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Osteology and relationships of *Lebrunichthys nammourensis* gen. and sp. nov. (Teleostei, Crossognathiformes, Pachyrhizodontidae), a fossil fish from the marine Upper Cretaceous of Lebanon

Ostéologie et relations de *Lebrunichthys nammourensis* gen. and sp. nov. (Teleostei, Crossognathiformes, Pachyrhizodontidae), un poisson fossile du Crétacé supérieur marin du Liban

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Résumé: L'ostéologie et les relations de *Lebrunichthys nammourensis* gen. and sp. nov., un nouveau poisson pachyrhizodonte du Cénomanien supérieur marin du Liban, sont étudiées en détails. Le nouveau genre appartient au sous-groupe des Pachyrhizodontidae ayant un processus postérieur pointu sur le ptérotique. Les caractères du squelette caudal indiquent que *Lebrunichthys* occupe une position systématique intermédiaire entre *Stanhopeichthys*, d'un côté, et de tous les autres genres du sous-groupe, de l'autre côté.

Mots-clés: Teleostei, Crossognathiformes, Pachyrhizodontidae, *Lebrunichthys nammourensis* gen. et sp. nov., ostéologie, relations, Cénomanien marin, Liban.

Abstract: The osteology and the relationships of *Lebrunichthys nammourensis* gen. and sp. nov., a new pachyrhizodontid fish from the marine Upper Cenomanian of Lebanon, are studied in details. The new genus belongs to the subgroup of Pachyrhizodontidae having a posterior pointed process on the pterotic. The characters of the caudal skeleton indicate that *Lebrunichthys* occupies an intermediate systematic position between *Stanhopeichthys*, one the one hand, and all the other genera of the subgroup, on the other hand.

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

INTRODUCTION

Pachyrhizodontidae is a family of primitive fossil teleosts that is generally ranged in the order Crossognathiformes. They had a fusiform body, a terminal mouth, long toothed jaws and a lateroparietal skull. The members of this lineage were fast-swimming predators that ate smaller fishes (TAVERNE, 1989: 103; TAVERNE & CAPASSO, 2020: 12; among others). Some large specimens can reach almost one meter in length. Their first occurrence dates back to the Upper Jurassic (ARRATIA & SCHULTZE, 1999). They had an almost worldwide distribution during the Cretaceous (TAVERNE, 1989: figs 11-13), with a dozen of genera. Only one genus, *Platinx* AGASSIZ, 1835, survived after the Cretaceous-Paleocene boundary (DANILCHENKO, 1968; TAVERNE, 1980).

During a long time, the presence of Pachyrhizodontidae was not mentioned in the abundant marine Upper Cretaceous fish fauna of Lebanon. GAYET *et al.* (2012: 114-115) were the firsts to figure two different pachyrhizodontid species from that Lebanese ichthyofauna. Unfortunately, the concerned samples belong to a private collection and are not available for a scientific study. Very recently and for the first time, an Upper Cretaceous Lebanese pachyrhizodontid new genus was finally studied and described (TAVERNE & CAPASSO, 2020).

The aim of the present paper is to study the skeleton and discuss the relationships of a second Upper Cretaceous Lebanese new pachyrhizodontid genus.

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MATERIAL AND METHODS

The material hereafter studied belongs to the CAPASSO collection (CLC) in Chieti (Italy). The concerned specimen was observed 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 and razing light were used to improve the 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

ASPH	=	autosphenotic
BRSTG	=	branchiostegal ray
CLT	=	cleithrum
DSPH	=	dermosphenotic
ENPT	=	entopterygoid
EP1-3	=	epurals 1 to 3
EPI	=	epiotic (= epioccipital)
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
HEM	=	haemal arch
HEMEP	=	haemal spine
HY 1-6	=	hypurals 1 to 6
HYOM	=	hyomandibula
IORB 1-5	=	infraorbitals 1 to 5
LEP	=	lepidotrich (= fin ray)
LETH	=	lateral ethmoid
METH	=	mesethmoid
MX	=	maxilla
NEUR	=	neural arch
NEUREP	=	neural spine
N PU1	=	neural arch of preural vertebra 1
NP PU2	=	neural spine of preural vertebra 2
OP	=	opercle
PA	=	parietal
PHY	=	parhypural
POP	=	preopercle
PS	=	parasphenoid
PT	=	posttemporal
PTE	=	pterotic
PU 1-4	=	preural vertebrae 1 to 4
QU	=	quadratic
SCU	=	caudal scute
SMX	=	supramaxilla
SOC	=	supraoccipital
SORB	=	supraorbital
ST	=	supratemporal (= extrascapular)
U 1, 2	=	ural vertebrae 1 and 2
UR 1-3	=	uroneurals 1 to 3
fr.	=	fragment
iorb. c.	=	infraorbital sensory canal
l.	=	left
ot. c.	=	otic 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 ***Lebrunichthys*** gen. nov.

Type-species: *Lebrunichthys nammourensis* gen. and sp. nov. (by monotypy)

Etymology

The generic name is chosen to honour Corneille LEBRUN (1652-1726) who was the first in 1698 to publish a figure of a Lebanese fossil fish, probably a specimen of *Prionolepis cataphractus* (PICTET & HUMBERT, 1866) from Haqel (CAPASSO, 2017: 56-57, fig. 4). The Greek word *ichthys*, fish, is added to his surname.

Lebrunichthys nammourensis gen. and sp. nov.

Diagnosis

Pachyrhizodontid fish of small size. Mesethmoid hypertrophied, with a pair of short lateral processes and a pair of short posterior processes. Frontal with a small crest in the posterior region. Lateroparietal skull. Parietals small, separated the one from the other by the supraoccipital. Pterotic with an enlarged acuminate posterior process. Supraoccipital bearing a long median crest. Well developed conical teeth on the jaws. Maxilla elongate, with a broadened posterior extremity, and reaching the preopercle. One long supramaxilla. No antorbital. Four infraorbitals, the third and the fourth ones being fused together. The posterior infraorbitals slightly enlarged. First infraorbital long and narrow. Supraorbital elongate. Preopercle with a well developed dorsal branch and no ventral branch. Opercle and subopercle large. Axial skeleton with 49 (26 + 23) vertebrae. Epineurals and epipleurals present. Dorsal fin with 23 rays. Origin of the dorsal fin located above the twenty-first vertebra. Preural centrum 1 and ural centra 1 and 2 autogenous. Complete neural spine on preural vertebra 3. Neural spine of preural vertebra 2 slightly reduced. 6 hypurals, all autogenous. Hypurals 1 and 2 fused by their articular heads but separated posteriorly. Hypural 1 and 3 enlarged. 3 epurals. 3 uroneurals. First uroneural anteriorly enlarged but not forked. Caudal fin forked, with 19 principal rays. Large cycloid scales, with a few short *radii* in the posterior field and a festooned anterior margin.

Etymology

The specific name refers to the locality of Ein Nammoura, Lebanon.

Holotype and only specimen

Sample CLC S-402. A complete specimen (Fig. 1). Total length: 11 cm.

Formation and locality

Marine Upper Cenomanian deposits of Ein Nammoura, Lebanon.

General morphology and morphometric data (Fig. 1)

The morphometric data are given in percentage (%) of the standard length (8.5 cm) of the holotype.
Length of the head (supraoccipital crest included) ..…….. 30.9 %
Maximum depth of the body ...…….. 21.8 %
Predorsal length ……. 59.1 %
Basal length of the dorsal fin ……. 19.1 %
Depth of the caudal peduncle …… 10.5 %
Length of the dorsal lobe of the caudal fin …… 27.3 %

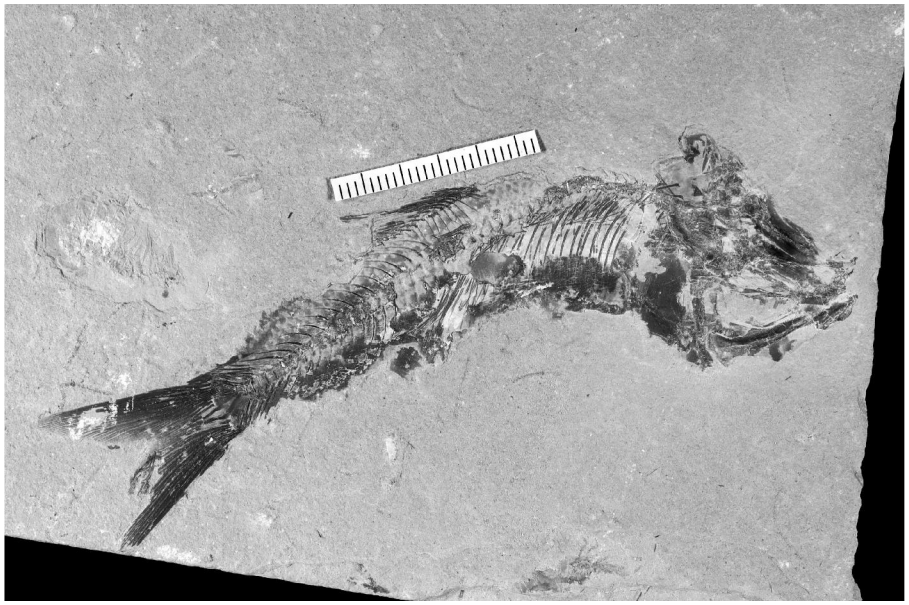

Fig. 1. *Lebrunichthys nammourensis* gen. and sp. nov. Holotype CLC S-402.

Osteology

The skull (Figs 2, 3)

The mesethmoid is a large and broad dermal bone (= rostral), with a short lateral process on each side and a pair of well marked posterior processes that reach the two frontals. There is a wide gap between these two processes and the two frontals, a gap probably occupied by an underlying cartilaginous component of the mesethmoid. Such a gap exists in other pachyrhizodontoid fishes (FOREY, 1977: figs 1, 12). The upper part of the right lateral ethmoid is visible just below the anterior extremity of the right frontal. Neither the nasals nor the vomer are preserved.

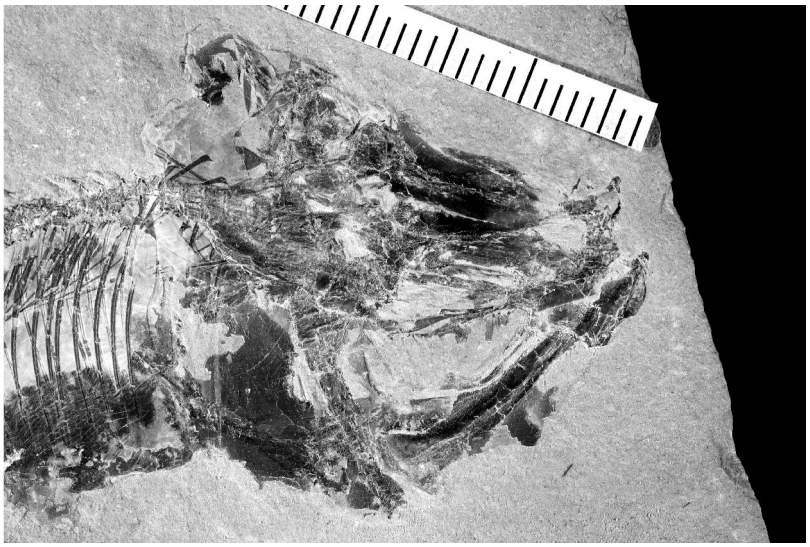

Fig. 2. *Lebrunichthys nammourensis* gen. and sp. nov. Head region of holotype CLC S-402.

The frontals form the major part of the skull roof. They have a more or less rounded anterior extremity. They are rather broad at the orbital level but still considerably broaden in the postorbital area. The most posterior part of each frontal bears a short but well marked crest and surrounds the anterior region of the supraoccipital. The parietals are small bones. The skull is lateroparietal, the two parietals being separated by the supraoccipital. A small epiotic (= epioccipital) is visible behind each parietal. The supraoccipital is rather small but it bears an elongate median crest. A wide autosphenotic is located at the anterior corner of the enlarged postorbital region of

the skull roof. The pterotics are very large bones. They exhibit a long, very broad and pointed posterior process, like the one present in *Nardopiscis cavini* TAVERNE, 2008, a pachyrhizodontid fish from the Upper Cretaceous of Nardò (TAVERNE, 2008: figs 4, 5). Fragments of a large supratemporal (= extrascapular, scale bone) are visible on the left side of the braincase. It reaches the mid-line of the skull and covers a part of the pterotic.

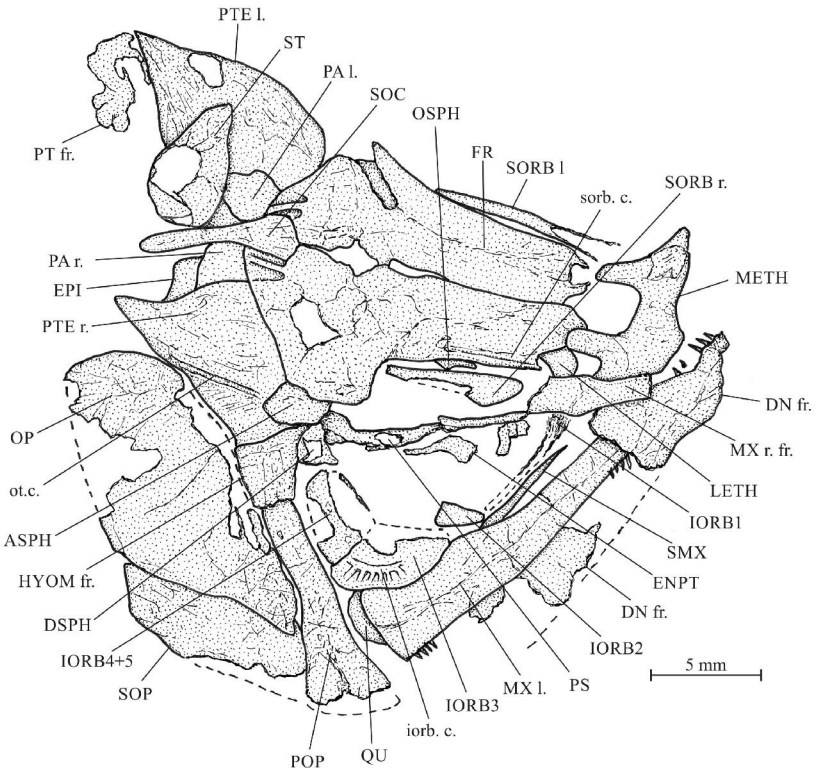

Fig. 3. *Lebrunichthys nammourensis* gen. and sp. nov. Skull of holotype CLC S-402.

A small orbitosphenoid, displaced by the fossilization, is visible between the margin of the right frontal and the right supraorbital. The toothless trabecular region of the parasphenoid is also preserved but broken. No basipterygoid process is present. The pleurosphenoid, the basisphenoid, the prootic, the exoccipital, the basioccipital are hidden by the skull roof.

A few fragments of the entopterygoid are preserved. A small part of the posterior region of the quadrate is visible just behind the left maxilla. Such a localization probably is due to a taphonomic displacement from the initial position.

The upper part of the hyomandibula is articulated with the pterotic and the autosphenotic. The ventral part of the bone is lost. The articular head is rectilinear.

The premaxilla is lost. The maxilla is a long, rectilinear bone that extends from the symphyseal region to the anterior margin of the preopercle. Its posterior region is broadened. A few small conical teeth are visible on the oral margin, at the beginning of the bone and at its posterior part, but not between these two regions. A fragment of a long and narrow supramaxilla is preserved above the maxilla. Only the anterior area and some other fragments of the dentary are present. The other bones of the lower jaw are missing. Some conical teeth occupy the most anterior part of the oral margin of the dentary. The length of the maxilla indicates that the articulation between the lower jaw and the quadrate is located behind the orbital level.

The orbital series is poorly preserved and the corresponding bones seem very thin. No antorbital is visible. The first infraorbital is long and very narrow. The second one is much shorter. The third one is the largest. The fourth and the fifth ones are fused. A small triangular dermosphenotic is also visible. The third and the fused fourth and fifth infraorbitals are less broad than usually in pachyrhizodontid fishes. The supraorbital is an extremely elongated and narrow bone but with an enlarged anterior region. The infraorbital sensory canal is visible on the third infraorbital. The canal bears a few short secondary tubules.

The preopercle has a deep dorsal branch but is devoid of ventral branch. The opercle is very large. The subopercle is smaller. The interopercle and the branchiostegal rays are not visible.

There is a pair of cephalic ribs articulated to the rear of the braincase.

The girdles

A small part of the right cleithrum is preserved but covered by the opercle. Fragments of the left posttemporal are also visible. The other elements of the pectoral girdle are lost. The right pectoral fin is partly visible but is backwardly displaced due to the fossilisation. Five rays are visible but the fin probably is incomplete.

The pelvic girdle is also missing. Fragments of six rays are located just over the vertebral axis, at the level of the dorsal fin. They seem to belong to a displaced ventral fin.

The axial skeleton (Fig. 1)

The axial skeleton contains 49 vertebrae, of which 26 are abdominal and 23 caudal, the two ural centra included. A strong median horizontally oriented crest is visible on the lateral face of the best preserved vertebrae. The crest separates two cavities. The neural and haemal arches are fused to the corresponding centra, except those of the posterior part of the caudal region that are articulated on the last vertebrae. The neural and haemal spines are long, thin and curved. The haemapophyses (= parapophyses) of the abdominal region are short. A few epineurals are visible at the level of the first vertebrae. However, the dorsal region is badly preserved between the head and the dorsal fin and it is probable that more epineurals were present in the living fish. No epicentral is visible. There are elongate epipleurals in the abdominal region. No supraneural is preserved. The ribs are long and thin.

The dorsal and anal fins (Fig. 4)

There are 23 rays in the dorsal fin. The best preserved of them are segmented but apparently not branched. Only 16 pterygiophores (= axonosts) are visible but the last ones are missing. The first pterygiophore is broadened and the following ones rod-like. The origin of the dorsal fin is located above the twenty-first vertebra.

The anal fin is not preserved.

Fig. 4. *Lebrunichthys nammourensis* gen. and sp. nov. Dorsal fin of holotype CLC S-402.

The caudal skeleton and fin (Figs 5, 6)

The four last preural vertebrae (PU1-4) and the two ural vertebrae (U1, 2) are progressively upturned and reduced in size. PU1, U1 and U2 are autogenous. U2 is small and triangle-shaped in lateral view. The last neural and haemal elements are articulated on the corresponding centra and not fused with them. The neural spines (NP) of PU3, 4 and 5 bear a small anterior wing-like component. NP PU3 is the last complete neural spine. NP PU2 is slightly shortened. PU1 only bears a neural arch but no neural spine. The haemal spines (HP) of PU2 and PU3 and the parhypural (PHY) of PU1 are a little broader than the preceding haemal spines. There are 6 autogenous hypurals (HY1-6). The two ventral hypurals (HY1, 2) are fused together at the level of their articular heads but separated the one from the other all along their length. HY1 and HY3 are broadened, while HY2, 4, 5 and 6 are rather narrow. HY1 and HY 2 are articulated on U1 and HY3 and HY4 on U2. There is a wide diastema between HY2 and HY3. There are 3 epurals (EP1-3). EP1 is longer than EP2 and EP3 and its anterior

extremity rests on the upper face of U1. Three uroneurals (UR1-3) are present. UR1 is the longer. Its anterior region is expanded but not forked and partly covers PU1. The anterior acuminate extremity of UR2 reaches the limit between U1 and PU1. UR3 is much shorter and more posteriorly positioned.

The caudal fin is forked, with the two lobes of the same length. There are 19 principal rays, 11 dorsal and at least 2 ventral procurrent rays (= basal fulcra). The most external dorsal and ventral principal rays are segmented and pointed. The seventeen other principal rays are segmented and branched. The segmentation of the rays is slightly sigmoid.

There are a dorsal and a ventral scute that precede the procurrent rays.

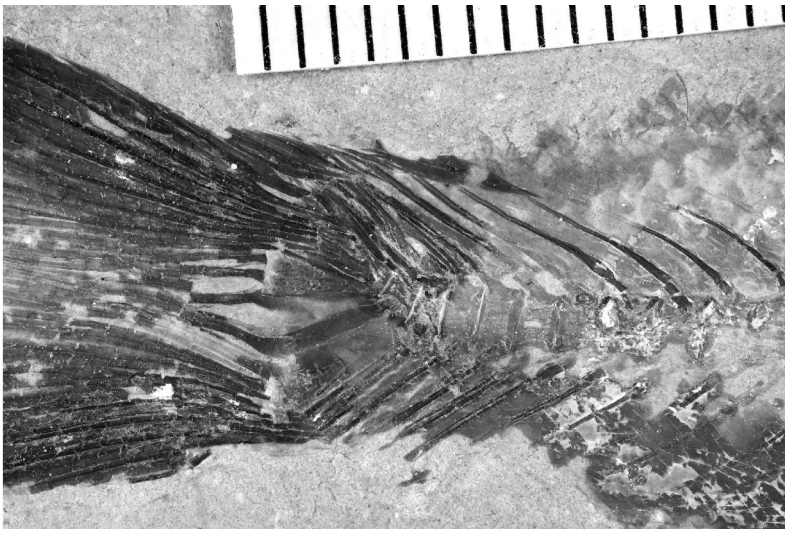

Fig. 5. *Lebrunichthys nammourensis* gen. and sp. nov. Tail region of holotype CLC S-402.

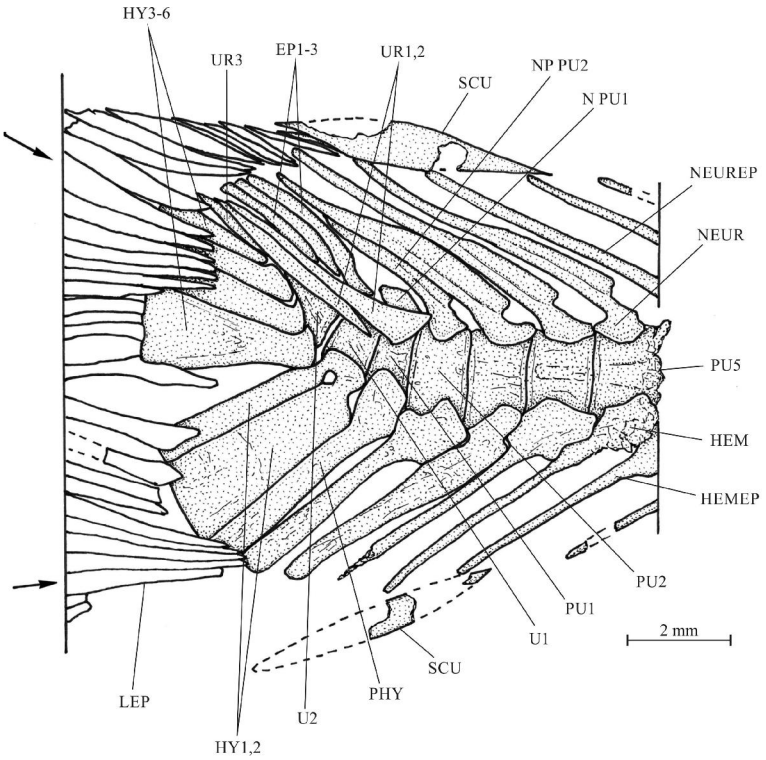

Fig. 6. *Lebrunichthys nammourensis* gen. and sp. nov. Caudal skeleton of holotype CLC S-402. The arrows point on the more external principal caudal rays.

The squamation

The squamation is badly preserved. However, some almost complete cycloid scales are visible in a few regions of the body. They are large and ovoid. A few short *radii* are located in the posterior field. The anterior margin of the scales is festooned.

DISCUSSION

The relationships of *Lebrunichthys* within Teleostei

Lebrunichthys has a long maxilla that borders the greatest part of the upper oral margin. The pelvic girdle are not associated with the pectoral one. PU1, U1 and U2 are autogenous. There are three epurals, three uroneurals and 19 principal caudal rays. The scales are cycloid. The new Lebanese genus is thus a primitive teleost.

However, some advanced characters are also present in *Lebrunichthys*. The posterior region of the frontal is ornamented with a short but well marked crest. The parietal are small and the skull is lateroparietal. The pterotic bears a strong pointed posterior process. The supraorbital is elongated and anteriorly broadened. There is no antorbital. A long and narrow supramaxilla is present. HY1 and HY2 are fused by their articular heads. The anterior extremity of UR1 is enlarged and covers the upper region of PU1.

Within the primitive teleostean fishes, only some Pachyrhizodontidae exhibit these specialized features. We can thus conclude that *Lebrunichthys* belongs to that family.

The relationships of *Lebrunichthys* within Pachyrhizodontidae

Within Pachyrhizodontidae, some genera share a peculiar apomorphy, the presence of a pointed posterior process on the pterotic (CAVIN, 2001: character 3 [1]). Other genera do not share this specialized character. With its enormous posterior process on the pterotic, *Lebrunichthys* obviously belongs to the first group, a lineage that also contains the genera *Platinx* AGASSIZ, 1935, *Rhacolepis* AGASSIZ, 1841, *Elopopsis* HECKEL, 1856, *Goulmimichthys* CAVIN, 1995, *Nardopiscis* TAVERNE, 2008, *Apricenapiscis* TAVERNE, 2013, *Motlayoichthys* ARRATIA *et al.*, 2018 and *Stanhopeichthys* TAVERNE & CAPASSO, 2020 (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; TAVERNE & CAPASSO, 2020: figs 6, 7). In *Tingitanichtys* TAVERNE, 1996, the posterior region of the pterotic is not known (TAVERNE, 1996: fig. 3). The relationship of this genus with one of the two subgroups is thus uncertain.

Until now, that is the recently described Lebanese genus *Stanhopeichthys* that exhibits the less specialized caudal skeleton of that subgroup, with autogenous PU1, U1 and U2, the neural and haemal spines, the parhypural and the hypurals not fused to the corresponding centra, three uroneurals, three epurals, seven hypurals, a complete neural spine on PU2, HY1 and HY2 only fused by their proximal extremities and UR 1 anteriorly enlarged but not forked (TAVERNE & CAPASSO, 2020: fig. 20).

The caudal skeleton of *Lebrunichthys* has almost the same primitive pattern but is a little more evolved by the loss of the seventh hypural and the shortening of the neural spine of PU2. A so little difference in the caudal endoskeleton could be interpreted as an individual variation within the same species. However, it is not possible to consider *Stanhopeichthys* and *Lebrunichthys* as the same fish. Indeed, *Stanhopeichthys* has a long and narrow mesethmoid and an axial skeleton comprising 83 vertebrae, while *Lebrunichthys* exhibits an extremely broad mesethmoid and only 49 vertebrae.

The caudal skeleton of *Rhacolepis* is already a little more evolved, with UR1 anteriorly forked, the loss of HY6, the two ventral hypurals more completely fused together and also fused to U1 (FOREY, 1977: fig. 24A, B; MAISEY, 1991: fig. p. 255). The other genera of the subgroup and *Tingitanichtys* exhibit a still more evolved caudal endoskeleton, with less elements and an important degree of fusion between these elements (TAVERNE, 1976: figs 1-3, 1980: figs 5, 6, 1996: fig. 5; CAVIN, 2001: fig. 11B). The caudal skeleton is unknown in *Nardopiscis* and *Motlayoichthys*.

Lebrunichthys and *Nardopiscis* share a very peculiar character not present in the other genera with a posterior process on the pterotic. There is a gigantic broadening of this posterior process. However, the two genera can not be confounded. They are separated by many osteological differences. *Nardopiscis* has a narrow mesethmoid with two long posterior processes, a short upper jaw not reaching the preopercle, very large posterior infraorbitals, a short supraorbital and a well developed ventral branch on the preopercle (TAVERNE, 2008: figs 3, 5). It is however possible that the two genera are closely related.

Motlayoichthys differs from *Lebrunichthys* by numerous characters. This Mexican pachyrhizodontid fish has a hypertrophied orbitosphenoid forming an ossified interorbital septum, very strong teeth on both jaws, an

evolved infraorbital series, a short supraorbital and a posterior ventral process on the preopercle (ARRATIA *et al.,* 2018: figs 4a, b, 5).

So, within the subgroup and on the basis of the caudal features, *Lebrunichthys* occupies an intermediate systematic position between the plesiomorphic *Stanhopeichthys*, on the one hand, and the more evolved genera, on the other hand.

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