Geo-Eco-Trop., 2020, 44, 1 : 147-160

Osteology and relationships of *Stanhopeichthys libanicus* gen. and sp. nov. (Teleostei, Crossognathiformes, Pachyrhizodontidae) from the marine Cenomanian (Upper Cretaceous) of Lebanon

Ostéologie et relations de *Stanhopeichthys libanicus* gen. et sp. nov. (Teleostei, Crossognathiformes, Pachyrhizodontidae) du Cénomanien marin (Crétacé supérieur) du Liban

Louis TAVERNE [1] & Luigi CAPASSO [2]

Résumé: L'ostéologie et les relations de *Stanhopeichthys libanicus* gen. and sp. nov., un nouveau poisson pachyrhizodonte du Cénomanien supérieur marin de Hgula (Liban), sont étudiées en détails. Le nouveau genre appartient au sous-groupe des Pachyrhizodontidae ayant un processus postérieur pointu sur le ptérotique. Avec les trois dernières vertèbres caudales non fusionnées, sept hypuraux autogènes, trois épuraux et trois uroneuraux, *Stanhopeichthys* possède le squelette caudal le moins évolué au sein de ce sous-groupe. *Stanhopeichthys* et le genre italien *Nardopiscis* partagent un caractère spécialisé qui n'est pas présent chez les autres Pachyrhizodontidae. Leurs pariétaux sont séparés l'un de l'autre par la région postérieure rétrécie des frontaux et non pas par le supraoccipital.

Mots-clés: Teleostei, Crossognathiformes, Pachyrhizodontidae, *Stanhopeichthys libanicus* gen. et sp. nov., ostéologie, relations, Cénomanien, Liban.

Abstract: The osteology and the relationships of *Stanhopeichthys libanicus* gen. and sp. nov., a new pachyrhizodontid fish from the marine Upper Cenomanian of Hgula (Lebanon), are studied in details. The new genus belongs to the subgroup of Pachyrhizodontidae having a posterior pointed process on the pterotic. With the three last caudal vertebrae not fused, seven autogenous hupurals, three epurals and three uroneurals, *Stanhopeichthys* exhibits the less evolved caudal skeleton within that subgroup. *Stanhopeichthys* and the Italian genus *Nardopiscis* share a specialized character not present in other pachyrhizodontid fishes. Their two parietals are separated from each other by the posterior narrow region of the frontals and not by the supraoccipital.

Key words: Teleostei, Crossognathiformes, Pachyrhizodontidae, *Stanhopeichthys libanicus* gen. and sp. nov., osteology, relationships, marine Cenomanian, Lebanon.

INTRODUCTION

With more than 500 species of animals and plants, the marine Cenomanian (Haqel, Hgula, Ein Namoura) and Santonian (Sahel Alma) biota of Lebanon is by far the richest one in the world for the Upper Cretaceous (GAYET *et al.*, 2012). The presence of fossil fishes in Lebanon is known at least since the 4th century, with the Chronicles of bishop Eusebius of Caesarea (ibid., 2012: 8; CAPASSO, 2017: 53-54, fig. 1). However, the first real scientific studies of these fossil fishes only begin in the second half of the 19th century (PICTET, 1850; PICTET & HUMBERT, 1866; DAVIS, 1887) and where continued during all the 20th century (HAY, 1903: WOODWARD, 1942; PATTERSON, 1967, 1970; GAUDANT, 1969, 1978; GAYET, 1993; among others) and even in the present days (FOREY *et al.*, 2003; TAVERNE, 2004; TAVERNE & GAYET, 2004; TAVERNE & CAPASSO, 2012; among others)

[1] Royal Institute of Natural Sciences of Belgium, Directorate Earth and History of Life, Vautierstreet, 29, B-1000 Brussels, Belgium. E-mail: louis.taverne@skynet.be
[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

Until very recently, the presence of Pachyrhizodontidae in the Upper Cretaceous ichthyofauna of Lebanon was unknown. GAYET *et al.* (2012: 114-115) presented for the first time photos of two different species of pachyrhizodontid fishes from the Cenomanian deposits of Haqel and Hgula. Unfortunately, the specimens of these two species belong to a private collection and are not available for a scientific study.

The aim of our present paper is to describe the osteology and to precise the relationships of a new Upper Cretaceous pachyrhizondontid fish from Lebanon that differs from the two figured in GAYET *et al.* (2012) and thus represents a third genus of that fossil family living in the same country at the same period.

Pachyrhizodontidae is one of the two families that constitute the Pachyrhizodontoidei, an extinct suborder of primitive teleosts often ranged within the order Crossognathiformes (TAVERNE, 1989; PATTERSON, 1993; ARRATIA, 2008), a position that is however denied by a few ones (CAVIN, 2001). Pachyrhizodontoidei are marine predators with a fusiform body, eating principally smaller fishes (TAVERNE, 1989: 103). Their size is highly variable, from a few centimetres to almost one meter in length. They appear during the Upper Jurassic (ARRATIA & SCHULTZE, 1999) and have a worldwide distribution during the Cretaceous (TAVERNE, 1989: fig. 11-13). They disappear at the Cretaceous/Paleocene boundary, except one genus, *Platinx* AGASSIZ, 1835, that survives till the Paleocene and even till the Middle Eocene (DANILCHENKO, 1968; TAVERNE, 1980).

MATERIAL AND METHODS

The specimen hereafter described belongs to the CAPASSO collection (CLC) in Chieti (Italy). The material was studied with a stereomicroscope Leica Wild M 8. The figures were drawn by the first author (L. T.) and the photos made by M. Luciano LULLO, from the University of Chieti-Pescara. Aspersions with ethanol were used to improve some observations.

The CAPASSO collection 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 specimens of this collection were also subject to prescription in order of conservation and availability to the studies on the basis of the article 30 of the Italian law N° 42/2004. The Soprintendenza per I Beni Archeologici dell'Abruzzo-Chieti has authorized the two 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 the text-figures

AN	=	angular
ART	=	articular
ASPH	=	autosphenotic
BRSTG	=	branchiostegal ray
CHY	=	anterior ceratohyal
CLT	=	cleithrum
DN	=	dentary
DSPH	=	dermosphenotic
ENPT	=	entopterygoid
EP1-3	=	epurals 1 to 3
EPI	=	epiotic (= epioccipital)
EXO	=	exoccipital
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
HEM	=	haemal arch
HEMEP	=	haemal spine
HY 1-7	=	hypurals 1 to 7
HYOM	=	hyomandibula
IC	=	intercalar
IORB 1-5	=	infraorbitals 1 to 5
LEP	=	lepidotrich (= fin ray)
LETH	=	lateral ethmoid
METH	=	mesethmoid
MPT	=	metapterygoid
MX	=	maxilla
NA	=	nasal
NEUR	=	neural arch

NEUREP	=	neural spine
N PU1	=	neural arch of preural vertebra 1 (shifted on ural vertebra 1)
NP PU2	=	neural spine of preural vertebra 2 (shifted on preural vertebra 1)
OP	=	opercle
PA	=	parietal
PHY	=	parhypural
PMX	=	premaxilla
POP	=	preopercle
PRO	=	prootic
PS	=	parasphenoid
PT	=	posttemporal
PTE	=	pterotic
PU 1-4	=	preural vertebrae 1 to 4
QU	=	quadratic
RART	=	retroarticular
SCU	=	caudal scute
SMX	=	supramaxilla
SOC	=	supraoccipital
SOP	=	subopercle
SORB	=	supraorbital
ST	=	supratemporal (= extrascapular)
U 1, 2	=	ural vertebrae 1 and 2
UHY	=	urohyal (= parahyoid)
UR 1-3	=	uroneurals 1 to 3
VO	=	vomer
f. VII	=	foramen for the *truncus hyoideomandibularis* of the facial nerve (VII)
iorb. c.	=	infraorbital sensory canal
l.	=	left
m. c.	=	mandibular sensory canal
o. c.	=	otic sensory canal
pop. c.	=	preopercular sensory canal
r.	=	rigth
sorb. c.	=	supraorbital sensory canal

SYSTEMATIC PALEONTOLOGY

Division Teleostei MÜLLER, 1846
Order Crossognathiformes TAVERNE, 1989
Suborder Pachyrhizodontoidei FOREY, 1977
Family Pachyrhizodontidae COPE, 1872
Genus ***Stanhopeichthys*** gen. nov.

Type-species: *Stanhopeichthys libanicus* gen. and sp. nov. (by monotypy)

Diagnosis

As for the species (monospecific genus).

Etymology

The name of the new genus is dedicated to Lady Hester STANHOPE (1776-1839), the niece of William PITT the Younger, a past British prime minister. She lived in Lebanon from 1818 to 1839, the year she died. She was the first to send large collections of Lebanese fossil fishes to different museums and private collectors in Europe and in North America (CAPASSO, 2014: 77-79, figs 17, 18, 2017: 58-59, fig. 6). The Greek word *ichthys*, fish, is added to her surname

Stanhopeichthys libanicus gen. and sp. nov.

Diagnosis

Pachyrhizodontid fish of medium size. Mesethmoid elongated. Lateral ethmoid strongly reduced. Nasal tubular. Vomer toothless. Latero-parietal skull. Parietals small, separated the one from the other by the posterior extension of the frontals and not by the supraoccipital. Pterotic with an acuminate posterior process. Supraoccipital bearing a large median crest. Parasphenoid toothless and devoid of basipterygoid process. Well developed conical teeth on the jaws. Premaxilla elongated, without ascending process. Maxilla long and narrow. One long supramaxilla. Articulation between the lower jaw and the quadrate located far behind the orbital posterior margin. Retroarticular autogenous. No antorbital. Five infraorbitals, the three posterior ones strongly enlarged. Long supraorbital reaching the first infraorbital. Preopercle with a broad dorsal branch and a very short ventral branch. Preopercular sensory canal with numerous secondary tubules. Subopercle large. Pectoral fin with 11 rays. Ventral fin with 8 rays, longer than the pectoral fin. Axial skeleton with 83 (55 + 28) vertebrae and 50 paired ribs. Numerous (probably around 30) supraneurals. Epineurals, epicentrals and epipleurals present. First epineurals fused with the neural arches, the following free. Dorsal fin with 26 rays and 23 pterygiophores. Origin of the dorsal fin located behind the level of the pelvic girdle. Anal fin with 25 rays and 19 pterygiophores. Preural centrum 1 and ural centra 1 and 2 autogenous. Last neural spine strongly reduced. 7 hypurals, all autogenous. 3 epurals. 3 uroneurals. Hypurals 1 and 2 fused by the articular head but separated posteriorly. Hypural 3 enlarged. Caudal fin forked, with 19 principal rays. Very small cycloid scales.

Etymology

The specific name refers to Lebanon.

Holotype and only specimen

Sample CLC S-473a, b. Part and counterpart of a complete specimen (Figs 1, 2). Total length: 22 cm.

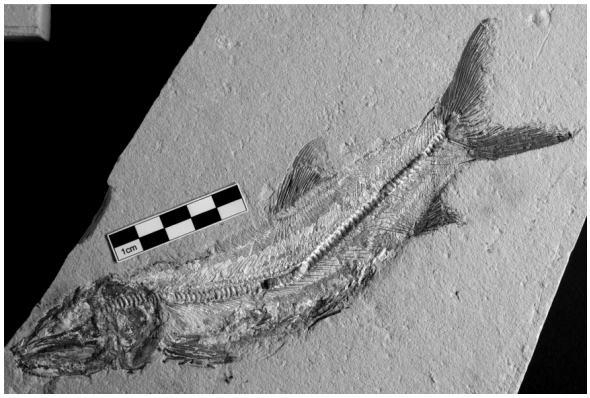

Fig. 1. *Stanhopeichthys libanicus* gen. and sp. nov. Holotype, side CLC S-473a.

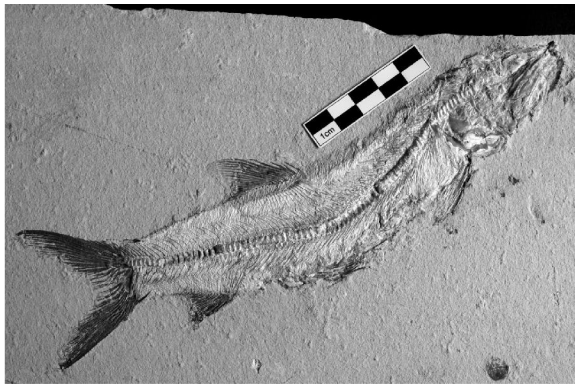

Fig. 2. *Stanhopeichthys libanicus* gen. and sp. nov. Holotype, side CLC S-473b.

Formation and locality

Marine Upper Cenomanian deposits of Hgula, Lebanon.

General morphology and morphometric data (Figs 1, 2)

As most pachyrhizodontid fishes, *Stanhopeichthys libanicus* has a fusiform body, a pointed snout and a large forked tail, the ideal shape for a rapid swimmer fish.

The morphometric data are given in percentage (%) of the standard length (18.3 cm) of the holotype.

Length of the head (opercle included) ..... 28.4 %
Depth of the head (in the occipital region) ..... 18.6 %
Maximum depth of the body (at the dorsal fin level) ..... 21.9 %
Prepelvic length ..... 56.3 %
Predorsal length ..... 60.1 %
Basal length of the dorsal fin ..... 13.7 %
Preanal length ..... 79.2 %
Basal length of the anal fin ..... 11.5 %
Length of the pectoral fin ..... 17.5 %
Length of the ventral fin ..... 27.3 %
Depth of the caudal peduncle ..... 13.1 %
Length of the two lobes of the caudal fin ..... 24.6 %

Osteology

The skull (Figs 3-7)

The mesethmoid is a rather long bone with a broadened anterior region. It represents the dermic part (= dermethmoid, rostral) of the bone. The endochondral part of the mesethmoid is not visible. This region probably was entirely cartilaginous and thus not preserved. The lateral ethmoid is very small. It is appended to the frontal and does not reach ventrally the parasphenoid. Such a reduced lateral ethmoid is unusual in Pachyrhizodontidae. The nasal is well visible on CLC S-473a. It is a long tubular bone located before the frontal, lying along the mesethmoid and bearing the most anterior part of the supraorbital sensory canal. A long, very thin, rod-like and apparently toothless vomer is positioned under the anterior tip of the parasphenoid on CLC S-473a.

Fig. 3. *Stanhopeichthys libanicus* gen. and sp. nov. Head region of holotype (CLC S-473a).

The frontals are large triangular bones forming the greatest part of the skull roof. They almost reach the posterior border of the braincase. There is no narrowing at the orbital level. The skull is latero-parietal. The parietal is a small bone. The two parietals are separated the one from the other by the most posterior parts of the frontals and not by the supraoccipital. That is once again an unusual situation. The supraoccipital bears a long, acuminate median crest. It meets anteriorly the frontals. The autosphenotic is a small bone that bears a short

pointed postorbital process. A part of a severely crushed pterotic is present on CLC S-473a, showing that the bone entirely supports the *dilatator fossa*. The pterotic is better preserved on CLC S-473b, showing a well developed acuminate posterior process. The epiotic is located just behind the parietal. A very wide plate-like supratemporal (= extrascapular, scale bone) is visible on CLC S-473a, just behind the epiotic and below the supraoccipital crest. The supraorbital sensory canal on the frontal and the otic sensory canal on the pterotic are in contact.

The parasphenoid is elongated, rather narrow, devoid of basipterygoid process and toothless. No orbitosphenoid, pleurosphenoid or basisphenoid is preserved.

The prootic, bearing a median foramen for the *truncus hyoideomandibularis* of the facial nerve (VII), a part of the exoccipital and a small portion of the intercalar are visible on CLC S-473a.

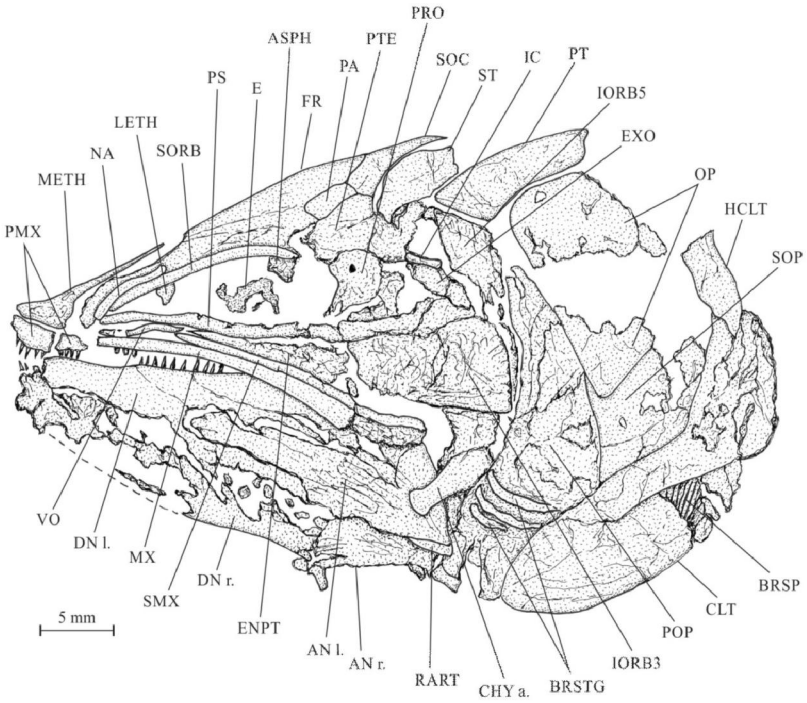

Fig. 4. *Stanhopeichthys libanicus* gen. and sp. nov. Skull and pectoral girdle of holotype (CLC S-473a).

The quadrate is triangle-shaped, with a well developed articular head for the lower jaw. Parts of the entopterygoid and of the metapterygoid are visible on CLC S-473b.

Fig. 5. *Stanhopeichthys libanicus* gen. and sp. nov. Head region of holotype (CLC S-473b).

The premaxilla is complete on CLC S-473a but broken in two pieces. The bone is rather long, devoid of ascending process and it bears nine conical teeth. The maxilla is narrow and very elongated. Three conical teeth are preserved on the anterior part of the oral border of the maxilla on CLC S-473b. There is only one long, thin and anteriorly pointed supramaxilla. The distal extremities of the maxilla and supramaxilla are located behind the level of the posterior border of the orbit. The lower jaw is elongated. The articulation with the quadrate is positioned far behind the level of the orbital posterior margin. A few conical teeth are visible on the oral margin of the dentary on CLC S-473a. The angular and the articular are fused and form together the articular fossa for the quadrate, as seen on CLC S-473a. There is a small autogenous retroarticular. The mandibular sensory canal is visible on the dentary and the angular on CLC S-473b.

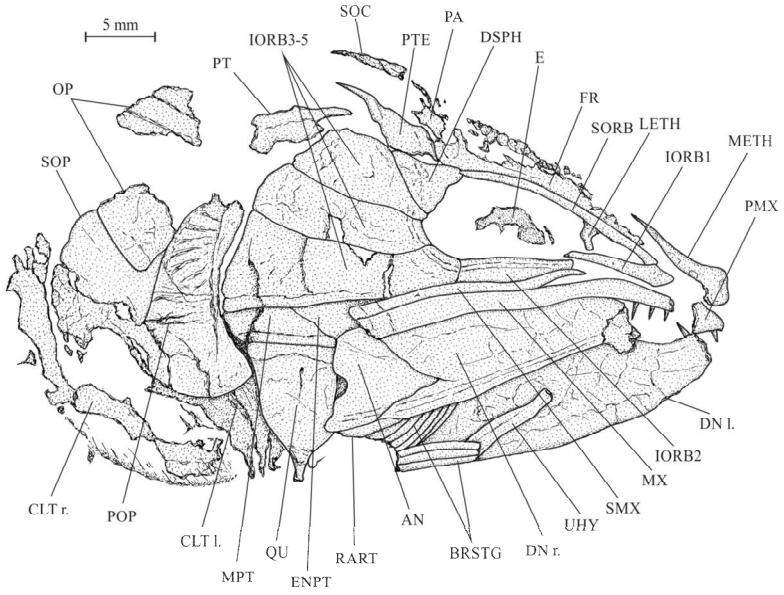

Fig. 6. *Stanhopeichthys libanicus* gen. and sp. nov. Skull and pectoral girdle of holotype (CLC S-473b).

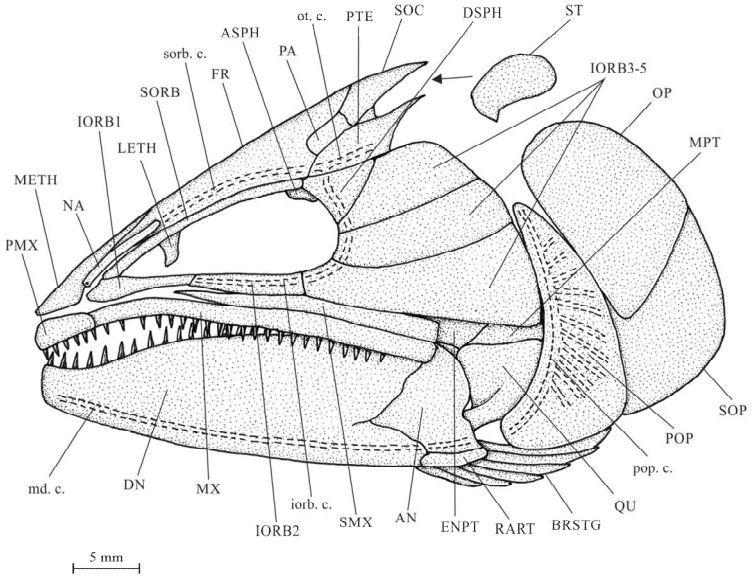

Fig. 7. *Stanhopeichthys libanicus* gen. and sp. nov. Restoration of the skull.

The orbital series is completely preserved on CLC S-473b. There is no antorbital. The first two infraorbital are long and narrow. The three posterior infraorbitals are extremely wide and extend till the anterior margin of the preopercle. The dermosphenotic is large and triangular. The supraorbital is narrow but extremely long. It lies against the lateral margin of the frontal and reaches anteriorly the first infraorbital. No sclerotic bone is

preserved. Traces of the eye are present on both sides of the holotype. The infraorbital sensory canal is preserved on the second, the third and the fourth infraorbitals.

Parts of the preopercle are visible on both sides of the holotype. The bone is very broad but its ventral branch is extremely short. The opercle is deeper than long. It is rather small compared to the size of the entire skull. The subopercle is wide and deep, with a long pointed antero-dorsal process. The interopercle is not visible. Fragments of a few branchiostegal rays are preserved. The preopercular sensory canal bears numerous long secondary tubules.

The hyoid and branchial skeleton (Figs 3-6)

Parts of the hyomandibula are present on CLC S-473a. Small fragments of ceratobranchials, epibranchials and branchiospines are visible under the missing region of the preopercle on CLC S-473b. The urohyal (= parahyoid) is also preserved on this side of the holotype.

The girdles (Figs 3-6, 8-11)

The pectoral girdle is better preserved on CLC S-473a than on S-473b. The postemporal is a long but not very deep bone. The hypercleithrum (= supracleithrum) is long and rather narrow. The ventral branch of the cleithrum is elongated and very broad, while the dorsal branch of the bone is shorter and a little narrower. The pectoral fin contains 11 rays. The first one is segmented and pointed, the others segmented and branched. The first two rays are much broader than the following ones.

The pelvic bones are long and rod-like. The ventral fin is longer than the pectoral and is formed by 8 rays, the first one being the broadest of the series. The origin of the ventral fins is located at the level of the thirty-eighth vertebra.

Fig. 8. *Stanhopeichthys libanicus* gen. and sp. nov. Pectoral fin of holotype (CLC S-473b).

Fig. 9. *Stanhopeichthys libanicus* gen. and sp. nov. Pectoral fin of holotype (CLC S-473a).

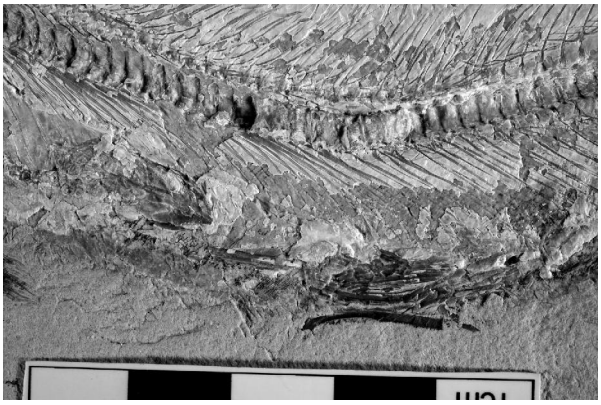

Fig. 10. *Stanhopeichthys libanicus* gen. and sp. nov. Pelvic girdle of holotype (CLC S-473b).

Fig. 11. *Stanhopeichthys libanicus* gen. and sp. nov. Pelvic girdle of holotype (CLC S-473a).

The axial skeleton (Figs 1, 2)

The axial skeleton is composed of 83 vertebrae, 55 in the abdominal region and 28 in the caudal region including the two ural centra. These vertebrae are deeper than long. Their lateral faces are ornamented with numerous thin and horizontally oriented crests. The first nine vertebrae are located under the preopercle, the opercle and the cleithrum but their traces are however well visible on both sides of the holotype. The neural and haemal arches are autogenous and simply articulated on the corresponding centra all along the vertebral axis. The neural and haemal spines are long, thin and obliquely oriented. The haemal arches are represented by paired haemapophyses (= parapophyses) in the abdominal region of the body. There are 50 pairs of ribs, the first one being associated with the sixth vertebra. They are long and narrow, except the last one, short and attached to the fifty-fifth vertebra.

Nineteen supraneurals are visible but the first ones are not preserved. The total number of elements in the supraneural series certainly is exceeding thirty. The last two supraneurals are located between the first pterygiophores of the dorsal fin.

Three strongly branched cephalic ribs are attached to the rear of the braincase. Epineurals are present in the abdominal region and the beginning of the caudal region of the body. They are fused to the neural arches, except the last ones that are free. The first epineurals are simple but they become bifurcated from the level of the twentieth vertebra till the last element of the series. Short epicentrals lie on the upper border of the centra at least at the level of the end of the abdominal and the beginning of the caudal region. There are epipleurals since the level of the twenty-sixth vertebra to the beginning of the caudal region. The first epipleurals are simple. They become bifurcated from the level of the thirty-sixth vertebra to the end of the series.

The dorsal and anal fins (Figs 12-14)

The origin of the dorsal fin is located above the forty-fourth vertebra. The fin contains 26 rays supported by 23 pterygiophores. The first five rays are short spines. The sixth ray is the first long one. It is segmented and pointed. The following rays are segmented and branched.

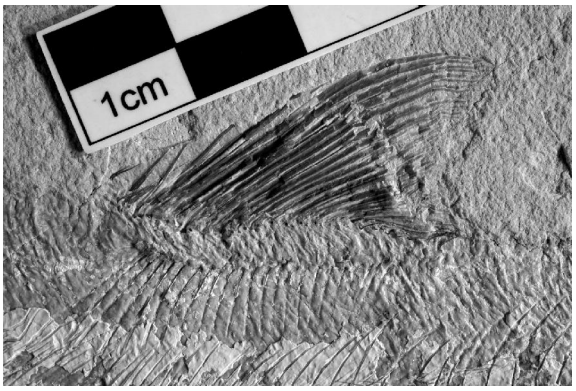

Fig. 12. *Stanhopeichthys libanicus* gen. and sp. nov. Dorsal fin of holotype (CLC S-473b)

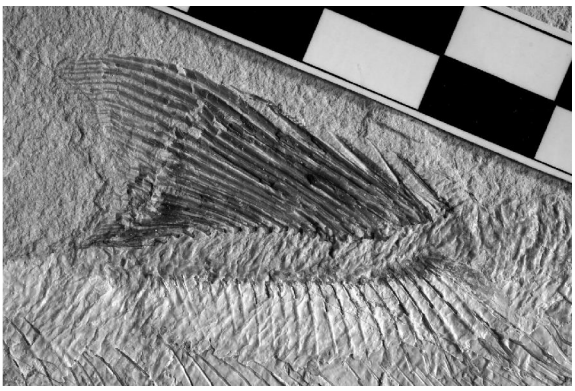

Fig. 13. *Stanhopeichthys libanicus* gen. and sp. nov. Dorsal fin of holotype (CLC S-473a)

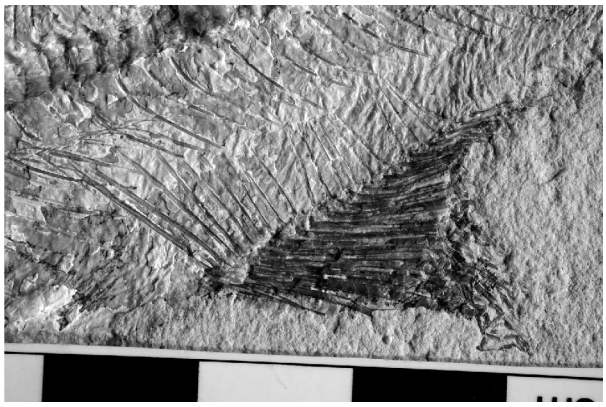

Fig. 14. *Stanhopeichthys libanicus* gen. and sp. nov. Anal fin of holotype (CLC S-473a)

The anal fin is located nearer to the tail than to the pelvic girdle, its origin being positioned at the level of the sixtieth vertebra. There are 19 pterygiophores supporting 25 rays. The first five rays are short spines and the first three are located just before the first pterygiophore. The first long ray is the sixth of the series. It is segmented and pointed, while the others are segmented and branched.

The caudal skeleton (Figs 15-19)

The caudal endoskeleton of holotype is rather peculiar. A double shifting is present. The neural pieces are pulled backwardly from one vertebra, while the haemal elements are pulled forwardly from one vertebra. Such morphology is really strange and is not due to an artefact of fossilisation. It is practically sure that the concerned specimen exhibits an individual abnormal variation not representing the usual caudal morphology of the species.

The last six preural (PU1-6) and the two ural vertebrae (U1, 2) and their associated elements support the caudal fin. PU1, U1 and the small U2 are strongly upturned. All the neural and haemal pieces of the caudal complex are autogenous. PU1 bears the last complete neural spine (normally associated to PU2), while U1 exhibits a strongly reduced neural spine (normally articulated to PU1). The haemal spine of PU6 is the first one connected to the ventral procurrent rays of the caudal fin. A supplementary haemal spine is intercalated between the normal haemal spines of PU3 and PU4. That is probably also an individual variation and not a specific character. The long and narrow parhypural is connected to PU2 (normally attached to PU1). There are seven hypurals (HY1-7). HY1 and HY2 are articulated on PU1 (normally connected to U1) and not fused with this vertebra. They are fused by their proximal heads but separated in their distal regions. A small hypural foramen is present in the most proximal region of this ventral hypural plate. The large HY3 is connected to U1 (normally linked to U2). The anterior heads of HY4 and HY5 are located just behind the small U2. HY6 and HY7 are more dorsally positioned. There are three uroneurals (UR1-3). UR1 has an enlarged but not forked anterior extremity and extends till the limit between PU1 and PU2. UR2 is preserved only on CLC S-473b. It extends till the lateral face of U1. A small UR3 is present behind U2. Three rod-like epurals (EP1-3) lie on the upper margin of UR1, just behind the reduced neural spine of U1. EP1 and EP 2 are long while EP3 is short.

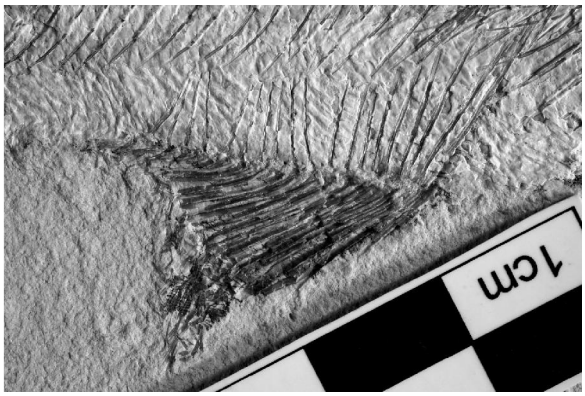

Fig. 15. *Stanhopeichthys libanicus* gen. and sp. nov. Anal fin of holotype (CLC S-473b)

Fig. 16. *Stanhopeichthys libanicus* gen. and sp. nov. Tail region of holotype (CLC S-473b)

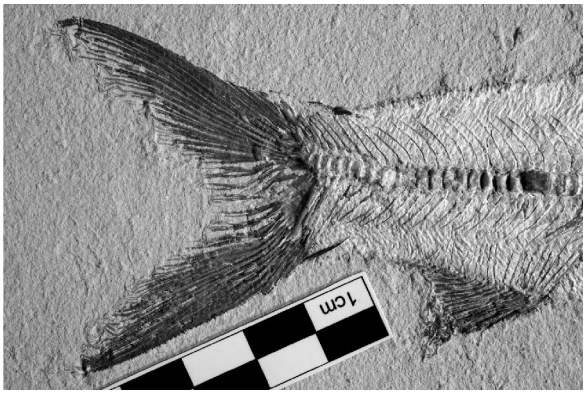

Fig. 17. *Stanhopeichthys libanicus* gen. and sp. nov. Tail region of holotype (CLC S-473a)

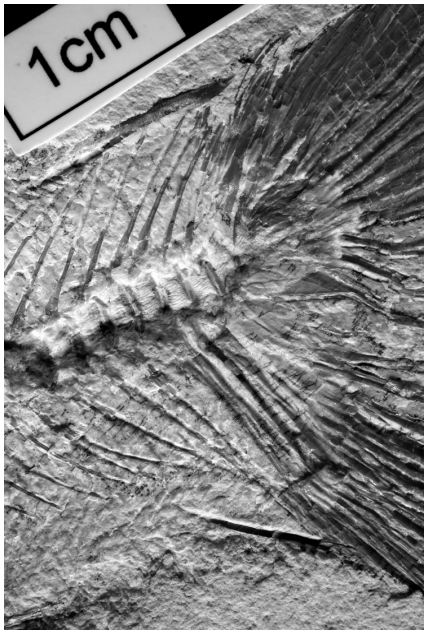

Fig. 18.
Caudal skeleton of holotype (CLC S-473a)

Fig. 19
Stanhopeichthys libanicus gen. and sp. nov.
Caudal skeleton of holotype (CLC S-473b)

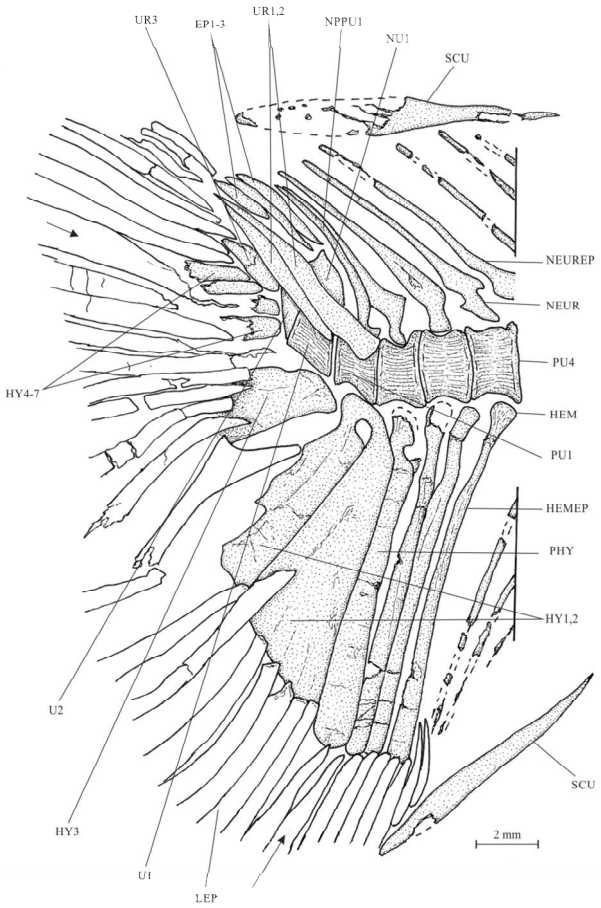

Fig. 20. *Stanhopeichthys libanicus* gen. and sp. nov. Caudal skeleton of holotype (principally based on CLC S-473b, completed with CLC S-473a)

The caudal fin is forked. The two lobes have the same length. A long, narrow and anteriorly pointed caudal scute precedes the first dorsal and the first ventral procurrent rays. There are 19 principal caudal rays, 8 dorsal and 7 ventral procurrent rays (= basal fulcra). The longest procurrent ray of each lobe is already segmented. The most external dorsal and ventral principal rays are segmented and pointed. The seventeen other principal rays are segmented and branched. The proximal head of the tenth principal ray, associated to HY3, is enlarged and triangular in shape.

The squamation

The scales are badly preserved on both sides of the specimen. They are cycloid and very small. Some of them exhibit very thin rectilinear *circuli* that are horizontally oriented.

The feeding (Figs 1, 2)

Stanhopeichthys libanicus was a predator of small fishes, as generally in Pachyrhizodontoidei (TAVERNE, 1989: 103). Indeed, the complete sketeton of a small teleost (total length: 34 mm) is preserved in the alimentary canal of the holotype from above the pectoral fin to the pelvic bones. This small fish was gulped in one piece, without any division in smaller elements.

DISCUSSION

The relationships of *Stanhopeichthys* within Teleostei

In *Stanhopeichthys*, the maxilla is the main bone of the upper jaw and it forms the greatest part of its oral margin. The posterior infraorbitals are large bones with well developed membranous components. There is a large scale-like supratempral. The retroarticular is autogenous. The pelvic girdle is abdominal. The dorsal and anal fins are devoid of strong spines. The supraneurals are numerous. The first epineurals are fused to the neural arches. PU1, U1 and U2 are autogenous. There are three epurals, three uroneurals and seven hypurals. The caudal fin contains 19 principal rays. The scales are cycloid. All these characters indicate that the new Lebanese genus belongs to the primitive Teleostei.

Stanhopeichthys also exhibits some specialized characters. The parietal is a small bone and the skull is latero-parietal. There is only one elongated and anteriorly acuminate supramaxilla. The antorbital is missing and the very long supraorbital reaches the first infraorbital. The parasphenoid is toothless and devoid of basipterygoid process. The articular fossa of the lower jaw for the quadrate is formed by the fused angular and articular. The two ventral hypurals are fused by their articular heads. The anterior extremity of the first uroneural is broadened and partly covers the lateral face of the vertebrae. Within primitive teleosts, only Pachyrhizodontidae share these evolved osteological features. *Stanhopeichthys* obviously belongs to that family.

The relationships of *Stanhopeichthys* within Pachyrhizodontidae

A few pachyrizodontid fishes have a peculiar apomorphy, the development of a posterior acuminate process on the pterotic (CAVIN, 2001, character 3[1]). *Stanhopeichthys* pertains to this group that also includes the genera *Platinx* AGASSIZ, 1835, *Rhacolepis* AGASSIZ, 1841, *Elopopsis* HECKEL, 1856, *Goulmimichtys* CAVIN, 1995, *Nardopiscis* TAVERNE, 2008, *Apricenapiscis* TAVERNE, 2013 and *Motlayoichthys* ARRATIA *et al.*, 2018 (FOREY, 1977: figs 12-14, 34; TAVERNE, 1980: fig. 1, 1994: fig. 3, 2008: figs 4, 5, 2013: figs 3, 5; CAVIN, 2001: fig. 2; ARRATIA *et al.*, 2018: fig. 4a, b). The situation is uncertain in *Tingitanichtys* TAVERNE, 1996, the most posterior part of the pterotic being unknown in this fish (TAVERNE, 1996: fig. 3). The other Pachyrhizodontidae are devoid of such a process.

Within the subgroup with a posterior process on the pterotic, *Stanhopeichthys* has the most primitive caudal pattern, with PU1, U1 and U2 separated, a complete neural spine on PU2 (on PU1 in the holotype because of the shifting), HY1 and HY2 not fused to the corresponding centrum, five autogenous dorsal hypurals, three epurals, three uroneurals and well developed caudal scutes (Fig. 13). *Rhacolepis* has a more advanced caudal morphology, with a shortened neural spine on PU2, two or three epurals, a forked UR1, only three autogenous dorsal hypurals, HY1 and HY2 fused to U1 and more completely fused together (FOREY, 1977: fig. 24A, B; MAISEY, 1991: fig. p. 255). *Tingitanichthys* also has a more evolved caudal pattern, with a short neural spine on PU2, HY1 and HY2 fused to U1, less dorsal hypurals and no epurals (TAVERNE, 1996: fig. 5). *Platinx*, *Elopopsis* and *Goulmimichthys* exhibit a still more specialized caudal endoskeleton with less elements and a high degree of fusion between the concerned pieces (TAVERNE, 1976: figs 1-3; 1980: figs 5, 6; CAVIN, 2001: fig. 11B). So, on the basis of the caudal data only, *Stanhopeichthys* seems the most primitive genus of the subgroup.

The caudal skeleton of *Motlayoichthys* is unknown. This Mexican pachyrhizodontid fish differs from *Stanhopeichthys* by its strong teeth on the jaws, its orbitosphenoid forming a bony interocular septum, its preopercle with a process at the posterior ventral corner and by its more specialized orbital series, with a short supraorbital and the infraorbitals fused in two elements (ARRATIA *et al.,* 2018: figs 4a, b, 5).

Stanhopeichthys and *Rhacolepis* exhibit another unusual character that is also present in *Nardopiscis* and *Apricenapiscis*. The mesethmoid is posteriorly elongated in a long process articulated with the frontals (FOREY, 1977: fig. 11A, B; TAVERNE, 2008: fig. 5, 2013: figs 3, 5). In other Pachyrhizodontidae, the mesethmoid is much shorter.

A last osteological feature is also useful to precise the relationships of the new Lebanese genus. Pachyrhizodontidae have a latero-parietal skull and the two parietals are disjoined by the supraoccipital, except in *Stanhopeichthys* and *Nardopiscis*. These two fishes share another exceptional character. Their skull also is latero-parietal but the two parietals are separated by the expanded posterior region of the frontals and not by the supraoccipital as in other pachyrhizodontid fishes (TAVERNE, 2008: fig. 5).

Thus, the cranial and caudal characters just discussed lead to the conclusion that *Stanhopeichthys* is the most primitive member of the pachyrhizodontid subgroup that has a pointed posterior process on the pterotic and also that *Stanhopeichthys* is closely related to *Nardopiscis*.

However, it is easy to distinguish the pachyrhizodontid of Nardò from *Stanhopeichthys*. Indeed, *Nardopiscis* exhibits a short upper jaw, a large lateral ethmoid, a broad supraorbital and a small preopercle with a well developed ventral limb (TAVERNE, 2008: figs 3, 4).

REFERENCES

ARRATIA, G., 2008. The varasichthyid and other crossognathiform fishes, and the break-up of Pangaea. *In*: CAVIN, L., LONGBOTTOM, A. & RICHTER, M. (eds). Fishes and the Break-up of Pangaea, *Geological Society, London, Special Publications*, 295: 71-92.

ARRATIA, G., GONZALEZ-RODRIGUEZ, K. A. & HERNANDEZ-GUERRERO, C., 2018. A new pachyrhizodontid fish (Actinopterygii, Teleostei) from the Muhi Quarry (Albian-Cenomanian), Hidalgo, Mexico. *Fossil Record*, 21: 93-107.

ARRATIA, G. & SCHULTZE, H.-P., 1999. Mesozoic fishes from Chile. *In*: ARRATIA, G. & SCHULTZE, H.-P. (eds). Mesozoic Fishes 2 – Systematics and Fossil Record, Verlag Dr. F. PFEIL, München: 565-593.

CAPASSO, L., 2014. The history of the fossil fish private collecting. *Bollettino del Museo Civico di Storia Naturale*, *Geologia Paleontologia Preistoria*, 38: 51-89.

CAPASSO, L., 2017. The history and situation of the world famous fossil fish quarries in Lebanon. *Bollettino del Museo Civico di Storia Naturale*, *Geologia Paleontologia Preistoria*, 41: 53-76.

CAVIN, L., 2001. Osteology and phylogenetic relationships of the teleost *Goulmimichthys arambourgi* Cavin, 1995, from the Upper Cretaceous of Goulmima, Morocco. *Eclogae geologicae Helvetiae*, 94: 509-535.

DANILCHENKO, P. G., 1968. Ryby verkhnego paleotsena Turkmenii. *In*: OBRUCHEV, D. V. (ed.), Ocherki po filogenii I sistematike iskapaemykh ryb I bezscheliustnykh. Nauka Press, Moscou: 113-156 (en russe).

DAVIS, J. W., 1887. The fossil fishes of the Chalk of Mount Lebanon, in Syria. *The Scientific Transactions of the Royal Dublin Society*, series 2, 3: 457-636.

FOREY, P. L., 1977. The osteology of *Notelops* WOODWARD, *Rhacolepis* AGASSIZ and *Pachyrhizodus* DIXON (Pisces: Teleostei). *Bulletin of the British Museum (Natural History)*, *Geology*, 28 (2): 123-204.

FOREY, P. L., YI, L., PATTERSON, C., DAVIES, C. E., 2003. Fossil fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon. *Journal of Systematic Palaeontology*, 1 (4): 227-330.

GAUDANT, M., 1969. Sur quelques nouveaux poissons bérycoïdes crétacés du Mont Liban. *Notes et Mémoires sur le Moyen-Orient*, 10: 273-283.

GAUDANT, M., 1978. Recherches sur l'anatomie et la systématique des Ctenothrissiformes et des Pattersonicnthyiformes (poissons téléostéens) du Cénomanien du Liban. *Mémoires du Muséum National d'Histoire Naturelle*, Paris, nouvelle série, Série C, *Sciences de la Terre*, 41: 1-124.

GAYET, M., 1993. Gonorhynchoidei du Crétacé supérieur marin du Liban et relations phylogénétiques des Charitosomidae nov. fam. *Documents du Laboratoire de Géologie de l'Université de Lyon*, 126: 1-131.

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.

MAISEY, J. G., 1991. *Rhacolepis* Agassiz, 1841. Santana Fossils. An Illustrated Atlas, T. H. F. (ed.), Neptune City, U.S.A.: 248-257.
PATTERSON, C., 1967. New Cretaceous berycoid fishes from the Lebanon. *Bulletin of the British Museum (Natural History)*, *Geology*, 14 (3): 69-109.
PATTERSON, C., 1970. Two Upper Cretaceous salmoniform fishes from the Lebanon. *Bulletin of the British Museum (Natural History)*, *Geology*, 19(5): 205-296.
PATTERSON, C., 1993. Osteichthyes: Teleostei. *In*: BENTON, M. J. (ed.). The Fossil Record 2, Chapman & Hall, London: 621-656.
PICTET, F. J., 1850. Description de quelques poissons fossiles du Mont Liban. Imprimerie J. G. Fick, Genève: 1-59.
PICTET, F. J. & HUMBERT, A., 1866. Nouvelles recherches sur les poissons fossiles du Mont Liban. Georg (editor), Genève, Imprimerie J.-B. Baillière et fils – F. Savy, Paris: 1-115.
TAVERNE, L., 1976. A propos *d'Elopopsis microdon* Heckel, J. J., 1856, du Crétacé moyen d'Afrique et d'Europe et des affinités systématiques de la famille fossile des Pachyrhizodontidae au sein des Téléostéens primitifs. *Revue de Zoologie Africaine*, 90 (2): 487-496.
TAVERNE, L., 1980. Ostéologie et position systématique du genre *Platinx* (Pisces, Teleostei) de l'Eocène du Monte Bolca (Italie). *Académie Royale de Belgique*, *Bulletin de la Classe des Sciences*, 5e série, 66 (11): 873-889.
TAVERNE, L., 1989. *Crossognathus* Pictet, 1858 du Crétacé inférieur de l'Europe et systématique, paléozoogéographie et biologie des Crossognathiformes nov. ord. (Téléostéens) du Crétacé et du Tertiaire. *Palaeontographica*, Stuttgart, A, 207 (1-3): 79-105.
TAVERNE, L., 1994. Ostéologie et affinités du Téléostéen crétacique *Elopopsis microdon* (Pisces, Crossognathiformes, Pachyrhizodontidae). *Biologish Jaarboek Dodonaea*, 61 (1993): 172-192.
TAVERNE, L., 1996. Révision de *Tingitanichthys heterodon* (ARAMBOURG, 1954) nov. gen. (Teleostei, Pachyrhizodontoidei) du Crétacé supérieur marin du Maroc. *Biologisch Jaarboek Dodonaea*, 63 (1995): 133-151.
TAVERNE, L., 2004. *Libanechelys bultyncki* gen. et sp. nov., une nouvelle anguille primitive (Teleostei, Anguilliformes) du Cénomanien marin du Liban. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 74, 2004: 73-87.
TAVERNE, L., 2008. Les poissons crétacés de Nardò. 29°. *Nardopiscis cavini* gen. et sp. nov. (Teleostei, Crossognathiformes, Pachyrhizodontidae). *Bollettino del Museo Civico di Storia Naturale di Verona*, *Geologia Paleontologia Preistoria*, 32: 19-28.
TAVERNE, L., 2013. Les poissons du Santonien (Crétacé supérieur) d'Apricena (Italie du Sud). 4°. *Apricenapiscis depotteri* gen. et sp. nov. (Teleostei, Crossognathiformes, Pachyrhizodontidae). *Bollettino del Museo Civico di Storia Naturale di Verona*, *Geologia Paleontologia Preistoria*, 37: 57-66.
TAVERNE, L. & CAPASSO, L., 2012. Osteology and relationships of *Prognathoglossum kalassyi* gen. and sp. nov. (Teleostei, Osteoglossiformes, Pantodontidae) from the marine Cenomanian (Upper Cretaceous) of En Nammoura (Lebanon). *Cybium*, 36 (4): 563-574.
TAVERNE, L. & GAYET, M., 2004. Ostéologie et relations phylogénétiques des Protobramidae (Teleostei, Tselfatiiformes) du Cénomanien (Crétacé supérieur) du Liban. *Cybium*, 28 (4): 285-314.
WOODWARD, A. S., 1942. Some new and little known Upper Cretaceous fishes from Mount Lebanon. *Annals and Magazine of Natural History*, series 11, 9: 537-568.