertebrae are as deep as long. The preural vertebrae 1 and 2 (PU1, PU2) and the ural vertebra 1 (U1) bear complete neural spines. The neural spine of U1 is a little broader than the preceding ones that are extremely narrow. The second ural centrum (U2) is fused to an upper hypural plate (HY3 + X) which is incompletely preserved. The rather large parhypural is fused to PU1. The two ventral hypurals (HY1, 2) are autogenous. Both are articulated on U1. Only a small fragment of HY1 is preserved. There is only one small thin uroneural (UR) located behind the neural spine of U1. No trace of epural is visible.

The caudal fin is forked. The total number of caudal rays is not known but the upper lobe contains 8 principal rays and at least 3 procurrent rays.

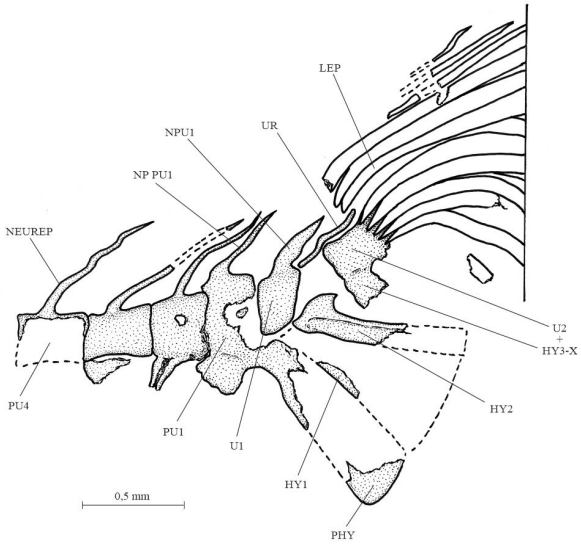


**Figure 4:** *Palaeopantodon vandersypeni* gen. and sp. nov. Caudal skeleton of holotype IRSNB P 8279.

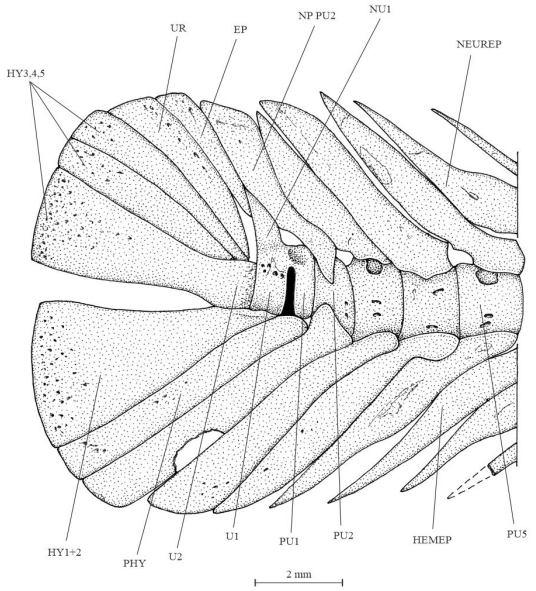


**Figure 5:** *Prognathoglossum kalassyi* TAVERNE & CAPASSO, 2012. Caudal skeleton of holotype CLC S-483, modified from TAVERNE & CAPASSO (2012: fig. 12).

### *Squamation*

No scale is visible. It seems that the squamation is not yet completely developed, the specimen being a juvenile one.

## DISCUSSION

### *Palaeopantodon* within Osteoglossiformes

The wide temporal fossa of *Palaeopantodon* is entirely located on the lateral side of the skull and the large parietal forms the dorsal margin of the fossa as in the other Pantodontidae (TAVERNE, 1978: figs 31, 32, 34, 2021: figs 4, 6, 2022: fig. 2; TAVERNE & CAPASSO, 2012: fig. 4). The parietal does not reach 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 a reduced region in Arapaimidae (TAVERNE, 1977: figs 104, 125; among others). A postfrontal is present in *Palaeopantodon* as in all Pantodontidae. Such a bone is missing in the other families of Osteoglossomorpha. *Palaeopantodon* clearly deserves its placement in the family Pantodontidae.

### *Palaeopantodon* within Pantodontidae

The data hereafter mentioned concerning *Pantodon*, *Prognathoglossum*, *Pankowskipiscis* and *Petersichthys* come from RIDEWOOD (1905), GREENWOOD & THOMPSON (1960), GREENWOOD (1967), KERSHAW (1970), TAVERNE (1978, 2021, 2022), HILTON (2003), HILTON & BRITZ (2010) and TAVERNE & CAPASSO (2012).

*Pantodon* has a very broad nasal, while *Prognathoglossum*, *Pankowskipiscis* and *Petersichthys* exhibit a short tubular nasal. *Palaeopantodon* has a longer and broader nasal than the one of the three other fossil pantodontid genera.

*Palaeopantodon* has the pelvic girdle in jugular position and the ventral fins are extremely elongated. The pelvic girdle of *Pantodon* is located in an advanced position just behind the pectoral level and the ventral fin rays are very long. In *Prognathoglossum*, *Pankowskipiscis* and *Petersichthys* the pelvic girdle is in abdominal position and the ventral fins are short.

The axial skeleton of *Pantodon* contains 30 (15 + 15) rarely 31 vertebrae. *Prognathoglossum* has a longer vertebral axis, with 77 (47 + 30) centra. *Pankowskipiscis* and *Petersichthys* respectively have 46 to 48 (23-25 + 23) and 49 (21 + 28) vertebrae. With 38 (16 + 22) centra, *Palaeopantodon* approaches the number found in *Pantodon*.

*Pantodon* and *Palaeopantodon* exhibit complete neural spines on PU1 and U1 and the epurals are lost. *Prognathoglossum*, *Pankowskipiscis* and *Petersichthys* have only neural arches on PU1 and U1 and one or two epurals are present. It is to be noted here that the two elements formerly named uroneural and hypural 6 in *Prognathoglossum* (TAVERNE & CAPASSO, 2012: fig. 12) are respectively an epural and an uroneural (cf. Fig. 5) by comparison with the caudal morphology of *Pankowskipiscis* and *Petersichthys*.

For all these characters *Palaeopantodon* undoubtedly is closer to the recent *Pantodon* than are *Prognathoglossum*, *Pankowskipiscis* and *Petersichthys*. Within the family Pantodontidae, *Palaeopantodon* thus appears to be the direct sister-genus of the modern *Pantodon*.


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