



Osteology and phylogenetic relationships of *Agoultpycnodus aldrovandii* gen. and sp. nov., a new pycnodont fish genus (Pycnodontidae) from the marine Upper Cretaceous of Morocco.

Ostéologie et relations phylogénétiques d'*Agoultpycnodus aldrovandii* gen. et sp. nov., un nouveau genre de poisson pycnodonte (Pycnodontidae) du Crétacé supérieur du Maroc.

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Résumé: L'ostéologie et la position systématique d'*Agoultpycnodus aldrovandii* gen. and sp. nov., un petit poisson pycnodonte du début du Crétacé supérieur du Maroc sont étudiés en détails. Le nouveau genre est principalement caractérisé par son corps peu élevé et par ses nageoires dorsale et anale extrêmement allongées. *A. aldrovandii* présente un processus en brosse sur le pariétal et appartient donc à la famille des Pycnodontidae. D'autres caractères du squelette indiquent qu'*A. aldrovandii* est un membre de la sous-famille des Pycnodontinae. Dans la phylogénie de la sous-famille, *A. aldrovandii* occupe une position intermédiaire entre le plésiomorphe *Sylvienodus* et l'apomorphe *Tergestia*.

Mots-clés: Pycnodontiformes, Pycnodontidae, *Agoultpycnodus aldrovandii* gen. and sp. nov., ostéologie, phylogénie, Cénomano-Turonien marin, Maroc.

Abstract: The osteology and the systematic position of *Agoultpycnodus aldrovandii* gen. and sp. nov., a small pycnodont fish from the early Late Cretaceous of Morocco, are studied in details. The new genus is more particularly characterized by its low body and its extremely elongated dorsal and anal fins. *A. aldrovandii* has a brush-like process on the parietal and thus belongs to the family Pycnodontidae. Other skeletal characters indicate that *A. aldrovandii* is a member of the subfamily Pycnodontinae. Within the phylogeny of the subfamily, *A. aldrovandii* occupies an intermediate position between the plesiomorphic *Sylvienodus* and the apomorphic *Tergestia*.

Key words: Pycnodontiformes, Pycnodontidae, *Agoultpycnodus aldrovandii* gen. and sp. nov., osteology, phylogeny, marine Cenomanian-Turonian, Morocco.

INTRODUCTION

The Gara es Sbâa member of the Akrabou geological Formation is located on a small mesa in the southeastern region of Morocco, near the Algerian boundary. These fossiliferous marine laminated limestones date back to the Late Cenomanian-Early Turonian. They are adjacent and overlies the continental Lower Cenomanian plateau of the Kem Kem deposits. The stratigraphy and the palaeoenvironment of the Akrabou Formation is now thoroughly described (FERRANDINI *et al.*, 1985; CAVIN *et al.*, 2001; ETTACHFINI & ANDREW, 2004; MARTILL *et al.*, 2011; MURRAY *et al.*, 2013; among others).

Most fossils collected in the Gara es Sbâa deposits come from the neighbourhood of Agoult, a small village at 100 km south-west of Erfoud. The rich fossil fish fauna of the Akrabou Formation includes members of various orders, suborders and families, Amiiformes, Macrosemiidae, Pycnodontidae, Ellimmichthiformes, Clupavidae, Aipichthyidae, Chanoidei, Dercetidae and Acanthomorpha (CAVIN & DUTHEIL, 1999; CAVIN *et al.*, 2010; MURRAY *et al.*, 2013). Some species are already well described, the clupavid *Lusitanichthys africanus* CAVIN, 1999, the macrosemiid *Agoullichthys chattertoni* MURRAY & WILSON, 2009, the sorbinichthyid *Sorbinichthys africanus* MURRAY & WILSON, 2011 and the paraclupeid *Thorectichthys marocensis* MURRAY & WILSON, 2013 and *Thorectichthys rhadinus* MURRAY & WILSON, 2013 (CAVIN, 1999; MURRAY & WILSON, 2009, 2001, 2013). Two different species of the pycnodont *Anomoeodus* FORIR, 1887 and the pycnodont new genus and species *Neomesturus asflaensis* COOPER & MARTILL, 2020 were recently described on the basis of isolated vomers and prearticulars from Asfla, another locality of the Akrabou Formation (COOPER & MARTILL, 2020).

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The aim of the present paper is to describe the osteology and precise the relationships of a new pycnodontid genus recently discovered in the deposits of Agoult

MATERIAL AND METHODS

The material hereafter studied belongs to the collection of the Museum of the University “Gabriele d’Annunzio” of Chieti-Pescara.

The specimen was studied with a stereomicroscope Leica Wild M 8. The figures were drawn by the first author (L. T.) and the photos made by Mr. Luciano LULLO, from the University of Chieti-Pescara. Aspersions with ethanol and razing light were used to improve the observations.

List of abbreviations used in text-figures

AN	=	angular
ART	=	articular
APTE	=	autopterotic
ASPH	=	autosphenotic
BO	=	basioccipital
CHY a.	=	ceratohyal (anterior)
CLT	=	cleithrum
DHYOM	=	dermohyomandibula
DN	=	dentary
DPTO	=	dermopterotic
DSOC	=	dermosupraoccipital
ENPT	=	entopterygoid (= endopterygoid)
EPCO 1-5	=	epichordals 1 to 5
EXO	=	exoccipital
FR	=	frontal
HHY	=	hypohyal
HP 11	=	haemal spine (eleventh)
HYCO 1-10	=	hypochordals 1 to 10
HYOM	=	hyomandibula
IC	=	intercalar
LEP	=	lepidotrichium (= ray)
METH	=	mesethmoid
MPT	=	metapterygoid
MX	=	maxilla
NP 2-5, 23	=	neural spine (second to fifth, twenty third)
OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
POP	=	preopercle
PRART	=	prearticular
PS	=	parasphenoid
PSPH	=	pleurosphenoid
QU	=	quadrate
SC	=	scales
SCU d. 5-8	=	scutes of the dorsal ridge (fifth to eighth)
SY	=	symplectic
UD	=	urodermal
VO	=	vomer
t. f.	=	temporal fenestra

SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii KLEIN, 1885

Series Neopterygii REGAN, 1923

Division Halecostomi REGAN, 1923 *sensu* PATTERSON, 1973

Superorder Pycnodontomorpha NURSALL, 2010

Order Pycnodontiformes BERG, 1937 *sensu* NURSALL, 2010

Family Pycnodontidae AGASSIZ, 1833 *sensu* NURSALL, 1996

Genus *Agoultpycnodus* gen. nov.

Type-species: *Agoultpycnodus aldrovandii* gen. and sp. nov. (by monotypy).

Diagnosis

As for the species (monospecific genus)

Etymology

The generic name of the new fossil fish refers to Agoult, the Moroccan locality where it was found. The name *Pycnodus* is added.

Species : *Agoultpycnodus aldrovandii* gen. and sp. nov.

Diagnosis

Small and low-bodied pycnodontid, with a weakly marked dorsal apex and a rounded ventral profile. Head with a long preorbital and a short postorbital region. Small dermosupraccipital. Brush-like process (= peniculus) on parietal. Long and narrow temporal fenestra. No prefrontal. Posterior region of endocranium exposed behind dermopterotic and over parasphenoid. Mouth gape obliquely oriented. Short dentary with 2 incisiform teeth. Coronoid process of the prearticular strongly developed. Opercle narrow and vertically elongated. Vertebral axis almost rectilinear. Notochord not completely surrounded by neural and haemal arches. 23 neural spines before the epichordal series. 11 haemal spines before the hypochordal series. Postcoelomic bone not reaching the vertebral axis. Origin of dorsal fin located at the dorsal apex. Dorsal fin with 38 segmented rays and 37 pterygiophores. First rays of the dorsal and anal fins strongly elongated, forming a whip-like structure. 5 epichordals. 10 hypochordals. One urodermal. Caudal fin double emarginated, with 20 principal rays. Reduced squamation present only in the abdominal region. 10 rows of bar-scales located above the axial skeleton. A few complete scales along the ventral margin. 10 scutellum-like dorsal ridge scutes, with micro-spines on the upper margin. 2 postcloacal spiny ventral keel scutes.

Etymology

The specific name of the new fossil fish is dedicated to Ulisse ALDROVANDI (1522-1605) who was the first author to figure a pycnodontid fish in his monumental book "Museum Metallicum" posthumously published in 1648 (cf. CAPASSO, 2021, figs 1, 2).



Figure 1: *Agoultpycnodus haqelensis* gen. and sp. nov. Holotype, Chieti Museum, N° 19591.

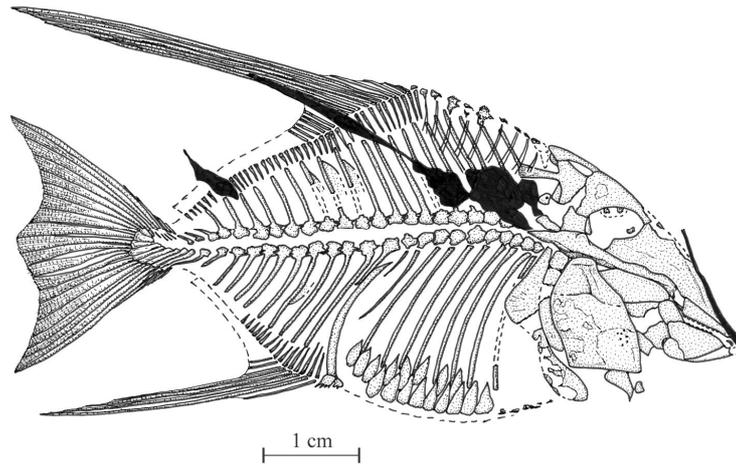


Figure 2: *Agoultpycnodus haqelensis* gen. and sp. nov. Reconstruction of the holotype, Chieti Museum, N° 19591.

Holotype

University of Chieti, Museum, N° 19591, a complete specimen (Fig.1). A part is preserved as bones and a part in imprints. Total length: 77 mm. Standard length: 63 mm.

Formation and locality

Gara es Sbâa member of the Akrabou Formation, marine Late Cenomanian-Early Turonian, Agoult, Morocco.

General morphology and morphometric data (Figs 1-2)

The new pycnodont genus is small and low-bodied. The dorsal apex is weakly marked and the ventral profile is rounded.

The morphometric data are given in % of the holotype standard length (63 mm).

Length of the head (opercle included)	42.1 %
Depth of the head (in the occipital region)	39.5 %
Maximum depth of the body (origin of the dorsal fin)	53.7 %
Prepelvic length	64.7 %
Predorsal length	74.2 %
Length of the dorsal fin	70.5 %
Basal length of the dorsal fin	43.7 %
Preanal length	74.7 %
Length of the anal fin	49.5 %
Basal length of the anal fin	?
Depth of the caudal peduncle	5.3 %

The skull (Figs 3-4)

The skull is elongated, triangular in lateral view, with a long and more or less pointed snout. The mouth gape is ventrally inclined. The frontal profile between the snout and the occipital region is almost rectilinear. The orbit is large. The preorbital part of the braincase is much longer than the postorbital region. The ornamentation of the dermal bones is very weakly marked. The sensory canals on the skull roof and on the preopercle are not observable.

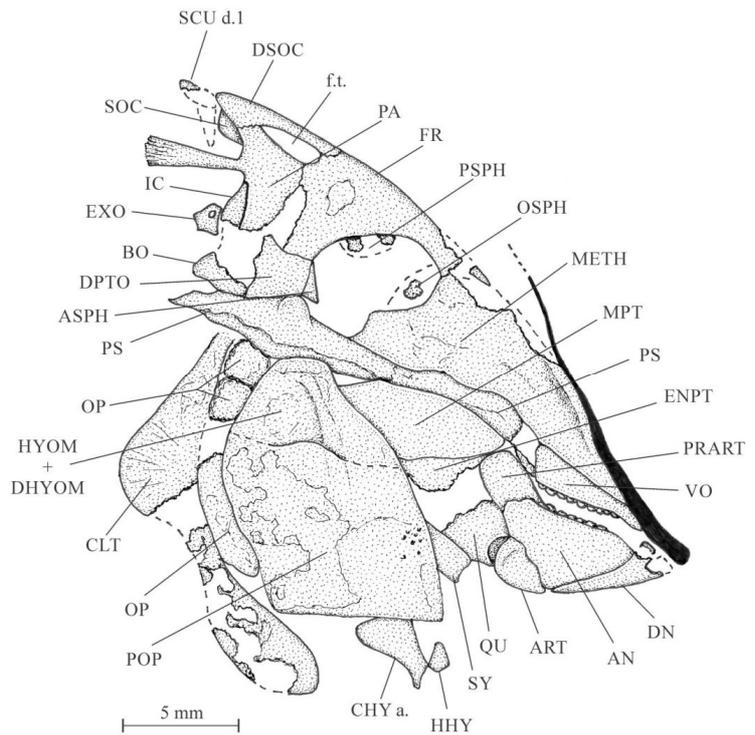
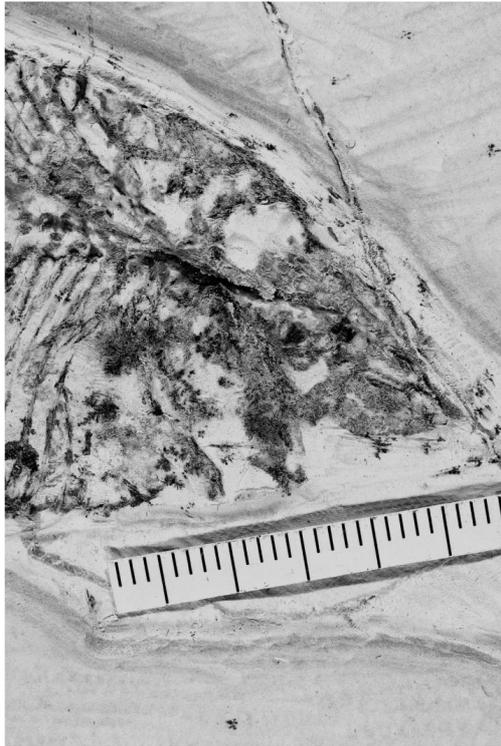


Figure 3 (gauche) : *Agoultpycnodus haqelensis* gen. and sp. nov. Head of the holotype.

Figure 4 (droite) : *Agoultpycnodus haqelensis* gen. and sp. nov. Skull and pectoral girdle of the holotype.

As usual in pycnodont fishes, the mesethmoid is the most massive bone of the braincase. No prefrontal is present. The vomer is seen in profile. At least 8 rounded teeth of the right lateral rank are partially visible. Their contour is smooth, not crenulated.

The skull roof is formed by the paired frontals, parietals and dermopterotics and by the impaired dermosupraoccipital. The frontal is rather short. The parietal bears a long and thin brush-like process (= peniculus). The upper posterior part of the supraoccipital (= supraotic) is visible just behind the suture between the dermosupraoccipital and the parietal. There is a small temporal (= dermocranial) fenestra between the frontal, the dermosupraoccipital and the parietal. A small triangular autosphenotic is placed against the anterior margin of the dermopterotic.

The broad posterior part of the parasphenoid supports the basioccipital and outpaces the level of the skull rear. The basioccipital, the exoccipital and the intercalar are also visible behind the parietal. A small foramen for the branches of the vagus nerve (X) is open in the exoccipital.

The parasphenoid is very long, toothless and almost straight. Fragments of the orbitosphenoid and of the pleurosphenoid are preserved in the orbit. The metapterygoid and a small part of the entopterygoid are visible between the parasphenoid and the hyomandibula. The quadrate and a large symplectic are also present.

The mouth gape is obliquely oriented. The premaxilla and the maxilla are not preserved. The lower jaw is composed by the traditional bones, the dentary, the prearticular, the articular and the angular. The dentary exhibits only the ventral branch, with a broad anterior extremity and an acuminate posterior one. Small fragments of two incisiform teeth are preserved. The articular is a massive bone connected to the quadrate. The angular covers the major part of the prearticular. Small parts of the prearticular teeth from the upper rank are visible but the exact number of these teeth is not determinable. The coronoid process of the prearticular is strongly developed.

No bone of the orbital series is preserved.

The hyomandibula-dermohyomandibula and the preopercle form a large lateral bony plate that is appended to the braincase. The position of the suture between the hyomandibula and the preopercle is uncertain. It is not possible to know precisely if the exposed part of the hyomandibula was smaller, equal or larger than the preopercle. The opercle is narrow but vertically elongated.

The anterior ceratohyal and one hypohyal are visible below the preopercle. The branchiostegal rays are not preserved.

The girdles (Figs 3-4)

Large fragments of the cleithrum are the only preserved elements of the pectoral girdle. The bone is shaped as the one figured by NURSALL (1996: fig. 11d) for a specimen named *Coelodus* sp., with the dorsal and the ventral parts of the same breadth and a narrow median region. No traces of the pelvic girdle are visible.

The axial skeleton (Figs 1-2)

The vertebral axis is almost rectilinear. The neural and ventral arches do not surround the notochord completely. There are 23 neural spines before the epichordal series. It is not possible to see if the first neural spines are autogenous or not. There are ten pairs of ribs. The ninth rib is shorter than the preceding ones and the tenth one is strongly reduced. There are 11 haemal spines before the hypochordal series. The first haemal spine is short and leans on the upper part of the postcoelomic bone. The neural and haemal spines bear an anterior bony sagittal wing, except the last ones. The postcoelomic bone is elongate and arched. Its ventral extremity rests on the second postcloacal scute. Dorsally, it does not reach the vertebral axis.

The dorsal and anal fins (Figs 1-2)

Both the dorsal and anal fins are strongly falcate. The dorsal fin origin is located at the level of the dorsal apex. The fin contains 38 rays and is supported by 37 pterygiophores. The first three rays are short. The first and the second rays are articulated on the first pterygiophore. Each following ray corresponds to one pterygiophore. From the fourth one to the eleventh, the dorsal rays form a very elongate whip-like structure. The anal fin is incompletely preserved. Only sixteen pterygiophores are visible. The second, third, fourth and fifth anal rays also form an elongate whip-like structure.

The caudal skeleton (Figs 5-6)

The caudal peduncle is short and not very broad. The caudal endoskeleton contains 5 epichordals, 10 hypochordals and 1 urodermal. Hypochordals 7, 8 and 9 are broadened but not really hypertrophied.

The caudal fin is double emarginated (POYATO-ARIZA & WENZ, 2002: fig. 36 E). There are 20 principal caudal rays, 4 dorsal and 7 ventral procurrent rays. The most dorsal and the most ventral principal rays are segmented and pointed. The other principal rays are segmented and branched.

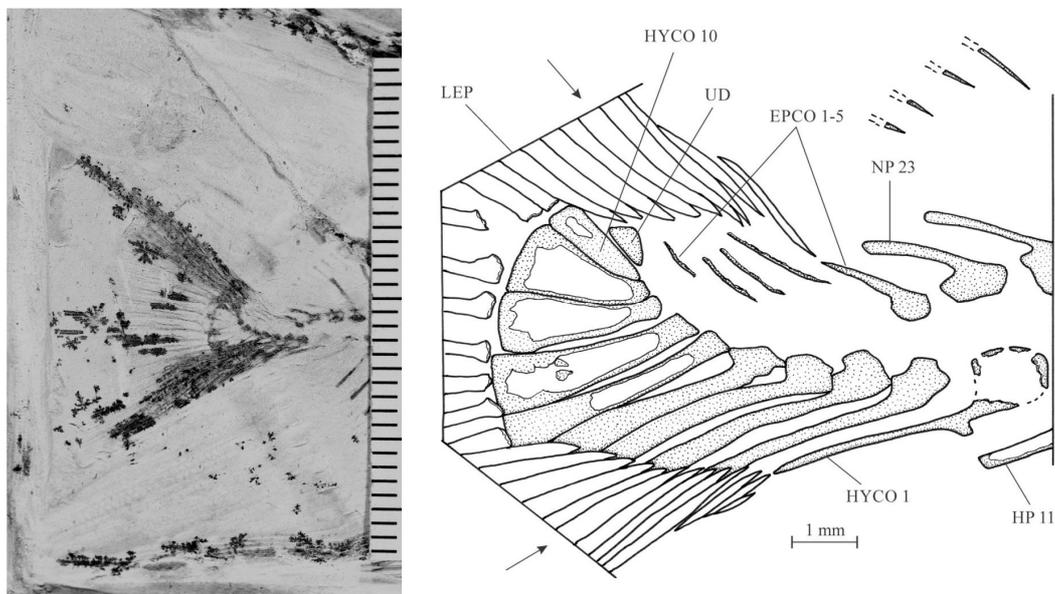


Figure 5 (gauche) : *Agoultpycnodus haqelensis* gen. and sp. nov. Caudal region of the holotype.

Figure 6 (droite) : *Agoultpycnodus haqelensis* gen. and sp. nov. Caudal skeleton of the holotype.

Squamation (Figs 7-8)

The squamation is strongly reduced and there are scales only in the abdominal region. There are 10 vertical rows of bar-scales that only extend above the vertebral axis. The upper bar-scales are associated to the dorsal ridge scutes. A few fragments of complete scales are present along the ventral border of the abdominal region.

There are 10 dorsal ridge scutes, most of them being preserved as fragments. The few complete ones are scutellum-like, with micro-spines on the upper border. A few fragments ventral keel scutes are preserved below the cleithrum but the exact number of precloacal scutes is not determinable. There are two postcloacal scutes. The first one bears two spines and is the smaller, while the second one is larger and bears four spines. The scales of the cloacal region are lost.

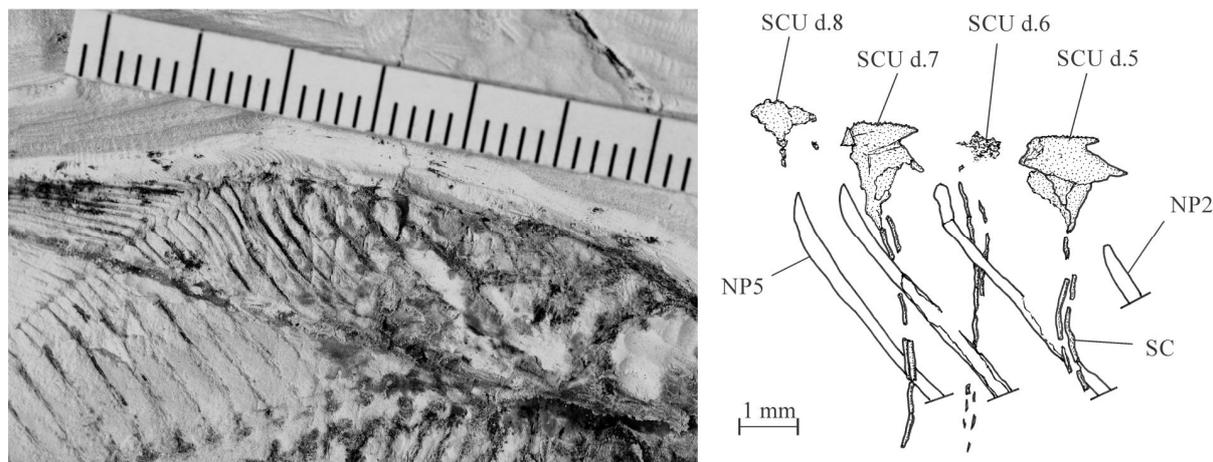


Figure 7 (gauche) : *Agoultpycnodus haqelensis* gen. and sp. nov. The dorsal ridge scutes of the holotype.
Figure 8 (droite) : *Agoultpycnodus haqelensis* gen. and sp. nov. The fifth to the eighth dorsal ridge scutes of the holotype.

DISCUSSION

***Agoultpycnodus aldrovandii* within Pycnodontiformes**

Agoultpycnodus aldrovandii has a large brush-like process (= peniculus) on the parietal. This anatomical structure is the major apomorphy of Pycnodontidae (POYATO-ARIZA & WENZ, 2002, node 13, character 14[1]). No other pycnodont fish exhibits such a process. The new genus certainly belongs to that family.

***Agoultpycnodus aldrovandii* within Pycnodontidae**

Agoultpycnodus aldrovandii exhibits two teeth on the dentary, only one urodermal, a strongly reduced flank squamation with bar-scales and only two postcloacal scutes. These four characters attest that the Moroccan new genus belongs to the group of the advanced Pycnodontidae and not to the primitive one.

The endocranium is posteriorly exposed in *Agoultpycnodus aldrovandii*, a feature that is present in the subfamily Pycnodontinae (POYATO-ARIZA & WENZ, 2002, node 24, character 19[1]), except in the tribe Nursalliini. The presence of a bifid cloacal scale is another important synapomorphy of the Pycnodontinae (ibid., 2002, node 23, character 104[1]). The cloacal region being missing, we do not know if this feature was present or not in *A. aldrovandii*.

The new genus has the dorsal ridge scutes scutellum-like, with micro-spines on the upper margin. This remarkable apomorphy is shared by three other pycnodontinid genera, *Pycnodus* AGASSIZ, 1833, *Tergestia* CAPASSO, 2000 and *Oropycnodus* POYATO-ARIZA & WENZ, 2002 (BLOT, 1987: fig. 29A, B; POYATO-ARIZA & WENZ, 2002: fig. 11B; TAVERNE *et al.*, 2019: fig. 3). No other pycnodont fish presents this very peculiar character, except *Sylvienodus* POYATO-ARIZA, 2013 that possesses at least partially the same feature (POYATO-ARIZA, 2013: fig. 6A). It is thus clear that *Agoultpycnodus aldrovandii* pertains to this group.

A temporal (= dermocranial) fenestra is present in *Agoultpycnodus*, *Pycnodus*, *Tergestia* and *Oropycnodus* (BLOT, 1987: fig. 2; POYATO-ARIZA & WENZ, 2002: fig. 11B; TAVERNE *et al.*: fig. 2) contrarily to *Sylvienodus* that does not exhibit such a specialized feature (POYATO-ARIZA, 2013: 94). On the other hand, *Pycnodus* and *Oropycnodus* share with the Nursalliini another highly advanced character, the arcocentra in complex or hyper-complex contact (POYATO-ARIZA & WENZ, 2002, nodes 24, 25, characters 54[2] and 54[3]). This evolved feature is missing in *Agoultpycnodus* and *Tergestia* (CAPASSO, 2000: figs 12-14).

Another feature allows to precise the systematic position of *Agoultpycnodus* within Pycnodontinae. The number of dorsal ridge scutes is reduced to 7-9 in *Tergestia*, *Pycnodus* and *Oropycnodus* (POYATO-ARIZA & WENZ, 2002, node 24, character 88[4]; TAVERNE *et al.*, 2019: 12), while *Agoultpycnodus* has still 10 dorsal ridge scutes, the primitive number of dorsal scutes (10-11) within the subfamily.

We can thus conclude that, within the phylogeny of the Pycnodontinae, *Agoultpycnodus* occupies an intermediate position between the plesiomorphic *Sylvienodus*, on the one hand, and the apomorphic *Tergestia*, on the other hand.

The validity of *Agoultpycnodus*

Two Pycnodontidae exhibit the same elongate and acute snout and the whip-like dorsal and anal fins as *Agoultpycnodus*. They are the genera *Scalacurvichthys* CAWLEY & KRIWET, 2017, from the Cenomanian of Israel, and *Flagellipinna* CAWLEY & KRIWET, 2019, from the Cenomanian of Lebanon.

However, *Scalacurvichthys* differs from *Agoultpycnodus* by many characters. The Israeli genus has a deep body, no temporal fenestra, a small narrow acuminate and vertically oriented dermosupraoccipital, a dorsal apex located in the occipital region, very short dorsal and anal fins, a few hypertrophied hypochordals and 31 rays in the caudal fin (CAWLEY & KRIWET, 2017).

Flagellipinna also differs from *Agoultpycnodus*. The Lebanese genus is deep-bodied and has a small prefrontal, no temporal fenestra, an extremely elongate opercle, 31 to 33 neural spines before the epichordal series, three hypertrophied hypochordals, a vertical-shaped caudal fin and 15 spiny dorsal scutes (CAWLEY & KRIWET, 2019; TAVERNE & CAPASSO, 2020).

The two genera are thus different from the new Moroccan genus. It is clear that no other genus within the subfamily Pycnodontinae or even in the family Pycnodontidae has the same morphology as *Agoultpycnodus* and thus the Moroccan pycnodont deserves a peculiar generic status.

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