Geo-Eco-Trop, 2015, 39, 2: 217-246

New data on the osteology and phylogeny of Gladiopycnodontidae (Pycnodontiformes), a tropical fossil fish family from the marine Upper Cretaceous of Lebanon, with the description of four genera

Nouvelles données sur l'ostéologie et la phylogénie des Gladiopycnodontidae (Pycnodontiformes), une famille de poissons fossiles tropicaux du Crétacé supérieur marin du Liban, avec la description de quatre genres

Louis TAVERNE [1] & Luigi CAPASSO [2]

Abstract: The skeleton of three new gladiopycnodontid genera from the marine Cenomanian of Lebanon, *Hayolperichthys pectospinus* gen. and sp. nov., *Ducrotayichthys cornutus* gen. and sp. nov. and of *Tricerichthys wenzi* gen. and sp. nov. is studied in details. The osteology of *Ichthyoceros spinosus* Gayet, 1984, another Lebanese gladiopycnodontid, is re-studied. *H. pectospinus* gen. and sp. nov. is characterised by the three strong spines borne by its pectoral girdle and the lost of the nuchal horn. *D. cornutus* gen. and sp. nov. had frontal and nuchal horns, an occipital hunch and an elongate dermosupraoccipital that overlies the basis of the nuchal horn. *T. wenzi* gen. and sp. nov. has frontal, occipital and nuchal horns and a long anterior spine on the cleithrum. Its hyomandibula, preopercle and opercle exhibit an unusual shape. They form a crescent-like bony wing over the cheek. *I. spinosus* is deep-bodied and entirely covered by large scutes. It bears frontal and occipital horns. The posterior region of the skull is elongated, forming a spiny occipital process. A phylogeny within the family Gladiopycnodontidae is proposed.

Key words: Pycnodontiformes, Gladiopycnodontidae, new genera, osteology, phylogeny, marine Cenomanian, Lebanon.

Résumé : Le squelette de trois nouveaux genres de Gladiopycnodontidae du Cénomanien marin du Liban, *Hayolperichthys pectospinus* gen. et sp. nov., *Ducrotayichthys cornutus* gen. et sp. nov. et *Tricerichthys wenzi* gen. et sp. nov. est étudié en detail. L'ostéologie d' *Ichthyoceros spinosus* Gayet, 1984, un autre gladiopycnodontidé, est ré-étudiée. *H. pectospinus* gen. et sp. nov. est caractérisé par trois longues épines portées par la ceinture scapulaire et par la perte de la corne nucale. *D. cornutus* gen. et sp. nov. possède des cornes frontale et nucale, une bosse occipitale et un dermosupraoccipital allongé qui recouvre la base de la corne nucale. *T. wenzi* gen. et sp. nov. présente des cornes frontale, occipitale et nucale ainsi qu'une longue épine antérieure sur le cleithrum. Ses hyomandibulaire, préoperculaire et operculaire montrent une morphologie inhabituelle. Ils forment sur la joue une aile osseuse en forme de croissant. *I. spinosus* a un corps élevé couvert de grands écussons. Il possède des cornes frontale et occipitale. La région postérieure du crâne est étirée en un processus occipital épineux. Une phylogénie au sein de la famille des Gladiopycnodontidae est proposée.

Mots-clés: Pycnodontiformes, Gladiopycnodontidae, nouveaux genres, osteologie, phylogénie, Cénomanien marin, Liban

[1] Royal Institute of Natural Sciences of Belgium, Directorate Earth and History of Life,, Vautierstreet, 29, B-1000 Brussels, Belgium. E-mail: louis.taverne@gmail.com
[2]Museo Universitario dell'Universitá "G. d'Annunzio" di Chieti-Pescara, Piazza Trento e Trieste, 1, I-661000 Chieti, Italy. E-mail: lcapasso@unich.it

INTRODUCTION

Gladiopycnodontidae is a highly specialized tropical family of fossil fishes that belong to the order Pycnodontiformes (TAVERNE & CAPASSO, 2013) and are represented by ten genera. Six genera are already published, *Stenoprotome* HAY, 1903, *Gladiopycnodus* TAVERNE & CAPASSO, 2013, *Monocerichthys* TAVERNE & CAPASSO, 2013, *Rostropycnodus* TAVERNE & CAPASSO, 2013, *Joinvillichthys* TAVERNE & CAPASSO, 2014 and *Pankowskichthys* TAVERNE & CAPASSO, 2014 (HAY, 1903; TAVERNE & CAPASSO, 2013, 2014a; TAVERNE *et al.*, 2015; MARRAMÀ *et al*, 2016). The Lebanese *Ichthyoceros* GAYET, 1984, originally included in the family Coccodontidae (GAYET, 1984: 297-300, pl. 3, figs 1, 2), represents a seventh gladiopycnodontid genus (TAVERNE & CAPASSO, 2014b: 38-39, fig. 43).

Gladiopycnodontidae are closely related to Coccodontidae and Gebrayelichthyidae, two other specialized pycnodontiform lineages. These three families are grouped in the Coccodontoidea. Members of this superfamily are small fishes. Most of them have a fusiform body. They have elaborated a remarkable and highly sophisticated defensive system, with a pointed rostrum, a cephalo-thorax, bony occipital processes, cranial and nuchal horns, pectoral and anal spines and large body scutes (TAVERNE & CAPASSO, 2013, 2014a, b, c; TAVERNE *et al.*, 2015; MARRAMÀ *et al.*, 2016). They represent an extraordinary and unique experiment of morphological diversification among the deep-bodied and not armoured pycnodont fishes. This experiment occurs only in Lebanon, in the Near-East realm of the Tethys Ocean, during the Cenomanian, a geological period of high diversification among teleosts and of important increase of temperature and oceanic level (GALE, 2000; CAVIN & FOREY, 2007; CAVIN *et al.*, 2007; among others). The coccodontoid attempt was thus geographically and chronologically very limited and was not a success as no specimen of this lineage has been found elsewhere neither in the marine Santonian of Lebanon nor in other Upper Cretaceous Mesogean deposits.

The aim of our present paper is quadruple: firstly, to describe the osteology of three new gladiopycnodontid genera, secondly, to study *Ichthyoceros* in a more detailed way than previously, thirdly, to give some comments on the newly erected *Gladiopycnodus byrnei* and, fourthly, to reconstruct the phylogeny within the family.

MATERIAL AND METHODS

The material hereafter studied belongs to the Capasso's registered collection (CLC) in Chieti and to the Muséum National d'Histoire Naturelle de Paris (MNHN).

The specimens were studied with stereomicroscopes Wild M 5 and Leica Wild M 8. The figures were drawn by the first author (L. T.) with a camera lucida and photos. 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).

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
Superfamily Coccodontoidea TAVERNE & CAPASSO, 2013
Family Gladiopycnodontidae TAVERNE & CAPASSO, 2013

Genus ***Hayolperichthys*** gen. nov.

Type-species: ***Hayolperichthys pectospinus*** gen. and sp. nov. (by monotypy).

Diagnosis

As for the species (monospecific genus)

Etymology

The generic name of this new gladiopycnodontid fish is dedicated to the American palaeontologist Oliver Perry HAY (1846-1930). He was the second scientist to describe a gladiopycnodontid fish (*Stenoprotome hamata*) that he ranged erroneously in the halecostomid family Belonorhynchidae (= Saurichthyidae) (cf. HAY, 1903; TAVERNE *et al.*, 2015). The Greek word *ichtys*, fish, is added.

Species ***Hayolperichthys pectospinus*** sp. nov.

Diagnosis

Gladiopycnodontid with a low and elongate cephalo-thorax. Long and anteriorly broadened frontal. Elongate lower jaw. Small dermosupraoccipital, devoid of any process. Exposed part of the hyomandibula-dermohyomandibula much smaller than the preopercle. Neither cephalic nor nuchal horns. Two strong spines articulated on the ventral margin of the hypertrophied cleithrum. One posterior strong spine fused to the hypertrophied hypercleithrum.

Etymology

The specific name refers to three strong spines of the pectoral girdle of the fish.

Holotype and unique specimen

Specimen CLC S-601, an isolated skull and pectoral girdle (Fig. 1, 2). Total length: 69 mm.

Figure 1: *Hayolperichthys pectospinus* gen. and sp. nov. Specimen CLC S-601, holotype (head and pectoral girdle only).

Formation and locality

Marine Upper Cenomanian, Haqel, Lebanon.

Osteology

The skull (Fig. 1, 2)

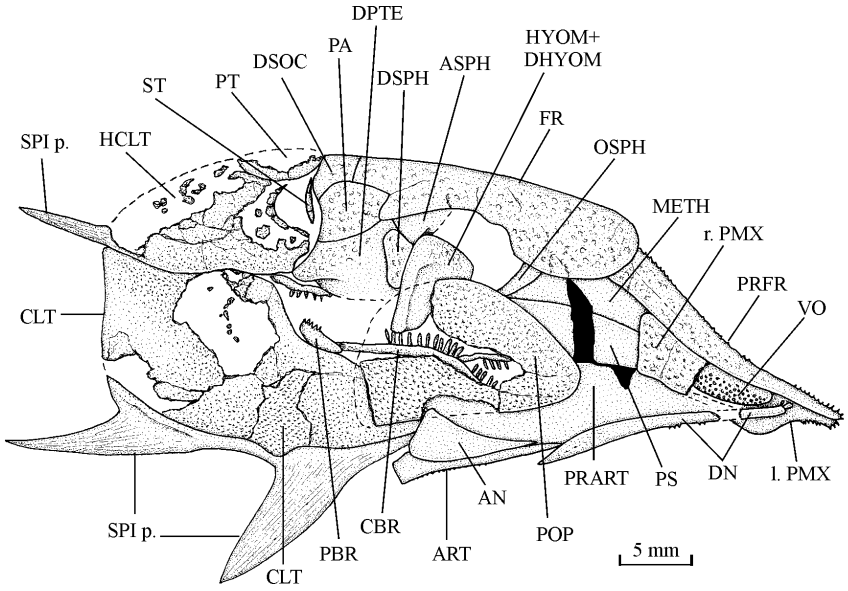

Figure 2: *Hayolperichthys pectospinus* gen. and sp. nov. Specimen CLC S-601, holotype. Skull and pectoral girdle.

The cephalo-thorax is much longer than deep. This feature implies that the body (not preserved) was fusiform. The dermal bones are ornamented with tubercles.

The long pointed rostrum slightly outpaces the lower jaw level and is formed by two large paired bones sutured together, a long prefrontal and an almost as long premaxilla. The anterior extremities of both bones become thinner and bear some small spines on their external margins. Only the most posterior part of the mesethmoid is visible. The right premaxilla is broken and a great part of the vomer is visible. The bone bears a patch of small rounded molariform teeth that are irregularly ranged.

The frontal is elongate, not curved and much broader anteriorly, in front of the orbit, than posteriorly. The posterior portion of the frontal outpaces the level of the orbit. The dermosupraoccipital is a rather small bone, smaller than the underlying parietal and dermopterotic. The dermosupraoccipital is devoid of a median crest. The supratemporal is a small and thin bone located just behind the parietal. A well developed autosphenotic is present on the posterior region of the orbit. There are no frontal, occipital or a nuchal horn.

Only a small part of the broad parasphenoid is visible between the preopercle and the premaxilla. The orbitosphenoid is pressed against the posterior border of the mesethmoid. No pleurosphenoid or basisphenoid is visible in the orbit. The other bones of the endocranium and those of the palato-quadrate arch are not known.

The premaxilla is a toothless, long and broad bone, except its anterior tip that is thinner. Its upper margin is sutured to the lower margin of the prefrontal. The maxilla is not preserved. The lower jaw is very elongated and comprises the dentary, the prearticular, the angular and the articular. The articulation with the quadrate is located at the level of the posterior border of the orbit. The long dentary, reduced to its ventral branch, bears two incisiform teeth. The anterior part of its lower margin bears some very small spines. The prearticular is the largest bone of the series but is partly covered by the preopercle. The teeth of the prearticular are not visible. The articular is

long and narrow. The small angular is triangular. It covers only a reduced surface in the posterior region of the prearticular.

The orbit is wide. The dermosphenotic is located in front of the dermopterotic and posterior to the hyomandibula. No other orbital bone is preserved.

The hyomandibula-dermohyomandibula and the preopercle are sutured together. The exposed part of the hyomandibula-dermohyomandibula is much smaller than the enlarged preopercle. The short ventral branch of the hyomandibula is visible under a missing part of the preopercle. The opercle is not preserved.

A fragment of a long ceratobranchial bearing a few short branchiospines and two small toothed pharyngeal bones are visible under the broken preopercle and near the cleithrum.

The pectoral girdle (Fig. 1, 2)

The pectoral girdle is composed of a greatly enlarged cleithrum, a hypertrophied hypercleitrum and a large posttemporal. Two long and strong spines are articulated on the ventral margin of the cleithrum. The anterior spine is broader than the posterior one. A smaller but however long spine is fused to the posterior ventral corner of the hypercleithrum.

Genus ***Ducrotayichthys*** gen. nov.

Type-species : ***Ducrotayichthys cornutus*** gen.and sp. nov. (by monotypy).

Diagnosis

As for the species (monospecific genus)

Etymology

The generic name of this new gladiopycnodontid fish is dedicated to the French zoologist Henri-Marie DUCROTAY DE BLAINVILLE (1777-1850) who was the first to have scientifically studied some fossil fishes from Lebanon in his "Nouveau Dictionnaire d'Histoire Naturelle" published from 1816 to 1818 (cf. GAYET *et al.*, 2012: 14). The Greek word *ichtys*, fish, is added.

Species ***Ducrotayichthys cornutus*** sp. nov.

Diagnosis

Gladiopycnodontid with a gigantic cephalo-thorax and a short body. Frontal short, broad, with a well marked frontal horn. Long spiny nuchal horn articulated with the dermosupraoccipital, the parietal and the dermopterotic. Very elongate dermosupraoccipital, with an anterior hunch and extending backwardly over the nuchal horn basis. Elongated parietal and dermopterotic. Short and massive lower jaw. Wide exposed part of the hyomandibula-dermohyomandibula. Small ovoid opercle. Small hypercleithrum. A short and broad pectoral spine partly fused to the hypertrophied cleithrum. Short dorsal fin with 8 rays. Short anal fin with one very small spine and 7 rays. About 15 vertebral segments before the caudal skeleton. Notochord not completely surrounded by the arcocentra. 8 epichordals. 8 hypochordals. 2 small spiny dorsal ridge scutes between the nuchal horn and the dorsal fin. Small needle-like scales on the body.

Etymology

The specific name comes from the Latin adjective *cornutus*, *-a*, *-um*, horny, and refers to the frontal and nuchal horn of the new fish.

Holotype and unique specimen

Specimen CLC S-591, a nearly complete specimen (a part of the caudal fin is missing) (Fig. 3, 4). Total length: 29 mm.

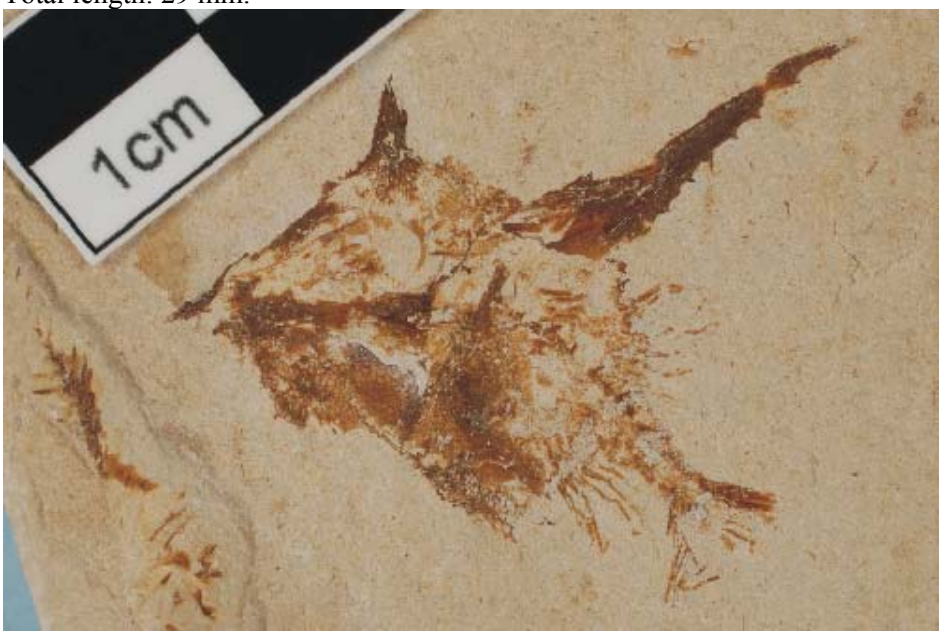

Figure 3: *Ducrotayichthys cornutus* gen. and sp. nov. Specimen CLC S-501, holotype. Complete fish.

Formation and locality

Marine Upper Cenomanian, Haqel, Lebanon.

Morphometric data (Fig. 3, 4)

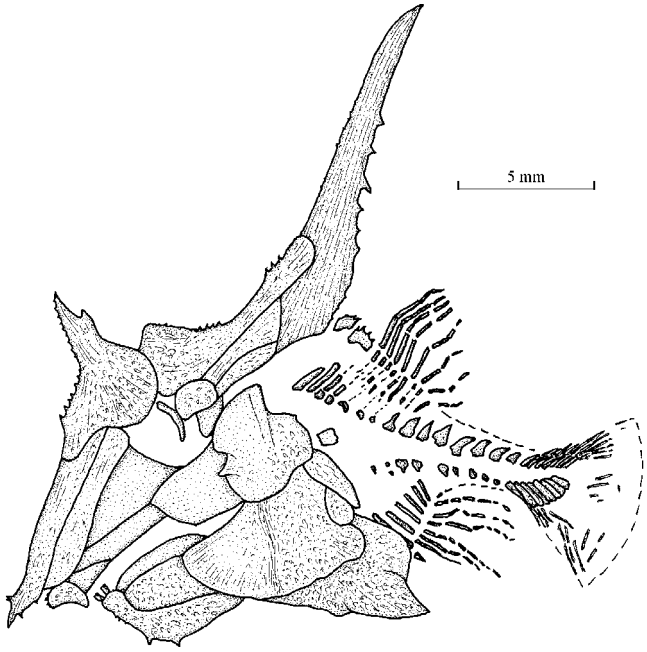

Figure 4: *Ducrotayichthys cornutus* gen. and sp. nov. Specimen CLC S-501, holotype. Reconstruction of the complete fish.

The morphometric data are given in percentage (%) of the standard length of the holotype (25 mm).

Length of the head (opercle included) ……..…… 69.1 %
Length of the cephalo-thorax (cleithrum included) ……. 78.8 %
Depth of the head (in the occipital region, without the nuchal horn) …..... 60.1 %
Length of the nuchal horn …… 69.7 %
Maximum depth of the body (behind the nuchal horn, cleithrum included) … 55.8 %
Predorsal length ……..... 66.7 %
Basal length of the dorsal fin ……..... 17.0 %
Preanal length …… 78.8 %
Basal length of the anal fin …… 12.7 %
Depth of the caudal peduncle …….. 7.9 %

Osteology

The skull (Fig. 5)

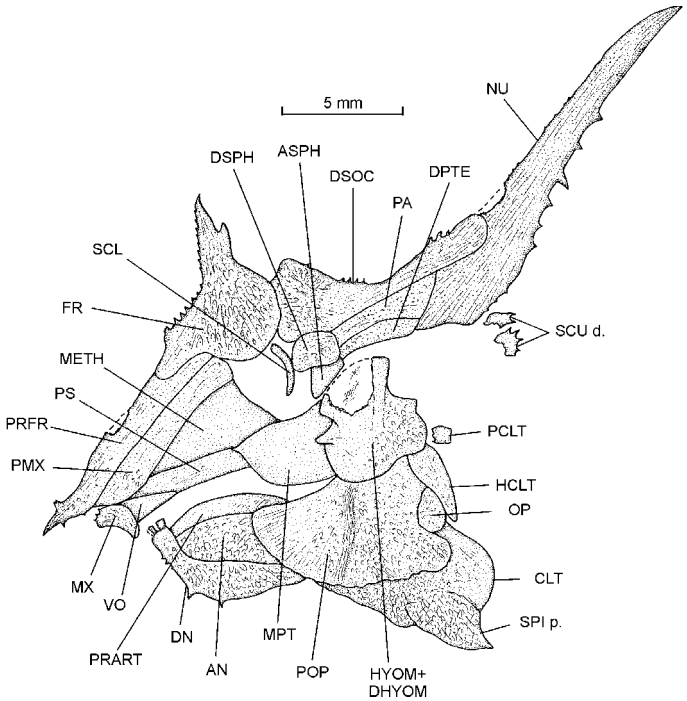

Figure 5: *Ducrotayichthys cornutus* gen. and sp. nov. Specimen CLC S-501, holotype. Skull and pectoral girdle.

As in all gladiopycnodontid fishes, the skull and the pectoral girdle are tightly connected, forming a very enlarge cephalo-thorax that is both longer and deeper than the body. The dermal bones are ornamented with large alveoli that are more or less ranged in rows.

The acuminate and spiny rostrum is formed by the long and broad prefrontal that is sutured to the underlying premaxilla. This rostrum anteriorly outpaces the lower jaw level. The prefrontal and the premaxilla cover the upper part of the large mesethmoid. The posterior region of the vomer is visible but its toothed region is hidden by the maxilla.

The frontal is short but rather broad above the orbit. It bears a series of small spines on the anterior part of its upper margin and a short pointed horn located just above the orbit. This frontal horn has spiny anterior and posterior margins. The dermosupraoccipital is extremely elongated, with some small spines on its upper margin. Anteriorly, just behind the frontal, the dermosupraoccipital broadens, forming a well marked hunch. The dermopterotic and the parietal are much longer than deep. The triangular autosphenotic is located before the dermopterotic and is partly covered by the large dermosphenotic. A strong and very long nuchal horn is articulated by its basis to the dermosupraoccipital, the parietal and the dermopterotic. This nuchal horn has a spiny

anterior margin and a posterior margin with some larger spines. The most posterior region of the dermosupraoccipital overlies the basis of the nuchal horn. No supratemporal is preserved.

The parasphenoid is long, straight, obliquely oriented and toothless. The endocranial bones of the braincase are not visible.

The large metapterygoid is the only bone of the palato-quadrate arch that is preserved.

The premaxilla and the maxilla are toothless. There is no supramaxilla. The premaxilla is long but however slightly shorter than the prefrontal to which it is sutured by its upper margin. The maxilla is reniform, located below the anterior extremity of the premaxilla and its anterior margin is spiny. The lower jaw is rather large. The dentary, reduced to its ventral branch, is a long, broad and curved bone. It bears two incisiform teeth. Its lower margin is spiny. The large angular covers the greatest part of the prearticular. The articular and the teeth of the prearticular are not visible.

The orbit is rather wide. There is a thin sclerotic bone. The large dermosphenotic is placed at the orbit posterior border. No other bone of the orbital series is present.

The hyomandibula and the preopercle are articulated together. The exposed part of the hyomandibula-dermohyomandibula is as deep as broad but however smaller than the hypertrophied preopercle that is greatly expanded along its lower margin. The opercle is a small ovoid bone located between the preopercle and the hypercleithrum.

The girdles (Fig. 5)

The hypertrophied pectoral girdle is pressed against the skull. The bones are ornamented with alveoli and some thin ridges. The anterior region of the cleithrum is covered by the preopercle. The posterior region of the cleithrum is enlarged and bears a short but very broad pectoral spine that is partially fused to the bone. The hypercleithrum (= supracleithrum) is rather small and much deeper than long. The posttemporal is not preserved. A small scute-like postcleithrum is present behind the hypercleithrum.

No pelvic girdle is visible. But it is probable that a small girdle was present as in other Gladiopycnodontidae but hidden by the cleithrum.

The axial skeleton (Fig. 3, 4)

The axial skeleton is composed of at least 15 vertebral segments. The neural and haemal arcocentra surround only very partially the notochord. The seventh neural arch is missing, due to preservation. The first neural arches bear well developed neural spines. At the level of the dorsal fin, these spines are short. The haemal arches are poorly developed at the level of the anal fin and the haemal spines are very short. In the long caudal peduncle, the neural and haemal arches are devoid of spines. Neither ribs nor the postcoelomic bone are visible. They are probably hidden by the cleithrum.

The dorsal and anal fins (Fig. 3, 4)

The dorsal fin contains 8 long segmented rays, the first one being broader than the others. Only fragments of some pterygiophores are preserved.

The anal fin is supported by 6 visible pterygiophores but there is probably a first one hidden by the cleithrum that sustains the small initial spine located at the origin of the fin. This short anal spine is formed by the last ventral keel scute. The spine is followed by 7 segmented rays. The first two rays are shorter than the others.

The caudal skeleton (Fig. 6)

The caudal peduncle is long and includes 5 vertebral segments. There are 8 epichordals and 8 hypochordals in the caudal endoskeleton. The last four hypochordals are slightly shorter than the preceding ones but also are slightly broader. No hypochordal is hypertrophied.

A large part of the caudal fin is lost. Only fragments of some principal rays and of a few procurrent rays in each lobe are preserved.

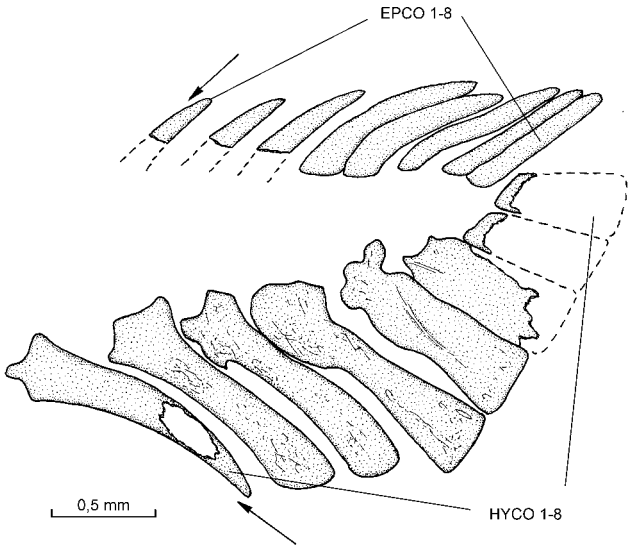

Figure 6: *Ducrotayichthys cornutus* gen. and sp. nov. Specimen CLC S-501, holotype. Caudal skeleton. The arrows indicate the anterior limit of the dorsal and ventral procurrent rays of the caudal fin.

Squamation (Fig. 7)

The body is covered by minute needle-like spines that are not connected to each other. Many of these are simple but some are tri- or tetraradiated.

There are two spiny scutes between the nuchal horn and the origin of the dorsal fin.

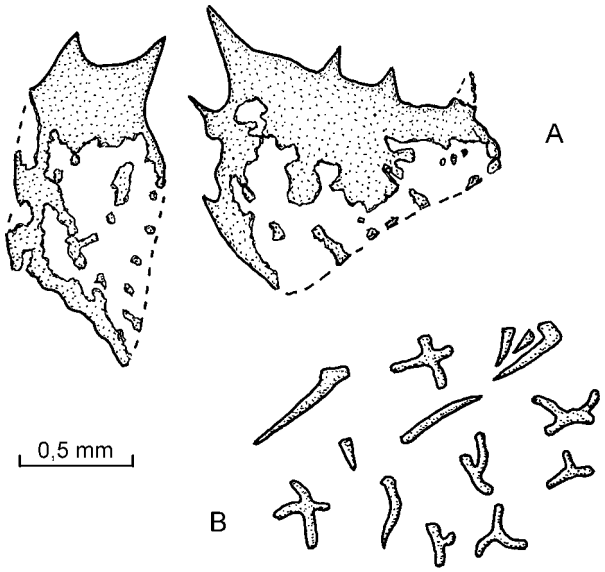

Figure 7: *Ducrotayichthys cornutus* gen. and sp. nov. Specimen CLC S-501, holotype. Scales. A: the two dorsal ridge scales. B: body scales.

Genus ***Tricerichthys*** gen. nov.

Type-species : ***Tricerichthys wenzi*** gen. and sp. nov. (by monotypy)

Diagnosis

As for the species (monospecific genus)

Etymology

From the Greek *threis*, three, *keras*, horn, and *ichthys*, fish. The generic name of the new fish refers to its three cephalic horns, one frontal, one occipital and one nuchal.

Species : ***Trichierichthys wenzi*** gen. and sp. nov.

Diagnosis

Gladiopycnodontid with an enlarged and longer than deep cephalo-thorax and a short body. Frontal short, anteriorly broad, posteriorly very narrow, with a well marked frontal horn. Long spiny nuchal horn articulated with the dermosupraoccipital and the parietal. Dermopterotic reaching the nuchal horn in only one point. Short dermosupraoccipital, with a broad spiny occipital horn. Autosphenotic sutured to dermosupraoccipital. Short parietal and dermopterotic. Short lower jaw. Hyomandibula, preopercle and opercle articulated together and forming a large crescent-like bony wing on the cheek . Wide exposed part of the hyomandibula-dermohyomandibula. Large opercle. Small hypercleithrum. Anterior ventral corner of the cleithrum expanded in a long acuminate spine. A short and massive pectoral spine articulated on the ventral margin of the hypertrophied cleithrum. Short dorsal fin with 5 pterygiophores. Anal fin with one strong spine supported by a long and thin pterygiophore. 10 vertebral segments in the caudal region of the body before the caudal skeleton. Notochord completely surrounded by the arcocentra. A golf-stick-like postcoelomic bone. First anal pterygiophore elongated. 4 epichordals. 9 hypochordals. 2 urodermals. Caudal fin with a convex posterior margin. 6 large spiny dorsal ridge scutes between the nuchal horn and the dorsal fin. 4 ventral keel scutes, the first one with a spiny lower margin. 3 large arrow-head shaped scutes and some smaller ones between the cleithrum and the postcoelomic bone. Caudal region of the body devoid of scales.

Etymology

The species name is chosen in honour of the French paleontologist Sylvie WENZ. Her works have greatly contributed to our present knowledge of the Pycnodontiformes.

Holotype

Specimen CLC S-92, a nearly complete specimen (parts of the caudal fin are missing) (Fig. 8). Total length: 64 mm.

Figure 8: *Tricerichthys wenzi* gen. and sp. nov. Specimen CLC S-92, holotype. Complete fish

Paratype

Specimen CLC S-353, a small incomplete and badly preserved specimen (the snout and a part of the caudal fin are missing). Total length: 33 mm.

Formation and locality

Marine Upper Cenomanian, Haqel, Lebanon.

Morphometric data (Fig. 8, 9)

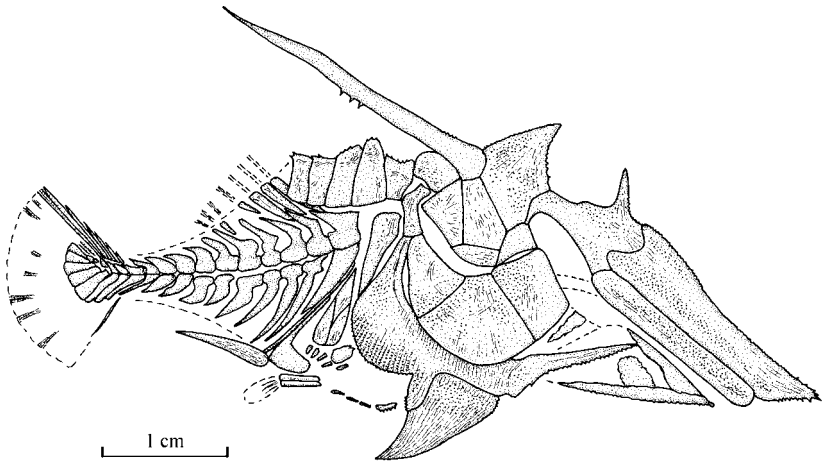

Figure 9: *Tricerichthys wenzi* gen. and sp. nov. Specimen CLC S-92, holotype. Reconstruction of the complete fish.

The morphometric data are given in percentage (%) of the standard length of the holotype (56 mm).

Length of the head (opercle included) ……. 62.4 %
Length of the cephalo-thorax (cleithrum included) …….. 67.5 %
Depth of the head (without the nuchal horn and the pectoral spine) …… 38.0 %
Length of the nuchal horn ……. 44.3 %
Maximum depth of the body (just behind the nuchal horn) ……. 37.1 %
Predorsal length ……..... 81.0 %
Basal length of the dorsal fin ……..... 9.7 %
Preanal length ……... 77.2 %
Depth of the caudal peduncle ……. 5.1 %

Osteology

The skull (Fig. 10)

The head and the pectoral girdle are closely associated. They form a cephalo-thorax that is enormous when compared to the body size. The dermal bones are ornamented with small tubercles and thin ridges.

The elongate rostrum is formed by two long, broad and paired bones that are sutured together, the premaxilla and the prefrontal. The upper margin and the anterior pointed extremity of the prefrontal are spiny. This rostrum greatly outpaces the lower jaw level. The vomer and the mesethmoid are hidden by the prefrontal and the premaxilla.

The frontal is short, anteriorly broad at the junction with the prefrontal, but very narrow posteriorly, above the orbit and at the contact with the dermosupraoccipital. The frontal bears a

small spiny horn. The dermosupraoccipital is a large bone not only contacting the parietal and the frontal but also the well developed autosphenotic, at the posterior margin of the orbit. The spiny upper margin of the dermosupraoccipital forms a short but very broad occipital horn. The dermosphenotic is integrated in the lateral wall of the skull roof and is sutured with the parietal and the dermopterotic. An extremely long nuchal horn with a spiny posterior margin is articulated on both the parietal and the dermosupraoccipital but reaches also the postero-dorsal corner of the dermopterotic. No supratemporal is present.

Neither the parasphenoid nor the bones the endocranium are visible, except the autosphenotic. A small fragment of the entopterygoid, located just before the preopercle, is the only preserved part of the palato-quadrate arch.

The premaxilla is an elongate, broad and toothless bone sutured with the prefrontal all along its upper margin. The maxilla is not preserved. The dentary, reduced to its ventral branch, is well developed. It bears only one very small incisiform tooth. It is possible that a second was present but lost due to the fossilisation. The lower margin of the dentary is spiny. Only a fragment of the angular and the upper margin region of the prearticular are preserved. The articular is lost.

The orbit is long but rather narrow. The dermosphenotic, sutured to the skull roof, is the only bone of the orbital series that is present.

The hyomandibula-dermohyomandibula, the preopercle and the opercle are articulated together, forming an unusual large, broad and crescent-like structure that completely covers the cheek. The hyomandibula-dermohyomandibula is articulated with the autosphenotic and is the anterior element of this bony crescent. The preopercle is positioned medially and the opercle posteriorly. These three bones are rather large, the preopercle being the largest and the opercle the smallest of the series.

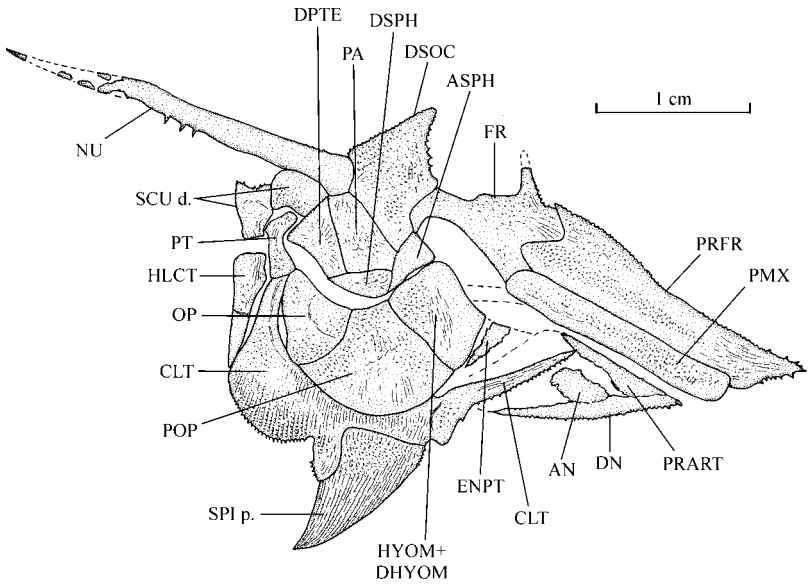

Figure 10: *Tricerichthys wenzi* gen. and sp. nov. Specimen CLC S-92, holotype. Skull and pectoral girdle.

The girdles (Fig. 10)

As in all Gladiopycnodontidae, the pectoral girdle is closely associated to the skull in a sort of cephalo-thorax. The bones are ornamented with ridges and tubercles sometimes ranged in regular rows. The cleithrum has well developed dorsal and ventral limbs. The dorsal branch is narrow in its upper part and broad in its lower part. The ventral branch is anteriorly prolonged by a long, narrow and acuminate process. A short, pointed and highly ornamented pectoral spine, with a very broad basis, is articulated with the ventral margin of the cleithrum. A deep and narrow hypercleithrum is positioned behind the dorsal limb of the cleithrum. A small posttemporal overlies the cleithrum and the opercle.

The pelvic girdle is small. Two short pelvic bones and fragments of ventral fin rays are visible in front of and below the postcoelomic bone.

The axial skeleton (Fig. 11)

The notochord is almost completely surrounded by the arcocentra. Traces of the axial skeleton and of ribs are not visible in the abdominal region of the body but these elements perhaps are hidden by the pectoral girdle and the opercle. In the caudal region, there are 10 neural spines and 9 haemal spines in front of the epichordal and hypochordal series. The neural spines are rather short. The first haemal spines are longer but the following ones shorten quickly.

The postcoelomic bone is like a golf-stick, with a greatly swollen ventral extremity and a short and thin dorsal limb that does not reach the vertebral axis.

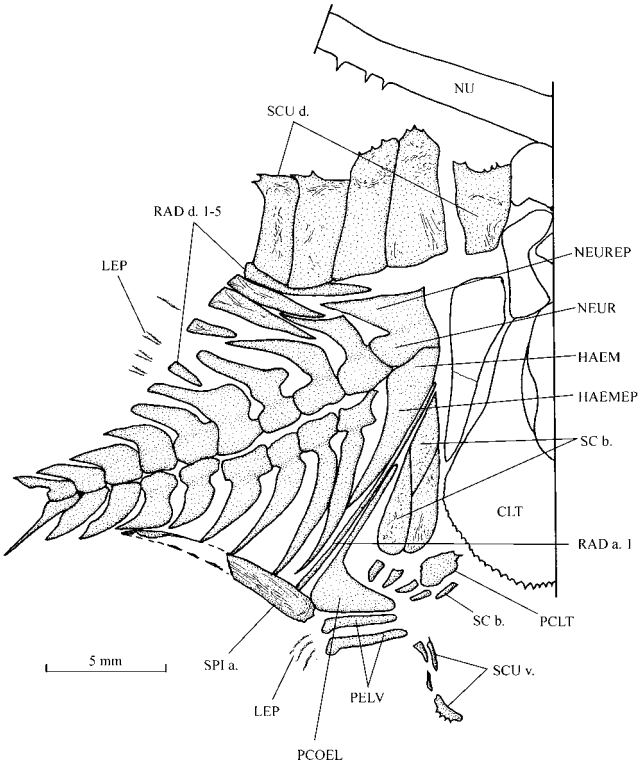

Figure 11: *Tricerichthys wenzi* gen. and sp. nov. Specimen CLC S-92, holotype. Axial skeleton, median fins, scales and scutes.

The dorsal and anal fins (Fig. 11)

The short dorsal fin is supported by 5 pterygiophores. The rays are lost.

The thin and very long first anal pterygiophore is pressed between the postcoelomic bone and the first haemal spine. It supports a long and strong anal spine. This spine, however, is shorter and less developed than that of *Gladiopycnodus* and *Rostropycnodus* (TAVERNE & CAPASSO, 2013: figs 1, 2, 4, 15-18, 20; MARRAMÀ *et al.*, 2016: fig. 2A, B). No other anal pterygiophore or ray is preserved but this apparent absence perhaps is due to an artefact of fossilisation.

The caudal skeleton (Fig. 12, 13)

The caudal peduncle is long and includes 5 vertebral segments as in *Ducrotayichthys* gen. nov. There are 4 epichordals, 9 hypochordals and 2 urodermals in the caudal endoskeleton. The fourth epichordal is slightly displaced, due to the fossilisation. The fifth to the eighth hypochordals are moderately broadened but there is no real hypertrophy.

A large part of the caudal fin is lost. Only fragments of rays and of a few procurrent rays are preserved. It is however possible to see that the posterior margin of the fin is convex.

Figure 12: *Tricerichthys wenzi* gen. and sp. nov. Specimen CLC S-92, holotype. Caudal region.

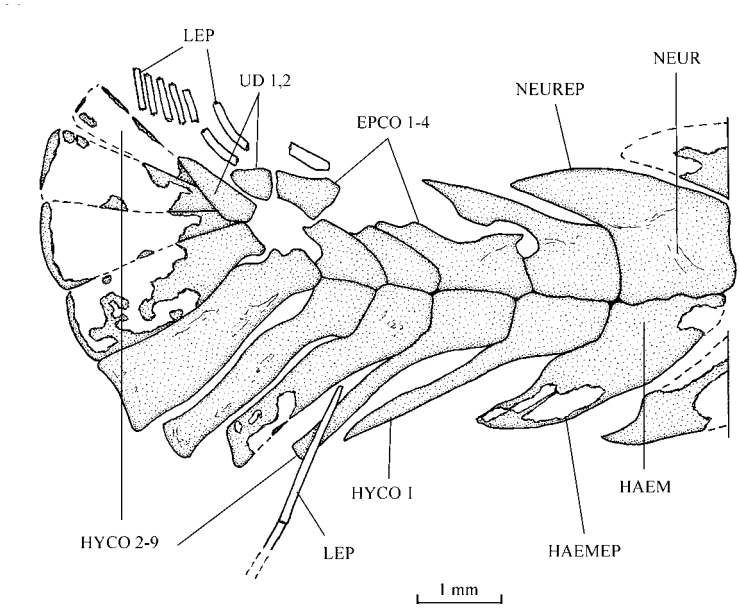

Figure 13: *Tricerichthys wenzi* gen. and sp. nov. Specimen CLC S-92, holotype. Caudal skeleton.

Squamation (Fig. 11)

There are 6 very large dorsal scutes with a spiny upper margin between the nuchal horn and the dorsal fin. They are alike those present in *Gladiopycnodus* (TAVERNE & CAPASSO, 2013: fig. 2). There are also 4 small ventral keel scutes between the cleithrum and the pelvic girdle. The first ventral scute has a spiny lower margin and is a little larger than the three following ones. 3 large scutes are located in the abdominal region of the body, between the cleithrum and the postcoelomic bone. They are connected together and they are arrow-head shaped, with an acuminate dorsal tip. 5 much smaller scutes are positioned below these three large scutes. There also is an ovoid scute with a spiny anterior margin in this region, just next to the cleithrum. This last scute perhaps represents a small postcleithrum. The caudal region of the body is devoid of scales.

Genus ***Ichthyoceros*** GAYET, 1984

Species : ***Ichthyoceros spinosus*** GAYET, 1984

Modified diagnosis

Gladiopycnopycnodontid with an enlarged, as deep as long cephalo-thorax and a short and deep body. Frontal short, broad, with three frontal horns, the middle one being the longest. No nuchal horn. Small horn on the dermosupraoccipital, just posterior to the frontal. Parietal and dermosupraoccipital forming a large elongate and spiny occipital process. Short lower jaw. Wide exposed part of the hyomandibula-dermohyomandibula. Rather small preopercle. Deep opercle, smaller than the preopercle. Posttemporal articulated with the dermopterotic. Hypertrophied hypercleithrum. Hypertrophied cleithrum, with an enlarged posterior region. A short pectoral spine articulated to the postero-ventral corner of the cleithrum. Short dorsal fin with 9 rays. Short anal fin with 7 to 9 rays. Notochord not completely surrounded by the arcocentra. Long postcoelomic bone reaching the vertebral axis. First anal pterygiophore elongated. Caudal fin with a convex posterior margin. Body entirely covered by large irregular scutes ornamented with tubercles and spines.

Holotype

Specimen MNHN N° HAK-106, a nearly complete specimen (the main part of the caudal fin is missing) (Fig. 14; GAYET, 1984: pl. 3, fig. 1). Total length: 65 mm.

Figure 14: *Ichthyoceros spinosus* GAYET, 1984. Specimen MNHN N° HAK-106, holotype. Complete fish (courtesy of Dr. Gaël CLÉMENT, copyright of the Muséum National d'Histoire Naturelle, Paris).

Other material

Specimen CLC S-134, a complete specimen (Fig. 15). Total length: 27 mm.
Specimen CLC S-296, a complete specimen (Fig. 16). Total length: 64 mm.
Specimen CLC S-569, a nearly complete specimen (a part of the caudal fin is missing) (Fig. 17). Total length: 67 mm.

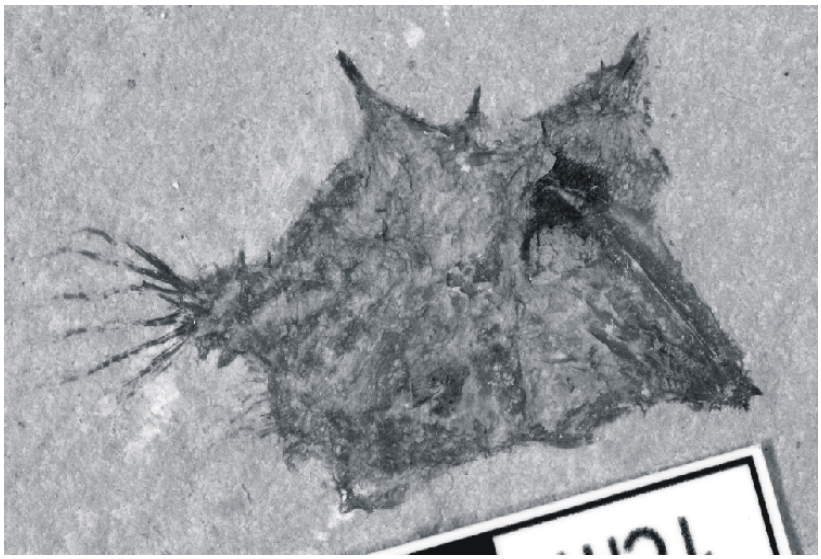

Figure 15: *Ichthyoceros spinosus* GAYET, 1984. Specimen CLC S-134. Complete fish.

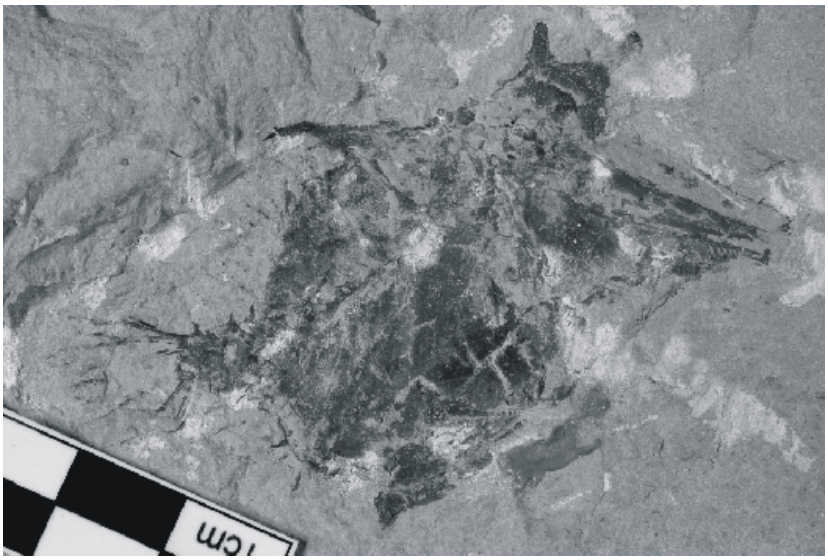

Figure 16: *Ichthyoceros spinosus* GAYET, 1984. Specimen CLC S-296. Complete fish.

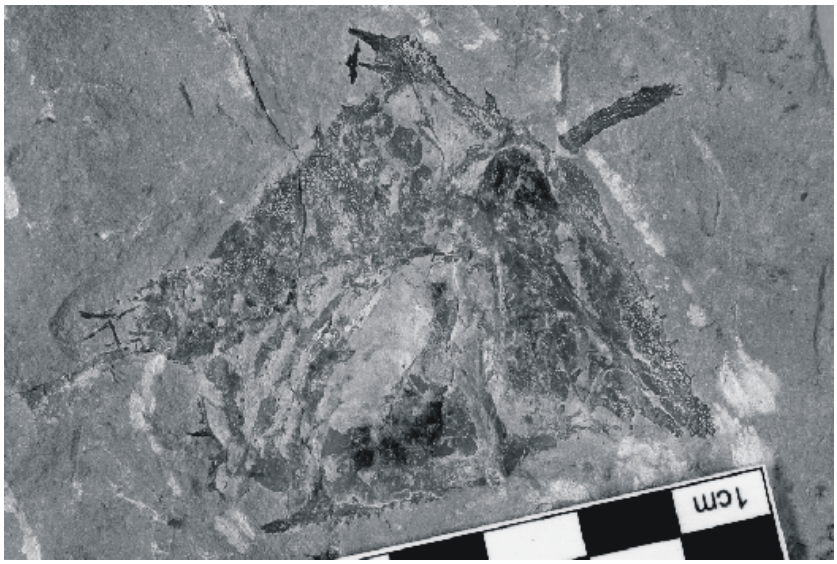

Figure 17: *Ichthyoceros spinosus* GAYET, 1984. Specimen CLC S-569. Complete fish.

Formation and locality

Marine Upper Cenomanian, Haqel, Lebanon.

Morphometric data (Fig. 14-18)

The morphometric data are given in percentage (%) of the standard length of the holotype (58 mm) and of specimen CLC S-569 (63 mm). They represent the extreme values of the four available samples.

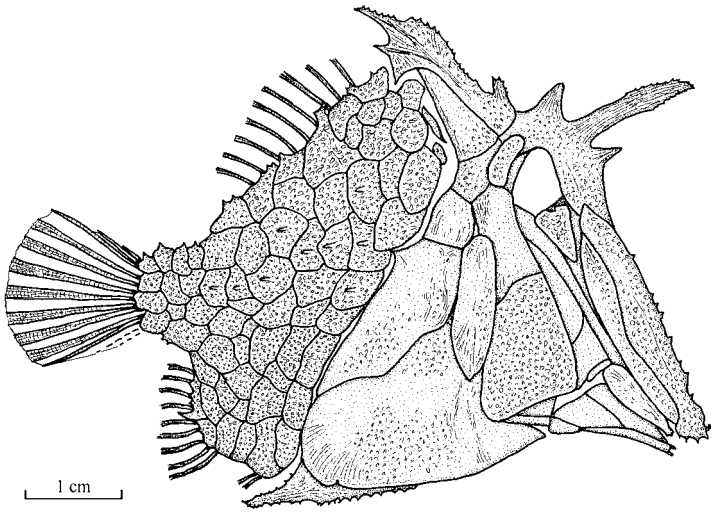

Figure 18: *Ichthyoceros spinosus* GAYET, 1984. Reconstruction of the complete fish based on the four available specimens. The scale refers to specimen CLC S-569.

	Holotype	CLC S-569
Length of the head (opercle included) …….	48.6 % ……..	46.5 %
Length of the cephalo-thorax (cleithrum included) ……..	75.7 % ……..	69.5 %
Depth of the head …….....	60.0 % ……..	69.3 %
Maximum depth of the body (just behind the head) ……	54.1 % ……..	70.3 %
Predorsal length ……	67.5 % ……..	–
Preanal length ……	78.4 % ……..	-
Depth of the caudal peduncle ……...	13.5 % ……..	13.9 %

Osteology

The skull (Fig. 19-23)

The skull is much deeper than long, with an elongate preorbital region. The dermal bones are strongly ornamented with small tubercles, large alveoli and some thin ridges.

The snout is formed by the very long prefrontal to which the almost as long toothless premaxilla is sutured. The snout slightly outpaces the lower jaw level. The anterior extremity and the dorsal border of the prefrontal are spiny. Only a small part of the mesethmoid is visible between the premaxilla and the parasphenoid. The vomer is unknown, being hidden by the premaxilla and the maxilla.

The frontal is rather short, limited to the orbital region and it bears three horns. The middle one is much longer than the two others and has spiny margins. The dermopterotic is sutured to the parietal, the frontal and the autosphenotic. The crown of the skull develops a very elongate occipital process that is formed by the dermosupraoccipital and the parietal. There is no free nuchal horn. The dermosupraoccipital bears a small pointed horn just posterior to the suture with the frontal. There are also one (CLC S-134), two (CLC S-296) or three horns (CLC S-569) or a series of

smaller horns (holotype) at the top of the dermosupraoccipital. These upper occipital horns overhang the beginning of the dorsal region of the body and perhaps are the result of the fusion between the nuchal horn and the dermosupraoccipital. A small and narrow supratemporal is visible behind the parietal.

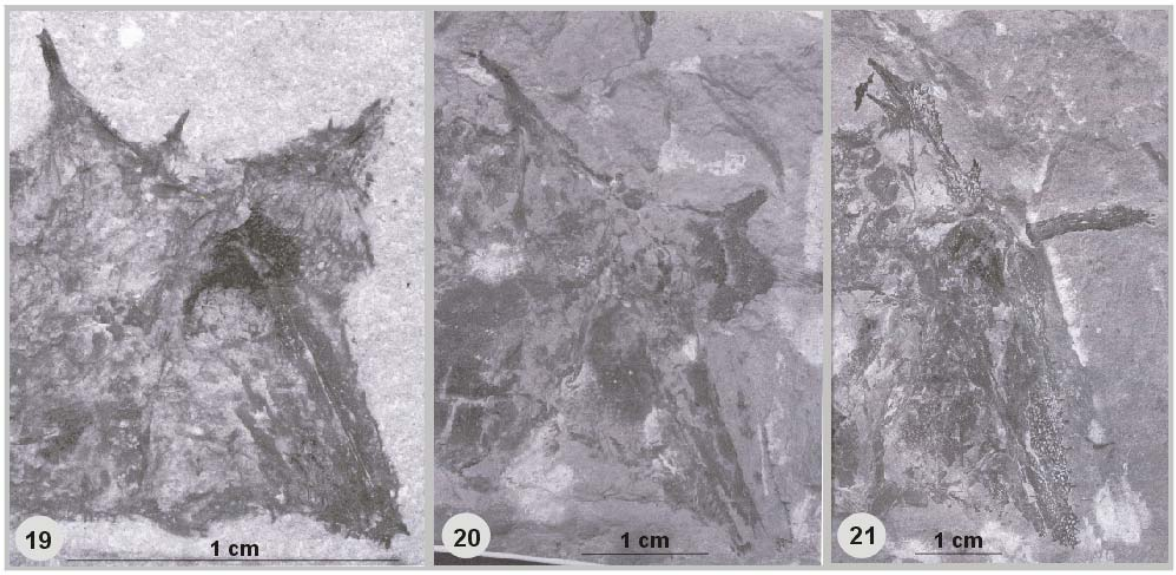

Figure 19: *Ichthyoceros spinosus* GAYET, 1984. Head region of specimen CLC S-134. Scale in mm.
Figure 20: *Ichthyoceros spinosus* GAYET, 1984. Head region of specimen CLC S-296.
Figure 21: *Ichthyoceros spinosus* GAYET, 1984. Head region of specimen CLC S-569.

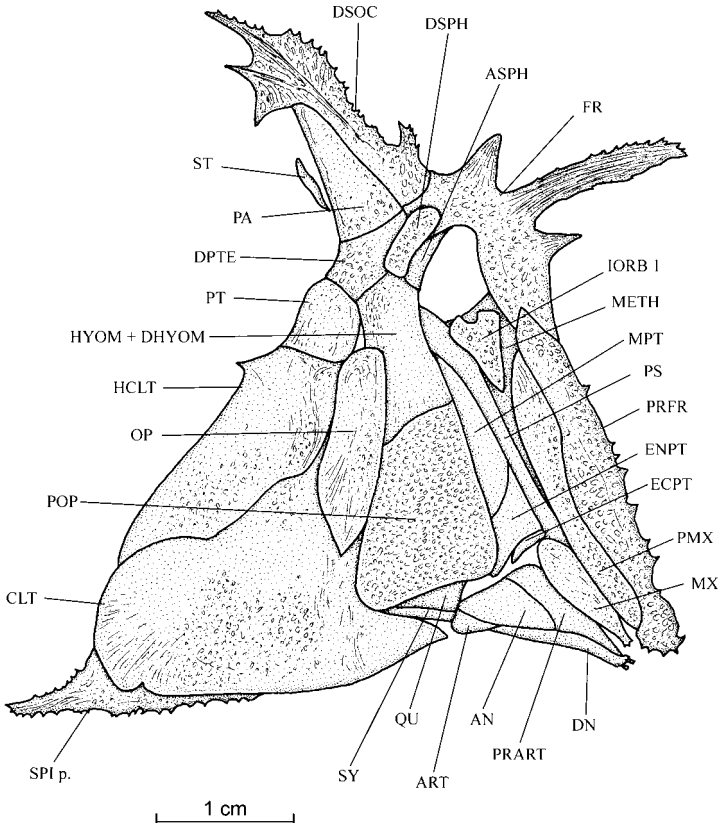

Figure 22: *Ichthyoceros spinosus* GAYET, 1984. Skull and pectoral girdle. Reconstruction based on the four available specimens. The scale refers to specimen CLC S-569.

The parasphenoid is long, toothless and its trabecular region is obliquely oriented. The endochondral bones of the braincase are hidden, except the autosphenotic that forms the posterior border of the orbit.

Small parts of the metapterygoid and of the entopterygoid and a very small ectopterygoid are visible between the preopercle and the parasphenoid. Both the quadrate and the symplectic articulate with the lower jaw as usual in pycnodont fishes.

The upper jaw contains the premaxilla and the maxilla. The long toothless premaxilla is sutured all along its upper margin with the lower margin of the prefrontal. GAYET (1984: 299) explains that "aucune trace de prémaxillaire n'est visible en avant du préfrontal". She considers the prefrontal and the premaxilla as only one bone, the prefrontal (ibid., 1984: 298, pl. 3, fig. 2). However, the suture between the true prefrontal and the premaxilla is clearly visible on the holotype as in the three other available specimens. The maxilla is narrow, rather long but much shorter than the premaxilla. Its anterior extremity is spiny. The lower jaw is triangular in shape, not very deep, without marked coronoid process and rather small while compared to the size of the skull. The dentary, reduced to its ventral branch, bears two small incisiform teeth. The angular partly covers the prearticular. There is a small articular. The inner face of the left prearticular is visible on sample CLC S-296. There are three rows of molariform teeth. Those of the middle row are the largest. They are much deeper than long and with a slightly sigmoid contour. Posteriorly, the two last elements of the middle row are divided in a small rounded upper tooth and a larger sigmoid lower tooth. The upper and the lower rows contain each two small and more or less ovoid teeth. More teeth were probably present in these two rows but were lost during the fossilisation.

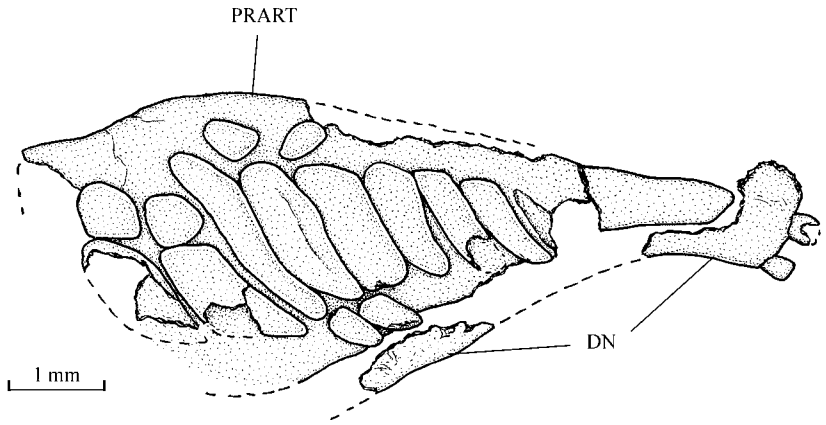

Figure 23: *Ichthyoceros spinosus* GAYET, 1984. Inner side of the left lower jaw of specimen CLC S-296, showing the dentary and the inner face of the prearticular.

A well developed dermosphenotic overlies the limit between the dermopterotic and the autosphenotic. The first infraorbital is large, triangle-shaped and it covers partially the mesethmoid..

The hyomandibula and the preopercle are sutured together. The exposed part of the hyomandibula-dermohyomandibula is important but, however, not as wide as the preopercle. However, this preopercle is proportionally less expanded than in most other Gladiopycnodontidae. The deep and narrow opercle is much smaller than the preopercle. In the holotype, the posterior margin of the opercle is ornamented with some small spines. GAYET (1984: pl. 3, fig.2) has interpreted this opercle as a narrow cleithrum (ibid., 1984: 299).

Some hook-like pharyngeal teeth are visible under broken parts of the opercle and of the hyomandibula on specimen CLC S-569.

The girdles (Fig. 19-22)

The enlarged pectoral girdle is closely connected to the skull, forming together a gigantic cephalo-thorax. This pectoral girdle was considered as enlarged scutes by GAYET (1984: 299). The posttemporal articulates with the dermopterotic, just behind the hyomandibula. The hypercleithrum is hypertrophied. The upper region of its posterior margin bears a small spine. The cleithrum has a

deep dorsal limb, a short anterior ventral limb and an extremely wide posterior ventral expansion. The pectoral spine articulates with the cleithrum and has spiny margins. GAYET (1984: 299, pl. 3, fig. 2) mentioned a pectoral fin emerging just behind the bone that we consider as the opercle (her "cleithrum"). We have not observed such a pectoral fin neither on the holotype nor on the three other specimens. There are very small bony fragments between the opercle and the cleithrum on the holotype but not a true pectoral fin.

Specimen CLC S-296 is the only one that exhibits some traces of a reduced pelvic girdle. In the other specimens, the small pelvic girdle is hidden by the cleithrum and the body scutes.

The axial skeleton

The vertebral axis is covered by the body scutes. Traces of dorsal and ventral arcocentra are visible in specimens CLC S-134 and S-296, showing that the neural and haemal arches do not completely surround the notochord.

A long and strong postcoelomic bone is partly preserved directly posterior to the hypercleithrum and the cleithrum in sample CLC S-569. It reaches dorsally the vertebral axis.

The dorsal and anal fins (Fig. 14-18)

The dorsal and anal fins of the holotype are severely crushed and it is not possible to count the rays. Specimens CLC S-134 and S-569 lack the dorsal fin, due to the fossilisation. In specimen CLC S-296, fragments and traces of 9 dorsal rays are preserved and the origin of the fin is located posterior to the occipital process of the skull. The anal fin is missing on specimen CLC S-569. There are respectively fragments and traces of 9 and 7 anal rays on specimens CLC S-134 and S-296. Specimen CLC S-296 also exhibits fragments of a very elongated first anal pterygiophore located directly posterior to the postcoelomic bone.

The caudal skeleton (Fig. 24)

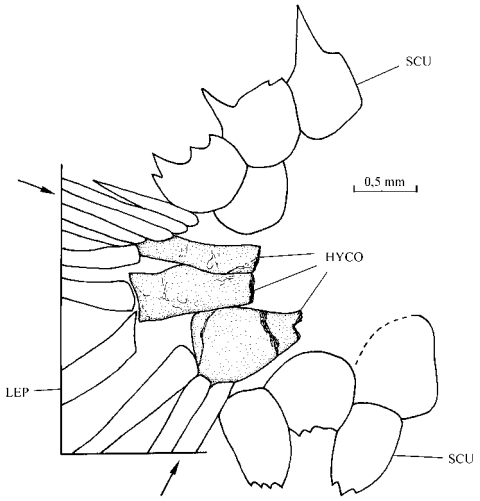

Figure 24: *Ichthyoceros spinosus* GAYET, 1984. Partial caudal skeleton of specimen CLC S-134. The arrows indicate the most external dorsal and ventral principal caudal rays.

The caudal endoskeleton is covered by the body scutes. However, three posterior hypochordals are visible in specimen CLC S-134. The two lower elements are broadened but not really hypertrophied.

A large part of the caudal fin is missing in the holotype. Fragments of 8 to 10 principal caudal rays are visible respectively on specimens CLC S-134 and CLC S-296. There are at least 2 upper procurrent rays. The posterior margin of the fin is convex.

Squamation (Fig. 14-18)

The body is entirely covered by large irregular scutes that are ornamented with tubercles. Some scutes bear a spine in their middle portion. At the level of the anal fin, one scute of the ventral margin bears a strong spine. The scutes of the caudal peduncle are smaller than those on the body and the scutes on the upper and lower borders of the peduncle have spiny margins.

DISCUSSION

The generic validity and the relationships of *Hayolperichthys* gen. nov.

Hayolperichthys gen. nov. is only known by its cephalo-thorax. It differs from all other Gladiopycnodontidae by its long and anteriorly broadened frontal and by the presence of three strong spines on each side of the pectoral girdle, two articulated with the cleithrum and one fused to the hypercleithrum. That is enough to justify the generic validity of this fish.

Hayolperichthys gen. nov. belongs to the most specialized members of the family, those having lost the nuchal horn.

Ducrotayichthys gen. nov., *Tricerichthys* gen. nov. , *Pankowskichthys* and their relationships

Data on *Pankowskichthys* mentioned in this chapter come from TAVERNE & CAPASSO (2014a: 19-24, fig. 17-21).

Ducrotayichthys gen. nov., *Tricerichthys* gen. nov. and *Pankowskichthys* share the same outline, with a greatly enlarged cephalo-thorax, a small and rather short body and a very long nuchal horn. Thus, eventually, someone could assume that the three fishes belong to the same genus. However, they greatly differ in many details of their anatomy, as explained hereafter.

(1) *Ducrotayichthys* gen. nov. and *Tricerichthys* gen. nov. have a well developed horn on the frontal, while *Pankowskichthys* has a frontal devoid of a horn.

(2) *Ducrotayichthys* gen. nov. exhibits elongated parietal, dermopterotic and dermosupraoccipital and this last bone has a well marked hunch just posterior to the frontal. In *Tricerichthys* gen. nov., these bones are shorter and the dermosupraoccipital bears a huge horn. *Pankowskichthys* has also shorter parietal, dermopterotic and dermosupraoccipital and there is neither a hunch nor a horn on the dermosupraoccipital.

(3) There is a hook-like process on the anterior extremity of the premaxilla in *Pankowskichthys*. The premaxilla of the two other genera is longer and devoid of such a process.

(4) In *Ducrotayichthys* gen. nov., the nuchal horn articulates with the dermosupraoccipital, the parietal and the dermopterotic. In *Pankowskichthys*, the dermopterotic has no contact with the horn. In *Tricerichthys* gen. nov., the dermopterotic reaches the occipital horn in only one point but does not really participate to its articulation with the skull.

(5) The dermosphenotic and the hyomandibula are much larger in *Ducrotayichthys* gen. nov. and *Tricerichthys* gen. nov. than in *Pankowskichthys*.

(6) The dermosphenotic of *Tricerichthys* gen. nov. is a part of the lateral margin of the skull roof. That is not the case in the two other genera.

(7) In *Trichérichthys*, the autosphenotic and the dermosupraoccipital are sutured together. That is not the case in the two other genera.

(8) The preopercle of *Ducrotayichthys* gen. nov. and *Tricerichthys* gen. nov. is greatly broadened in its lower region, whereas *Pankowskichthys* has a preopercle deeper than long.

(9) The opercle is ovoid in *Ducrotayichthys* gen. nov. and rod-like in *Pankowskichthys*. *Tricerichthys* gen. nov. has a larger opercle than that of the two other genera.

(10) In *Tricerichthys* gen. nov., there is an unusual position of the hyomandibula, preopercle and opercle. These three bones are arranged in a large, broad, horizontally oriented and crescent-like structure. These bones have the normal “pycnodontid” position in the two other genera.

(11) The cleithrum has a completely different shape in *Tricerichthys* gen. nov. than in the two other genera.

(12) The hypercleithrum is larger in *Pankowskichthys* than in *Ducrotayichthys* gen. nov. and *Tricerichthys* gen. nov.

(13) The pectoral spine is huge and articulated on the cleithrum in *Tricerichthys* gen. nov. but is much smaller and partially fused to the cleithrum in the two other genera.

(14) The postcoelomic bone has a greatly swollen ventral extremity in *Tricerichthys* gen. nov. This bone is less developed in *Pankowskichthys*. The coelomic bone is unknown in *Ducrotayichthys* gen. nov.

(15) The rays of the dorsal and anal fin are long in *Ducrotayichthys* gen. nov. and short in *Pankowskichthys*. The situation is unknown in *Tricerichthys* gen. nov.

(16) The anal fin begins with a long and strong spine in *Tricerichthys* gen. nov. This spine is very small in the two other genera.

(17) The notochord is completely surrounded by the arcocentra in *Tricerichthys* gen. nov. That is not the case in the two other genera.

(18) There is an enlarged hypural plate in the caudal endoskeleton of *Pankowskichthys*. In *Ducrotayichthys* gen. nov. and in *Tricerichthys* gen. nov., the hypochordals are not fused in such a broad plate.

(19) There are 2 small spiny dorsal ridge scutes in *Ducrotayichthys* gen. nov. between the nuchal horn and the dorsal fin and 6 enlarged dorsal scutes in *Tricerichthys* gen. nov. The dorsal fin begins just behind the nuchal horn in *Pankowskichthys* and there is no dorsal scute.

(20) *Tricerichthys* gen. nov. has a few ventral keel scutes between the cleithrum and the pelvic girdle. The two other genera are devoid of such ventral scutes.

(21) The body of *Ducrotayichthys* gen. nov. is entirely covered by very small needle-like scales and by large scutes ornamented with tubercles in *Pankowskichthys*. In *Tricerichthys* gen. nov., there are a few scutes between the cleithrum and the postcoelomic bone but the caudal region of the body is naked.

Such an amount of important differences clearly indicate that these three fishes represent three different genera in spite of their overall morphological similarity.

Ducrotayichthys gen. nov. and *Tricerichthys* gen. nov. are related to the primitive genera of the family, those that have a nuchal horn. They are the most evolved members of this subgroup, as shown by their frontal horn and their occipital hunch or horn. These structures are missing in the primitive genera of this subgroup.

***Ichthyoceros*, a valid gladiopycnodontid genus, and its relationships**

GAYET (1984: 297-300, pl. 3, fig. 1, 2) provided a succinct description of *Ichtyoceros* based on a single specimen, the holotype. She includes this fossil fish in the Coccodontidae and considered that it was closely allied to *Trewavasia* WHITE & MOY-THOMAS, 1941, another coccodontid genus. This systematic relationship was accepted by ulterior authors, such as POYATO-ARIZA & WENZ (2002). Indeed, the two fishes share the same general morphology. They are deep-bodied, with a huge head, frontal horns, a well marked occipital process and wide scutes that cover entirely their body.

However, the bones of the skull and of the pectoral girdle greatly differ in size, shape and position in these two genera, as shown by TAVERNE & CAPASSO (2014b: 38-39, fig. 43). Moreover, *Trewavasia* exhibits the classical "pycnodontid" morphology of the jaws (ibid., 2014b: figs 35-37), while *Ichthyoceros* has an elongate snout, outpacing the lower jaw level and formed by a long prefrontal and a long toothless premaxilla sutured together, *i. e.,* the characteristic "gladiopycnodontid" snout morphology. *Ichthyoceros* thus belongs to Gladiopycnodontidae and not to Coccodontidae. The apparent similarity between *Trewavasia* and *Ichthyoceros* is only a matter of morphologic convergence.

Ichthyoceros is the only deep-bodied fish within Gladiopycnodontidae and its cranial anatomy, with an occipital process, markedly differs from that of all the other members of this family. This confirms the generic validity of *Ichthyoceros*.

Ichthyoceros does not exhibit a nuchal horn. Thus, the genus belongs to the evolved subgroup of the family, the one that has lost the free nuchal horn. Its frontal and occipital horns place it as a primitive member of this subgroup, seeing that such horns are also present in the most

evolved genera of the subgroup that exhibits a nuchal horn but absent in the most specialized genera of the subgroup devoid of nuchal horn.

Comments on *Gladiopycnodus byrnei* and the supposed pectoral fin in Gladiopycnodontidae (Fig. 25)

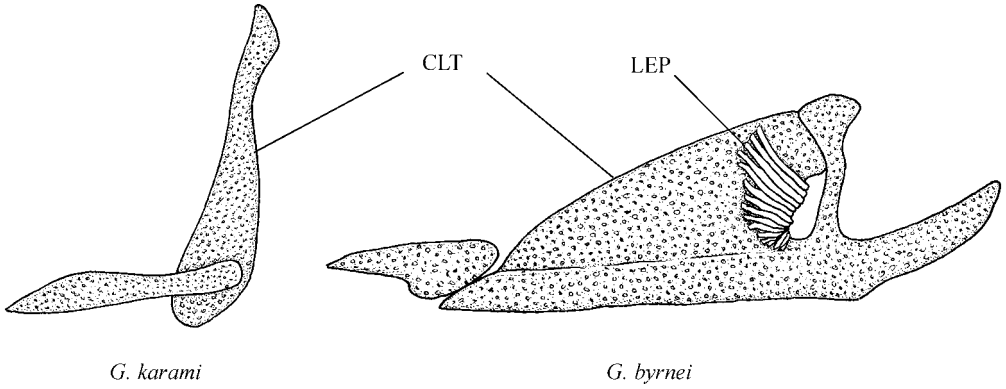

Figure 25: Comparison between the cleithra of *Gladiopycnodus karami* (left; modified from TAVERNE & CAPASSO, 2013: fig. 4) and *Gladiopycnodus byrnei* (right; modified from MARRAMÀ *et al.*, 2016: figs 2B, 3, 5A, B) (not to scale).

Gladiopycnodus karami TAVERNE & CAPASSO, 2013 is the first species described and assigned to the family Gladiopycnodontidae (TAVERNE & CAPASSO, 2013: 4, 5). A second species, *Gladiopycnodus byrnei* MARRAMÀ *et al.*, 2016 from the marine Cenomanian beds of Hgula (Lebanon), has been described very recently on the basis of one specimen and included in the genus *Gladiopycnodus* (MARRAMÀ *et al.*, 2016).

The two species exhibit the same general morphology, the same long, sword-like, acuminate rostrum and the same gigantic anal spine derived from the last ventral keel scute. Thus, at first sight, they seem very closely allied (TAVERNE & CAPASSO, 2013: fig. 1, 2; MARRAMÀ *et al.*, 2016: fig. 2A, B).

However, the osteological differences between them are numerous and important (TAVERNE & CAPASSO, 2013: fig. 3, 4, 5, 6C; MARRAMÀ *et al.*, 2016: fig. 2B, 3-5A, B). *G. byrnei* has a much shorter and broader frontal, much smaller parietal, preopercle, opercle and lower jaw and a wider posttemporal than *G. karami*. *G. byrnei* also possesses a pair of highly enlarged supratemporals (= extrascapulars) that form a bridge between the dermosupraoccipital and the first pair of dorsal ridge scutes. *G. karami* has lost the supratemporals and its dermosupraoccipital is directly connected to the first pair of dorsal ridge scutes. *G. byrnei* is devoid of pelvic girdle, while such a girdle is present of in *G. karami*. The body of *G. byrnei* is entirely covered with irregularly imbricated flake-like scales, even in the tail region. *G. karami* exhibits the same body scales but its caudal peduncle is covered with large rounded scales ornamented with tubercles that are missing in *G. byrnei*. The origin of the anal fin is much closer to the skull in *G. karami* than in *G. byrnei*, a position which is due to the different shape and size of their cleithra.

But the main difference separating the two species is located in the pectoral girdle (Fig. 25). The cleithrum of *G. karami* is a deep, strong but narrow rod-like bone vertically oriented that bears a long pectoral spine. There is no anterior process and the wide posterior process normally present on the cleithrum of the other Gladiopycnodontidae is lost in this species. The cleithrum of *G. byrnei* has a completely different shape. The bone has also a median rod-like vertical structure. But, contrarily to the case of *G. karami*, an enlarged posterior process and a pointed anterior process are also present. A short pectoral fin containing sixteen rays emerges by a broad notch that is open between the posterior process and the median bony bar of the cleithrum. That is a unique feature among Gladiopycnodontidae, the pectoral fin being lost in all the other known species of this family. A notch piercing the cleithrum is also absent in the other gladiopycnodontid fishes and is a peculiar character of *G. byrnei*.

Contrarily to us, MARRAMÀ *et al.* (2016: 36-37) consider that a pectoral fin is present in all Gladiopycnodontidae. They write that "the inadequate preservation of the specimens described by TAVERNE and CAPASSO (2013, 2014a) prevented the recognition of the pectoral fin, whose apparent absence was erroneously regarded as a diagnostic character of *Gladiopycnodus*, and, more generally, of the whole family". That is a rather rash and gratuitous affirmation, since these authors have not seen our material. They have studied only one specimen from only one gladiopycnodontid species. We have studied twenty one specimens from eleven species and some of our specimens were well preserved. We have never found a pectoral fin or a pectoral notch in the cleithrum of any specimen.

MARRAMÀ *et al.* (2016: 36) also state that "although the available material of *Stenoprotome hamata* clearly exhibits some fin rays in the position of the pectoral fin, these elements were considered as pertaining to the pelvic fins, and their unusual displacement due to the taphonomic biases". Indeed, a few long rays are associated to the cleithrum in the preserved pectoral girdle of the holotype of *Stenoprotome* (TAVERNE *et al.*, 2015: fig. 5). However, these rays have not a normal position for a pectoral fin. They emerge before the cleithrum and not behind. The occurrence of a taphonomic displacement is thus certain. On the other hand, a pair of strongly developed pelvic bones is visible just below the posterior process of the cleithrum and these two bones have lost their corresponding fin rays. Moreover, the cleithrum of *Stenoprotome* is not pierced by a pectoral notch. That is why we have considered these displaced rays as belonging to the ventral fins and not to an eventual pectoral fin that we have never found in our other studied material.

Concerning the supposed pectoral fin in Gladiopycnodontidae, we must also add that, in many samples, the pelvic girdle is partly or totally hidden by the enlarge cleithrum. Parts of the pelvic bones and of the ventral fin rays often are visible just behind the cleithrum. This unusual situation could give the false impression that a pectoral fin is present.

To conclude, we interpret the presence of a pectoral fin in *G. byrnei* as a reversion that recalls the case of Coccodontidae, the most primitive family within the Coccodontoidea. A pectoral fin is also present in Gebrayelichthyidae but extremely reduced and composed of one or two long rays (TAVERNE & CAPASSO, 2014c: figs 9, 20).

Phylogeny within Gladiopycnodontidae (Fig. 26)

The anatomical data used here come from TAVERNE & CAPASSO (2013, 2014a, b, c), TAVERNE *et al.* (2015), MARRAMÀ *et al.* (2016) and the present paper.

The three highly specialized families Coccodontidae, Gebrayelichthyidae and Gladiopycnodontidae are grouped in the superfamily Coccodontoidea. The most primitive members of this lineage share a few advanced characters not present in other pycnodontiform fishes.

(1) The skull and the pectoral girdle are intimately associated and form together an enlarged cephalo-thorax.

(2) The body is small, fusiform, without dorsal and ventral apex.

(3) The supratemporal is articulated with the dermosupraoccipital, the parietal and the dermopterotic (the supratemporal is lost in Gebrayelichthyidae).

(4) The posttemporal is sutured to the supratemporal or to the parietal when the supratemporal is absent.

(5) The cleithrum is greatly hypertrophied.

(6) The hypercleithrum is hypertrophied.

(7) There are less than 20 vertebral segments before the epichordal series.

(8) The neural and haemal spines are short (linked to character 2).

(9) The dorsal fin is short and located in the middle of the back.

(10) The anal fin is short and largely separated from the tail.

Gebrayelichthyidae and Gladiopycnodontidae exhibit some new specialized characters that are absent in Coccodontidae.

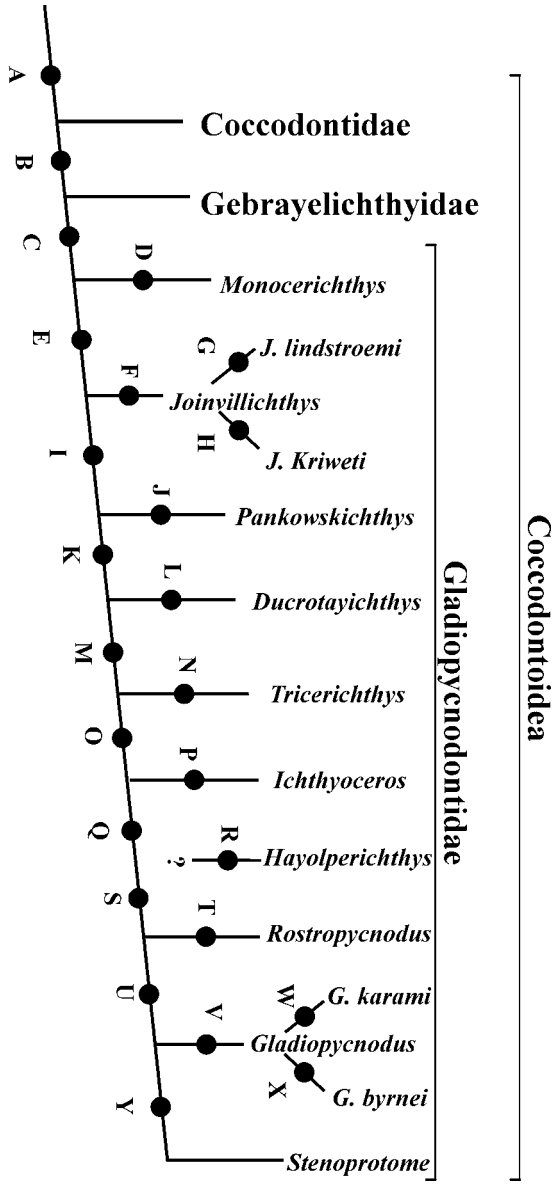

Figure 26: Phylogeny within Coccodontoidea and within Gladiopycnodontidae. The numbers refer to the characters discussed in the text. **Node A**: 1-10. **Node B**: 11-18. **Node C**: 11-24. **Node D**: 25-27. **Node E**: 28-29. **Node F**: 30-31. **Node G**: 32. **Node H**: 33-35. **Node I**: 36-39. **Node J**: 40-42, 26. **Node K**: 43-44. **Node L**: 45-48. **Node M**: 49-52. **Node N**: 53-55. **Node O**: 56. **Node P**: 57-61. **Node Q**: 62. **Node R**: 63-65. **Node S**: 66. **Node T**: 67-70. **Node U**: 71-72. **Node V**: 73-77. **Node W**: 78-80. **Node X**: 81-84. **Node Y**: 85-88.

(11) A long nuchal horn is articulated to the occipital region of the skull.

(12) The prefrontal forms a rostrum that anteriorly outpaces the level of the lower jaw.

(13) The premaxilla is toothless but sometimes bears small spines.

(14) There is a wide postero-ventral process on the cleithrum.

(15) The shortened abdominal region is totally or partially enclosed in the two expanded cleithra.

(16) The pectoral fin is reduced to one or two long rays.

(17) The reduced pelvic girdle is partly or totally hidden by the postero-ventral process of the cleithrum.

(18) There are scales on the whole body. These scales have a completely different shape than those in other Pycnodontiformes.

Comments on the phylogeny within Coccodontidae and Gebrayelichthyidae are given in TAVERNE & CAPASSO (2014b, c).

Six new apomorphies distinguish Gladiopycnodontidae.

(19) Both the prefrontal and the toothless premaxilla are very elongated. The upper margin of the premaxilla is strongly sutured to the lower margin of the prefrontal. The two bones form together a spiny prominent rostrum.

(20) The vomer bears a patch of very small ovoid teeth that are irregularly ranged (this character is present in all the species in which the vomer is known [Fig. 2; TAVERNE & CAPASSO, 2013: fig. 10, 2014a: fig. 7]).

(21) The pectoral fin is lost (except in *Gladiopycnodus byrnei* [reversion])

(22) A strong pectoral spine is articulated or partially fused to the cleithrum.

(23) The nuchal horn bears a series of strong spines on its posterior margin.

(24) The body is entirely covered by small flake-like scales.

Monocerichthys seems to be the most primitive member of the family. Its cranial skeleton is still rather similar to that of the other pycnodontiform fishes. The genus exhibits at least three autapomorphies.

(25) The nuchal horn basis is greatly broadened. The horn is not only articulated on the dermosupraoccipital, the posttemporal and the supratemporal but extends also on the body back.

(26) The dorsal ridge scutes are lost (this feature probably is linked to character 25).

(27) The ventral keel scutes are lost.

Joinvillichthys and the more advanced genera differ from *Monocerichthys* by two new characters.

(28) The rostrum becomes longer and more acuminate.

(29) The caudal region of the body is covered by large scute-like scales, those of the abdominal region remaining small and flake-like.

Joinvillichthys presents a few autapomorphies.

(30) The dermosupraoccipital is enlarged and becomes the only bone forming the occiput.

(31) The nuchal horn is articulated only on the dermosupraoccipital (linked to character 30).

Joinvillichthys lindstroemi possesses at least one autapomorphy.

(32) The opercle is reduced to a deep and extremely thin strip-like bone.

Joinvillichthys kriweti exhibits some autapomorphies.

(33) The parietal is enlarged and the dermopterotic reduced.

(34) The anterior ventral limb of the cleithrum is lost.

(35) The pectoral spine is articulated on the ventral margin of the cleithrum and not on the posterior corner of the bone.

Pankowskichthys and the remaining gladiopycnodontid genera share new apomorphies.

(36) The posttemporal and the supratemporal are no more articulated with the skull roof and they do not support the nuchal horn.

(37) The posterior ventral keel scute associated with the postcoelomic bone becomes a small spine located at the origin of the anal fin.

(38) The body is entirely covered by scute-like scales.

(39) The precloacal ventral keel scutes are lost.

Pankowskichthys shows some autapomorphies.

(40) The dermopterotic is reduced and largely separated from the nuchal horn.

(41) The dorsal fin becomes longer and its origin is located just behind the nuchal horn.

(42) Some hypocordals are fused, forming a broad hypural plate.

(26) The dorsal ridge scutes are lost (linked to character 41 and not to the broadening of the nuchal horn basis as in *Monocerichthys*).

Ducrotayichthys gen. nov. and the following genera exhibit two new specialized characters.

(43) The frontal bears a horn.

(44) The dermosupraoccipital develops a well marked hunch.

Ducrotayichthys gen. nov. is characterized by a few autapomorphies.

(45) The dermosupraoccipital is greatly elongated and extends on the basis of the nuchal horn.

(46) The hyomandibula-dermohyomandibula is enlarged.

(47) The lower jaw is deep and massive.

(48) The size of the body scales is severely reduced. The scales become minute needle-like spines.

Tricerichthys gen. nov. and the remaining gladiopycnodontid genera offer a series of new apomorphies.

(49) There is a true horn on the dermosupraoccipital and no more a simple hunch.

(50) The anal spine grows longer.

(51) The postcoelomic bone broadens and supports the long anal spine (linked to character 50).

(52) The first anal pterygiophore is greatly elongated, pressed against the posterior margin of the postcoelomic bone and supports also the anal spine (linked to characters 50 and 51).

Tricerichthys gen. nov. presents some autapomorphies.

(53) The hyomandibula, preopercle and opercle are sutured together , forming an unusual crescent-like structure that is horizontally positioned.

(54) The cleithrum is anteriorly expanded, forming a long spiny process.

(55) There are only a few large scales in the abdominal region and some scutes on the dorsal ridge, the scales of the caudal region being lost.

Ichthyoceros and the more evolved genera differ from the preceding by at least one character.

(56) The free nuchal horn is lost.

Ichthyoceros is characterized by a series of autapomorphies.

(57) The frontal bears three horns.

(58) The dermosupraoccipital and the parietal are elongate and form an occipital process.

(59) The dorsal margin of the dermosupraoccipital is horny.

(60) The body is short and deep.

(61) The anal spine is lost.

The cephalo-thorax is the only preserved region of *Hayolperichthys*. Its body is unknown and its systematic position is unclear. However, this fish must be ranged in the gladiopycnodontid subgroup that has lost the nuchal horn, *i. e.*, the level of *Ichthyoceros* and the more specialized genera. On the other hand, it does not possess the elongate sword-like rostrum that characterizes *Rostropycnodus*, *Gladiopycnodus* and *Stenoprotome*. Thus, it occupies a plesiomorphic position in regard to these three genera.

Hayolperichthys, *Rostropycnodus*, *Gladiopycnodus* and *Stenoprotome* share one new character.

(62) The horn on the dermosupraoccipital is lost.

Hayolperichthys has at least three autapomorphies.

(63) The frontal is elongate and anteriorly broadened.

(64) The hypercleithrum bears a long posterior spine.

(65) Two strong pectoral spines are articulated on the cleithrum and not only one.

Rostropycnodus and the two remaining genera differ from the preceding gladiopycnodontid fishes by at least one new feature.

(66) The rostrum is extremely elongated and sword-like.

Rostropycnodus presents some autapomorphies.

(67) The dermosupraoccipital is enlarged, forming a massive sabot-like process that extends on the back and reaches the dorsal fin.

(68) The anterior ventral limb of the cleithrum is enlarged.

(69) The postcoelomic bone is extremely broadened.

(70) The basis of the anal spine is highly broadened (characters 69 and 70 are linked).

Gladiopycnodus and *Stenoprotome* share two new characters.

(71) The frontal horn is lost.

(72) The posterior margin of the dermosupraoccipital bears a median spine (feebly marked in *Gladiopycnodus* and strongly marked in *Stenoprotome*).

Gladiopycnodus is characterized by a few peculiar features.

(73) The long sword-like rostrum has a thin and very acuminate anterior extremity.

(74) A vertically oriented median bar-like component of the cleithrum is individualized.

(75) The anal spine becomes extremely elongate and largely outpaces the caudal fin level.

(76) A series of numerous paired dorsal ridge scutes covers the full length of the back and surround the dorsal fin.

(77) All or most of the body scales are flake-like (complete or partial reversion to character 24).

Gladiopycnodus karami presents a few peculiar apomorphies.

(78) The cleithrum is reduced to its median vertical bar-like component, the anterior ventral limb and the posterior process being lost.

(79) The ventral margin of the enlarged preopercle forms a part of the ventral border of the skull (linked to the loss of the anterior ventral branch of the cleithrum, cf. character 78).

(80) Some ovoid ornamented scute-like scales are present in the tail region.

Gladiopycnodus byrnei also exhibits some peculiar apomorphies.

(81) Paired highly hypertrophied supratemporals are sutured to the dermosupraoccipital and to the first pair of dorsal ridge scutes.

(82) The cleithrum is pierced by a large notch open between its posterior ventral process and its median bar-like component.

(83) A pectoral fin emerges from a notch piercing the cleithrum (characters 82 and 83 are linked).

(84) The pelvic girdle is lost.

Stenoprotome differs from the preceding Gladiopycnodontidae by a series of new specialized characters.

(85) The frontals are strongly shortened but rather broad.

(86) The parietals are enlarged and ovoid.

(87) The elongate dermopterotic lies along the frontal, the parietal and the dermosupraoccipital and bears a long lateral horn.

(88) The cleithrum, hypercleithrum and postcleithrum bear large spines on their posterior margins.

ACKNOWLEDGMENTS

We greatly thank Dr. Silvano AGOSTINI, Superintendant of the Soprintendenza per i Beni Archeologici dell'Abruzzo – Chieti, for allowing us to study the fossil fishes of the Luigi CAPASSO's 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, for their technical help. We also thank Dr. Gaël CLÉMENT, from the Muséum National d'Histoire Naturelle de Paris, for providing photos of one specimen and Dr. Jurgen KRIWET, from the University of Vienna, for his constructive comments. We are also indebted to the anonymous reviewers who have read and commented our text.

ABBREVIATIONS USED IN THE TEXT-FIGURES

AN: angular
ART: articular
ASPH: autosphenotic
CBR: ceratobranchial
CLT: cleithrum
DHYOM: dermohyomandibula
DN: dentary
DPTE: dermopterotic
DSOC: dermosupraoccipital
DSPH: dermosphenotic
ECPT: ectopterygoid
ENPT: entopterygoid (= endopterygoid)
EPCO 1-8: epichordals 1 to 8
FR: frontal
HAEM : haemal arch
HAEMEP: haemal spine
HCLT: hypercleithrum (= supracleithrum)

HYCO 1-9: hypochordals 1 to 9
HYOM: hyomandibula
IORB 1: infraorbital 1
LEP: lepidotrichium (= fin ray)
METH: mesethmoid
MPT: metapterygoid
MX: maxilla
NEUR: neural arch
NEUREP: neural spine
NU: nuchal horn
OP: opercle
OSPH: orbitosphenoid
PA: parietal
PBR: pharyngobranchial
PCLT: postcleithrum
PCOEL: postcoelomic bone
PELV: pelvic bone
PMX: premaxilla
POP: preopercle
PRART: prearticular
PRFR: prefrontal (= lateral dermethmoid ?)
PS: parasphenoid
PT: posttemporal
QU: quadrate
RAD d.: pterygiophores (= radials) of the dorsal fin
RAD v.: pterygiophores (= radials) of the anal fin
SC b.: body scales
SCL: sclerotic bone
SCU: scute
SCU d. : scutes of the dorsal ridge
SCU v.: scutes of the ventral keel
SPI a.: anal spine
SPI p.: pectoral spine
ST: supratemporal
SY: symplectic
UD 1, 2: urodermals 1 and 2
VO: vomer
f. V: foramen of the trigeminal nerve (V)
l.: left
r.: rigth

REFERENCES

CAVIN, L. & FOREY, P. L. 2007. Using ghost lineages to identify diversification in the fossil record. *Biology Letters*, 3: 201-204.

CAVIN, L., FOREY, P. L. & LÉCUYER, C. 2007. Correlation between environment and Late Mesozoic ray-finned fish evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 245: 353-367.

GALE, A. S. 2000. The Cretaceous world. *In*: Culver S. J. & Rawson P. F. (eds) *Bioticresponse to global change. The last 145 million years*: 1-19. Cambridge University Press, Cambridge.

GAYET, M. 1984. *Ichthyoceros spinosus* nov. gen., nov. sp., du Cénomanien inférieur de Hakel (Liban) et ses affinités avec le genre *Trewavasia* (Pisces, Pycnodontiformes, Coccodontidae). *Bulletin du Muséum National d'Histoire Naturelle*, Paris, 4^{e} série, 6, section C, 3: 287-307.

GAYET, M., ABI SAAD, P. & GAUDANT, O. 2012. Les fossiles du Liban. Mémoire du temps.184 p. Méolan-Revel: Éd. Désiris.

HAY, O. P. 1903. On a collection of Upper Cretaceous fishes from Mount Lebanon, Syria, with descriptions of four new genera and nineteen new species. *Bulletin of the American Museum of Natural History*, 19(10): 395-452.

KRIWET, J. 2001. Palaeobiogeography of pycnodontiform fishes (Actinopterygii, Neopterygii). *In*: MELENDEZ, G., HERRERA, Z., DELVENE, G. & AZANZA, B. (eds) *Los fósiles y la paleogeographia. XII Jornadas de la Sociedad Española de Paleontologia*: 121-130. Universidad de Zaragoza, Zaragoza.

MARRAMÀ, G., VILLIER, B., DALLA VECCHIA, F. M. & CARNEVALE, G. 2016. A new species of *Gladiopycnodus* (Coccodontoidea, Pycnodontomorpha) from the Cretaceous of Lebanon provides new insights about the morphological diversification of pycnodont fishes through time. *Cretaceous Research*, 61: 34-43.
MARTIN-ABAD, H. & POYATO-ARIZA, F. J. 2013. Historical patterns of distribution in Pycnodontiform and Amiiform fishes in the context of moving plates. *Geologica Belgica*, 16 (4): 217-226.
NURSALL, J. R. 1996. Distribution and ecology of pycnodont fishes. *In*: ARRATIA, G. & VIOHL, G. (eds) Mesozoic Fishes – Systematics and Paleoecology, Verlag Dr. F. PFEIL, München: 115-124.
NURSALL, J. RA. 2010. The case for pycnodont fishes as the fossil sister-group of teleosts. *In*: NELSON, J. S., SCHULTZE, H.-P. & WILSON, M. V. H. (eds) Origin and phylogenetic interrelationships of teleosts, Verlag Dr. F. PFEIL, München: 37-60.
POYATO-ARIZA, F. J. 2015. Studies on pycnodont fishes (I): evaluation of their phylogenetic position among actinopterygians. *Rivista Italiana di Paleontologiae Stratigrafia*, 121(3): 329-343.
POYATO-ARIZA, F. J. & WENZ, S. 2002. A new insight into pycnodontiform fishes. *Geodiversitas*, 24(1): 139-248.
TAVERNE, L. & CAPASSO, L. 2013. Gladiopycnodontidae, a new family of pycnodontiform fishes from the Late Cretaceous of Lebanon, with the description of three genera. *European Journal of Taxonomy*, 57: 1-30.
TAVERNE, L. & CAPASSO, L. 2014a. On the « *Coccodus* » *lindstroemi* species complex (Pycnodontiformes, Gladiopycnodontidae) from the marine Late Cretaceous of Lebanon, with the description of two new genera. *European Journal of Taxonomy*, 2014 (101): 1-27.
TAVERNE, L. & CAPASSO, L. 2014b. Ostéologie et phylogénie des Coccodontidae, une famille remarquable de poissons Pycnodontiformes du Crétacé supérieur marin du Liban, avec la description de deux nouveaux genres. *Palaeontos*, 25: 3-43.
TAVERNE, L. & CAPASSO, L. 2014c. Ostéologie et relations phylogénétiques des Gebrayelichthyidae (Halecostomi, Pycnodontomorpha), une extraordinaire famille de poissons du Crétacé supérieur marin du Liban, avec la description d'un nouveau genre. *Palaeontos*, 25: 44-68.
TAVERNE, L., MAISEY, J. G. & CAPASSO, L. 2015. A third longirostrine gladiopycnodontid fish genus (Pycnodontiformes) from the marine Late Cretaceous of Lebanon. *Palaeontos*, 28: 37-42.