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A horny pycnodont fish (Pycnodontiformes) in the continental Middle Jurassic (Stanleyville Formation) of the Democratic Republic of Congo

Un poisson pycnodonte à corne (Pycnodontiformes) dans le Jurassique moyen continental (Formation de Stanleyville) de la République Démocratique du Congo

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Résumé: Un fragment crânien et des cornes nucales de *Congopycnodus cornutus* gen. et sp. nov., du Jurassique moyen continental (Formation de Stanleyville) de la République Démocratique du Congo, sont décrits. Le nouveau genre de poisson pycnodonte est rapporté à la superfamille des Coccodontoidea, la seule lignée de Pycnodontiformes qui contient des membres cornus. Des comparaisons sont faites avec les trois familles de coccodontoïdes, les Coccodontidae, les Gebrayelichthyidae et les Gladiopycnodontidae. *Congopycnodus* n'appartient à aucune de ces familles mais est considéré comme le précurseur anatomique des Gebrayelichthyidae et des Gladiopycnodontidae. Des commentaires zoogéographiques sont avancés pour expliquer la présence d'un poisson pycnodonte en Afrique Centrale au Jurassique moyen.

Mots-clés: Pycnodontiformes, Coccodontoidea, *Congopycnodus cornutus* gen. et sp. nov., ostéologie, relations, Jurassique moyen continental, Formation de Stanleyville, République Démocratique du Congo.

Abstract: A skull fragment and nuchal horns of *Congopycnodus cornutus* gen. and sp. nov., from the continental Middle Jurassic (Stanleyville Formation) of the Democratic Republic of Congo, are described. This new pycnodont fish genus is referred to the superfamily Coccodontoidea, the only lineage of Pycnodontiformes with members bearing horns. Comparisons are done with the three coccodontoid families, Coccodontidae, Gebrayelichthyidae and Gladiopycnodontidae. *Congopycnodus* does not belong to these families but is thought to be an anatomical precursor of Gebrayelichthyidae and Gladiopycnodontidae. Some zoogeographical comments are done to explain the presence of a pycnodont fish in Central Africa during the Middle Jurassic.

Key words: Pycnodontiformes, Coccodontoidea, *Congopycnodus cornutus* gen. and sp. nov., osteology, relationships, continental Middle Jurassic, Stanleyville Formation, Democratic Republic of Congo.

INTRODUCTION

The continental Middle Jurassic Stanleyville Formation, near Kisangani in the Democratic Republic of Congo, dates back from the Aalenian-Bathonian (COLIN, 1994: 34), with an age comprised between 165 to 175 MY. These geological deposits yield a rich and various fish fauna that was firstly studied more than a half-century ago (DE SAINT-SEINE, 1950, 1955; DE SAINT-SEINE & CASIER, 1962) and is presently re-studied in a more detailed way (TAVERNE, 1975, 2001, 2011a, b, c, 2014a, b, 2015a, b, 2017).

The aim of the present paper is to describe some skeletal remains of a horny pycnodont fish present in this fossil ichthyofauna and found in the sediments of the Hamamba, a small stream that runs into the Lualaba river, and in those near the Otraco installations.

Pycnodontomorpha are by far the largest lineage within fossil Neopterygii, with about 50 genera and more than 650 nominal species. Most of them are tropical reefal fishes. They appear during the Late Triassic and disappear at the Middle Eocene, with a nearly worldwide distribution during the Late Cretaceous (NURSALL, 1996; KRIWET, 2001a; POYATO-ARIZA & MARTIN-ABAD, 2013; MARTIN-ABAD & POYATO-ARIZA, 2013). They are generally considered as closely related to Teleostei (NURSALL, 2010; among others) but a recent phylogenetic study concludes on the contrary that they are basal Neopterygii (POYATO-ARIZA, 2015). Most pycnodont fishes are deep-bodied (NURSALL, 1999; POYATO-ARIZA, 2005).

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They have a duraphagous mode of feeding, as shown by their molariform teeth on the vomer and the prearticulars (NURSALL, 1996, 1999; KRIWET, 2001b). During a long period, all the pycnodontid fishes were grouped in only one order, the Pycnodontiformes. Recently, NURSALL (2010) has divided the taxon in two orders, the Gyrodontiformes and the Pycnodontiformes *sensu stricto*, grouped in one superorder, the Pycnodontomorpha.

MATERIAL AND METHODS

The specimens hereafter described belong to the paleontological collection of the Department of Geology and Mineralogy of the Royal Museum for Middle Africa (MRAC), Tervuren, Belgium, and were studied with a Leica MZ8 stereomicroscope. The drawings of the figures were made by the author with a camera lucida.

List of abbreviations used in the text-figures

AN	=	angular
ART	=	articular
DHYOM	=	dermohyomandibula
DN	=	dentary
DPTE	=	dermopterotic
DSOC	=	dermosupraoccipital
DSPH	=	dermosphenotic
ENPT	=	entopterygoid (= endopterygoid)
FR	=	frontal
HO	=	nuchal horn
HYOM	=	hyomandibula
IORB 1	=	first infraorbital
METH	=	mesethmoid
MPT	=	metapterygoid
MX	=	maxilla
OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
PMX	=	premaxilla
POP	=	preopercle
PRART	=	prearticular
PRFR	=	prefrontal
PS	=	parasphenoid
PT	=	posttemporal
QU	=	quadratic
ST	=	supratemporal
SY	=	symplectic
VO	=	vomer

SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii KLEIN, 1885
Series Neopterygii REGAN, 1923
Superorder Pycnodontomorpha NURSALL, 2010
Order Pycnodontiformes BERG, 1937 *sensu* NURSALL, 2010
Superfamily Coccodontoidea TAVERNE & CAPASSO, 2013
Family *incertae sedis*
Genus ***Congopycnodus*** gen. nov.

Diagnosis

As for the species (monospecific genus)

Etymology

The name of the new genus refers to the Democratic Republic of Congo. The generic name *Pycnodus* is added to emphasize the pycnodontiform appurtenance of this fossil fish.

Congopycnodus cornutus gen. and sp. nov.

Diagnosis

Small coccodontoid pycnoditorm fish. Occipital region deep and conical. Upper margin of dermosuproccipital straight, flat and supporting a nuchal horn. Nuchal horn short, acuminate, ornamented with crest and alveoli and with a smooth posterior border.

Etymology

From the Latin *cornutus*, *a*, *um*, horny.

Holotype

Specimen MRAC RG 10.284. The postorbital region of a skull (Fig. 1)

Paratypes

Specimen MRAC RG 8.041. A complete well preserved nuchal horn, with a fragment of the dermosupraoccipital (**Fig. 2A**).

Specimen MRAC RG 8.041. A complete broken nuchal horn, with a fragment of the dermosupraoccipital (**Fig. 2B**).

Specimen MRAC RG 8.045a, b. A complete but badly preserved nuchal horn; face "a" an imprint and face "b" a bony fragment.

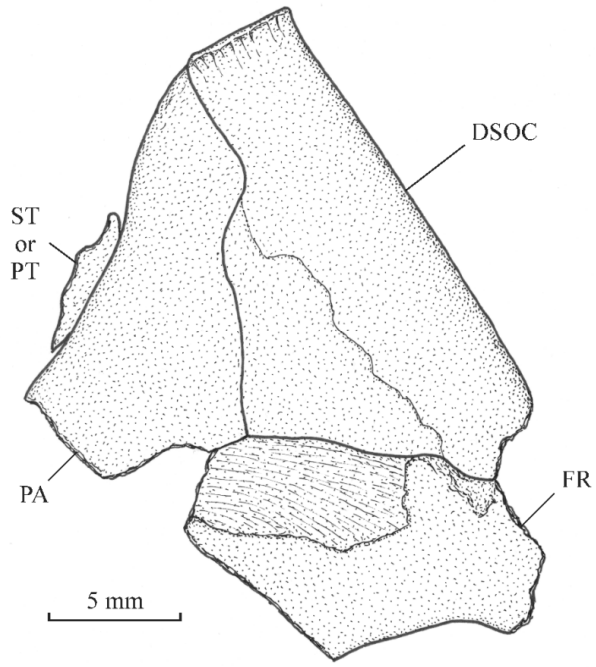

Figure 1: *Congopycnodus cornutus* gen. and sp. nov. Holotype MRAC RG 10.284 (occipital region of the skull).

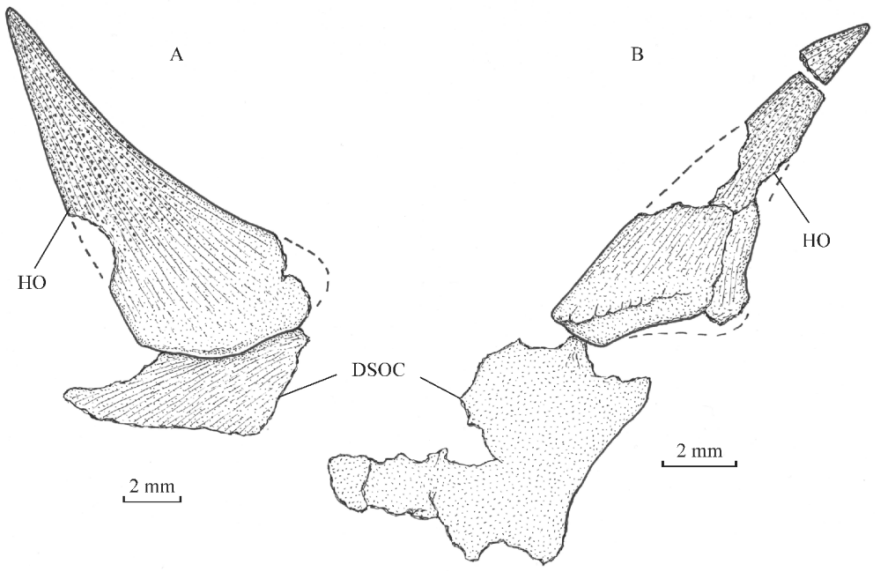

Figure 2: *Congopycnodus cornutus* gen. and sp. nov. Nuchal horns of (A) paratype MRAC RG 8.028 and of (B) paratype MRAC RG 8.041.

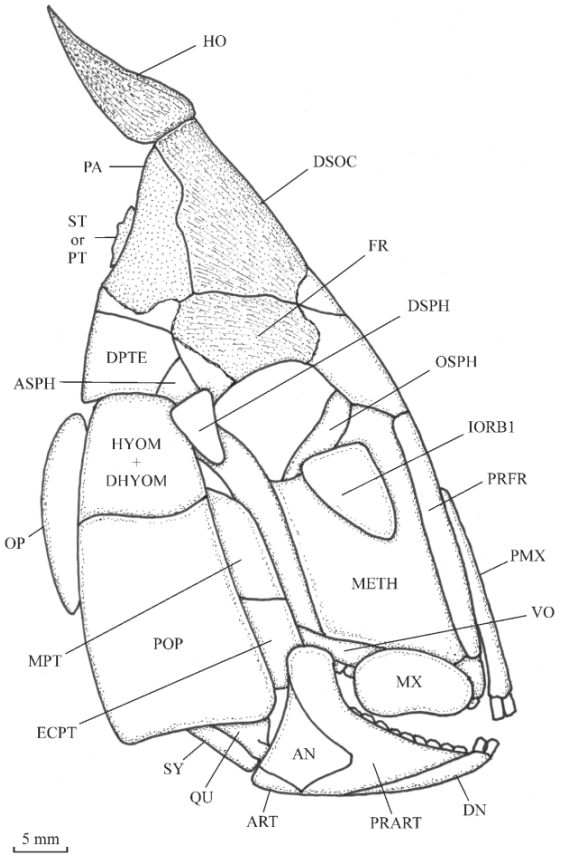

Figure 3: *Congopycnodus cornutus* gen. and sp. nov. Reconstruction of the skull. The scale refers to holotype.

Formation and locality

Stanleyville Formation, level 4 (black bituminous shales), Stanleyville Otraco (holotype) and Hamamba river (paratypes), 50 km South-East to Kisangani, Democratic Republic of Congo.

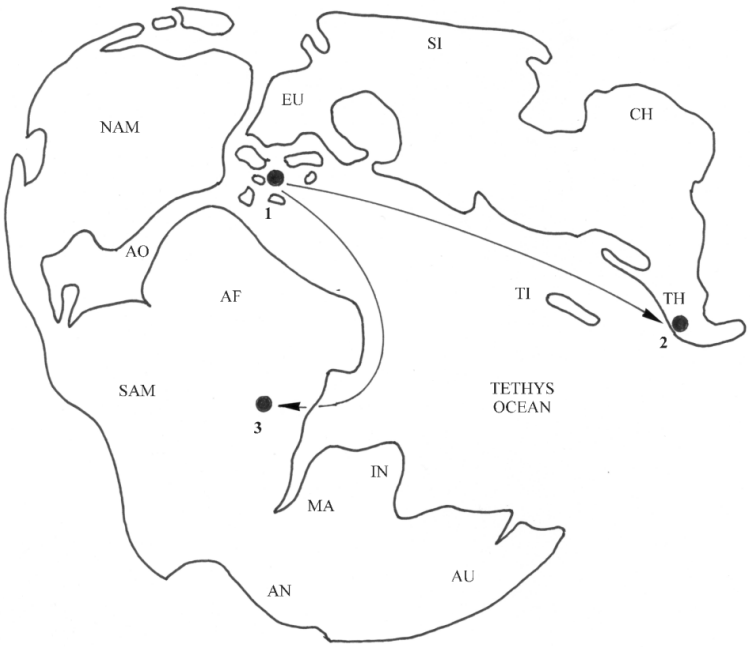

Figure 4: Schematic map of the Earth during the Middle Jurassic, showing the distribution of Pycnodontomorpha during that geological period and their two roads of dispersion from Europe to Asia and Africa. AF: Africa, AN: Antarctica, AO: Central Atlantic Ocean (in formation), AU: Australia, CH: China, EU: Europa, IN: India, MA: Madagascar, NAM: North America, SAM: South America, SI: Siberia, TH: Thailand, TI: Tibet. 1: The pycnodont fishes from Western-Central Europe (present there since the Late Triassic). 2: The pycnodont fishes from the Far East (Thailand). 3: The pycnodont fishes (*Congopycnodus*) from Central Africa.

Osteology

The skull **(Figs 1, 2A, B, 3)**

Only a few cranial fragments are known. Unfortunately, no other part of this fish is preserved.

The postorbital region visible on holotype RG 8.041 is deep, conical in shape and contains the posterior part of the frontal, the dermosupraoccipital and the parietal. The preserved portion of the frontal overhangs the orbit. A small part of the frontal at the suture with the dermosupraoccipital has retained the external layer of the bone. This part is ornamented with long, thin and feebly marked ridges. The dermosupraoccipital is a large and deep bone, broader at its basis than at its top. Its dorsal margin is broad and straight, forming a flat surface for the articulation of a nuchal horn. The fragment of dermosupraoccipital preserved on sample RG 8.028 exhibits the same ornamentation as the frontal, with weakly marked ridges. The parietal also is a large bone broader at the level of its basis than at its dorsal extremity. The bone is devoid of brush-like process and does not participate to the articulation surface for the horn. A small narrow bone is visible along the posterior margin of the parietal. It is the posttemporal or the supratemporal.

The nuchal horn is strongly built, straight but not very long. The basis is considerably enlarged and the tip acuminate. The external surface of the horn is ornamented with long and thin crests. Series of alveoli are visible in the grooves between the crests. The posterior border is devoid of spines and denticles. This horn can not be confounded with the spine of *Hybodus* AGASSIZ, 1837, a primitive shark also present in the deposits of the Stanleyville Formation (DE SAINT-SEINE & CASIER, 1965: 4-5, pl. 6, fig. 6). The spine of *Hybodus* is

much longer, with well marked crests but no alveoli between them and a strongly developed denticulation on the posterior margin (CASIER, 1961: pl. 1, figs 1a-d, 2)

DISCUSSION

Congopycnodus within Neopterygii

The deep conical shape of the occipital region, the size of the different bones that compose this part of the skull and the relations between them are typical of the Pycnodontomorpha. No other actinopterygian fishes possess such a morphologic architecture of the postorbital region of the skull. Moreover, the presence of only one dermosupraoccipital reveals that the new Congolese fossil fish belongs to the Pycnodontiformes and not to the Gyrodontiformes that exhibit two dermosupraoccipitals.

Pycnodont fishes in a freshwater environment

Most Pycnodontomorpha are marine fishes. However, the occurrence of a pycnodont in continental sediments (Stanleyville Formation) is not really astonishing. Indeed, other occurrences of pycnodonts in fresh and brackish water deposits are known (POYATO-ARIZA *et al.*, 1998; KOCSIS *et al.*, 2009; SZABO *et al.*, 2016).

Congopycnodus within Pycnodontiformes

The absence of a brush-like process on the parietal indicates that *Congopycnodus* does not belong to the Pycnodontidae. Besides, no member of this family exhibits a nuchal horn articulated on the top of the skull.

Horny Pycnodontiformes are extremely rare. A nuchal horn articulated on the dermosupraoccipital probably is the result of the hypertrophy of the first dorsal ridge scute. All the known horn-bearing pycnodonts are included in the Coccodontoidea, a superfamily that contains three highly specialized families endemic from the marine Cenomanian (Upper Cretaceous) of Lebanon, the Coccodontidae (GAYET, 1984; KRIWET, 2004; NURSALL & CAPASSO, 2008: CAPASSO *et al.*, 2010; TAVERNE & CAPASSO, 2014b), the Gebrayelichthyidae (NURSALL & CAPASSO, 2004; TAVERNE & CAPASSO, 2014c) and the Gladiopycnodontidae (TAVERNE & CAPASSO, 2013, 2014a, 2016; TAVERNE *et al.*, 2015; MARRAMA *et al.*, 2016).

The family Coccodontidae contains five genera, *Coccodus* PICTET, 1850, *Trewavasia* WHITE & MOY-THOMAS, 1941, *Hensodon* KRIWET, 2004, *Paracoccodus* TAVERNE & CAPASSO, 2014 and *Corusichthys* TAVERNE & CAPASSO, 2014. *Coccodus* and *Paracoccodus* have a well developed horn fused to the anterior region of the dermosupraoccipital (TAVERNE & CAPASSO, 2014b: figs 4, 15, 19), while *Trewavasia*, *Hensodon* and *Corusichthys* exhibit frontal horns and a well marked occipital process (ibid., 2014b: figs 23, 29, 35). However, the coccodontid skull has not a conical occipital region and is devoid of the free nuchal horn articulated on the top of the dermosupraoccipital that is present in *Congopycnodus*. We can conclude that the new Congolese pycnodont is not a member of the Coccodontidae.

Gebrayelichthyidae comprises only two genera, *Gebrayelichthys* NURSALL & CAPASSO, 2004 and *Maraldichthys* TAVERNE & CAPASSO, 2014. This lineage is certainly the most extraordinary family within Pycnodontiformes. The skull has the pycnodont typical morphology but is narrower and deeper than in other Pycnodontiformes. The caudal part of the body is extremely reduced and very short, while the abdominal region is considerably deepened, dorsally by an elongate nuchal horn associated with the dorsal pterygiophores or with the dorsal ridge scutes and ventrally by the extremely expanded cleithrum (TAVERNE & CAPASSO, 2014c: figs 1, 2, 4-9, 12, 14-21). In *Congopycnodus*, the nuchal horn is short and not associated to the dorsal pterygiophores or to the dorsal scutes. In consequence, the new Congolese pycnodont can not be reported to the family Gebrayelichthyidae.

Gladiopycnodontidae are the most numerous among the three families. They contain ten genera, *Stenoprotome* HAY, 1903, *Ichthyoceros* GAYET, 1984, *Gladiopycnodus* TAVERNE & CAPASSO, 2013, *Monocerichthys* TAVERNE & CAPASSO, 2013, *Rostropycnodus* TAVERNE & CAPASSO, 2013, *Joinvillichthys* TAVERNE & CAPASSO, 2014, *Pankowskichthys* TAVERNE & CAPASSO, 2014, *Hayolperichthys* TAVERNE & CAPASSO, 2016, *Ducrotayichthys* TAVERNE & CAPASSO, 2016 and *Tricherichthys* TAVERNE & CAPASSO, 2016. Five genera, *Rostropycnodus*, *Joinvillichthys*, *Pankowsichthys*, *Ducrotayichthys* and *Tricerichthys*, exhibit a nuchal horn. The five other genera of the family have lost the nuchal horn. But, the horny gladiopycnodontid fishes differ from *Congopycnodus*. They have a rather flat occipital region and a long horn with a spiny posterior margin (TAVERNE & CAPASSO, 2013: fig. 9, 2014: figs 6, 14, 19, 2016: figs 5, 10). Thus, *Congopycnodus* can not be referred to the Gladiopycnodontidae.

However, *Congopycnodus* can be considered as an anatomical precursor of Gebrayelichthyidae and Gladiopycnodontidae. Indeed, the gebrayelichtyid cranial morphology differs from that of *Congopycnodus* simply by the deepening and the narrowing of the occipital region, by the important lengthening of the nuchal horn and its association with the dorsal pterygiophores or with the dorsal ridge scutes. As for the horny Gladiopycnodontidae, their skull differs from that of *Congopycnodus* principally by the flattening of the occipital region, the lengthening of the nuchal horn and the development of spines on the posterior border of this horn.

The validity of *Congopycnodus*

No other horny pycnodond fish than *Congopycnodus* exhibits a deep conical occipital region associated to a rather short free nuchal horn. These features justify the peculiar generic status of the new Middle Jurassic African pycnodontiform.

As previously written, the coccodontoid *Congopycnodus* does not belong to the three families already ranged within the superfamily Coccodontoidea. However, the osteology of the new Congolese pycnodont remains for a great part unknown. In these conditions, I prefer to let *Congopycnodus* family *incertae sedis* than to erect for it a peculiar new family.

Zoogeographical implications (Fig. 4)

As already said, the oldest known Pycnodontomorpha appear in Europe (Austria, Italy, Belgium, Luxemburg) during the Late Triassic (GORJANOVIC-KRAMBERGER, 1905; TINTORI, 1980; DELSATE & KRIWET, 2004; NURSALL, 2010). Until recently, their only occurrences during the Lower and the Middle Jurassic were also confined to Europe (NURSALL, 1996; KRIWET, 2001a; STUMPF *et al.*, 2017). But pycnodont remains (cf. *Gyrodus* AGASSIZ, 1833) were recorded in the Lower-Middle Jurassic of Thailand a few years ago (CAVIN *et al.*, 2009).

So, during the time period separating the Late Triassic from the Middle Jurassic, pycnodont fishes were able to cross all the length of the Tethys Ocean from Europe to the Far East, by longing the Asian southern coast.

It is reasonable to think that the same kind of explanation is valid to explain the Congolese geographic position of *Congopycnodus* during the Middle Jurassic, *i. e.,* a migration from Europe along the northern and eastern coasts of the African region of the partly broken Gondwana. A lineage of horny pycnodont fishes probably expanded there, in the marine area of the break that began to separate the two large provinces of Gondwana, the western South America-Africa on the one hand and the eastern Madagascar-India-Antarctica-Australia on the other hand. One of these marine horny pycnodonts migrated via the regional hydrographic net from the African eastern coast into the large lake occupying the region of Kisangani during the Middle Jurassic. The distance to pass over is not very important. That fish became the freshwater genus *Congopycnodus*.

***Congopycnodus* and its bearing on the origin of coccodontoid pycnodont fishes**

Coccodontoidea are by far the most highly specialized lineage among Pycnodontomorpha. But, until now, no pycnodont precursor of this assemblage was known. So, the sudden apparition of a so advanced group in the Lebanese sea during the Cenomanian remained mysterious. *Congopycnodus* and the marine horny pycnodont fishes supposed to be present along the eastern African coast during the Jurassic (see the preceding subchapter) could explain that strange event. Some of these East African horny pycnodonts probably migrated northward during the Early Cretaceous and reached the Near East realm of the Mesogea to become there the Coccodontoidea.

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