



Osteology and phylogenetic relationships of *Haqelpycnodus picteti* gen. and sp. nov., a new pycnodont fish genus (Pycnodontidae) from the marine Late Cretaceous tropical sea of Lebanon

Ostéologie et relations phylogénétiques d'*Haqelpycnodus picteti* gen. et sp. nov., un nouveau genre de poisson pycnodonte (Pycnodontidae) de la mer tropicale néocrétacée du Liban

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Résumé: L'ostéologie et les relations phylogénétiques d'*Haqelpycnodus picteti* gen. et sp. nov., un poisson pycnodonte du Cénomaniens marin (Crétacé supérieur) du Liban, sont étudiées en détails. Le nouveau genre fossile appartient à la famille des Pycnodontidae, comme le montre la présence d'un processus en brosse sur le pariétal. *H. picteti* partage quelques caractères spécialisés avec la sous-famille des Pycnodontinae. La région postérieure de l'endocrâne est exposée. Le dermosphénotique est suturé au toit crânien. Le bord inférieur du dermoptérotique et du dermosphénotique est situé au niveau du bord ventral de l'orbite. La *dilatator fossa* est profonde et bien visible au-dessus de l'hyomandibulaire. Cependant, l'un des principaux caractères des Pycnodontinae manque chez *H. picteti*, à savoir la présence d'une écaille cloacale bifide pourvue de deux branches ventrales étroites et pointues. Dans la phylogénie des Pycnodontidae, *H. picteti* est le taxon-frère plésiomorphe immédiat des Pycnodontinae.

Mots-clés: Pycnodontiformes, Pycnodontidae, *Haqelpycnodus picteti* gen. and sp. nov., ostéologie, phylogénie, Cénomaniens marin, Liban.

Abstract: The osteology and the phylogenetic relationships of *Haqelpycnodus picteti* gen. and sp. nov., a pycnodont fish from the marine Cenomanian (Late Cretaceous) of Lebanon, are studied in details. The new fossil genus belongs to the family Pycnodontidae, as shown by the presence of a brush-like process on the parietal. *H. picteti* shares a few specialized characters with the members of the subfamily Pycnodontinae. The posterior region of the endocranium is exposed. The dermosphenotic is sutured to the skull roof. The lower margin of the dermopterotic and the dermosphenotic is located at the level of the orbital lower border. The *dilatator fossa* is deep and well visible above the hyomandibula. However, one of the main characters of Pycnodontinae is missing in *H. picteti*, i. e., the presence of a bifid cloacal scale, with two narrow and acuminate ventral branches. Within the phylogeny of Pycnodontidae, *H. picteti* is the immediate plesiomorphic sister-taxon of Pycnodontinae.

Key words: Pycnodontiformes, Pycnodontidae, *Haqelpycnodus picteti* gen. and sp. nov., osteology, phylogeny, marine Cenomanian, Lebanon.

INTRODUCTION

Pycnodont fishes are the largest group within fossil Neopterygii, with almost 50 genera and more than 650 nominal species. They appear in the Late Triassic and their last occurrences date back to the Eocene. They reach a nearly worldwide distribution during the Late Cretaceous. They are mostly marine fishes. The Cenomanian tropical sea of Lebanon is particularly rich in pycnodonts of all sorts, including the highly specialized members of the superfamily Coccodontoidea.

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Most pycnodonts are deep-bodied fishes. They bear molariform teeth on the vomer and the prearticulars and have a durophagous mode of feeding. They are now ranged in Pycnodontomorpha, a super-order comprising two orders, Gyrodontiformes and Pycnodontiformes (NURSALL, 2010). The aim of the present paper is to describe a new pycnodont fish genus from the marine Cenomanian of Lebanon and to define its phylogenetic relationships.

MATERIAL AND METHODS

The material hereafter studied belongs to the CAPASSO registered collection (CLC) in Chieti.

The specimens were 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 were used to improve some observations.

The Capasso collection (CCL) in Chieti (Italy) is legally registered by a decree of the Ministero per I Beni e le Attività Culturali under the date of October 11th 1999, following the disposition of the Italian law 1089/39. The Soprintendenza per I Beni Archeologici dell'Abruzzo-Chieti has authorized the authors to study this collection by two letters bearing the dates of May 5th, 2011 (ref.: MBAC-SBA-ABR PROT 0004537 05/05/ 2011 Cl. 34.25.01/2.1) and July 30th, 2014 (ref.: MBAC-SBA-ABR PROT 0005618 31/07/2014 Cl. 34.25.01/2.1).

List of abbreviations used in text-figures

AN	=	angular
ART	=	articular
APTE	=	autopterotic
ASPH	=	autosphenotic
BHY	=	basihyal
BO	=	basioccipital
BRSTG	=	branchiostegal rays
CHY a., p.	=	ceratohyal (anterior, posterior)
CIRC	=	tubular bones of the circumorbital sensory canal
CLO	=	cloaca
CLT	=	cleithrum
DHYOM	=	dermohyomandibula
DN	=	dentary
DPTE	=	dermopterotic
DSOC	=	dermosupraoccipital
DSPH	=	dermosphenotic
ECPT	=	ectopterygoid
ENPT	=	entopterygoid (= endopterygoid)
EPCO 1-6	=	epichordals 1 to 6
EXO	=	exoccipital
FR	=	frontal
HAEM	=	haemal arch
HAEMEP	=	haemal spine
HCLT	=	hypercleithrum (= supracleithrum)
HHY d., v.	=	hypohyals (dorsal, ventral)
HP 14	=	haemal spine (fourteenth)
HYCO 1-12	=	hypochordals 1 to 12
HYOM	=	hyomandibula
IORB 1-3	=	infraorbital 1 to 3
LEP	=	lepidotrichium (= ray)
METH	=	mesethmoid
MPT	=	metapterygoid
MX	=	maxilla
NEUR	=	neural arch
NEUREP	=	neural spine
NP 34	=	neural spine (thirty fourth)
OP	=	opercle

OSPH	=	orbitosphenoid
PA	=	parietal
PCLT	=	postcleithrum
PCOEL	=	postcoelomic bone
PELV	=	pelvic (= ventral) rays
PMX	=	premaxilla
POP	=	preopercle
PRART	=	prearticular
PRFR	=	prefrontal (= lateral dermethmoid ?)
PRO	=	prootic
PS	=	parasphenoid
PSPH	=	pleurosphenoid
PT	=	posttemporal
QU	=	quadrate
RAD	=	pterygiophores (= radials)
SC	=	scales
SC clo.	=	cloacal scales
SCL	=	sclerotic bone
SCU d. 1-10	=	scutes of the dorsal ridge (first to tenth)
SCU v. 1-6	=	precloacal scutes of the ventral keel (first to sixth)
SCU v. po.	=	postcloacal scutes of the ventral keel
ST	=	supratemporal
SY	=	symplectic
PT	=	posttemporal
UD	=	urodermal
VO	=	vomer
b. pr.	=	brush-like process of the parietal
br.	=	broken
d. f.	=	<i>dilatator fossa</i>
f. X	=	foramen for the vagus nerve (X)
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 *Haqelpycnodus* gen. nov.

Type-species: *Haqelpycnodus picteti* gen. and sp. nov. (by monotypy).

Diagnosis

As for the species (monospecific genus)

Etymology

The generic name of the new fish refers to the village of Haqel (Lebanon) where the two specimens hereafter studied were discovered. The taxon *Pycnodus* is added.

Species *Haqelpycnodus picteti* gen. and sp. nov.

Diagnosis

Small-sized and deep-bodied pycnodontid fish. Maximum body depth exceeding the standard length. Large head, with a long preorbital and a short postorbital region. Small dermosupraccipital. Brush-like process on parietal. Small temporal fenestra. Prefrontal present. Dermosphenotic sutured with dermopterotic and frontal. Ventral borders of dermopterotic and dermosphenotic located at the

level of the orbital lower margin. Deep and well visible *dilatator* fossa. Posterior region of endocranium exposed behind dermopterotic and over parasphenoid. Mouth gape obliquely oriented. Premaxilla with 2 incisiform teeth. Short dentary with 3 incisiform teeth. Preopercle much larger than the exposed region of hyomandibula-dermohyomandibula. Maximum body depth exceeding the standard length. Notochord not completely surrounded by neural and haemal arches. 33 or 34 neural spines before the epichordal series. 14 haemal spines before the hypochordal series. First 8 or 9 neural spines autogenous. Origin of dorsal fin located at the highest point of the dorsal profile. Dorsal fin with 4 small spiny rays + 59 to 64 segmented rays and 62 to 65 pterygiophores. Anal fin with 3 small spiny rays + 42 to 44 segmented rays and 45 to 47 pterygiophores. 6 or 7 epichordals. 12 hypochordals. One urodermal. Caudal fin double emarginated, with 28 principal rays. Body scales only in the abdominal region. Scale bars dorsally and complete scales ventrally. 10 spiny dorsal ridge scutes. 8 pre- and 2 postcloacal spiny ventral keel scutes. A bifid cloacal scale, with a short rounded anterior branch and a long acuminate posterior branch. 3 cloacal scales before and 3 cloacal scales beneath the bifid scale. One ovoid cloacal scale associated with the two ventral branches of the bifid scale.

Etymology

The new species is named in honour of the Swiss paleontologist François-Jules PICTET (1807-1872) who was one of the first scientists having studied the Late Cretaceous Lebanese fossil fishes.

Holotype

Sample CLC S-317, a complete specimen (Fig.1). Total length: 12.4 cm. Standard length: 9.5 cm.



Figure 1: *Haqelpycnodus picteti* gen. and sp. nov. Holotype CLC S-317

Paratype

Sample CLC S-376a, b, part and counterpart of a complete specimen (Figs 2, 3). Total length: 15.4 cm. Standard length: 11.8 cm. A partial skeleton of a small aulopiform fish bearing a few large scutes is visible near the tail of the paratype.

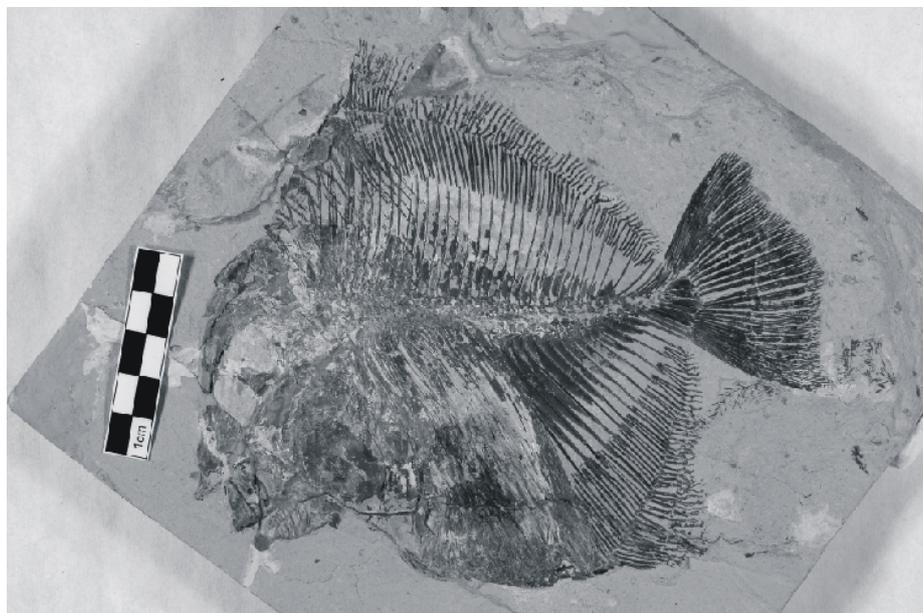


Figure 2: *Haqelpycnodus picteti* gen. and sp. nov. Paratype CLC S-376 a.



Figure 3: *Haqelpycnodus picteti* gen. and sp. nov. Paratype CLC S-376b.

Formation and locality

Marine Upper Cenomanian deposits of Haqel, Lebanon.

General morphology and morphometric data (Figs 1-5)

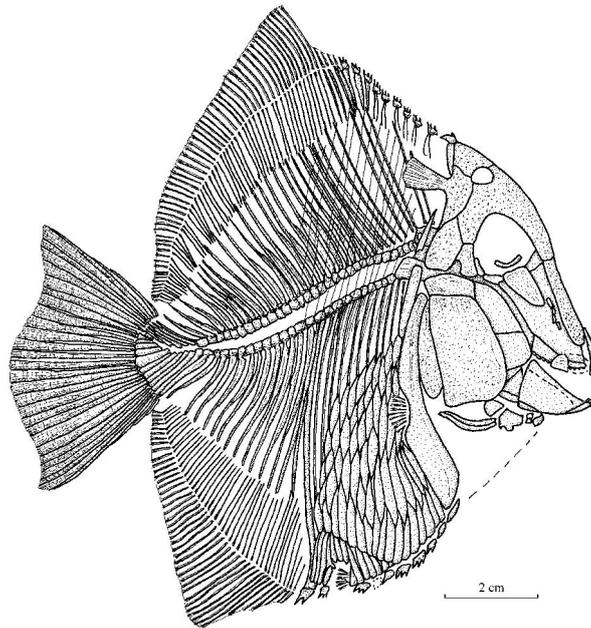


Figure 4: *Haqelpycnodus picteti* gen. and sp. nov. Reconstruction based on holotype CLC S-317, completed by paratype CLC S-376a, b. The scale refers to holotype.

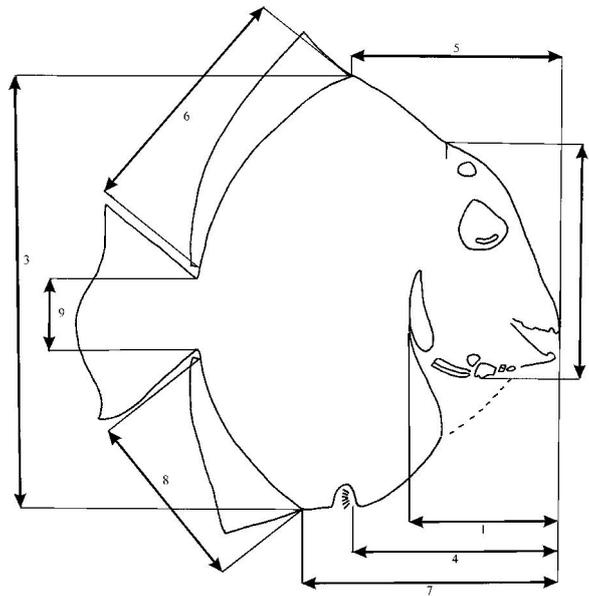


Figure 5: schema showing how the morphometric data are measured. 1: length of the head. 2: depth of the head. 3: Maximum depth of the body. 4: Prepelvic length. 5: predorsal length. 6: length of the basis of the dorsal fin. 7: preanal length. 8: length of the basis of the anal fin. 9: depth of the caudal peduncle.

The new pycnodont genus is rather small but extremely deep-bodied, the maximum body height exceeding the standard length. However, this depth decreases gradually as the specimens grow larger. The dorsal and the ventral profiles are rounded and devoid of a well marked apex.

The morphometric data are given in % of the standard length (holotype CLC S-317: 95 mm, paratype CLC S-376a, b: 118 mm).

	S-317	S-376
Length of the head (opercle included)	46.7 %	42.4 %
Depth of the head (in the occipital region))	68.8 %	60.6 %
Maximum depth of the body (origin of the dorsal fin) ...	121.3 %	101.2 %
Prepelvic length	64.0 %	58.2 %
Predorsal length	53.3 %	57.6 %
Basal length of the dorsal fin	68.7 %	66.7 %
Preal length	73.1 %	70.9 %
Basal length of the anal fin	50.7 %	44.2 %
Depth of the caudal peduncle	19.3 %	17.0 %

Osteology

The skull (Figs 6-14)

The head is large when compared to the body size and deeper than long. The length of the preorbital part of the braincase is equal to that of the orbital and postorbital regions together. The orbit is wide. The dermal bones of the skull are ornamented with small tubercles. However, this ornamentation is weakly developed, except on the anterior extremity of the prefrontal that is strongly ornamented. The mouth gape is ventrally inclined.



Figure 6: *Haqelpycnodus picteti* gen. and sp. nov.
Head region of holotype CLC S-317.

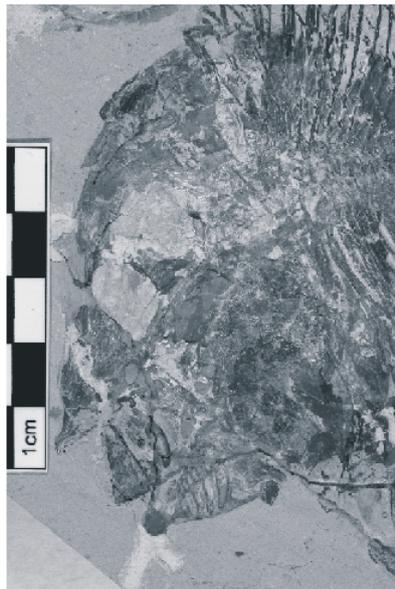


Figure 7: *Haqelpycnodus picteti* gen. and sp. nov.
Head region of paratype CLC S-376^a



Figure 8: *Haqelpycnodus picteti* gen. and sp. nov.
Head region of paratype CLC S-376^b.

The mesethmoid is a long and thick bone. Its upper margin is covered by a pair of broad prefrontals. The orbitosphenoid is present just behind the posterior margin of the mesethmoid. The vomer, seen in profile, is well preserved on holotype CLC S-317. It is a long toothed bone, deeper posteriorly than anteriorly. There are probably three rows of teeth. The right lateral row is complete and contains 9 molariform teeth, longer than broad. The four posterior ones are much larger than the first five. Other teeth, rounded or ovoid, seem to belong to the middle row.

The frontal is short and surrounds the orbital region. The small dermosupraoccipital has a pointed dorso-posterior extremity. The parietal bears a well developed brush-like process. A small temporal fenestra is opened between the frontal, the dermosupraoccipital and the parietal. The dermopterotic is deeper than long. The dermosphenotic is sutured with the frontal and the dermopterotic, forming a part of the lateral wall of the skull roof. The ventral margin of the

dermopterotic and of the dermosphenotic is located at the same level as the lower border of the orbit. The dermopterotic and the dermosphenotic surround a small but deep *dilatator fossa*, well visible above the hyomandibula. The parasphenoid is long, broad, toothless and its trabecular region is obliquely inclined. The broad posterior part of the parasphenoid supports the basioccipital and largely outpaces the level of the skull rear. The basioccipital and the exoccipital also outpace this level. A large foramen for the branches of the vagus nerve (X) is open in the exoccipital. The supratemporal, an large scale, sustains the first dorsal ridge scute and is pressed against the posterior margin of the dermosupraoccipital.

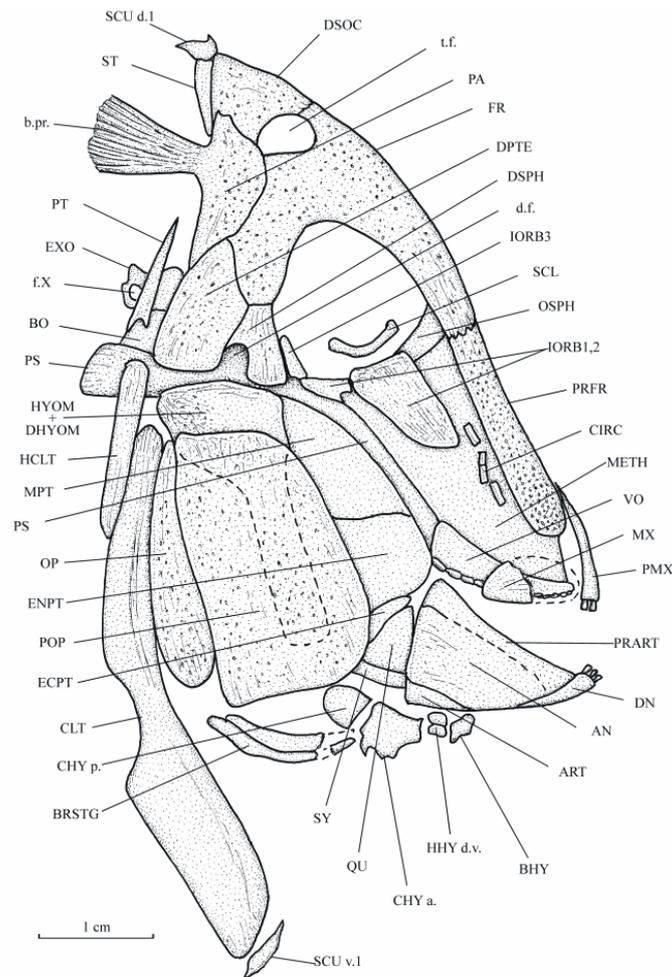


Figure 9: *Haqelpycnodus picteti* gen. and sp. nov. Reconstruction of the skull and the shoulder girdle based on holotype CLC S-317, completed by paratype CLC S 376a, b. The scale refers to holotype.

The metapterygoid and the entopterygoid are large bones whereas the ectopterygoid is small. Both the quadrate and the symplectic are articulated with the lower jaw.

The long and narrow premaxilla bears 2 incisiform teeth. Only fragments of the maxilla are preserved and the shape of the bone is not determinable. The dentary is very short and bears 3 incisiform teeth. The articular is small. Only a reduced part of the angular is preserved. The prearticular is a large bone. It bears three rows of molariform teeth. On holotype, the upper row contains 20 more or less ovoid teeth, the anterior ones being much smaller than the posterior. The middle row is composed of 13 large, very deep and generally claw-shaped teeth. In the middle of this row, two rounded teeth, one upon the other, replace the normal claw-shaped tooth. The lower row contains 18 very small rounded teeth. On paratype, the three rows are not complete, some teeth being lost. The disposition of these teeth differs from that on the holotype. On that sample, the small rounded teeth are located in the upper row and not in the lower one.

Three bones compose the orbital series. The first infraorbital is a long triangular bone. The second and third infraorbitals are tubular bones. There is a sclerotic ring. A few tubular bones, located at the level of the mesethmoid, link the infraorbital and the rostral sensory canals.

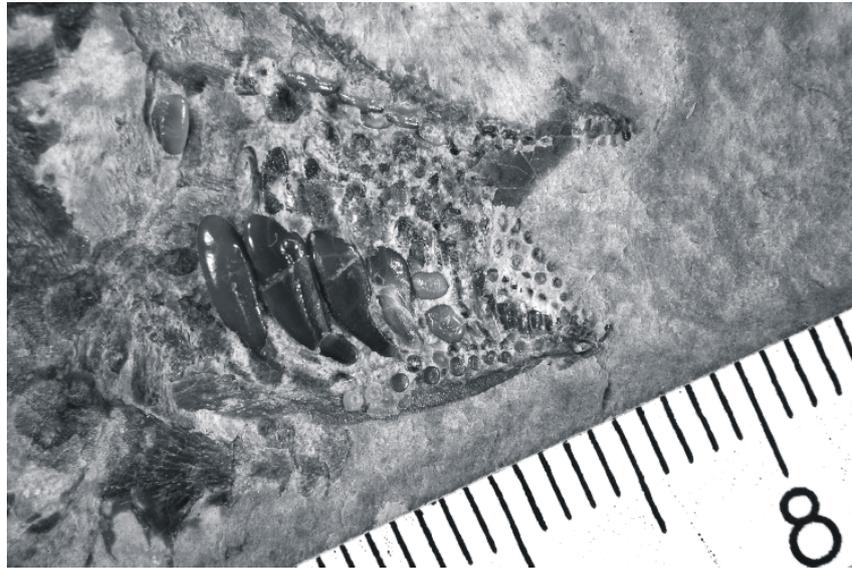


Figure 10: *Haqelpycnodus picteti* gen. and sp. nov. Vomer, premaxilla, prearticular and dentary of holotype CLC S-317.

Only a small part of the hyomandibula-dermohyomandibula is exposed above the preopercle to which it is sutured. The long ventral branch of the hyomandibula is visible under the preopercle. The upper margin of the hyomandibula does not bear a dorsal process. The preopercle is deep and broad, with a rather narrow dorsal margin. The opercle is well developed, with an acuminate dorsal tip and a broader lower part.



Figure 11: *Haqelpycnodus picteti* gen. and sp. nov. Prearticular and dentary of paratype CLC S-376b.

The basihyal, the dorsal and ventral hypohyals, the large anterior ceratohyal, the small posterior ceratohyal and two branchiostegal rays are preserved on holotype. It is to be noted that normally the pycnodontid fishes possess only one ossified hypohyal (LAMBERS, 1991: fig. 13b; NURSALL & MAISEY, 1991: fig. page 131; GARDINER *et al.*, 1996: fig. 5) as in primitive Actinopterygii.

However, dorsal and ventral hypohyals exist at least in some specimens of the genus *Pycnodus* Agassiz, 1833 (TAVERNE, 1997: fig. 5).

Some small hook-like branchial teeth are visible on both specimens. Long, very thin and pointed branchiospines are preserved just behind the lower jaw of paratype. They are pressed the one against the others.

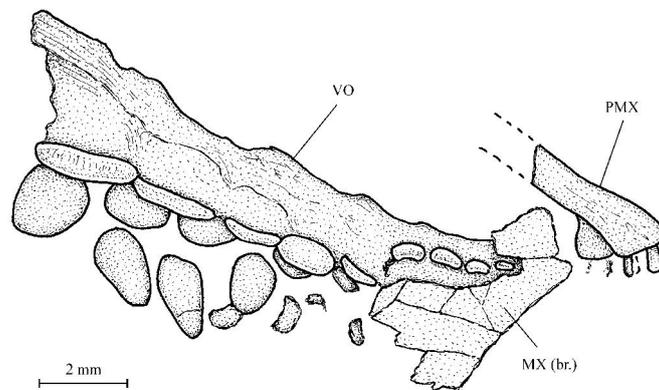


Figure 12: *Haqelpycnodus picteti* gen. and sp. nov. Vomer and premaxilla of holotype CLC S-317.

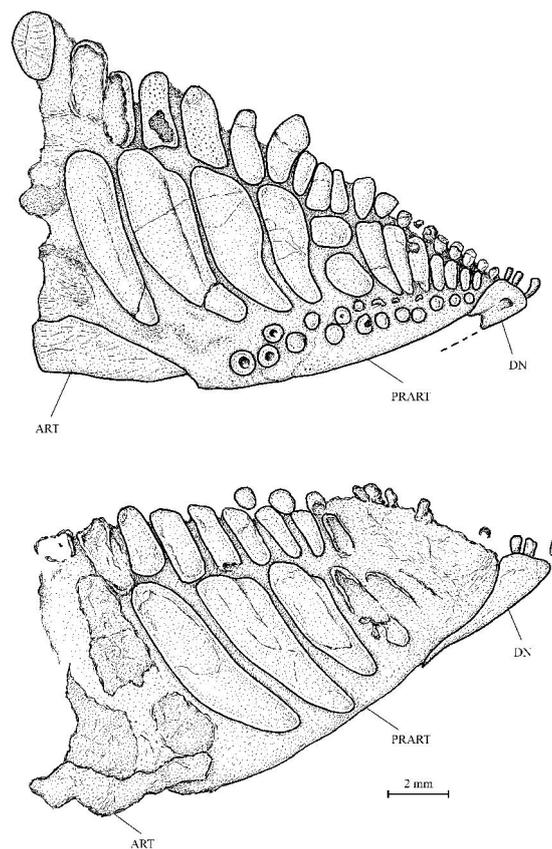


Figure 13: *Haqelpycnodus picteti* gen. and sp. nov. Lower jaw in internal view of holotype CLC S-317 (above) and of paratype CLC S-376b (below).

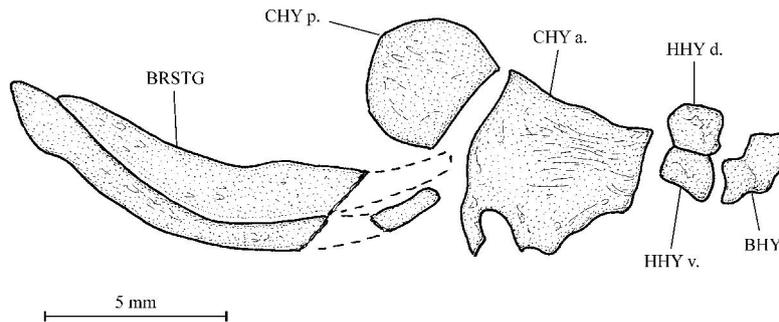


Figure 14: *Haqelpycnodus picteti* gen. and sp. nov. Hyoid bar and branchiostegal rays of holotype CLC S-317.

The girdles (Figs 6-9)

A small needle-shaped posttemporal is preserved behind the skull, at the level of the parietal and the dermopterotic. The hypercleithrum is a long and thin bone. The cleithrum is divided in two long and narrow branches, one above the pectoral fin, the other below. The ventral branch is a little broader than the dorsal one. Only fragments of the pectoral pterygiophores and rays are preserved.

Fragments of small ventral rays are visible in the cloacal region of the two available specimens.

The axial skeleton (Figs 1-4)

The axial skeleton progressively elevates from the caudal region and reaches anteriorly the orbit level. The vertebrae are formed by separated dorsal and ventral arcocentra. The neural and haemal arches are well developed. However, the notochord is not completely surrounded by those bony elements. In the caudal region, each neural and haemal arches are linked with the following one by means of one pre- and one postzygapophysis. There are 33 (holotype) or 34 (paratype CLC S-376a, b) neural spines before the epichordal series and 14 (both specimens) haemal spines before the hypochordal pieces. The first haemal spine is incomplete and does not reach the vertebral axis. These neural and haemal spines bear anterior bony sagittal wings. The first 8 or 9 neural spines are autogenous and devoid of sagittal wing. There are 11 or 12 pairs of long ribs. The postcoelomic bone is long and narrow. It contacts the axial skeleton.

The dorsal and anal fins (Fig. 1-4)

The dorsal and anal fins are long and strip-like (type A 2 of POYATO-ARIZA & WENZ, 2002: fig. 34). The origin of the dorsal fin is located before that of the anal fin and corresponds to the highest point of the dorsal profile. In holotype, the dorsal fin contains 4 small spiny rays, 59 branched rays and 62 pterygiophores. The anal fin begins with 3 small spiny rays followed by 42 branched rays and is supported by 45 pterygiophores. In paratype, the dorsal fin is composed of 4 small spiny rays, 64 branched rays and 65 pterygiophores. The anal fin contains 3 small spiny rays, 44 branched rays and 47 pterygiophores.

The caudal skeleton (Figs 15-18)

The caudal skeleton is better preserved in paratype CLC S-376a, b than in holotype in which a great part of that skeleton is only present as imprints.

The caudal peduncle is rather broad but very short, the dorsal and anal fins ending near the tail. The caudal endoskeleton is composed of 6 (paratype CLC S-378a, b) or 7 epichordals (holotype), 12 hypochordals (both specimens) and 1 urodermal (both specimens). The first four or five epichordals are thin and elongate. The last two elements of the series are shorter. The hypochordals are longer and wider than the epichordals. Some posterior hypochordals are slightly broadened.

The caudal fin is double emarginated (POYATO-ARIZA & WENZ, 2002: fig. 36 E). There are 28 principal caudal rays, 2 or 3 dorsal and 3 ventral procurent rays in the two samples. The most dorsal and the most ventral principal rays are segmented and pointed. The other principal rays are segmented and branched.

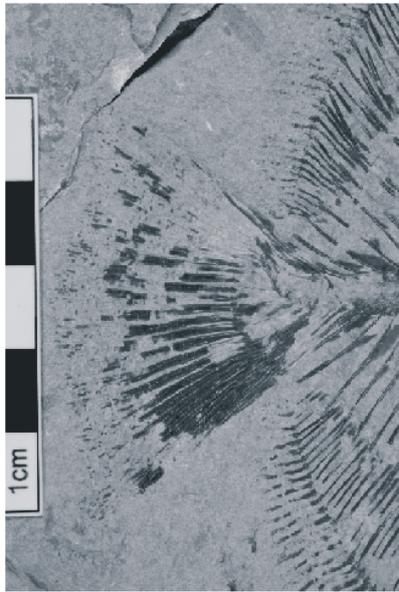


Figure 15: *Haqelpycnodus picteti* gen. and sp. nov. Tail region of holotype CLC S-317.

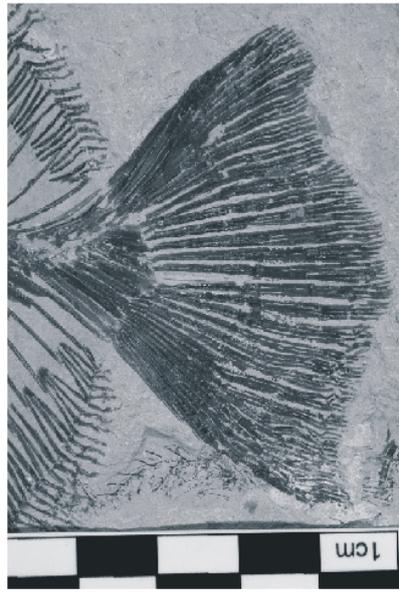


Figure 16: *Haqelpycnodus picteti* gen. and sp. nov. Tail region of paratype CLC S-376a.



Figure 17: *Haqelpycnodus picteti* gen. and sp. nov. Tail region of paratype CLC S-376b.

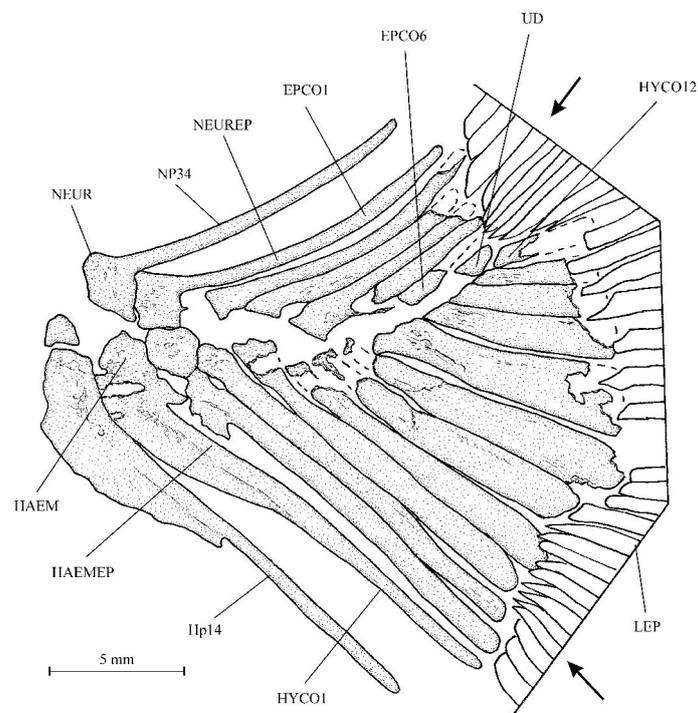


Figure 18: *Haqelpycnodus picteti* gen. and sp. nov. Caudal skeleton of paratype CLC S-376a.

Squamation (Figs 1-4, 19-21)

The flank scales are present only in the abdominal region of the body in the two adult specimens. Dorsally and in the upper part of the ventral region, they are reduced to scale bars. More ventrally, the flank scales are broader and they join together. These complete scales are not ornamented.

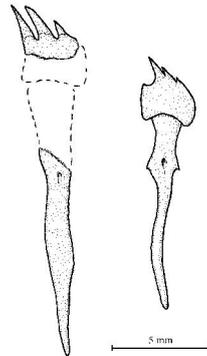


Figure 19: *Haqelpycnodus picteti* gen. and sp. nov. Seventh and tenth dorsal ridge scutes of holotype CLC S-317.

The dorsal ridge scutes are incompletely preserved on paratype CLC S-376a, b but the fragments and the associated scales visible on this sample allow counting a total of 10 scutes. The preservation is better on the holotype but, unfortunately, not perfect. However, it is possible to number also 10 dorsal scutes. The first dorsal scute bears one spine on its dorsal margin and is articulated with the dermosupraoccipital. This first scute is associated to the supratemporal. From the second to the sixth, the scutes are each articulated with a pair of short scale bars. A broader scale sustains the scutes from the seventh to the tenth of the series. Three spines are visible on the scutes that follow the first one, the first spine being the smaller and the third spine the larger.

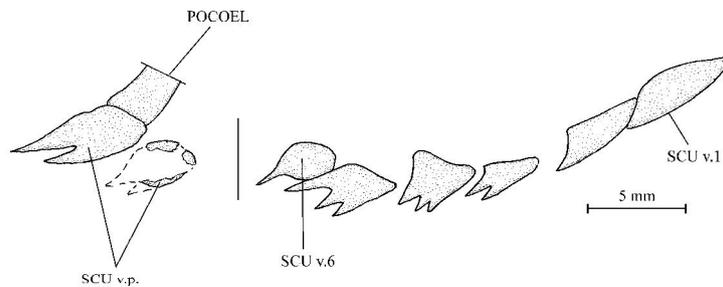


Figure 20: *Haqelpycnodus picteti* gen. and sp. nov. Incomplete series of ventral keel scutes of holotype CLC S-317. The last precloacal scutes are missing in this specimen.

Most of the precloacal ventral ridge scutes are missing in paratype CLC S-376a, b. In holotype, 6 precloacal ventral ridge scutes are preserved but at least two posterior scutes of this region are lost due to the fossilization. The total number of precloacal scutes must be around 8. The first scute is located beneath the cleithrum. The first two and the sixth scutes bear only one spine, the third one two spines and the fourth and fifth scutes three spines. In paratype CLC S-376a, b, the last precloacal scute bears three spines. The two specimens exhibit two postcloacal ventral ridge scutes. The first scute is badly preserved in holotype but is complete, with three spines, in paratype CLC S-376a, b. The second postcloacal scute is articulated with the postcoelomic bone and bears two large spines in holotype and four smaller spines in paratype.

The cloacal region is not preserved in holotype, except the presence of fragmented ventral rays, but is well visible in paratype. Two complete scales are located just before the cloaca, a long anterior

and a short posterior one. Five scales are positioned just above the cloaca. The first three are normal elongate complete scales. The fourth scale is long and divided in two ventral branches, a short rounded anterior branch and a longer acuminate posterior branch. A large ovoid scale is associated to these two ventral branches. Three other long complete scales are present between the bifid scale and the postcoelomic bone.

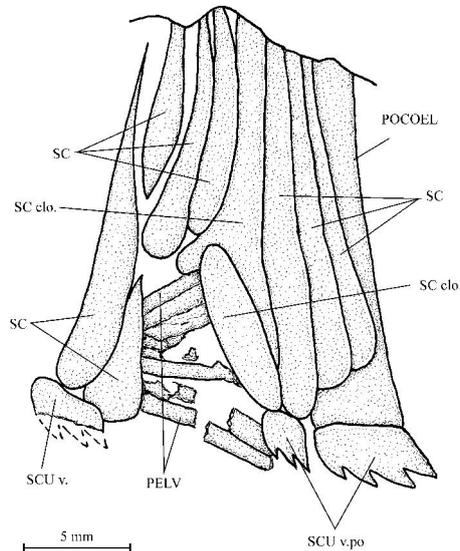


Figure 21: *Haqelpycnodus picteti* gen. and sp. nov. Scales of the cloacal region of paratype CLC S-376a, b.

DISCUSSION

Haqelpycnodus picteti within Pycnodontiformes

Haqelpycnodus picteti has a large brush-like process 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.

Haqelpycnodus picteti within Pycnodontidae

The most posterior part of the endocranium (basioccipital and exoccipital) is well exposed in *Haqelpycnodus picteti*. That peculiar character is known in the Pycnodontinae (POYATO-ARIZA & WENZ, 2002: node 24, character 19[1]) and seems present in all the members of the subfamily (TAVERNE, 1997: figs 2, 4; CAPASSO, 2000: figs 3, 7A, 8; POYATO-ARIZA & WENZ, 2002: fig. 11B; POYATO-ARIZA, 2010: fig. 3, 2013: 94), except in those of the tribe Nursalliini. The same pattern also exists in *Rhinopycnodus gabriellae* TAVERNE & CAPASSO, 2013, another pycnodontid fish from the Cenomanian of Lebanon (TAVERNE & CAPASSO, 2013: fig. 4) that belongs to Pycnodontidae but not to Pycnodontinae.

In *Haqelpycnodus picteti*, the dermosphenotic is not a free bone. It is sutured to the frontal and the dermopterotic and becomes a part of the lateral wall of the skull roof. The lower margin of the dermosphenotic and of the dermopterotic occupies a low position, at the level of the orbital ventral margin. These two bones surround a deep and well visible *dilatator fossa* that overhangs the hyomandibula. These characters also are typical of Pycnodontinae (TAVERNE & CAPASSO, 2012: fig. 13, characters 1, 3).

However, one of the principal characters of the Pycnodontinae is the presence of a peculiar bifid cloacal scale, *i. e.*, a scale ventrally divided in two thin and acuminate branches (POYATO-ARIZA &

WENZ, 2002: node 23, character 104[1]), a feature also present in some Nursalliinae. In *Haqelpycnodus picteti*, the bifid cloacal scale differs from that definition. Its ventral extremity is effectively divided in two branches. The posterior branch is long, thin and acuminate. But the anterior branch is short and rounded, not acuminate. The bifid cloacal scale of *Haqelpycnodus picteti* announces the peculiar bifid cloacal scale of Pycnodontinae.

Thus, *Haqelpycnodus picteti* possesses some features typical of Pycnodontinae but not the peculiar bifid cloacal scale, one of the most important characters of the subfamily. In consequence, *Haqelichthys* can not be ranged within Pycnodontinae but, in the phylogenetic tree proposed by POYATO-ARIZA & WENZ (2002: fig. 43), the new Lebanese genus becomes the direct plesiomorphic sister-lineage of the subfamily Pycnodontinae. *Haqelpycnodus* occupies exactly the same position in the phylogeny proposed by TAVERNE & CAPASSO (2012: fig. 13).

Nursalliinae versus Nursalliini

POYATO-ARIZA & WENZ (2002: 216 and Fig. 43) defined two new sister-subfamilies to group the most evolved Pycnodontidae, the Pycnodontinae for the genera *Pycnodus* and *Oropycnodus* POYATO-ARIZA & WENZ, 2002 and the Nursalliinae for the genera *Nursallia* BLOT, 1987, *Abdabalistum* POYATO-ARIZA & WENZ, 2002 and *Palaeobalistum* DE BLAINVILLE, 1818.

TAVERNE & CAPASSO (2012: fig. 13) maintained the same subdivision in two subfamilies but added three other genera to the Pycnodontinae, *Tergestina* CAPASSO, 2000, *Pseudopycnodus* TAVERNE, 2003 and *Polazzodus* POYATO-ARIZA, 2010. Later, other new genera were still reported to this subfamily.

However, the most recent phylogenetic analyses concerning the Pycnodontidae (EBERT, 2016: figs 21, 22; CAWLEY & KRIWET, 2017: fig. 6) lead to the conclusion that the Pycnodontinae are a paraphyletic group, while the Nursalliinae remain a valid subfamily.

A possible way to restore the validity of the Pycnodontinae as a homogenous subfamily is to include the nursalliid fishes in the lineage as a simple tribe, the Nursalliini.

Haqelpycnodus* and *Scalacurvichthys

Scalacurvichthys naishi CAWLEY & KRIWET, 2017 is a newly described pycnodont fish from the marine Cenomanian of Israel, with a high but narrow skull, a short dermosupraoccipital, an extremely acuminate occipital region, a thin brush-like process on the parietal (= postparietal in CAWLEY, J. J. & KRIWET, J., 2017) and bifurcated scales in the cloacal region (ibid., 2017: figs 2, 3, 5). In the phylogeny of Pycnodontiformes, these two authors placed *S. naishi* as the most primitive member of Pycnodontinae (ibid., 2017: fig. 6). Such a position places *S. naishi* just above *Haqelichthys picteti* in the pycnodont phylogenetic tree.

However, *S. naishi* seems devoid of the main features characterizing the Pycnodontinae. The *dilatator fossa* is not visible above the hyomandibula and the ventral margin of the dermopterotic-dermosphenotic is located at the level of the upper border of the orbit and not the lower border (ibid., 2017: figs 2, 3). Some bifurcated scales are present in its cloacal region. Those bifurcated scales have two long dorsal branches (ibid., 2017: fig. 5) but not two acuminate ventral branches as in a bifid cloacal scale *sensu* POYATO-ARIZA & WENZ (2002; fig. 42).

The only apomorphic character shared by *S. naishi* and Pycnodontinae is the posteriorly exposed endocranium (CAWLEY, J. J. & KRIWET, J., 2017: figs 2, 3). But that only feature is not sufficient to allow ranging a pycnodont fish in the subfamily as that cranial morphology is also present in *Rhinopycnodus gabriellae*, a pycnodont fish that does not belong to Pycnodontinae. Moreover, the endocranium of *S. naishi* is rather strange. Normally, the endocranial exposed part of Pycnodontinae is located posterior to the dermopterotic, below the brush-like process of the parietal, at the level of the connexion with the axial skeleton, and consists in a series of bones, the basioccipital, the exoccipital and sometimes the intercalar and the opisthotic. In *S. naishi*, the endocranial exposed part is a single triangular bone located along the parietal, above the brush-like process and also well above the level of the vertebral axis (ibid., 2017: fig. 2A). That is really an unusual shape and position for the posterior portion of the endocranium. The shape and position of that bone would better correspond to a posttemporal or a supratemporal than to the endocranium.

In those conditions, it is really difficult to agree with the placement of *S. naishi* within Pycnodontinae.

The specialized characters shared by *Haqelichthys picteti* and Pycnodontinae, but absent in *S. naishi*, show that *H. picteti* is closer to that subfamily than is *S. naishi*. So, the conclusion seems clear. *H. picteti* occupies a more apomorphic position than *S. naishi* in the pycnodont phylogenetic tree.

ACKNOWLEDGMENTS

We greatly thank Dr. Dr. Silvano AGOSTINI, Superintendant of the Soprintendenza per i Beni Archeologici dell'Abruzzo – Chieti, for allowing us to study the fossil fishes of the CAPASSO collection. We are grateful to M. Adriano VANDERSYPEN, from the Royal Institute of Natural Sciences of Belgium, and to M. Luciano LULLO, from the University of Chieti-Pescara, for their technical help. We are also indebted to the anonymous reviewers who have read and commented our text.

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